# Peter Castro Michael E. Huber

fourth edition

biology

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Front Matter

Preface

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# preface

People around the world are fascinated and inspired by marine life. With the global trend of migration to the coast, the growth of such pastimes as scuba diving, recreational fishing, and aquarium keeping, and the increasing accessability of travel to exotic seaside destinations, more people than ever before are able to experience firsthand the sea's beauty, mystery, and excitement. Even those not lucky enough to do so can learn about the life of the ocean not only through the many excellent film and television documentaries and photo essays that are available, but more and more over the Internet, where one can now follow the day-by-day progress of research expeditions, listen to whale songs, or view underwater scenes in real time. Partly as a result of this, awareness of human impacts on the oceans and of the importance of the oceans to our affairs continues to grow. This interest in the oceans is reflected in the continuing popularity of marine biology and related subjects in high schools, colleges and universities, and adult education programs.

While keeping in mind the range of potential users of this text, we have written it primarily for lower-division, nonscience majors at colleges and universities. These students may enroll in marine biology not only out of personal interest in the subject, but also to fulfill a general science requirement. Many will take no other college science course. We have made a special effort to include the solid basic science content needed in a general education course, including fundamental principles of biology, the physical sciences, and the scientific method. Our general aim was to integrate this basic science content with a stimulating, up-to-date overview of marine biology. We hope this approach demonstrates the relevance of the physical sciences to biology and makes the study of all sciences less intimidating.

At the same time, we recognize that general science content will not be needed in all marine biology courses, either because the course is not intended to satisfy general education requirements or because students already have some scientific background. To balance the needs of instructors teaching courses with and without prerequisites in basic biology or other sciences, we have designed the book to provide as much flexibility as possible in the amount of basic science coverage, the order in which topics are presented, and in overall emphasis and approach. We have tried to meet the needs and expectations of a wide variety of students, from the humanities major who likes to go fishing to the biology major considering a career in marine science. We also hope that a variety of readers other than university students find the book useful and enjoyable.

Another feature of Marine Biology, fourth edition, is its global, non-regional perspective. That the world's oceans and seas function as a vast integrated system is among the most important messages of our book. For many students this is a new perspective. One aspect of our global approach is the deliberate inclusion of examples from many different regions and ecosystems so that as many students as possible will find something relevant to their local areas or places they have visited. We hope this will stimulate them to think about the many relationships between their own shores and the one world ocean that so greatly influences our lives.

# CHANGES IN THE FOURTH EDITION

Perhaps the most significant changes in this edition of *Marine Biology* involve the *treatment of microorganisms*. We have adopted an increasingly accepted threedomain classification system that considers bacteria and archaea to be as different from each other as they are from eukaryotic organisms. An entire chapter, Chapter 5, is now devoted to microorganisms in recognition of the growing evidence of the importance of these organisms in the ocean. New and updated information on the role of microorganisms and viruses in the marine environment is presented in several other chapters.

As in previous editions we have updated the text to reflect recent events, new research, and changes in perspective. The fourth edition presents new information on phylogenetics, nucleic acid sequencing, molecular adaptations to pressure in deep-sea organisms, the feeding habits of whales, bioturbation, endangered marine species, the global effects of marine pollution and toxic algal blooms on human health, hydrothermal vents, invasive species, and many other topics. The coverage of salt marshes and mangroves, seagrass beds, and competing hypotheses to explain the structure of coral-reef fish communities has been expanded. There are new boxed readings on symbiotic bacteria, the use of nucleic acid sequencing in studying marine life, and the diversity of the deep-sea benthos. As in previous editions we have updated facts and figures, corrected errors, and reorganized some sections to provide more balanced coverage and improve the logical sequence. At the request of several reviewers, we have slightly raised the level of the text while being careful to preserve the informal writing style that our readers tell us they enjoy.

We have continued to improve the art program with many new or revised illustrations and photographs, and the interior design has again been improved to make better use of space and improve readability. The home page for *Marine Biology* continues to develop and the fourth edition more than previous editions has been written with the opportunities for online learning specifically in mind. The home page can be found at: www.mhhe.com/marinebiology (click on this book's cover). Preface

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# **Preface** ix

# ORGANIZATION

Marine Biology is organized into four parts. Part 1 (Chapters 1 through 3) introduces students to marine biology and related fields of science. Chapter 1 describes the history of marine biology. It also covers the fundamentals of the scientific method, which are essential in understanding the workings of science. This feature presents science as a process, an ongoing human endeavor. We believe it is important for students to realize that science does have limitations and that there is still much to be learned. Chapters 2 and 3 present basic material in marine geology, physics, and chemistry. Marine Biology includes more information on these subjects than other texts, but we kept Chapters 2 and 3 as short as possible. Wherever possible, physical and chemical aspects of marine environment are discussed in the chapters where they are most relevant to the biology. Wave refraction, for example, is covered in conjunction with intertidal communities (Chapter 11), estuarine circulation is discussed as part of the ecology of estuaries (Chapter 12), and upwelling is covered with the epipelagic zone (Chapter 15). This approach provides the general science coverage that some instructors need, but allows those who don't to use these chapters for background reference. It also emphasizes the importance of the physical and chemical environment to the organisms of the sea. Like the rest of the book, Chapters 2 and 3 include original world maps that were drawn using the Robinson projection to minimize distortion.

The exciting nature of life in the sea is the subject of Part 2 (Chapters 4 through 9). Chapter 4, "Some Basics of Biology," is a brief introduction to basic biology aimed at students with a limited background in biology. As with the fundamentals of geological, physical, and chemical oceanography, basic biological concepts are reviewed throughout the book in "In-text Glossary." Because the most important material is reviewed in these boxes, Chapter 4 may be omitted if

students have an adequate background in basic biology. Chapters 5 through 9 survey the major groups of marine organisms from the perspective of organismal biology. As in the first part of the book, we provide introductory information that is reviewed and expanded upon in future chapters. In discussing the various groups of organisms, we emphasize functional morphology, outstanding ecological and physiological adaptations, and economic importance or significance to humanity. Classification and phylogeny are not stressed, although a general classification scheme is presented in graphical form at the beginning of each chapter. Here and throughout the book we selected organisms from around the world for illustration in photographs, line drawings, and color paintings, but organisms from the coasts of North America are emphasized. Organisms are referred to by their most widely accepted common names; one or two common or important genera are noted in parentheses the first time a group is mentioned in a chapter, but we have not attempted to be comprehensive in listing genera. Indeed, at the suggestion of reviewers we have reduced the number of genera that are listed to make the text easier to read. Nomenclature follows for the most part the FAO Species Catalog and Species Identification Guides for groups covered by these references.

The third and most extensive part (Chapters 10 through 16) constitutes the heart of the book. The first chapter of this section (Chapter 10) introduces some fundamental principles of ecology. As in Chapter 4, important concepts presented here are reviewed elsewhere in the In-text Glossary boxes. In the remaining six chapters of Part 3, we describe the major environments of the world ocean, proceeding from nearshore to offshore and from shallow to deep water. This sequence is admittedly arbitrary but conforms to the teaching sequence followed by the greatest number of our reviewers. The chapters, however, are designed so that they can be covered in any sequence according to instructors' preferences and needs. The basic themes are adaptation to the physical constraints

of the environment and the interaction of organisms within the environment. Most chapters include generalized food webs that follow a standardized scheme of color coding to indicate the nature of the trophic relationships.

The final part of the book looks at the many ways that humans interact with the world ocean: the use of resources, our impact on the marine environment, and the influence of the ocean on culture and the human experience. These chapters present an up-to-date, comprehensive view of issues and concerns shared by many students. The chapter on resource utilization (Chapter 17) looks not only at traditional uses such as fisheries and mariculture, but also at more modern aspects such as the pharmacological use of marine natural products and the application of genetic engineering to mariculture. In Chapter 18, a discussion of human-induced degradation of the marine environment is balanced by an examination of the conservation and enhancement of the marine environment. The book closes with an essay on the impact of the ocean on human affairs (Chapter 19) that we hope will stimulate students to reflect on the past and future significance of the world ocean.

# TEACHING AND LEARNING AIDS

Because courses vary in content and sequence, Marine Biology was designed to be a flexible and efficient teaching aid. Chapters are written as short, readily absorbed units to increase instructors' flexibility in selecting topics. It is not assumed that instructors will follow the order in which material is presented in the book. For this reason, we provide an In-text Glossary that briefly explains key terms and concepts from other chapters. Some are illustrated by line drawings. Each box refers to the chapter and page where the concept is explained if more detailed information is needed. We hope this feature reduces the distraction of searching the index for unfamiliar terms.

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Key concept summaries, printed in italics, highlight the most important terms and ideas presented in preceding paragraphs. The text is accompanied by a superb collection of photographs and illustrations that were carefully designed and selected to complement and reinforce the text. Some of their captions contain questions that seek to further stimulate the student. There are many maps specifically created for Marine Biology to our specifications. The extensive Glossary provides complete definitions, and often refers to illustrations in the text or other key terms in the glossary that help explain a concept.

All chapters contain short **boxed essays** that present interesting supplementary information—material as varied as experimental setups, John Steinbeck, intelligence in dolphins, and marine archaeology.

Each chapter concludes with material to promote students' Interactive Exploration of topics covered in the chapter. This material is specifically designed to be used in conjunction with the book's Online Learning Center. Several Critical Thinking questions are posed at the end of each chapter to challenge students and stimulate class discussion. Many of these have no "right" answer-that is often the point. A brief annotated list of recent readings, For Further Reading, is provided for students who want to learn more. As in previous editions the list includes richly illustrated General Interest articles in publications such as Scientific American, Discover, and National Geographic that are appropriate for students with limited backgrounds in science. For the first time, a list of In Depth readings is also provided as a starting point for students who want to study particular topics in detail. An icon indicates articles that can be freely accessed online, and links to the articles are provided within the Marine Biology Online Learning Center. Students can use the online Do-It-Yourself Summary, Key Terms flashcards, and Quiz Yourself resources to review the chapter and test their understanding. The Online Learning Center also provides links to web sites related to each chapter. For most chapters the Online Learning Center also provides short video clips showing interesting habitats and animal behaviors.

# SUPPLEMENTARY MATERIALS

# Instructor's Manual

Prepared by Peter Castro, this helpful ancillary provides chapter outlines and summaries, a listing of audiovisual materials and software that complement each chapter, and answers to the Critical Thinking Questions within the text. Instructors will also find suggestions on how to present concepts to students and how to organize materials for class presentation. The Instructor's Manual is available in the Online Learning Center, within the Instructor Resources, at <u>www.mhhe.com/marinebiology</u> (click on this book's cover).

# **Test Item File**

This user-friendly computerized testing software includes 470 multiple-choice questions and answers, sorted by chapter. The Test Item File is available as a CD-ROM, and is available free of charge to instructors using the textbook.

# **Digital Content Manager**

Available through the Online Learning Center and on CD-ROM, instructors will have access to the Digital Content Manager (DCM). This multimedia collection of visual resources allows instructors to utilize artwork from the text in multiple formats to create customized classroom presentations, visually-based tests and quizzes, dynamic course website content, or attractive printed support materials. The digital assets on this crossplatform CD-ROM are grouped by chapter within easy-to-use folders. On the CD-ROM version of the Digital Content Manager, instructors will have access to 34 video segments from Scripps Institution of Oceanography, grouped by chapter to go with the fourth edition of this text. The Scripps video segments are also available on videotape.

# **Transparencies**

A set of 75 full-color overhead transparencies of key illustrations from the text is available to instructors at no cost.

# www.mhhe.com/marinebiology

# Laboratory Manual

Laboratory and Field Investigations in Marine Life, 7<sup>th</sup> edition, by James L. Sumich and Gordon Dudley, is a manual written specifically for a one-semester course. Each of the fifteen laboratory exercises in this collection has been designed for approximately a 3-hour laboratory period. Suggested topics for further investigation are also incorporated into the exercises. A collection of field studies, as well as six informative appendices, can be found at the back of this manual.

# Marine Biology Online Learning Center

This text-specific web site allows students and instructors from all over the world to communicate. Instructors can create a more interactive course with the integration of this site, and students will find many tools to help them improve their grades and learn that marine biology can be fun. Check out the Online Learning Center for this text at <u>www.mhhe.com/</u><u>marinebiology</u> (just click on this book's cover). See page xii for more details.

# ACKNOWLEDGMENTS

The many contributors of photographs that add so much to the book are acknowledged in the credits section, but we extend special thanks to A. Charles Arneson, who provided many excellent photos. We are also grateful for the outstanding artwork of Bill Ober and Claire Garrison. LouAnn Wilson has been a great help in locating new photographs for this edition.

We also thank the exceptional staff at McGraw-Hill Publishers, particularly Marge Kemp, Publisher, Donna Nemmers, Senior Developmental Editor, and Rose Koos, Project Manager, for their patience in dealing with us while we worked in our separate corners of the world, and for their efficiency in managing an enormous amount of detail.

Finally, we thank the students, friends, colleagues, former teachers, and reviewers who answered questions, pointed out errors, and made suggestions that have greatly improved the book. We take full credit, however, for any errors or shortcomings that remain. Preface

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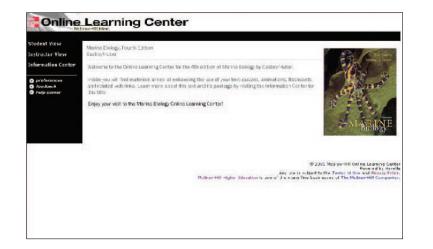
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Online Learning Center

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# online learning center www.mhhe.com/marinebiology

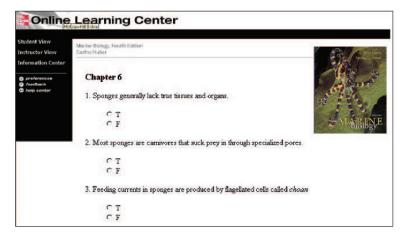
For every chapter in this textbook, a variety of useful study tools are available on the *Marine Biology* Online Learning Center. Students will discover chapter-sorted **Marine Biology on the Net** links to web pages of related content for further reading and research. Key terms from each chapter can be studied interactively as **Key Terms Flashcards**. The **Do-It-Yourself Summary** helps students review material learned in each chapter, and the **Quiz Yourself** allows students to test themselves on important concepts learned in each chapter.





See It In Motion underwater video clips display interesting habitats and behaviors for many animals in the ocean. For Further Reading sections provide links to online articles for further study and research. Careers in Marine Biology offers links to interesting careers in the field of marine biology, and Marine Biology Case Studies detail stories of endangered species, marine habitats, and more.

Instructors will find that the Online Learning Center hosts the **Instructor's Manual**, plus eight **Field and Laboratory Exercises** that may be printed and used in the laboratory section for this course. **Sample Syllabi** and a **List of Transparencies** are also available within the Instructor Resources section of the Online Learning Center. The *Marine Biology* Online Learning Center can be accessed by visiting <u>www.mhhe.com/</u> <u>marinebiology</u> (just click on this book's cover).



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# The Science of Marine Biology



arine biology is the scientific study of the organisms that live in the ocean. The ocean is a vast realm that contains many strange and wonderful creatures. It is often the beauty, mystery, and variety of life in the sea that attracts students to a course in marine biology. Even professional marine biologists feel a sense of adventure and wonder in their studies.

There are also many practical reasons to study marine biology. Marine life represents a vast source of human wealth. It provides food, medicines, and raw materials, in addition to offering recreation to millions and supporting tourism all over the world. On the other hand, marine organisms can also create problems. For example, some organisms harm humans directly by causing disease or attacking people. Others may harm us indirectly by injuring or killing other marine organisms that we value for food or other purposes. Marine organisms may erode piers, walls, and other structures we build in the ocean, foul the bottoms of ships, and clog pipes. They may even interfere with our weapons of war, for better or for worse.

At a much more fundamental level, marine life helps determine the very nature of our planet. Marine organisms produce much of the oxygen we breathe and help regulate the earth's climate. Our shorelines are shaped and protected by marine life, at least in part, and some marine organisms even help create new land. In economic terms, it has been estimated that the ocean's living systems are worth more than \$20 *trillion* a year.

To make both full and wise use of the sea's living resources, to solve the problems



Diver and Crown-of-Thorns sea star (*Acanthaster planci*). Photograph courtesy of the Great Barrier Reef Marine Park Authority.

marine organisms create, and to predict the effects of human activities on the life of the sea, we must learn all we can about marine life. In addition, marine organisms provide clues to the earth's past, the history of life, and even our own bodies that we must learn to understand. This is the challenge, the adventure, of marine biology.

# THE SCIENCE OF MARINE BIOLOGY

Marine biology is not really a separate science but rather the more general science of biology applied to the sea. Nearly all the disciplines of biology are represented in marine biology. There are marine biologists who study the basic chemistry of living things, for example. Others are interested in marine life as whole organisms: the way they behave, where they live and why, and so on. Other marine biologists adopt a global perspective and look at the way entire oceans function as systems. Marine biology is thus both part of a broader science and itself made up of many different disciplines, approaches, and viewpoints.

Marine biology is closely related to oceanography, the scientific study of the oceans. Like marine biology, oceanography has many branches. Geological

oceanographers, or marine geologists, study the sea floor. Chemical oceanographers study ocean chemistry, and physical oceanographers study waves, tides, currents, and other physical aspects of the sea. Marine biology is most closely related to biological oceanography, so closely in fact that the two are difficult to separate. Sometimes they are distinguished on the basis that marine biologists tend to study organisms living relatively close to shore, while biological oceanographers focus on life in the open ocean, far from land. Another common distinction is that marine biologists tend to study marine life from the perspective of the organisms (for example, studying how organisms produce organic matter), while biological oceanographers tend to take the perspective of the ocean (for example, studying how organic matter cycles through the system). In practice there are so many exceptions to these distinctions that many marine scientists consider marine biology and biological oceanography to be the same. The disciplines are sometimes divided for administrative rather than scientific reasons. Legend has it that separate departments of Marine Biology and Biological Oceanography at one major institution were established because two senior scientists didn't get along!

A marine biologist's interests may also overlap broadly with those of biologists who study terrestrial organisms. Many of the basic ways in which living things make use of energy, for example, are similar whether an organism lives on land or in the sea. Nevertheless, marine biology does have a flavor all its own, partly because of its history.

# The History of Marine Biology

People probably started learning about marine life from the first time they saw the ocean. After all, the sea is full of good things to eat. Archaeologists have found piles of shells, the remains of ancient "clambakes," dating back to the Stone Age. Ancient harpoons and simple fish-

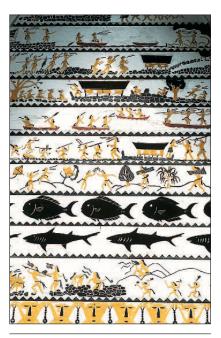


FIGURE 1.1 The Micronesian inhabitants of Palau have traditionally carved storyboards on wood to illustrate their traditional legends, many of which tell about their encounters with marine animals.

hooks of bone or shell have also been found. While they gathered food, people learned through experience which things were good to eat and which were badtasting or harmful. The tomb of an Egyptian pharaoh, for example, bears a warning against eating a pufferfish, a kind of poisonous fish. Coastal peoples in virtually every culture developed a store of practical knowledge about marine life and the oceans.

Knowledge of the ocean and its organisms developed as people gained skills in seamanship and navigation. Ancient Pacific Islanders had detailed knowledge of marine life, which their descendants still retain (Fig. 1.1). They were consummate mariners, using clues such as wind, wave, and current patterns to navigate over vast distances. Some groups recorded these clues on unusual three-dimensional maps made of sticks and shells. The Phoenicians were the first accomplished

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**FIGURE 1.2** This Greek plate from around 330 B.C. reflects a considerable knowledge of marine life. The fish at the right is an electric ray (*Torpedo*), which the ancient Greeks used to deliver the first electrical stimulation therapy.

Western navigators. By 2000 B.C. they were sailing around the Mediterranean Sea, Red Sea, eastern Atlantic Ocean, and Indian Ocean.

By the time of the ancient Greeks, a fair amount was known about the things that live near shore (Fig. 1.2). The Greek philosopher Aristotle, who lived in the fourth century B.C., is considered by many to be the first marine biologist. He described many forms of marine life, and many of his descriptions are considered valid to this day. Aristotle made other studies as well. He recognized, for example, that gills are the breathing apparatus of fish (see "Constructing the Hypothesis," p. 13.)

During the centuries popularly known as the Dark Ages, scientific inquiry in most of Europe came to a grinding halt. Progress in the study of marine biology ceased. Indeed, much of the knowledge of the ancient Greeks was lost or distorted. Not all exploration of the ocean stopped, however. During the ninth and tenth centuries the Vikings continued to explore the northern Atlantic. In A.D. 995 a Viking party led by Leif Eriksson discovered Vinland, what we now call North America. Arab traders were also Castro–Huber: Marine Biology, Fourth Edition I. Principle of Marine Science 1. The Science of Marine Bioloav © The McGraw-Hill Companies, 2003

active during the Middle Ages, voyaging to eastern Africa, southeast Asia, and India. In the process they learned about wind and current patterns, including the monsoons, strong winds that reverse direction with the seasons. In the Far East and the Pacific, people also continued to explore and learn about the sea.

In the Renaissance, spurred in part by the rediscovery of ancient knowledge preserved by the Arabs, Europeans again began to investigate the world around them. At first there were mainly voyages of exploration. Christopher Columbus rediscovered the "New World" in 1492-word of the Vikings' find had never reached the rest of Europe. In 1519 Ferdinand Magellan embarked on the first expedition to sail around the globe. Many other epic voyages contributed to our knowledge of the oceans. Fairly accurate maps, especially of places outside Europe, began to appear for the first time (see "Oceans as Barriers and Avenues," p. 429).

Before long, explorers became curious about the ocean they sailed and the things that lived in it. An English sea captain, James Cook, was one of the first to make scientific observations along the way and to include a full-time naturalist among his crew. In a series of three great voyages, beginning in 1768, he explored all the oceans. He was the first European to see the Antarctic ice fields and to land in Hawai'i, New Zealand, Tahiti, and a host of other Pacific islands. Cook was the first to make use of the chronometer, an accurate timepiece. This new technology enabled him to accurately determine his longitude, and therefore prepare reliable charts. From the Arctic to the Antarctic, from Alaska to Australia, Cook extended and reshaped the European conception of the world. He brought back specimens of plants and animals and tales of strange new lands. Though Cook was generally respectful and appreciative of indigenous cultures, he was killed in 1779 in a fight with native Hawaiians at Kealakekua Bay, Hawai'i.

By the nineteenth century it was common for vessels to take along a naturalist to collect and study the life forms

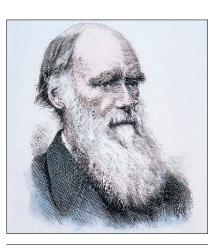


FIGURE 1.3 Charles Darwin (1809–1882), most often associated with the theory of evolution by natural selection, was also an able marine biologist and geologist.

that were encountered. Perhaps the most famous of these shipboard naturalists was Charles Darwin (Fig. 1.3), another Englishman. Beginning in 1831, Darwin sailed around the world on HMS Beagle for five years, horribly seasick most of the time. The Beagle's primary mission was to map coastlines, but Darwin used the opportunity to make detailed observations of all aspects of the natural world. This set off a train of thought that led him, years later, to propose the theory of evolution by natural selection (see "Natural Selection and Adaptation." p. 84). Though best known for the theory of evolution, Darwin made many other contributions to marine biology. For example, he proposed an explanation for the formation of atolls, distinctive rings of coral reef. Though it wasn't until the 1950s that supporting evidence was obtained, his explanation is now almost universally accepted (see "How Atolls Grow," p. 310). He also used nets to capture the tiny drifting creatures known as plankton. A group of animals called barnacles was another of Darwin's many interests, and specialists still refer to his treatise on the subject.

# The Challenger Expedition

By the middle of the nineteenth century a few scientists were able to undertake voyages for the specific purpose of studying the oceans. One was Edward Forbes, who in the 1840s and 1850s carried out extensive dredging of the sea floor, mostly around his native Britain but also in the Aegean Sea and other places. Forbes died prematurely in 1854, at the age of 39, but was the most influential marine biologist of his day. He discovered many previously unknown organisms and recognized that sea-floor life is different at different depths (see "Biodiversity in the Deep Sea," p. 372). Perhaps his most important contribution, however, was to inspire new interest in the life of the sea floor.

Many of Forbes's contemporaries and successors, especially from Britain, Germany, Scandinavia, and France, carried on his studies of sea-floor life. Though their ships were poorly equipped and the voyages short, their studies yielded many interesting results. They were so successful, in fact, that in 1872 British scientists managed to convince their government to fund the first major oceanographic expedition, under the scientific leadership of Charles Wyville Thompson. The British navy supplied a light warship to be fitted out for the purpose. The ship was named HMS *Challenger*.

*Challenger* underwent extensive renovations in preparation for the voyage. Most of her guns were removed—two were left, probably for moral support more than anything else. Laboratories and quarters for the scientific crew were added, and gear for dredging and taking water samples in deep water was installed. Though primitive by modern standards, the scientific equipment on board was the best of its day. Finally, in December 1872, *Challenger* set off.

During the three and a half years that followed, *Challenger* and her crew sailed around the world gathering information and collecting samples (Fig. 1.4). The sheer volume of the data was enormous. After the *Challenger* expedition returned to port, it took 19 years to publish the results, which fill 50 thick volumes.

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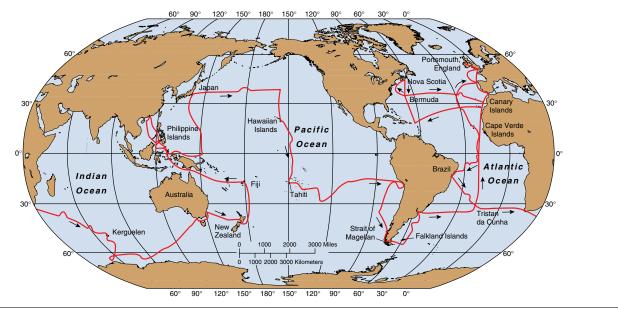


FIGURE 1.4 The route of the *Challenger* expedition.

*Challenger* brought back more information about the ocean than had been gathered in all previous human history.

It was not just the duration of the voyage or the amount of information collected that set the Challenger expedition apart from earlier efforts. More important, the expedition set new standards for studying the ocean. Measurements were made systematically and carefully, and meticulous records were kept. The crew worked with great efficiency and dedication to the task. For the first time, scientists began to get a coherent picture of what the ocean was like. They also got a glimpse of the enormous variety of marine life, for Challenger brought back samples of thousands of previously unknown species. Thus, the Challenger expedition laid the foundations of modern marine science.

In the years that followed, a series of other expeditions continued the work begun by *Challenger*. Major oceanographic cruises continue to this day. In many ways, though, the voyage of the *Challenger* remains one of the most important in the history of oceanography.

# The Growth of Marine Labs

Even before the *Challenger* set off, biologists were excited about the organisms

brought back by ocean expeditions. Unfortunately, oceanographic vessels had quarters for only a limited number of scientists. Most biologists just got to see the dead, preserved specimens that the ships brought back to port. This was fine as long as biologists were content with simply describing the structure of new forms of marine life. They soon became curious, however, about how the organisms actually lived: how they functioned and what they did. Living specimens were essential for the study of these aspects of biology, but ships usually stayed in one place only for a short time, making long-term observations and experiments impossible.

Rather than study the ocean from ships, some biologists began to conduct their studies at the seashore. Among the first of these were two Frenchmen, Henri Milne Edwards and Victor Andouin, who around 1826 began making regular visits to the shore to study the life there. Other biologists soon followed suit. These excursions offered the opportunity to study live organisms, but there were no permanent facilities and only a limited amount of equipment could be taken along. This restricted the scope of the investigations. Eventually, permanent laboratories dedicated to the study of marine life were established. These labs allowed

marine biologists to keep organisms alive and to work over long periods. The first such laboratory was the Stazione Zoologica, founded in Naples, Italy, by German biologists in 1872—the same year the *Challenger* embarked. The laboratory of the Marine Biological Society of the United Kingdom was founded at Plymouth, England, in 1879.

The first major American marine laboratory was the Marine Biological Laboratory at Woods Hole, Massachusetts (Fig. 1.5). It is hard to pinpoint the exact date when this laboratory was established. The first marine laboratory at Woods Hole was initiated by the United States Fish Commission in 1871, but it did not flourish. Several other short-lived laboratories were subsequently established in the area around Woods Hole. In 1888 one of these, established in 1873 by Harvard biologist Louis Agassiz on Cape Ann, Massachusetts, moved to Woods Hole and officially opened its doors as the Marine Biological Laboratory. It is still one of the world's most prestigious marine stations.

After these early beginnings, other marine laboratories were established. Among the earliest in the United States were the Hopkins Marine Station in Pacific Grove, California; Scripps Institution

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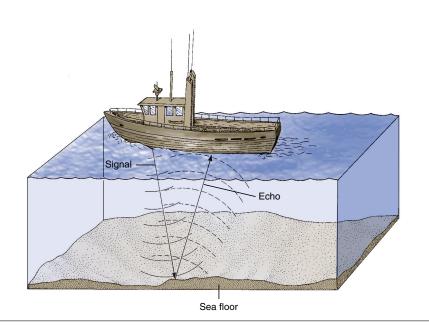


FIGURE 1.5 Woods Hole, Massachussetts, home of the Marine Biological Laboratory and the Woods Hole Oceanographic Institution.

of Oceanography in La Jolla, California; and the Friday Harbor Marine Laboratory in Friday Harbor, Washington. In the ensuing years, more laboratories appeared all over the world. These labs played a vital role in the growth of marine biology and remain active to this day.

The onset of World War II had a major effect on the development of marine biology. A new technology, sonar, or sound navigation ranging, was developed in response to the growing importance of submarine warfare. Sonar is based on the detection of underwater echoes-a way of listening to the sea (Fig. 1.6). The ocean, long thought of as a silent realm, was suddenly found to be full of sound, much of it made by animals! During wartime, learning about these animals was no longer the casual pursuit of a few interested marine biologists but a matter of national security. As a result of this urgency, several marine laboratories, such as Scripps and the Woods Hole Oceanographic Institution (established in 1929), underwent rapid growth. When the war ended, these labs not only remained vital research centers but continued to grow.

The years immediately after World War II saw the refinement of the first really practical **scuba**, or *s*elf-*c*ontained *u*nderwater *b*reathing *a*pparatus. The basic technology used in scuba was developed in occupied France by the engineer Èmile Gagnan to allow automobiles to run on compressed natural gas. After the war, Gagnan and fellow Frenchman Jacques Cousteau modified the apparatus, using it to breathe compressed air under water. Cousteau went on to devote his life



Chapter 1 The Science of Marine Biology

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**FIGURE 1.6** A ship uses sonar by "pinging," or emitting a loud pulse of sound, and timing how long it takes the echo to return from the sea floor. From this the depth of the water can be determined. This, the most common form of sonar, is called "active sonar" because the sounds used are actively generated by the equipment (see "Eyes (and Ears) in the Ocean," p. 11).



**FIGURE 1.7** Scuba is an important tool in the work of many marine biologists.

to scuba diving and the oceans. His films, books, and television programs inspired a fascination with the oceans in people all over the world and alerted them, often for the first time, to growing threats to the health of the marine environment.

Using scuba, marine biologists could, for the first time, descend below the surface of the water to observe marine organisms in their natural environment (Fig. 1.7). They could now work comfort-



FIGURE 1.8 These marine scientists are hauling in a net known as a "bongo net" used to capture minute marine organisms. One is signaling instructions to the winch operator.

ably in the ocean, collecting specimens and performing experiments, though they were still limited to relatively shallow water, generally less than 50 m (165 ft).

# Marine Biology Today

Oceanographic ships and shore-based laboratories are as important to marine biology now as they were in the past (Fig. 1.8). Today many universities and



FIGURE 1.9 The R/V Thomas G. Thompson, operated by the University of Washington, was the first of a new generation of research vessels. These vessels offer increased work space and the ability to travel to research sites quickly and stay there longer.



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FIGURE 1.10 Alvin, a deep-sea submarine operated by the Woods Hole Oceanographic Institution. The mechanical arm below the round porthole is used to collect samples and place them in the basket below. Alvin is one of the most famous vessels in the history of marine science.

other institutions operate research vessels (Fig. 1.9). Modern ships are equipped with the latest equipment for navigation, sampling, and studying the creatures that are collected. Many of these, like Challenger, were originally built for other uses, but a growing number of vessels are being custom-built for scientific research at sea.

In addition to ships as we normally think of them, some remarkable craft are used to study the marine world. Hightech submarines can descend to the deepest parts of the ocean, revealing a world that was once inaccessible (Fig. 1.10). A variety of odd-looking vessels ply the oceans, providing specialized facilities for marine scientists (Fig. 1.11). Marine biologists are making increasing use of remotely operated vehicles (ROVs), underwater robots that can take photos, collect samples, and make measurements (see Fig 16.25). They have developed a variety of automated instruments that can remain in the sea for long periods, even permanently, continuously collecting data.



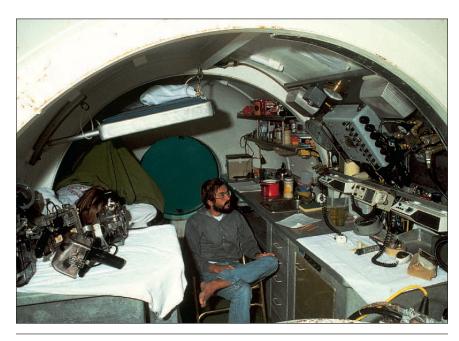


FIGURE 1.11 R/V FLIP, short for floating instrument platform, operated by Scripps Institution of Oceanography, provides a stable platform for research at sea. It is towed to the location (a); then one end of the hull is flooded, and as the flooded end sinks, FLIP swings into position (b).

Marine laboratories, too, have come a long way since the early days. Today such labs dot coastlines around the world and are used by an international community of scientists. Some are equipped with the most up-to-date facilities available. Others are simple field stations, providing a base for scientists to work in remote areas. There are even undersea habitats where scientists can live for weeks at a time, literally immersed in their work (Fig. 1.12).

Marine laboratories are important not only as research institutions, but also as centers of education. Many offer summer courses that allow students to learn about marine biology firsthand (Fig. 1.13). Most labs provide facilities for graduate students from various universities to pursue their studies, and some offer graduate degrees in marine biology on their own. Thus, in addition to furthering today's research, marine

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**FIGURE 1.12** This scientist is working inside *Hydrolab*, one of several undersea habitats that have been used to help marine biologists pursue their studies. These cramped quarters served as laboratory, living room, bedroom, and kitchen. The "office," however, was much larger; scientists just went out the front door to begin their underwater work.

laboratories are busy training the profes-

9

Chapter 1 The Science of Marine Biology

sional marine biologists of tomorrow. New technology offers exciting opportunities for the study of the oceans. Computers have had a tremendous impact because they allow scientists to rapidly analyze huge amounts of information (Figs. 1.14 and 1.15). Space technology has also aided the study of the sea. Satellites now orbit the earth, peering down at the ocean below. Because they are so far away, these satellites can capture the big picture, viewing broad areas of the ocean

all at once (Fig. 1.16). With the aid of computers, scientists use the information gathered by satellites to measure the temperature of the sea surface, track ocean currents, determine the abundance and kinds of organisms present, and monitor human impacts on the oceans. Much of our knowledge of large-scale features like ocean currents could not have been obtained without the use of this **remote sensing** technology, or technology used



FIGURE 1.13 A marine biology class at Duke University's marine laboratory in Beaufort, North Carolina.



**FIGURE 1.14** The computer room aboard the R/V *Thompson*, the research vessel shown in Figure 1.9. Only a few years ago such sophisticated equipment was not available anywhere, let alone on a ship that sails the open ocean.

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# FIGURE 1.15 This

computer-generated image represents the flash of light from a shrimp-like animal called a krill that produces light much as fireflies do. The plot shows the brightness of the light and its color, or wavelength, at different times. A millisecond (msec) equals one one-thousandth of a second; each flash lasts less than a second! This plot could not have been produced without modern computers and light-sensing technology that was originally developed to study distant stars.

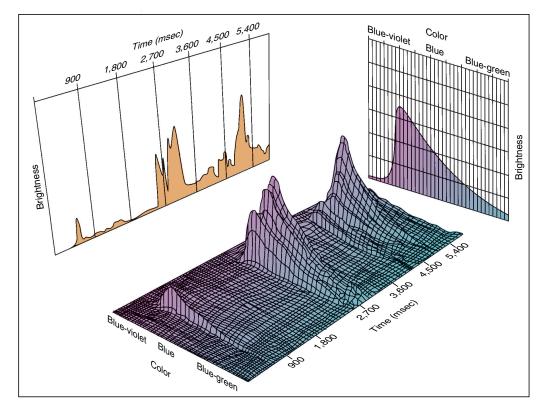
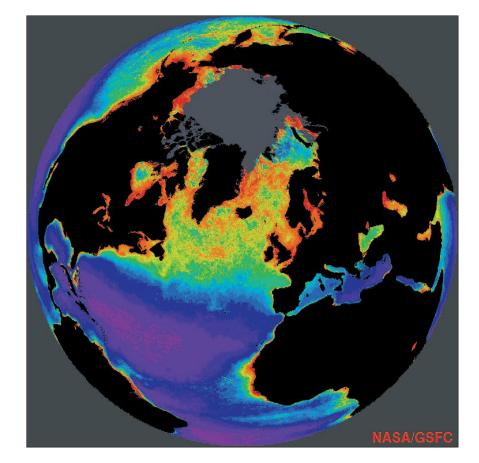


FIGURE 1.16 A satellite image showing the abundance of photosynthetic organisms in the ocean, as indicated by the amount of pigment in the water. This photo was taken by the Coastal Zone Color Scanner (CZCS), which was mounted on the *Nimbus-7* satellite. It is actually a composite of information gathered over nearly an eightyear period. Advances in computer and space technology made this image possible.

| .1<br>.2 | Phytoplankton<br>Pigment |
|----------|--------------------------|
| .4       | Concentration            |
| .6       | (mg/m3)                  |
| .8       |                          |
| 1        |                          |
| 10       | NASA/GSFC                |



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# EYES (AND EARS) IN THE OCEAN

Marine biologists are often frustrated by how hard it is to actually *see* what is going on in the ocean. They can collect samples with nets and dredges, make measurements with automated instruments, and do experiments in the laboratory, and in these ways have learned a great deal about marine life. We humans are visual creatures, though, and no amount of sampling, measurement, or experimentation can completely substitute for actually watching organisms in their natural habitats.

One solution is to enter the ocean and observe with our own eyes. Scuba and research submersibles have tremendously aided the study of the ocean, allowing us not only to see the organisms we study, but also to conduct experiments in the natural environment. These methods have their limitations, though. Scuba divers can penetrate only the shallowest parts of the ocean, and then only for short periods on the order of a few hours. Scuba diving is also physically demanding. Submarines are extremely expensive and can accommodate only a very few very cramped scientists at a time. They also involve an element of risk. Compared to fishes, whales, seals, and other fast-moving animals, both scuba divers and submarines are slow, cumbersome, and highly intrusive.

Another approach is to use still or video cameras that operate automatically or can be controlled from the surface. Such cameras are unlikely to be in the right place at the right time just by chance, so bait is usually used to attract the animals of interest to the camera (see Fig. 16.28). Such systems have captured new and unusual deep-sea animals on film, and provided useful information about their lifestyles.

Observing the complex behavior of large animals like seals, sea lions, whales, and other marine mammals has always been a problem. They move too fast, and too far, for a human diver, much less a stationary camera, to possibly record their behavior. Even if people could somehow keep up with them we would almost certainly be a disruptive presence, and the animals would be unlikely to behave normally. So, why not let the animals themselves take the pictures? This is the idea behind "crittercam," a compact, streamlined, underwater video camera that can be attached to animals including sea turtles, sharks, whales, seals, and sea lions. Our knowledge of these animals' behavior once came almost entirely from watching them on land and at the surface. Crittercam lets us observe them underwater, where they spend most of their time. This has given us new, and constantly growing, insight into their lives.

Not all efforts to "see" in the ocean rely on vision as we normally think of it. Light does not penetrate very far in seawater (see "Transparency," p. 51), which means not only that most of the ocean is too dark to see, but also that even with artificial light visibility is quite limited. Sound, on the other hand, travels long distances underwater, which is the basis of sonar. Modern sonar and computerized data processing produce detailed three-dimensional



Wearing crittercam doesn't seem to bother this female northern elephant seal (*Mirounga angustirostris*), or her neighbors. The ability to record social behavior with minimal human interference is one of crittercam's advantages.

images of the sea floor (see Fig. 2.19). Scientists are also developing sonar systems that are "passive," that is, they use the existing background noise produced by animals, waves, passing ships, and other sources instead of generating their own sound. Just as we see when light bounces off an object into our eyes, sound bouncing off an object—a whale, for example—can be picked up by underwater microphones and, with the aid of computers, processed into moving images. Such systems can work in the dark, potentially over relatively long distances, and reduce noise disturbance to the animals.

New technology is also being used to spy on the tiny, drifting organisms known as plankton (see "Ecological Zonation of the Marine Environment," p. 229). These organisms are among the most important on earth, but until recently have been studied mainly by catching them in nets. This usually damages or kills them. At the very least it removes them from their environment and completely disrupts their natural behavior. Imagine how limited our understanding of birds would be if our knowledge was based entirely on catching them in nets towed behind airplanes!

Some systems for visualizing plankton rely solely on video. Four cameras are required to accurately track these organisms in their three-dimensional world, which lacks fixed reference points. Other systems use a kind of sonar, and some use a combination of sonar and video. The sonar is used to determine the organisms' size and position, and when they are in range a digital camera takes a snapshot using a red flash, which most of the organisms are unable to see. Still other systems use lasers to detect the tiny microorganisms and even to produce three-dimensional holograms of them that can be stored in a computer and examined in the laboratory. All of these systems are giving us revealing new glimpses of the nature of life in the ocean.

to study the earth and its oceans from afar. The technology is also being applied at smaller scales. For example, satellites are used to track the migrations of whales, fish, and other organisms that have been fitted with miniature transmitters. Electronic buoys released at oil spill sites drift along with the oil and are tracked by satellite to monitor the path of the spill. These are just a few of the many and ever-increasing applications of remote sensing.

Marine biologists today use every available tool in their study of the sea. Information about the ocean pours in at an ever-increasing pace. Much remains to be learned, however, and the oceans remain a realm of great mystery and excitement. Castro–Huber: Marine Biology, Fourth Edition I. Principle of Marine Science 1. The Science of Marine Biology © The McGraw–Hill Companies, 2003

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## 12 **Part One** Principles of Marine Science

# THE SCIENTIFIC METHOD

Marine biology is an adventure, to be sure, but it is also a science. Scientists, including marine biologists, share a certain way of looking at the world. Students of marine biology need to be familiar with this approach and how it affects our understanding of the natural world, including the ocean.

We live in an age of science. Advertisers constantly boast of new "scientific" improvements to their products. Newspapers regularly report new breakthroughs, and many television stations have special science reporters. Governments and private companies spend billions of dollars every year on scientific research and science education. Why has science come to occupy a position of such prestige in our society? The answer, quite simply, is that it works! Science has been among the most successful of human endeavors. Modern society would be impossible without the knowledge and technology produced by science. The lives of almost everyone have been enriched by scientific advances in medicine, agriculture, communication, transportation, art, and countless other fields.

Much of the practical success of science results from the way it is done. Scientists do not see the world as a place where things happen haphazardly or for no reason. They assert instead that all events in the universe can be explained by physical laws. Scientists don't go about discovering these laws haphazardly either; they proceed according to time-tested procedures. The set of procedures by which scientists learn about the world is known as the **scientific method**.

Scientists sometimes disagree over the fine points of exactly what constitutes the scientific method. As a result, they often apply the method in slightly different ways. In spite of these minor differences, most scientists do agree on the basic principles of the scientific method. The scientific method should not be seen as a fixed set of rules to be rigidly followed but rather as a flexible framework that guides the study of nature.

# Observation: The Currency of Science

The goal of science is to discover facts about the natural world and the principles that explain these facts. At the heart of the scientific method is the conviction that we can learn about the outside world only through our senses. Scientists concern themselves solely with what they can see, hear, feel, taste, and smell, though they often use tools to extend their senses. For example, they use microscopes to improve their vision. In other words, scientific knowledge is based only on what can be directly observed. Anything that cannot be observed is outside the realm of science.

One of the advantages of relying on observations is that these findings are accessible to others. A person's thoughts, feelings, and beliefs are internal. No one really knows what goes on in the mind of another. On the other hand, the world studied by scientists is external to any single person. Many people can look at the same object. Even though sensory perception may be imperfect and the scientist, like anyone else, may not be completely impartial, the object is there for all to see. Thus, there is a way to check and verify any one person's observations.

# Two Ways of Thinking

Scientists don't always agree on the best way to do science. In the past there were serious disputes over which methods of scientific reasoning were acceptable. Some people thought that the only truly scientific form of thinking was **induction**, in which one starts with a number of separate observations and then arrives at general principles. Others believed that scientists should use **deduction**, and reason from general principles to specific conclusions. Most scientists now agree that both ways of thinking are indispensable.

## Induction

When using induction, a scientist starts by making a series of individual observations. Ideally, he or she has no goal or hunch about the outcome and is com-

FIGURE 1.17 The Indo-Pacific sailfish (*Istiophorus platypterus*). The long projection on the snout is called the bill.

pletely objective. The combination of these observations suggests a general conclusion. For example, suppose a particular marine biologist examined a sailfish (Fig. 1.17), a shark (Fig. 1.18), and a tuna (Fig. 1.19), and found that they all had gills. Because sailfish, sharks, and tuna are all fishes, he might draw the general conclusion, *All fishes have gills*. This is an example of induction.

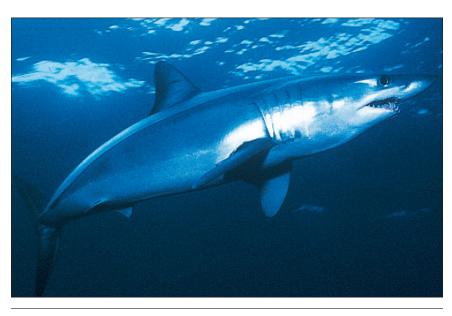
In the process of induction, general conclusions are made on the basis of specific observations.

The scientist must be careful in making inductions. The step from isolated observations to a general statement critically depends on the number and quality of the observations and on recognizing their limitations. If the biologist had stopped after examining the sailfish, which happens to have a bill, he might use induction to make the false conclusion *All fishes have bills*. Even after examining all three fishes, he might have concluded *All marine animals have gills* instead of just *All fishes have gills*. This is where deduction comes into play.

## Deduction

In deductive reasoning, scientists start with a general statement about nature and predict what the specific consequences would be if the general statement is true. They might arrive at the general statement by hunch or intuition,





**FIGURE 1.18** The shortfin make shark (*Isurus oxyrinchus*). The vertical lines in front of the pectoral fins are the gill slits, where water exits after passing over the gills. © Bob Cranston.



**FIGURE 1.19** The northern bluefin tuna (*Thunnus thynnus*). These fish grow to nearly 700 kg (1,500 lb).

but usually the statement is the result of induction, that is, it is based on observations. Suppose our marine biologist used induction to make the general statement *All marine animals have gills*. He might then reason that if all marine animals have gills and whales are marine animals, then whales must have gills. The biologist has used a general statement about all marine animals to make a statement about a particular kind of marine animal. In the process of deduction, specific predictions are made by applying a general principle.

# **Testing Ideas**

Scientists are never content to simply make statements about the world and let it go at that. Instead, they are obsessed with testing the statements to see whether they are, in fact, true. Both induction and deduction lead the scientist to make statements that *might* be true. A statement that might be true is called a **hypothesis**. A crucial feature of the scientific method is that all hypotheses are tested, usually again and again. This insistence on testing is one of the great strengths of the scientific method. Incorrect hypotheses are usually quickly weeded out and discarded.

# Constructing the Hypothesis

Scientific hypotheses must be stated in a way that allows them to be tested. What this means is that it must be possible, at least potentially, to prove that the hypothesis is false if it really is false. Sometimes this is simple. For example, the hypothesis that whales have gills is easy to test. All the biologist has to do is examine a whale to see whether it has gills. By doing so, he would find that whales have lungs, not gills (Fig. 1.20). He would have proven the hypothesis Whales have gills false. He would also have disproved the more general hypothesis All marine animals have gills. The steps our marine biologist used to construct and test these hypotheses are illustrated in Figure 1.21. Actually, this line of reasoning is not entirely imaginary. Aristotle, one of the first marine biologists, used similar logic in the fourth century B.C. He observed not only that whales breathe with lungs and not gills, but that unlike most fishes they give birth to live young instead of laying eggs. Unfortunately, Aristotle's recognition that whales and other marine mammals are not fishes was lost for more than two millenia.

People sometimes make the mistake of proposing hypotheses that cannot be fairly tested. Someone who believes in mermaids might say, *Somewhere in the* 

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**FIGURE 1.20** This gray whale (*Escbrichtius robustus*) is spouting, or exhaling a breath of air. The whale breathes air with lungs, rather than using gills to get oxygen from water as fishes do. The spout is mostly water vapor, like fog, rather than liquid water.

ocean there are mermaids. The problem with this hypothesis is that it could never be proved to be false. An army of marine biologists could spend their entire careers looking for a mermaid without success, but the true believer could always say, *The mermaids are there, you just didn't find them.* No matter how hard they look, the biologists could never prove that there are no mermaids. Therefore the statement, *There are mermaids in the ocean,* is not a valid scientific hypothesis because it is not **testable.** 

A scientific hypothesis is a statement about the world that might be true and is testable. A testable hypothesis is one that at least potentially can be proved false.

# The Nature of Scientific Proof

It must be at least possible to disprove a hypothesis before the hypothesis can be considered scientific. But how can a hypothesis be proved to be true? This question has always troubled scientists, and the answer may trouble you too. In general, no scientific hypothesis can be absolutely proved true. For example, consider the hypothesis that all fishes have gills. It is easy to see that this hypothesis can be proved false by finding a fish without gills. But even though every fish so far examined has gills, this does not prove that *all* fishes have gills. Somewhere out there may lurk a fish without them. Just as it cannot be proved that there are no mermaids, it can never be proved that all fish have gills.

In science, then, there are no absolute truths. Knowing this, the scientist could throw up his hands and look for another line of work. Fortunately, most scientists have learned to accept and deal with the lack of absolute certainty that is inherent in science by making the best of the available evidence. Any scientific hypothesis is examined and tested, poked and prodded, to see if it agrees with actual observations of the world. When a hypothesis withstands all these tests, it is conditionally accepted as "true" in the sense that it is consistent with the available information. Scientists speak of

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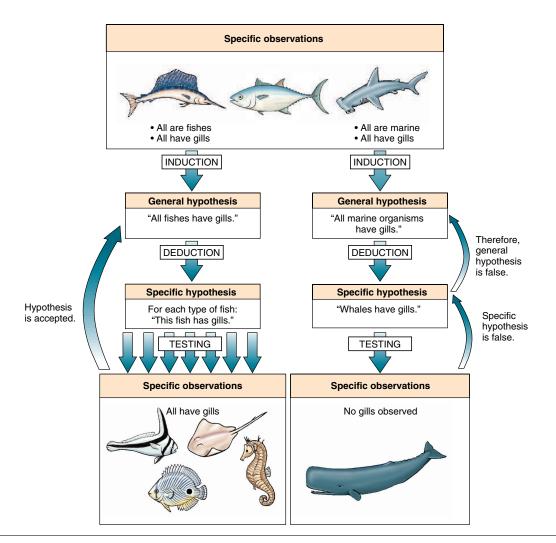


FIGURE 1.21 The steps involved in the scientific method. Two hypotheses were derived from the same observations. When tested by further observations, one hypothesis (left) is accepted and one (right) is rejected.

accepting hypotheses, not proving them. They accept the hypothesis that all fish have gills because every attempt to reject it has failed. At least for the time being, the hypothesis fits the observations. The good scientist, however, never quite forgets that any hypothesis, even one of his or her favorites, could suddenly be thrown out the window by new information. No hypothesis in science is exempt from testing, and none is immune to being discarded if it conflicts with the evidence. The bottom line in science is observation of the world, not preconceived human ideas or beliefs.

No hypothesis can be scientifically proved to be true. Instead, hypotheses are accepted for as long as they are supported by the available evidence.

# Testing the Hypothesis

Because hypotheses generally can't be proved to be true, scientists, somewhat surprisingly, spend most of their time trying to disprove, not prove, hypotheses. The basic idea is that more confidence can be placed in a hypothesis that has stood up to hard testing than in an untested one. Thus, the role of the scientist is to be a skeptic.

Often scientists are trying to decide among two or more competing hypotheses. After looking at the sailfish, shark, and tuna, our imaginary marine biologist advanced two possible hypotheses: that all fish have gills and that all marine animals have gills. Both hypotheses were consistent with his observations to that point. After examining a whale, he rejected the second hypothesis and, in doing so, strengthened the first one. He arrived at the best hypothesis by a process of elimination. I. Principle of Marine Science 1. The Science of Marine Biology © The McGraw–Hill Companies, 2003

16 Part One Principles of Marine Science



Most people know the American writer John Steinbeck as the author of such beloved works as *The Grapes of Wrath, Of Mice and Men,* and *East of Eden.* Less well known are Steinbeck's contributions to marine biology, which resulted largely from his close friendship with a man named Ed Ricketts.

Steinbeck and Ricketts first met in 1930—by Steinbeck's account, in a dentist's office in Pacific Grove, California. Steinbeck had a long-standing interest in marine biology and had even taken college courses in the subject at the nearby Hopkins Marine Station. He had wanted to meet Ricketts for some time. Ricketts owned and operated the Pacific Biological Laboratory, located near the Hopkins station and the present site of the Monterey Bay Aquarium. Working out of his laboratory, Ricketts collected specimens of marine life along the Pacific coast and sold them to universities and museums. He was immensely popular in the area and knew more about marine biology than anyone around.

The two men became close friends almost immediately. Before long Steinbeck, then struggling as a writer, was spending a lot of time hanging around his friend's laboratory. He gave his interest in marine biology free rein and soon was helping Ricketts in his business, going on collecting trips and assisting in day-to-day operations. Steinbeck got so involved in this work that he could even get excited about a microscope:

My dream for some time in the future is a research scope with an oil immersion lens, but that costs about 600 dollars and I'm not getting it right now. . . . Oh boy! Oh boy! Sometime I'll have one. (From *Steinbeck: A Life in Letters* by Elaine A. Steinbeck and Robert Wallsten, editors, copyright 1952 by John Steinbeck, © 1969 by The Estate of John Steinbeck, © 1975 by Elaine A. Steinbeck and Robert Wallsten. Used by permission of Viking Penguin, a division of Penguin Putnam Inc.)



Ed Ricketts.

Scientific knowledge is based on observation, and sometimes simple observation is the best way to test a hypothesis. The marine biologist was able to test the hypothesis that all marine animals have gills just by examining a whale. Often, however, the conditions required to test a hypothesis do not occur naturally and cannot merely be observed. The scientist must perform an **experiment**, or artificially create a situation to test the hypothesis.

In experiments scientists create situations to test hypotheses instead of relying on simple observations of nature.

Suppose another marine biologist decides that she wants to find out whether water temperature affects the growth of mussels. One approach would be to find two places, one warm and one cold, and measure how fast mussels grow at each place. The temperature at any given place changes all the time, however, and the biologist would have difficulty finding two locations where one is always warmer than the other. Even if she does, there might be many differences between the two places besides temperature. The mussels might be of different types at the two places, for example. They might be eating different foods or different amounts of food. There might be pollution or an outbreak of disease at one of the sites. In any natural situation, there will be countless factors other than temperature that might affect how fast the mussels grow. Factors that might affect observations are called **variables**.

Faced with all these variables, the biologist decides to perform an experiment. She collects mussels from one place and divides them at random into two groups. Now she knows that the mussels in the two groups are pretty much the same. She places the two groups in holding tanks, where she can regulate the water temperature with

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John Steinbeck would eventually credit Ed Ricketts with shaping his views of humanity and the world. Steinbeck was so taken with his friend that he included Ricketts in his writing. Characters in at least six of Steinbeck's novels were based on Ricketts. The most famous is Doc, the main character of *Cannery Row*, who runs the "Western Biological Laboratory":

It sells the lovely animals of the sea, the sponges, tunicates, anemones, the stars and buttlestars [sic], the sunstars, the bivalves, barnacles, the worms and shells, the fabulous and multiform little brothers, the living moving flowers of the sea, nudibranchs and tectibranchs, the spiked and nobbed and needly urchins, the crabs and demi-crabs, the little dragons, the snapping shrimps, the ghost shrimps so transparent that they hardly throw a shadow. . . . You can order anything living from Western Biological and sooner or later you will get it. (From *Cannery Row*, by John Steinbeck. Copyright 1945 by John Steinbeck. Renewed © 1973 by Elaine Steinbeck, John Steinbeck IV, and Thom Steinbeck. Used by permission of Viking Penguin, a division of Penguin Putnam Inc.)

The friendship was beneficial to marine biology as well as to literature. One long trip to Mexico resulted in their collaboration on *The Sea of Cortez.* This book is part literature, part travelogue, and part scientific report. It contains lists and descriptions of the marine life the two men encountered on their expedition.

Ed Ricketts' most enduring contribution to marine biology was the publication in 1939 of *Between Pacific Tides*. Written with Jack Calvin, a mutual friend of Ricketts and Steinbeck, *Between Pacific Tides* is a comprehensive guide to the seashore life of the Pacific coast of North America. Revised and updated—it's now in its fifth edition—it is still used by amateurs and professionals alike.

Though Ricketts was an able biologist and was largely responsible for the content of *Between Pacific Tides*, he had difficulty getting his observations and ideas down on paper. Steinbeck almost certainly helped him write the book. Steinbeck, who was beginning to achieve success as a writer, also helped Ricketts get the book published. At one point, Ricketts felt that the publisher, Stanford University Press, was dragging its feet, and Steinbeck fired off this sarcastic letter:

Gentlemen:

May we withdraw certain selected parts of *Between Pacific Tides* which with the passing years badly need revision. Science advances but Stanford Press does not.

There is the problem also of the impending New Ice Age.

Sometime in the near future we should like to place our order for one (1) copy of the forthcoming (1948, no doubt) publication, The Internal Combustion Engine, Will it Work?

> Sincerely, John Steinbeck Ed Ricketts

### P.S. Good Luck with A Brief Anatomy of the Turtle.

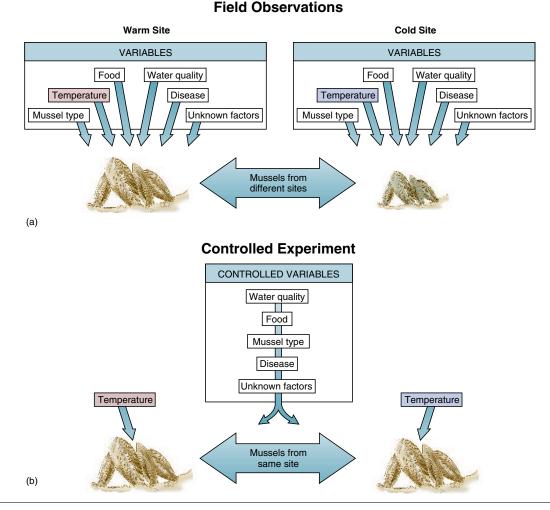
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Ed Ricketts was killed in a train accident in 1948. Steinbeck, saddened at the death of his friend, wrote, "There died the greatest man I have ever known and the best teacher." The memory of Ed Ricketts, and the love of marine biology he inspired, would remain with Steinbeck for the rest of his life.

thermostats, and grows one group in warm water, the other in cold. She feeds all the mussels the same amounts of the same food at the same time, protects the mussels from pollution and disease, and supplies both holding tanks with seawater from the same source. She also keeps all the other living conditions exactly the same for both groups. Because all these variables are the same for both groups, the biologist knows that they cannot be responsible for any differences she observes in the growth of the mussels. The only difference between the two groups is temperature. To prevent a variable from affecting an experiment, the scientist has two options. One is to artificially keep the variable from changing, for example, by giving all the mussels exactly the same food. The other is to make sure that any changes that do occur are identical for both groups. By supplying both tanks with seawater from the same source, for example, our biologist ensures that any changes in the quality of the water affect both groups of mussels equally. Variables that are prevented from affecting an experiment are said to be **controlled**, and the experiment is called a **controlled**  **experiment** (Fig. 1.22). Since the biologist has controlled the effects of other variables while growing the mussels at different temperatures, she can be more confident that any difference in growth rate between the two groups is due to temperature.

Similarly, the biologist could study how food supply affects mussel growth by keeping the mussels at the same temperature but giving them different amounts of food. Experiments thus allow the effects of different variables to be separated. The way that variables interact can also be studied. The mussels could be

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**FIGURE 1.22** Many different variables might produce differences between groups of mussels observed at two different locations (*a*). Controlling the variables in an experiment (*b*) allows the effects of a single factor, in this case temperature, to be tested.

maintained in different *combinations* of temperature and food supply, for example, to see whether the temperature at which they grow fastest depends on how much food they get.

# The Scientific Theory

Many people think of a theory as a rather shaky proposition, and most of us have heard people ridicule some idea or other because it was "only theoretical." The public usually reserves such scorn for controversial or unpopular theories. The theory of gravity, for instance, is rarely criticized for being "only a theory." In reality, a scientific theory is on much firmer ground than most people realize. To the scientist, the term **theory** refers to a hypothesis that has passed so many tests that it is generally regarded as true. In science, the status of theory is a lofty one indeed. Because it has been extensively tested, scientists place considerable confidence in it. They use it as a framework to order their thinking and move on to new discoveries.

It must be remembered, however, that a theory is still a hypothesis, though a welltested one. As with other hypotheses, theories cannot be absolutely proved and are accepted as true only as long as they are supported by evidence. Good scientists accept theories for the time being because the best available evidence supports them. They also recognize that any theory may be overturned at any time by new evidence.

A scientific theory is a hypothesis that has been so extensively tested that it is generally regarded as true. Like any hypothesis, however, it is subject to rejection if enough evidence accumulates against it. Castro-Huber: MarineI. Principle of Marine1. The Science of Marine© The McGraw-HillBiology, Fourth EditionScienceBiologyCompanies, 2003

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# *Limitations of the Scientific Method*

No human enterprise, including science, is perfect. Just as it is important to understand how and why the scientific method works, it is important to understand the limitations of the scientific method. For one thing, remember that scientists are people too; they are prone to the same human shortcomings as anyone else. Scientists may be attached to favorite theories even when confronted with contradictory evidence—being wrong can be hard to accept. Like anyone else, they may let their personal biases affect their thinking. No one can be completely objective all the time. Fortunately, factual errors are usually corrected because hypotheses are tested not just by one person but by many. The practical success of science is evidence that the self-checking nature of the scientific method does work most of the time.

Science also has some built-in limitations. Ironically, these limitations arise from the same features that give the scientific method its power: the insistence on direct observation and testable hypotheses. This means that science cannot make judgments about values, ethics, or morality. Science can reveal how the world is, but not how it should be. Science cannot decide what is beautiful. Science can't even tell humanity how to use the knowledge and technology it produces. These things all depend on values, feelings, and beliefs, which are beyond the scope of science.



# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

# **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. Nearly all the major advances in marine biology have come in the last 200 years. What do you think are the reasons for this?
- 2. In Chapter 1 it was explained that the statement "There are mermaids in the ocean" is not a valid scientific hypothesis. Can the same be said of the statement "There are *no* mermaids in the ocean"? Why?
- 3. Imagine that you are a marine biologist and you notice that a certain type of crab tends to be considerably larger in a local bay than the same type of crab is in the waters outside the bay. What hypotheses might account for this difference? How would you go about testing these hypotheses?
- 4. Many species of whale have been hunted to the brink of extinction. Many people think that we do not have the right to kill whales and that all whaling should cease. On the other hand, in many cultures whales have been hunted for

centuries and still have great cultural importance. People from such cultures argue that limited whaling should be allowed to continue. What is the role that science can play in deciding who is right? What questions cannot be answered by science?

# For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol \_\_\_\_\_, and will contain live links when you visit this page in the Online Learning Center.

- Access to the sea. *Oceanus*, vol. 40, no. 1, 1997. This issue of *Oceanus* focuses on the ships, submersibles, unmanned vehicles, and other tools that marine scientists use to study the ocean.
- Buckingham, M. J., J. R. Potter and C. L. Epifanio, 1996. Seeing underwater with background noise. *Scientific American*, vol. 274, no. 2, February, pp. 86–90. How the sounds of animals, waves, and ships are used to "see" underwater.
- Edmunds, P. J., 1996. Ten days under the sea. *Scientific American*, vol. 275, no. 4, October. Six marine biologists spend ten days living and working in the world's only underwater habitat and laboratory.
- McGovern, T. H. and S. Perdikaris, 2000. The Vikings' silent saga. *Natural History*, vol. 109, no. 8, October, pp. 50–57. The story of the Vikings' discovery of America and why their attempt to colonize the New World was not successful.

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- Mayr, E., 2000. Darwin's influence on modern thought. *Scientific American*, vol. 283, no. 1, July, pp. 78–83. Darwin's ideas and writings had a profound influence not only upon science but upon society at large.
- Ocean observatories. *Oceanus*, vol. 42, no. 1, 2000. Hightech instrument packages stay deep in the oceans for months, even years, at a time, sending back key information to
- scientists on the surface. Pain, S., 1998. Fellini with flippers. *New Scientist*, vol. 158, no. 2129, 11 April 1998, pp. 32–35. More information on "crittercam," the underwater video camera used to spy on the underwater lives of marine mammals.

"The oceans." *Scientific American Presents*, vol. 9, no. 3, August 1998. A collection of articles about the ocean.

# See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

- Juvenile lemon shark being captured for research (Bahamas)
- Juvenile lemon shark being measured prior to release (Bahamas)

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- Sampling the estuary using a seine—a messy job! (Baruch Research Station, South Carolina)
- Marine research: sorting, identifying, cataloging estuary sample (Baruch Marine Research Station, South Carolina)

# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- The science of marine biology
- · Aquaria and research station sites
- · Marine archaeology and maritime history
- Science as a process
- Introductory sites
- Careers in science
- Scientific method

# Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

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# The Sea Floor



The oceans are not just places where the land happens to be covered by water. The sea floor is geologically distinct from the continents. It is locked in a perpetual cycle of birth and destruction that shapes the oceans and controls much of the geology and geological history of the continents. Geological processes that occur beneath the waters of the sea affect not only the oceans, but dry land as well.

The processes that mold ocean basins occur slowly, over hundreds of millions of years. On this timescale, where a human lifetime is but the blink of an eye, solid rocks flow like liquid, entire continents move across the face of the earth, and mountains grow from flat plains. To understand the sea floor, we must learn to adopt the unfamiliar point of view of geological time.

It may seem odd to devote an entire chapter in a marine biology book to geology, but geology is important to the marine biologist. **Habitats**, or the natural environments where organisms live, are directly shaped by geological processes. The form of coastlines; the depth of the water; whether the bottom is muddy, sandy, or rocky; and many other features of a marine habitat are determined by its geology. Even the history of marine life is related to geology.

# THE WATER PLANET

The presence of large amounts of liquid water makes our planet unique. Most other planets have very little water, and on those that do the water exists only as perpetually frozen ice or as vapor in the atmosphere. The earth, on the other



Earth: the ocean planet.

hand, is very much a water planet. The oceans cover most of the globe and play a crucial role in regulating our climate and atmosphere. Without water, life itself would be impossible.

# The Geography of the Ocean Basins

The oceans cover 71% of the earth's surface. They are not distributed equally with respect to the Equator. About twothirds of the earth's land area is found in the Northern Hemisphere, which is only 61% ocean. About 80% of the Southern Hemisphere is ocean.

The oceans are traditionally classified into four large basins (Fig. 2.1). The **Pacific** is the deepest and largest ocean, almost as large as all the others combined (Table 2.1). The **Atlantic** Ocean is a little larger than the **Indian** Ocean, but the two are similar in average depth. The **Arctic** is the smallest and shallowest ocean. Connected or marginal to the main ocean basins are various shallow seas, such as the Mediterranean Sea, the Gulf of Mexico, and the South China Sea.

Though we usually treat the oceans as four separate entities, they are actually interconnected. This can be seen most easily by looking at a map of the world as seen from the South Pole (Fig. 2.2). From this view it is clear that the Pacific, Atlantic, and Indian oceans are large branches of one vast system. The connections among

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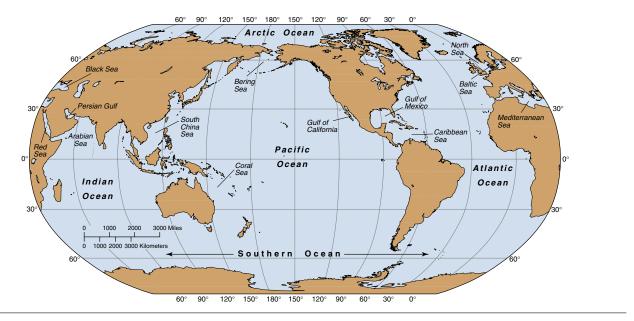


FIGURE 2.1 The major ocean basins and some of the marginal seas.

Table 2.1Average Depths and Total Areas of the Four<br/>Major Ocean Basins

|          | Ar                          | Average                     | e Depth |        |
|----------|-----------------------------|-----------------------------|---------|--------|
| Ocean    | Millions of km <sup>2</sup> | Millions of mi <sup>2</sup> | Meters  | Feet   |
| Pacific  | 166.2                       | 64.2                        | 4,188   | 13,741 |
| Atlantic | 86.5                        | 33.4                        | 3,736   | 12,258 |
| Indian   | 73.4                        | 28.3                        | 3,872   | 12,704 |
| Arctic   | 9.5                         | 3.7                         | 1,330   | 4,364  |

the major basins allow seawater, materials, and some organisms to move from one ocean to another. Because the oceans are actually one great interconnected system, oceanographers often speak of a single **world ocean.** They also refer to the continuous body of water that surrounds Antarctica as the **Southern Ocean.** 

The world ocean, which covers 71% of the planet, is divided into four major basins: the Pacific, Atlantic, Indian, and Arctic oceans.

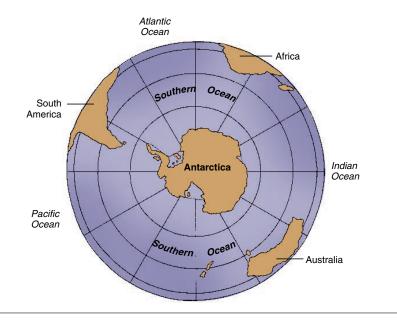
# The Structure of the Earth

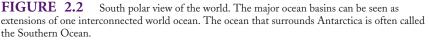
The earth and the rest of the solar system are thought to have originated about 4.5 billion years ago from a cloud or clouds of dust. This dust was the debris remaining from a great cosmic explosion called the **big bang**, which astrophysicists estimate occurred about 15 billion years ago. The dust particles collided with each other, merging into larger particles. These larger particles collided in turn, joining into pebblesized rocks that collided to form larger rocks, and so on. The process continued, eventually building up the earth and other planets.

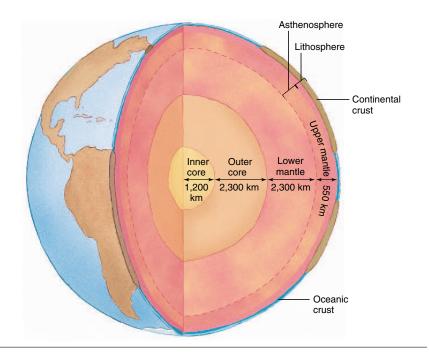
So much heat was generated as the early earth formed that the planet was probably molten. This allowed materials to settle within the planet according to their density. Density is the weight, or more correctly the mass, of a given volume of a substance. Obviously, a pound of styrofoam weighs more than an ounce of lead, but most people think of lead as "heavier" than styrofoam. This is because lead weighs more than styrofoam if equal volumes of the two are compared. In other words, lead is denser than styrofoam. The density of a substance is calculated by dividing its mass by its volume. If two substances are mixed, the denser material will tend to sink and the less dense to float.

Density is the mass of a substance per unit volume. Substances of low density will float on substances of higher density.

 $density = \frac{mass}{volume}$ 







**FIGURE 2.3** The interior of the earth is divided into the core, mantle, and crust. The core is subdivided into the solid inner core and the liquid outer core. The mantle is also subdivided into upper and lower layers. The very upper layer of the upper mantle is solid, and together with the crust forms the lithosphere. The upper mantle below the lithosphere is relatively fluid and is called the asthenosphere. The thickness of the crust and lithosphere is exaggerated here, and the thicknesses of all layers vary.

# Chapter 2 The Sea Floor 23

During the time that the young earth was molten, the densest material tended to flow toward the center of the planet, while lighter materials floated toward the surface. The light surface material cooled to make a thin crust. Eventually, the atmosphere and oceans began to form. If the earth had settled into an orbit only slightly closer to the sun, the planet would have been so hot that all the water would have evaporated into the atmosphere. With an orbit only slightly farther from the sun, all the water would be perpetually frozen. Fortunately for us, our planet orbits the sun in the narrow zone in which liquid water can exist. Without liquid water there could be no life as we know it on earth.

# Internal Structure

The internal structure of the earth reflects the planet's early beginnings. As materials sank or floated according to their density, they formed concentric layers like those of an onion (Fig. 2.3). The innermost layer, the **core**, is composed mostly of mixtures, or alloys, of iron. The pressure in the core is more than a million times that at the earth's surface, and the temperature is estimated to be over 4,000°C (7,200°F). The core is made up of a solid inner core and a liquid outer core. It is thought that swirling motions of the liquid material in the iron-rich outer core produce the earth's magnetic field.

The layer outside the earth's core is the **mantle**. Though most of the mantle is thought to be solid, it is very hot—near the melting point of the rocks. Because of this, much of the mantle actually flows almost like a liquid, though much slower. Over hundreds of millions of years, the mantle swirls and mixes like very thick soup heating in a saucepan.

The **crust** is the outermost, and therefore most familiar, layer of the earth. Compared with the deeper layers, it is extremely thin, like a rigid skin floating on top of the mantle. The composition and characteristics of the crust differ greatly between the oceans and the continents.

The earth is composed of three main layers: the iron-rich core, the semiplastic mantle, and the thin outer crust. I. Principle of Marine Science 2. The Sea Floor

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# Table 2.2Comparison of the Characteristics of Continental<br/>and Oceanic CrustsOceanic Crust (basalt)Continental Crust (granite)Density about 3.0 g/cm³Density about 2.7 g/cm³Only about 5 km (3 mi) thick20 to 50 km (12 to 30 mi) thickGeologically youngCan be very oldDark in colorLight in colorRich in iron and magnesiumRich in sodium, potassium, calcium, and aluminum

# Continental and Oceanic Crusts

The geological distinction between ocean and continents is caused by physical and chemical differences in the rocks themselves (Table 2.2), rather than whether or not the rocks happen to be covered with water. The part of the earth covered with water, the ocean, is covered because of the nature of the underlying rock.

Oceanic crust, which makes up the sea floor, consists of a type of mineral called basalt that has a dark color. Most continental rocks are of a general type called granite, which has a different chemical composition than basalt and is lighter in color. Oceanic crust is denser than continental crust, though both are less dense than the underlying mantle. Oceanic crust has a density of about 3.0 g/cm<sup>3</sup>, compared with about 2.7 g/cm<sup>3</sup> for continental crust. The continents can be thought of as thick blocks of crust floating on the mantle much as icebergs float in water. Oceanic crust floats on the mantle too, but because it is denser it doesn't float as high. This is why the continents lie high and dry above sea level and oceanic crust lies below sea level and is covered with water. Oceanic crust is also much thinner-about 5 km (3 mi) compared with 20 to 50 km (12 to 30 mi) for continental crust.

Oceanic and continental crusts also differ in geological age. The oldest oceanic rocks are less than 200 million years old, quite young by geological standards. Continental rocks, on the other hand, can be very old, as old as 3.8 billion years.

# THE ORIGIN AND STRUCTURE OF THE OCEAN BASINS

For centuries people viewed the earth as static and unchanging. Evidence of geological change was all around, however, from catastrophic earthquakes and volcanic eruptions to the slow erosion of river valleys. People gradually began to see that the face of the earth did indeed change. Today scientists recognize the earth as a world of constant transformation where even the continents move.

# Early Evidence of Continental Drift

As early as 1620 the English philosopher, writer, and statesman Sir Francis Bacon noted that the coasts of the continents on opposite sides of the Atlantic fit together like pieces of a puzzle (Fig. 2.4). It was later suggested that the Western Hemisphere might once have been joined to Europe and Africa. Evidence that the continents were once merged slowly accumulated over the centuries. Coal deposits and other geological formations, for example, match up on opposite sides of the Atlantic. Fossils collected on opposing coasts are also similar.

In 1912 a German geophysicist, Alfred Wegener, combined the evidence available at the time and proposed the first detailed hypothesis of **continental**  www.mhhe.com/marinebiology

drift. Wegener suggested that all the continents had once been joined in a single "supercontinent," which he called **Pangaea.** He thought that Pangaea began breaking up into the continents we know today about 180 million years ago.

# The Theory of Plate Tectonics

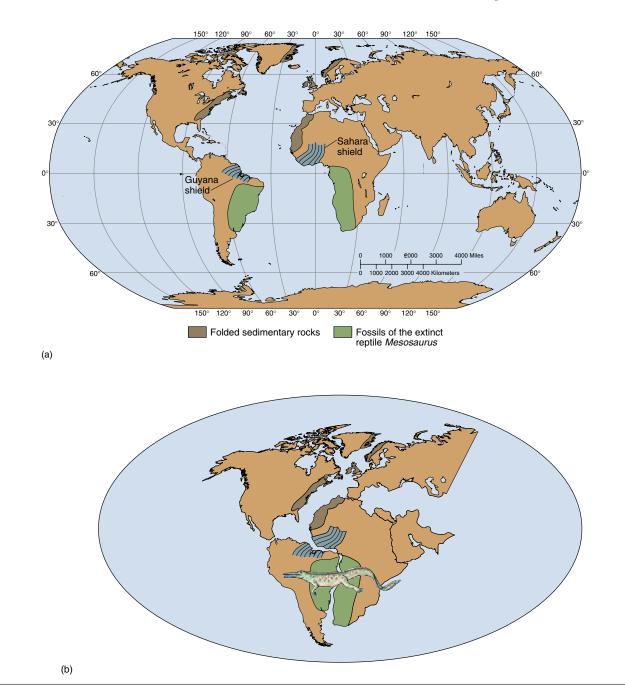
Wegener's hypothesis was not widely accepted because he could not supply a plausible mechanism to account for the motion of the continents. Later proposals of continental drift also failed to provide a workable mechanism, though evidence continued to accumulate. In the late 1950s and the 1960s scientists were able to put all the evidence together. They concluded that the continents *did* drift, as part of a process that involves the entire surface of our planet. This process is called **plate tectonics.** 

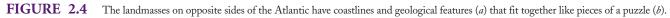
# Discovery of the Mid-Ocean Ridge

In the years after World War II, sonar allowed the first detailed surveys of large areas of the sea floor. These surveys resulted in the discovery of the mid-ocean ridge system, a continuous chain of volcanic submarine mountains that encircles the globe like the seams on a baseball (Figs. 2.5 and 2.6). The mid-ocean ridge system is the largest geological feature on the planet. At regular intervals the midocean ridge is displaced to one side or the other by cracks in the earth's crust known as transform faults. Occasionally the submarine mountains of the ridge rise so high that they break the surface to form islands, such as Iceland and the Azores.

The portion of the mid-ocean ridge in the Atlantic, known as the **Mid-Atlantic Ridge**, runs right down the center of the Atlantic Ocean, closely following the curves of the opposing coastlines. The ridge forms an inverted Y in the Indian Ocean and runs up the eastern side of the Pacific (Fig. 2.6). The main section of ridge in the Eastern Pacific is called the **East Pacific Rise**.

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The mid-ocean ridge system is a continuous, submarine range of volcanic mountains that runs through all of the ocean basins.

Surveys of the sea floor also revealed the existence of a system of deep depressions in the sea floor called **trenches** (Figs. 2.5 and 2.6). Trenches are especially common in the Pacific. How they are formed will be discussed later in this chapter (see "Sea-Floor Spreading and Plate Tectonics," p. 30).

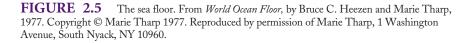
# Significance of the Mid-Ocean Ridge

When the mid-ocean ridge system and trenches were discovered, geologists wanted to know how they were formed and began studying them intensively. They found that there is a great deal of geological activity around these features. Earthquakes are clustered at the ridge, for example, and volcanoes are especially common near trenches (Fig. 2.7).

The characteristics of the sea floor are also related to the mid-ocean ridge. The layer of **sediment**, loose material such as mud or sand that settles to the bottom, gets thicker and thicker moving away from the crest of the mid-ocean ridge. Beginning in 1968 a deep-sea drilling ship, the *Glomar Challenger*, obtained samples of the actual sea-floor rock. It was found that the farther rocks are from the ridge crest the older they are. The deepest sediment, that lying directly on the sea-floor rock, also gets older moving away from the ridge crest.

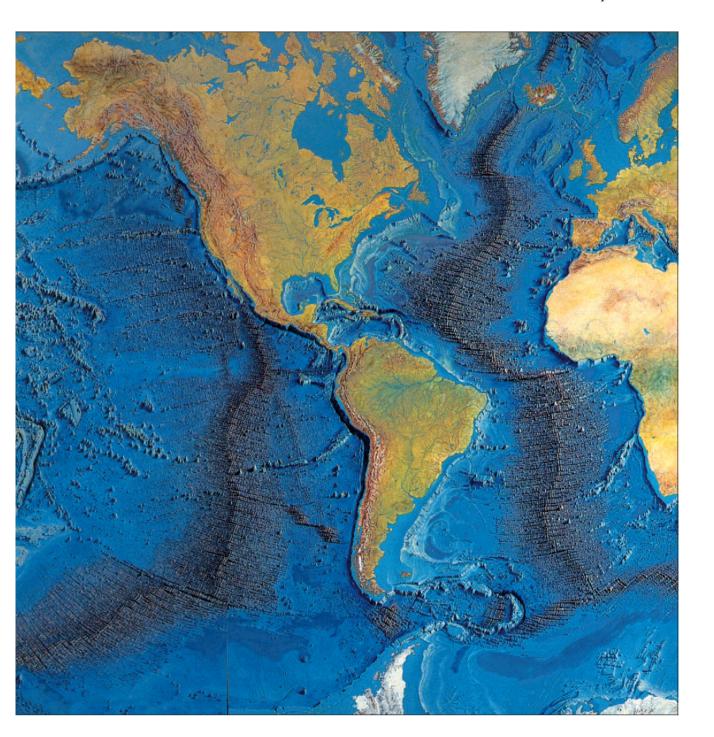
One of the most important findings came from studying the magnetism of rocks on the sea floor. Geologists already knew that the earth's magnetic field reverses direction a few times every million years. The present orientation, where a magnetic compass points north, is arbitrarily called the "normal" orientation. During magnetic reversal periods, the earth's magnetic north pole is opposite to where it is now. During a reversal, a compass would point toward what is now the South Pole! The cause of these reversals is unknown but is thought to be related to changes in the movement of material in the molten outer core.





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Many rocks contain tiny magnetic particles. When a rock is molten these particles are free to move and act like tiny compasses, pointing toward the magnetic north pole, wherever it happens to be. Thus, the magnetic particles will point in opposite directions during times of normal and reversed magnetic fields. When the rocks cool the particles are frozen in place and keep their orientation even after the magnetic field changes. It is therefore possible to tell what the orientation of the earth's magnetic field was when the rocks cooled.

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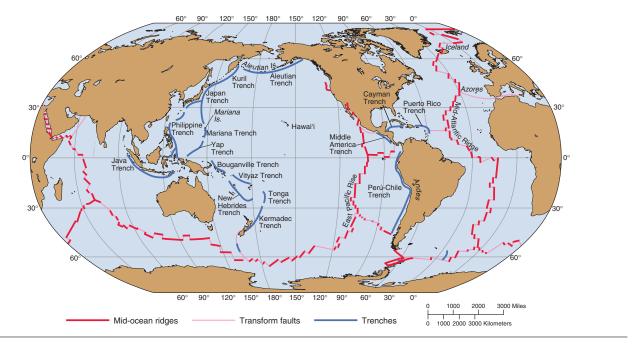


FIGURE 2.6 The major features of the sea floor. Compare this map with Figure 2.5.

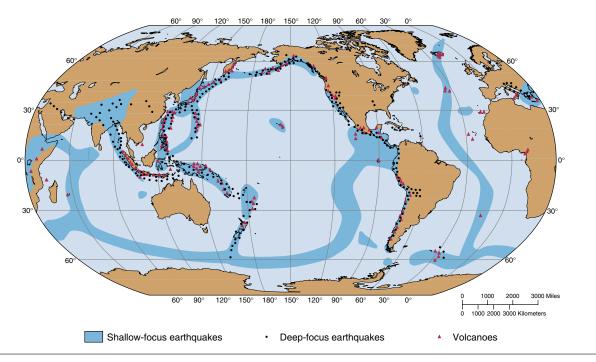


FIGURE 2.7 The world distribution of earthquakes and volcanoes. Compare these with the locations of mid-ocean ridges and trenches shown in Figure 2.6.

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Iceland

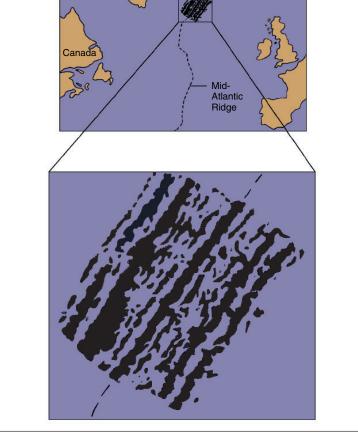
Geologists studying the mid-ocean ridge system discovered a pattern of magnetic bands or "stripes" in the sea floor (Fig. 2.8). The stripes run parallel to the mid-ocean ridge and represent zones in which the rocks on the sea floor alternate between normal and reversed magnetization. The bands are symmetric around the ridge, so that the pattern on one side of the ridge is a mirror image of the pattern on the other side. The discovery of these magnetic bands, called magnetic anomalies, was important because the bands of normally magnetized sea floor must have formed-that is, cooled from molten material-at different times from the reverse magnetized bands. The sea floor, then, was not formed all at once but in strips that parallel the mid-ocean ridge.

Earthquakes and volcanoes are associated with the mid-ocean ridge. The sediments are thicker and the rock of the actual sea floor is older the farther they are from the ridge. Bands of rock alternating between normal and reversed magnetism parallel the ridge.

## Creation of the Sea Floor

It was the discovery of magnetic anomalies on the sea floor, together with the other evidence, that finally led to an understanding of plate tectonics. The jump from the various observations of the sea floor and mid-ocean ridges to the theory of plate tectonics is a good example of the use of **induction** in science.

Huge pieces of oceanic crust are separating at the mid-ocean ridges. As the pieces move apart they create a crack in the crust called a rift. When a rift occurs it releases some of the pressure on the underlying mantle, like removing the cap from a bottle of soda pop. Because of the reduced pressure, some of the hot mantle material melts and rises up through the rift. The ascending mantle material pushes up the oceanic crust around the rift to form the mid-ocean ridge (Fig. 2.9). When this molten material reaches the earth's surface it cools and solidifies to form new oceanic crust. The process repeats itself as the sea floor continues to move away from the midocean ridge. The entire process by which the sea floor moves away from the mid-



Greenland

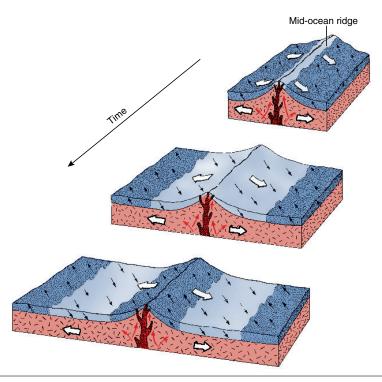
**FIGURE 2.8** Rocks with normal magnetization cooled from molten rocks at a time when the earth's magnetic field was "normal," that is, the same as it is today. If the positions of sea-floor rocks with normal (dark) and reversed (light) magnetization are drawn on a map, they form bands running parallel to the mid-ocean ridge. Note that the rocks at the ridge crest have normal magnetization.

ocean ridges to create new sea floor is called **sea-floor spreading**, and the ridges are called spreading centers.

Sea-floor spreading explains many observations related to the mid-ocean ridge. Right at the ridge crest the crust is new and has not had time to accumulate a layer of sediment. As the crust moves away from the ridge it ages and sediment builds up. This explains why the sediment gets thicker and the rocks get older as one moves away from the ridge. Seafloor spreading also explains the pattern of magnetic stripes. As new sea floor is created, it freezes the magnetic field prevailing at the time and preserves that magnetization as it moves away from the ridge. Eventually the earth's magnetic field reverses, starting a new stripe.

**Induction** The development of a generalized conclusion from a series of isolated observations.

Chapter 1, p. 12



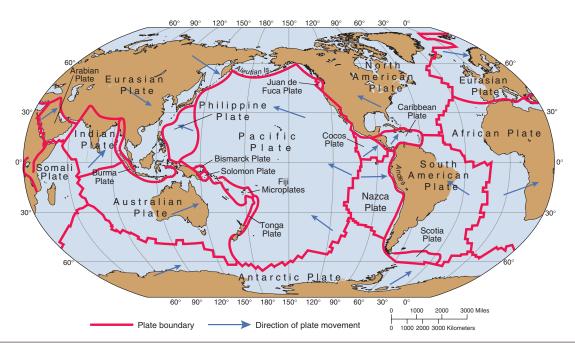
**FIGURE 2.9** Cross section of the sea floor at a mid-ocean ridge showing the mechanism of sea-floor spreading. As the sea floor moves away from the rift, molten material rises from the mantle and cools to form new sea floor. When the rocks cool, they "freeze" whatever magnetic orientation, normal or reversed, is present at the time. The entire floor of the ocean was created at the mid-ocean ridge in this manner.

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# Sea-Floor Spreading and Plate Tectonics

Sea-floor spreading is only part of the story of plate tectonics. The earth's surface is covered by a fairly rigid layer composed of the crust and the uppermost part of the mantle. This layer, approximately 100 km (60 mi) thick, is called the lithosphere, meaning "rock sphere" (see Fig. 2.3). The lithosphere is broken into a number of plates called lithospheric plates (Fig. 2.10). A plate can contain continental crust, oceanic crust, or both. The lithospheric plates float on the rest of the upper mantle, called the asthenosphere, which is denser and more plastic. While the crust, mantle, and core are distinguished by their chemical composition, the distinction between the lithosphere and the asthenosphere is based on how easily the rock flows. It is the slow, swirling motion of the asthenosphere that drives the motion of lithospheric plates.

The earth's surface is broken up into a number of plates. These plates, composed of the crust and the top part of the mantle, make up the lithosphere. The plates are about 100 km (60 mi) thick.



**FIGURE 2.10** The division of the earth's surface into lithospheric plates. Some areas are not fully understood, and there may be more plates than are shown here. Compare this map with those in Figures 2.6 and 2.7.

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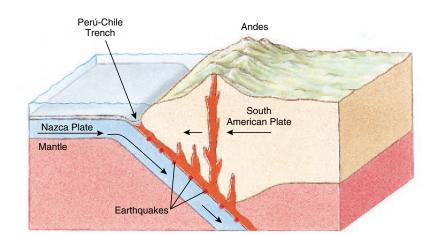
The mid-ocean ridges form the edges of many of the plates. It is at the ridges that the lithospheric plates move apart and new sea floor—that is, new oceanic lithosphere—is created by sea-floor spreading. If the plate includes a block of continental crust, the continent is carried along with the plate as it moves away from the ridge. This is the mechanism of continental drift. The plates move apart at between 2 and 18 cm (0.8 to 7 in) per year. For comparison, human fingernails grow at about 6 cm (2.4 in) per year.

As new lithosphere is created, old lithosphere is destroyed somewhere else. Otherwise, the earth would have to constantly expand to make room for the new lithosphere. Lithosphere is destroyed at trenches, which are another important type of boundary between lithospheric plates. A trench is formed when two plates collide and one of the plates dips below the other and sinks back down into the mantle (Figs. 2.11 and 2.12). This downward movement of the plate into the mantle is called **subduction**. Because subduction occurs at trenches, trenches are often called **subduction zones**.

As the plate sinks, it weakens under the heat and pressure of the mantle and begins to break up. The movements produced as the plate sinks and breaks up cause earthquakes. Eventually the plate gets so hot that it melts. Some of the molten material rises back to the surface to form volcanoes. The rest of the molten rock continues to sink into the mantle. Some of this material may eventually be recycled, rising again at another mid-ocean ridge several hundred million years later.

At trenches a lithospheric plate descends into the mantle, where it breaks up and melts. This process, called subduction, produces earthquakes and volcanoes.

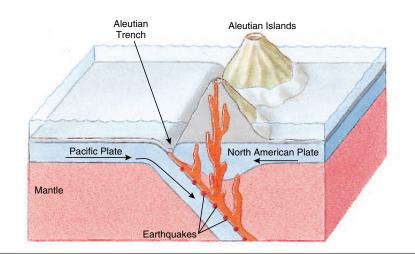
The collision that produces a trench can be either between an oceanic plate and a continent or between two oceanic plates. When an oceanic plate collides with a continent, it is always the oceanic plate that descends into the mantle. This is because the continental block is less dense than the oceanic plate and floats on top. This explains why very old rocks are



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**FIGURE 2.11** Some trenches are formed by the collision of continental and oceanic plates. In this example the Nazca Plate dips beneath the South American Plate. Earthquakes are produced as the Nazca Plate descends into the mantle. The lighter materials from the sinking plate rise back to the surface as they melt, creating the volcanic Andes (see Figs. 2.5, 2.6, and 2.7).



**FIGURE 2.12** Trenches can also be caused by the collision of two oceanic plates. The oceanic portion of the North American Plate has collided with the Pacific Plate. In this case, the Pacific Plate dipped below the North American Plate, but either of the two plates could have done so. Earthquakes are produced by the descending plate. The volcanoes associated with the trench have produced the Aleutian Island arc (see Figs. 2.5, 2.6, and 2.7).

found only on the continents: Because oceanic crust is eventually destroyed at trenches, it never gets old by geological standards. Continental crust, on the other hand, is not destroyed in trenches and can therefore last for billions of years.

A collision between oceanic and continental plates causes the development of continental volcanoes associated with the trench. These volcanoes may form coastal mountain ranges. The Andes on the Pacific coast of South America are a good example of this (Fig. 2.11).

When two oceanic plates collide, one of the plates dips beneath the other to form the trench. Again the trench is associated with earthquakes and volcanoes (Figs. 2.12 and 2.13). The volcanoes may rise from the sea floor to create chains of volcanic islands. As viewed on a map, trenches are curved because of the earth's spherical shape. The volcanic island chains



**FIGURE 2.13** Mount Veniaminof, an active volcano on the Alaska Peninsula. Geologically, the Alaska Peninsula is part of the Aleutian Island chain that has formed behind the Aleutian Trench (see Figs. 2.6 and 2.12).

associated with the trenches follow the trenches' curvature and are called **island arcs.** Examples include the Aleutian and Mariana islands (see Figs. 2.5 and 2.6).

Occasionally two continental plates collide. Because of the relatively low density of continental crust, both plates tend to float and neither is subducted. Therefore no trench is formed. Instead, the two continental blocks push against each other with such tremendous force that the two continents become "welded" together. The force is eventually too much for the rocks, which buckle and fold like an accordion. The huge folds form mountain ranges. The Himalayas, for example, were formed when India collided with the rest of Asia (see "Continental Drift and the Changing Oceans," p. 33).

There is a third type of plate boundary in addition to trenches and midocean ridges. Sometimes two plates are moving in such a way that they slide past each other, neither creating nor destroying lithosphere. This type of plate boundary is called a **shear boundary**. In the zone where the two plates move past each other, called a **fault**, there is a great deal of friction between the plates. This friction prevents the plates from sliding smoothly. Instead they lock, and stress builds up until the plates break free and slip all at once, causing an earthquake. The San Andreas Fault in California is the largest and most famous example of a shear boundary (Fig. 2.14).

#### The Dynamic Mantle

The slow swirling motions of the mantle not only drive the movement of lithospheric plates, they also shape the earth's surface in other ways. At 45 or so places scattered around the world, for example, plumes of hot, molten rock called magma well up from deep within the mantle. Hot magma from the hot spots sporadically forces its way up through the lithosphere to erupt in volcanic activity.

The geysers and bubbling mud pools at Yellowstone are a famous example of the volcanic activity produced by hot spots. While a few other hot spots lie beneath continents, most of them are below the sea floor, producing volcanic underwater mountains, or seamounts, that sometimes grow high enough to become islands. Some hot spots lie under the middle of a plate, creating long lines of seamounts and islands (see "Hot Spots and the Creation of the Hawaiian Islands," p. 40), including many island www.mhhe.com/marinebiology



FIGURE 2.14 The San Andreas Fault. This photo was taken on the Carrizo Plain, California.

chains in the South Pacific. Others are intimately associated with mid-ocean ridges. They too form islands, but because mid-ocean ridges are not carried along like the lithospheric plates these islands do not form chains. Instead, single islands or clumps of islands are formed. Examples include Iceland, the Azores, and the Galápagos Islands. Even larger masses of hot rock called superplumes also rise slowly from deep in the mantle, lifting up great areas of the lithosphere. A superplume under southern Africa, for example, is thought to have uplifted a vast plateau region there.

Not all rock movements in the mantle cause uplift. When an oceanic plate slides under the continent at a trench (Fig. 2.11), it does slightly lift the edge of the continent. As the slab of cold lithosphere continues to sink deeper in the mantle under the continent, however, it tends to drag the continent down with it. The central part of the continent subsides, sometimes by so much that seawater floods in to form shallow seas. After tens of millions of years the continent breaks free of the sinking plate and floats back up to its normal elevation, and the shallow sea disappears. It is thought that this occurred in North America when a huge Castro–Huber: Marine Biology, Fourth Edition I. Principle of Marine Science 2. The Sea Floor

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slab of oceanic lithosphere called the Farallon Plate slid under the west coast. This explains why Denver, Colorado, the "mile-high city," is surrounded by rocks formed from marine sediments.

## Geological History of the Earth

We now realize that the earth's surface has undergone dramatic alterations. The continents have been carried long distances by the moving sea floor, and the ocean basins have changed in size and shape. In fact, new oceans have been born. Knowledge of the process of plate tectonics has allowed scientists to reconstruct much of the history of these changes.

#### Continental Drift and the Changing Oceans

About 200 million years ago all the continents were joined in the supercontinent Pangaea, just as Wegener proposed. Antarctica was in approximately the same place it is today, but all the other continents were in different positions (Fig. 2.15*a*). India was attached to Antarctica and Africa, rather than to Eurasia as it is now.

Pangaea was surrounded by a single vast ocean called **Panthalassa**. Panthalassa, which covered all of the rest of the planet, was the ancestor of the modern Pacific Ocean. A relatively shallow sea, the **Tethys Sea**, separated Eurasia from Africa. The Tethys Sea, the precursor of the present-day Mediterranean, was home to many of the world's shallow-water organisms. Another indentation in the coast of Pangaea, the Sinus Borealis, was to become the Arctic Ocean. Before Pangaea began to break up, there was no sign of the modern Atlantic or Indian oceans.

Approximately 180 million years ago a new rift appeared between North America and the combined continents of South America and Africa (Fig. 2.15b). This rift was the beginning of the Mid-Atlantic Ridge, and its formation marked the birth of the northern Atlantic Ocean. Pangaea was now separated into two large continents. One was **Laurasia**, composed of what is now North America and Eurasia. South America, Africa, Antarctica, India, and Australia made up the southern continent of **Gondwana**.

At around the same time another rift began to split up Gondwana, marking the beginning of the Indian Ocean. South America and Africa began to move to the northeast, and India, separated from the other continents, began to move north.

About 135 million years ago the South Atlantic was born when a new rift occurred between South America and Africa (Fig. 2.15c). This rift eventually joined the mid-ocean ridge in the North Atlantic to form a single mid-ocean ridge. As the Atlantic Ocean grew, the Americas were carried away from Eurasia and Africa. To make room for the new sea floor produced in the Atlantic, the Pacific Ocean—the descendant of Panthalassa steadily shrank. The Atlantic is still growing, and the Pacific shrinking.

The Y-shaped ridge that produced the Indian Ocean gradually extended to separate Australia from Antarctica (Fig. 2.15*d*). The base of the inverted Y extended into the African continent, forming the Red Sea, which is actually a young ocean. India continued to move to the north until it collided with Asia (Fig. 2.15*e*) to create the Himalayas.

The continents were once united in a single supercontinent called Pangaea that began to break up about 180 million years ago. The continents have since moved to their present positions.

The breakup of Pangaea to form today's continents is only the most recent turn of a continuing cycle. For hundreds of millions of years the continents have been adrift. They alternately collide and re-form into larger landmasses, only to break up and drift apart again.

#### The Record in the Sediments

We have already seen how the increase in sediment thickness moving away from mid-ocean ridges gave a clue to the workings of plate tectonics. Marine sediments also provide a wealth of other information about the earth's past. The type of sediment laid down on the sea floor often reflects the prevailing conditions in the ocean above. By studying sediments that were deposited in the past, oceanographers have learned a great deal about the history of the planet.

Two major types make up most of the sediments found in the sea. The first of these is lithogenous sediment, which is derived from the physical and chemical breakdown, or weathering, of rocks, mostly on the continents. Coarse sediments, which consist of relatively large particles, tend to sink to the bottom rapidly rather than being carried out to sea by ocean currents (see "The Shifting Sediments," p. 253). Most coarse lithogenous sediments, therefore, are deposited near the edges of the continents. Finer material sinks much more slowly and is carried far out to sea by ocean currents. Some fine material is even transported as dust by the wind. The most common kind of lithogenous sediment on the open ocean floor is a fine sediment called **red clay**.

The second major type of marine sediment, biogenous sediment, is made up of the skeletons and shells of marine organisms including diatoms, radiolarians, and forams. Some biogenous sediments are composed of the mineral calcium carbonate (CaCO<sub>3</sub>). This type of sediment is called calcareous ooze. The other type of biogenous sediment is made of silica (SiO<sub>2</sub>), which is similar to glass. It is called siliceous ooze.

The two most abundant types of marine sediment are lithogenous sediment, which comes from the weathering of rocks on land, and biogenous sediment, which is composed of the shells of marine organisms. Biogenous sediment is made mostly of calcium carbonate or silica.

**Diatoms** Single-celled, photosynthetic organisms that have a shell, or test, made of silica.

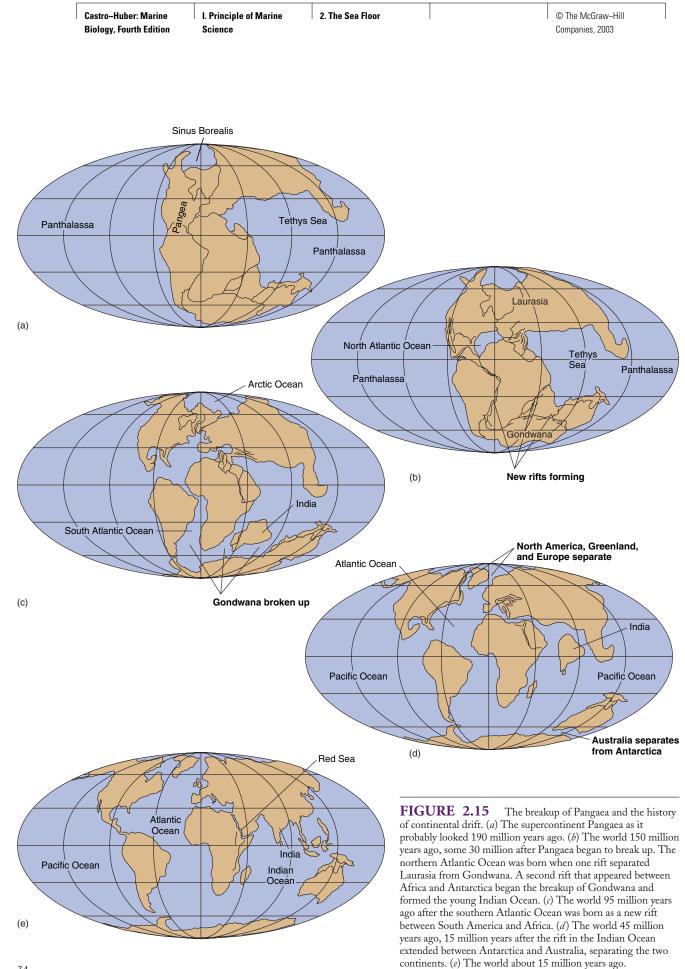
Chapter 5, p. 96, Figure 5.5

**Radiolarians** Single-celled protozoans with a test made of silica.

Chapter 5, p. 102, Figure 5.11

**Foraminiferans (Forams)** Protozoans, often microscopic, with a calcium carbonate shell.

Chapter 5, p. 101, Figure 5.10



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**FIGURE 2.16** The fossil shell of a foraminiferan (*Textularia*).

Though large fossils such as whale bones and shark teeth can be found, most of the organisms that produce biogenous sediments are microscopic, or nearly so. The sediment particles are sometimes called **microfossils** since each particle represents the preserved remains of a dead organism (Fig. 2.16). Microfossils tell scientists what organisms lived in the ocean in the past. Because some of these organisms are known to prefer cold or warm water, microfossils also give clues to ancient ocean temperatures. Ocean temperatures are determined by the earth's climate and ocean currents.

The climate of the earth in the past can also be determined by the chemical composition of the microfossils. By various methods including carbon dating, a procedure in which the ratios of different atomic forms, or isotopes, of carbon are measured, the age of the microfossils can be determined. It is also possible to tell the temperature of the water in which the organisms lived by measuring the ratios of different isotopes of oxygen in the microfossils. Thus, microfossils have preserved a detailed record of the earth's past climate. Though the record in the sediments is not always easy to read, it has been supplemented by other information. The ratio of the elements strontium (Sr) and calcium (Ca) in ancient coral skeletons, for example, also records past ocean temperatures. Ice cores from polar areas like Greenland and Antartica also preserve a record of past temperatures, as well as samples of the ancient atmosphere in the form of tiny bubbles trapped in the ice. These and other studies are providing an increasingly more detailed picture of the earth's past climate.

#### Climate and Changes in Sea Level

The climate of the earth has fluctuated rhythmically through much of its history, with relatively brief warm periods alternating with longer cold periods, or **ice ages.** The earth is presently in a warm, or **interglacial**, period. During the ice ages, great glaciers build up on the continents. Because large amounts of water are trapped as ice instead of flowing to the sea in rivers, there is less water in the ocean. Thus, sea level falls during ice ages.

The **Pleistocene**, which began a little less than 2 million years ago, was the last major period of glaciation. During the Pleistocene a series of ice ages was interspersed by brief warm periods of melting. The peak of the last ice age occurred about 18,000 years ago. At that time, vast ice sheets as thick as 3 km (2 mi) covered much of North America and Europe. Sea level was about 130 m (425 ft) lower than it is today.

Sea level falls during ice ages because water is trapped in glaciers on the continents. The last major ice age occurred about 18,000 years ago.

Sea level continues to rise, though the rate of melting slowed during the past 3,000 years. Some scientists think that without the influence of humans there would eventually be another ice age. Human impact on the atmosphere, however, has intensified the **greenhouse effect**. Global temperatures, and the rate of glacial melting, now appear to be increasing and sea level is projected to continue to rise for at least the next century (see "Living in a Greenhouse: Our Warming Earth," p. 410).

## THE GEOLOGICAL PROVINCES OF THE OCEAN

The structure of the ocean floor is dominated by the workings of plate tectonics. Because this is a global process, the major features of the sea floor are quite similar from place to place around the world. The sea floor is divided into two main regions: the **continental margins**, which represent the submerged edges of the continents, and the deep-sea floor itself.

Chapter 2 The Sea Floor

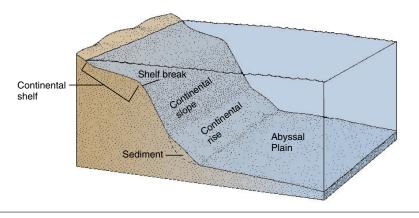
## **Continental Margins**

The continental margins are the boundaries between continental crust and oceanic crust. Most of the sediment from the continents settles to the bottom soon after reaching the sea and accumulates on the continental margins. Sediment deposits on the continental margins may be as thick as 10 km (6 mi). Continental margins generally consist of a shallow, gently sloping **continental shelf**, a steeper **continental slope** seaward of the continental shelf, and another gently sloping region, the **continental rise**, at the base of the continental slope (Fig. 2.17).

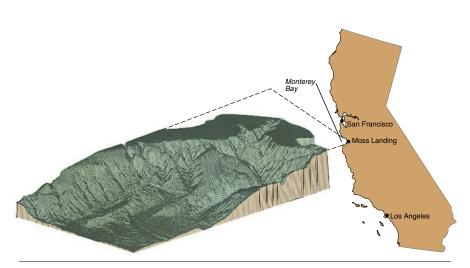
#### The Continental Shelf

The shallowest part of the continental margin is the continental shelf. Though they make up only about 8% of the ocean's surface area, continental shelves are the biologically richest part of the ocean, with the most life and the best fishing. The shelf is composed of continental crust and is really just part of the continent that presently happens to be under water. During past times of low sea level, in fact, most of the continental shelves were exposed. At these times, rivers and glaciers flowed across the continental shelves and eroded deep canyons. When sea level rose, these canyons were submerged and gave rise to much larger submarine canyons (Fig. 2.18).

The continental shelf extends outward at a gentle slope that in most places is too gradual to see with the naked eye. The shelf varies in width from less than 1 km (0.6 mi) on the Pacific coast of South America and other places to more than 750 km (470 mi) on the Arctic coast of Siberia. The continental shelf ends at the **shelf break**, where the slope abruptly gets steeper. The shelf break usually occurs at depths of 120 to 200 m (400 to 600 ft) but can be as deep as 400 m (1,300 ft).



**FIGURE 2.17** An idealized continental margin consists of a continental shelf, continental slope, and a continental rise. Seaward of the continental rise lies the deep-sea floor, or abyssal plain. These basic features vary from place to place.



**FIGURE 2.18** The Monterey Canyon originates less than 1 km (0.6 mi) off Moss Landing in Monterey Bay, California, and extends offshore for about 175 km (110 mi).

#### The Continental Slope

The continental slope is the closest thing to the exact edge of the continent. It begins at the shelf break and descends downward to the deep-sea floor. Submarine canyons beginning on the continental shelf cut across the continental slope to its base at a depth of 3,000 to 5,000 m (10,000 to 16,500 ft; Fig. 2.19). These canyons channel sediments from the continental shelf to the deep-sea floor.

#### The Continental Rise

Sediment moving down a submarine canyon accumulates at the canyon's base in a deposit called a **deep-sea fan**, similar to a river delta. Adjacent deep-sea fans may merge to form the continental rise. The rise consists of a thick layer of sediment piled up on the sea floor. Sediment may also be carried along the base of the slope by currents, extending the continental rise away from the deepsea fans. www.mhhe.com/marinebiology

Continental margins have three main parts. The continental shelf is the submerged part of the continent and is almost flat. The relatively steep continental slope is the actual edge of the continent. The continental rise is formed by sediments building up on the sea floor at the base of the continental slope.

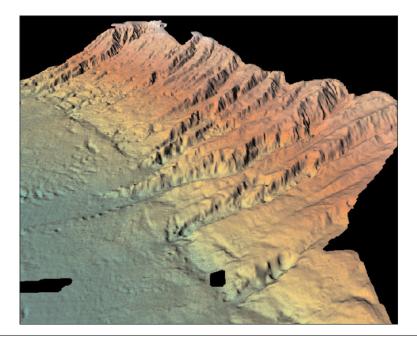
#### Active and Passive Margins

The nature of the continental margin, and therefore of the biological habitats on the coast, depends to a large extent on the plate tectonic processes occurring in the region. The continent of South America provides a good example of the relationship between the continental margin and plate tectonics (Fig. 2.20). The South American Plate (see Fig. 2.10) consists of both the continent itself and the part of the Atlantic sea floor created by the Mid-Atlantic Ridge. South America is carried westward along with the plate as new sea floor is created. The west coast of South America is colliding with the Nazca Plate, leading to the creation of a trench (see Figs. 2.6 and 2.11). Trenches are zones of intense geological activity, including earthquakes and volcanoes, so this type of continental margin is called an active margin. The west coast of North America also has a type of active margin, but it is much more complex than that of South America.

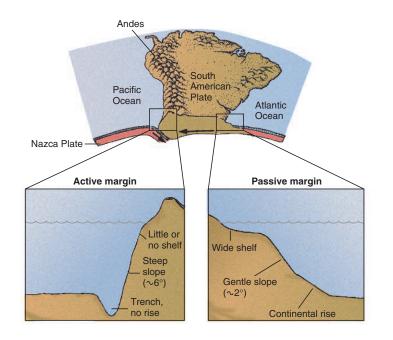
As the colliding plate descends into the trench, some of the sediment gets scraped off, folded, and "plastered" onto the continental margin. The edge of the continent is lifted by the oceanic plate passing below (see "The Dynamic Mantle," p. 32), and the coast is built up by volcanoes. These processes give active margins steep, rocky shorelines (Fig. 2.21), narrow continental shelves, and steep continental slopes. Because the sediments at the base of the continental slope are either carried down into the trench or scraped onto the continent, active margins usually lack a well-developed continental rise.

South America's east coast, on the other hand, is not a boundary between plates and is therefore relatively inactive

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**FIGURE 2.19** The continental slope along the Atlantic coast of the United States off New Jersey, Delaware, and Maryland is furrowed with marine canyons. The slope runs down from the upper right to the deep-sea floor at the lower left. This image was created with a sophisticated form of sonar known as multibeam sonar. The black areas have not been surveyed.



**FIGURE 2.20** The opposite sides of South America have very different continental margins. The leading edge, or west coast, is colliding with the Nazca Plate. It has a narrow shelf and steep slope and has a trench rather than a continental rise. On the trailing edge—that is, the Atlantic coast—there is a wide shelf, a relatively gentle continental slope, and a well-developed continental rise. The steepness of all the slopes is exaggerated for illustrative purposes. Compare this with the map in Figure 2.6.

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geologically. The continental margin here can be thought of as the trailing edge left when South America separated from Africa. This type of margin is called a **passive margin**. Passive margins typically have flat coastal plains (Fig. 2.22), wide shelves, and relatively gradual continental slopes. Because there are no tectonic processes to remove it, sediment accumulates at the base of the continental slope. Passive margins therefore usually have a thick continental rise.

Active continental margins have narrow shelves, steep slopes, and little or no continental rise. Passive margins have wide shelves, relatively gentle slopes, and a well-developed rise.

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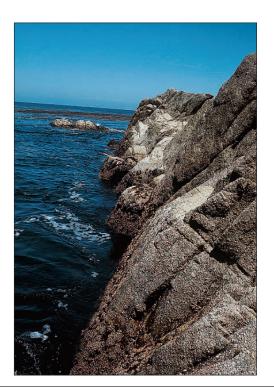
#### **Deep-Ocean Basins**

Most of the deep-sea floor lies at a depth of 3,000 to 5,000 m (10,000 to 16,500 ft), averaging about 4,000 m (13,000 ft). The sea floor is almost flat and is called the **abyssal plain**. It is not perfectly flat, however, and rises toward the mid-ocean ridges at a very gentle slope of less than one degree. The abyssal plain is dotted with submarine volcanoes called **seamounts** and volcanic islands. Distinctive flat-topped seamounts called **guyots** are common in parts of the Pacific Ocean. The abyssal plain also has a number of plateaus, rises, and other features.

At trenches, where the plate descends into the mantle, the sea floor slopes steeply downward. Trenches are the deepest parts of the world ocean. The Mariana Trench in the western Pacific is the deepest place of all, at 11,022 m (36,163 ft) deep.

## The Mid-Ocean Ridge and Hydrothermal Vents

The mid-ocean ridge itself is an environment that is unique in the ocean. As noted previously, the ridge is formed when material rising from the mantle pushes up the oceanic crust. Right at the center of the ridge, however, the plates



**FIGURE 2.22** The Atlantic coast of North America has a passive margin. Because of the lack of geological activity and the buildup of sediments, most of the eastern seaboard has a broad coastal plain, with barrier islands, salt marshes, lagoons, and estuaries.

**FIGURE 2.21** Steep, rocky shorelines like this one along the Pacific coast of North America at Monterey Bay, California, are typical of active margins, although they occur in other places. The special problems of the organisms living on shores like this are discussed in Chapter 11.

are pulling apart. This leaves a great gap or depression known as the **central rift valley**, which has been called a "wound in the earth's crust." The floor and sides of the valley are riddled with crevices and fractures. Seawater seeps down through these cracks until it gets heated to very high temperatures by the hot mantle material (Fig. 2.23). The heated water then forces its way back up through the crust and emerges in **hydrothermal vents**, or **deep-sea hot springs**.

The water coming from many hydrothermal vents is warm, perhaps  $10^{\circ}$  to  $20^{\circ}$ C ( $50^{\circ}$ to  $68^{\circ}$ F), much warmer than the surrounding water (see "The Three-Layered Ocean," p. 64). At some vents, however, the water is blisteringly hot, up to  $350^{\circ}$ C ( $660^{\circ}$ F). The water is so hot that when scientists first tried to measure its temperature the thermometer they were using started to melt! To take accurate readings, they had to return with a specially designed thermometer.

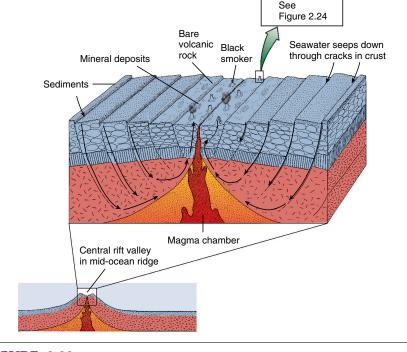
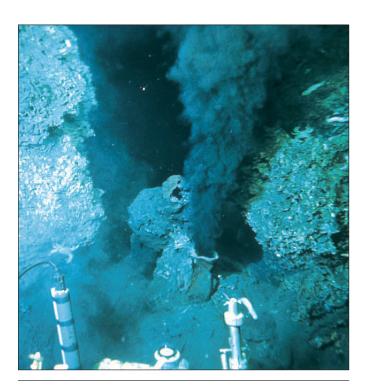


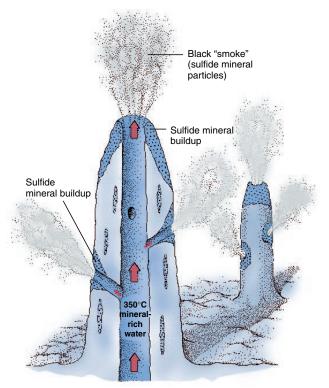
FIGURE 2.23 A cross section of a mid-ocean ridge showing how seawater seeps down through cracks in the crust, is heated, and reemerges in underwater hot springs.

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**FIGURE 2.24** Black smokers are common in hydrothermal vent areas. The black "smoke," actually composed of mineral particles, rises because the water emerging from the black smoker is much warmer than the surrounding water. This photo was taken at the Galápagos vent, a part of the East Pacific Rise. The instruments in the foreground belong to *Alvin*, from which the photo was taken.



**FIGURE 2.25** Cross section of a black smoker. Minerals are deposited as a precipitate when hot, mineral-laden water emerging from the rift zone meets the cold ocean water. Over time this builds up the chimney of the black smoker.

As the hot water seeps through cracks in the earth's crust, it dissolves a variety of minerals, mainly those known as **sulfides**. When the mineral-laden hot water emerges at the vent, it mixes with the surrounding cold water and is rapidly cooled. This causes many of the minerals to solidify, forming mineral deposits around the vents. **Black smokers** (Figs. 2.24 and 2.25) are one type of mineral deposit found at hydrothermal vents. These are chimney-like structures that progressively build up around a vent as the minerals solidify. The "smoke" is actually a dense cloud of mineral particles. When hydrothermal activity was first discovered it was thought to be confined to mid-ocean ridges. Hydrothermal vents, complete with black smokers and other mineral deposits, have since been discovered behind trenches. They result from the same volcanic activity that creates island arcs (see "Sea-Floor Spreading and Plate Tectonics," p. 30). Relatively cool (40° to 75°C, or 105° to 170°F) vents have also been discovered near, but not at, mid-ocean ridges. These vents produce chimneys of carbonate rather than sulfide minerals and are caused by chemical reactions between seawater and newly formed oceanic crust rather than by volcanic activity. A chimney like this has been found that rises 60 m (200 ft) above the sea floor, making it the tallest hydrothermal vent known.

Deep-sea hot springs are of great interest not only to geologists, but also to biologists. One of the most exciting developments ever in marine biology has been the discovery of unexpectedly rich marine life around hydrothermal vents. These organisms are discussed in Chapter 16 (see "Hot Springs, Cold Seeps, and Dead Bodies," p. 377). I. Principle of Marine Science 2. The Sea Floor

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Hot spots, the columns of hot magma that rise up from deep in the mantle, remain more or less stationary. When they occur under an oceanic plate, the plate moves along above them, each new eruption of magma breaking out at a slightly different place. The result is a linear chain of volcanoes. The Hawaiian Islands are part of one such chain called the Hawaiian Ridge. The Ridge is connected to the Emperor Seamount chain, a string of seamounts stretching to the northwest. Each seamount and island in the chain was produced when magma erupted while the plate was over the hot spot. The volcanoes therefore get older moving away from the hot spot. The island of Hawai'i, the youngest of the Hawaiian Islands, began forming less than a million years ago. It is still erupting today, and the island grows as the lava from the eruptions solidifies into new rock (see Fig. 11.1). Much of the island is smooth, bare volcanic rock because there has not been enough time for erosion or for vegetation to grow. Kaua'i, at more than 5 million years old, is the oldest of the main Hawaiian Islands. It is densely vegetated, and erosion has produced steep, jagged cliffs.

The remaining islands and seamounts of the Hawaiian Ridge and the seamounts of the Emperor chain get progressively older moving to the northwest. For example, Midway, about two-thirds of the way up the Hawaiian Ridge, is about 25 million years old. The bend that separates the Emperor chain from the Hawaiian Ridge was caused when the Pacific Plate changed its direction of movement a little less than 40 million years ago. Meiji Seamount, at the northernmost end of the chain, is 70 million years old.

The ancient Hawaiians had a remarkably similar explanation for the formation of their islands centuries before the days of detailed geological studies. They recognized both that the islands were formed by volcanoes and that the eroded, densely forested Kaua'i was older than the erupting, relatively barren island of Hawai'i. They had no way of knowing that their islands were moving along on a lithospheric plate, of course, so they concluded that it was the volcanoes that moved. Hawaiian tradition has it that Pele, the Goddess of Fire, originally lived on Kaua'i but, under repeated attacks from her sister Namakaokaha'i, Goddess of the Sea, moved from island to island to her present home in the Kilauea Volcano on Hawai'i.

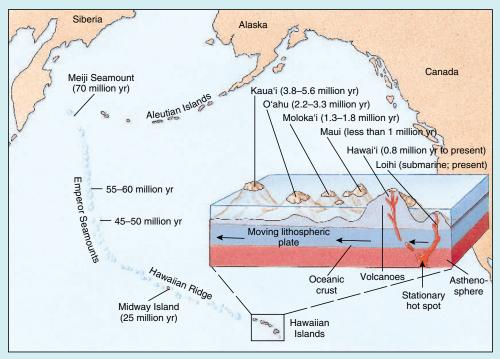
The formation of the Hawaiian Islands by a hot spot provides the solution to a mystery that once puzzled biologists. The Hawaiian Islands contain more than 800 different species of fruit flies, most of which are found nowhere else. And yet the islands are geologically very young. How could so many different kinds of fruit fly have evolved in such a short time?

The answer is that they didn't. The fruit flies have been around a lot longer than today's Hawaiian Islands. They once lived on older islands in the chain, most of which have sunk below sea level and are now seamounts. The flies island-hopped to the new islands that appeared

over the hot spot. A new Hawaiian island may be on the way. A young submarine volcano called Loihi has been found southeast of the island of Hawai'i. Loihi probably won't break the surface for several million years, so don't get your surfboard ready yet.



Pele's house: volcanic eruption at Kilauea, Hawai'i.



The Emperor Seamounts and Hawaiian Island chain.

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# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

## **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

## Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

## **Critical Thinking**

- 1. The process of plate tectonics is occurring today in the same way as in the past. Can you project the future positions of the continents by looking at a map of their present positions and the positions of the mid-ocean ridges (see Fig. 2.6)?
- 2. Why are most oceanic trenches found in the Pacific Ocean?
- 3. Scientists who study forms of marine life that lived more than approximately 200 million years ago usually have to obtain fossils not from the sea floor, but from areas that were once undersea and have been uplifted onto the continents. Why do you think this is?
- 4. What are some of the major pieces of evidence for the theory of plate tectonics? How does the theory explain these observations?

## For Further Reading

### **General Interest**

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## See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

- Typical south Atlantic coast (Cape Hatteras, North Carolina)
- Typical Florida coast, sand and worm reef (Fort Pierce, Florida)
- Coast of Aruba, situated on plate margin, showing volcanic rock and rough shore

## Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Plate tectonics
- · Undersea tectonic and volcanic activity
- The coast and the continental shelf
- The marine deep-sea zone

## Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

Castro–Huber: Marine Biology, Fourth Edition I. Principle of Marine Science 3. Chemical & Physical Features of Seawater & the World Ocean © The McGraw–Hill Companies, 2003

# Chemical and Physical Features of Seawater and the World Ocean



r verybody talks about the weather, but nobody does any-✓ thing about it." This famous quotation expresses the plight of the organisms that live in the sea as well as that of human beings. The sea stars, mussels, and other organisms in this photo are being buffeted by waves that were generated by a distant storm. The mussels are immersed at high tide and dry at low tide, while the sea stars must move up and down the rock with the tides in order to stay wet. The saltiness or temperature of the water changes with the season, fluctuations in rainfall, and ocean currents. From the point of view of marine organisms, wind and waves, tides and currents, temperature and salt all make up the "weather." All are beyond the control of the sea stars or any other marine organism.

Because marine organisms can't control the physical and chemical nature of their environment, they simply have to "grin and bear it," that is, they have to *adapt* to the place where they live, or move somewhere else. The types of organisms found at a given place in the ocean, and the way those organisms live, is controlled to a large extent by chemical and physical factors. To understand the biology of marine organisms, therefore, we must know something about the environment in which they live. Chapter 3 describes the chemistry and physics of the oceans in relation to life in the sea.



Waves crash over ochre sea stars (Pisaster ochraceus) and other intertidal organisms.

## THE WATERS OF THE OCEAN

Everyone knows that the ocean is full of water. Many people think of water as commonplace because there is so much of it around. From a cosmic perspective, though, water is not so common. Earth is the only known planet that has liquid water on its surface.

Even so, most of us never give water a second thought, unless we happen to be hot or thirsty. Water quenches our thirst because it makes up most of our bodies. Marine organisms, too, are mostly water— 80% or more by weight in most cases, in jellyfishes over 95%. Water not only fills the ocean, it makes possible life itself.

## The Unique Nature of Pure Water

All matter is made of tiny particles called **atoms.** Of all the substances known, only 115 or so are composed of a single kind of atom; these are called **elements.** In all other substances two or more atoms are chemically combined into larger particles



called **molecules**. Water molecules are made up of one oxygen atom, which is relatively large, combined with two small hydrogen atoms. Water molecules have an unusual structure that causes them to "stick" together, or, more properly, to attract each other (Fig. 3.1). The attractions between liquid water molecules are called **hydrogen bonds**. Hydrogen bonds are not very strong, but they make water different from any other substance on earth.

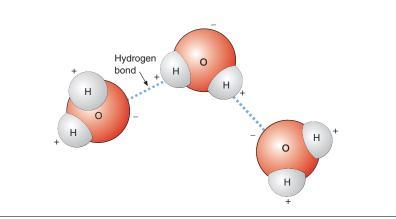
#### The Three States of Water

Any substance can exist in three different physical forms, called states or phases. A substance can occur as a solid, a liquid, or a gas. Water is the only substance that naturally occurs in all three states on earth.

The molecules in liquid water move constantly. Hydrogen bonds hold small groups of molecules together (Fig. 3.2), but the bonds are weak and the groups continually form and break apart. Any particular molecule in liquid water spends most of its time as part of a group, connected to other molecules by hydrogen bonds.

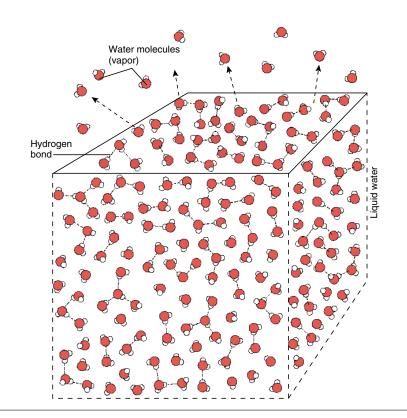
Temperature is a reflection of the average speed of the molecules-the faster they move, the higher the temperature. If a water molecule moves fast enough, it may break free of all the hydrogen bonds. In this process, called evaporation, the molecules go from the liquid phase to the gaseous or vapor phase. The molecules in water vapor are not held together by hydrogen bonds. They are separate and much farther apart than in the liquid (Fig. 3.2). As the temperature rises so does the rate of evaporation, since the molecules move faster and more of them escape the hydrogen bonds. If the water gets hot enough, nearly all of the hydrogen bonds are broken and the molecules try to enter the vapor state all at once; in other words, the water boils.

When liquid water cools, the molecules not only move slower, they pack closer together and take up less space. In other words, the volume of the water decreases. Because the volume decreases without changing the mass, the water gets denser. As seawater gets colder, therefore, it gets more dense. As we shall see, cold seawater tends to sink in the ocean. Fresh water is a little different. Like seawater, fresh water gets denser as



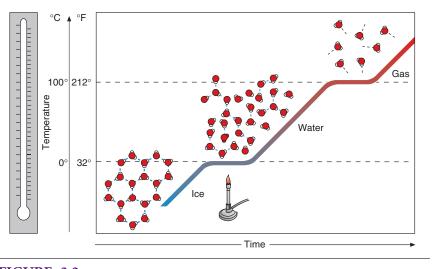
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**FIGURE 3.1** The different ends of water molecules have opposite electrical charges. The oxygen (O) end of the molecule has a weak negative charge, the hydrogen (H) end a slight positive charge. Opposite charges attract each other much like the opposite poles of a magnet attract, so the oxygen end of one molecule is attracted to the hydrogen end of neighboring molecules. These weak attractions between water molecules are known as hydrogen bonds.



**FIGURE 3.2** The molecules in liquid water form groups of various sizes held together by hydrogen bonds. The molecules are moving too rapidly to be held permanently in place, so the groups constantly break up and re-form. Evaporation occurs when molecules break free of all hydrogen bonds and enter the gaseous state. Molecules of water vapor are much farther apart than in the liquid state.





**Chapter 3** Chemical and Physical Features of Seawater and the World Ocean 45

**FIGURE 3.3** The molecular structure of water changes with temperature. In ice, hydrogen bonds hold the molecules in a hexagonal, or six-sided, pattern. As heat is added, the ice warms up and the molecules vibrate more rapidly until they break free of the crystal structure. When this happens, the ice melts. While the ice is melting, heat that is added is absorbed by breaking hydrogen bonds, not by increasing the temperature. When the ice is completely melted, additional heat again causes the temperature to rise. Some of the molecules gain enough speed to break free of all the bonds and evaporate. At 100°C (212°F) nearly all the hydrogen bonds are broken and the water boils.

it gets colder, but only down to a temperature of about 4°C (39°F). Below 4°C fresh water gets less dense as it cools.

## Seawater becomes more dense as it cools.

As the water continues to cool, the molecules move slower and more weakly. Eventually the hydrogen bonds overcome the motion of the molecules. The bonds hold the molecules in a fixed three-dimensional pattern, and the water changes from liquid to a solid. Solids that consist of such regular patterns of molecules are called **crystals**. The solid form of water, of course, is ice.

In ice crystals, the water molecules are spaced farther apart than in liquid water. This means that water expands as it freezes, as anyone who has made ice cubes knows. Since the same weight of water occupies more volume in ice than in liquid water, ice is less dense than liquid water. That is why ice floats.

It is extremely unusual for a substance's solid phase to be less dense than its liquid phase. This unique characteristic of water is important to aquatic organisms, both marine and freshwater. Because ice floats, it acts as an insulating blanket that helps keep the water below from rapidly cooling off in cold weather. Organisms can live below the surface ice. If ice were denser than liquid water, it would sink. In cold regions, ice forming at the surface would keep sinking and build up at the bottom. Lakes and some parts of the ocean would freeze solidly, and only a thin surface layer would melt in the summer. Lakes and the ocean would be much less hospitable to life.

#### Heat and Water

It takes a large amount of heat to melt ice. Water molecules in ice vibrate but do not move from place to place within the crystal. As heat energy is added and the temperature of the ice rises (Fig. 3.3), the molecules vibrate faster, eventually breaking some of the hydrogen bonds that hold the crystal together. The molecules then start to move around as well as vibrate. As a result, the ice begins to melt. Because hydrogen bonds must be broken, ice melts-or, moving in the opposite direction, freezes-at a much higher temperature than similar substances that do not form hydrogen bonds. If not for the hydrogen bonds, ice would melt at about -90°C (-130°F) instead of 0°C (32°F)!

Not only does ice melt at a comparatively high temperature, it absorbs a lot of heat when it melts. The amount of heat required to melt a substance is called the **latent heat of melting.** Water has a higher latent heat of melting than any other commonly occurring substance. The reverse is also true: A great deal of heat must be removed from liquid water to freeze it. It thus takes a long period of very cold weather before a body of water will freeze.

Once ice begins to melt, added heat energy goes into breaking more hydrogen bonds rather than increasing the speed of molecular motion. As long as some ice is left to be melted, the temperature of the ice-water mixture remains at a constant  $0^{\circ}$ C (32°F). This is why ice works so well as a refrigerant in a drink or insulated cooler: Heat that enters the glass or cooler goes into melting the ice, not into raising the temperature.

Once all the ice has melted, adding more heat causes the molecules to move more rapidly, thereby raising the temperature. Some of the heat energy, however, goes into breaking the hydrogen bonds that hold groups of molecules together. Because not all the energy goes into increasing the speed of molecular motion, it takes a large amount of heat to raise the temperature. The amount of heat that must be added to raise the temperature of a substance by a given amount, or heat capacity, reflects how much heat the substance can store. Water has one of the highest heat capacities of any naturally occurring substance. This is why water is used as an engine coolant in cars: It can absorb a lot of heat without greatly increasing in temperature. The high heat capacity of water also means that most marine organisms are not subjected to the rapid and sometimes drastic changes in temperature that occur on land (Fig. 3.4).

**Density** The mass of a given volume of a substance.

density =  $\frac{\text{mass}}{\text{volume}}$ Chapter 2, p. 22 World Ocean

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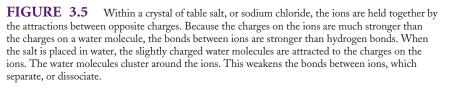
Water also absorbs a great deal of heat when it evaporates; that is, it has a high **latent heat of evaporation**. Again this is due to hydrogen bonding: Only the fastest moving molecules, those with the most energy, can break free of the hydrogen bonds and enter the gaseous phase. Because the fastest molecules leave the liquid phase, those left behind have a lower average velocity and therefore a lower temperature. This is known as **evaporative cooling**. Our bodies take advantage of evaporative cooling: When perspiration evaporates, it cools our skin.

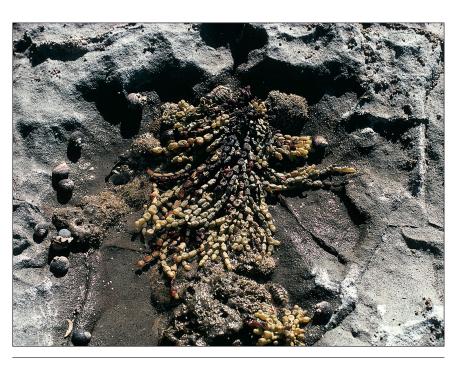
Water has the highest latent heats of melting and evaporation and one of the highest heat capacities of any natural substance.

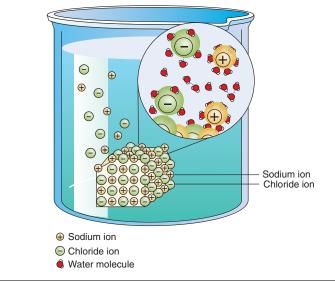
#### Water as a Solvent

Water can dissolve more things than any other natural substance, and is often called the universal solvent. Water is especially good at dissolving a general class of molecules called salts. Salts are made of combinations of particles that have opposite electrical charges. Such electrically charged particles, which can be either single atoms or groups of atoms, are known as ions. For example, ordinary table salt, or sodium chloride (NaCl), consists of a positively charged sodium ion (Na+) combined with a negatively charged chloride ion (Cl<sup>-</sup>). Recall that hydrogen bonds form because the hydrogen end of the water molecule has a slight positive charge and is attracted to the slightly negative oxygen end of other water molecules. Ions have much stronger electric charges than the opposite ends of the water molecule, so the electrical attraction between ions is much stronger than the hydrogen bonds that form between water molecules. If no water is present, the ions bind strongly together to form salt crystals (Fig. 3.5).

When a salt crystal is placed in water, the strongly charged ions attract the water molecules—with their weak charges—like iron filings are attracted to a magnet. A layer of water molecules surrounds each ion, insulating it from the surrounding ions (Fig. 3.5). This greatly weakens the electrical attractions that hold the salt crystal together. The ions pull apart, or **dissociate**, and the salt dissolves. **FIGURE 3.4** In the heat of the sun, this seaweed (*Hormosira banksii*) in New Zealand is beginning to shrivel. Shore organisms that are exposed to the air during low tide are subjected to much more extreme temperatures than organisms that are always submerged.

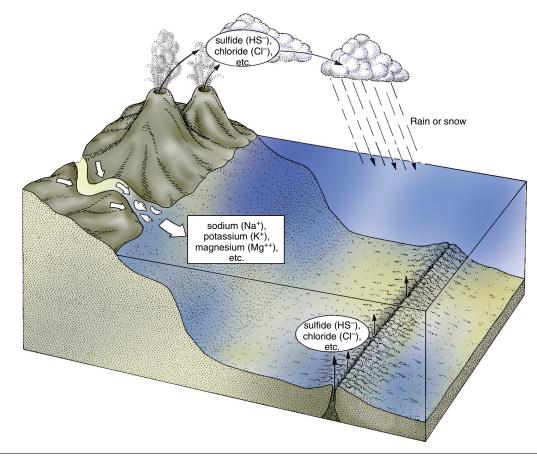






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**FIGURE 3.6** Not all ions in seawater enter the ocean at the same place. Positive ions like sodium and magnesium mostly come from the weathering of rocks and are carried to the sea by rivers. Negative ions like chlorine and sulfide enter the ocean at hydrothermal vents and from volcanoes via rain. If the ocean was not thoroughly mixed, coastal water would have a relatively high proportion of sodium and magnesium. Deeper water, influenced by hydrothermal input, would be rich in chloride and sulfate, which is produced from sulfide. Actually, the proportions of ions do vary right near river mouths and hydrothermal vents, but most of the ocean is well mixed and the rule of constant proportions holds.

#### Seawater

The characteristics of seawater are due both to the nature of pure water and to the materials dissolved in it. Some of the solids dissolved in seawater are produced by the chemical **weathering** of rocks on land and are carried to the sea by rivers (Fig. 3.6). Other materials come from the earth's interior. Most of these are released into the ocean at **hydrothermal vents.** Some are released into the atmosphere from volcanoes and enter the ocean in rain and snow.

#### Salt Composition

Seawater contains at least a little of almost everything, but most of the **solutes**, or dissolved materials, are made up of a surprisingly small group of ions. In fact, only six ions compose over 98% of the solids dissolved in seawater (Table 3.1). Sodium and chloride account for about 85% of the dissolved solids, which is why seawater tastes like table salt.

If seawater is evaporated, the ions in it are left behind and combine to form various salts. **Salinity** is defined as the total amount of salt dissolved in seawater. Salinity is usually expressed as the number of grams of salt left behind when 1,000 grams of seawater are evaporated. If we evaporated 1,000 grams of seawater and were left with 35 grams of salt, we would say the seawater had a salinity of 35 parts per thousand, or 35‰. The salinity of water strongly affects the organisms that live in it. Most marine organisms, for instance, die in fresh water. Even slight changes in salinity will harm some organisms. Many, especially those that live in river mouths or other places where the salinity is prone to fluctuations, have specific mechanisms that allow them to cope with salinity changes (see "Regulation of Salt and Water Balance," p. 79).

Organisms are affected not only by the total amount of salt, but also by the

Weathering The physical or chemical breakdown of rocks.

Chapter 2, p. 33

**Hydrothermal Vents** Undersea hot springs associated with mid-ocean ridges. *Chapter 2, p. 38* 



The Composition of Seawater of 35 ‰ Salinity. While the concentration varies slightly from place to place in the ocean, the percentage of total salinity of each ion remains constant

| Ion   | Concentration ‰ | Percentage of Total Salinity |
|---|-----------------|------------------------------|
| Chloride (Cl <sup>-</sup> )                           | 19.345          | 55.03                        |
| Sodium (Na+)  | 10.752          | 30.59                        |
| Sulfate (SO <sub>4</sub> <sup>-2</sup> )              | 2.701           | 7.68                         |
| Magnesium (Mg <sup>+2</sup> )                         | 1.295           | 3.68                         |
| Calcium (Ca <sup>+2</sup> )                           | 0.416           | 1.18                         |
| Potassium (K+)  | 0.390           | 1.11                         |
| Bicarbonate (HCO3 <sup>-</sup> )                      | 0.145           | 0.41                         |
| Bromide (Br-)   | 0.066           | 0.19                         |
| Borate (H <sub>2</sub> BO <sub>3</sub> <sup>-</sup> ) | 0.027           | 0.08                         |
| Strontium (Sr <sup>+2</sup> )                         | 0.013           | 0.04                         |
| Fluoride (F <sup>_</sup> )                            | 0.001           | 0.003                        |
| Everything else                                       | <0.001          | <0.001                       |

kind of salt. The composition of the ions in seawater can be determined by analyzing the salts left after evaporation. In fact, that is how the information in Table 3.1 was obtained.

The chemist William Dittmar analyzed 77 seawater samples brought back by the *Challenger* expedition and found that the relative amounts of the various ions were constant. In other words, the *percentage* accounted for by each ion is always the same, even though the total amount of solid material dissolved in seawater varies from place to place. Chloride ion, for example, always makes up 55.03% of however much salt is present. This principle is called the **rule of constant proportions**.

The rule of constant proportions states that the relative amounts of the various ions in seawater are always the same.

The rule of constant proportions has important implications. Though marine organisms may be exposed to changes in total salinity, they do not have to deal with changes in the ratios of the various ions. This makes it much easier for them to control their internal salt and water balance. The rule of constant proportions also indicates that the oceans are chemically well-mixed, and that ocean salinity varies almost entirely as a result of the addition or removal of pure water, not the addition or removal of salt. If salinity varied by adding or removing any particular salt, then the relative amounts of the ions in the seawater would change. If magnesium chloride (MgCl<sub>2</sub>) were added, for example, then the proportions of magnesium and chloride in the water would go up.

Water is removed from the ocean primarily by evaporation, but it may also be removed by freezing. When salt water freezes, the ions are not included in the forming ice. They are left behind in the unfrozen water, increasing its salinity, and the ice is almost pure water. This is why icebergs are not salty. Water is added to the ocean by **precipitation** rain and snow—and to a lesser extent by the melting of glaciers and polar ice.

The average salinity of the ocean is about 35%. The open ocean varies relatively little, between about 33% and 37%, depending mostly on the balance between evaporation and precipitation. Partially enclosed seas may have much more extreme salinities. The Red Sea, for instance, is in a hot, dry region where evaporation predominates over precipitation. As a result the Red Sea is very salty,

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about 40‰. Near coasts or in enclosed basins, runoff from rivers may have a strong effect. The Baltic Sea gets a lot of river runoff, for example, and has a typical salinity of only about 7‰ at the surface.

#### Salinity, Temperature, and Density

We have already seen that temperature greatly affects the density of water. Salinity also influences the density of seawater: The saltier the water, the denser it is. The density of seawater therefore depends on both the temperature and the salinity of the water.

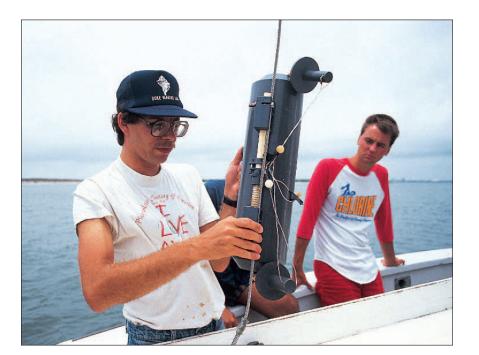
The temperature and salinity of seawater determine its density: It gets denser as it gets saltier, colder, or both.

Temperature in the open ocean varies between about  $-2^{\circ}$  and  $+30^{\circ}$ C (28° to 86°F). Temperatures below 0°C (32°F) are possible because salt water freezes at a colder temperature than pure water. This is one reason that the ocean is less prone to freezing than lakes and rivers.

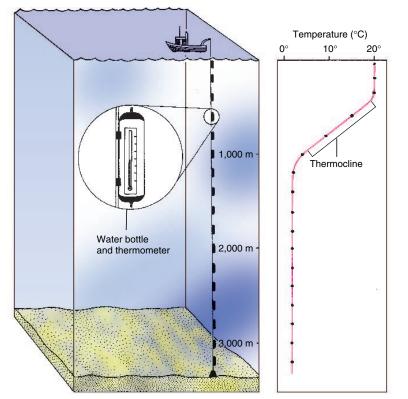
Temperature in the ocean varies considerably more than salinity, so as a practical matter density is controlled more by temperature than salinity. Exceptions do occur, however, and both the temperature and salinity of ocean water still need to be measured to determine the density.

Temperature and salinity can be measured by lowering specially designed bottles fitted with thermometers into the ocean to collect water samples that are analyzed to determine salinity (Fig. 3.7). Ordinary thermometers cannot be used to measure the temperature at depth because the temperature reading would change as the thermometer was brought back to the surface. To overcome this problem, oceanographers may use special reversing thermometers to measure temperature in the ocean. Reversing thermometers are made so that the mercury column breaks when the thermometer is turned upside down, preventing the temperature reading from changing after that. The thermometers are mounted onto spring-loaded racks that flip the thermometers over when a trigger is activated. A weight called a messenger slides down the wire to trigger the thermometer rack.

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**FIGURE 3.7** Niskin bottles are one of several types of water sampling bottles. The bottles are clamped to a cable and lowered to the desired depth with both ends open. A weight called a messenger is sent down from the surface. The spring-loaded end caps then snap shut, trapping a sample of seawater in the bottle.



A series of bottles can be attached to the cable, allowing the user to determine temperature and salinity, and therefore density, at several depths at the same time (Fig. 3.8). A graph that shows the temperature at different depths in the ocean is called a temperature **profile**. A temperature profile obtained from a given location can be thought of as showing the temperature in a vertical shaft of water, or **water column**, extending down from the surface. Profiles can also be plotted for salinity, density, or any other characteristic. In a profile the vertical axis appears "upside down," as shown in Figure 3.8.

A profile is a plot that shows temperature, salinity, or any other characteristic of seawater at various depths in the water column.

Using bottles and reversing thermometers is time-consuming and expensive. Today oceanographers usually use electronic sensors that quickly and accurately measure the salinity, temperature, and depth as they are lowered through the water (Fig. 3.9). These instruments take measurements throughout the water column, rather than just at certain depths, and tend to be less expensive to operate. One type that measures temperature profiles, the expendable bathythermograph (XBT), is even disposable.

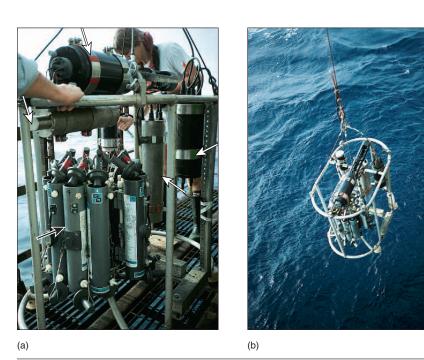
Though temperature, salinity, and various other things can be measured electronically, many other measurements require a water sample. Niskin bottles and similar devices are still widely used. These days, oceanographers usually mount all the

The *Challenger* expedition (1872–1876) marked the birth of modern oceanography. *Chapter 1, p. 5* 

FIGURE 3.8 A series of bottles hung on a wire is used to measure the temperature and salinity at several depths at once. Such information can be used to plot a profile, or a graph showing how temperature, salinity, or any other property varies with depth. In this case, temperature measurements were used to plot a temperature profile. Temperature is measured only where the bottles are (dots). Water temperature between the bottles (colored line) must be inferred. The zone where the temperature drops rapidly as it gets deeper is called a thermocline. Castro–Huber: Marine Biology, Fourth Edition I. Principle of Marine Science 3. Chemical & Physical Features of Seawater & the World Ocean

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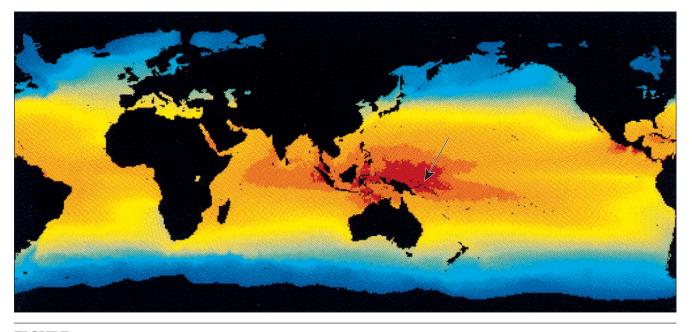
**FIGURE 3.9** Instead of being hung on a wire individually, water sampling bottles (black arrow) are now usually mounted in a "rosette" (*a*) to a single frame. A variety of electronic instruments (white arrows) that measure temperature, salinity, light, water clarity, and other factors can also be mounted on the frame, which is then lowered through the water column (*b*). Many of the instruments provide instantaneous information to computers on the surface.

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open bottles to a single rack (Fig. 3.9) rather than stringing them along the wire. As the rack is lowered, the bottles are closed at different depths to obtain water samples. The rack is easier to use than a series of individual bottles. Various electronic instruments are also mounted on the rack.

Even with electronic instruments, measurements from ships can be made in only one place at a time. To gather information over a large area, the ship has to steam from place to place. In the meantime, conditions might change because of currents or the weather. One alternative is to use a number of ships at once. This is very expensive, however, and is not done often. Today oceanographers increasingly make their measurements with automated instruments that are left in the ocean. Depending on the objectives of the study, the instruments may be moored in one location or may drift with the currents. Another way to get the big picture is to use satellites to study the ocean from space.

Satellites can measure conditions only near the surface, but they give instantaneous coverage of a large area (Fig. 3.10). Furthermore, a series of measurements can be made in a short time. This makes it



**FIGURE 3.10** This satellite image shows the temperature of the ocean surface. The coldest water is shown in blue, the warmest in red. The large patch of very warm  $(29.5^{\circ}C, 85.1^{\circ}F)$  water (arrow) just north of the island of New Guinea contains the ocean's largest reservoir of heat. This area is thought to control or at least strongly influence the climate of the entire planet. During El Niño years, for example, the pool of warm water moves east to the central Pacific (see "The El Niño—Southern Oscillation Phenomenon," p. 351).

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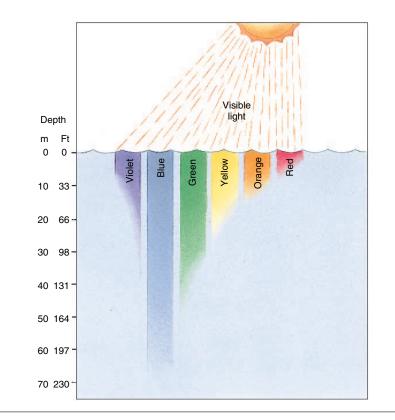
FIGURE 3.11 Sophisticated electronic instruments, such as those mounted to the frame in Figure 3.9, allow precise measurements of water clarity and color and light penetration. For surface waters, however, this simple instrument called a Secchi disk gives surprisingly useful information about water clarity. The disk is slowly lowered, and the depth where the disk is no longer visible is recorded. The greater this depth is, the clearer the water.

possible to follow rapid changes in surface conditions that result from currents, weather, and so forth.

Oceanographers use automated instruments and satellites to measure temperature, track ocean currents, determine the concentration of **photosynthetic pigments**, and monitor many other water characteristics. Such information is greatly increasing our understanding of the ocean, and of human impacts on it.

#### **Dissolved Gases**

There are gases as well as solid materials dissolved in seawater. For living things, the three most important gases in the ocean are oxygen  $(O_2)$ , carbon dioxide  $(CO_2)$ , and nitrogen  $(N_2)$ . All three of these gases are found in the earth's atmosphere and dissolve in seawater at the sea surface. Sometimes the reverse occurs and the sea surface releases gases to the atmosphere. This process is known as gas exchange between the ocean and atmosphere. Whereas most solids dissolve



**FIGURE 3.12** Different colors of light penetrate to different depths in the ocean. Blue light penetrates the deepest, red light the least.

better in warm water than in cold, gases are the opposite; they dissolve better in cold water. This is particularly important for animals in the sea (see "Stability and Overturn," p. 63 and "The Oxygen Minimum Layer," p. 367). Marine organisms themselves also affect the amount of dissolved gases in the water. For example, animals use up oxygen in respiration.

#### Transparency

One of the most biologically important properties of seawater is that it is relatively transparent, so sunlight can penetrate into the ocean. This is vital because all photosynthetic organisms need light to grow. If seawater were not transparent, there would be very little **photosynthesis** in the sea, and then only right at the surface.

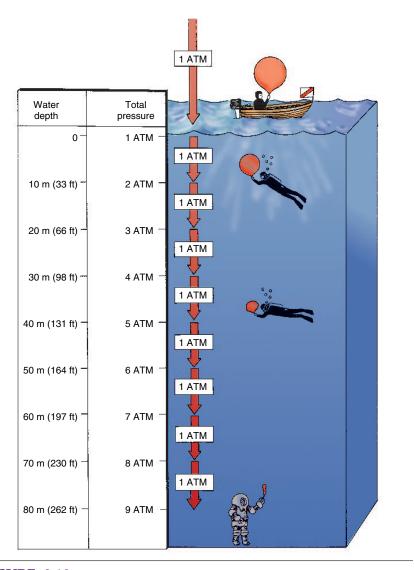
The transparency of water (Fig. 3.11) depends to a large extent on how much and what kind of material is suspended and dissolved in the water. Obviously, muddy water is not as clear as clean water. Large quantities of microorganisms also reduce the transparency of water. Water near coasts often contains a lot of material brought in by rivers. This material gives coastal waters a greenish tint and makes them less transparent than the deep blue waters of the open ocean.

Sunlight contains all the colors of the visible spectrum, but not all colors of light penetrate seawater equally well. The ocean is most transparent to blue light. Other colors are absorbed more than blue, so as depth increases more and more of these other colors are filtered out. Before long, only blue light remains (Fig. 3.12).

Photosynthetic Pigments Chemical compounds used by organisms to capture light energy for photosynthesis. *Chapter 4, p. 72* 

**Photosynthesis**  $CO_2 + H_2O + sun$ energy  $\rightarrow$  glucose +  $O_2$ *Chapter 4, p. 71* 

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**FIGURE 3.13** The pressure at any place depends on the weight pressing down from above. At the sea surface or on land, the atmosphere is the only thing above. Divers and marine organisms, however, are also under the weight of the water column. The deeper the diver goes, the more water is pressing down from above and the greater the pressure. As the pressure increases, flexible gas-filled structures like the red balloon are compressed.

Things that appear red on the surface look grey or black at depth because there is no red light to reflect off them and be seen. At greater depths even the blue light gets absorbed, and there is total darkness.

#### Pressure

**Pressure** is another factor that changes dramatically with depth in the ocean. Organisms on land are under 1 **atmosphere** (14.7 pounds per square inch, or psi) of pressure at sea level—the weight of all the air above them. Marine organisms, however, are under the weight of the water above them as well as the atmosphere. Since water is much heavier than air, marine organisms are under much more pressure than those on land. The pressure increases dramatically with depth because the amount of water above gets greater (Fig. 3.13). With each 10 m (33 ft) of increased depth, another atmosphere of pressure is added.

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As the pressure increases, gases are compressed. Gas-filled structures inside organisms like air bladders, floats, and lungs shrink or collapse. This limits the depth range of many marine organisms. It also means that submarines and housings for scientific instruments must be specially engineered to withstand pressure. This greatly increases the difficulty, expense, and sometimes the danger of studying the sea. The reverse effect also causes problems: Organisms that contain gas-filled structures may be injured when brought up from the deep (Fig. 3.14).

## MOTION IN THE OCEAN

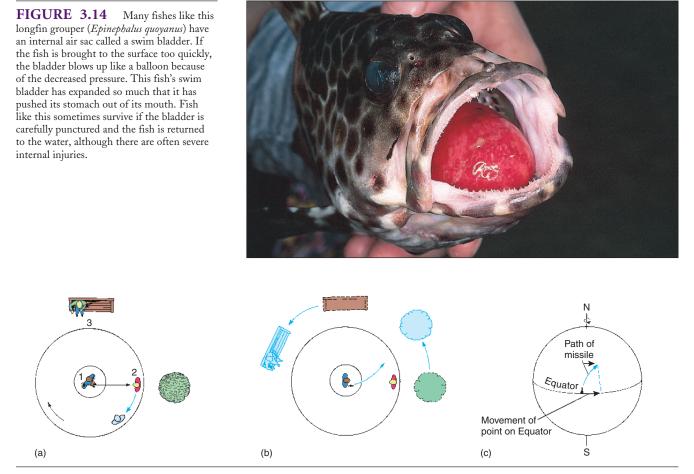
The ocean never rests. Anyone who has gone swimming in, sailed on, or simply walked beside the sea knows that it is in constant motion. Waves, currents, and tides all move and mix ocean waters, and all have important effects on life in the sea.

## Surface Circulation

The most intense motion of the ocean occurs at the surface in the form of surface currents and waves. Both currents and waves are driven by the wind, which in turn is driven by heat from the sun. Winds and currents are also strongly influenced by what is known as the Coriolis effect.

#### The Coriolis Effect

Because the earth is rotating, anything that moves over its surface tends to turn a little to one side rather than moving in a straight line. One way to understand this bending, called the **Coriolis effect**, is to try a simple experiment. Put a piece of paper on a record turntable or some other rotating surface. Try to draw a straight line. The line will come out curved because the paper is spinning, moving under the pen. Figure 3.15 shows some other ways to understand the Coriolis effect. *Chapter 3 Chemical and Physical Features of Seawater and the World Ocean* 53



**FIGURE 3.15** One way to understand the Coriolis effect is to think of a merry-go-round. (a) Imagine that someone at the center (1) throws a ball at someone on the outside (2). An observer on the ground (3) can see that the rider on the outside moved to a new position (shown in blue) while the ball was in the air. (b) To the people on the merry-go-round, however, it looks like the ball veered off to the side. Try it yourself! (c) Places at the Equator travel faster than those near the poles: Both places make one full revolution every day, but the place at the Equator has to travel a lot farther. If a missile is fired from the Equator, it continues to move at the speed it had when fired. This means that as it moves toward the pole, it moves faster than the ground below. Thus, it appears to curve relative to the earth's surface.

The Coriolis effect is too slight to notice when you're walking along or driving in a car, so most people aren't aware of it. It is very important, however, for things like winds and ocean currents that move over large distances. In the Northern Hemisphere the Coriolis effect always deflects things to the right. In the Southern Hemisphere, things are deflected to the left.

The Coriolis effect deflects large-scale motions like winds and currents to the right in the Northern Hemisphere and to the left in the Southern Hemisphere.

#### Wind Patterns

The winds in our atmosphere are driven by heat energy from the sun. Most of this solar energy is absorbed near the Equator. This makes sense: It is generally warm at the Equator and cold at the poles. The warm air at the Equator rises. Air from adjacent areas gets sucked in to replace the rising equatorial air, creating wind (Fig. 3.16). The winds do not move straight toward the Equator, but are bent by the Coriolis effect. These winds, called the **trade winds**, approach the Equator at an angle of about 45°. Over the ocean, where they are not affected by land, the trade winds are the steadiest winds on earth.

Other winds are also driven by solar energy but tend to be more variable than the trades. At middle latitudes lie the **westerlies** (Fig. 3.17), which move in the opposite direction to the trade winds. At high latitudes are the **polar easterlies**, the most variable winds of all.

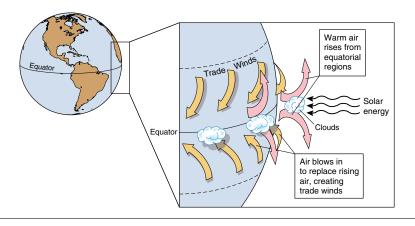
#### Surface Currents

The major wind fields of the atmosphere push the sea surface, creating currents. All the major currents of the open ocean, in fact, are driven by the wind.  

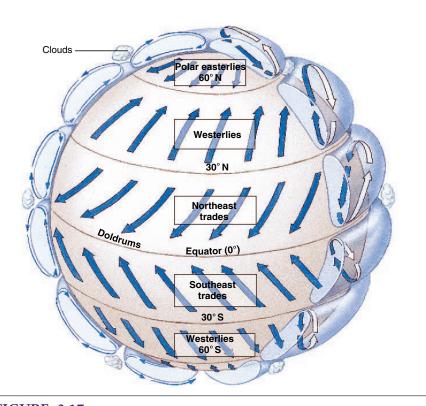
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**FIGURE 3.16** Air near the Equator is warmed by solar heating and rises. Air from higher latitudes rushes in over the earth's surface to replace the rising air, creating wind. These winds, the trades, are deflected by the Coriolis effect and approach the Equator at an angle of about 45°.



**FIGURE 3.17** The major wind patterns on earth are created by the rising of sun-warmed air and the sinking of cold air. The trade winds lie between about 30° north and south latitude and are the steadiest of all winds. The westerlies are found from about 30° to 60°, and above 60° lie the most variable winds, the polar easterlies. The transition zones or boundaries between these major wind belts have very light and changeable winds (see "Tall Ships and Surface Currents," p. 59). The wind fields are pictured here as they would look on an imaginary water-covered earth. In actuality they are modified somewhat by the influence of the continents (see Fig. 3.19).

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When pushed by the wind, surface water does not move in the same direction as the wind but, because of the Coriolis effect, moves off at an angle of 45° (Fig. 3.18). The surface currents driven by the trade winds, for example, do not move toward the Equator at all. Instead, these **equatorial currents** move parallel to the Equator (Fig. 3.19). Under the influence of the Coriolis effect, the winddriven surface currents combine into huge, more or less circular systems called **gyres.** 

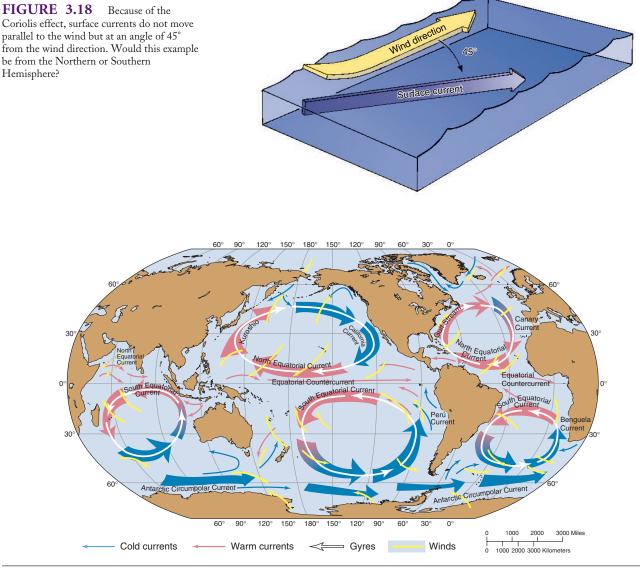
Global wind patterns and the Coriolis effect produce gyres, large circular systems of surface currents.

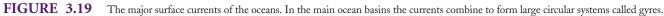
Recall that water is particularly good at transporting heat because of its high heat capacity. The warm currents on the western sides of the gyres carry vast amounts of solar heat from the Equator to higher latitudes. Cold currents flow in the opposite direction on the eastern sides. Ocean currents thus act like a giant thermostat, warming the poles, cooling the tropics, and regulating the climate of our planet. Large-scale fluctuations in current patterns such as El Niño can dramatically affect weather around the world (see "The El Niño-Southern Oscillation Phenomenon," p. 351). Recent studies indicate that the onset of ice ages is directly related to major changes in ocean circulation.

The role of surface currents in transporting heat is reflected in the temperature of the sea surface (Fig. 3.20). Surface temperature is higher on the western sides of the oceans, where currents carry warm water away from the Equator, than on the eastern sides, where cold currents flow toward the Equator. Because of this, tropical organisms like corals tend to extend into high latitudes on the west sides of the oceans (see "Conditions for Reef Growth," p. 302 and Fig. 14.10). Coldloving organisms like kelps, on the other hand, occur closest to the Equator on the eastern shores of the oceans (see "Kelp Communities," p. 290 and Fig. 13.21).



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The currents shown in Figure 3.19 are average patterns over large distances and a long time span. At a given place on a given day the current might be different: Currents shift with the season and the weather. On the continental shelf, currents are strongly affected by the bottom, the shape of the coastline, and the tides (see "Physical Characteristics of the Subtidal Environment," p. 277).

#### Waves

The wind not only drives surface currents, it causes **waves**. Waves are among the most familiar of all ocean phenomena, easily visible at the shore. They also affect the organisms that live on the shore.

The highest part of a wave is called the **crest** and the lowest part the **trough** (Fig. 3.21). The size of an ocean wave is usually expressed as the wave **height**, which is the vertical distance between the trough and the crest. Wave crests or troughs can be close together or far apart. The distance between them is called the **wavelength.** The time a wave takes to go by any given point is called the **period** of the wave.

When under a wave crest the water moves up and forward; under the troughs

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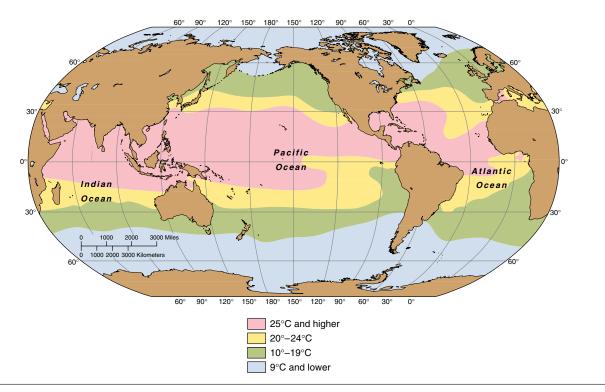
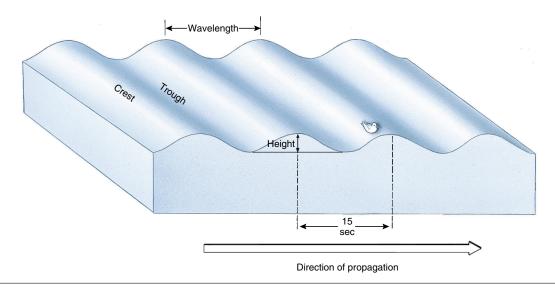
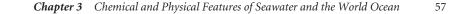


FIGURE 3.20 The average sea-surface temperatures of the oceans. Compare with the map in Figure 3.19.



**FIGURE 3.21** An idealized series of waves, or wave train. The highest point of a wave is called the crest, the lowest point the trough. The wavelength is the distance between crests. The wave period refers to how long it takes the wave to go by. In this example the period is 15 seconds, which is how long it will take for the next crest to reach the bird.





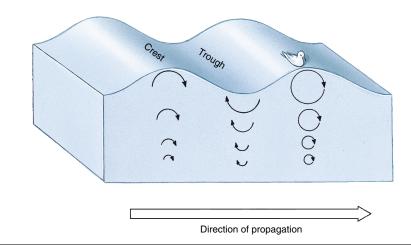
it moves down and back. On the whole the water particles don't go anywhere at all as the wave passes; they just move in circles (Fig. 3.22). Though waves carry energy across the sea surface, they do not actually transport water.

Waves begin to form as soon as the wind starts to blow. The faster and longer the wind blows, the larger the waves get. The size of waves generated by the wind also depends on the **fetch**, the span of open water over which the wind blows (Fig. 3.23).

While the wind is blowing it pushes the wave crests up into sharp peaks and "stretches out" the troughs (Fig. 3.24). Waves like this are called **seas**. The waves move away from where they are generated slightly faster than the speed of the wind. Once away from the wind the waves settle into **swells**. With their smoothly rounded crests and troughs, swells are very similar to the ideal waves shown in Figure 3.21.

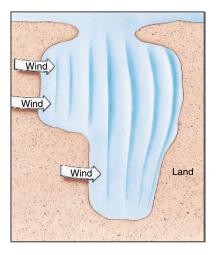
When the waves approach shore and get into shallow water, they begin to "feel" the bottom. They slow down and "pile up," becoming higher and steeper. Eventually they become so high and so steep that they fall forward and break, creating **surf.** The energy that was put into the wave by the wind is expended on the shoreline as the wave breaks.

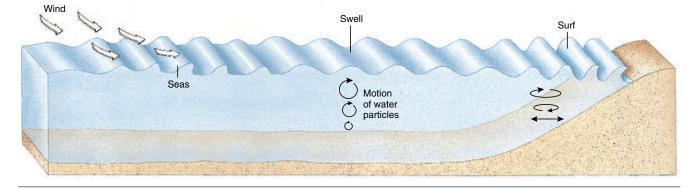
The sea surface is usually a confused jumble instead of a series of nice, regular waves moving in one direction. This is because the surface at any given location



**FIGURE 3.22** Water particles do not move along with a wave but instead move in circles. When under the crest they move up and forward with the wave, then they are pulled back down. As wave after wave passes, the water and anything floating in or on it moves in circles.

FIGURE 3.23 The wind is blowing at the same speed and has been blowing for the same length of time over this entire imaginary bay. On the top side of the bay, however, the wind is blowing over a much longer stretch of water. In other words, the fetch is longer on the top side, and so the waves are bigger there.





**FIGURE 3.24** Storm winds generate seas, peaked waves with relatively flat troughs. The waves move out of the storm area, carrying energy away, and become swells, with rounded crests and troughs. When the waves reach shallow water, they get higher and shorter, that is, closer together. Eventually they become unstable and break, expending their energy on the shoreline. Water particles under swells have the ideal circular motion shown in Figure 3.22. In shallower water the influence of the bottom causes the particle motion to flatten out into back-and-forth movement known as surge.

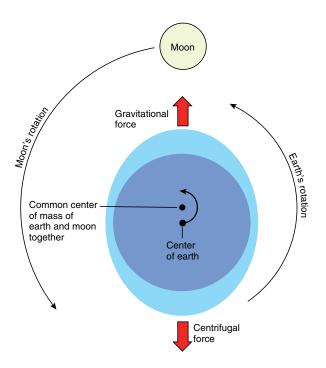
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**FIGURE 3.25** These grunion (*Leuresthes tenuis*) are laying eggs high on a California beach. Their spawning is precisely timed to coincide with the peak of the highest tides, when they can reach the uppermost parts of the beach. Hatching of the eggs, not quite a month later, also corresponds to high tides so that the fry can swim away.



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is affected by a mixture of waves coming from many different places, generated by winds of different speeds blowing in different directions for different lengths of time. When the crests of two waves collide, they add together, producing a higher wave (see "Waves That Kill," p. 60). The crests pass through each other, however, and the high peak disappears. Similarly, when a crest and trough intersect they tend to cancel each other. The complex surface of the ocean results from many such interactions.

## Tides

The sea surface has been rising and falling in the rhythmic pattern known as the **tides** for billions of years. The tides are a dominant influence on nearshore sea life. They alternately expose and submerge organisms on the shore (see Chapter 11), drive the circulation of bays and estuaries (see Chapter 12), trigger spawning (Fig. 3.25), and influence the lives of marine organisms in countless other ways.

#### Why Are There Tides?

The tides are caused by the gravitational pull of the moon and sun and by the rotations of the earth, moon, and sun. Strictly speaking, the moon does not revolve around the earth. Instead the earth and moon both rotate around a common point, their combined center of mass (Fig. 3.26). This rotation produces centrifugal force, which is the same force that pushes you outward when you ride on a merry-go-round. The centrifugal force just balances the gravitational attraction between the earth and moon otherwise the two would either fly away from each other or crash together.

Centrifugal force and the moon's gravity are not in perfect balance everywhere on the earth's surface, however.

**FIGURE 3.26** The moon does not exactly rotate around the earth. Instead, both the moon and earth rotate around their common center of mass, which lies inside the earth. Thus, the earth actually "wobbles" a bit, like an unbalanced tire. Centrifugal force produced by the earth's motion causes the water to bulge outward, away from the moon. On the side of the earth closest to the moon, however, the moon's gravitational pull overcomes the centrifugal force and pulls the water into a bulge *toward* the moon. Castro–Huber: Marine Biology, Fourth Edition I. Principle of Marine Science 3. Chemical & Physical Features of Seawater & the World Ocean © The McGraw–Hill Companies, 2003

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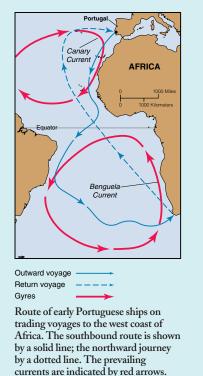
## TALL SHIPS AND SURFACE CURRENTS

For purely practical reasons winds and surface currents were among the first oceanic phenomena to be observed and documented. For centuries ships were at the mercy of the wind, and the names sailors gave to various areas reflected their knowledge of global wind patterns. Many of these names are still used. The trade winds got their name from the traders who relied on them during their voyages. The equatorial region where the winds are light and variable because of the rising air masses there (see Fig. 3.16) is called the doldrums. Winds are also variable at 30° north and south latitudes, where the trade winds and westerlies are moving apart (see Fig. 3.17). At these latitudes, sailors, becalmed and short of drinking water, sometimes had to throw their dying horses overboard. To this day these are known as the horse latitudes.

Sailors also knew about surface currents. A clever navigator could shorten a passage by weeks or months by riding favorable currents and avoiding unfavorable ones. In the fifteenth century, Portuguese sailors under the guidance of Prince Henry the Navigator made careful observations of currents along the west coast of Africa. Soon they were using their knowledge of these currents on their trading voyages. On the southbound journey, the ships sailed close to shore while in the Northern Hemisphere, riding the Canary Current. When they crossed the Equator they swung to the west to avoid the Benguela Current. On the voyage home, they took the opposite path, completing a figure eight.

Other currents were known to early mariners. Christopher Columbus noted the existence of the North Atlantic Equatorial Current on his third voyage to the New World. While searching for the "Fountain of Youth" the Spaniard Juan Ponce de León described the Florida Current. In the Pacific, fishermen recorded their knowledge of the Perú Current and the Kuroshio.

Even Ben Franklin has a place in this story. While serving as colonial postmaster he noticed that mail ships routinely made the trip to Europe two weeks faster than they returned. He began to



question sea captains, particularly those of the Nantucket whaling fleet, about their knowledge of surface currents. Using this information, he published the first chart of the mighty Gulf Stream and issued instructions on how to avoid it when returning from Europe.

On the side of the earth nearest the moon, the moon's gravity is stronger and pulls the water toward the moon. On the side away from the moon, centrifugal force predominates, pushing the water away from the moon. If the earth were completely covered with water, the water would form two bulges on opposite sides of the planet. The water would be relatively deep under the bulges and shallower away from the bulges.

In addition to the rotation of the earth and moon illustrated in Figure 3.26, the earth is spinning like a top on its own axis. As it does so, any given point on the planet's surface will first be under a bulge and then away from it (Fig. 3.27). High tide occurs when the point is under a bulge. Because the earth takes 24 hours to complete a rotation, the point will have two high tides and two low tides every day. Actually, the moon advances a little in its own orbit in the course of a day. It takes the point on earth an extra 50 minutes to catch up and come directly in line with the moon again. A full tidal cycle therefore takes 24 hours and 50 minutes.

The sun produces tidal bulges in the same way as the moon. Though the sun is much larger than the moon, it is 400 times farther away, so the effect of the sun on the tides is only about half as strong as the moon's. When the sun and moon are in line with each other, which happens at the full and new moons (Fig. 3.28), their effects add together. At these times the **tidal range**, or difference in water level between successive high and low tides, is large. Such tides are called **spring tides**. This name is a bit confusing because spring tides occur throughout the year, about once every two weeks, and not just in springtime.

When the sun and moon are at right angles their effects partially cancel each other. During these **neap tides** the tidal range is small. Neap tides occur when the moon is in the first and third quarters.

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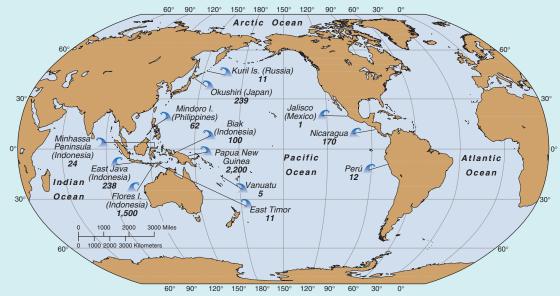
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## WAVES THAT KILL

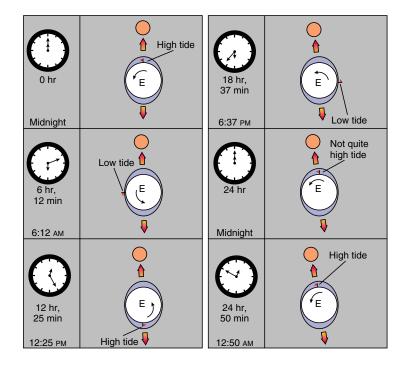
Most of the time, waves are benign, providing entertainment for coast watchers and thrills for surfers. Sure, they may sometimes cause seasickness or give the unwary beachgoer a tumble, but by and large they are relatively harmless. On rare occasions, however, waves can unleash all the awesome power of the sea.

Every year, severe waves and tidal surges caused by violent storms cause massive damage somewhere in the world, and sometimes even kill people. So-called rogue waves, giant waves that appear seemingly out of nowhere, have also been blamed for sinking ships, sometimes with loss of life. Oceanographers have never been



Death toll from tsunamis between 1992 and 2000. The figures are almost certainly underestimates; in remote areas many casualties go unreported, and deaths from disease because of disrupted sanitation, medical care, and food supplies are usually not included.

FIGURE 3.27 As the earth spins on its axis, a given point on earth like the one marked by the flag alternates between being under a bulge, making it high tide, and being between the bulges, making it low tide. Because the moon moves while the earth is rotating, a full tidal cycle takes 50 minutes longer than the 24 hours it takes the earth to make a complete rotation.



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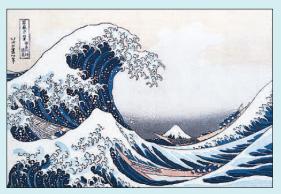
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able to observe rogue waves, but if they exist they almost certainly arise when the crests of different waves happen to meet at the same place and time. When this happens, the waves reinforce each other, combining to form a crest that is much larger than the individual waves. Certainly, rogue waves are extremely rare, since they have never been documented. It has even been suggested that they are nothing more than a convenient excuse for mistakes at sea!

The deadliest waves by far are **tsunamis**, a Japanese word meaning "harbor waves." Tsunamis were once called tidal waves, but they have nothing to do with the tides. They are produced instead by earthquakes and other seismic disturbances of the sea floor, so they are more properly called **seismic sea waves**. When such a disturbance occurs, it can produce very long, fast-moving waves. Tsunamis may have wavelengths of 240 km (150 mi) and can travel at over 700 km/hr (435 mi/hr)—as fast as a jet airplane. In the open ocean, tsunamis are not very high, usually less than 1 m (40 in). Most of the time ships at sea don't even notice the passing of a tsunami. Tsunamis usually get higher when they approach shore. In most cases, the increase in height is relatively minor. A few tsunamis occur almost every year, but most are not very damaging. Occasionally, however, the waves grow huge and cause great death and destruction.

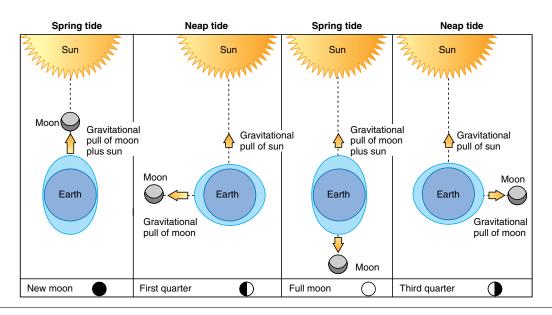
Perhaps the most famous tsunamis were caused not by an earthquake but by the explosion in 1883 of the volcanic island of Krakatoa in the Indian Ocean. These tsunamis caused destruction over half the globe and killed more than 35,000 people.

Hawai'i is exposed to tsunamis caused by earthquakes around the Pacific Rim, and averages about one tsunami per year. About every seven years the tsunami is dangerous, and Hawai'i, especially the town of Hilo, has suffered tremendous damage. A tsunami in 1946 took 159 lives. A 1960 earthquake in Chile caused tsunamis around the Pacific, including one that killed 61 people in Hilo. Death and destruction occurred along the west coast of the United States as a result of both the 1960 Chile earthquake and the great Alaska earthquake of 1964.



The Great Wave at Kanagawa.

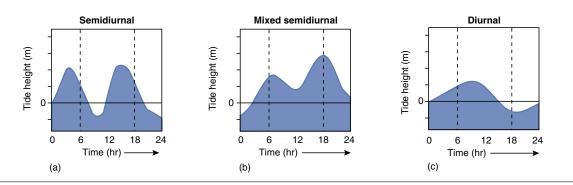
Today a worldwide network of seismic monitoring stations provides instant notice of an earthquake or other seismic disturbance. A tsunami watch is issued whenever there is an earthquake stronger than 6.75 on the Richter scale. This system has saved lives, but is far from perfect. Scientists can't predict which particular earthquakes will produce killer tsunamis, or where, so there are often false alarms. Much more serious in terms of protecting human life is that many people, especially in developing countries, do not receive the warnings. In some cases the earthquakes occur near the coast, and there is no time to issue a warning. Between 1992 and 2000 more than 4,000 people are known to have been killed by tsunamis, and the actual toll may be much higher. For example, a tsunami that struck Papua New Guinea in 1998—the deadliest in decades—left thousands unaccounted for in addition to the 2,200 confirmed dead.



**FIGURE 3.28** The tidal bulges are largest, and therefore the tidal range is greatest, when the moon and sun are in line and acting together. This happens at new and full moon. When the moon and sun are pulling at right angles, which occurs when the moon is in quarter, the bulges and tidal range are smallest.

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**FIGURE 3.29** Types of tides. In most places the tide is semidiurnal; that is, there are two high and two low tides per day. (a) In some places, successive high tides are nearly equal in height. (b) In many other places, one of the highs is considerably higher than the other. This is called a mixed semidiurnal tide. (c) A few places have a diurnal tide, with only one high and one low tide per day.

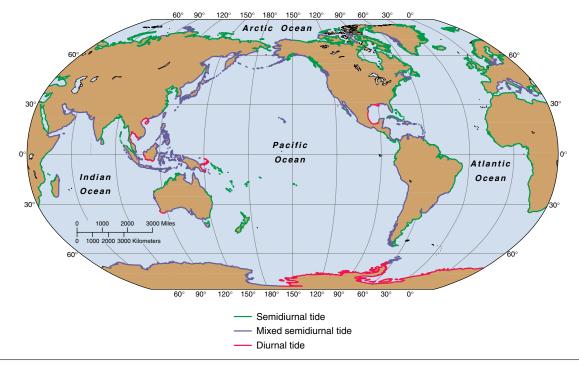


FIGURE 3.30 The worldwide distribution of semidiurnal, mixed semidiurnal, and diurnal tides. This map shows the dominant type of tide. At most places there is variation; a place that usually has, say, a mixed semidiurnal tide may occasionally experience diurnal tides.

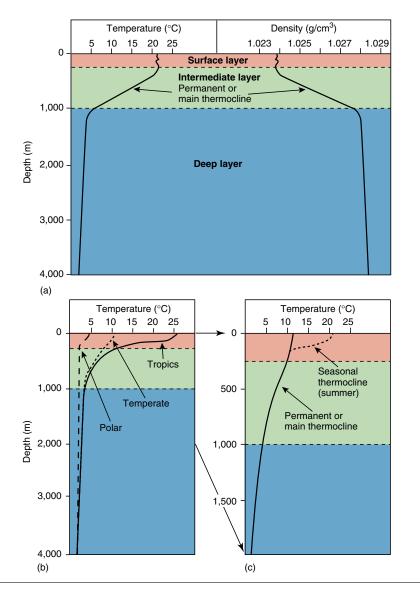
The tides are caused by a combination of the gravity of the sun and moon and the centrifugal force that results from the rotation of the earth, moon, and sun.

#### Tides in the Real World

Fortunately for us, the earth is not completely covered with water. Largely because of the continents and the shape of the sea floor, tides in the real world behave somewhat differently than they would on a water-covered earth. The tides vary from place to place depending on the location and on the shape and depth of the basin.

As predicted, most places do have two high tides and two low tides a day (Fig. 3.29a and b); that is, they have **semidiurnal tides**. The east coast of North America and most of Europe and Africa have semidiurnal tides (Fig. 3.30). Some places have a **mixed semidiurnal tide**, with successive high tides of different height (Fig. 3.29*b*). Mixed semidiurnal tides are characteristic of most of the west coast of the United States and Canada. **Diurnal tides** occur when there is only one high and one low tide every day (Fig. 3.29*c*). Diurnal tides are uncommon. They occur on the coast of Antarctica and in parts of the Gulf of Mexico, Caribbean, and Pacific (Fig. 3.30).

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|--------------------------------|------------------------|----------------------------|-------------------|--|
| <b>Biology, Fourth Edition</b> | Science                | Features of Seawater & the | Companies, 2003   |  |
|                                |                        | World Ocean                |                   |  |



**FIGURE 3.31** Typical profiles of temperature and density in the ocean away from the poles (*a*). Temperature and density profiles are usually mirror images of each other because density in the ocean is controlled largely by temperature. Surface water is usually warmer and therefore less dense than the water below. The temperature of the surface, as you might expect, varies with latitude, with the highest surface temperature occurring in the tropics (*b*). Deep-water temperatures are much more uniform. In temperate and polar waters, thermoclines may develop in the surface layer during the summer when the sun warms the uppermost part of the water column (*c*). Note that the depth scale in (*c*) is different from that in (*a*) and (*b*).

**Tide tables** that give the predicted time and height of high and low tides are available in most coastal areas. These tables give the values for one particular place. Other places in the area may have slightly different tides, depending on how far away they are and on the effects of channels, reefs, basins, and other local features. Weather patterns can also influence the tides. Strong winds, for instance, can pile up water on shore, causing higher tides than predicted. On the whole, however, tide tables are remarkably accurate.

## VERTICAL MOTION AND THE THREE-LAYERED OCEAN

63

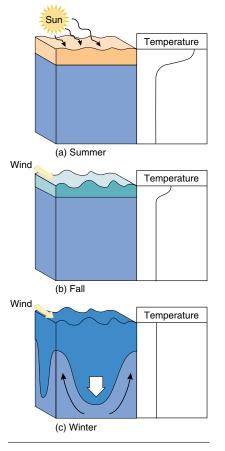
The oceans are a three-dimensional habitat. They vary not only horizontally—from north to south and east to west—but vertically, that is, at different depths. In many ways, changes in living conditions that are due to the third dimension, depth, are more important than changes due to geographic location. Much of the threedimensional structure of the sea, especially in relation to depth, is controlled by the density of the water. That is why oceanographers take such pains to measure the temperature and salinity of ocean water, the two factors that determine its density.

## **Stability and Overturn**

Because the densest water sinks, the ocean is usually layered, or **stratified**, with the densest water on the bottom and the least dense at the surface. This can be seen in typical profiles of density and temperature (Fig. 3.31). Deep water is normally cold and dense, whereas the surface water is relatively warm and "light." The surface water tends to stay where it is and float on the denser water below, so the water column is said to be **stable.** Unless some type of energy, like wind or storm waves, stirs up the water column, the surface water will not mix with the deep water.

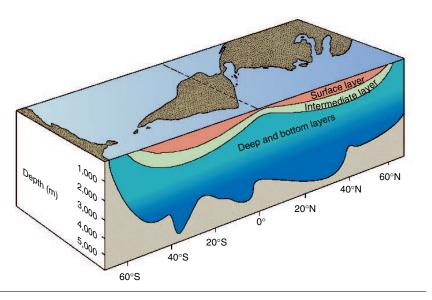
*How* stable the water column is depends on the difference in density between the surface and deep water. If the surface water is only slightly more dense than the deep water, it will be relatively easy to mix the two. In this case the water column would be said to have low stability. A highly stable water column, on the other hand, would result from a large density difference between deep and shallow water.

The water column in the ocean is usually stratified, with the densest water on the bottom. The greater the difference in density between surface and deep water, the more stable the water column is and the harder it is to mix vertically.



**FIGURE 3.32** Overturn of the water column often occurs in temperate and polar waters. (*a*) In summer the sun warms up the surface layer, which therefore becomes much less dense than the water below. (*b*) When fall comes, the surface water cools and storm winds mix colder deep water to the surface. (*c*) If the surface water gets cold enough, usually during winter, it gets denser than the deeper water and sinks.

Occasionally surface water becomes more dense than the water below. Such a water column is called unstable because the situation cannot last long. The surface water sinks, displacing the less dense water below in a process known as **overturn** (Fig. 3.32). Since surface water, all with the same temperature and density, is descending through the water column, the temperature and density profiles are vertical straight lines. In fact, oceanographers identify conditions of overturn by looking for such straight-line profiles. Overturn



**FIGURE 3.33** Greatly simplified, the ocean can be thought of as having three main layers or water masses. The warm surface layer is relatively thin. The intermediate layer, the region of the main thermocline, is a transition between the surface layer and the cold, deep, and bottom layers.

usually occurs in temperate and polar regions during the winter when the surface water cools.

After the water leaves the surface, it descends to a depth determined by its density. If the water is very dense, it will sink all the way to the bottom. This only happens at a few places (see p. 357). Water of intermediate density will descend only part way, to a level where it is denser than the water above but less dense than the water below. The stability of the water column is quickly restored as the densest water sinks to the bottom and the least dense water rises to the surface.

The processes that change salinity in the open ocean-precipitation, evaporation, and freezing-occur only at the surface. Temperature also changes primarily at the surface, through evaporative cooling, solar heating, or the exchange of heat with the atmosphere. Once surface water has sunk, therefore, its salinity and temperature do not change. From then on the volume of water, or water mass, has a "fingerprint," a characteristic combination of temperature and salinity. Oceanographers can use this to follow the movement, or circulation, of water masses over great distances. Because this form of circulation is driven by changes

in density, which in turn is determined by temperature and salinity, this form of circulation is known as **thermohaline circulation**.

Unlike wind-driven currents, which occur only near the surface, thermohaline circulation extends throughout the ocean depths (see Figs. 16.2 and 16.3). It is critically important in regulating earth's climate and chemically mixing the oceans. Descending surface water also brings dissolved oxygen to the deep sea (see "The Oxygen Minimum Layer," p. 367). This effect is enhanced because oxygen dissolves best in cold water (see "Dissolved Gases," p. 51). Overturn is also an important factor in determining the abundance of life in the oceans (see "Patterns of Production," p. 343).

### The Three-Layered Ocean

Although there are actually many thin layers of water, each of slightly different density, it is not a bad approximation to view the ocean as being made of three principal layers (Fig. 3.33). The **surface layer** is usually around 100 to 200 m (330 to 660 ft) thick. Much of the time the surface layer is mixed by wind, waves, and currents, so it is also known as the **mixed layer**. The surface

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*Chapter 3 Chemical and Physical Features of Seawater and the World Ocean* 65

layer is not always well mixed, however. Sometimes, usually in the spring and summer in temperate and polar water, the very uppermost part of the surface layer gets heated by the sun. The warm water floats in a shallow "lens" on top, and there is a sharp transition to the cooler water below. These sudden changes in temperature over small depth intervals, called **thermoclines**, are often noticed by divers. When the weather becomes colder, wind and waves again mix the water column and the thermocline breaks down. The intermediate layer lies below the surface layer to a depth of around 1,500 m (5,000 ft). The main thermocline, a zone of transition between warm surface water and the cold water below, lies in the intermediate layer. The main thermocline should not be confused with the shallower, seasonal thermoclines previously described. The main thermocline rarely breaks down, and then only in a few places. The main thermocline is a feature of the open ocean. The waters over the continental shelf are not deep enough to have the main thermocline. Indeed, shelf waters are often mixed all the way to the bottom.

Below about 1,500 m (5,000 ft) lie the **deep** and **bottom layers**. Technically, deep water and bottom water are different, but they are similar in being uniformly cold, typically less than  $4^{\circ}$ C ( $39^{\circ}$ F).

The ocean has three main layers: the surface or mixed layer, the intermediate layer, and the deep layer.

•



## interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

## **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject matter.

## Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

## **Critical Thinking**

- The winter of 1984–85 was particularly cold in Europe. The northern part of the Black Sea, which lies between the Ukraine, Russia, and Turkey, froze, which is rare in the normally mild climate. The Adriatic Sea, located to the east, had just as cold a winter but never froze. The Black Sea has an unusually low salinity of about 18‰. What would you guess about the salinity of the Adriatic?
- 2. Just for the fun of it, someone walking along the shore in Beaufort, South Carolina, throws a bottle with a message in it into the sea. Some time later, someone in Perth, on the west coast of Australia, finds the bottle. Referring to Figure 3.19 and Appendix B of this book, can you trace the path the bottle probably took?
- 3. If you owned a seaside home and a bad storm brought heavy winds and high surf to your coastline, would you prefer it to be during a new moon or a quarter moon? Why?

4. Most tsunamis occur in the Pacific Ocean, as indicated by the map in the "Waves That Kill" boxed reading (see p. 60). How would you explain this?

## For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol , and will contain live links when you visit this page in the Online Learning Center.

#### **General Interest**

- Cromwell, D., 2000. Ocean circulation. New Scientist, vol. 166, no. 2239, 20 May, Inside Science supplement no. 130, pp. 1–4. A summary of what is known about ocean currents and current research efforts to learn more.
- González, F. I., 1999. Tsunami! *Scientific American*, vol. 280, no. 5, May, pp. 56–65. Detailed explanations of how tsunamis form and behave, and a review of their worldwide impacts.
- Krajik, K., 2001. Message in a bottle. *Smithsonian*, vol. 32, no. 4, July, pp. 36–47. An oceanographer studies ocean currents by tracking the paths taken by rubber duckies, tennis shoes, and other floating objects.
- Kunzig, R., 1996. In deep water. *Discover*, vol. 17, no. 12,
   December, pp. 86–96. An interesting account of ocean circulation, its link to climate, and the scientists that are unraveling these mysteries.

Castro-Huber: Marine **Biology, Fourth Edition**  I. Principle of Marine Science

3. Chemical & Physical Features of Seawater & the World Ocean

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66 Part One Principles of Marine Science

- Kunzig, R., 2001. The physics of . . . deep-sea animals: They love the pressure. Discover, vol. 22, no. 8, August, pp. 26-27. Deep-sea organisms feel the squeeze under the pressure of the deep sea.
- Linn, A., 1983. Oh, what a spin we're in, thanks to the Coriolis effect. Smithsonian, vol. 13, no. 11, February, pp. 66-73. A detailed explanation of the Coriolis effect and a look at some of its consequences.
- Matthews, R., 1997. Wacky water. New Scientist, vol. 154, no. 2087, 21 June, pp. 40-43. Plain water, so familiar to us all, still holds scientific secrets.
- Oceans and climate. Oceanus, vol. 39, no. 2, Fall/Winter 1996. This issue provides more information on the link between the oceans and global climate patterns.

#### In Depth

- Koeve, W. and H.W. Ducklow, 2001. JGOFS synthesis and modeling: The North Atlantic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography, vol. 48, no. 10, pp. 2141-2154.
- Read, J. F., 2001. CONVEX-91: Water masses and circulation of the northeast Atlantic subpolar gyre. Progress in Oceanography, vol. 48, nos. 2-3, 2001, pp. 461-510.
- Weaver, A. J., C. M. Bitz, A. F. Fanning and M. M. Holland, 1999. Thermohaline circulation: High-latitude phenomena and the difference between the Pacific and Atlantic. Annual Review of Earth and Planetary Sciences, vol. 27, pp. 231-285.

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Wunsch, C. and D. Stammer, 2001. Satellite altimetry, the marine geoid, and the oceanic general circulation. Annual Review of Earth and Planetary Sciences, vol. 48, pp. 219–253.

## See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

- Intertidal wave action (Bermuda)
- · Wave crashing on a rocky shore (Galápagos Islands)

## Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Inorganic chemistry
- Atoms
- Molecules
- Bonds
- · Waves, tides, and currents

## **Quiz Yourself**

Take the online quiz for this chapter to test your knowledge.

4. Some Basics of Biology

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# Some Basics of Biology



ow that we have discussed some of the major features of the marine environment, we can turn our attention to life in the sea. Perhaps the most basic question we could ask is, What *is* life? Most people have a pretty good feel for what the word *living* means, but it is difficult to come up with a precise definition. About the best we can do is to describe the properties that living things have in common.

All living things use **energy**, the ability to do work, to maintain themselves and grow. This is accomplished by means of a vast number of chemical reactions that together are called **metabolism.** Living things also use energy to regulate their internal environments, that is, to maintain livable conditions inside themselves no matter what their surroundings are like. They are able to sense and react to the external environment. In addition, all life forms reproduce to perpetuate their kind, and they pass their characteristics on to their offspring.

All living things grow, metabolize, react to the external environment, and reproduce.

The most basic features of living things are shared by all organisms, not just those that live in the sea. Here, however, we will pay particular attention to the lives of marine organisms.



Flatworms (Pseudoceros bifurcus) joust in a mating ritual known as penis fencing.

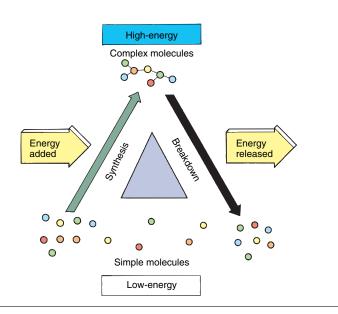
# THE INGREDIENTS OF LIFE

The process of life involves an intricate series of interactions among an immense variety of chemicals. The most important of these chemicals is also one of the simplest: water. As the universal solvent, water provides the medium in which all the other molecules dissolve and interact. Water is the base of a complex "chemical soup" inside all organisms where the chemical reactions of metabolism take place.

# **The Building Blocks**

The processes that make life possible involve an enormous number of chemicals in addition to water. Most of these chemicals are **organic compounds**, molecules that contain atoms of **carbon**, **hydrogen**,

Water is called the universal solvent because it can dissolve more different substances than any other liquid. *Chapter 3, p. 46* 



**FIGURE 4.1** Chemical reactions can be divided into those that require energy and those that release it. Organisms need energy to make complex molecules from simple ones, much as energy is required to push a rock uphill. The breakdown of energy-rich complex molecules is a "downhill" process that releases energy.

and usually **oxygen**. Organic compounds are high-energy molecules; that is, it takes energy to make them (Fig. 4.1). The ability to use energy to make, or synthesize, organic compounds is an important characteristic of living things. Organic compounds tend to fall apart, or break down, when left to themselves. When this happens they release the energy that went into their construction. Organisms have developed the ability to control this breakdown, often in order to harness the energy that is released.

### Carbohydrates

Most organic molecules belong to one of four main groups. **Carbohydrates** are composed mainly of just the basic elements of most organic molecules: carbon, hydrogen, and oxygen. The simplest carbohydrates are **glucose** and a few other **simple sugars**. More complex carbohydrates are formed by the combination of simple sugars into chains. Ordinary table sugar, for example, consists of two simple sugar molecules joined together. **Starches** and other complex carbohydrates consist of much longer chains, which may contain components other than simple sugars. Carbohydrates serve a variety of functions. Simple sugars play a vital role in the most basic metabolic processes, as we shall see. Complex carbohydrates like starches are often used to store energy reserves. Other carbohydrates are important **structural molecules**, that is, they provide support and protection. Plants and many algae (see Table 5.1, p. 92) make use of a structural carbohydrate called **cellulose**, the main ingredient of wood and plant fibers. Some animals use a modified carbohydrate called **chitin** as a skeletal material.

### Proteins

**Proteins** are another important group of organic molecules. Proteins are the most varied and complex organic compounds. Like complex carbohydrates, proteins are composed of chains of smaller subunits. In proteins the subunits are **amino acids**, which contain atoms of **nitrogen** as well as the carbon, hydrogen, and oxygen typical of all organic compounds.

Proteins have an extraordinary variety of functions. Muscles are made largely of protein. **Enzymes** are proteins that speed up specific chemical reactions. Without enzymes, many metabolic reactions would proceed very slowly or not at all. There

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are also many structural proteins, such as those that help make up skin, hair, and the skeletons of some marine animals. Some **hormones**, chemicals that act as messengers to help different parts of the body work together, are proteins. Other proteins carry oxygen in the blood and muscles. Proteins also act as poisons, are used to send chemical signals, produce light, and have countless other functions.

### Lipids

Fats, oils, and waxes are examples of **lipids**, another group of organic chemicals. Lipids are often used for energy storage (Fig. 4.2). Another useful property of lipids is that they repel water. Many marine mammals and birds, for instance, use a coating of oil to keep their fur or feathers dry. Some marine organisms that are exposed to the air at low tide have a coating of wax that helps keep them from drying out. Lipids are also useful in buoyancy because they float, and for insulation from the cold. Some hormones are lipids rather than proteins.

### Nucleic Acids

Nucleic acids store and transmit the basic genetic information of all living things. Nucleic acid molecules are chains of repeating subunits called nucleotides that consist of a simple sugar joined to molecules containing phosphorus and nitrogen. One type of nucleic acid is DNA (deoxyribonucleic acid). An organism's DNA molecules specify the "recipe" for the organism-all the instructions for its construction and maintenance. An organism's complete genetic information is called its genome. The organism inherits this genetic information, in the form of DNA, from its parents and passes it on to its offspring. The DNA chains are often tens or hundreds of millions of nucleotides long, but contain only four different types of nucleotides. The order, or sequence, of the different nucleotides on the chain forms a code, like a four-letter alphabet, that contains the genetic information. Four letters may not sound like much, but Morse code can express any written message with an alphabet of only two symbols: dots and dashes. Modern computers also use a twoletter alphabet, known as binary code.

4. Some Basics of Biology

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**FIGURE 4.2** The thick layers of blubber on this whale are composed almost entirely of lipid. Whales can go without eating for long periods by using the energy stored in the blubber. The whale's blubber also helps protect it from the cold and gives it buoyancy. People once used the energy contained in blubber by burning oil made from it for light and heat. Most industrial whaling has ceased but so-called traditional whaling, such as that undertaken by these Alaskan Inuit, continues legally in some places.



**FIGURE 4.3** Kelp, a kind of seaweed that lives in sub-polar and temperate waters, captures the sunlight streaming down through the water to perform photosynthesis. The kelp uses the light energy to grow. Other organisms eat the kelp, making use of the energy that originally came from the sun.

The other group of nucleic acids is **RNA (ribonucleic acid).** Like DNA, RNA consists of chains of only four types of nucleotides, but one of these is different from that in DNA. RNA translates the genetic information contained in an organism's DNA into protein molecules, and ultimately into the organism itself.

Because organisms' nucleic acids define so much about them, sequencing nucleic acids-determining their nucleotide sequences-has become one of the hottest fields of biological research. Complete genome sequences are known for only a small but increasing number of organisms, most notably humans. Partial nucleic acid sequences are available for many more organisms and contain a wealth of information that biologists are only beginning to learn how to use. Just as a few signature notes immediately identify a song, or a classic line a movie, certain characteristic partial sequences of DNA or RNA can identify organisms or reveal details of their metabolism (see "Tiny Cells, Big Surprises," p. 99).

Organic compounds are chemicals that contain carbon, hydrogen, and usually oxygen. The main types of organic compounds are carbohydrates, proteins, lipids, and nucleic acids.

# The Fuel of Life

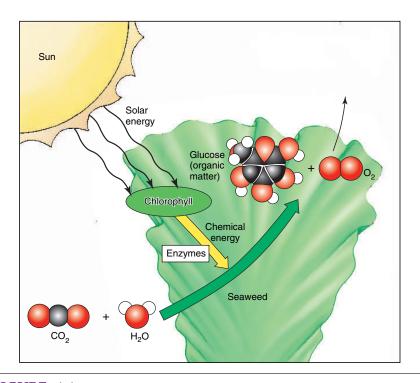
The molecules that make up living things interact in many complex chemical reactions. The most basic of these chemical systems have to do with the capture, storage, and use of energy. More simply put, they deal with the production and use of food.

## Photosynthesis: Making the Fuel

Almost all living things ultimately get their energy from the sun (Fig. 4.3). In a process called **photosynthesis**, algae, plants, and some other organisms capture the sun's energy and use it to make glucose, a simple sugar, some of which is converted into

**Molecules** Combinations of two or more *atoms;* most substances are composed of molecules rather than individual atoms.

Chapter 3, p. 43



**FIGURE 4.4** In photosynthesis, carbon dioxide and water are used to make glucose. The energy for this comes from sunlight. Oxygen is given off as a by-product.

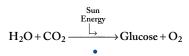
other organic compounds. Most other organisms use these organic molecules as a source of energy. Organic material contains a tremendous amount of energy. As food it fuels our bodies and those of most other creatures. In such forms as oil, gas, and coal it heats our homes, runs our factories, and powers our cars.

Photosynthesis (Fig. 4.4) begins when solar energy, in the form of sunlight, is absorbed by chemicals within an organism called **photosynthetic pigments**. The most common photosynthetic pigment is **chlorophyll**. The bright green color characteristic of plants is caused by chlorophyll. Most algae have additional pigments that may mask the green chlorophyll (see Table 5.1, p. 92). Because of these pigments, algae may be brown, red, or even black in addition to green.

In a long series of enzyme-controlled reactions, the solar energy captured by chlorophyll and other pigments is used to make glucose, with **carbon dioxide** (CO<sub>2</sub>) and water ( $H_2O$ ) as the raw materials. Carbon dioxide is one of very few carbon-containing molecules not considered to be

an organic compound. Photosynthesis, then, converts carbon from an inorganic to an organic form. This is called **fixing** the carbon or carbon fixation. In this process, the solar energy that was absorbed by chlorophyll is stored as chemical energy in the form of glucose. The glucose is then used to make other organic compounds (see "Primary Production," p. 73). In addition, photosynthesis produces oxygen gas (O<sub>2</sub>), which is released as a by-product. All the oxygen gas on earth, both in the atmosphere we breathe and in the ocean, was produced by photosynthetic organisms. Photosynthesis constantly replenishes the earth's oxygen supply. Thus, we rely on photosynthesis not only for food, but for the very air we breathe.

Photosynthesis captures light energy from the sun to produce glucose. Carbon dioxide and water are used to make the glucose, and oxygen gas is liberated as a by-product:



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Organisms that are capable of photosynthesis can obtain all the energy they need from sunlight and do not need to eat. Such organisms are called **autotrophs** ("self-feeders"). Plants are the most familiar autotrophs on land. In the ocean, however, algae and bacteria are the most important autotrophs.

Many organisms cannot produce their own food and must obtain energy by eating organic matter that already exists. These organisms, which include all animals, are called **heterotrophs**.

### Respiration: Burning the Fuel

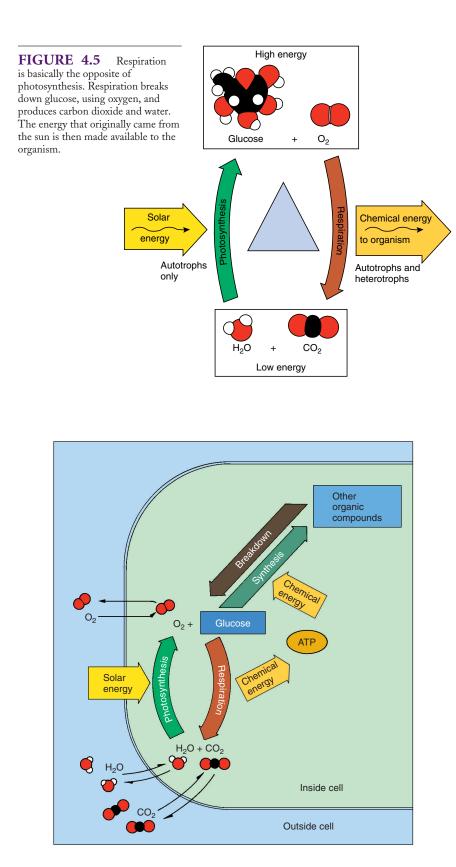
Both autotrophs and heterotrophs perform **respiration** to make use of the solar energy stored in organic chemicals by photosynthesis. Though the chemical reactions are different, the net result of respiration is essentially the reverse of photosynthesis (Fig. 4.5). Sugars are broken down using oxygen, and carbon dioxide and water are given off. This process is sometimes called cellular respiration to distinguish it from the physical act of breathing. Since breathing acts to provide oxygen for cellular respiration, the two processes are closely related.

Respiration, which occurs in all organisms, breaks down glucose, releasing the energy it contains. Respiration consumes oxygen and produces carbon dioxide and water:

$$\begin{array}{c} Glucose + O_2 & \longrightarrow & CO_2 + H_2O \\ & & & \downarrow & \\ & & & Chemical \\ & & & Energy \end{array}$$

Respiration is similar to the burning of wood or oil in that organic material is broken down, oxygen is consumed, and the energy contained in the material is released. This is why weight watchers speak of "burning calories." In respiration, however, the energy stored in the organic material is not released in flames. Instead, it is stored as chemical energy in a special molecule called ATP (adenosine triphosphate) that is based upon adenosine, one of the nucleotides in nucleic acids. ATP provides a way to keep the energy available until it is needed. Most of the chemical reactions in metabolism use ATP as an energy source rather than being tied directly to respiration. Thus, cells use ATP as a





### Chapter 4 Some Basics of Biology 73

sort of "energy currency." In an average day you go through 57 kg (125 lb) of ATP. Whales must use tons!

The energy released from glucose by respiration is used to make ATP, the "energy currency" of life.

### **Primary Production**

The sugars produced by photosynthesis supply both the raw material and the energy, via respiration, for the manufacture of other organic compounds. Through elaborate chemical processes, some of the glucose formed during photosynthesis is converted into other types of organic molecules-carbohydrates, proteins, lipids, and nucleic acids (Fig. 4.6). The energy for these conversions, in the form of ATP, comes from "burning up," or metabolizing, much of the rest of the glucose. Thus, most of the glucose produced by photosynthesis is either converted to other types of organic matter or respired to fuel this conversion.

When autotrophs produce more organic matter than they use in respiration, there is an overall gain of organic matter. This net increase in organic matter is called **primary production**. The autotrophs use the extra organic material to grow and reproduce. In other words, the extra organic matter forms more living material, and that means more food for animals and other heterotrophs. Organisms that perform this primary production of food are called **primary producers**, or sometimes just **producers**.

Primary production is the net gain in organic matter that occurs when autotrophs photosynthesize more than they respire.

FIGURE 4.6 In photosynthesis, autotrophs capture energy from the sun and store it in chemical form in simple sugars like glucose. Some of the sugars are broken down in respiration, and the energy is stored in ATP. The energy can now be used by the rest of the organism's metabolism, for example, to make other organic matter from the rest of the glucose. If there is no light, autotrophs can perform only respiration, like animals and other heterotrophs. The small black arrows represent molecules moving in and out of the cell.

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### The Importance of Nutrients

Only carbon dioxide, water, and sunlight are needed to make glucose by photosynthesis, but other materials are needed to convert the glucose into other organic compounds. These raw materials, called nutrients, include minerals, vitamins, and other substances. Primary producers need many different nutrients, but those needed in the largest amounts are nitrogen and phosphorus. Nitrogen is needed to make proteins; both nitrogen and phosphorus are needed to make nucleic acids. In one form or another, nitrogen and phosphorus are the main ingredients of most garden fertilizers. They are important "fertilizers" in the ocean as well. The most important form of nitrogen in the sea is nitrate (NO<sub>3</sub><sup>-1</sup>). Phosphate  $(PO_4^{-3})$  is the main source of phosphorus.

Primary production requires nutrients, as well as light. Nitrogen and phosphorus are usually the most important nutrients for plant growth in the ocean.

## LIVING MACHINERY

The chemical reactions of metabolism make life possible, but chemical reactions are not living things and organisms are not just bags of chemical soup in which reactions take place. If you ran a fish, say, through a blender, you would still have all the same molecules, but the fish would definitely not be alive. The molecules in living things are *organized* into structural and functional units that work in a coordinated way. It is this living machinery that is responsible for many of the properties of living things.

## **Cells and Organelles**

The basic structural unit of life is the **cell**. All organisms are made of one or more cells. Cells contain all the molecules needed for life packaged in a living wrapper called the **cell membrane** or **plasma membrane**. This membrane isolates the gelatinous contents of the cell, or **cytoplasm**, from the outside world. The cell membrane allows some subPlasma (cell) membrane Cell wall

**FIGURE 4.7** Prokaryotic cells like this bacterium are fairly simple. The cell is surrounded by a plasma membrane. Outside the membrane lies a cell wall. In this bacterium, which performs photosynthesis, the cell membrane is folded into the cell's interior. The membrane folds contain chlorophyll, and are the sites where photosynthesis takes place. There is also a large, ring-like molecule of DNA. Otherwise, there is little structure inside the cell.

stances to pass in or out but prevents others from doing so.

There are a number of structures within the cytoplasm. Among the most important are membranes similar to the outer cell membrane. These interior membranes act as sites for such chemical processes as photosynthesis and respiration. Membranes may also divide the cell into compartments that enclose still more complex structures specialized for particular tasks. These membrane-bound structures are known as **organelles**. It is the presence of organelles that separates the two major types of cells.

## Structurally Simple Cells: Prokaryotes

**Prokaryotic cells** are primitive in the sense that they are the most ancient type of cell. They are also the simplest and smallest cells. Prokaryotic cells are distinguished by the absence of membrane-bound organelles (Fig. 4.7). Organisms with prokaryotic cells are called **prokaryotes**. With very few exceptions (see Fig. 5.2) prokaryotes are microscopic, and most are tiny even by the standards of microscopic organisms. The most well-known group of prokaryotes is the **bacteria**.

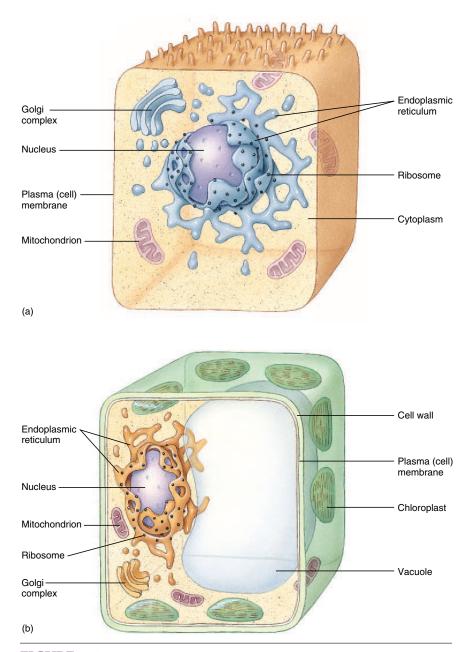
Outside the cell membrane of prokaryotes lies a supportive **cell wall.** Inside, the cell has a single, ring-like molecule of DNA. Scattered through the cytoplasm are small structures called **ribosomes** that are made of protein and RNA. The cell's proteins are made in the ribosomes. In photosynthetic bacteria the cell membrane folds into the cell's interior. The photosynthetic pigments lie in these folds. Some prokaryotes possess one or more whip-like extensions known as **flagella** (singular, **flagellum**). These cells move by rotating their flagella like tiny propellers.

The most primitive cells are prokaryotic. They have relatively little internal structure and lack membrane-bound organelles.

## Structurally Complex Cells: Eukaryotes

**Eukaryotic cells,** the second major cell type, are much more organized and complex than prokaryotic cells (Fig. 4.8). Various membrane-bound organelles do special jobs inside the cell. The **nucleus** contains structures called **chromosomes** that carry most of the cell's DNA. The nucleus thus holds the cell's genetic information and directs most of its activities. The nucleus can be thought of as the cell's headquarters.





**FIGURE 4.8** Typical cells of animals (*a*) and algae and plants (*b*) and some of the structures they contain.

The "factories" of eukaryotic cells are two structures, mostly folded membranes, called the **endoplasmic reticulum** and the **Golgi complex**. These organelles make, package, and transport many of the organic molecules that the cell needs. Ribosomes sit in some of the endoplasmic reticulum. Respiration in eukaryotes takes place in special organelles called **mitochondria**. Mitochondria are the cell's power plants, breaking down organic molecules to provide energy. Plant and algal cells have two important structures that animals don't. First, they have **chloroplasts**, chlorophyllcontaining organelles where photosynthesis takes place. Second, except for some single-celled algae they have a cell wall.

Many eukaryotic cells have flagella. When they are short and numerous the flagella are called **cilia**, but the structure is exactly the same. Like prokaryotes, eukaryotes often use their flagella or cilia to swim. They are also used to push water or particles through or past the organism, rather than to push the organism through the water. Many marine animals, for example, use cilia to push food particles to the mouth. Cilia in your lungs carry away dust and other irritants.

The cells of eukaryotes are more structured than those of prokaryotes. They have membranebound organelles, including a nucleus in which the DNA is carried in chromosomes.

The cell may also have a complex internal framework made of protein fibers. This framework, called the **cytoskeleton**, supports the cell, allows it to move and change shape, and helps it divide. The cytoskeleton is normally invisible under the microscope and not usually shown in drawings.

## Levels of Organization

A cell is a self-contained unit that can carry out all the functions necessary for life. Indeed, many organisms get by just fine with only a single cell. One-celled organisms are called **unicellular**. All prokaryotes and some eukaryotes are unicellular. Most eukaryotic organisms, however, are **multicellular**; that is, they have more than one cell. The human body, for instance, contains something like 100 trillion cells.

There is a division of labor among the cells of multicellular organisms, with different cells becoming specialized for particular jobs. Groups of specialized cells that perform the same task may be organized into more complex structures. The extent of this specialization and organization is referred to as the **level of organization** (Table 4.1).

### Organization Within the Body

At the simplest, or **cellular**, level each cell is essentially an independent, self-sufficient unit. Each can perform all of the functions

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| Table 4      | Levels of Organization of  | f Biological Systems                        |                             |
|--------------|--|---|-----------------------------|
| Level        | Description  | Examples                                    |                             |
| Ecosystem    | A community or communities in a large<br>area, together with their physical<br>environment | Nearshore ecosystem                         |                             |
| Community    | All the populations in a particular habitat  | Rocky shore community                       | One or more organisms       |
| Population   | Group of organisms of the same species that occur together                                 | All the mussels on a stretch of rocky shore |                             |
| Individual   | A single organism  | One mussel                                  | )                           |
| Organ system | A group of organs that work in cooperation   | Digestive system                            | lexity                      |
| Organ        | Tissues organized into structures  | Stomach                                     | Iuo                         |
| Tissue       | Groups of cells specialized for the same<br>function that are bound together<br>organisms  | Muscle tissue                               | Within individual organisms |
| Cell         | Independent cells, the fundamental unit of living things                                   | Muscle cell, single-celled organisms        | ) "                         |
| Organelle    | A complex structure within cells;<br>bound by a membrane                                   | Nucleus, mitochondrion                      | ]                           |
| Molecule     | Combinations of atoms that are bound together  | Water, proteins                             | Within cells                |
| Atom         | The fundamental units of all matter  | Carbon, phosphorus                          | J                           |

needed to sustain the organism and reproduce, and there is little or no cooperation among the cells.

Only a few multicellular organisms remain at the cellular level (Fig. 4.9). In most, certain groups of cells act together to do a particular job. These specialized, coordinated groups of cells are called **tissues**. Some cells, for example, are specialized to contract and do work. These cells are bound together to form muscle tissue. Nervous tissue, specialized to collect, process, and transmit information, is another example.

In most animals organization doesn't stop at the tissue level either. Their tissues are further organized into structures known as **organs** that carry out specific functions. The heart is an example of an organ. There are several different tissues that make up the heart. Muscle tissue, for example, allows the heart to contract and pump blood, and nervous tissue controls the muscle.

Different organs act together in organ systems. The digestive system, for instance, includes many organs: a mouth,

stomach, intestine, and so on. Animals usually have a number of organ systems, including nervous, digestive, circulatory, and reproductive systems.

### Interactions Among Individuals

Not only are there different levels of organization within individual organisms, but individuals interact with each other at still higher levels of complexity. A **population** is a group of organisms of the same kind, or **species**, that lives in one place. The mussels on a stretch of rocky shore, for example, form a population (Fig. 4.10).

Populations of different species that occur in the same place form **communities**. A community is often more than just a collection of organisms that happen to live in the same area. The characteristics of communities are determined in large part by the way the organisms *interact* which organisms eat each other, which organisms compete, and which depend on each other. Rocky shores, for example, are home to many organisms in addition



**FIGURE 4.9** Sponges are the only multicellular animals that are at the cellular level of organization (see "Sponges," p. 118). Even sponges have specialized cells, though they don't form tissues.

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Prokaryotes were the first life on earth. There are fossil bacteria that are 3.8 *billion* years old, nearly as old as the oceans themselves. Being prokaryotes, these early cells did not have organized organelles enclosed by membranes. Prokaryotic life came on the scene very early in the earth's history, but the next step took much longer. It was a billion years or more before complex cells with organelles, or eukaryotic cells, appeared. Strangely enough, this advance in cell design, shared by all multicellular life, probably started with a simple meal.

Biologists believe that mitochondria, the "powerhouses" of the cell (see Fig. 4.8), were once free-living bacteria. They are 1 to 3 microns ( $\mu$ m) long, about the same size as many bacteria. Like many bacteria, they contain layers of folded membranes. Although most of the cell's DNA is contained in the nucleus, mitochondria have a small amount of their own DNA. This DNA is even in the form of a single, circular molecule like the chromosome of bacteria. When a cell needs new mitochondria it does not make them from scratch. Instead, the mitochondria within the cell divide in two, much as bacteria divide by cell division. Mitochondria resemble bacteria in several other respects.

Because of these similarities, biologists believe that mitochondria were originally bacteria that came to live inside other cells. The most likely scenario is that relatively large prokaryotic cells that ate smaller ones were unable to digest all of their food. It is also possible that the small cells were disease bacteria that invaded the larger cell but were unable to kill it. Both phenomena have been observed in the laboratory in living cells. Either way, the small cells eventually took up permanent residence in the larger cells, using them as hosts. The living together of different kinds of organisms like this is called **symbiosis** (see "Living Together," p. 220).

According to this theory, the host cells could not use oxygen in respiration. The smaller, symbiotic, bacteria did use oxygen and gave this ability to their hosts. This gave the host cells an advantage over cells that didn't have symbiotic bacteria.

Over the course of time, the host cells were able to transfer most of the symbiotic bacteria's genes into their own nuclei, and thus came to control the symbionts. The bacteria and host cells became more and more dependent on each other. Eventually the bacteria became mitochondria.

Chloroplasts, the organelles that perform photosynthesis, are also thought to have arisen from symbiotic bacteria. Like mitochondria,



Prochloron.

they are about the right size, have a circular DNA molecule, and can reproduce themselves. Chloroplasts also contain folded membranes very similar to those of photosynthetic bacteria that we see today (see Figs. 4.7 and 5.1). In fact, biologists have found a possible "missing link" between photosynthetic bacteria and chloroplasts. Some sea squirts and other invertebrates contain symbiotic, photosynthetic bacteria called *Prochloron* that are similar to the chloroplasts of green algae and higher plants. It is thought that these chloroplasts arose from *Prochloron*-like bacteria when host cells ate the bacteria, some of which managed to resist being digested and became symbiotic.

The hypothesis that mitochondria and chloroplasts arose from bacteria, once highly controversial, is now almost universally accepted by biologists. Some biologists now even classify mitochondria and chloroplasts as symbiotic bacteria rather than organelles. Several other types of organelles may have similar origins. All multicellular organisms, including humans, carry in their very cells the legacy of these bacterial partnerships, probably the result of an ancient snack.



to mussels: seaweeds, crabs, barnacles, snails, and sea stars, to name a few (Fig. 4.11). It is the interactions among all these organisms that give the rocky shore community its own unique structure.

A community, or more often several communities, together with the physical, or non-living, environment, make up an **ecosystem.** The rocky shore community, for instance, along with other nearby communities, is part of a larger ecosystem that includes the tides, currents, nutrients dissolved in the water, and other physical and chemical aspects of the area.

**FIGURE 4.10** These blue mussels (*Mytilus edulis*) growing on a rocky shore in New Zealand are part of a population.

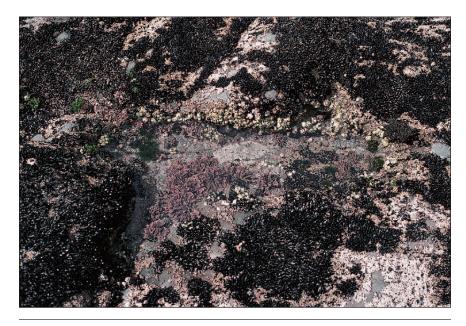
# CHALLENGES OF LIFE IN THE SEA

Every **habitat** has its own unique set of characteristics and presents special challenges to the organisms that live there. Thus, marine organisms must cope with problems unlike those of land dwellers. Even within the marine environment there are different habitats, each of which poses special difficulties. For example, **planktonic** organisms—those that drift in the water—face much different

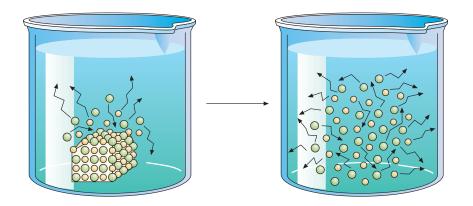
Habitat The natural environment where an organism lives. *Chapter 2, p. 21* 

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**FIGURE 4.11** The community that lives on this rocky shore is made up of populations of blue mussels, barnacles, seaweeds, and many other species.



**FIGURE 4.12** Ions and molecules that are dissolved in water tend to move around randomly just like water molecules do. When a crystal of salt dissolves in water, the ions start out concentrated in one part of the solution but eventually spread out because of their random movement. This process, called diffusion, results in the flow of ions from areas of high concentration to areas of low concentration.

conditions than **benthic** organisms—those that live on the bottom—or **nekton** organisms that are strong swimmers (see Fig. 10.19). Organisms have evolved innumerable ways to adapt to the conditions of their habitats.

Many of the adaptations of marine organisms have to do with maintaining

suitable conditions inside their bodies. The living machinery inside most organisms is rather sensitive and can only operate properly within a narrow range of conditions. Living things have therefore devised ways to keep their internal environments within this range no matter what the external conditions are like. www.mhhe.com/marinebiology

# Salinity

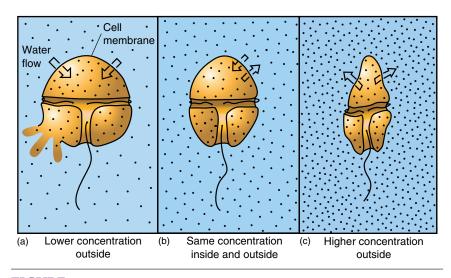
Many enzymes and other organic molecules are very sensitive to changes in the concentrations of the **ions** that are common in seawater. Marine organisms are immersed in a medium that has the potential to profoundly alter their metabolism. To fully understand the problems posed by **salinity**, we must know something about how dissolved ions and molecules behave.

### Diffusion and Osmosis

When in solution, ions and molecules move around just like water molecules do. If the molecules are concentrated in one part of the solution, this random movement spreads them out until they are evenly distributed (Fig. 4.12). The overall result is that the molecules move from areas of high concentration to areas of low concentration. This process is called **diffusion**.

Whenever the internal composition of a cell differs from that on the outside, substances will tend to move in or out of the cell by diffusion. If the surrounding seawater contains more sodium, say, than the cell's interior, sodium will tend to diffuse into the cell. If the organism is sensitive to sodium, this presents a problem. Similarly, substances that are concentrated inside cells tend to diffuse out. Many of the cell's precious molecules like ATP, amino acids, and nutrients are much more concentrated in the cell than in seawater. Therefore, they tend to leak out of the cell.

One answer to this problem is to have some kind of barrier that prevents materials from diffusing in and out. The cell membrane is just such a barrier. It blocks the passage of the common ions in seawater, as well as many organic molecules. The membrane cannot be a complete barrier, however, because the cell needs to exchange many materials-like oxygen and carbon dioxide-with its surroundings. The cell membrane is selectively permeable; that is, it allows some substances to enter and leave the cell but prevents others from doing so. Water and other small molecules pass readily through the cell membrane, for example, whereas ATP and many proteins do not.



**FIGURE 4.13** Osmosis. If there is more dissolved material, and therefore less water, inside a cell than outside (*a*), water will move into the cell by osmosis (a special case of diffusion). The cell will swell until it bursts. If the internal and external concentrations are the same (*b*), water moves in and out of the cell equally, and the cell stays in balance. When the outside water is *more* concentrated (*c*), the cell loses water by osmosis and shrivels.

The selective permeability of the cell membrane solves the problem of diffusion of ions and organic molecules, but it creates a new problem. Like any other molecule, water will diffuse from areas where it is concentrated to areas of lower concentration. If the total concentration of solutes inside the cell is higher than that outside, the concentration of water will be lower. Because water molecules are free to cross the cell membrane, they will stream into the cell, causing it to swell (Fig. 4.13). On the other hand, the cell will tend to lose water and shrivel if the total salt concentration outside the cell is higher than that inside. The diffusion of water across a selectively permeable membrane is known as osmosis.

Diffusion and osmosis always move materials from high concentration to low. The selective permeability of the cell membrane can control this movement, but not reverse it. Cells often need, however, to move materials in the opposite direction. They may, for example, need to rid themselves of excess sodium even though the seawater outside is more concentrated than the inside of the cell, or to take up sugars and amino acids from the surroundings even though they are already more concentrated inside the cell. In the process of **active transport**, proteins in the cell membrane pump materials in the opposite direction to which they would move by diffusion. This process requires energy, in the form of ATP. Active transport is so important that it represents over one-third of cells' total energy expenditure.

Diffusion is the movement of ions and molecules from areas of high concentration to areas of low concentration. Osmosis is the diffusion of water across a selectively permeable membrane. In active transport the cell uses energy to move materials in the opposite direction to diffusion.

•

## Regulation of Salt and Water Balance

Marine organisms have adapted to the problems of maintaining the proper balance of water and salts in various ways. Actually, some do not actively maintain salt and water balance at all; their internal concentrations change as the salinity of the water changes (see Fig. 12.6). Such organisms are called **osmoconformers**. Osmoconformers often have to stay where the salinity of the water matches that of their fluids. Outside a narrow range of salinity, they experience osmotic problems. If placed in fresh water, they would swell up and burst because of the osmotic flow of water into their tissues. In areas such as the open ocean, where salinity doesn't fluctuate much, osmoconformers have few difficulties.

Other marine organisms osmoregulate, or control their internal concentrations to avoid osmotic problems. One way they adapt to different salinities is by adjusting the concentration of solutes in their body fluids so that the overall concentration of their fluids matches that of the water outside. It doesn't matter if there are the same dissolved chemicals inside and out as long as the total amount of dissolved material is the same. Therefore, some organisms osmoregulate by changing the amount of just one particular chemical to match changes in the salinity outside. Sharks, for example, increase or decrease the amount of a chemical called urea in their blood (see Fig. 8.18). A onecelled marine alga called Dunaliella uses a different chemical, glycerol, to do the same thing. Dunaliella may be the champion osmoregulator. It can maintain its water balance in water ranging from nearly fresh to more than nine times saltier than normal seawater.

By contrast, many osmoregulators maintain blood concentrations that are different from the surrounding seawater. Most marine fishes have body fluids considerably more dilute than seawater (Fig. 4.14a) and tend to lose water by

**Ions** *Atoms* or groups of atoms that have a positive or negative charge. The most common ions in seawater are chloride, sodium, and potassium.

Chapter 3, p. 46

Salinity The total amount of *salts* dissolved in water. Salts are combinations of ions. Solute Ions, organic molecules, or anything else that is dissolved in a solution.

*Chapter 3*, *p. 47* 

Salts pass

through gut

(a) Marine fish

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osmosis. They replace the lost water by drinking seawater. They also conserve water by producing only a very small amount of urine. Some of the excess salts that are taken in with the seawater they drink are never absorbed and pass right through the gut, but some salts are absorbed. Marine fishes must actively rid themselves of, or **excrete**, these excess salts. Some salts are excreted in the urine, but because so little urine is produced this is not enough. Most of the excess salts are excreted through the the gills (see "Regulation of the Internal Environment," p. 166).

Freshwater fishes have the reverse problem: Their blood has a higher concentration of salt than the surrounding water, and they take in water by osmosis. Their adaptations are opposite those of marine fishes (Fig. 4.14b).

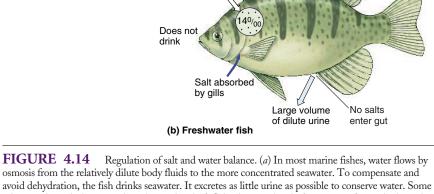
Marine birds and reptiles, and some marine plants, also have special cells or glands to rid themselves of excess salt (Fig. 4.15). Marine plants and most algae have the added advantage of a fairly rigid cell wall that helps them resist the swelling caused by osmotic water gain.

## Temperature

Organisms are greatly affected by temperature. Metabolic reactions proceed faster at high temperatures and slow down dramatically as it gets colder. A general rule of thumb is that most reactions occur about twice as fast with a  $10^{\circ}$ C ( $18^{\circ}$ F) rise in temperature. At extreme temperatures, however, most enzymes cease to function properly.

Most marine organisms are adapted to live in particular temperature ranges. Many polar species, for instance, have enzymes that work best at low temperatures, and they cannot tolerate warm water. The reverse is true of many tropical species. As a result, temperature plays a major role in determining where different organisms are found in the ocean (Fig. 4.16).

All organisms generate heat through their metabolism, but most are **ectotherms**, meaning that this heat is quickly lost to the environment and has little effect upon body temperature. They are commonly known as "cold-blooded." As a result, all ectotherms are also **poikilotherms**. This



Salts excreted

Water gain

ov osmosis

by gills

00/00

Drinks

seawater

Water loss

by osmosis

Small volume

of relatively

salty urine

osmosis from the relatively dilute body fluids to the more concentrated seawater. To compensate and avoid dehydration, the fish drinks seawater. It excretes as little urine as possible to conserve water. Some salts pass through the gut without being absorbed. Salts that are absorbed are excreted, mostly through the gills but also in the urine. (*b*) Freshwater fishes are in the reverse situation: The outside water has a very low salinity, so they tend to gain water by osmosis. To avoid swelling up, they refrain from drinking and produce large amounts of dilute urine. Salts are absorbed by the gills to replace those lost in the urine.



**FIGURE 4.15** Sea turtles have glands near the eyes that excrete excess ions, producing salty "tears." This is a hawksbill turtle (*Eretmochelys imbricata*).

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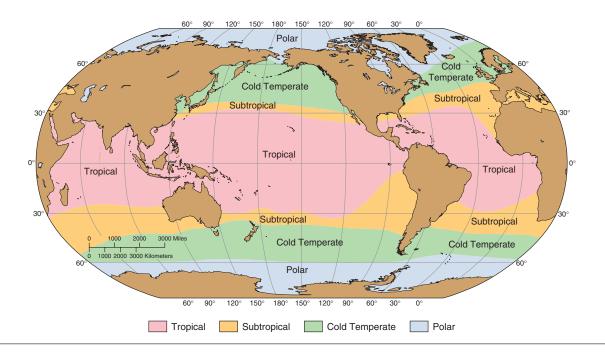


FIGURE 4.16 Marine organisms are often restricted to specific regions that correspond to average water temperatures. The major divisions are the polar, cold temperate, subtropical (or warm temperate), and tropical regions. The boundaries of these regions are not absolute and change slightly with the seasons and shifts in current patterns.

means that as the temperature of the surrounding water rises and falls so does their body temperature, and consequently their metabolic rate. Many such animals become quite sluggish in unusually cold water.

The slowing down caused by cold water is a disadvantage for highly active animals. Some large fishes, like certain tunas and sharks, can retain the metabolic heat produced by their large muscles (see "Swimming: The Need for Speed," p. 338). This enables them to maintain body temperatures that are considerably warmer than the surrounding water, and thus to remain active even in cold water and to move over broader geographic areas. These fishes are **endotherms**, meaning that their metabolic heat significantly affects their body temperature.

Mammals and, to a lesser extent, birds, are able to keep their body temperatures more or less constant even when the external temperature varies. They are called **homeotherms**, or "warm blooded." Like the fishes mentioned in the previous paragraph, they are endotherms and retain metabolic heat. More importantly, they control their metabolism, producing heat when needed by burning up fats and other energy-rich molecules. The heat maintains a warm body temperature in cold water. This allows them to remain highly active regardless of water temperature, but it also uses up a lot of energy. To reduce the "heat bill"—the energy cost of maintaining their body temperatures mammals and birds are often insulated with feathers, hair, or blubber.

## Surface-to-Volume Ratio

Adaptations to salinity and temperature are needed because salts and heat can flow in and out of organisms—if organisms were not affected by their environment, they would not have to adapt. Organisms also exchange nutrients, waste products, and gases. Such materials often move in and out across the surface of marine organisms, so the amount of surface area is very important. More precisely, it is the amount of surface area relative to the total volume of an organism—in other words, the **surface-to-volume ratio**, or **S/V ratio**—that determines how rapidly heat and materials flow in and out. One thing that determines the S/V ratio is the size of the organism. As organisms grow larger, their volume increases faster than their surface area. Small organisms have a larger S/V ratio than big ones (Fig. 4.17). Small organisms, especially single-celled ones, can therefore rely on simple diffusion across their surfaces for the exchange of materials. Larger organisms must develop supplementary mechanisms, like respiratory and excretory systems.

## **PERPETUATING LIFE**

One of the most basic characteristics of living things is the ability to reproduce to generate offspring similar to themselves. Any life form that failed to replace itself with new individuals of its own kind would soon vanish from the planet. It is only by reproducing that a species ensures its own survival.

Organisms must do two things when they reproduce. First, they must produce new individuals to perpetuate the species. Second, they must pass on to this new

S/V ratio

Surface area

Volume

FIGURE 4.17 A cube that is 1 cm on a side (top) has a volume of 1 cm<sup>3</sup> and, because it has six sides, a surface area of 6 cm<sup>2</sup>. Eight such cubes (middle) will, of course, have both eight times the volume and eight times the surface area, so the ratio of the surface area to the volume of the cubes, or surface-to-volume (S/V) ratio, will stay the same: 1/6. If the eight cubes are combined into a single large one (bottom), half the surfaces are hidden in the interior. The S/V ratio, like the surface area, is reduced by half, to 1/3. A large cube, therefore, has a lower S/V ratio than a small one.

generation the characteristics of the species in the form of genetic information. The transfer of genetic information from one generation to the next is called heredity.

Given the amazing variety of organisms that inhabit the earth, it should not surprise you that organisms achieve the first objective, the production of offspring, in many different ways. What is a little surprising is that there are relatively few ways through which organisms pass on genetic information. This similarity of hereditary mechanisms is evidence that living things are all fundamentally related.

## Modes of Reproduction

The only way that individual cells reproduce is by dividing to form new daughter cells (Fig. 4.18). In prokaryotes, where the DNA that carries the genetic information is not enclosed in a nucleus, the cell divides into two new ones by a simple process called cell fission. Before dividing, the cell copies, or replicates, its DNA. Each daughter cell gets one of the copies, as well as the rest of the cellular machinery it needs to survive.

In eukarvotes the DNA lies on several different chromosomes. Before a cell

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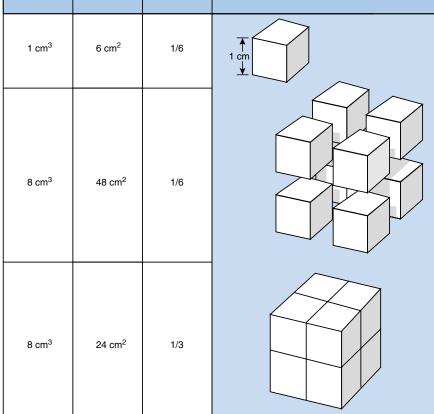
FIGURE 4.18 Two cells of a microscopic organism called a dinoflagellate (Dinophysis tripos). These cells were formed by the division of a single cell. The two cells, joined here, will soon separate.

divides, each chromosome is replicated. The most common form of eukaryotic cell division, mitosis, is a complex process that takes place in the nucleus. Mitosis ensures that each daughter cell gets a copy of every chromosome. As in bacterial cell division, the end result is two daughter cells that are exact duplicates of the original, with the same genetic information.

### Asexual Reproduction

Cell division is the primary way that single-celled organisms reproduce. Because a single individual can reproduce itself without the involvement of a partner, this form of reproduction is called asexual reproduction. All forms of asexual reproduction are similar in that the offspring inherit all the genetic characteristics of the parent. They are, in fact, exact copies, or clones.

Many multicellular organisms also reproduce asexually (Fig. 4.19). Some sea anemones, for example, simply split in half to create two smaller anemones. This process is known as fission. Another common form of asexual reproduction is budding. Instead of dividing into two new individuals of equal size, the parent develops small growths, or **buds**, that eventually break away and become separate individuals. Many plants reproduce asexually by sending out various kinds of runners that take root and then sever their connection to the parent (Fig 4.19a). Because it is so common in plants, asexual



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(a)

(b)

**FIGURE 4.19** (a) Seagrasses reproduce asexually by sending out rhizomes, or "runners" that take root and form new plants. (b) Budding is a common form of reproduction in marine animals like this sponge (*Tethya*). The small, round bodies surrounded by spine-like filaments are "baby" sponges budding off their parent. They break off and are carried by currents until settling on the bottom to form a new sponge.

reproduction is sometimes called **vegetative reproduction,** even when it occurs in animals.

Asexual, or vegetative, reproduction can be performed by single individuals and produces offspring that are genetically identical to the parent.

### Sexual Reproduction

Most multicellular and some unicellular organisms reproduce part or all of the time by **sexual reproduction**, in which new off-spring arise from the union of two separate cells called **gametes**. Usually each of the gametes comes from a different parent.

Organisms that reproduce sexually have a special kind of tissue called **germ tissue**. Whereas all the other cells in the body divide only by mitosis, germ cells are capable of a second type of cell division, **meiosis**.

In most of the cells of eukaryotic organisms the chromosomes occur in pairs, with each chromosome of a pair storing similar genetic information. Such cells are said to be **diploid**, designated **2***n*. Meiosis produces daughter cells that have copies of only half the parents' chromosomes—

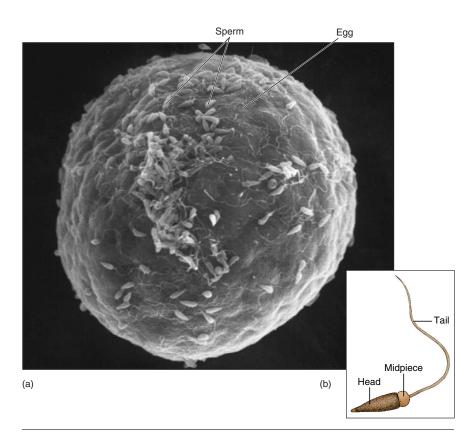
one of each pair. Cells with half the normal number of chromosomes are called haploid, designated *n* or **1***n*. The haploid daughter cells produced in meiosis are the gametes. In some seaweeds and microscopic organisms, all the gametes are the same. Most organisms, however, have two types of gametes: female gametes called eggs and male gametes called sperm. In animals the germ tissue is usually contained in gonads, the organs that produce the gametes. Ovaries are the female gonads, which produce eggs. In animals the male gonads, or testes, produce sperm. In seaweeds sperm is also produced by gonads (see Fig. 6.11), while in flowering plants sperm develop within pollen, which is produced by organs in the flower called anthers.

Eggs are large cells, usually an organism's largest (Fig. 4.20). They contain all of the cellular machinery—organelles and cytoplasm—characteristic of regular cells. The eggs of many species also contain large amounts of energy-rich yolk. Sperm, by contrast, are usually an organism's smallest cells, with almost no cytoplasm and few of the typical organelles. Sperm are little more than tiny packages of chromosomes equipped with flagella, powered by mitochondria, that enable the sperm to swim. Mitosis, the most common form of cell division, produces two daughter cells that are identical to the original cell. Meiosis, on the other hand, produces daughter cells that have half the normal number of chromosomes; that is, they are haploid. These daughter cells are called gametes. Eggs and sperm are the female and male gametes, respectively.

Sperm are attracted to eggs from the same species. When egg and sperm come into contact, they fuse; in other words, fertilization occurs. The genetic material contained in the two gametes combines. Since both haploid gametes had 1n chromosomes—or half the normal number-the fertilized egg, called a **zygote**, is back to the normal diploid, or 2*n*, number of chromosomes for the species. It has DNA from *both* parents, however, and is therefore different from either. This recombination of genetic information to produce offspring that differ slightly from their parents is the most important feature of sexual reproduction.

In sexual reproduction, eggs and sperm fuse to create a genetically distinct individual.

The fertilized egg begins to divide by ordinary mitosis. Now called an **embryo**,



**FIGURE 4.20** The egg of the variegated sea urchin (*Lytechinus variegatus*) is many times larger than sperm from the same species (*a*). Though many sperm surround the egg, only one will fertilize it. The egg contains a large amount of cytoplasm and the organelles characteristic of other cells. It also contains yolk to nourish the developing embryo. (*b*) The head of a sperm cell is made up almost entirely of the cell nucleus and contains the genetic material. The midpiece contains mitochondria that power the tail, or flagellum, with which the sperm swims.

it is nourished by the yolk. Through an extraordinarily complex process called embryological development, the embryo eventually becomes a new adult of the species. Along the way, most marine organisms pass through immature, or **larval**, stages that often look completely different from the adults (see Figs. 7.37 and 15.11).

## **Reproductive Strategies**

The goal of reproduction for any organism is to pass on its hereditary characteristics to a new generation. There is a nearly endless variety of ways to achieve this (Fig. 4.21). Some species release millions of eggs and sperm into the water, where fertilization occurs, and never see their offspring. This is called **broadcast spawning**. Others issue only a few offspring and invest a lot of time and energy in caring for them. Some species have many different larval stages, whereas others develop directly from egg to adult. Some reproduce asexually, some sexually, and some do both.

The particular combination of methods used by a given species is called its **reproductive strategy**. The strategy used by a species depends on its size, on where and how it lives, on what kind of organism it is—in fact, on just about everything about it and its environment. Learning how reproductive strategies relate to lifestyles is a common pursuit of marine biologists. www.mhhe.com/marinebiology

# THE DIVERSITY OF LIFE IN THE SEA

There are so many different living things in the sea that it almost boggles the mind. From microscopic bacteria to gigantic whales, marine organisms come in all shapes, sizes, and colors. The ways in which they live are just as varied. Making sense of all this **diversity** might seem a hopeless task. Fortunately, there is a unifying concept that helps make the bewildering diversity of life comprehensible. This concept is the theory of evolution. Remember that scientists do not use the term "theory" lightly. Evolution, the gradual alteration of a species' genetic makeup, is supported by a vast body of evidence. It is as well established as the theory of gravity. The way in which evolution occurs, on the other hand, never ceases to fascinate biologists.

# Natural Selection and Adaptation

Evolution occurs because individual organisms have genetic differences in their ability to find food and avoid being eaten, in their success at producing offspring, in metabolism, and in countless other attributes. The best-adapted individuals are those that are most successful at meeting the challenges of the environment. They will, on average, produce more offspring than those that are not so well adapted. This process was called natural selection by Charles Darwin, the nineteenth-century English naturalist who along with another Englishman, Alfred Wallace, first proposed the modern theory of evolution.

The best-adapted individuals not only will produce more offspring, but also will pass their favorable characteristics on to those offspring. The favorable traits will therefore grow more common, and over generations the population as a whole will gradually become more similar to the best-adapted individuals. Thus, the result of natural selection is that the population continually adapts to its environment; that is, it evolves.

4. Some Basics of Biology

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(a)

Natural selection occurs when some members of a population survive and reproduce more successfully than others. Evolution is the genetic change in the population that results because these more successful individuals pass their favorable characteristics on to their young.

Every population is constantly adapting to its environment. The world is an ever-changing place, however, and organisms are always being faced with new challenges. Populations either adapt to the changes in the environment or become extinct, making way for others. As a result, evolution is an endless process.

## Classifying Living Things

Since the appearance of life on earth some 3.8 billion years ago, the adaptation of various populations to different environments has produced a fantastic variety of



(b)



(c)

life forms. It is difficult to study and discuss the millions of life forms on earth unless we first classify them, or sort them into groups. One of the goals of biological classification is to give a universally accepted name to different types of organisms so that scientists from all over the world can call a species by the same name.

### The Species Concept

We have loosely defined a species as a "type" of organism, but what exactly does that mean? After all, fishes are all the same general type of animal, but a sailfish is obviously not the same species as a tuna (see Figs. 1.17 and 1.19). No definition is perfect, but here we will define species as populations of organisms that have common characteristics and can successfully breed with each other. Successful breeding means that the offspring produced are fertile and can themselves propagate the species. Dogs, to use a familiar example,

### Chapter 4 Some Basics of Biology 85



(d)

FIGURE 4.21 Marine organisms have many different reproductive strategies, a few of which are shown here. (a) Like many marine organisms, giant clams (Tridacna gigas) simply spawn into the water, a strategy known as broadcast spawning. Successful fertilization requires that other members of their species are spawning nearby and that currents will mix their eggs and sperm together. (b) Some fishes, like this yellow jawfish (Opistognathus macrognathus), carry the eggs in their mouths until they hatch. In jawfishes the males incubate the eggs. (c) Marine mammals like this New Zealand fur seal (Arctocephalus forsteri) take care of their young for much longer than most marine animals. (d) Marine plants like seagrasses flower (arrow) to reproduce. Most seagrasses have even more inconspicuous flowers than this one (Enhalus acaroides).

are all the same species because all breeds of dog—no matter how different they may look—can interbreed to produce fertile offspring. Organisms that cannot breed with each other are not members of the same species no matter how similar they look. When two populations are unable to interbreed successfully, they are said to be **reproductively isolated**.

A species is a population of organisms that share common characteristics, can breed with each other, and are reproductively isolated from other populations.

**Scientific Theory** A *hypothesis* that is accepted as "true" for the time being because it has passed test after test and is supported by a large body of evidence.

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### 86 **Part Two** Life in the Marine Environment

### Biological Nomenclature

Organisms are identified biologically by two names, their species name and the name of their genus. A genus is a group of very similar species. Dogs, for example, have the scientific name of Canis familiaris. They are closely related to other species in the genus Canis, like wolves, Canis lupus, and coyotes, Canis latrans. Similarly, the genus Balaenoptera contains several related species of whales, including the blue whale, Balaenoptera musculus; the fin whale, Balaenoptera physalus; and the minke whale, Balaenoptera acutorostrata. This two-name system is called **binomial nomenclature**. It was first introduced in the eighteenth century by the Swedish biologist Carolus Linnaeus. At that time, Latin was the language of scholars, and Latin is still used for scientific names, along with Greek. By convention, binomial names are always underlined or italicized. The first letter of the generic name, but not the species name, is capitalized. When the name of the genus has been previously mentioned it may be abbreviated. Thus, the blue whale could be identified as B. musculus.

Students often ask why biologists have to use complicated, hard-topronounce Latin or Greek names rather than ordinary common names. The trouble with common names is that they are not very precise. The same common name may be applied to different species, and the same species may have different common names. The name "spiny lobster" (Fig. 4.22), for example, is applied to many different species that are not even all in the same genus. Australians call spiny lobsters "crayfish." Americans reserve the name "crayfish" for freshwater relatives of lobsters. Things get even more confusing when people speak different languages. In Spanish, spiny lobsters are called langostas, which can also refer to grasshoppers. Another example is the name "dolphin," which is applied not only to the lovable relatives of whales, but to a delicious game fish. Dolphin fish are called *dorado* in Latin America and mahimahi in Hawai'i. At



**FIGURE 4.22** *Panulirus interruptus*, the Pacific spiny lobster, is sometimes called a rock lobster or a crayfish.

the local seafood grotto this confusion is only a minor annoyance. To biologists, however, it is absolutely essential to identify precisely whatever species they are discussing. The use of scientific names that are accepted worldwide avoids confusion.

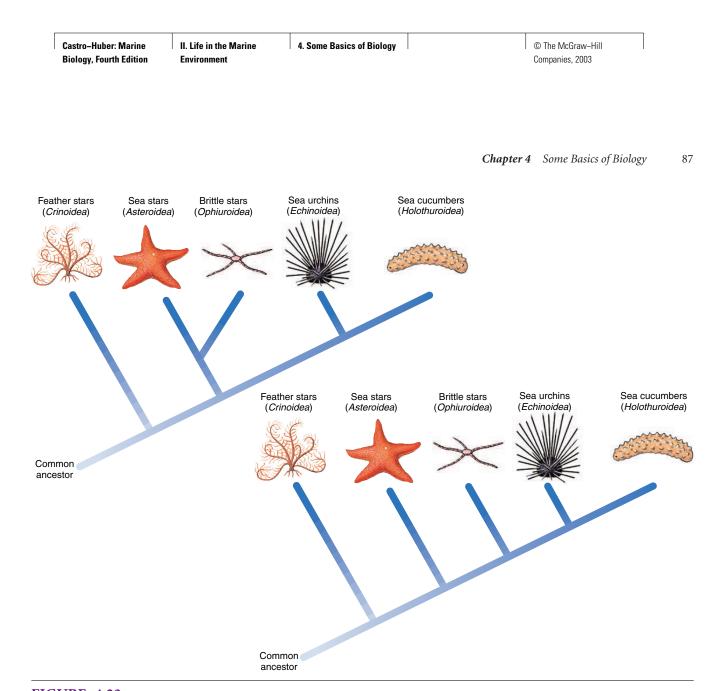
Confusion over common names can have practical implications as well. After a dive on a coral reef near Australia, one of the authors mentioned to his dive buddy that he had seen a gray reef shark. Gray reef sharks, although not so dangerous as to force you out of the water, can be aggressive and merit some attention and respect. The diving partner, who was familiar with the area, replied that the shark was not a gray reef, but a "graceful whaler." "Looks just like a gray reef shark to me," said the author but, reassured, he continued diving, blissfully ignoring the "graceful whalers" that swam by. Only later did he discover that "graceful whaler" was just a local name for the gray reef shark, Carcharhinus amblyrhynchos! (See Fig. 8.5*a*)

## Phylogenetics: Reconstructing Evolution

The goals of biological classification include not only assigning agreed-upon names to organisms, but also to group them according to their relatedness. Most people instinctively understand that a seal is related to a sea lion, for example, or that oysters and clams are related. They might be hard-pressed, though, to explain exactly what they mean by "related." To a biologist, saying that two groups of organisms are "related" means that they share a common evolutionary history, or phylogeny. In particular, it means that both groups evolved from a common ancestral species. Closely related groups evolved from common ancestors relatively recently, while the common ancestors of distantly related groups occurred further in the past. The study of such evolutionary relationships is called **phylogenetics**.

It is almost always difficult to determine the phylogenetic relationships among organisms. Very few groups have

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**FIGURE 4.23** Alternative proposals for the phylogeny of the major groups of echinoderms. Both schemes accept that feather stars diverged early from the common ancestor of all echinoderms, and that urchins and sea cucumbers are more closely related to each other than to other echinoderms. The proposals differ, however, with regard to the phylogeny of sea stars and brittle stars.

a good record of fossils that trace their evolutionary past. Usually the fossil record is incomplete or even nonexistent. Biologists have to try to piece together an organism's evolutionary history from other evidence. Body structure, reproduction, embryological and larval development, and behavior all provide clues to the past. In recent years biologists have increasingly relied on molecular studies, and in particular, on DNA and RNA sequences. Because evolution is genetic change by definition, the study of the nucleic acids that store organisms' genetic information reveals a great deal about evolutionary history. Unfortunately, different methods of studying phylogeny sometimes yield different results, and experts in a particular group often disagree about its phylogeny (Fig. 4.23). Classification schemes change and new arguments arise as fresh information comes in.

As noted previously, biological classification seeks to group organisms according to their relatedness. Species that are very closely related, for example, are grouped into the same genus. Genera with similar phylogenies can also be grouped together into a larger group, called a family. This process can be continued to sort organisms into progressively larger groups. All the members of a group, or **taxon** (plural, **taxa**), have certain common characteristics and are thought to share a common ancestry. Taxa are systematically arranged in a hierarchy that extends from the most general classification, the domain, down to the species (Table 4.2).

### The Tree of Life

For many years, all known organisms were classified as either plants (kingdom **Plantae**) or animals (kingdom **Animalia**), and the kingdom was considered the most

Table 4.2

Biological Classification of Humans (*Homo sapiens*) and the Bottlenose Dolphin (*Tursiops truncatus*)

|         | Taxonomic Level | Example     |   |
|---------|-----------------|-------------|---|
|         | Domain          | Eukaryota   |   |
|         | Kingdom         | Animalia    |   |
|         | Phylum          | Chordata    |   |
|         | Class           | Mammalia    |   |
| Human   | Order           | Primates    |   |
|         | Family          | Hominidae   |   |
|         | Genus           | Homo        |   |
|         | Species         | sapiens     |   |
|         | Domain          | Eukaryota   |   |
| Dolphin | Kingdom         | Animalia    |   |
|         | Phylum          | Chordata    | A CONTRACTOR OF                           |
|         | Class           | Mammalia    |   |
|         | Order           | Cetacea     |   |
|         | Family          | Delphinidae | Tursiops truncatus, the bottlenose dolphi |
|         | Genus           | Tursiops    |   |
|         | Species         | truncatus   |   |

general taxon in biological classification. As biologists learned more about the living world, however, they discovered many organisms that didn't fit this neat, two-kingdom system. To take this new information into account, the classification scheme was changed to recognize additional kingdoms. A system of five kingdoms came to be widely accepted. In addition to the Animalia and Plantae, this system includes fungi (kingdom Fungi), protists (kingdom Protista), and prokaryotes (kingdom Monera). The fungi are multicellular, somewhat plantlike organisms with unique characteristics that separate them from both plants and animals. Protists are an extremely

varied group of organisms, some plantlike, others animal-like, that include both unicellular organisms and the multicellular seaweeds. According to this five-kingdom system, the prokaryotic Monera consists of bacteria.

In recent years, studies of the RNA and cellular chemistry of prokaryotes have led biologists to conclude that there are two main groups of prokaryotes that are as different from each other as they are from all eukaryotic organisms (see "Prokaryotes," p. 92). To recognize this, some classification systems place these two groups of prokaryotes into two new kingdoms, the **Bacteria** (sometimes called Eubacteria or "true bacteria") and the Archaea (sometimes called Archaebacteria). Other systems recognize a new taxon, the domain, that is even more general than the kingdom; in this system the Bacteria and Archaea are separate domains that each include a number of different kingdoms. In this text we use the three-domain system of classification (Fig. 4.24), but not all biologists agree with this system.

It is not clear whether **viruses** should be included in this system because biologists do not agree on whether they are alive or not. Viruses are extremely simple, made of only nucleic acids and protein, but they can reproduce. Viruses are best known for causing disease.

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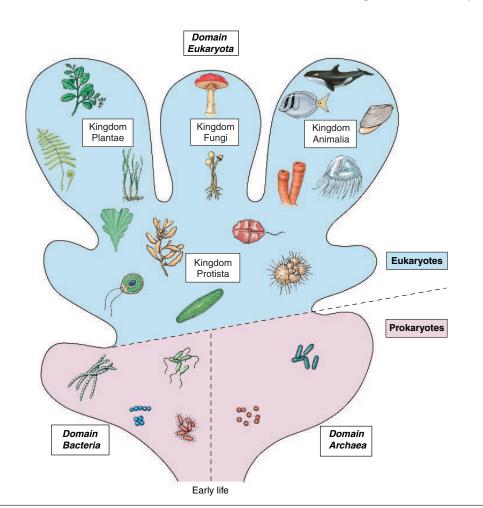


FIGURE 4.24 The tree of life.



# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

# **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. During the day, algae carry out both photosynthesis and respiration, but at night, when there is no light, they can only perform respiration. Small, isolated tide pools on rocky shores are often inhabited by thick growths of seaweeds, which are algae. Would you expect the amount of oxygen in the water to differ between night and day? How?
- 2. The cells of some marine organisms are known to have high concentrations of ions found in minute amounts in seawater. Could these organisms accumulate the ions by diffusion? Formulate a hypothesis to explain how this accumulation is accomplished. How might this hypothesis be tested?

## **For Further Reading**

Some of the recommended readings listed below may be available online. These are indicated by this symbol (, and will contain live links when you visit this page in the Online Learning Center.

## **General Interest**

- Brown, G. C., 2000. Symbionts and assassins. *Natural History*, vol. 109, no. 6, July–August, pp. 66–71. Mitochondria are the source of our energy—and perhaps our mortality as well.
- De Duve, C., 1996. The birth of complex cells. *Scientific American*, vol. 274, no. 4, April, pp. 38–45. More information on how eukaryotic cells arose from symbiosis among primitive bacteria.
- Dicks, L., 2000. The creatures time forgot. New Scientist, vol. 164, no. 2209, 23 October, pp. 36–39. Species such as the horseshoe crab and coelocanth have not changed much for hundreds of millions of years.
- Doolittle, W. F., 2000. Uprooting the tree of life. *Scientific American*, vol. 282, no. 2, February, pp. 90–95. Recent controversies about the phylogeny of living organisms are explored.
- Ingber, D. E., 1998. The architecture of life. *Scientific American*, vol. 278, no. 1, January, pp. 30–39. The structure of the cytoskeleton—the internal scaffolding of cells—is

based on the same principles as abstract sculpture, geodesic domes, and a giraffe's neck.

Lewin, R., 1998. Family feuds. New Scientist, vol. 157, no. 1998, 24 January, pp. 36–40. The bodies of organisms and their molecules tell us different things about the tree of life.

## In Depth

- Bramhill, D., 1997. Bacterial cell division. *Annual Review of Cell* and Developmental Biology, vol. 13, pp. 395–424.
- Brower, A. V., R. DeSalle and A. Vogler, 1996. Gene trees, species trees, and systematics: A cladistic perspective. *Annual Review of Ecology and Systematics*, vol. 27, pp. 423–450.
- De Weer, P., 2000. A century of thinking about cell membranes. Annual Review of Physiology, vol. 62, pp. 919–926.
- Dutta, A. and S. P. Bell, 1997. Initiation of DNA replication in eukaryotic cells. *Annual Review of Cell and Developmental Biology*, vol. 13, pp. 293–332.
- Williams. D. M. and T. M. Embley, 1996. Microbial biodiversity: Domains and kingdoms. *Annual Review of Ecology and Systematics*, vol. 27, pp. 569–595.
- Woese, C. R., O. Kandler and M. L. Wheelis, 1990. Towards a natural system of organisms: Proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences of the USA*, vol. 87, pp. 4576–4579.

## See It in Motion

Video footage of the following animals and their behaviors can be found for this chapter on the Online Learning Center:

• Sea cucumber releasing sperm (Papua New Guinea)

# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

Chemistry of biology

• Prokaryotes and eukaryotes

- Aerobic respirationPhotosynthesis
- Cell theory
  - Primary productivity
  - Classification and phylogeny of animals
  - Methods of classification
- The cell membrane Cellular respiration

Cellular organelles

# Quiz Yourself

DNA

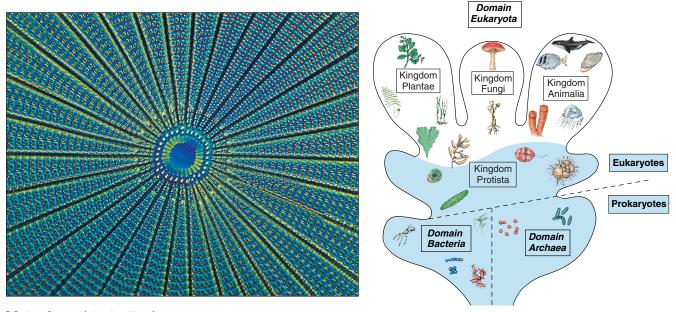
### Take the online quiz for this chapter to test your knowledge.

5. The Microbial World

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# The Microbial World





Marine diatom (Arachnodiscus).

This chapter, the first in our survey of life in the ocean, is devoted to marine microorganisms, which are easily the most abundant forms of marine life. Microorganisms live everywhere in the ocean, from the deepest trenches to the highest tide pools. The microbial world includes an incredibly diverse assortment of organisms, and new microorganisms are discovered regularly. Except for being small, the various groups of microorganisms discussed in this chapter have little in common. All three biological domains, the most basic divisions of life (see "The Tree

of Life," p. 87), include microorganisms. The diversity of the microbial world can be bewildering even to biologists. Indeed, much of the scientific debate about how to group organisms into kingdoms within domains centers on microorganisms. One thing is for sure: The familiar concepts of "plants" and "animals" have been modified in classification schemes that consist of more than two kingdoms.

Though marine microorganisms include some of the smallest and structurally simplest organisms on earth, they have played critical roles in the evolution of life on our planet. Without them, the world we live in would be very different. Microorganisms are the most important **primary producers** in many marine environments, and directly or indirectly feed most marine animals. Some microorganisms make essential nutrients

**Primary Producers** Organisms that manufacture organic matter from CO<sub>2</sub>, usually by photosynthesis.

Chapter 4, p. 73

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# Table 5.1

Chemical Compounds Used in the Characterization of Marine Photosynthetic Organisms

|                                    | Photosynthetic Pigments                              | Major Storage Products | Major Cell-Wall Components               |
|------------------------------------|--|------------------------|--|
| Bacteria (except<br>Cyanobacteria) | Bacteriochlorophyll a, b, c, d, e                    | Variety of types       | Peptidoglycan containing<br>muramic acid |
| Cyanobacteria                      | Chlorophyll a  | Cyanophycean starch    | Chains of amino sugars and amino acids   |
|                                    | Phycobilins (phycocyanin, phycoerythrin, and others) | Cyanophycin (protein)  |  |
|                                    | Carotenoids  |                        |  |
| Archaea                            | Bacteriorhodopsin                                    | Variety of types       | Variety of types, no muramic acid        |
| Diatoms                            | Chlorophyll <i>a</i> , <i>c</i>                      | Chrysolaminarin        | Silica                                   |
|                                    | Carotenoids  | Oil                    | Pectin                                   |
| Dinoflagellates                    | Chlorophyll <i>a</i> , <i>c</i>                      | Starch                 | Cellulose                                |
|                                    | Carotenoids  | Oil                    |  |
| Green algae                        | Chlorophyll <i>a</i> , <i>b</i>                      | Starch                 | Cellulose                                |
|                                    | Carotenoids  |                        | Carbonates in calcareous algae           |
| Brown algae                        | Chlorophyll <i>a</i> , <i>c</i>                      | Laminarin              | Cellulose                                |
|                                    | Carotenoids (fucoxanthin, and others)                | Oil                    | Alginates                                |
| Red algae                          | Chlorophyll a  | Starch                 | Agar                                     |
|                                    | Phycobilins (phycocyanin,                            |                        | Carrageenan                              |
|                                    | phycoerythrin)                                       |                        | Cellulose                                |
|                                    | Carotenoids  |                        | Carbonates in coralline algae            |
| Flowering plants                   | Chlorophyll <i>a</i> , <i>b</i>                      | Starch                 | Cellulose                                |
|                                    | Carotenoids  |                        |  |

available to other primary producers, either for the first time or by recycling them. Others swim about in the water to ingest food very much like animals do, and play critical roles in marine food chains.

## PROKARYOTES

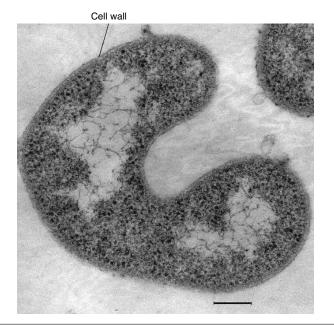
**Prokaryotes** are the smallest and structurally simplest organisms, and the oldest forms of life on earth. Nonetheless, they carry out nearly all the chemical processes performed by supposedly more complex organisms—most of which evolved in prokaryotes in the first place—as well as some that are unique to prokaryotes. Prokaryotes cells are enclosed by a protective **cell wall**. The **plasma membrane**, or **cell membrane**, lies immediately inside the cell wall (see Fig. 4.7). In addition to lacking membrane-bound organelles, prokaryotes differ from eukaryotes in the circular shape of the DNA molecules that encode their genetic information, in the size of their ribosomes, and in a number of other ways.

Despite their similarities, the two prokaryotic domains, **Bacteria** and **Archaea**, also have important differences, including the chemistry of their cell walls (Table 5.1) and plasma membranes, and the cellular machinery that manufactures proteins. In fact, genetic analyses indicate that bacteria and archaea are as different from each other as they are from humans!

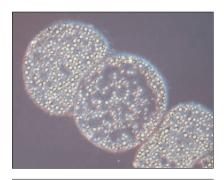
# Bacteria

**Bacteria** (domain **Bacteria**) appear to have branched out very early on the tree of life and are genetically distant from both archaea and eukaryotes. Because they are prokaryotes, bacteria (singular, **bacterium**), have remained structurally simple, but they have evolved a great range of metabolic abilities and chemical features. They are abundant in all parts of the ocean.

Bacterial cells have many shapes, including spheres, coils, rods, or rings (Fig. 5.1) depending on the species. The cells are very small (see Appendix A for relative size), much smaller than those of single-celled eukaryotes. About 250,000 average bacterial cells would fit on the period at the end of this sentence. There are



**FIGURE 5.1** A high-magnification photograph taken with an electron microscope showing *Cyclobacterium marinus*, a ring-forming marine bacterium. The bar represents 0.1 micron (µm).



**FIGURE 5.2** Three cells of *Thiomargarita namibiensis*, the largest bacterium known so far. Cells can be 0.75 mm (0.03 in) wide. The round, white structures are sulfur granules.

exceptions, however, such as a sediment bacterium discovered off Namibia, southwest Africa, with cells in filaments as wide as 0.75 mm (0.03 in), large enough to be seen with the naked eye (Fig. 5.2)! Another giant bacterium (0.57 mm or 0.02 in long) is found inside the intestines of a coral reef fish.

The unique chemistry of bacterial cell walls (Table 5.1) makes them rigid

and strong. A stiff or gelatinous covering often surrounds the cell wall as additional protection or a means to attach to surfaces.

Bacteria can grow to extremely high numbers in favorable environments such as sediments or decomposing organic matter. In large numbers, marine bacteria are sometimes visible as iridescent or pink patches on the surface of stagnant pools in mudflats and salt marshes. Sometimes gigantic strands of cells can be seen as whitish hairs on rotting seaweed.

### Heterotrophic Bacteria

Most bacteria, like animals, are **heterotrophs** and obtain their energy from organic matter. Most of these bacteria are **decomposers**, which break down waste products and dead organic matter and release nutrients into the environment. These bacteria, the **decay bacteria**, are vital to life on earth because they ensure the recycling of essential nutrients. They are found everywhere in the marine environment—on almost all surfaces as well as in the water column. They are especially abundant in bottom sediments,

### Chapter 5 The Microbial World 93

which are usually rich in organic matter. All organic matter is sooner or later decomposed, though in very deep, cold water the process is slower than elsewhere (see "Bacteria in the Deep Sea," p. 374).

Decay and other types of bacteria play a crucial role because they constitute a major part of the organic matter that feeds countless bottom-dwelling animals. Even many organic particles in the water column are composed mostly of bacteria. Marine bacteria are also important in recycling dissolved organic matter in oceanic food webs (see "The Microbial Loop," p. 343). Other marine bacteria are beneficial because they are involved in degrading oil and other toxic pollutants that find their way into the environment. The same process of decomposition is unfortunately involved in the spoilage of valuable fish and shellfish catches.

### Autotrophic Bacteria

Autotrophic bacteria make their own organic compounds and thus are primary producers. Some of them are **photosynthetic** (or **photoautotrophs**; see Fig. 4.7). They contain chlorophyll or other photosynthetic pigments (Table 5.1) and, like seaweeds and plants, tap light energy to manufacture organic compounds from  $CO_2$ . Photosynthetic bacteria are now known to account for much of the primary production in many open-ocean areas. The biochemistry of bacterial photosynthesis, however, is different from that of algae and

**Prokaryotes** Organisms with cells that do not have a nucleus or other organelles.

Chapter 4, p. 74; Figure 4.7

**Eukaryotes** Organisms with cells that contain a nucleus and other organelles that are enclosed by membranes.

Chapter 4, p. 74; Figure 4.8

Heterotrophs Organisms that cannot make their own food and must eat the organic matter produced by autotrophs. Autotrophs Organisms that can use energy (usually solar energy) to make organic matter.

Chapter 4, p. 72

5. The Microbial World

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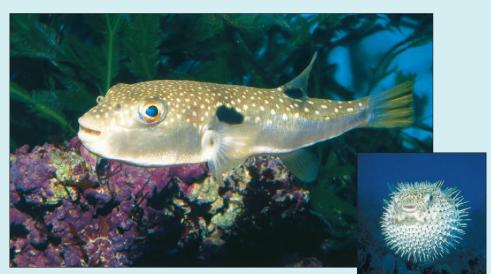
#### 94 Part Two Life in the Marine Environment



# SYMBIOTIC BACTERIA—THE ESSENTIAL GUESTS

Some bacteria live in close, or symbiotic, associations with other marine organisms. Some symbiotic bacteria are parasites that may ultimately cause a disease. Others, on the other hand, benefit their hosts. These symbiotic bacteria began their association by increasing the chances of survival of the host and evolve to become essential-hosts cannot survive without them. In many cases the symbiotic bacteria are even sheltered in special tissues or organs that evolve in the host.

All eukaryotic organisms, including humans, shelter bacteria without which life would be impossible. The chloroplasts and mitochondria of eukaryotic cells evolved from symbiotic bacteria (see "From Snack to Servant: How Complex Cells Arose,"



A Japanese pufferfish, or fugu (Takifugu niphobles), and an inflated pufferfish (Diodon histrix).

p. 77). Indeed essential, these bacteria have become an integral part of all complex cells.

There are many cases of symbiotic bacteria among marine organisms. Symbiotic bacteria, for example, are involved in digesting the wood that is ingested by shipworms (Teredo), which happen to be bivalve molluscs, not worms. Like all wood-eating animals, shipworms lack cellulase, the enzymes needed to digest cellulose, the main component of wood. Wood is a surprisingly common habitat in many marine environments, and so everything from driftwood to boat bottoms is exploited by shipworms thanks to their symbiotic bacteria.

Symbiotic bacteria are also responsible for the light, or bioluminescence, that is produced by some fishes, squids, octopuses, and other animals of the deep (see "Bioluminescence," p. 365). The bacteria are usually sheltered in special light-producing organs, or photophores. These deep-sea animals, which live in darkness, use light to communicate with other members of their species, lure prey, blend with the light that filters from the surface, and for other functions. Flashlight fishes (Anomalops), which live in shallow tropical waters, lodge their symbiotic bacteria in an organ beneath each eye. A shutter mechanism controls the emission of light so that the fish are provided with the ability of "blinking" at night! Groups of fish blink in synchrony, a behavior that is involved in attracting prey.

Chemosynthetic bacteria symbiotic with mussels, clams, and tube worms that live around deep-sea hydrothermal vents have a very particular role: manufacturing organic matter from CO2 and the abundant hydrogen sulfide (H2S) from the vents. The symbiotic bacteria live in a special organ, the feeding body, of the giant hydrothermalvent tube worm Riftia (see Fig. 16.31).

Symbiotic bacteria are also involved in some unexpected ways. Pufferfishes are known to store a toxin that is deadly to any predators (or humans) who eat the fish. The fish, or fugu, is a delicacy in Japan. Licensed chefs must prepare the fish, otherwise the toxin (tetrodotoxin) will kill anyone feasting on fish that has been improperly prepared. Tetrodotoxin is a deadly neurotoxin (that is, it affects the nervous system). In fact, it is one of the most powerful poisons known, and there is no antidote! The deadly toxin is stored mostly in the liver and gonads of the fish, so the internal organs must be expertly removed. Mistakes do happen and numerous deaths (including the suicides of disgraced cooks) take place every year in Japan. Cooks may still be guilty, but not the puffers: The toxin is now known to be produced not by the fish but by symbiotic bacteria. No one knows yet how the fish is immune to the bacteria toxins.

Tetrodotoxin and very similar toxins have also been found in a variety of marine organisms such as flatworms, snails, crabs, sea stars, and several species of fishes. It has also been found in the blue-ring octopus, a notoriously toxic animal. We are not yet sure if in all of these animals the toxin is produced, as in *fugu*, by symbiotic bacteria or if it is accumulated from their food. Tetrodotoxin of an unknown source has also been found in dead sea urchins and is suspected as their cause of death.

The production of powerful toxins that are used by other organisms is just one example of the amazing abilities of bacteriainvisible to the eye but powerful giants when it comes to their role in the environment.

plants, and varies considerably among different groups of bacteria. Some bacteria, for example, have a kind of chlorophyll unique to prokaryotes and produce sulfur (S) instead of oxygen ( $O_2$ ).

Other bacterial autotrophs, called **chemosynthetic** or **chemoautotrophic**, derive energy not from light but from chemical compounds such as hydrogen (H<sub>2</sub>), ammonia (HN<sub>3</sub>), **hydrogen sulfide** (H<sub>2</sub>S), and other sulfur or iron compounds. Many other ways of obtaining energy to manufacture organic matter are found among chemosynthetic bacteria.

Bacteria are structurally simple microorganisms that are especially significant as decomposers, breaking down organic compounds into nutrients that can be used by other organisms. They are also an important food source and help degrade pollutants. Some species are autotrophic, and account for much of the oceanic primary production.

### Cyanobacteria

Cyanobacteria, once known as bluegreen algae, are a group of photosynthetic bacteria. In addition to having chlorophyll, most contain a bluish pigment called phycocyanin (Table 5.1). Most marine cyanobacteria also have a reddish pigment, phycoerythrin. The visible color of the organism depends on the relative amounts of the two pigments. When phycocyanin predominates, the bacteria appear blue-green, when phycoerythrin predominates they appear red. Photosynthesis takes place on folded membranes within the cell (as in Fig. 4.7) rather than in chloroplasts as in eukaryotic photosynthetic organisms such as seaweeds and plants. Unlike other photosynthetic bacteria, cyanobacteria do share with eukaryotic photosynthetic organisms a type of chlorophyll, chlorophyll a (Table 5.1), and liberate gaseous oxygen in photosynthesis. Most marine cyanobacteria are microscopic, though some form long filaments, strands, or thick mats visible to the naked eye.

Cyanobacteria were perhaps among the first photosynthetic organisms on earth. They are thought to have had an im-



**FIGURE 5.3** Stromatolites, calcareous mounds deposited by cyanobacteria are frequently found as fossils. These, however, are living stromatolites growing in shallow water in the Exuma Cays, Bahama Islands.

portant role in the accumulation of oxygen in our atmosphere. Fossil **stromatolites**, massive **calcareous** mounds formed by cyanobacteria, are known to date back some 3 billion years. Stromatolites are still being formed in tropical seas (Fig. 5.3).

Many species of cyanobacteria can tolerate wide ranges of salinity and temperature and are therefore found practically everywhere in the marine environment, including some unexpected places like the hair of polar bears! Some cyanobacteria, called endolithic, burrow into calcareous rocks and coral skeletons. Others form thick, dark crusts along the wave-splashed zone of rocky coasts. Some cyanobacteria exploit oxygen-poor sediments, which may include polluted sites. Planktonic species may rapidly multiply and change the color of the water. Even some of the so-called red tides (see "Red Tides and Harmful Algal Blooms," p. 326) are caused by cyanobacteria that contain a red pigment. A few species are responsible for skin rashes on swimmers and divers.

Many cyanobacteria are known to carry out **nitrogen fixation**, converting

gaseous nitrogen  $(N_2)$  into other nitrogen compounds that can be used by other primary producers (see "Cycles of Essential Nutrients," p. 227). Some cyanobacteria live on the surface of seaweeds and seagrasses. Photosynthetic organisms that live on other algae or plants are called **epiphytes.** Some cyanobacteria live *inside* algae and are called **endophytes.** Other cyanobacteria are known to lose their ability to photosynthesize, thus becoming heterotrophs.

Cyanobacteria are photosynthetic bacteria widely distributed in the marine environment.

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**Calcareous** Made of calcium carbonate (CaCO<sub>3</sub>).

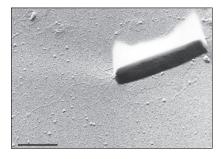
Chapter 2, p. 33

**Plankton** Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.

Chapter 10, p. 230; Figure 10.19

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**FIGURE 5.4** Pyrobacterium aerophilum is a rod-shaped marine archaeum that grows best at temperatures of 100°C. Each cell is about 0.5 microns (µm) in diameter.

## Archaea

Archaea (domain Archaea), often called archaebacteria, are the simplest, most primitive forms of life. Some look very similar to the oldest fossils ever found, cells estimated to be at least 3.8 billion years old. Like bacteria, their cells are small and may be spherical, spiral, or rod-shaped (Fig. 5.4). In fact, until recently archaea (singular, archaeum) were thought to be bacteria. It is now thought, however, that despite being prokaryotic, archaea are more closely related to eukaryotes than to bacteria.

Archaea may be heterotrophs or autotrophs and like bacteria exhibit a great variety of metabolic processes. One group, the methanogens is the only group of organisms that produces methane (CH<sub>4</sub>). They are important decomposers and extremely abundant in sediments, especially in organic-rich environments like salt marshes and mudflats. Some are nitrogen fixers. They are also important in breaking down organic matter in sewage treatment plants and landfills.

Other groups of archaea were discovered only recently, first in extreme environments on land such as hot sulfur springs, saline lakes, and highly acidic or alkaline environments. Marine archaea were subsequently found in extreme marine environments, such as in very deep water, where they survive at pressures of 300 to 800 atmospheres. Other archaea are associated with **hydrothermal vents** or coastal saltpans.

Because these groups of archaea were first known only from such extreme environments, they were thought to depend on them. Indeed, the term "extremophiles" ("lovers of extremes") became almost synonymous with archaea. Some archaea, for example, cannot grow in temperatures less than  $70^{\circ}$  to  $80^{\circ}$ C (158° to  $176^{\circ}$ F), and one species can live at 113°C (235°F), the highest of any living organism known. Others depend on extremely acid, alkaline, or salty conditions. New techniques based on detecting nucleic acid sequences characteristic of archaea, however, have shown that they are exceedingly common in the water column and other marine environments (see "Tiny Cells, Big Surprises," p. 99). Thus, the hypothesis that archaea are restricted to extreme environments was proven false.

Archaea are prokaryotic microorganisms once thought to be bacteria, but are more closely related to eukaryotes. Most were thought to be restricted to extreme environments but are now known to be very common in the water column and elsewhere.

## UNICELLULAR ALGAE

Algae (singular, alga) are a very diverse group of simple, mostly aquatic (that is, marine and freshwater), mostly photosynthetic organisms. They are eukaryotic, and as such their cells contain organelles enclosed by membranes. Photosynthesis takes place in chloroplasts-green, brown, or red organelles with layers of internal membranes that contain photosynthetic pigment (see Fig. 4.8b). The color of algae is a reflection of the pigments and their concentration. In contrast to the land plants with which we are familiar, algae lack flowers and have relatively simple reproductive structures. Their nonreproductive cells are also mostly simple and unspecialized. Algae lack true leaves, stems, and roots.

Biologists used to refer to algae as plants. Many of the unicellular algae, however, show animal-like characteristics. Some swim by moving their flagella. Distinguishing these free-swimming algae from some of the structurally sim-

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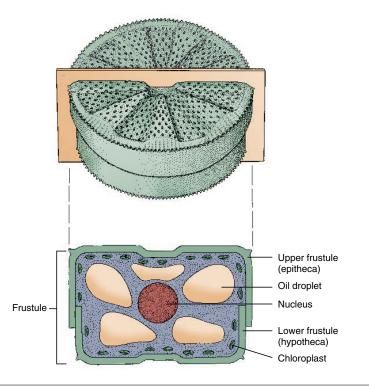
pler animals becomes rather difficult, especially when there are species that carry out photosynthesis like plants, and very similar ones move and eat food particles like animals. Some are claimed by both botanists (plant biologists) and zoologists (animal biologists)! These unicellular organisms are grouped in a separate kingdom, **Protista**. Seaweeds, though multicellular, are algae that are generally placed in the kingdom Protista mostly because they lack the specialized tissues of plants. Seaweeds, together with other multicellular primary producers, the marine plants, are discussed in Chapter 6.

Algae are protists. They are mostly aquatic primary producers that lack the specialized tissues of plants. They range in size and complexity from single cells to large multicellular seaweeds.

## Diatoms

Diatoms (phylum Bacillariophyta) are unicellular, though many species aggregate into chains or star-like groups. Diatom cells are enclosed by cell walls made largely of silica (SiO<sub>2</sub>), a glass-like material (Table 5.1). This glassy shell, or frustule, consists of two tightly fitting halves often resembling a flat, round, or elongate box (Fig. 5.5). The frustule typically has intricate perforations and ornaments such as spines or ribs, making diatoms strikingly beautiful when seen under a microscope (see figure on page 91). The frustule allows light to pass through, so that the conspicuous golden-brown chloroplasts can capture light energy for photosynthesis. The minute perforations allow dissolved gases and nutrients to enter and exit. The sinking of open-ocean diatoms below the well-lit surface layer is often slowed by oil droplets in their cells and spines on the frustules. (see "Staying Afloat," p. 333).

The characteristic color of diatoms is due to yellow and brown **carotenoid** pigments present in addition to two types of chlorophyll, a and c (Table 5.1). Diatoms are efficient photosynthetic factories, producing much-needed food (the food being the diatoms themselves), as well as oxygen for other forms of life. They are very important open-water primary producers in



**FIGURE 5.5** Diagrammatic representation of a diatom cell (also see Fig. 15.3).

temperate and polar regions (see "Epipelagic Food Webs," p. 341). In fact, billions of diatom cells in the ocean account for a hefty share of the organic carbon and oxygen produced on planet earth.

Around half the estimated 12,000 living species of diatoms are marine. Most are planktonic, but many produce a stalk-like structure for attachment to rocks, nets, buoys, and other surfaces. The brownish scum sometimes seen on mudflats or glass aquaria often consists of millions of diatom cells. Some are able to slowly glide on surfaces. A few are colorless and, having no chlorophyll, live on the surfaces of seaweeds as heterotrophs.

Diatoms are unicellular organisms that live mostly as part of the plankton. A silica shell is their most distinctive feature. They are important open-water primary producers in cold waters.

Diatoms reproduce mostly by cell division, a type of **asexual reproduction**. The overlapping halves of the frustule separate, and each secretes a new, smaller half (Fig. 5.6). Diatoms may also reproduce by **sexual reproduction.** Some cells develop eggs, others develop flagellated sperm (Fig. 5.6). Fertilization then results in the development of resistant stages known as **auxospores.** 

Favorable environmental conditions, such as adequate nutrients and temperature, trigger periods of rapid reproduction called **blooms.** This is a general phenomenon that also occurs in other algae. During blooms, most diatoms get progressively smaller, partly because they use up the silica dissolved in the water and partly because the smaller frustule becomes the larger one in many of the new cells. Full size may be regained by the development of auxospores. The auxospores eventually give rise to larger cells that display the frustule characteristic of the species.

The glassy frustules of dead diatoms eventually settle to the bottom of the sea floor. Here they may form thick deposits of siliceous material that cover large portions of the ocean floor. Such sediments are known as **diatomaceous ooze**. Huge fossil

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deposits of these sediments can now be found inland in various parts of the world. The siliceous material, or **diatomaceous earth**, is mined and used in products such as filters for swimming pools, for clarifying beer, as temperature and sound insulators, and as mild abrasives that may find their way into toothpaste.

## **Dinoflagellates**

The **dinoflagellates** (phylum **Dinoflagellata** or **Pyrrhophyta**) make up another large group of planktonic, unicellular organisms. Their most outstanding characteristic is the possession of two flagella, one wrapped around a groove along the middle of the cell (Fig. 5.7) and one trailing free. These flagella direct movement in practically any direction. Most dinoflagellates have a cell wall that is armored

**Ribosomes** Structures inside the cell, consisting of proteins and RNA, where proteins are manufactured.

Chapter 4, p. 74; Figure 4.8

**Hydrothermal Vents** Undersea hot springs associated with mid-ocean ridges and other geologically active environments. *Chapter 2, p. 38* 

**Nucleic Acids** DNA and RNA, complex molecules that store and transmit genetic information.

Chapter 4, p. 70

**Hypothesis** A statement about the world that might be true.

Chapter 1, p. 13

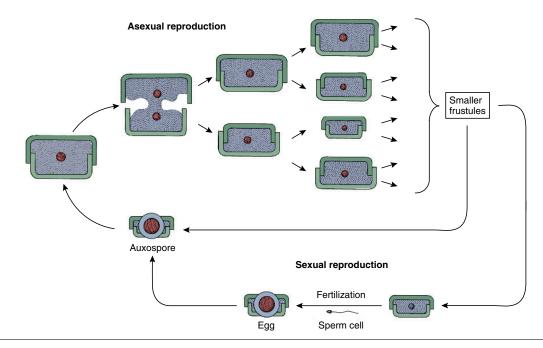
Types of reproduction:

Asexual (or *vegetative*) The production of new individuals by simple division (or other means) without involving *gametes*, so that the offspring are genetically identical to the parents.

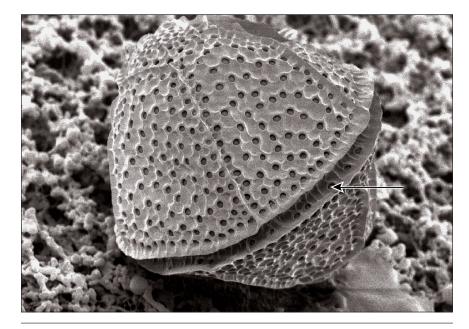
Chapter 4, p. 82

**Sexual** The production of new individuals by the formation of *gametes* (sperm and eggs), so that the offspring are genetically different from the parents. *Chapter 4, p. 83* 

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**FIGURE 5.6** The usual method of reproduction in diatoms is by cell division. Most, but not all, frustules get smaller with time. Resistant cells called auxospores are produced two ways: directly from the expansion of a smaller frustule or by sexual reproduction when an egg is fertilized by a sperm cell, both of which are liberated from separate frustules.



**FIGURE 5.7** Dinoflagellates such as *Gonyaulax polyedra* have a cell wall, or theca, that consists of cellulose plates. The theca is marked by grooves for the flagella; only one groove is visible here (arrow). This species is bioluminescent and also responsible for red tides.

with plates made of **cellulose**, the characteristic component of the cell walls of seaweeds and land plants (Table 5.1). The plates may have spines, pores, or other ornaments.

Though most dinoflagellates photosynthesize, many can also ingest food particles. A few have a light-sensitive pigment spot that acts as a crude eye. It has been suggested that during their evolution dinoflagellates gained the ability to function as primary producers by capturing and using chloroplasts from other algae. Almost all known dinoflagellates, around 1,200 living species, are marine. Dinoflagellates are important planktonic primary producers, especially in warm water.

Dinoflagellates reproduce almost exclusively by simple cell division (see Fig. 4.18). They sometimes form blooms that color the water red, reddish-brown, yellow, or other unusual shades (see "Red Tides and Harmful Algal Blooms," p. 326). Some of these dinoflagellates release toxic substances, and seafood collected during red tide periods may be poisonous. Other dinoflagellates are noted

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TINY CELLS, BIG SURPRISES

It is surprising how little biologists know about the lives of marine microbes. We know they are everywhere but we are not sure how many types there are, how common they are, and what exactly they are up to. The situation is rapidly changing as we apply new techniques and approaches studying the private lives of marine microorganisms that call the ocean home.

Information about marine microbes was traditionally gathered largely by growing them in artificial cultures inoculated with seawater samples. This information (what nutrients the microbes need to grow, the type of compounds they produce, and such) was gathered mostly from organisms collected in water samples and then grown under artificial conditions. Even worse, many organisms would not grow in the lab and their presence in the sample went undetected. At least some of this information was used by marine ecologists to deduce the role of microbes in the big ocean world-the role of decay bacteria in releasing nutrients, for example, and of bacteria that convert free nitrogen into nitrates or make dissolved organic matter (DOM) available to larger forms of life. Still, bacteria and other marine microbes remained vital but little-understood forms of life. Some groups of microbes remained undiscovered for a long time. Most archaea, for instance, have been known only since the 1970s. Certainly, other groups remain to be discovered.

The minute prokaryotic cells of bacteria and archaea and the smallest eukaryotic cells of some algae seem to be everywhere but are very difficult to collect and characterize by the microscopic examination of cells. Instead of culturing or filtering out these cells, fragments of nucleic acid (see "Nucleic Acids," p. 70) are collected from the water and **sequenced.** The presence of organisms can be detected by identifying characteristic DNA or RNA sequences. Furthermore, the partial sequences can yield information about the unique characteristics of these microbes, even if whole cells or whole nucleic acid molecules are not collected.

The presence of RNA sequences characteristic of archaea in seawater and sediment samples has shown archaea to be abundant. In 2001 two groups of archaea were found to be extremely abundant in water samples collected from depths below the photic zone, that is, where light does not penetrate (see Chapter 16). The samples, collected from the Pacific Ocean south of Hawai'i, showed that archaea were rare at the surface but sharply increased in abundance below depths of 250 m (720 ft). They were as common as bacteria below 1,000 m (3,280 ft). Judging from their numbers and the huge volume of the ocean in question, these archaea are among the ocean's most abundant forms of life.

Similar techniques based on the detection of characteristic nucleic acid sequences have been used to identify previously unknown eukaryotic microorganisms. These eukaryotes are larger than prokaryotes but still minute (smaller than 2 to 3 µm), making them difficult to collect and study. This sharply contrasts other unicellular but larger eukaryotes in the phytoplankton, which are relatively easy to collect using plankton nets (see "The Plankton: A New Understanding," p. 324). In 2001 two new groups related to dinoflagellates were discovered at depths of 250 to 3,000 m (720 to 9,840 ft) near Antarctica. Similar but unique groups of eukaryotic microorganisms (including yet another new group related to dinoflagellates) were reported at the same time by another team working at depths of 75 m (246 ft) in the tropical Pacific. The fact that these microorganisms collected in relatively shallow water (where light still penetrates) are photosynthetic adds a new dimension to the discovery. They represent a previously unknown source of primary production in typically unproductive tropical waters. Other groups of minute algae have been discovered in recent years, including three groups that are related to dinoflagellates. It will not be surprising if additional groups are discovered in the future.

for the production of light, or bioluminescence (see "The Bay of Fire," on page 100). Though bioluminescence has also been observed in some bacteria and many types of animals, dinoflagellates are generally responsible for the diffuse bioluminescence sometimes seen on the sea surface. This effect is of course seen only at night. It is especially bright if the water is disturbed by a boat or when a wave crashes on the shore.

A variety of marine animals contain in their tissues round, golden-brown photosynthetic cells known as **zooxanthellae**. These cells are actually dinoflagellates adapted to live in close association with an animal host. Though hosts range from sponges and sea anemones to giant clams, it is perhaps in reef-building corals where zooxanthellae are most significant (see Fig. 14.7). They fix carbon dioxide by photosynthesis, release organic matter used by the coral, and help in the formation of the coral skeleton (see "Coral Nutrition," p. 301).

A few highly modified dinoflagellates are parasites of seaweeds and some marine animals. Like zooxanthellae, these highly specialized forms reveal their true nature by having life cycles that include free-swimming stages resembling typical dinoflagellates.

One such dinoflagellate is *Pfiesteria*, sometimes called the "phantom dinoflagellate" because they spend most of their lives as harmless resting stages, or cysts, in the sediments. Coastal pollution in the form of excessive nutrients can trigger blooms of *Pfiesteria*, which release powerful poisonous substances that stun fishes. *Pfiesteria* and other *Pfiesteria*-like microorganisms have been linked to deadly open sores on the fishes. These parasites are also known to be harmful to crabs, oysters, and clams, and have been implicated with sores and symptoms such as temporary memory loss in humans.

**Cellulose** Complex carbohydrate characteristic of plants and other primary producers.

Chapter 4, p. 70

5. The Microbial World

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Imagine entering a quiet tropical bay at night. There are no lights on shore, and on a moonless night the spectacle is unforgettable. As the propeller of your boat churns the black water, an intense blue-green light is left behind, like an eerie trail of cool fire. Outside the bay you see a few sparks of light as you approach, but inside the bay things are very different. Long streaks of light shoot like fireworks beneath the boat. They are created by fleeing fish. A swim in the bay is even more spectacular. Your dive into the water is accompanied by a blinding flood of light, and sparks scatter out as you wave your arms.

Such light effects result from an unusual concentration of bioluminescent dinoflagellates, a natural and permanent phenomenon in a few select locations such as *Bahía Fosforescente*, or Phosphorescent Bay, in southwestern Puerto Rico.

Bioluminescent Bay might be a more apt name because the light is produced by living organisms. The bay's most important source of bioluminescence is Pyrodinium bahamense, a unicellular, photosynthetic dinoflagellate about 40 microns (µm) (0.004 cm or 0.0015 in) in diameter. As many as 720,000 individuals are found in a gallon of water, many more than outside the bay. The bay is small, about 90 acres, and fan-shaped, and it does not exceed 4.5 m (15 ft) in depth. The main reason that the dinoflagellates are concentrated here is that the bay is connected to the open sea by a narrow, shallow channel. As water containing the dinoflagellates flows into the bay, evaporation in the shallow water causes the surface water to sink because of the increase in salinity, and therefore density. Evaporation is enhanced by the dry and sunny days. The Pyrodinium stays near the surface and is therefore not carried out as the denser water flows out along the bottom of the shallow entrance. The tidal range here is only about a foot at the most, so water exchange with the outside is limited. The bay thus acts as a trap that keeps the dinoflagellates from leaving.



Bahía Fosforescente in Puerto Rico.

Of all the planktonic organisms that enter the bay, why is *Pyro-dinium* favored? A key factor seems to be the thick mangrove trees bordering the bay. They grow along the muddy shores, together with all kinds of organisms living attached to their roots. Mangrove leaves fall into the water, where intense bacterial decomposition increases the organic nutrient levels in the water. Some nutrients essential to the growth of *Pyrodinium*, perhaps vitamins, may be released by bacteria or other microorganisms.

*Bahia Fosforescente* is protected to keep the critical natural balance intact, but bioluminescence has noticeably decreased during recent years. The same phenomenon in a bay in the Bahamas disappeared when its narrow entrance was dredged to allow larger boats, with larger loads of tourists, to pass through.

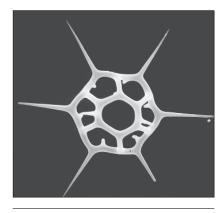
Dinoflagellates are unicellular organisms that have two unequal flagella. They are mostly marine and are particularly common in the tropics. Some are noted for their emission of light; others are closely associated with marine animals, especially reef corals.

## **Other Unicellular Algae**

Three additional groups of primary producers may be abundant in some areas. **Silicoflagellates** (phylum **Chryosphyta**) are characterized by a star-shaped internal skeleton made of silica (Fig. 5.8) and a single flagellum. **Coccolithophorids** (phylum **Haptophyta**) are flagellated, spherical cells covered with button-like structures called **coccoliths** that are made of calcium carbonate (Fig. 5.9). Coccolith may be found in sediments as fossils. **Cryptomonads** (phylum **Cryptophyta**) have two flagella and lack a skeleton. Members of these three groups are so small that hundreds could fit into a large diatom or dinoflagellate cell.

# PROTOZOANS: THE ANIMAL-LIKE PROTISTS

**Protozoans** are structurally simple and very diverse organisms that are traditionally considered to be animal-like. Most biologists agree that protozoans (meaning



**FIGURE 5.8** Skeleton of *Dictyocha speculum*, a silicoflagellate.



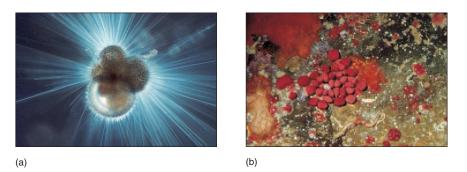
**FIGURE 5.9** Coccolithophorids, like *Umbilicosphaera sibogae* from Australia, are tiny single-celled phytoplankton that can be very important primary producers in the open ocean. The plates that cover the cell are made of calcium carbonate.

"the first animals") are actually composed of several groups of urelated origins. Like animals, they ingest food (that is, they are heterotrophs) and are eukaryotic. Some protozoans, however, contain chlorophyll and photosynthesize. Although a few form colonies, most are single-celled, unlike true animals, and only visible under a microscope.

Having a single cell is about the only thing that all protozoans, which show an enormous diversity in structure, function, and lifestyle, have in common. There is little agreement as to how to classify the estimated 50,000 species of protozoans, but for now biologists group them in the kingdom Protista with unicellular algae and seaweeds.

Protozoans are the most animal-like of the protists. They are eukaryotic and unicellular. They are heterotrophic and ingest food like true animals.

The minute size and apparent simplicity of protozoans disguise a complex nature. Each cell might be described as a "super cell" because it can perform many



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**FIGURE 5.10** Foraminiferans. (*a*) Foraminiferans typically have calcareous shells that consist of a spiral arrangement of chambers. The thin, long strands are the pseudopodia used to capture food. (*b*) *Homotrema rubrum* is a foraminiferan that forms bright red calcareous growths several millimeters in diameter at the base of corals in the tropics. It is so common in Bermuda that their skeletons are responsible for the island's famous pink beaches.

of the same functions carried out by the multitude of cells in the structurally more complex organisms. They inhabit water everywhere, living not only in marine and freshwater environments, but even inside other organisms. Many kinds of marine protozoans can be readily collected from sediments rich in organic debris, the surface of seaweeds, the guts of animals, and plankton samples.

## **Foraminiferans**

The foraminiferans, (phylum Foraminifera), better known as forams, are marine protozoans that usually have a shell, or test, made of calcium carbonate (CaCO<sub>3</sub>). The test is usually microscopic and may have several chambers (Fig. 5.10a) that increase in size as the foram grows. Pseudopodia-extensions of the jelly-like contents of the cell, or cytoplasm-are thin, long, and retractable in forams. The pseudopodia protrude through pores in the shell and form a network used to trap diatoms and other organisms suspended in the water (see Fig. 15.5). Food is then moved into the interior of the cell as if on a conveyor belt.

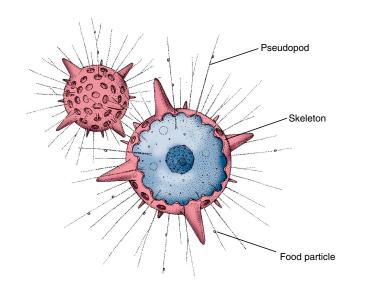
Most forams live on the bottom, either free or attached. Attached forams may develop into conspicuous growths as much as 5 cm (2 in) in diameter (Fig. 5.10*b*). Each growth consists of a single cell that forms a shell, though

some may be covered with sand grains or other materials instead. The shells of bottom-living forams can be important contributors of calcareous material on coral reefs and sandy beaches. Only a few species are planktonic, but these can be very abundant. Their shells are smaller and thinner than those that live on the bottom and may have delicate spines that aid in flotation. The shells of planktonic forams eventually sink to the bottom in such high numbers that large stretches of the ocean floor are covered by foraminiferan ooze, a type of calcareous ooze. Many limestone and chalk beds around the world, like the white cliffs of Dover in England, are products of foram sediments that were uplifted from the ocean floor.

Forams are protozoans characterized by a shell usually made of calcium carbonate. Most live on the bottom. The shells of planktonic species are important components of marine sediments.

**Biogenous Sediments** Sediments made of the skeletons and shells of marine organisms; *calcareous ooze* is made of calcium carbonate and *siliceous ooze* of silica.

Chapter 2, p. 33



**FIGURE 5.11** A typical radiolarian cell consists of a dense central portion surrounded by a less dense zone that is involved in the capture of food particles and in buoyancy.

Most species of forams are known only as microfossils. The distribution of these microfossils in sediments is very important to geologists. Shells of warmwater species are slightly larger and more porous than those from colder water. Past water temperatures can be estimated from the distribution of certain marker species. Their distribution is also valuable in the search for oil because it is used to determine the age of sediments.

## Radiolarians

**Radiolarians** (phylum **Polycystina**) are planktonic marine protozoans that secrete elaborate and delicate shells made of glass (silica) and other materials. Typical shells are spherical with radiating spines (Fig. 5.11), though the structure varies. Thin, needle-like pseudopodia capture food, as in forams.

Most radiolarians are microscopic, but some form bizarre, sausage-shaped colonies that reach 3 m (9 ft) in length, making them true giants among protozoans. Radiolarians inhabit open water throughout the oceans. When abundant, the remains of their shells settle to the bottom and form a siliceous ooze known as **radiolarian ooze**. This ooze is more extensive in deep water because radiolarian shells are more resistant to dissolving under pressure than those of forams.

The shells of radiolarians are made primarily of silica (glass). These shells form siliceous sediments that cover large areas of the ocean floor.

## Ciliates

Ciliates (phylum Ciliophora) are protozoans that have many hair-like cilia that are used in locomotion and feeding. The most familiar ciliates are freshwater forms such as Paramecium. Marine ciliates are usually found creeping over seaweeds and in bottom sediments. Some live on the gills of clams, in the intestines of sea urchins, on the skin of fish, and in other unusual places. Other ciliates live attached to surfaces, even forming branched colonies of tiny individuals. Tintinnids are common ciliates that build vase-like cases, or loricas, loosely fitting shells that drift in the water (Fig. 5.12). The cases may be transparent or made of bits of particles.



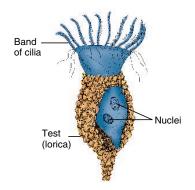


FIGURE 5.12 *Tintinnopsis* is a marine tintinnid that forms a vase-like lorica made of sand grains. Specialized cilia on one end are used in feeding.

## **FUNGI**

**Fungi** (kingdom **Fungi**) are eukaryotic and mostly multicellular, although some, such as molds and yeasts, are unicellular. Many fungi appear superficially plantlike but are heterotrophs that lack chloroplasts and chlorophyll and cannot perform photosynthesis.

There are at least 500 known species of marine fungi. They are mostly microscopic. Many, like bacteria, are decomposers of dead organic matter. They are the most important decomposers of mangrove plants and thus contribute to the recycling of nutrients in mangrove forests (see "Mangroves," p. 115). Some are parasites of seagrasses or borers in mollusc shells. Others are parasites that cause diseases of economically important seaweeds, sponges, shellfish, and fish. Some marine fungi are being investigated as a source of antibiotics for use in medicine. Still others live in close association with algae to form unique entities, the lichens. In lichens the long, filament-like growths of the fungi provide support, while the algae provide food manufactured by photosynthesis. Marine lichens can be found as thick, darkbrown or black patches in the wave-splashed zone of rocky shores, particularly on North Atlantic shores. By comparison with the multitude of lichen species on land, there are very few species of marine lichens.

5. The Microbial World



# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

# **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. Scientists use the particular structure of nucleic acids and other chemical differences to separate the archaea from the bacteria. Can you think of other characteristics that could be used to separate not only these two kingdoms but also between them and members of the kingdom Protista?
- 2. An autotrophic protist, such as a diatom or a dinoflagellate, can evolve into a heterotrophic protist (and therefore a protozoan) simply by losing its chloroplasts. Under what conditions could such a situation take place?

# For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol \_\_\_\_\_, and will contain live links when you visit this page in the Online Learning Center.

## **General Interest**

- Burkholder, J. M., 1999. The lurking perils of *Pfiesteria*. *Scientific American*, vol. 281, no. 2, August, pp. 42–49. The life cycle and other aspects of the biology of this potentially harmful parasite.
- Furlow, B., 2001. The freelance poisoner. *New Scientist*, vol. 169, no. 2274, 20 January, pp. 30–33. As in the case of the deadly toxins found in pufferfishes, similar toxic chemicals in other marine organisms may actually be produced by bacteria.
- Hoppert, M. and F. Mayer, 1999. Prokaryotes. *American* Scientist, vol. 87, no. 6, November–December, pp. 518–525.
  Prokaryotic cells show a complex organization, even when organelles are absent.

- Jarrell, K. F., D. P. Bayley, J. D. Correia and N. A. Thomas, 1999. Recent excitement about the Archaea. *BioScience*, vol. 49, no. 7, July, pp. 530–541. The archaea are useful tools in efforts to understand some of the basic characteristics of life.
- Knight, J., 1999. Blazing a trail. New Scientist, vol. 164, no. 2213, 20 November, pp. 28–32. Bioluminescent phytoplankton is used to study the swimming ability of dolphins.
- Leslie, M., 2001. Tales of the sea. *New Scientist*, vol. 169, no. 2275, 27 January, pp. 32–35. New techniques allow the sampling of previously unknown unicellular organisms in the ocean.
- Zimmer, C., 2000. Sea sickness. Audubon, vol. 102, no. 3, May–June, pp. 38–45. Bacteria, fungi, and other microorganisms cause serious diseases in marine life, from seagrasses and corals to cetaceans.

## In Depth

- Cahoon, L. B., 1999. The role of benthic microalgae in neritic ecosystems. Oceanography and Marine Biology: An Annual Review, vol. 37, pp. 47–86.
- Fleming, L. E., J. Easom, D. Baden, A. Rowan and B. Levin, 1999. Emerging harmful algal blooms and human health: *Pfiesteria* and related organisms. *Environmental Toxicologic Pathology*, vol. 27, pp. 573–581.
- Hyde, K. D., E. B. G. Jones, E. Leano, S. B. Pointing, A. D. Poonyth and L. L. Vrijmued, 1998. Role of fungi in marine ecosystems. *Biodiversity and Conservation*, vol. 7, pp. 1147–1161.
- McFall-Ngai, M. J., 1999. Consequences of evolving with bacterial symbionts: Insights from the squid-Vibrio associations. *Annual Review of Ecology and Systematics*, vol. 30, pp. 235–256.
- Rowan, R., 1998. Diversity and ecology of zooxanthellae on coral reefs. *Journal of Phycology*, vol. 34, pp. 407–417.

# See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center.

• Brown algae moving in surge (Honduras)

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# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Photosynthetic marine organisms
- Diversity of algae
- Economic and ecological importance of algae
- Diversity of eubacteria
- Cyanobacteria

- Pfiesteria
- · Diversity of archaea
- · Marine protozoans and invertebrates
- Diversity of fungi
- Lichens

# Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

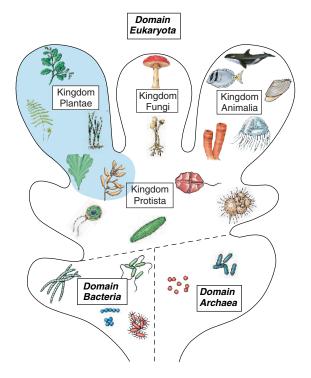
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# Multicellular Primary Producers: Seaweeds and Plants





Brown seaweeds, Pacific coast of North America.



s inhabitants of land, our perception of the world of photosynthetic organisms is based mostly on plants like trees, ferns, and mosses. Many fascinating photosynthetic organisms populate the oceans, but for the most part they are very different from the land plants that surround us. Most, in fact, are not generally considered plants at all. **Plants** are members of the kingdom **Plantae**, and most of the photosynthetic organisms found in the sea (the unicellular algae described in Chapter 5

and the seaweeds covered here) are classified by most biologists as **Protists**.

What makes practically all of the organisms covered in this chapter "plant-like" is that they are **primary producers** capable of using light energy to perform photosynthesis, like photosynthetic bacteria and the unicellular algae discussed in Chapter 5. While many other bacteria *are* primary producers but do *not* perform photosynthesis, almost all the seaweeds and marine plants discussed in Chapter 6 are photosynthetic. There are always exceptions, and a few seaweeds are not primary producers but parasites of other seaweeds!

Seaweeds play an important role in many coastal environments. The seaweeds illustrated above, for example, not only

**Primary Producers** Organisms that manufacture organic matter from  $CO_2$ , usually by photosynthesis.

Chapter 4, p. 73

transform light energy from the sun into chemical energy but also make it available to a long list of hungry creatures, which may include humans. Other organisms live on or even in the tissues of seaweeds. Those on land as well as organisms living in the ocean also utilize some of the oxygen seaweeds produce.

# MULTICELLULAR ALGAE: THE **SEAWEEDS**

The most familiar types of marine algae are those popularly known as seaweeds. This, however, is a rather unfortunate term. For one thing, the word "weeds" does not do justice to these conspicuous and often elegant inhabitants of rocky shores and other marine environments. Some biologists opt for the more formal names of macrophytes or macroalgae. On the other hand, the term "seaweeds" is useful in distinguishing them from the unicellular algae surveyed in Chapter 5 and the seagrasses and saltmarsh grasses described later in Chapter 6. The structures of seaweeds are far more complex than those of unicellular algae, and reproduction is also more elaborate. Seaweeds are all eukaryotic. By definition they are all multicellular; unicellular green and red algae are therefore not considered seaweeds. The classification of seaweeds takes into consideration not only structure but also other features such as the types of pigments and food products they store (see Table 5.1, p. 92).

Though structurally more complex than unicellular algae, seaweeds still lack the highly specialized structures and reproductive mechanisms characteristic of the mostly terrestrial plants. Some biologists, however, consider some or all seaweeds to be plants.

The range of variation observed among seaweeds is spectacular. Those we see on rocky shores at low tide are usually small and sturdy as an adaptation to withstand waves. Some small, delicate ones live as epiphytes or parasites on other seaweeds. Kelps found offshore in cold waters are true giants that form dense underwater forests (see Fig. 6.8b).

Pneumatocyst Holdfast

FIGURE 6.1 The giant kelp (Macrocystis).

The multicellular condition of seaweeds allows many adaptations not available to unicellular forms. Their ability to grow tall and rise off the bottom provides new opportunities as well as challenges: wave action, competition for space and light, and the problem of predation by sea urchins and fishes.

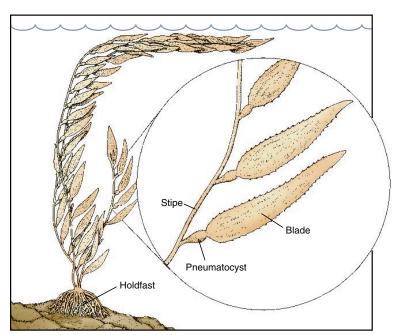
# **General Structure**

Seaweeds show a wide range of growth forms and complexity of structures. Nevertheless, several unifying features are worth mentioning. Seaweeds lack the true leaves, stems, and roots of plants. The complete body is known as the thallus, whether it is a filament, a thin leafy sheet, a crusty cushion, or a giant kelp.

The leaf-like, flattened portions of the thallus of many seaweeds are known as blades (Fig. 6.1). They increase the surface area and are the main photosynthetic regions. All portions of the thallus are able to photosynthesize in light as long as they have chlorophyll. Blades are technically not true leaves because there are no veins. Another difference is that in contrast to true leaves, the upper and

lower surfaces of blades are identical to each other. Blades are sometimes kept close to the sea surface by means of gasfilled bladders known as pneumatocysts (Fig. 6.1), thereby maximizing their exposure to the sunlight. The mixture of gases in the pneumatocysts of some seaweeds includes carbon monoxide, a gas that is toxic to humans.

Some seaweeds have a distinct stemlike structure to provide support, the stipe, from which blades originate. It is long and tough in the large kelps. A structure that looks like roots, the **holdfast**, glues the thallus to the bottom. Holdfasts are particularly well developed in the kelps (Fig. 6.1). They are not involved in any significant absorption of water and nutrients and do not penetrate through the sand or mud as true roots would. Seaweeds cannot anchor in soft sediments and are therefore restricted to hard bottoms. Water and nutrients, which bathe the entire thallus, are picked up directly across the surface without the need of roots, as in land plants. Also in contrast to the leaves and stems of plants, the stipe and holdfast usually lack tissues specialized in the transport of water and nutrients.



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Seaweeds typically consist of a thallus, which is sometimes provided with leaf-like blades, and a root-like holdfast. They lack true leaves, stems, or roots.

# Types of Seaweeds

There are three types of seaweeds: the green, brown, and red algae. It is not always easy to recognize the groups by their color in nature since the proportion of chlorophyll and other pigments (see Table 5.1, p. 92) can vary. When the pigments are chemically separated however, the types present are characteristic for each group.

#### Green Algae

Most green algae (phylum Chlorophyta) are restricted to freshwater and terrestrial environments. Only around 10% of the estimated 7,000 species are marine. This, however, does not mean that green algae are uncommon in the sea. Some species are dominant in environments with wide variations in salinity such as bays and estuaries and in isolated tide pools on rocky coasts.

Few green algae are as complex as the other two groups of seaweeds in terms of the general structure of the thallus. Most are unicellular or filamentous; many are microscopic. Their pigments and food reserve, however, are the same as those in plants (see Table 5.1, p. 92), so it is thought that land plants evolved directly from green algae very similar to those we see today. Chlorophyll in both green algae and plants is not normally masked by any other pigments, so the thallus is typically bright, or grass, green. Because of these similarites, green algae are more frequently considered to be plants than the brown and red algae.

The green algae are largely unicellular and nonmarine. They are typically bright green because chlorophyll is not masked by other pigments.

The simplest marine green algae are unicellular and planktonic and possess one

to four flagella, which they use to swim. Some are responsible for blooms in salt marshes and tide pools, especially in the tropics. Some species are **epiphytes** on

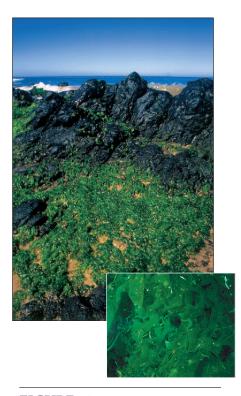


FIGURE 6.2 Ulva, or sea lettuce, is a green alga that is common on rocks where fresh water, often containing high amounts of nutrients, reaches the sea.

other seaweeds, and a few actually live as endophytes within their tissues. Other species bore by chemically dissolving into coral skeletons or the shells of other animals. Filamentous forms grow on a wide variety of surfaces such as rocks in shallow water, other seaweeds, and rocky shore tide pools. The filaments of these species may be branched or unbranched. Species of Enteromorpha are characterized by a thin thallus in the form of a hollow tube. They sometimes flourish in areas disturbed by pollution. Sea lettuce (Ulva; Fig. 6.2) forms paper-thin sheets whose shape varies depending on environmental factors. Different species of Ulva are widespread, from Arctic to tropical waters. Some species are particularly common in brackish water. Valonia, another green alga, forms large spheres or curious spherical clusters in the tropics and subtropics.

Several other green algae consist of branched, thin tubes (siphons) with many



FIGURE 6.3 The dead man's fingers seaweed (*Codium fragile*) forms branched clumps on rocky shores. Its chloroplasts remain alive, and still photosynthesize, in some shell-less gastropods that feed on the seaweed.

nuclei. Such is the case in Caulerpa, which is restricted to the tropics and subtropics. Its many species show a great variety of shapes. Dead man's fingers (Codium; Fig. 6.3) is a green alga that extends into temperate waters, including both sides of North America. It consists of multinucleated filaments woven into a spongy, often branching thallus. Halimeda is characterized by a thallus consisting of numerous segments with deposits of calcium carbonate (see Fig. 14.9). Halimeda thus is known as a calcareous green alga. The accumulation of its dead, calcified segments has an important role in the formation of coral reefs (see "Other Reef Builders," p. 301).

## Brown Algae

The characteristic color of the **brown algae** (phylum **Phaeophyta**), which actually varies from olive green to dark brown, is due to a preponderance of yellow-brown pigments, particularly **fucoxanthin**, over chlorophyll (see Table 5.1, p. 92). Almost all of the approximately 1,500

**Epiphytes** Photosynthetic organisms that live on algae or plants. **Endophytes** Photosynthetic organisms that live within algae or plants.

Chapter 5, p. 95

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**FIGURE 6.4** *Padina*, a brown alga, consists of clusters of flat blades that are rolled into circles. This species is from the Hawaiian Islands.



**FIGURE 6.5** The spiral rockweed (*Fucus spiralis*) is common on rocky shores on the Atlantic coasts of temperate North America and Europe. Its thallus lacks the air bladders that characterize a similar species, the bladder rockweed (*Fucus vesiculosus*).

known species are marine. Brown algae are often the dominant primary producers on temperate and polar rocky coasts. They include the most complex and the largest of the seaweeds, the kelps.

The brown algae include seaweeds that are the largest and structurally most complex algae. Chlorophyll is found together with yellowbrown pigments.

The simplest brown algae have a finely filamentous thallus, as in the widely distributed species of *Ectocarpus*. The thallus is flat and branched in *Dictyota* and fan-shaped in *Padina* (Fig. 6.4). Both are found mostly in tropical and subtropical waters. The thallus of most species of *Desmarestia* is branched, though the branching pattern varies widely. *Desmarestia* is found in cold waters. It ranges from the Antarctic, where it is one of the dominant species, to the deep water in the Caribbean and temperate shores elsewhere.

Some of the most conspicuous of all brown algae are those exposed at low tides at the middle and upper levels of rocky shores. Their thick, leathery thalli can withstand exposure to air (see "Exposure at Low Tide," p. 236). Many species have gas-filled floats. Known locally as **rockweeds**, or **wracks**, *Fucus* (Fig. 6.5) is found on the Atlantic and Pacific coasts of North America and other temperate shores, and Ascophyllum is found on the temperate Atlantic coasts (Fig. 6.6). In warm waters, including the Gulfs of Mexico and California, these temperate species are replaced by sargasso weed (Sargassum). The sargasso weed has spherical air bladders that keep the small, leaf-like blades afloat at the sea surface. Most species grow on rocks, but at least two float offshore in huge masses. They give the Sargasso Sea, an area in the Atlantic north of the West Indies (see Fig. 8.24), its name. Sargasso weed drifts in other regions of the world as well. It is particularly common in the Gulf of Mexico.

The large group known as the **kelps** includes the most complex and largest of all brown algae. Most kelps are found in great abundance below the low tide level in temperate latitudes and in the Arctic. In these environments, they are a most important element of the marine life, providing food and shelter for many organisms.

Some kelps consist of a single large blade, as in the many species of *Laminaria* (see Figs. 13.20*a* and *b* and 13.25). Their large blades, up to 3 m (almost 10 ft) in length, are harvested for food in several parts of the world (see "Seaweeds for Gourmets," p. 113). In some species the blade is split or even branched; several blades may grow from a single holdfast. In *Agarum* and *Alaria* (see Fig. 13.20*c*), a



**FIGURE 6.6** The knotted rockweed (*Ascophyllum nodosum*) occurs on the North American and European coasts of the North Atlantic.

conspicuous rib runs along the middle of the single blade. The blade of *Alaria* can be as long as 25 m (82 ft). *Postelsia*, commonly known as the sea palm because of its appearance (Fig. 6.7), grows on intertidal rocks exposed to heavy waves. It occurs in thick clusters from central California to British Columbia. Two branched forms, the feather-boa kelp (*Egregia*; see Fig. 13.25) and the southern sea palm (*Eisenia*), are also common on Pacific rocky shores.

In the Pacific the largest kelps are found in deeper water just below the lowest tide level. The bullwhip kelp, *Nereocystis*, consists of a long, whip-like stipe up to 30 m (almost 100 ft) in length with

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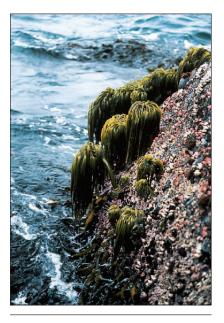


FIGURE 6.7 Stands of the sea palm (*Postelsia palmaeformis*) are common on rocky shores exposed to heavy wave action on the Pacific coast of North America (also see Figs. 11.11 and 11.15).

a large spherical pneumatocyst at the upper end (see Fig. 13.25). Another large kelp is *Pelagophycus* (see Figs. 13.22 and 13.25). It is similar to the bullwhip kelp, but it has impressive antler-like branches.

Macrocystis (Fig. 6.1) is the largest of the kelps. Its massive holdfast, which is attached to a hard bottom, may weigh several kilograms. Several long stipes grow from the holdfast, from which elongate blades develop (Fig. 6.8a). At the base of each blade a pneumatocyst eventually develops, which is filled with gas, thereby helping keep the blades close to the surface. This body plan rivals that of many land plants in its complexity. Individuals as long as 100 m (330 ft) have been recorded! It has been estimated that such kelps can grow 50 cm (20 in) or more per day for short periods. Many individuals, each with many fastgrowing and intertwined stipes, form dense and very productive kelp beds, or forests (Fig. 6.8b), in the colder waters of the North and South Pacific (see the map in Fig. 13.21). Kelp beds are harvested by chopping off the tops for the extraction of several natural products (see



(a)



(b)

**FIGURE 6.8** (*a*) Growing end of a stipe of the giant kelp (*Macrocystis pyrifera*). (*b*) A kelp forest in California (also see Figs. 13.23 and 13.25).

"Economic Importance," p. 112). Kelp beds are among the richest, most productive environments in the marine realm and will be discussed under "Kelp Communities" (p. 290).

## Red Algae

There are more species of marine **red algae** (phylum **Rhodophyta**) than of marine green and brown algae combined. Among other features, they are characterized by having red pigments called **phycobilins**, which mask chlorophyll (see Table 5.1, p. 92). Most species are actually red, though some may show different colors depending on their daily exposure to light. The group is essentially marine; only a few of the approximately 4,000 species live in fresh water or soil. Red algae are found in most shallow-water marine environments. Some are of significant commercial importance and are harvested for food and for the extraction of many different products (see "Economic Importance," p. 112).

The structure of the thallus of red algae does not show the wide variation in complexity and size that is observed in the brown algae. Some reds have become greatly simplified, at least in their structure, by becoming parasites of other seaweeds. A few have lost all trace of chlorophyll and have become heterotrophs, depending entirely on their host for nutrition. Most red algae are filamentous, but the thickness, width, and arrangement of the filaments vary a great deal. Dense clumps are more common on the upper levels of rocky shores that are exposed at low tide; longer and flatter branches predominate in areas less exposed to air and in deeper water. These variations are observed, for example, among the many species of Gelidium and Gracilaria that are found worldwide. Endocladia forms wiry clumps on rocky shores from Alaska to Southern California.

Some species of Gigartina, are characterized by large blades as long as 2 m (6 ft). These are among the most massive of the red algae. Numerous species of Porphyra are common on rocky shores above the lowest tide marks from polar to tropical coasts (Fig. 6.9). A thallus consisting of thin, large blades is the most common growth form. Palmaria is common in the North Atlantic. Its blades may reach 1 m (3 ft) in length. Another North Atlantic red alga is Irish moss (Chondrus). It can tolerate wide ranges of temperature, salinity, and light, and its shape varies greatly in response to these physical factors.

The red algae are the largest group of seaweeds. Their chlorophyll is typically masked by a red pigment.

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FIGURE 6.9 Many species of *Porphyra*, a red alga, inhabit temperate, polar, and tropical rocky shores around the world. Some are of significant economic importance.

The coralline red algae are important in several marine environments. They deposit calcium carbonate within their cell walls. The calcified thallus takes a variety of shapes: thin disks growing over other seaweeds, branches with numerous joints (Corallina; Fig. 6.10), smooth or rough encrusting growths on rocks. The color of these seaweeds varies from light to intense reddishpink; dead calcified thalli are white. Warm-water coralline algae are actively involved in the formation and development of coral reefs (see "Other Reef Builders," p. 301). Other species thrive in temperate and polar waters, often attaining a large size.



FIGURE 6.10 Corallina, a coralline red alga.

# Life History

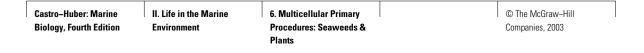
Reproduction is a complex affair in the seaweeds. **Asexual**, or vegetative, reproduction is common. It is possibly more important than **sexual** reproduction in most species. Fragments of the thallus can often grow into new individuals, as occurs in the floating masses of *Sargassum* of Sargasso Sea fame. Some seaweeds produce a variety of asexual, single-celled stages. These stages, named **spores**, are cells specialized in dispersing to new locations. Some spores are protected by resistant cell walls; others are provided with flagella for movement and are known as **zoospores**.

Sexual reproduction, an uncommon phenomenon among the unicellular marine algae, is widespread in the seaweeds. The production of **gametes** is a key event in sexual reproduction. Gametes from two different individuals fuse so that the new generation contains genetic information from both parents. Genetic variation is thus ensured generation after generation. Gametes produced by all members of a seaweed species may be similar in appearance or may consist of larger, nonmotile eggs and smaller sperm that can swim by means of flagella. Male gametes in the red algae lack flagella and are nonmotile. They may be released in strands of slime. Male and female gametes may be formed in the same thallus, but the chances are good that fusing gametes will be from separate thalli.

Cells of seaweeds (and of us all clam, fish, or human) divide and produce identical cells by **mitosis**. Seaweeds may also produce haploid spores or gametes by **meiosis**. The existence of diploid and haploid cells is fundamental in understanding the often complex life histories, or life cycles, of seaweeds. Their life histories can be divided into four basic types.

The first type (Fig. 6.11*a*) is the most common among all three groups of seaweeds, and it involves two types of thalli. The first is a diploid (2n) **sporophyte** generation that through meiosis, produces not gametes but haploid (n, or 1n) spores. Except in the red algae, these spores are typically motile. They divide and develop into the second kind of thallus, a haploid (n) **gametophyte** generation. The gametophyte is the one that produces haploid gametes. In some species there are separate male (sperm-producing) and female (egg-producing) thalli; in others, both types of gametes are produced by

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#### Chapter 6 Multicellular Primary Producers: Seaweeds and Plants 111

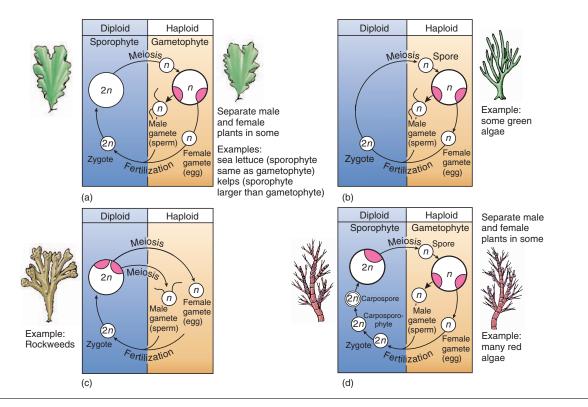


FIGURE 6.11 Basic patterns of sexual reproduction in the life histories of seaweeds (see text below). These patterns are not absolute, and many modifications have been described.

every thallus. The gametes are released and, upon fertilization, develop into the diploid sporophyte. A life history with two generations, a sporophyte and a gametophyte, is an example of the phenomenon of alternation of generations. In some algae such as sea lettuce (Ulva) and the brown Dictyota, the sporophyte and gametophyte are structurally identical. On the other hand, in kelps (Laminaria, Macrocystis, and others) the large plant we see is the sporophyte, whereas the gametophyte is minute and barely visible (see Fig. 13.24). A similar type of alternation of generations takes place in flowering plants, when a sporophyte dominates over a minute gametophyte.

In the second type of life history, as in some green algae (Fig. 6.11b), the dominant thallus is haploid (*n*) and produces haploid gametes. On fertilization the gametes form a diploid (2*n*) zygote. It is in the zygote where meiosis takes place, resulting in haploid spores. Each of these spores develops into a haploid individual, the only kind of thallus in the cycle.

The third type of life history (Fig. 6.11c) is perhaps the easiest to understand because it is similar to that of animals, including humans. There is only one thallus, and it is diploid (2n). The thallus then produces haploid (n) gametes by meiosis. After fertilization the resulting zygote develops into a new diploid thallus. This type of life history is observed in some brown algae such as *Fucus* and other rockweeds and in some green algae (*Codium, Halimeda*).

The fourth type, unique to the red algae, is more complex, involving three generations (Fig. 6.11d). It is similar to the life history illustrated in Figure 6.11a, but a third generation, a diploid **carposporophyte**, results from the fertilization of gametes. **Carpospores**, diploid spores produced by the carposporophyte, develop into sporophytes.

Reproduction in seaweeds is by asexual and sexual means. Sexual reproduction is usually complex. It may involve an alternation of a haploid (or gametophyte) and a diploid (or sporophyte) generation.

Type of cell division: **Mitosis** Cell division wherein the resulting cells are identical to the original cell, having their chromosomes in pairs (diploid cells, or 2n), as in the case of our body cells.

#### Chapter 4, p. 82

**Meiosis** Cell division wherein the resulting cells are haploid (n, or 1n), as in the case of gametes (spores in seaweeds), because they contain only half the number of the parent's chromosomes.

Chapter 4, p. 83

There are many known exceptions to these basic schemes, and certainly there must be combinations and variants of life histories waiting to be discovered. Other aspects of the life history of seaweeds are also interesting. It has been shown, for example, that the development of gametes or spores in some seaweeds can be influenced by the amounts of nutrients in the water, by temperature, or even by day length. High levels of nitrogen nutrients in the water cause the development of asexual spores in sea lettuce  $(\hat{U}lva)$ , but low levels stimulate the development of gametes instead. The release of gametes and spores may be triggered by the splashing of water in an incoming tide (and therefore by the cycles of the moon) or by chemical messengers received from cells of the opposite sex. It is also known that in some seaweeds the release of male and female gametes is timed to take place at about the same time. Furthermore, gametes must recognize gametes of the opposite sex that belong to the same species. Such mechanisms help ensure that gametes will not be wasted and that as many successful fertilizations as possible will take place.

## **Economic Importance**

People have used seaweeds since time immemorial. Around the world, workers harvest seaweeds to be used in many ways. The most obvious use is as a food source. People from different cultures have discovered that many seaweeds are edible, especially some of the red and brown algae. They are consumed in a variety of ways (see "Seaweeds for Gourmets" p. 113). The farming, or mariculture, of seaweed is big business in China, Japan, Korea, and other nations (see Table 17.3, p. 399).

Seaweeds produce several types of gelatinous chemicals called phycocolloids that are used in food processing and in the manufacture of different products. These phycocolloids are valuable because of their ability to form viscous suspensions or gels even at low concentrations.

One important phycocolloid, algin (which comprises alginic acid and its salts, the alginates), is used extensively as a stabilizer and emulsifier in the manufacture of dairy products such as ice

FIGURE 6.12 The Kelstar, a kelp harvester based in San Diego, California. It is 55 m (180 ft) long and has a capacity of 600 tons.

cream, cheese, and toppings, which need to be smooth and not likely to separate. Algin is also used in the baking industry to prevent frostings and pies from becoming dry. As a thickener and emulsifier it is also used in the pharmaceutical and chemical industries and in the manufacture of various products, from shampoo and shaving cream to plastics and pesticides. Algin also has uses in the making of rubber products, paper, paints, and cosmetics. One of its biggest applications is in the textile industry-algin thickens the printing paste and provides sharper prints. A major source of algin for commercial uses is the giant kelp, Macrocystis. The west coast of temperate North America, particularly California, is home to extensive kelp forests, making this an important algin-producing area. The forests are leased from the state of California, and large barges equipped with rotating blades cut and collect the stipes and fronds to a depth of 1 to 2 m (up to 6 ft) below the surface (Fig. 6.12). The stipes quickly grow back toward the surface. An additional important source of algin is Laminaria, another brown alga that is harvested in the North Atlantic.

A second phycocolloid, carrageenan, is obtained from red algae such as Irish moss (Chondrus) in the North Atlantic and Eucheuma in the tropics. Several species of Eucheuma are farmed extensively in the Philippines. Carrageenan is especially valued as an emulsifier. It is used to give body to dairy products and an amazing variety of processed foods, including instant puddings.

Another phycocolloid extracted for its ability to form jellies is agar. Agar is employed to protect ham, fish, and meats during canning, in low-calorie foods (because it is not digestible by humans), and as a thickener. It is also used in laxatives and other pharmaceuticals (see "Take Two Sponges and Call Me in the Morning," p. 401) and in cosmetics. Biologists use agar as a medium in which to grow bacteria and molds; it is widely used in medical research for this purpose. Agar is obtained commercially from several red algae, especially from species of Gelidium, Gelidiella, and Pterocladiella.

Seaweed may also be used as fertilizers, food additives in animal feeds, and wound dressings in hospitals. Coralline red algae are sometimes marketed in Europe to reduce the acidity of soils. The future may see new uses for seaweeds. Their fermentation to produce methane for fuel has been proposed.



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# SEAWEEDS FOR GOURMETS

Seaweeds, raw, cooked, or dried, are used as food in many cultures. Seaweeds are good sources of some vitamins and minerals, and some are said to contain substantial amounts of protein. Unfortunately, we cannot digest many of the complex carbohydrates in the plants, but this may be an advantage for those counting calories. Seaweeds can add variety and taste to bland foods and may be used to wrap such foods as rice. Cookbooks containing seaweed recipes have been written to whet the appetites of the most demanding gourmets.

Ulva is not called sea lettuce for nothing. It can be eaten fresh in salads. Seaweeds (or *limu*), including *limu 'ele 'ele* (the green *Enteromorpha prolifera*) and *limu manauea* (the red *Gracilaria coronopifolia*), are beloved by the Hawaiians. Purple laver (a species of *Porphyra*, a red alga) prepared in various ways is still eaten in some parts of the British Isles. It is washed and boiled, then formed into flat cakes, rolled in oatmeal, and fried; it is then called laverbread. Purple laver is also eaten as a hot vegetable or fried with bacon. Irish moss (*Chondrus*, a red alga and a source of carrageenan) is dried and used in preparing *blancmange* and other desserts in eastern Canada, New

England, and parts of northern Europe. *Palmaria*, another red alga, is dried and eaten, mostly by those living along the Atlantic coasts of Canada and northern Europe. Called *dulse*, it is sometimes still used in making bread and several types of desserts. For those on a diet, dulse can also be chewed like tobacco (of course it's nicotine-free).

It is in the Orient, however, that preparing seaweed for food has reached the level of an art. Several species are carefully cultivated, supporting multimillion-dollar operations. Seaweed culture is a very old tradition in Japan, and Japanese cuisine uses seaweed in many ways. Species of *Laminaria* and *Alaria* are dried and shredded, then prepared in various ways. *Laminaria japonica* is heavily cultivated in Japan and when processed is known as *kombu*. They are even used to make tea and candy. *Undaria*, or *wakame*, is another edible kelp that is best when fresh or cooked for a very short time. *Porphyra*, a red alga, is used to make thin sheets of *nori*, widely used in soups, and for wrapping *sushi*, boiled rice stuffed with bits of raw fish, sea urchin roe, or other ingredients (see Fig. 17.8).

Mariculture of edible seaweed is a growing business in many parts of the world (see Table 17.3, p. 399). Seaweeds are harvested by hand, rinsed in water, dried on lines, and sold at health food stores or through the Internet. Connoisseurs use seaweed in salads, soups, omelets, casseroles, and sandwiches. Sea palm (*Postelsia*), also known as "sea noodles," is a best-seller. It is reported to be excellent when sautéed in honey or in butter and garlic. Coastal Indians cooked it in ovens and made it into cakes. Its indiscriminate collection is endangering its survival, which is also true for other edible seaweeds. Pickled bullwhip kelp (*Nereocystis*) tastes even better than regular pickled cucumbers. Bladder rockweed (a type of *Fucus*) makes great tea. Are you ready for feather-boa burgers, French-fried sea palm, and *wakame* shakes?



Harvesting kelp (Laminaria japonica) in Japan.

Some additional food for thought: seaweeds at their best.

#### Seaweed Cake\*

- 1 1/2 cups salad oil
- 2 cups sugar
- 3 eggs
- 2 cups grated or chopped seaweed: sea palm (Nereocystis),
- *ogo (Gracilaria coronopifoloia), Eucheuma* (local species from Hawaiʻi), or local equivalent
- 2 cups grated carrots
- 1 cup crushed, drained pineapple (or 1 cup grated coconut, preferably fresh)
- 2 1/2 cups flour
- 1 teaspoon baking soda
- 1 teaspoon salt
- 1 teaspoon cinnamon
- 1 cup chopped walnuts (optional)
- Mix well the sugar and salad oil. Add the eggs, one at a time, beating well after each egg is added. Add the seaweed, carrots, and pineapple (or coconut). Sift together the flour, baking soda, salt, and cinnamon and add to mixture; mix well. Add the chopped walnuts if desired. Bake in oblong or bread-loaf pan at 160°C (350°F) for 45 to 50 minutes. Cake may be covered with buttercream frosting. Enjoy.

\*Adapted from I. A. Abbot, *Limu, An Ethnobotanical Study of Some Hawaiian Seaweeds*, 4th edition, National Tropical Botanical Garden, Lawa'i, Kaua'i, Hawai'i, 1996.

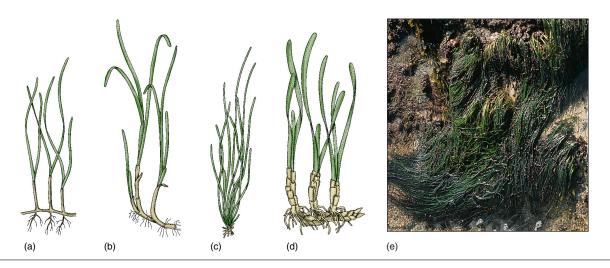
 

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**FIGURE 6.13** Seagrasses are flowering plants adapted to live under seawater. Some of the most common are (*a*) manatee grass (*Syringodium*), (*b*) eelgrass (*Zostera*), (*c*) surf grass (*Phyllospadix*), (*d*) turtle grass (*Thalassia*), and (*e*) surf grass (*Phyllospadix scouleri*).

# **FLOWERING PLANTS**

The 250,000 species of flowering plants, or angiosperms (division Magnoliophyta), are the dominant plants on land. Like other groups of land plants (ferns, conifers, and other groups) they have true leaves, stems, and roots, all provided with specialized tissues to transport water, nutrients, and the food manufactured during photosynthesis. As such, they are grouped in the kingdom Plantae. Reproduction involves a dominant sporophyte that features an elaborate reproductive organ, the flower. Few of these "higher" plants are successful in the oceans. Of all flowering plants, only the seagrasses are truly marine. They spend almost their entire lives submerged by seawater, rarely exposed at low tide. Salt-marsh grasses and mangroves inhabit estuaries and shores protected from wave action. They are not completely at home in the ocean, and usually only their roots are covered by water at high tide. There are also many flowering plants adapted to colonize coastal areas exposed to salt-laden winds and occasional sea spray, though they do not tolerate immersion in seawater. Such plants may be found on sand dunes or living along the edges of salt marshes.

# Seagrasses

**Seagrasses** superficially resemble grass, but actually are not grasses at all. The closest relatives of certain seagrasses appear to be members of the lily family.

Seagrasses have adapted to life in the marine environment. They have horizontal stems called rhizomes that commonly grow beneath the sediment. Roots and erect shoots grow from the stems (Figs. 6.13 and 4.19*a*). Seagrass flowers are typically very small and inconspicuous (see Fig. 4.21d), because there is no need to attract insects for pollination. Pollen, which contains the male gamete, is carried instead by water currents. For this reason it is often released in strands. In some seagrasses the pollen grains are long and thread-like, instead of tiny and round as in land plants. Tiny seeds, which in some species develop inside small fruits within the flower, are the result of successful fertilization. These seeds are dispersed by water currents and perhaps in the feces of the fish and other animals that browse on the plants.

Eelgrass (species of *Zostera*) is the most widely distributed of the 50 to 60 species of seagrasses known. It is found on the temperate North Atlantic and Pacific oceans, the tropical southwestern Pacific, and in other regions of the world, where it inhabits shallow, wellprotected coastal waters such as bays and estuaries (see Fig. 13.15). It has distinctively flat, ribbon-like leaves (Figs. 6.13*b* and 13.17). It is common in oxygen-poor sediments. Thick *Zostera* beds are highly productive and provide shelter and food to a variety of animals, some of considerable economic importance (see "Seagrass Beds," p. 286). Surf grass (*Phyllospadix*; Fig. 6.13*c* and *e*) is an unusual seagrass because it is an inhabitant of rocky coasts exposed to wave action, as its common name implies. Some species may become exposed at low tides. It is found on the Pacific coast of North America.

Most species of seagrasses are found in tropical waters, and most of these are found in the Indian and western Pacific oceans. In the Western Hemisphere most species are in the Caribbean Sea and the Gulf of Mexico. One common tropical seagrass is turtle grass (Thalassia). It looks similar to eelgrass, but its leaves are broader and more strap-like (Fig. 6.13d). Highly productive turtle grass beds can be found on muddy and sandy bottoms in water that is calm and of moderate depth, down to approximately 10 m (30 ft). The meadows are especially well developed in Caribbean coral reefs, where they play an important role in the stabilization of sediments on the landward side of the reef. Other tropical seagrasses are manatee grass (Syringodium; Fig. 6.13a), Cymodocea, Halophila, and in estuaries Ruppia.

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# Salt-Marsh Plants

The cordgrasses (species of Spartina; see Fig. 12.7) are true members of the grass family. They are not really marine species, but rather land plants tolerant of salt. Unlike seagrasses, which are true marine species, cordgrasses do not tolerate total submergence by seawater. They live in salt marshes and other soft-bottom coastal areas throughout temperate regions. Cordgrasses inhabit the zone above mudflats that becomes submerged by seawater only at high tide, so their leaves are always partly exposed to air. Salt glands in the leaves excrete excess salt. Other salt-tolerant plants, or halophytes, such as pickle weed (Salicornia; see Fig. 12.8), may be found at higher levels on the marsh. Salt-marsh plants and their adaptations to the estuarine environment along the mouths of rivers are discussed in "Salt Marshes" (p. 268).

## Mangroves

**Mangroves** are shrubs and trees adapted in the most unique ways to live along tropical and subtropical shores around the world. They are essentially land plants that can tolerate salt. Luxuriant and very productive mangrove forests flourish along muddy or sandy shores protected from waves (Fig. 6.14).

At least 80 mostly unrelated species of flowering plants receive the common name of mangrove. They are adapted in various ways to survive in an uninviting salty environment where water loss from leaves is high and where sediments are soft and poor in oxygen. Adaptations become more crucial in those species living right on the shore, such as the red mangrove (Rhizophora). Several species are found throughout the tropics and subtropics. The extreme northern and southern limits of the red mangrove are those areas in which killing frosts begin. Salt marshes replace red mangrove forests in areas exposed to frosts.

The leaves of the red mangrove are thick, an adaptation to reduce water loss. As in several other mangroves, seeds germinate while still attached to the parent tree (Fig. 6.15*a*). They develop into elongate, pencil-shaped seedlings with a pointed end and growing as long as 30 cm

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(almost a foot), before they eventually fall off. Successful seedlings stick in the soft muddy sediment like a knife thrown into a lawn, or float in the water to be carried by currents to new locations (Fig. 6.15b). The types and distribution of mangroves and their significance in the marine environment are discussed in "Mangrove Forests" (p. 271).

Flowering plants, dominant on land, have few marine representatives. Seagrasses, which are true marine species, and salt-tolerant plants like salt-marsh plants and mangroves are exceptions. They have successfully adapted to softbottom coastal regions, developing as highly productive meadows and, in the case of mangroves, forests along the shore.



**FIGURE 6.14** The red mangrove (*Rhizophora mangle*) forms lush forests along shores in Florida, the Caribbean, the Gulf of California, and other tropical regions of the Western Hemisphere and West Africa. Notice the long roots extending into the mud, exposed here at low tide. Other species of mangroves can be found further inland (see Fig. 12.18).



(a)



(b)

**FIGURE 6.15** A seedling of the red mangrove (*Rhizophora mangle*) as it appears in the tree (*a*) and one that has taken root in the soft sediment (*b*).

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# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

# **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- Some biologists place the seaweeds in the kingdom Plantae, others in the kingdom Protista. Assume that a better arrangement is to group the green, brown, and red algae in their own kingdom, which we will call Macrophyta. Characterize the new kingdom by first giving its unique characteristics and then differentiate it from the protists and the true plants. Be sure to consider major exceptions or overlaps.
- 2. Only very few flowering plants have invaded the oceans, but those that have are very successful. What are some possible reasons for the small number of marine flowering plants? How do those that have taken the step manage to thrive in some environments?

# **For Further Reading**

Some of the recommended readings listed below may be available online. These are indicated by this symbol **(**), and will contain live links when you visit this page in the Online Learning Center.

# **General Interest**

- Genthe, H., 1998. The Sargasso Sea. *Smithsonian*, vol. 29, no. 8, November, pp. 82–93. The sargasso weed manages to thrive in a nutrient-poor environment.
- Glenn, E. P., J. J. Brown and J. W. O'Leary, 1998. Irrigating crops with seawater. *Scientific American*, vol. 279, no. 2, August, pp. 76–81. Pickle weed and other salt-tolerant plants irrigated with seawater may one day be used to feed farm animals and humans.
- Jacobs, W. P., 1994. Caulerpa. *Scientific American*, vol. 271, no. 6, December, pp. 100–105. How this green alga, the largest single-celled organism, grows a complex structure.
- Rützler, K. and I. C. Feller, 1996. Caribbean mangrove swamps. *Scientific American*, vol. 274, no. 3, March, pp. 94–99. Many forms of life, both from land and sea, live in association with mangroves.

# In Depth

- Edwards, M. S., 2000. The role of alternate life-history stages of a marine macroalga: A seed bank alternative? *Ecology*, vol. 81, pp. 2404–2415.
- Hurd, C. L., 2000. Water motion and marine macroalgal physiology and production. *Journal of Phycology*, vol. 36, pp. 453–472.
- Lapointe, B. E., 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography*, vol. 42, pp. 1119–1131.
- Pearson, G. A. and S. H. Brawley, 1998. Sensing hydrodynamic conditions via carbon acquisition: Control of gamete release in fucoid seaweeds. *Ecology*, vol. 79, pp. 1725–1739.
- Trowbridge, C. D., 1998. Ecology of the green macroalga Codium fragile (Suringar) Hariot 1889: Invasive and non-invasive subspecies. Oceanography and Marine Biology: An Annual Review, vol. 36, pp. 1–64.

# See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

- *Caulerpa*, a green alga (Palau)
- Floating kelp (Alaska)
- Black mangrove roots (pneumatophores) and flowers (Bermuda)
- Red mangrove roots (Bermuda)
- Brown algae moving in surge (Honduras)

# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Primary productivity
- Kelp forests
- Rhodophyta
- Phaeophyta
- Chlorophyta
- Economic and ecological importance of algae
- Macroscopic algae and sea grasses

# Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

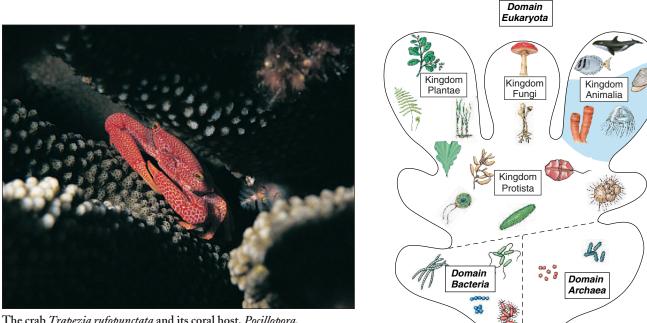
II. Life in the Marine Environment

7. Marine Animals without a Backbone

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# Marine Animals without a Backbone





The crab Trapezia rufopunctata and its coral host, Pocillopora.

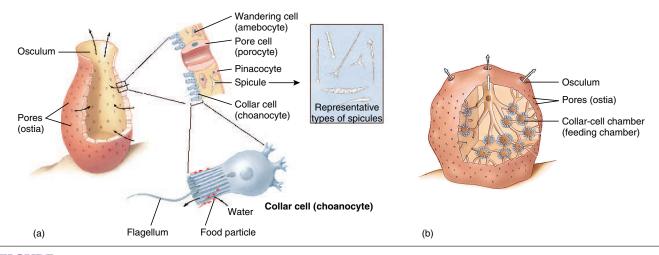
tured by a fish or an octopus, the crabs are usually safe hiding among the coral branches. The crabs repay the favor by using their pincers to drive away other animals that have a taste for coral tissue.

Zooxanthellae Dinoflagellates (single-celled algae) that live within animal tissues. Chapter 5, p. 99; Figure 14.7

ost species of multicellular organisms inhabiting our planet are **animals** (kingdom Animalia). In contrast to photosynthetic organisms like algae and plants, we animals cannot manufacture our own food and must therefore obtain it from others. The need to eat has resulted in the evolution of ingenious and diverse ways of obtaining and processing food, as well as equally diverse ways of avoiding being eaten by others.

The colorful crab in the photo above is a good example. It inhabits reef-building corals, relying on them for food and shelter. The crabs feed on mucus, which the coral produces to keep its surface free from debris. The coral is also an animal, though it may not look like one. It gets some of its food from zooxanthellae that live in its tissues. The coral also eats small planktonic organisms that it captures by using special stinging cells in its tentacles. Though an absent-minded crab is occasionally cap-





**FIGURE 7.1** Sponges consist of complex aggregations of cells that carry out specific functions. In both simple (*a*) and complex (*b*) sponges, collar cells are the cells in charge of trapping food particles.

Our survey of the many kinds of marine animals follows the traditional way of classifying them into two major groups: the **vertebrates**, which have a **backbone** (a row of bones called **vertebrae**), and those without a backbone, the **invertebrates**.

It is estimated that at least 97% of all species of animals are invertebrates. All major groups of invertebrates have marine representatives, and many are exclusively marine. Only a few groups have successfully invaded dry land. Were it not for one of these groups, the insects, we could boast without hesitation that most species of invertebrates, and therefore most animals, are marine.

# **SPONGES**

**Sponges** are animals that are best described as complex aggregations of specialized cells. These cells are largely independent of each other and do not form true **tissues** and **organs**. Sponges are among the structurally simplest multicellular animals. Nearly all sponges are marine. All are **sessile**, living attached to the bottom or a surface. They show an amazing variety of shapes, sizes, and colors but share a relatively simple body plan. Numerous tiny pores, or **ostia**, on the surface allow water to enter and circulate through a series of canals where **plankton** and organic particles are filtered out and eaten (Fig. 7.1*a*). This network of canals and a relatively flexible skeletal framework give most sponges a characteristic spongy texture. Because of this unique body plan, sponges are classified as the phylum **Porifera**, or "pore bearers."

Sponges may be similar to the first multicellular animals, which were probably simple colonies in which some cells became specialized for such functions as feeding and protection. Sponges have only a cellular level of organization because the cells are not combined into different tissues (see Table 7.1, pp. 148–149). Sponge cells are very plastic and easily change from one type to another. If experimentally separated, the cells can even regroup and form a new sponge (Fig. 7.2).

The architecture of sponges is best understood by examining the simplest kind of sponge (Fig. 7.1*a*). The outer surface is covered with flat cells called **pinacocytes** and occasional tube-like **pore cells**, or **porocytes**, through which a microscopic canal allows water to enter. Water is pumped into a larger feeding chamber lined with **collar cells**, or **choanocytes**. Each choanocyte has a flagellum that creates currents and a thin collar that traps food particles, which are then ingested by the body of the cell. Water then leaves through the **osculum**, a large opening on top of the sponge. Sponges are an example of **suspension feeders**, animals that eat food particles suspended in the water. Because sponges actively filter the food particles, they are a type of suspension feeder known as **filter feeders** (see Fig. 7.16).

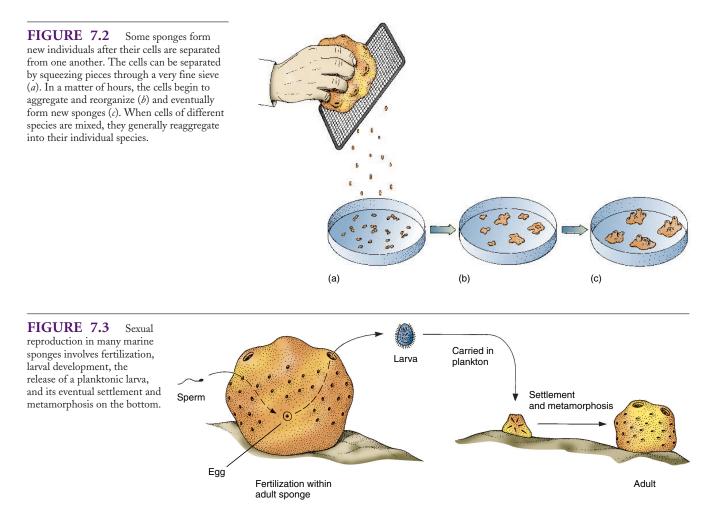
Most marine sponges show a more complex arrangement in which the collar cells are restricted to chambers connected to the outer pores by a network of canals (Fig. 7.1b). Water exits not through a single osculum, but through several oscula, each of which serves as the exit for many canals. This increased complexity is associated with increased size, which demands higher water flow through the sponge and therefore a larger surface area of collar cells.

Sponges are among the structurally simplest multicellular animals, lacking true tissues and organs. They are mostly marine, living as attached filter feeders.

As sponges get larger, they need structural support. Most have **spicules**, transparent **siliceous** or **calcareous** supporting structures of different shapes and sizes (Fig. 7.1*a*). Many also have a skeleton of tough, elastic fibers made of a protein called **spongin**. Spongin may be the only means of support, or it may be found together with spicules. When present, spongin and spicules are mostly embedded in a gelatinous layer between the outer and



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inner layers of cells. Wandering cells, or **amebocytes**, secrete the spicules and spongin (Fig. 7.1*a*). Some of these wandering cells also transport and store food particles. Some can even transform themselves into other types of cells, quickly repairing any damage to the sponge.

Many sponges reproduce **asexually** when branches or buds break off and grow into separate sponges identical to the original one. Sponges also reproduce **sexually** when collar cells or cells in the gelatinous layer develop into **gametes**. Unlike most animals, sponge gametes are not produced by **gonads**. Instead, specialized collar cells or cells in the gelatinous layer develop into gametes. The gametes themselves are like those of other animals: large, nutrient-rich eggs and smaller sperm cells that have a flagel-lum (Fig. 7.3). Most individual sponges

can produce both male and female gametes. Some sponges, however, have separate males and females, which is the case in most other invertebrates. Sponges typically release gametes into the water, which is called **spawning**. The eggs, however, are usually retained inside the

**Tissues** Specialized, coordinated groups of cells.

**Organs** Structures consisting of several types of tissues grouped together to carry out particular functions.

Chapter 4, p. 76

**Plankton** Organisms that drift with the currents.

Chapter 10, p. 230; Figure 10.19

body and fertilization takes place internally after the sperm enter the sponge.

The early stages of development take place inside the sponge. Eventually a tiny, flagellated sphere of cells is released into the water (Fig. 7.3). This planktonic **larva**, called the parenchymula larva, is carried

Siliceous Made of silica (SiO<sub>2</sub>). Calcareous Made of calcium carbonate (CaCO<sub>3</sub>).

Chapter 2, p. 33

**Gametes** Specialized reproductive cells usually produced by organs called *gonads: sperm* (male gametes produced by the *testes*) and *eggs* (female gametes produced by the *ovaries*).

Chapter 4, p. 83

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#### 120 **Part Two** Life in the Marine Environment

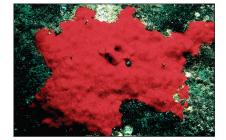


FIGURE 7.4 (a) Verongia archeri, a tubular sponge from the Caribbean. (b) An encrusting sponge from Hawai'i. (c) Ceratoporella nicholsoni, a coralline sponge, or sclerosponge, photographed at a depth of 52 m (170 ft) in Puerto Rico

(also see Fig. 4.9).

by currents until it settles on the bottom and develops into a minute sponge. Most marine invertebrates have life histories involving characteristic larvae that eventually change into juvenile adults. This drastic change from the larva to the adult is called **metamorphosis** (Fig. 7.3).

Almost all of the approximately 9,000 species of sponges are marine. Sponges live from the poles to the tropics, but the largest number of species inhabits shallow tropical waters. Sponges (Fig. 7.4) may grow into branching, tubular, round, or volcano-like masses that may reach a huge size. Encrusting sponges form thin, sometimes brightly colored growths on rocks or dead coral (Fig. 7.4b). Glass sponges, such as the Venus flower basket sponge (Euplectella), live anchored in deep-water sediments and are characterized by a lace-like skeleton of fused siliceous spicules. Boring sponges (Cliona) actively bore thin channels through calcium carbonate, such as





(c)

(b)

oyster shells and corals. In the **sclerosponges**, or **coralline sponges** (*Ceratoporella*; Fig. 7.4*c*), a calcium carbonate skeleton forms beneath the body of the sponge, which contains siliceous spicules and spongin. Sclerosponges were first known as fossils, but living specimens were discovered in underwater caves and on steep coral reef slopes after the advent of scuba diving.

Some marine sponges are of commercial importance. Bath sponges (Spongia) are still harvested in a few locations in the Gulf of Mexico and the eastern Mediterranean in what remains of a once flourishing occupation. Bath sponges, not to be confused with synthetic sponges, consist of the spongin fibers remaining after cells and debris are washed away. Some marine sponges produce chemicals that are potentially of commercial importance to humans (see "Take Two Sponges and Call Me in the Morning," p. 401). www.mhhe.com/marinebiology

# CNIDARIANS: A RADIALLY SYMMETRICAL BODY PLAN

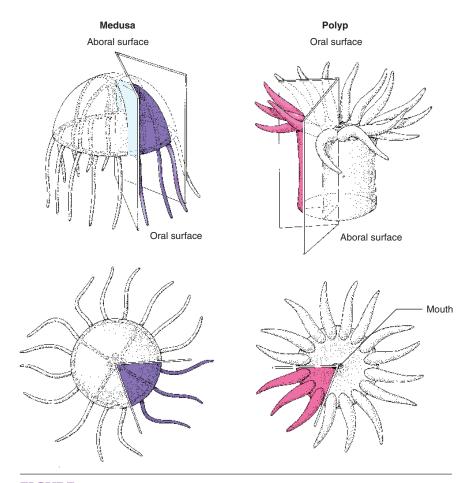
The next level of organizational complexity among animals after the sponges involves quite a big step. This difference is the evolution of tissues that perform specific functions. This development makes it possible to swim, respond to external stimuli, and engulf prey, among other things. Cnidarians, sometimes called coelenterates (phylum Cnidaria or Coelenterata), includes the sea anemones, jellyfishes, corals, and their relatives. Besides having a tissue level of organization, cnidarians display radial symmetry, where similar parts of the body are arranged and repeated around a central axis (Figs. 7.5 and 7.11). If a radially symmetrical animal were cut like a pizza, all of the resulting slices would be similar. Animals with radial symmetry look the same from all sides and have no head, front, or back. They do, however, have an oral surface, where the mouth is, and an aboral surface on the opposite side (Fig. 7.5).

Cnidarians occur in one of two basic forms (Fig. 7.5): a **polyp**, a sac-like attached stage, or a bell-like **medusa**, or jellyfish, which is like an upside-down polyp adapted for swimming. The life history of some cnidarians includes both polyp and medusa stages. Others spend their entire lives as either polyp or medusa.

The polyp and the medusa share a similar body plan. Both have a centrally located mouth surrounded by **tentacles**, slender, finger-like extensions used to capture and handle food. The mouth opens into a **gut** where food is digested. The cnidarian gut is a blind cavity with only one opening, the mouth. Cnidarians capture small prey by discharging their **nematocysts**, unique stinging structures found on the tentacles (see Fig. 7.7).

The radially symmetrical cnidarians exist as polyps, medusae, or both, in alternation. Nematocysts, stinging structures unique to cnidarians, are present in tentacles used to capture prey.





**FIGURE 7.5** The flower-like appearance of many cnidarians is a consequence of their radial symmetry. In both the medusa and polyp, tentacles are arranged and repeated around a central axis that runs through the mouth.

Two layers of cells form the body wall of cnidarians. One of these, the **epidermis** (see Fig. 7.7), is external, whereas the other, the **gastrodermis**, lines the gut. There is also a narrow middle layer, or **mesoglea** (see Fig. 7.7), that usually does not contain cells. In medusae this layer is expanded to form the domed bell. The layer is also gelatinous, hence their common name of jellyfish. They are of course not related to fish at all.

# **Types of Cnidarians**

The basic cnidarian body plan, though structurally simple, has been very successful. Some 9,000 species are known, almost all of which are marine. The variety of shapes and colors of cnidarians contributes much to the beauty of the oceans.

## Hydrozoans

The **hydrozoans** (class **Hydrozoa**) have a wide range of forms and life histories. Many consist of feathery or bushy colonies of tiny polyps. They attach to pilings, shells, seaweeds, and other surfaces (Fig. 7.6). The polyps may be specialized for feeding, defense, or reproduction.

Reproductive polyps produce minute, transparent medusae. These medusae, usually planktonic, release gametes. The fertilized eggs develop into free-swimming larvae. The characteristic larva of most cnidarians is the **planula**, a

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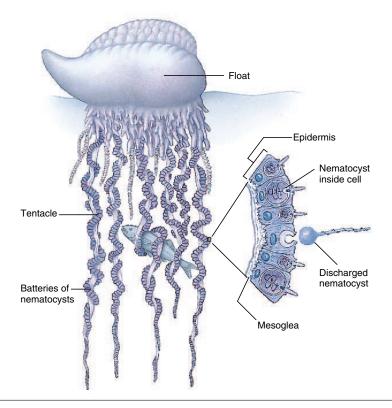
**FIGURE 7.6** Colonial hydrozoans include this feather-like colony of a hydroid living on a seagrass (*Thalassia*) leaf.

cylindrical, ciliated stage consisting of two layers of cells. After a time in the plankton, the planula settles on the bottom and metamorphoses into a polyp. This first polyp divides repeatedly and develops into a colony of many interconnected polyps. Some hydrozoans lack a polyp stage and, instead, their planula develops into a medusa. Others lack a medusa stage and, instead, the polyp produces gametes directly.

**Siphonophores** are hydrozoans that form drifting colonies of polyps. Some polyps in a siphonophore colony may be specialized as floats, which may be gasfilled, as in the Portuguese man-of-war (*Physalia physalis*; Fig. 7.7), or contain droplets of oil. Other siphonophore polyps form long tentacles used to capture prey. Toxins from the nematocysts can produce painful reactions in swimmers or divers (see "The Case of the Killer Cnidarians," p. 123).

## Scyphozoans

The larger jellyfishes common in all oceans are quite different from the often tiny hydrozoan medusae. These medusae (Fig. 7.8) are the dominant stage of the



**FIGURE 7.7** A diagrammatic representation of the Portuguese man-of-war (*Physalia physalis*). It consists of a colony of specialized polyps, one of which forms a gas-filled float that may reach 30 cm (12 in) in length. The long tentacles, here contracted, are armed with nematocysts notorious for their ability to sting swimmers.

life cycle of scyphozoans (class Scyphozoa). The polyps of scyphozoans, are very small and release juvenile medusae. A few species lack a polyp stage altogether. The rounded body, or **bell**, of some scyphozoan medusae may reach a diameter of 2 m (6.6 ft) in some species. Scyphozoans swim with rhythmic contractions of the bell, but their swimming ability is limited and they are easily carried by currents. Some scyphozoan medusae are among the most dangerous marine animals known, giving extremely painful and sometimes fatal stings. This is particularly true of cubomedusae, once classified as scyphozoans but now placed in their own cnidarian group, the class Cubozoa (see "The Case of the Killer Cnidarians," p. 123).

## Anthozoans

Anthozoans (class Anthozoa), solitary or colonial polyps that lack a medusa stage, include the largest number of cnidarian species. The anthozoan polyp is more complex than hydrozoan or scyphozoan polyps. The gut, for instance, contains several thin partitions, or septa, that provide additional surface area for the digestion of large prey (see Fig. 14.1). Sea anemones are common and colorful anthozoans that often have large polyps (see Fig. 11.24). Colonial anthozoans occur in an almost infinite variety of shapes. The mostly colonial stony corals have calcium carbonate skeletons that may form coral reefs. Though stony corals can be found in cold waters, it is in the tropics that they are active in reefbuilding (see "Reef Corals," p. 298). Gorgonians, such as sea fans (Fig. 7.9), are colonial anthozoans that secrete a tough branching skeleton made of protein. Precious corals are gorgonians with fused red or pink calcareous spicules in addition to the protein skeleton. Black corals, which are neither gorgonians nor stony corals, secrete a hard, black, pro-

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**FIGURE 7.8** Scyphozoan medusae are larger and more complex than hydrozoan medusae. This example is the sea nettle (*Chrysaora quinquecirrba*), which is found from Cape Cod to the Gulf of Mexico. It is especially common in Chesapeake Bay.



**FIGURE 7.9** Sea fans are gorgonians with branches that grow in only one plane and have many cross-connections.

tein skeleton. Both precious and black corals are carved into jewelry. Some anthozoans form fleshy colonies with large polyps and no hard skeletons. Examples of these are the soft corals, sea pens (see Fig. 13.13), and sea pansies.

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The stings of most cnidarians are harmless to humans, but there are exceptions. Delicate and innocent-looking, some cnidarians are among the most dangerous marine animals. The sinister side of these creatures is due to the potent toxins released by their nematocysts.

The Portuguese man-of-war (*Physalia*), a siphonophore, is found in warm waters around the world. Though its blue, sail-like float can be seen fairly easily, its long tentacles are nearly invisible. Armed with thick batteries of nematocysts, these tentacles may reach 50 m (164 ft) in length. Portuguese men-of-war may occur by the thousands, sometimes forcing the closure of beaches. Pieces of tentacle that wash ashore can be as nasty as the whole animal.

*Physalia* stings are very painful, like being repeatedly burned with a hot charcoal. The pain may last for hours, especially if sensitive areas of the body are affected. Red lines appear wherever tentacles have touched the skin, and welts usually follow. Both of the authors have had encounters with *Physalia*, painful but fortunately less severe than the experiences of others. One of us saw a man get stung on the hand. When the wave of intense pain reached his armpit, the man passed out. Even more severe reactions may occur. There can be nausea and difficulty in breathing. Contact of tentacles with the eye may damage the cornea. Allergic reactions to the toxin may cause shock and even death, and swimmers may drown because of pain or shock.

If you are stung, the best thing to do is not to panic. Carefully wash the area with seawater, but don't rub the area or wash with fresh water because this stimulates firing of the nematocysts. Vinegar and alcohol will inactivate the nematocysts. Urine may be useful if nothing else is available. The toxin is a protein, and some recommend papain, a protein-digesting enzyme found in meat tenderizer. The meat tenderizer is of little help, however, because the poison is injected into the skin while the meat tenderizer remains on the surface. Severe reactions should be treated in a hospital.



Sting of Chiropsalmus, a cubomedusa.

A group of medusae, the cubomedusae, release even more powerful toxins. The sea wasp, or box jellyfish, *Chironex fleckeri*, of northern Australia, Southeast Asia, and the Indian Ocean, has been responsible for many known deaths. Its stings cause immediate, extreme pain. Death due to heart failure may follow within minutes, especially in children. Skin that touches the tentacles swells up, and the purple or dark brown lines that are left are slow to heal. Fortunately, an antivenin ("antivenom") has been developed. Otherwise, the recommended first aid is to dowse the sting with vinegar. There are other tropical cubomedusae that give severe stings, particularly in Australia and the West Indies.

Cubomedusae (class Cubozoa) are more common along the coast during summer. Their transparent, almost square bells are difficult to see in the water. Most are small, but in the sea wasp the bell may reach 25 cm (almost 10 in) in diameter, and the tentacles may stretch to 4.5 m (15 ft).

# **Biology of Cnidarians**

The presence of tissues allows cnidarians to perform more complex functions than sponges can. In particular, cnidarians display advances in feeding and can sense and respond to their environment.

#### Feeding and Digestion

Practically all cnidarians are **carnivores**, animals that prey on other animals. Many must capture and digest prey much bigger than that of filter feeders such as sponges. Nematocysts are used primarily to capture prey. They consist of a fluid-filled capsule containing a thread that can be quickly ejected (Fig. 7.7). The thread may be sticky or armed with spines, or be a long tube that wraps around parts of the prey. Some nematocysts contain toxins. After ingestion, food passes into the gut where it is digested. The initial phase of digestion is said to be **extracellular** because it takes place outside cells. **Intracellular digestion** within cells lining the gut completes the breakdown of food.

### Behavior

Though cnidarians lack a brain or true nerves, they do have specialized **nerve cells**. These cells interconnect to form a **nerve net** that transmits impulses in all directions. This simple nervous system can produce some relatively sophisticated behaviors. Some anemones can tell whether other members of the same species are also members of the same group, or clone. They are known to attack using special nematocysts that may actually kill anemones from other clones! Some medusae have primitive eyes. Medusae also have **stato-cysts**, small calcareous bodies in fluid-filled chambers surrounded by sensitive hairs. Statocysts give medusae a sense of balance.

# COMB JELLIES: RADIAL SYMMETRY ONE MORE TIME

The **comb jellies**, or **ctenophores** (phylum **Ctenophora**), are an exclusively marine group of about 100 species. Their radially symmetrical and gelatinous body resembles that of a medusa (Fig. 7.10), but a closer look reveals some unique traits. Eight rows of **ciliary combs**, long cilia fused at the base like combs, beat in



FIGURE 7.10 This comb jelly (*Mnemiopsis leidyi*) displays the rows of ciliary combs characteristic of the group. Four rows are visible here, the middle ones appearing as multicolored bands. The species is common along the Atlantic coast of North America but it has been accidentally introduced into other locations.

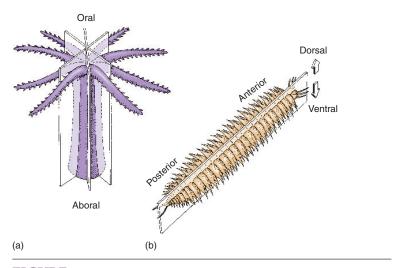
waves and are used in swimming. The continuous beating of the ciliary combs refracts light, creating a prism-like multicolor effect. Body length varies from a few millimeters in the sea gooseberry (*Pleuro-brachia*) to 2 m (6.6 ft) in the elongated Venus's girdle (*Cestum*; see Fig. 15.12c).

Comb jellies, or ctenophores, are radially symmetrical invertebrates similar in appearance to cnidarians but possessing eight rows of ciliary combs.

Comb jellies are common in both warm and cold waters. They are carnivores with a voracious appetite. Swarms of comb jellies may consume large numbers of fish larvae and other plankton (see "Biological Invasions: The Uninvited Guests," p. 420). Many capture their prey using two long tentacles armed with sticky cells named **colloblasts.** Unlike cnidarians, comb jellies lack nematocysts.

# BILATERALLY SYMMETRICAL WORMS

Radial symmetry works fairly well in animals that attach to surfaces or drift in currents, but animals that crawl or swim in



**FIGURE 7.11** The radial symmetry of a soft coral's polyp (a) in contrast to the bilateral symmetry of a worm (b). Notice that bilateral symmetry implies the development of an anterior end with a head, brain, eyes, and all the other features demanded by more complex behaviors.

one direction have different needs. Most animals show bilateral symmetry, the arrangement of body parts in such a way that there is only one way to cut the body and get two identical halves (Fig. 7.11b). Bilaterally symmetrical animals, including humans, have a front, or anterior, end and a rear, or posterior, end. At the anterior end is a head with a brain, or at least an accumulation of nerve cells, and sensory organs such as eyes. Similarly, bilaterally symmetrical animals have a back, or dorsal surface, that is different from the belly, or ventral surface. Bilateral symmetry allows for animals to be more active in the pursuit of prey and to develop more sophisticated behaviors than those of radially symmetrical animals.

## **Flatworms**

The simplest bilaterally symmetrical body plan is seen in elongate, creeping worms. In the marine world worms come in all shapes and sizes. Among the structurally simplest are the **flatworms** (phylum **Platyhelminthes**), so called because they are dorsoventrally flattened, that is, they have flat backs and bellies. Flatworms also are the simplest animals in which tissues are organized into real organs and organ systems.

The presence of a central nervous system in which information is stored and processed is of special significance. In flatworms it typically consists of a simple brain, which is just an aggregation of nerve cells in the head. There are also several nerve cords running from the brain through the length of the worm. The nervous system coordinates the movements of a well-developed muscular system. The gut is similar to those of cnidarians and ctenophores in having only one opening to the outside, the mouth. The space between the outer and inner tissue layers, however, is no longer thin or gelatinous as in cnidarians and ctenophores, but is filled with tissue. In developing embryos this middle layer of tissue, the mesoderm, gives rise to muscles, the reproductive system, and other organs-not only in flatworms, but also in higher animals.

Flatworms are bilaterally symmetrical invertebrates typically flattened in appearance. They have true organs and organ systems, including a central nervous system.

There are approximately 20,000 species of flatworms. The most commonly seen marine flatworms are the **turbellarians**, a group consisting mostly of free-living

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FIGURE 7.12 A turbellarian flatworm from a coral reef in Chuuk (Truk) Island, Micronesia. Cilia on the underside and mucus help in movement. Also see the photo on page 69.

carnivores. Most are small, but some are obvious because of their striking color patterns (Fig. 7.12). Some turbellarians live inside or on the surface of oysters, crabs, and other invertebrates.

The largest group of flatworms, more than 6,000 species, is the **flukes**, or **trematodes.** All flukes are **parasites**, which live in close association with other animals and feed on their tissues, blood, or intestinal contents. Like most parasites, flukes have complex life histories with amazing reproductive abilities, a key to their success. Adult flukes always live in a vertebrate. Larvae may inhabit invertebrates like snails or clams or vertebrates like fish. The larva must then be eaten by the vertebrate destined to harbor the adult. Flukes are common in fishes, seabirds, and whales.

Tapeworms, or cestodes, are parasitic flatworms that, with a few exceptions, have a long body that consists of repeated units. These unique worms hang inside the intestine of most species of vertebrates, including marine ones. The head of the worm attaches to the walls of the gut by means of suckers, hooks, or other structures. Tapeworms lack a gut or mouth. They absorb nutrients from their host's intestinal contents directly across the body wall. Their larvae are found in invertebrates or vertebrates. Tapeworms may reach a prodigious length. The record appears to be a species found in sperm whales that is 15 m (50 ft) long!

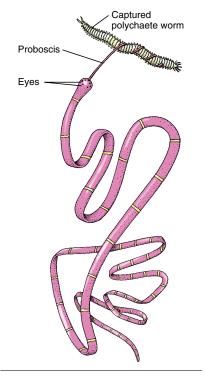


FIGURE 7.13 Ribbon, or nemertean, worms use a proboscis to entangle prey. It may be armed at the tip with a spine and secrete toxins. Once the prey is captured, the proboscis is pulled back and it's dinner time.

## **Ribbon Worms**

Though they look like long flatworms, ribbon, or nemertean, worms (phylum Nemertea) show several features that indicate a more complex degree of organization. Their digestive tract is complete, with a gut that includes a mouth and an anus to get rid of undigested material. They also have a circulatory system, by which blood transports nutrients and oxygen to tissues. The most distinctive feature of ribbon worms, however, is a proboscis (Fig. 7.13), a long, fleshy tube used to entangle prey. It is everted from a cavity above the mouth like the finger of a glove. All ribbon worms are predators that feed on worms and crustaceans.

There are approximately 900 species of ribbon worms, most of which are marine. They are found throughout all oceans but are more common in shallow temperate waters. Some are nocturnal

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and not easily seen; others are brightly colored and may be found under rocks at low tide. Ribbon worms are incredibly elastic, and the proboscis may extend a meter or more beyond the body. One species reaches 30 m (100 ft) long, which makes it the longest animal on earth!

# Nematodes

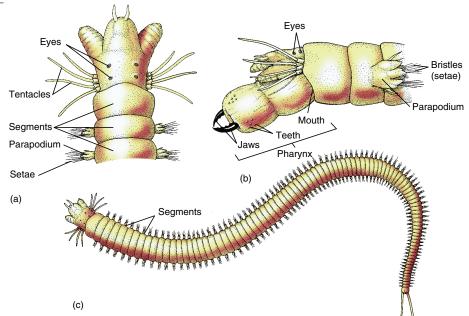
Nematodes (phylum Nematoda), some of which are known as roundworms, are hardly ever seen, but their numbers in sediments, particularly those rich in organic matter, can be staggering. Many species are parasitic, and most groups of marine organisms have nematode parasites. Nematodes are perfectly adapted to live in sediments or the tissues of other organisms. They are mostly small, and their slender and cylindrical bodies are typically pointed at both ends (see the figure in "Life in Mud and Sand," p. 283). Nematodes that inhabit sediments feed mostly on bacteria and organic matter. The gut, which ends in an anus, lies within a body cavity filled with fluid that transports nutrients. A layer of muscles in the tough but flexible body wall pushes and squeezes against the fluid, which acts as a hydrostatic skeleton that provides support and aids in locomotion.

Nematodes are very common inhabitants of marine sediments and are widespread parasites of most groups of marine animals.

The actual number of species of nematodes is debatable. Estimates vary between 10,000 and 15,000 species, but some biologists believe there may be as many as half a million species, most of which remain to be discovered.

The adults of *Anisakis* and a few related nematodes inhabit the intestine of seals and dolphins. Their larvae, however, are found in the flesh of many types of fish and may infect humans when raw or poorly cooked fish is eaten. Often the larvae are vomited or coughed up without further complications. Sometimes, however, larvae penetrate into the walls of the stomach or intestine, causing symptoms similar to those of ulcers. It is a risk that lovers of raw fish dishes such as *sashimi* and *ceviche* must take.

**FIGURE 7.14** This sandworm (*Nereis*) illustrates the meaning of the name polychaetes—"many setae, or bristles." (*a*) Dorsal view of the head, with the pharynx retracted, showing the sensory tentacles and eyes. (*b*) Side view of the head, showing the large pharynx in an extended position. (*c*) Dorsal view of the worm.



# Segmented Worms

A large group of perhaps as many as 15,000 species, the segmented worms, or annelids (phylum Annelida), includes earthworms and many marine worms. Their body plan includes innovations that have been incorporated in some of the more structurally complex groups of animals. The body consists of a series of similar compartments or segments, a condition known as segmentation. Segmentation can be clearly seen in the rings of the familiar earthworm. The gut goes through all the segments and lies in a cavity known as a coelom. The coelom is lined with a different type of tissue, which develops from mesoderm in contrast to the simpler body cavity of nematodes. The coelom is filled with fluid and divided by partitions that correspond to the external segments. The segments act as a hydrostatic skeleton and can be contracted in sequence by means of muscles in the body wall. These movements, plus the flexibility given by segmentation, make annelids efficient crawlers and burrowers.

### Polychaetes

Almost all marine annelids are **polychaetes** (class **Polychaeta**), which are common and important in many environments. Each of their body segments has a pair of flattened extensions, or **parapodia**, which are provided with stiff and sometimes sharp bristles, or **setae** (Fig. 7.14).

Annelids have a body consisting of similar segments and a coelom. Most marine annelids are polychaetes, segmented worms that have parapodia.

Like all annelids, polychaetes have a circulatory system that transports nutrients, oxygen, and carbon dioxide. Circulating blood always remains within distinct blood vessels, making it a **closed circulatory system.** Muscular contraction of vessels helps in the circulation of blood.

In small animals, oxygen—essential in the release of energy through **respiration** can easily move from the water across the body wall to all the tissues. In the larger and relatively more active polychaetes, however, obtaining enough oxygen from the water is a potential problem. Polychaetes have solved this problem by evolving **gills** on the parapodia or elsewhere (see Fig. 7.15*a*). The gills are thinwalled extensions of the body wall that have many blood vessels called **capillaries**, which allow for the easy absorption of oxygen. This absorption of oxygen, along with the elimination of carbon dioxide, is known as gas, or respiratory, exchange.

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The life history of many polychaetes involves a planktonic larval stage known as the **trochophore**, which has a band of cilia around the body (see Fig. 15.11*d*). The trochophore is of considerable interest because it is also a larval stage in other groups of invertebrates.

The more than 10,000 species of polychaetes are almost entirely marine. Length varies a great deal but is typically around 5 to 10 cm (2 to 4 in). Many polychaetes crawl on the bottom, hiding under rocks or coral. These crawling worms, such as most sandworms (*Nereis*), are mostly carnivores. They feature heads provided with several pairs of eyes and other sense organs (Fig. 7.14) used to search for small invertebrates. A proboscis, often armed with jaws, is used to capture prey. The parapodia are well developed and are used in locomotion.

Other polychaetes burrow in mud or sand (see Fig. 11.29). Many, like bloodworms (*Glycera*), capture small prey. Others, like lugworms (*Arenicola*), feed on organic particles that settle on the bottom. This feeding technique is known as **deposit feeding**, in contrast with

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(a)

(b)

**FIGURE 7.15** Polychaetes are common inhabitants of most marine bottoms. (*a*) The anterior end of a free-living polychaete (*Hermodice carunculata*), a fireworm that feeds on corals. The bright-red structures are gills. (*b*) Sabella melanostigma, a feather-duster worm, inhabits leathery tubes.

suspension feeding, which involves feeding on organic particles and plankton in the water (Fig. 7.16).

Many polychaetes live singly or in aggregations in a wide variety of tubes they build, either temporary or permanent (see Figs. 12.11h and 13.6i). The tubes may be made of mucus, protein, bits of seaweed, cemented mud particles, sand grains, or tiny fragments of shells. Tubedwelling polychaetes usually have reduced parapodia. Some, such as Terebella and related forms (see Fig. 13.11), are suspension feeders. Their tentacles have cilia and mucus that catch organic particles in the water and move them to the mouth (Fig. 7.16). Fanworms, or feather-duster worms (Sabella; Fig. 7.15b), use feathery tentacles covered with cilia to capture, sort, and transport particles. Serpulids (Serpula) and spirorbids (Spirorbis), also suspension feeders, extend feather-like tentacles from calcium carbonate tubes they build on rocks and other surfaces (see Fig. 13.17*d*).

Polychaetes are successful at other lifestyles. Species of *Tomopteris* are planktonic throughout life. Their parapodia are flat and expanded to help in swimming (see Fig. 15.12*d*). In the tropical Pacific the bodies of the Palolo worm (*Eunice*) periodically break off and the posterior half swims up to the surface to spawn. This behavior, known as **swarming**, is timed in some areas with the phases of the moon, reaching its peak just after full moon. Some polychaetes live on the external surface of such invertebrates as sea stars and sea urchins. Several species live in the burrows of other invertebrates or inhabit shells occupied by hermit crabs.

## Oligochaetes

**Oligochaetes** are small worms found in mud and sand (see "Life in Mud and Sand," p. 283), where they feed on organic matter. They are the marine relatives of earthworms. Some species may be very abundant. Unlike polychaetes, oligochaetes lack parapodia.

## Leeches

Bloodsucking **leeches** (class **Hirudinea**) live mostly in fresh water but marine species can be found attached to marine fishes and invertebrates. Leeches are highly specialized annelids distinguished by a sucker at each end and no parapodia.

# Odds and Ends in the World of Worms

A few unique groups, minor but hardy branches of the animal family tree, are variants of the worm body plan. Some show similarities to the segmented worms.

#### Peanut Worms

Often called **peanut worms**, the **sipunculans** (phylum **Sipuncula**) have soft, unsegmented bodies. They burrow in muddy bottoms, rocks, and corals, or hide in empty shells. All are marine, living mostly in shallow water. The long anterior portion contains a mouth and a set of small lobes or branching tentacles (Fig. 7.17). These can be pulled into the remaining portion of the body, and the worm then becomes a compact bundle that looks like a large peanut. Most peanut worms are from 1 to 35 cm (0.4 to 14 in) long. More than 250 species are known, all deposit feeders.

## Echiurans

All of the over 100 species of **echiurans** (phylum **Echiura**) are marine. They look like soft, unsegmented sausages buried in the mud. They are similar to peanut worms in shape and size except for having a non-retractable, spoon-like or forked proboscis (see Fig. 13.9). Echiurans are deposit feeders that use the proboscis to gather organic matter. The "fat innkeeper" (*Urechis caupo*) of the western coast of North America lives in U-shaped tubes in mud (see Fig. 12.11*e*).

## Beard Worms

**Beard worms,** or **pogonophorans** (phylum **Pogonophora**), are unique in several ways. These long, thin worms lack a digestive system—mouth and gut included.

**Respiration** Glucose  $+ O_2 \rightarrow CO_2 + H_2O + energy$ *Chapter 4, p. 72* 

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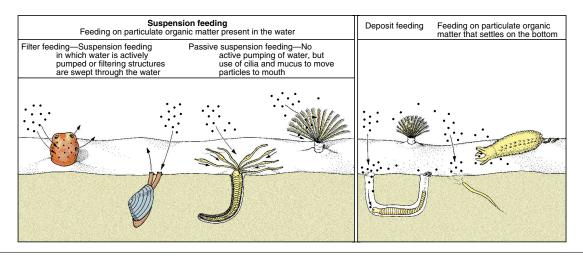


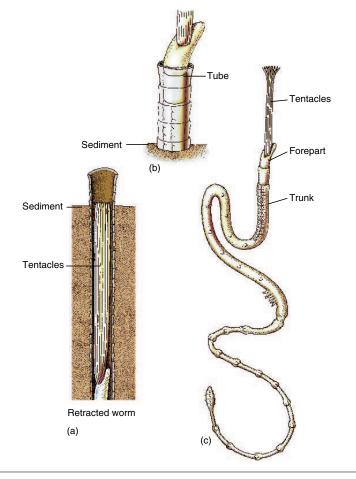
FIGURE 7.16 Feeding on particulate organic matter can be classified as suspension or deposit feeding. The difference between these two types of feeding is not always well defined. Fanworms, for instance, are tube-dwelling polychaetes that switch back and forth between suspension and deposit feeding, depending on the strength of the water current.



**FIGURE 7.17** *Phascolosoma antillarum*, a peanut worm (or sipunculan), burrows in coral and rocks in the Caribbean. The anterior portion, which is extended in this specimen, can be retracted.

Except for sponges and tapeworms, this is an uncommon phenomenon in animals. A tuft of one to many thousand long tentacles (Fig. 7.18), responsible for the group's common name, appears to be involved in absorbing nutrients dissolved in the water. Beard worms have **symbiotic** bacteria that use the nutrients to manufacture food, which in turn is used by the worms.

Approximately 135 species of beard worms are known. They are mostly restricted to deep water, which helps explain why they remained unknown until 1900 (see "How to Discover a New



**FIGURE 7.18** Diagrammatic representation of a beard worm, or pogonophoran. (*a*) Most secrete and live in tubes buried in the soft sediment. (*b*) Only the upper end of the tube protrudes, with the tentacle or tentacles extending from it. (*c*) Worm removed from its tube.

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13.34

# HOW TO DISCOVER A NEW PHYLUM

It is not very difficult to discover a new marine invertebrate species. Small animals living in sediments, among rocky shore seaweeds, or in deep water are good candidates. Discovering a new phylum, however, is a different story.

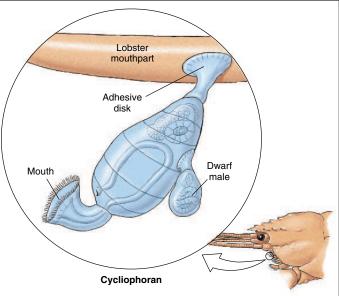
The founding species of four phyla escaped description until last century. All three are exclusively marine. The first new phylum of the century was created for the beard worms, or pogonophorans (see Fig. 7.18). The first beard worm was dredged in Indonesia in 1900, but it was not formally described until 1914. The second species, from the Sea of Okhotsk in eastern Siberia, was described in 1933. More new species were and still are being described, mostly from deep water. A new phylum, **Pogonophora** was officially created for them in 1955.

The first species of what eventually became the new phylum **Gnathostomulida** was not officially described until 1956. Gnathostomulids are a group of about 80 species of minute worms living among sediment particles around the world (see the figure in "Life in Mud and Sand," p. 283). They are similar to the flatworms but possess unique features, including a set of toothed jaws to scrape bacteria, diatoms, and other organisms from sand grains.

The next of the new phyla has a short but turbulent history. In 1961 Robert Higgins, then at the Smithsonian Institution in Washington, D.C., predicted the existence of a group that lived in the spaces between clean, coarse sediment particles in deep water. He actually found a specimen in 1974 but unfortunately did not realize it was something new.

One year later, in 1975, Reinhardt Kristensen of the University of Copenhagen, Denmark, collected a specimen, but it was destroyed while being prepared for microscopic examination. Kristensen later found larvae of the elusive animal in coarse sediments from western Greenland and the Coral Sea. In 1982 he was working with a large sample off the coast of Brittany in France. It was his last day at the Roscoff Biological Station, and to save time he washed the sample with fresh water instead of following the standard but more time-consuming method. It happened to loosen the grip of the animals on the sediment particles, and Kristensen got a complete series of larval and adult specimens!

The microscopic animals Kristensen found have a body encased by six plates. The head, which can be retracted, bears a set of spines and a mouth at the end of a cone. Kristensen got together with Higgins, and they concluded that the specimens Higgins examined in 1974 and those subsequently found by Kristensen were members of a new phylum. They found additional adults in eastern Florida, which further confirmed the new status of the group.



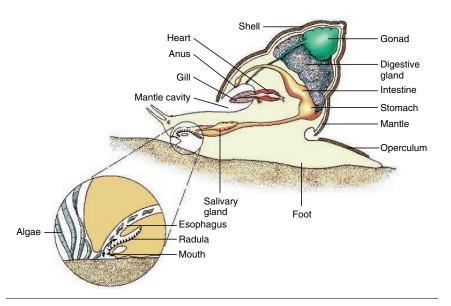
The new phylum **Loricifera** (meaning "armor bearer") was officially born in 1983 when Kristensen published a paper in a German scientific journal. The first species was named *Nanaloricus mysticus* ("mystic, or enigmatic, dwarf armor") and the larva was baptized the Higgins larva in honor of Higgins, a nice consolation prize indeed! Some 12 additional species have so far been described.

The latest new phylum comes from another unexpected location: the hairs around a lobster's mouth! Though first observed in the 1960s, the phylum **Cycliophora** was not described until 1995. So far it consists of one species, *Symbion pandora*, a tiny bottleshaped sac with a disk-like mouth. Cilia around the mouth sweep food particles that come off the lobster's mouth at mealtime.

This strange lifestyle coincides with a bizarre life cycle. The minute but multicellular animal—hundreds often live on a lobster—alternates sexual and asexual generations. Dwarf males, which live attached to females, exist only to produce sperm. Females also reproduce asexually, but they produce only females that develop inside box-like structures inside their mothers. The new generation of females is set free from the boxes as it bursts out from the mothers. The Greek myth of a box that Pandora (and hence the name of the first cycliophoran) opened to allow all human ills to escape is thus re-created around a lobster's mouth.

Phylum," above). The total length of the worms ranges from 10 cm to 2 m (4 in to 7 ft). Vestimentiferans are even longer. Large numbers of these worms have been found at hydrothermal vents (see Figs. 16.30 and 16.31). Vestimentiferans are usually considered to be pogonophorans but some scientists think they are actually polychaetes, while others think they are a phylum of their own.

Symbiosis The living together in close association of two different species. *Chapter 10, p. 220* 



**FIGURE 7.19** The general body plan of a snail, indicating the most important internal structures. In many species the head and foot can be retracted into the shell, leaving a tough operculum blocking the shell opening.

# MOLLUSCS: THE SUCCESSFUL SOFT BODY

Snails, clams, octopuses, and other familiar forms are members of the phylum **Mollusca. Molluscs** have been very successful: There are more species of molluscs in the ocean than of any other animal group. There may be as many as 200,000 species of molluscs, which are surpassed only by the arthropods as the largest phylum of animals.

Molluscs feature a soft body with a calcium carbonate shell (Fig. 7.19). The body is covered by a mantle, a thin layer of tissue that secretes the shell. The unsegmented body is typically bilaterally symmetrical. There is a ventral, muscular foot, usually used in locomotion. Most molluscs have a head that normally includes eyes and other sensory organs. A unique feature is the radula, a ribbon of small teeth used in feeding, usually to rasp food from surfaces (Figs. 7.19 and 7.20). It is made largely of chitin, a highly resistant carbohydrate also found in other invertebrates. Gas exchange is through paired gills.

All molluscs have this basic body plan, but it is often greatly modified. The shell, for example, is internal in squids and absent in octopuses and a few other groups. In snails, portions of the body are coiled and asymmetrical. In some molluscs the radula is modified or even absent.

The molluscs constitute the largest group of marine animals. Their body is soft with a muscular foot. They usually have a shell and most have a radula, a rasping "tongue" unique to the group.

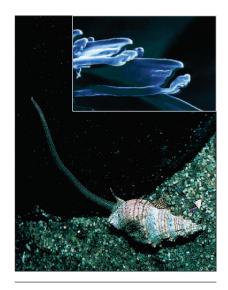
# **Types of Molluscs**

Molluscs exhibit an immense diversity of structure and habit. They occupy all marine environments from the wave-splashed zone of rocky shores to hydrothermal vents in the deep sea. They thrive on practically every conceivable type of diet. For all their diversity, though, most molluscs belong to one of three major groups.

#### Gastropods

The **gastropods** (class **Gastropoda**), are the largest, most common, and most varied group of molluscs. Snails are the most familiar gastropods, but the group in-

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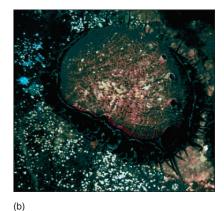
**FIGURE 7.20** The Cooper's nutmeg snail (*Cancellaria cooperi*) seeks out electric rays, which rest partially buried in sand. It then extends its long proboscis, makes a tiny cut in the ray's skin with the radula at the end of the proboscis, and then sucks the ray's blood. A high magnification photo (inset) shows the teeth of the radula.

cludes other forms such as limpets, abalones, and nudibranchs (Fig. 7.21). There are perhaps 75,000 species, mostly marine. A typical gastropod (the term means "stomach footed") can best be described as a coiled mass of vital organs enclosed by a dorsal shell (Fig. 7.19). The shell rests on a ventral creeping foot and is usually coiled.

Most gastropods use their radula to scrape algae from rocks, as in periwinkles (Littorina; see Fig. 11.2), limpets (Fissurella, Lottia; Fig. 7.21a), and abalones (Haliotis; Fig. 7.21b). Some, like mud snails (Hydrobia), are deposit feeders on soft bottoms. Whelks (Nucella, Buccinum; see Fig. 11.19), oyster drills (Murex, Urosalpinx), and cone shells (Conus; Fig. 7.21c), are carnivores. They prey on clams, oysters, worms, or even small fishes. The violet snail Janthina (see the photo on page 323) has a thin shell and produces a bubble raft out of mucus to float on the surface looking for siphonophores, its prey. Sea hares (Aplysia), which graze on seaweeds, have small, thin shells buried in tissue.

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(a)



(c)

(d)

**FIGURE 7.21** Gastropods come in all shapes, colors, and habits. (*a*) The giant keyhole limpet (*Megathura crenulata*), from the Pacific coast of North America, photographed on a bottom covered by encrusting red coralline algae. (*b*) The red abalone (*Haliotis rufescens*) is much sought after for food and is now rare in some areas. (*c*) Cone shells, such as *Conus geographus*, are carnivorous snails that bury themselves in sand, waiting for prey such as small fishes. Their radula is modified into a dart-like tooth that is shot—together with a poison—into the unsuspecting prey, which is eaten whole, very much as in snakes. (*d*) A flashy nudibranch (*Phidiana crassicornis*).

Nudibranchs, or sea slugs, are gastropods that have lost the shell altogether. Colorful branches of the gut or exposed gills make sea slugs among the most beautiful of all marine animals (Fig. 7.21*d*). They prey on sponges, hydroids, and other invertebrates. As a defensive mechanism, sea slugs often retain noxious chemicals or undischarged nematocysts taken undigested from their prey.

## Bivalves

**Bivalves** (class **Bivalvia**) are the clams, mussels, oysters, and similar molluscs. Bivalves retain the basic molluscan body plan, but it is modified. (Fig. 7.22). The body is laterally compressed and enclosed in a two-valved shell. There is no head to speak of, and no radula. The gills, expanded and folded, are used not only to obtain oxygen, but also to filter and sort small food particles from the water. The inner surface of the shell is lined by the mantle, so that the whole body lies in the **mantle cavity**, a large space between the two halves of the mantle. Strong muscles are used to close the valves.

Clams (Macoma, Mercenaria) use their shovel-shaped foot to burrow in

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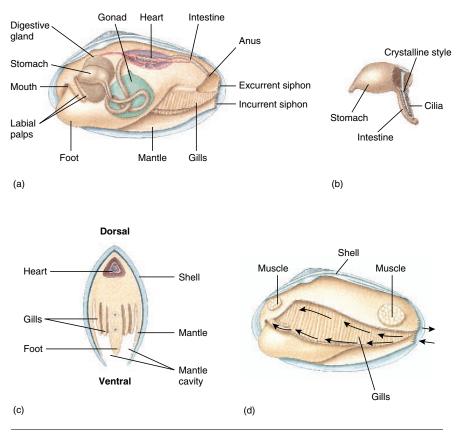
sand or mud (see Figs. 11.28 and 12.11*f*). When the clam is buried, water is drawn in and out of the mantle cavity through **siphons** formed by the fusion of the edge of the mantle (Fig. 7.22*a* and *d*). This allows clams to feed and obtain oxygen while buried in sediment.

Not all bivalves are burrowers. Mussels (Mytilus; see Fig. 11.4), for instance, secrete strong byssal threads that attach them to rocks and other surfaces. Oysters (Ostraea, Crassostrea; Fig. 7.23a) cement their left shell to a hard surface, often the shell of another oyster. Aphrodisiac or not, they have been lustfully swallowed by lovers of good food for thousands of years. Pearl oysters (Pinctada) are the source of most commercially valuable pearls. Pearls are formed when the oyster secretes shiny layers of calcium carbonate to coat irritating particles or parasites lodged between the mantle and the iridescent inner surface of the shell, which is called mother-of-pearl. Cultured pearls are obtained by carefully inserting a tiny bit of shell or plastic in the mantle. Some scallops (Pecten; Fig. 7.23b) live unattached and can swim for short distances by rapidly ejecting water from the mantle cavity and clapping the valves. The largest bivalve is the giant clam (Tridacna; see Fig. 14.34), which grows to more than 1 m (3 ft) in length.

Many bivalves bore in coral, rock, or wood. The shipworm (*Teredo*) bores in mangrove roots, driftwood, and wooden structures such as boats and pilings. They use their small valves to excavate the wood, which is eaten. Symbiotic bacteria in the shipworm's gut digest the wood. The rasping valves lie at the inner end of a tunnel lined with calcium carbonate, and a tiny siphon protrudes from the entrance at the other end. Shipworms are an example of a **fouling organism**, one that settles on the bottoms of boats, pilings, and other submerged structures.

## Cephalopods

The **cephalopods** (class **Cephalopoda**), voracious predators that are specialized for locomotion, include the octopuses, squids, cuttlefishes, and other fascinating creatures. Cephalopods adapt the molluscan



**FIGURE 7.22** A laterally compressed body is the most distinctive feature of bivalves, illustrated here by a clam. The gills, which hang on both sides of the body (a, c), sort out food particles and transport them to the mouth with the help of cilia and mucus. The palps then push the food into the mouth. Food is then digested in the stomach with the help of the crystalline style (b). The path of the particles from the incurrent siphon to the mouth is indicated by arrows (d).

body plan to an active way of life. Many are agile swimmers with a complex nervous system and a reduction or loss of the shell. All 650 living species are marine. A cephalopod (the name means "headfooted") is like a gastropod with its head pushed down toward the foot. The foot is modified into arms and tentacles, usually equipped with suckers that are used to capture prey (Fig. 7.24). The large eyes, usually set on the sides of the head, are remarkably like ours. The body, rounded in octopuses and elongate in squids, is protected by a thick and muscular mantle. The mantle forms a mantle cavity behind the head that encloses two or four gills. Water enters through the free edge of the mantle and leaves through the siphon, or funnel, a muscular tube formed by what

remains of the foot, which projects under the head. Cephalopods swim by forcing water out of the mantle cavity through the siphon. The flexible siphon can be moved around, allowing the animal to move in practically any direction, an example of jet propulsion in nature.

Octopuses (*Octopus*)—not "octopi" have eight long arms and lack a shell (Fig. 7.24). They are common bottom dwellers. Including arms, the size varies from 5 cm (2 in) in the dwarf octopus (*Octopus joubini*) to a record of 9 m (30 ft) in the Pacific giant octopus (Fig. 7.25*a*).

Octopuses are efficient hunters, with crabs, lobsters, and shrimps among their favorite dishes. The prey is bitten with a pair of beak-like jaws. The radula may help in rasping away flesh. They also se-

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(a)



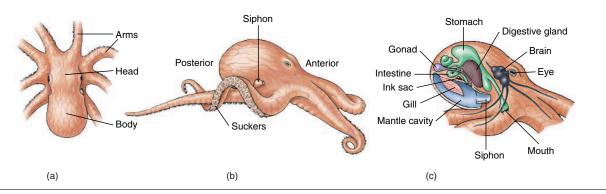
(b)

**FIGURE 7.23** Oysters such as *Crassostrea virginica* (*a*) are harvested commercially around the world (see Fig. 17.15). Some scallops, such as *Pecten ziczac* (*b*), live free on the bottom. Other bivalves bury themselves in sand or mud.

crete a paralyzing substance, and some have a highly toxic bite. Most, however, are harmless. They use crevices in rocks, and even discarded bottles and cans, as homes. Their shelters are given away by the presence of rocks, which they move around, and by the remains of crabs. Like most other cephalopods, they can distract potential predators by emitting a cloud of dark fluid produced by the **ink sac** (Fig. 7.24*c*).



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**FIGURE 7.24** External (*a* and *b*) and internal (*c*) structure of the octopus. In the male the tip of the third right arm is modified to transfer packets of sperm from his siphon into the mantle cavity of the female. Copulation is preceded by courtship behavior that includes intricate color changes.



**FIGURE 7.25** (a) The Pacific giant octopus (*Octopus dofleini*). (b) Mating squids (*Loligo opalescens*). Notice the masses of white, gelatinous egg cases on the bottom.

Squids (Loligo; Fig. 7.25b) are better adapted for swimming than are octopuses. The body is elongate and covered by the mantle, which also, forms two triangular fins. Squids can remain motionless in one place or move backward or forward just by changing the direction of the siphon. Eight arms and two tentacles, all with suckers, circle the mouth. The tentacles are long and retractable and have suckers only at the broadened tips. They can be swiftly shot out to catch prey. The shell is reduced to a chitinous pen that is embedded in the upper surface of the mantle. Adult size varies from tiny individuals of a few centimeters in length to 20 m (66 ft) in the giant squid (Architeuthis), the largest living invertebrate. The giant squid is a deep-water species known mostly from specimens that have been washed ashore or found in the stomachs of sperm whales. Various aspects of the biology of deep-water squids are discussed in "Adaptations of Midwater Animals" (p. 361).

Cuttlefishes (*Sepia*) resemble squids in having eight arms and two tentacles, but the body is flattened and has a fin running along the sides. Cuttlefishes, which are not fish at all, have a calcified internal shell that aids in buoyancy. This shell is the "cuttlebone" sold as a source of calcium for cage birds.

An unusual external shell characterizes the chambered nautilus (*Nautilus*; see "The Chambered Nautilus," p. 376). The impressive shell is smooth, coiled, and up to 25 cm (10 in) in diameter. The shell contains a series of gas-filled chambers that serves as a buoyancy organ. The body—which occupies the outer, largest chamber—has 60 to 90 short, suckerless tentacles used to capture crabs and fish.

**FIGURE 7.26** Chitons such as *Tonicella lineata* use their strong foot and the flexibility provided by the eight articulated shells to fit tightly to the irregular surface of rocky shores.

### Other Molluscs

About 800 species of **chitons** (class **Polyplacophora**) are known, all marine. They can be readily identified by the eight overlapping shell plates that cover their slightly arched dorsal surface (Fig. 7.26). Their internal organs are not coiled as in snails.

Almost all chitons are restricted to rocky shores. Most species use the radula to graze algae from the rocks. Many of them return to a homesite after feeding. One species, however, captures small crustaceans and other invertebrates with a flap-like extension of the mantle that surrounds the mouth.

The 350 or so species of **tusk shells**, or **scaphopods**, (class **Scaphopoda**), have an elongate shell, open at both ends and tapered like an elephant tusk. They live in sandy or muddy bottoms. The narrow end of the shell protrudes from the bottom, Castro–Huber: Marine II. Life Biology, Fourth Edition Enviro

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whereas the foot projects from the wide end. Many species have thin tentacles with adhesive tips. They are used to capture **forams**, young bivalves, and other small organisms from the sediment. Tusk shells are most common in deep water, but empty shells sometimes wash ashore.

The **monoplacophorans** (class **Monoplacophora**) are represented by only a handful of limpet-like molluscs. They were thought to be extinct until their discovery as "living fossils" in 1952. They have now been collected, mostly from deep water, in scattered locations around the world. Monoplacophorans are peculiar because their gills and other organs are repeated along the body, which is reminiscent of the segmentation of annelids.

# **Biology of Molluscs**

The business of life is far more complex in molluscs than in cnidarians and worms. Does this complexity result from their abundance and variety, or is the variety and abundance of molluscs due to their complexity? The answer probably lies somewhere in the middle.

## Feeding and Digestion

The molluscan gut has a separate mouth and anus. Digestion involves **salivary** and **digestive glands** (Fig. 7.19) that release digestive **enzymes**, which break down food into simpler molecules. Other aspects of the digestive system differ among groups and according to diet.

Chitons and many snails are grazers. They have a rasping radula that removes minute algae from surfaces or cuts through large seaweeds. Their relatively simple digestive system can efficiently process large amounts of hard-to-digest plant material. Digestion is partly extracellular in the gut cavity and partly intracellular in the digestive glands. Some shell-less gastropods that feed on seaweeds keep the seaweeds' **chloroplasts** intact. The chloroplasts are kept in the digestive gland and continue to carry out photosynthesis, providing nourishment for the gastropod.

Carnivorous snails have a radula modified to drill, cut, or even capture prey.

The radula and mouth are contained in a proboscis that can be protruded to strike the prey (Fig. 7.20). Jaws may even be present. In these snails, digestion is extracellular and takes place in the stomach.

Bivalves ingest food particles that are filtered and sorted out by the cilia on the gills. The radula is absent, and food enters the mouth trapped in long strings of mucus. An enzyme-secreting rod in the stomach, the crystalline style (Fig. 7.22b), continually rotates the food to help in its digestion. The stomach's contents eventually pass into a large digestive gland for intracellular digestion. The giant clam not only filters food but obtains nutrients from zooxanthellae that live in tiny branches of the gut that extend into its expanded mantle (see Fig. 14.34). This extra nourishment may allow them to attain their giant size.

All cephalopods are carnivores that have to digest large prey. The stomach is sometimes connected to a sac in which digestion is rapidly and efficiently completed. It is entirely extracellular.

Molluscs have a circulatory system that transports nutrients and oxygen. A dorsal, muscular heart pumps blood to all tissues. Most molluscs have an **open circulatory system** in which blood flows out of vessels into open blood spaces. Cephalopods, on the other hand, have a closed circulatory system in which the blood always remains in vessels and can be more effectively directed to oxygendemanding organs such as the brain.

#### Nervous System and Behavior

The nervous system of molluscs shows a wide range of complexity. The relatively simple behaviors of gastropods, bivalves, and chitons do not call for a well-developed brain. Chitons have a nervous system much like that of flatworms. Rather than a single brain, gastropods and bivalves have a set of **ganglia**, or "local brains," clusters of nerve cells located in several parts of the body.

Complexity of the nervous system reaches its highest point in cephalopods, not just for molluscs but for all invertebrates. The separate local brains of other molluscs are fused into a single large brain that coordinates and stores information received from the environment. Different functions and behaviors of cephalopods are controlled by particular regions of the brain, as in humans. Giant nerve fibers rapidly conduct impulses, allowing cephalopods to capture prey or escape at amazing speeds. The strikingly complex eyes of cephalopods reflect the development of their nervous system. Octopuses and cuttlefishes have considerable intelligence and a remarkable capacity for learning. Most cephalopods, especially cuttlefishes, display color changes correlated with particular behaviors and moods, from intricate sexual displays to camouflage. Some cuttlefishes flash two large black spots resembling eyes, perhaps to fool potential predators. Some octopuses even change color and behavior to mimic, or imitate, poisonous fishes and sea snakes.

## Reproduction and Life History

Most molluscs have separate sexes, but some species are **hermaphrodites**, animals in which individuals have both male and female gonads. In bivalves, chitons, tusk shells, and some gastropods, sperm and eggs are released into the water and fertilization is external. Fertilization is internal in cephalopods and most gastropods. When cephalopods mate, the male uses a modified arm to transfer a **spermatophore**, an elongate packet of sperm, to the female. Males of gastropods that copulate have a long, flexible penis.

Some molluscs have a trochophore larva like polychaetes, a characteristic often used as evidence for close affinities among molluscs, the segmented worms, and other groups. In gastropods and bivalves the trochophore usually develops into a veliger, a planktonic larva that has a tiny shell (see Fig. 15.11a). In many gastropods, part or all of development takes place within strings or capsules of eggs. Cephalopods lack larvae, and the young develop from large yolk-filled eggs. Female octopuses protect their eggs until they hatch. The female usually dies afterward because she eats little or nothing while guarding the eggs.

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# ARTHROPODS: THE ARMORED ACHIEVERS

Arthropods (phylum Arthropoda) comprise the largest phylum of animals, with more than a million known species and several million remaining undiscovered. Of all the animals on earth, three out of four are arthropods. They have invaded all types of environments on the earth's surface, including, of course, the oceans. Marine arthropods encompass a huge variety of animals such as barnacles, shrimps, lobsters, and crabs, to name a few.

The arthropod body is segmented and bilaterally symmetrical. In addition to a flexible, segmented body, arthropods have the benefit of jointed appendages such as legs and mouthparts. Another characteristic of arthropods is a chitinous external skeleton, or **exoskeleton**, secreted by the underlying layer of tissue. The exoskeleton is tough and non-living. The body and appendages, all covered by exoskeleton, are moved by sets of attached muscles.

To grow, arthropods must **molt**, or shed their exoskeleton (Fig. 7.27). The rigid old skeleton is discarded, and a new one develops after the animal takes in water to expand itself. Most arthropods are small. The rigid exoskeleton imposes limitations in terms of size and growth. We will never see arthropods as big as giant squids or whales. The exoskeleton and jointed appendages provide protection, support, flexibility, and increased surface area for muscle attachment. These advantages allow arthropods to be very active.

More species belong to the arthropods than to any other animal group. Arthropods have a segmented and bilaterally symmetrical body. Their success in adapting to all types of environments is due in part to a resistant exoskeleton and jointed appendages.

# Crustaceans

The overwhelming majority of marine arthropods are **crustaceans** (subphylum **Crustacea**), a large and extremely diverse group that includes shrimps, crabs, lobsters, and many less familiar animals.



**FIGURE 7.27** This is not really a live Galápagos shore crab (*Grapsus grapsus*) but its exoskeleton, or molt. The old exoskeleton covered the entire external surface of the crab, even its mouthparts and eyes. Molting, which is regulated by hormones, results in a soft, helpless crab that must find shelter for a few days until its new, larger skeleton hardens.

Crustaceans are specialized for life in water and possess gills to obtain oxygen. Their chitinous skeleton is usually hardened by calcium carbonate. The appendages are specialized for swimming, crawling, attaching to other animals, mating, and feeding. Crustaceans possess two pairs of **antennae** (Figs. 7.28 and 7.32), which are usually involved in sensing the surroundings.

There may be as many as 150,000 species of crustaceans, mostly undiscovered. Most are marine. Whereas insects are by far the dominant arthropods on land, crustaceans are their counterparts at sea. The crustacean body plan is repeated in myriad forms, from the familiar to the not so familiar.

Crustaceans are arthropods adapted to live in water. They share the presence of two pairs of antennae, gills, and a calcified exoskeleton.

## The Small Crustaceans

Small crustaceans are everywhere: in the plankton, on the bottom, among sediments, on and in other animals, crawling among seaweeds. **Copepods** are extremely abundant and important in the plankton (see "Copepods," p. 329). They use their mouthparts to filter out or capture food. Some species are so abundant that they are among the most common animals on earth. Many planktonic species keep from sinking by using their enlarged first pair of antennae (Fig. 7.28) to swim. Many species are parasitic, some being so simplified that they look like small bags of tissue.

Barnacles are filter feeders that usually live attached to surfaces, including living surfaces like whales and crabs.

Foraminiferans or Forams Protozoans with tiny calcareous shells.



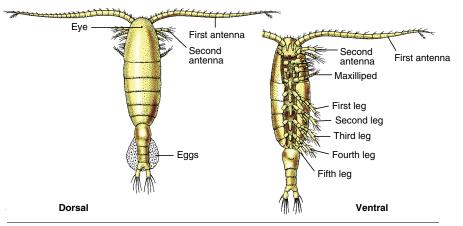
Chapter 5, p. 101; Figure 5.10

**Enzymes** Substances that speed up specific chemical reactions.

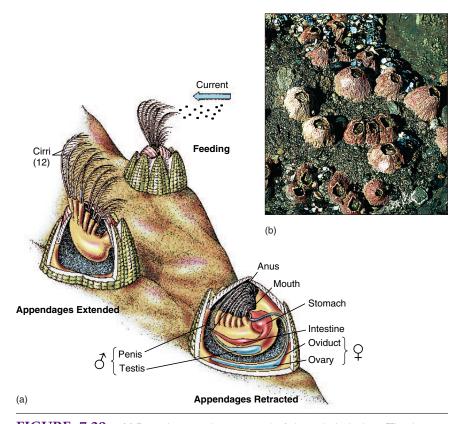
## Chapter 4, p. 70

**Chloroplasts** Cell organelles in plants and other primary producers in which the process of photosynthesis takes place.

Chapter 4, p. 75; Figure 4.8b



**FIGURE 7.28** The structurally simplest and most primitive crustaceans, like this planktonic copepod, tend to be small and have appendages that are similar to each other, that is, less specialized. One exception here is the first antenna, which is specialized for swimming (also see Figs. 15.6 and 15.7). All appendages are paired, but the ventral view above shows only those on one side.



**FIGURE 7.29** (*a*) Barnacles conceal a crustacean body beneath thick plates. They lie on their backs and use their legs to filter feed. Note that barnacles are hermaphrodites. Individuals, however, mate with each other, alternatively taking different sex roles. One individual may act as "male" by inserting its extended penis into a nearby "female." It may then turn into a "female" by accepting the penis of a neighbor. (*b*) The thatched barnacle (*Tetraclita squamosa*) from the Pacific coast of North America.

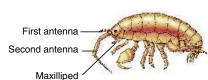


FIGURE 7.30 Most amphipods, like this beach hopper (*Orchestoidea*), can be recognized by their laterally compressed, curved bodies. The skeleton shrimps common among seaweeds and hydroids, however, are amphipods with bizarre skinny bodies. A giant deep-sea amphipod is illustrated in Figure 16.26.

Many are very particular about the type of surface on which they live. Some are among the most important types of fouling organisms.

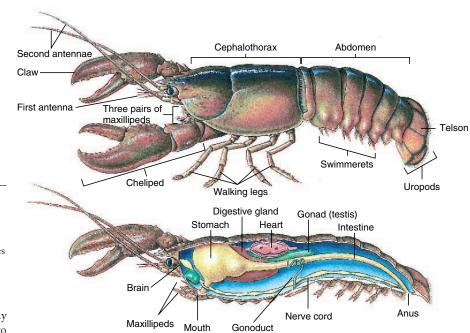
The common barnacles look almost like molluscs because their bodies are enclosed by heavy calcareous plates (Fig. 7.29). The plates on the upper surface open to allow the feathery filtering appendages (**cirri**), which are actually the legs, to sweep the water. Some barnacles have become highly modified parasites and lack plates. All barnacles, however, have typical crustacean larvae, which swim and attach to surfaces before metamorphosis into adults (see Fig. 7.37).

Amphipods are small crustaceans with a body distinctively compressed from side to side (fig. 7.30). Most amphipods are under 2 cm (3/4 in) in length. The head and tail typically curve downward, and the appendages are specialized according to function. Beach hoppers, common among debris washed ashore, are strong jumpers that spring about by briskly stretching their curved bodies. Other amphipods crawl among seaweeds. Burrowing in the skin of whales (as whale lice; see Fig. 10.9) and living as part of the plankton are some other lifestyles in this large, mostly marine group of over 5,000 species.

**Isopods** are found in many of the same environments exploited by amphipods. They are about the same size as amphipods, but isopods are easily identifiable because they are flat from top to bottom (dorsal to ventral) and have legs that are similar to each other (Fig. 7.31). Pill bugs, or roly-polies, are common

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FIGURE 7.31 The sea louse, or sea roach (*Ligia oceanica*), is neither a louse nor a roach but an isopod. It feeds mainly on decaying seaweeds carried in to shore by the waves. Some isopods live as parasites on fishes (see Fig. 10.10).

land isopods that are similar to many marine species. **Fish lice** (no relation to lice of birds and land mammals, which are insects) and other isopods are parasites of fishes (see Fig. 10.10) and other crustaceans.

**Krill,** or **euphausiids**, are planktonic, shrimp-like crustaceans of moderate size, up to 6 cm (2.5 in). The head is fused with some of the body segments to form a distinctive **carapace** that covers the anterior half of the body like armor (see Fig. 17.12). Most krill are filter feeders that feed on diatoms and other plankton. They are extremely common in polar waters, aggregating in gigantic schools of billions of individuals. They are an almost exclusive food source for whales, penguins, and many types of fish (see Fig. 10.12). Other species of krill live in the deep sea (see Fig. 16.4*a*).

#### Shrimps, Lobsters, and Crabs

With around 10,000 species, the **decapods** (the term means "ten legs") are the largest group of crustaceans. They include the shrimps, lobsters, and crabs. Decapods are also the largest crustaceans in size. Many are prized as food and are of great commercial importance.

Decapods feature five pairs of walking legs, the first of which is heavier and usually has claws used for feeding and defense (Fig. 7.32). The carapace is well developed and encloses the part of the body

**FIGURE 7.32** The American lobster (*Homarus americanus*) illustrates the basic body plan of decapod crustaceans. One significant omission from this drawing is the feathery gills, which lie in a chamber on each side of the cephalothorax. The ducts from the gonads, the gonoducts, open at the base of the last pair of walking legs in males and at the base of the second pair in females. Be sure to check next time you eat a lobster.

known as the **cephalothorax**. The rest of the body is called the **abdomen**.

Shrimps and lobsters tend to have laterally compressed bodies with distinct and elongate abdomens, the "tails" we like to eat so much. Shrimps are typically scavengers, specialists in feeding on bits of dead organic matter on the bottom. They have other lifestyles. Many colorful shrimps, particularly in the tropics, live on the surface of other invertebrates (Fig. 7.33) or remove parasites from the skin of fish (see "Cleaning Associations," p. 221). Others live in deep water (see Fig. 16.4c and d). Ghost and mud shrimps burrow in muddy bottoms (see Fig. 12.11d). Lobsters, such as the American, or Maine, lobster (Homarus; Fig. 7.32) and the clawless spiny lobster (Panulirus; see Fig. 4.22) are mostly nocturnal and hide during the day in rock or coral crevices. Their feeding habits are similar to those of shrimps, but they are also known to catch live prey. Hermit crabs, which are not true crabs, are also



**FIGURE 7.33** This shrimp (*Periclimenes*) is beautifully camouflaged to live on the branching arms of crinoids (see Fig. 7.47) in the tropical Pacific.

scavengers. They hide their long, soft abdomens in empty gastropod shells (see Fig. 10.5). Some hermit crabs cover their shells with sea anemones (Fig. 7.34) or sponges for added protection and camouflage. One type, however, doesn't hide the abdomen (Fig. 7.35).



**FIGURE 7.34** Hermit crab (*Dardanus* sp.) with sea anemones living on its shell. The hermit crab is protected by the nematocysts on the sea anemone's tentacles, and the sea anemones get to eat food particles that are let loose when the hermit crab feeds.



(a)



**FIGURE 7.35** The coconut crab (*Birgus latro*) is a large, land-dwelling hermit crab that does not use a shell as an adult (*a*). Females return to seawater only to release their eggs. After a planktonic existence, the young settle on the bottom and use shells for a home (*b*) as they crawl out of the sea to begin life on land. Coconut crabs, so called because they often eat coconuts, are found in the tropical Pacific and Indian oceans. They have been known to reach 13.5 kg (30 lb) in weight, thus being the largest and heaviest of all land arthropods.

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In the **true crabs** the abdomen is small and tucked under the compact and typically broad cephalothorax. The abdomen is visible as a flat, V-shaped plate in males; in females it is expanded and U-shaped for carrying eggs (Fig. 7.36). Crabs may be highly mobile, and most can easily move sideways when in a hurry. They make up the largest and most diverse group of decapods, more than 4,500 species strong. Most are scavengers, but some have specialized diets such as seaweeds, organic matter in mud, molluscs, or even coral mucus (see the photo on page 117). Many crabs live along rocky shores or sandy beaches, exposed to air much of the time. Land crabs actually spend most of their lives on land, returning to the sea only to release their eggs.

# **Biology of Crustaceans**

The diversity of forms among crustaceans is paralleled by equally diverse functional features.

### Feeding and Digestion

Filter feeding is very common in copepods and many of the small planktonic crustaceans (see Fig. 15.7). Stiff, hair-like bristles on some appendages are used to catch food particles in the water. Particles are carried to the bristles by currents induced by the beating of other appendages. Still other specialized appendages move food from the bristles to the mouth. Parasitic crustaceans have appendages adapted for piercing and sucking.

Bottom-dwelling crustaceans like lobsters have some of their body appendages specialized as walking legs. The appendages closest to the mouth, such as the **maxillipeds**, are turned forward and are specialized to sort out food and push it toward the mouth. Decapods have three pairs of maxillipeds (Fig. 7.32). They are used as filtering devices in decapods that eat small food particles in water or mud.

Food passes to a stomach that typically has chitinous teeth or ridges for grinding and bristles for sifting. The stomach, two-chambered in decapods, is connected to digestive glands that secrete digestive enzymes and absorb nutrients.

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FIGURE 7.36 The abdomen is V-shaped in male crabs (bottom) and larger and U-shaped in females (top). This is the mangrove crab (*Scylla serrata*).

Digestion is essentially extracellular. The intestine ends in an anus.

As in molluscs, absorbed nutrients are distributed by an open circulatory system. Gas exchange is carried out by gills attached to some appendages. In most decapods the gills lie in a chamber under the carapace, where they are constantly bathed by water. In land crabs, however, the gill chamber, though moistened, is filled with air and acts almost like our lungs.

#### Nervous System and Behavior

The nervous system of the structurally simplest crustaceans is ladder-like, but it is more centralized in decapod crustaceans. Crustaceans have a small, relatively simple brain (Fig. 7.32).

The sensory organs of crustaceans are well developed. Most have **compound eyes,** which consist of a bundle of up to 14,000 light-sensitive units grouped in a mosaic. In decapods the compound eyes are at the end of movable stalks and can be used like periscopes. Crustaceans have a keen sense of "smell," that is, they are very sensitive to chemicals in the water. Many crustaceans have a pair of statocysts for balance. Crustaceans are among the most behaviorally complex invertebrates. They use a variety of signals to communicate with each other. Many of these signals involve special body postures or movements of the legs and antennae. This type of communication has been shown to be very important in settling disputes between neighbors and in courtship. Courtship behavior can be especially elaborate (see "Fiddler on the Mud," p. 269).

## Reproduction and Life History

The sexes are separate in most crustaceans. Gametes are rarely shed into the water. Instead, males use specialized appendages to transfer sperm directly to the female. Even hermaphroditic species transfer sperm between individuals. Barnacles, for instance, have a penis that can stretch to reach other barnacles in the neighborhood. Mating in decapods usually takes place immediately after the female molts, while the exoskeleton is still soft. Females of many species can store sperm for long periods and use it to fertilize separate batches of eggs. In amphipods, isopods, decapods, and other groups, females carry their eggs using specialized appendages beneath the body.

Most crustaceans have planktonic larvae that look nothing like the adult. Probably the most characteristic crustacean larva is the **nauplius**, but the type and number of larval stages vary widely from group to group (Fig. 7.37).

# **Other Marine Arthropods**

Very few arthropods other than crustaceans are common in the ocean. Most belong to two small and entirely marine groups. A third group, huge and mostly terrestrial, includes a few shy invaders of the sea.

## Horseshoe Crabs

The horseshoe crabs are the only surviving members of a group (class Merostomata) that is widely represented in the fossil record. The five living species of horseshoe crabs (*Limulus*) are not true crabs but "living fossils," not unlike forms that became extinct long ago. Horseshoe

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crabs live on soft bottoms in shallow water on the Atlantic and Gulf coasts of the United States, Southeast Asia, and the Indian Ocean. Their most distinctive feature is a horseshoe-shaped carapace that encloses a body with five pairs of legs (Fig. 7.38).

### Sea Spiders

Sea spiders (class Pycnogonida) only superficially resemble true spiders. Four or more pairs of jointed legs stretch from a small body (Fig. 7.39). A large proboscis with the mouth at the tip is used to feed on soft invertebrates such as sea anemones and hydrozoans. Sea spiders are most common in cold waters, but they occur throughout the oceans.

#### Insects

**Insects** (class **Insecta**) are distinguished from other arthropods by having only three pairs of legs as adults. They are the largest and most diverse group of animals on earth but are rare in the sea. Most marine insects live at the water's edge, where they scavenge among seaweeds, barnacles, and rocks. Many inhabit the decaying seaweed that accumulates at the high tide mark. One marine insect that *is* found far from shore is the water strider (see Fig. 15.16).

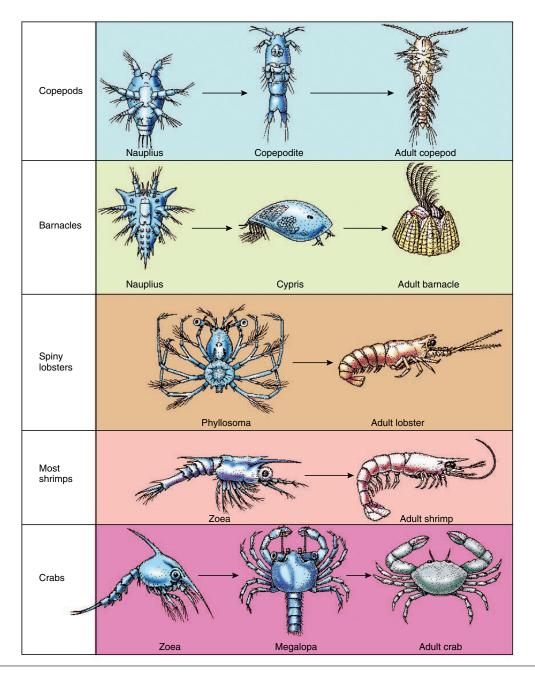
# **LOPHOPHORATES**

Three groups of marine invertebrates are linked by the presence of a unique feeding structure, the **lophophore**. It consists of a set of ciliated tentacles arranged in a horseshoe-shaped, circular, or coiled fashion. Lophophorates are suspension feeders, using their cilia to create feeding currents. They share other important traits: lack of segmentation, bilateral symmetry, a coelomic cavity, and a U-shaped gut.

## Bryozoans

**Bryozoans** ("moss animals") are invertebrates that form delicate colonies on seaweed, rocks, and other surfaces. Approximately 4,500 species, almost all marine, are grouped in the phylum

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**FIGURE 7.37** Eggs of marine crustaceans hatch into planktonic larvae that undergo consecutive molts. Each molt adds a new pair of appendages, with the ones already present becoming more specialized. The last larval stage eventually metamorphoses into a juvenile (see Fig. 13.5). The larvae and adults shown here are not drawn to scale. In most cases, each arrow represents several molts. Other crustacean larvae are shown in Figure 15.13.

**Ectoprocta.** Bryozoan colonies consist of minute interconnected individuals called **zooids** that secrete skeletons of a variety of shapes. The colonies may be encrusting or take an upright form that looks like tufts of crusty lace (Fig. 7.40). A

close look often reveals the rectangular, round, or vase-like compartments occupied by zooids (see Fig. 13.17e). The lophophore is retractable. The U-shaped gut ends in an anus outside the edge of the lophophore.

# Phoronids

At first sight, **phoronids** (phylum **Phoronida**) may be easily confused with polychaetes. They are worm-like and build tubes made in part of sand grains.

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FIGURE 7.39 Sea spiders, or

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Proboscis

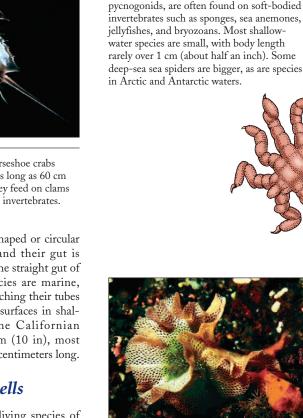


FIGURE 7.40 Sertella and other bryozoans form crusty, lace-like colonies.

one of the most common and important members of the plankton. Their bodies are very different from those of bottomdwelling worms. They are almost transparent, streamlined, with fish-like fins and tail (Fig. 7.41). The head has eyes, grasping spines, and teeth. Total length ranges from a few millimeters to 10 cm (up to 4 in).

Arrow worms are voracious carnivores with efficient sensory structures to detect their prey. They prey on small crustaceans, eggs and larvae of fishes and other animals, other arrow worms, and practically anything else that is small. They spend most of their time motionless in the water but will swim in rapid, darting movements to grab their prey.

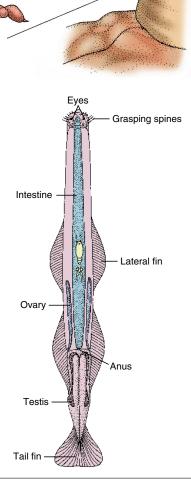


FIGURE 7.41 Arrow worms, or chaetognaths, are characterized by a transparent, fish-like body, an adaptation to living as planktonic predators. *Sagitta elegans* ("elegant arrow"), illustrated here, is widely distributed throughout the oceans. Notice that individuals have both testes and ovaries. A partially digested copepod, a favorite food, is inside the transparent intestine.



FIGURE 7.38 Horseshoe crabs (*Limulus polyphemus*) grow as long as 60 cm (2 ft), including the tail. They feed on clams and other small soft-bottom invertebrates.

They have a horseshoe-shaped or circular lophophore, however, and their gut is U-shaped in contrast to the straight gut of polychaetes. All 15 species are marine, burrowing in sand or attaching their tubes to rocks and other hard surfaces in shallow water. Though one Californian species may reach 25 cm (10 in), most phoronids are only a few centimeters long.

# Lamp Shells

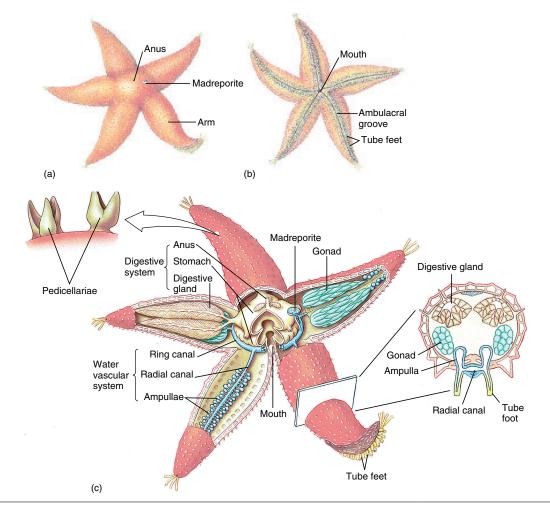
There are close to 350 living species of lamp shells, or brachiopods (phylum Brachiopoda). Thousands of other species are known only as fossils. Lamp shells have a shell with two parts, or valves, like the unrelated clams. The two valves are dorsal and ventral to the body, in contrast to the lateral (right and left) valves of clams. When the valves are opened, another major difference between lamp shells and clams is apparent. Lamp shells have a conspicuous lophophore, consisting of at least two coiled and ciliated arms, that occupies most of the space between the valves. Most brachiopods are found attached to rocks or burrowing in soft sediments.

## ARROW WORMS

In terms of number of species the **arrow worms**, or **chaetognaths** (phylum **Chaetognatha**), rank among the smallest animal phyla. Only about 100 species, all marine, are known. They are nevertheless



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**FIGURE 7.42** Aboral (*a*) and oral (*b*) surfaces of a sea star (*Asterias vulgaris*) common on the Atlantic and Gulf coasts of North America. Internal structure (*c*), with an arm cut across to show the relationship between tube feet, the internal sacs (ampullae), and the canals that make up the water vascular system. This and other carnivorous sea stars event their thin-walled stomach and begin digesting prey without having to eat it.

# ECHINODERMS: FIVE-WAY SYMMETRY

Sea stars, sea urchins, sea cucumbers, and several other forms make up the **echinoderms** (phylum **Echinodermata**). The echinoderms display many traits that are unique among invertebrates.

Echinoderms are radially symmetrical, like cnidarians and comb jellies. The radial symmetry of echinoderms, however, is only a secondary development. Their planktonic larvae are bilaterally symmetrical, and only the adults develop radial symmetry. Unlike cnidarians and comb jellies, most echinoderms have **pentamerous** radial symmetry, that is, symmetry based on five parts (Fig. 7.42). As might be expected in a radially symmetrical animal, echinoderms lack a head. They have no anterior or posterior end or dorsal or ventral side. It is useful instead to refer to one surface of echinoderms as oral, because that is where the mouth is located and the opposite surface as **aboral** (Fig. 7.42*a* and *b*).

Echinoderms typically have a complete digestive tract, a well-developed coelom, and an internal skeleton. This skeleton, like ours, is an **endoskeleton**. It is secreted within the tissues, rather than externally like the exoskeleton of arthropods. Though sometimes it looks external, as in the spines of sea urchins, the endoskeleton is covered by a thin layer of ciliated tissue. Spines and pointed bumps give many echinoderms a spiny appearance, and hence the name Echinodermata, meaning "spiny-skinned."

Unique to echinoderms is the water vascular system, a network of waterfilled canals (Fig. 7.42c). Tube feet are muscular extensions of these canals. They are extended when filled with water, sometimes by the action of muscular sacs, the **ampullae**, that extend inside the body opposite the tube feet. Tube feet often end in a sucker and are used for attachment, locomotion, and for receiving chemical and mechanical stimuli. In most species the system connects to the outside through the **madreporite**, a porous plate on the aboral surface.

Echinoderms are radially symmetrical as adults. They are characterized by an endoskeleton and a unique water vascular system.

## **Types of Echinoderms**

The echinoderms are a large group of about 7,000 species, all marine. They are important members of bottom communities from the poles to the tropics.

## Sea Stars

Sea stars (class Asteroidea), sometimes called starfishes, most clearly display the distinctive echinoderm body plan (Fig. 7.42). Most species have five arms that radiate from a central disk, though some have more than five, sometimes close to 50. Hundreds of tube feet protrude from the oral surface along radiating channels on each arm called **ambulacral grooves** (Fig. 7.42*b*). Sea stars can move in any direction, though slowly, by reaching out their tube feet and pulling themselves along.

The endoskeleton of sea stars consists of interconnected calcium carbonate plates that form a relatively flexible framework. This allows their arms to be somewhat flexible. The aboral surface of many sea stars is often covered with spines modified into minute pincer-like organs called **pedicellariae** (Fig. 7.42*c*). They help keep the surface clean.

Most sea stars are predators of bivalves, snails, barnacles, and other attached or slow-moving animals. Typical examples include *Asterias* (Figs. 7.42), common on rocky shores from the North Atlantic to the Gulf of Mexico, and *Pisaster* (Fig. 7.43*a*), its counterpart on the west coast of North America.

### **Brittle Stars**

The star-shaped body architecture is repeated in the **brittle stars** (class **Ophiuroidea**). The five arms, however, are long, very flexible, and sharply demarcated from the central disk (Fig. 7.44). The swift, snake-like movements of the arms



**FIGURE 7.43** (a) The giant spined sea star (*Pisaster giganteus*) from the Pacific coast of North America. (b) Linckia guildingi, from the Caribbean, shows remarkable regenerating abilities; here the larger arm regenerated the central disk and four small arms to form a complete individual.



**FIGURE 7.44** *Ophiothrix spiculata* is a brittle star typically found under rocks and on seaweed holdfasts in California.

are used in locomotion. The tube feet, which lack suckers, are used in feeding.

Most brittle stars eat particulate organic matter and small animals they pick up from the bottom or the water. Particles are collected by the tube feet and passed from foot to foot to the mouth. They lack an anus. There are more species of brittle stars, around 2,000, than of any other group of echinoderms. They are widely distributed but not always visible, often hiding under rocks and corals or covering themselves with mud or sand.

## Sea Urchins

In sea urchins (class Echinoidea) the endoskeleton forms a round, rigid, shell-like test with movable spines and pedicellariae (Fig. 7.45). Locomotion is achieved by the movable spines, jointed to sockets in the test, and the sucker-tipped tube feet. The flat and radiating body plan of sea stars can be transformed into a sea urchin by dropping the arms and pulling the oral and aboral surfaces to form a sphere. The five rows of ambulacral grooves with their

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**FIGURE 7.45** (*a*) The green sea urchin (*Strongylocentrotus droebachiensis*) is found on rocky shores and kelp forests on the Atlantic, Arctic, and Pacific coasts of North America. (*b*) *Mellita sexiesperforata*, the six-hole sand dollar from sandy bottoms along the southern United States and the Caribbean. The five-part pattern characteristic of all echinoderms can be seen in the light star pattern in the center of the sand dollar.

tube feet now extend along the outer surface of the sphere. The mouth is on the bottom and the anus on top. The plates that make up the test can be seen in a sea urchin cleaned of spines and tissue. Bands of pores along the ambulacral grooves correspond to the bands of tube feet.

Sea urchins graze on attached or drifting seaweeds and seagrasses. In the process, they also ingest dead organic matter and encrusting animals such as sponges and bryozoans. The mouth, directed downward, has an intricate system of jaws and muscles called Aristotle's lantern that is used to bite off algae and other bits of food from the bottom. Sea urchins are a common sight on rocky shores throughout the world. Examples are species of Arbacia from the Atlantic Ocean and Gulf of Mexico and Strongylocentrotus from most North American polar and temperate coasts (Figs. 7.45a and 13.19). Those in the tropics show an even richer variety of shapes and sizes, particularly on coral reefs (Echinometra, Diadema; see Fig. 14.33).

Not all of the approximately 1,000 species in the class Echinoidea have round tests with prominent spines. **Heart urchins** (see Fig. 13.7) and **sand dollars** (Figs. 7.45*b* and 13.8) are echinoids adapted to live in soft bottoms by having flattened bodies and short spines. They are deposit feeders that use their tube feet and sometimes strands of mucus to pick up organic particles.

## Sea Cucumbers

In yet another modification of the echinoderm body plan, sea cucumbers (class Holothuroidea) are superficially wormlike (Fig. 7.46). They do not have spines and lack an obvious radial symmetry. The basic body plan of sea urchins appears to have been elongated along the oral-aboral axis, as if they were pulled from the mouth and anus and stretched. The animal lies on one side, where the five rows of tube feet are concentrated. The oral and aboral surfaces are at the ends. The endoskeleton consists of microscopic, calcareous spicules scattered throughout the warty, often tough, skin. Like sea urchins, most species have five rows of tube feet extending from mouth to anus.

Many sea cucumbers are deposit feeders. The tube feet around the mouth are modified into branched tentacles that are used to pick up organic matter from the bottom or scoop sediment into the mouth (see Fig. 7.16). Some sea cucumbers burrow or hide and extend only their tentacles to obtain food directly from the water.

Many sea cucumbers have evolved novel defensive mechanisms that compensate for the lack of a test and spines. Some secrete toxic substances. When disturbed, some species discharge sticky, sometimes toxic filaments through the anus to discourage potential predators. www.mhhe.com/marinebiology

Others resort to a startling response, the sudden expulsion of the gut and other internal organs through the mouth or anus, a response known as **evisceration**. It is assumed that evisceration distracts the offender while the sea cucumber, which will eventually grow back the lost organs, escapes. Messy, perhaps, but effective!

## Crinoids

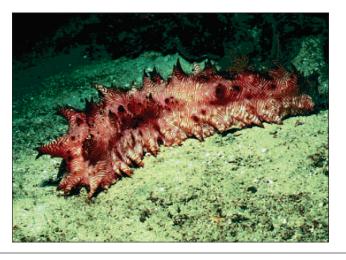
**Crinoids** (class **Crinoidea**) are suspension feeders that use outstretched, feathery arms to obtain food from the water. Crinoids are represented by close to 600 species of **feather stars** (Fig. 7.47) and **sea lilies**. Sea lilies are restricted to deep water and attach to the bottom. Feather stars, on the other hand, crawl on hard bottoms in shallow to deep waters, especially in the tropical Pacific and Indian oceans.

The body plan of crinoids is best described as an upside-down brittle star with the ambulacral grooves and mouth directed upward. The mouth and larger organs are restricted to a small cup-shaped body from which the arms radiate. Some crinoids have only five arms but most have many-up to 200-because of branching of the initial five. The arms also have small side branches (Fig. 7.33). Tiny tube feet along these side branches secrete mucus, which aids in catching food particles. Food makes its way into the mouth by way of ciliated ambulacral grooves. Feather stars perch on hard surfaces using claw-like appendages. These appendages tilt the body so that the extended arms orient to currents for efficient suspension feeding.

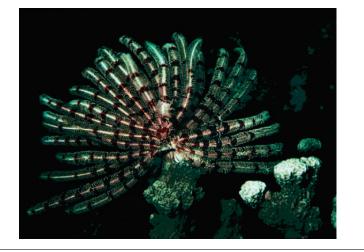
## **Biology of Echinoderms**

Radial symmetry, so effective for suspension feeding, is associated with sedentary lifestyles. With the exception of limited swimming in some feather stars and some deep-water sea cucumbers, adult echinoderms are slow bottom crawlers. But do they need to be fast to be successful? Certainly not. More than anything, echinoderms are fascinating because of the extraordinary ways in which they handle day-to-day life.

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**FIGURE 7.46** A sea cucumber (*Thelenota rubralineata*) from Papua New Guinea. Sea cucumbers, among the largest echinoderms, reach 2 m (6.6 ft) in length.



**FIGURE 7.47** A feather star, or crinoid, photographed at night at Kwajalein atoll, Marshall Islands. Feather stars are among the most spectacular of all marine animals. The outstretched arms of feeding individuals can reach a diameter of 70 cm (more than 2 ft). See Fig. 7.33 for a close-up of an arm.

### Feeding and Digestion

The digestive system of echinoderms is relatively simple. Most sea stars are carnivorous. Many feed by extending, or everting, part of their stomach inside out through the mouth to envelop the food. The stomach then secretes digestive enzymes produced by large digestive glands that extend into the arms (Fig. 7.42c). The digested food is carried into the glands for absorption and the stomach pulled back inside the body. The intestine is short or missing. Brittle stars and crinoids also have simple, short guts. Brittle stars lack an anus.

The gut of sea urchins and sea cucumbers is long and coiled. In sea urchins, this is an adaptation for the lengthier digestion needed for the breakdown of plant material. A long gut is advantageous in sea cucumbers because they need to remove organic matter from the large amounts of sediment they ingest. In all echinoderms nutrients are transported in the fluid that fills the extensive body cavity. The fluid is called **coelomic fluid** because the body cavity of echinoderms is a coelom.

The coelomic fluid also transports oxygen because most echinoderms lack a distinct circulatory system. In sea stars and sea urchins gas exchange takes place across small, branched projections of the body wall connected at the base to the coelomic cavity. In sea cucumbers water is drawn in through the anus into a pair of thin, branched tubes called **respiratory trees**. The respiratory trees are extensions of the gut and are suspended in the body cavity, surrounded by coelomic fluid. They provide a large surface area in close proximity to the coelomic fluid, thus allowing considerable gas exchange.

## Nervous System and Behavior

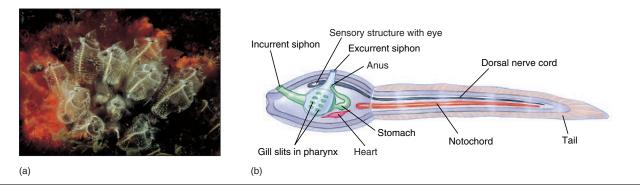
Our knowledge of the nervous system of echinoderms is rather limited. The presence of a nerve net is reminiscent of cnidarians. The nervous system coordinates movements of tube feet and spines in the absence of a brain. Nevertheless, more complex behaviors, such as the righting of the body after being turned over and camouflaging with bits of debris in sea urchins, are evidence that the nervous system may not be as simple as it looks.

## Reproduction and Life History

The sexes are separate in most echinoderms. In most groups, five, ten, or more gonads shed sperm or eggs directly into the water. The gonads are usually located in the body cavity and open to the outside by way of a duct (Fig. 7.42*c*). Gametes do not survive long in the water, so in many species individuals spawn all at once to ensure fertilization.

Development of the fertilized egg proceeds in the plankton and typically results in a ciliated larva characteristic of each group (see Fig. 15.11b and c). Echinoderm larvae are bilaterally symmetrical and it is not until metamorphosis that radial symmetry develops. Some echinoderms do not have planktonic larvae and brood their offspring in special pouches or under the body.

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**FIGURE 7.48** (a) Clavelina lepadiformis is a colonial sea squirt, or ascidian. Its outer covering, the tunic, contains cellulose, a substance typical of plants. (b) The tadpole larva of ascidians exhibits all the distinguishing characteristics of chordates. Some of these characteristics, however, are missing in the adults.

Asexual reproduction takes place regularly in some sea stars, brittle stars, and sea cucumbers by the separation of the central disk or body into two pieces. The resulting halves then grow into complete individuals. **Regeneration**, the ability to grow lost or damaged body parts, is highly developed in echinoderms. Sea stars, brittle stars, and crinoids regenerate lost arms. In some sea stars a severed arm can grow into a new individual (Fig. 7.43*b*). In most sea stars, however, only arms that include portions of the central disk can regenerate.

# HEMICHORDATES: A "MISSING LINK"?

The search for evolutionary links between the chordates, our own phylum, and other groups of animals has been a most provocative challenge. As strange as it may seem, echinoderms and chordates share several features related to the development of their embryos. The wide evolutionary gap between echinoderms and chordates, however, may be filled by a small and infrequently seen group of worms, the hemichordates (phylum Hemichordata). Hemichordates share the same basic developmental characteristics of chordates and echinoderms. Some hemichordates also have a larva similar to that of some echinoderms. Hemichordates share with we chordates some of the

features used to define our phylum. These characteristics, a dorsal, hollow nerve cord and openings along the anterior part of the gut, will be discussed in the following text. In contrast to chordates, however, there is also a ventral nerve cord along the proboscis and the rest of the body.

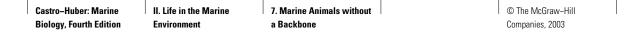
The hemichordates include approximately 90 species. Most of these are **acorn worms**, or **enteropneusts**, wormlike deposit feeders that live free or in U-shaped tubes. Some acorn worms have been found around hydrothermal vents, often occurring in large numbers. They generally range in length from about 8 to 45 cm (3 to 18 in) but some reach 2.5 m (more than 8 ft). Like sea cucumbers they ingest sediment, but they use a thick, mucus-secreting proboscis to collect organic material that is then swept toward the mouth.

# CHORDATES WITHOUT A BACKBONE

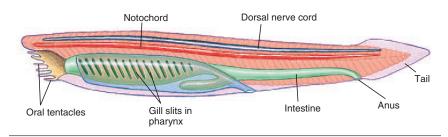
The phylum **Chordata** is divided into three major groups, or subphyla. Two of these lack a backbone and, for this reason, are discussed here with the invertebrates. These invertebrate chordates are collectively called **protochordates.** The third and by far the largest chordate subphylum comprises the vertebrates, the subject of Chapters 8 and 9.

Humans share the phylum Chordata with many distant cousins. Some of these chordates are in fact invertebrates similar in appearance and lifestyle to some of the groups we have reviewed. The estimated 49,000 living species of chordates share many characteristics, but four stand out. During at least part of their development, all chordates, including humans, have (1) a single, hollow nerve cord that runs along the dorsal length of the animal, (2) gill (or pharyngeal) slits, small openings along the anterior part of the gut (or phar**ynx**), (3) a **notochord**, a flexible rod for support that lies between the nerve cord and the gut, and (4) a post-anal tail, that is, a tail that extends beyond the anus. (Figs. 7.48b and 7.49). All chordates also have a ventral heart. In most chordates the notochord is surrounded or replaced by a series of articulating bones, the backbone, or vertebral column. Recall that this is the characteristic that defines and separates vertebrates from the invertebrates. The realm of invertebrates extends well into the chordates because the most primitive chordates lack a backbone.

All chordates possess—at least during part of their lives—a dorsal nerve cord, gill slits, a notochord, and a post-anal tail. Vertebrate chordates also have a backbone.



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**FIGURE 7.49** Though it looks like a fish, the lancelet (*Branchiostoma*) is an invertebrate because it lacks a backbone. The notochord, dorsal nerve cord, and gill slits show it is a chordate.

## **Tunicates**

The largest group of protochordates is the tunicates (subphylum Urochordata). All 3,000 species are marine. Those we are most apt to see are the sea squirts, or ascidians (class Ascidiacea). Their saclike bodies are attached to hard surfaces, often as fouling organisms, or anchored in soft sediments. They are the only sessile, or attached, chordates. To the inexperienced eye, some sea squirts may be confused with sponges because of their general appearance. The body of the sea squirt, however, is protected by a tunic, a leathery or gelatinous outer covering that often has a different texture than that of sponges, and the internal structure is completely different.

Sea squirts are filter feeders. Water typically flows through the mouth, or **incurrent siphon**, and is filtered by a ciliated, sieve-like sac. This sac represents the pharynx, and the openings are derived from the gill slits. Food is filtered from the water and passed into a U-shaped gut. Filtered water is expelled through a second opening, the **excurrent siphon**. When disturbed or expelling debris, ascidians force a jet of water out of both siphons, giving them their common name of sea squirts. Some sea squirts are colonial, some consisting of clumps of separate individuals (Fig. 7.48*a*) and others of a circular, flower-like arrangement of individuals sharing a common tunic and excurrent siphon (see Fig. 13.17*c*).

Were it not for their planktonic larvae, the headless, attached sea squirts could easily pass as anything but chordates. The adults possess neither a notochord nor a dorsal nerve cord. Ascidian larvae are known as tadpole larvae because of their superficial resemblance to the tadpoles of frogs (Fig. 7.48b). Tadpole larvae clearly display the fundamental chordate traits. They have gill slits, a dorsal nerve cord, a notochord, and a well-developed post-anal tail. They also have an eye. Tadpole larvae do not feed; their only purpose is to find a suitable surface on which to settle. The metamorphosis of a tadpole larva into a juvenile ascidian is nothing short of spectacular.

The notochord and tail are reabsorbed, the filtering sac and siphons develop, and free existence is no more.

Some tunicates lead a planktonic existence throughout their lives. These are among the most remarkable examples of life in the sea. Salps (class Thaliacea) have a transparent, barrel-shaped body with muscle bands for locomotion (see Fig. 15.8). Water enters through the anterior mouth, or incurrent siphon, and it is forced out through the excurrent siphon on the posterior end. Salps can be extremely abundant, particularly in warm water. Some are colonial, much like floating colonies of sea squirts, and may reach several meters in length. Larvaceans, or appendicularians, (class Larvacea) retain the body of a tadpole larva through life. Each tiny individual secretes a complex but delicate gelatinous "house" for protection and to filter water for food (see Fig. 15.9).

## Lancelets

The second group of invertebrate chordates consists of about 29 species of **lancelets** (subphylum **Cephalochordata**). The body, up to 7 cm (close to 3 in) long, is laterally compressed and elongate like that of a fish (Fig. 7.49). The basic chordate characteristics are well developed through life. Only the lack of a backbone separates lancelets from vertebrates. Lancelets are inhabitants of soft bottoms. They are filter feeders, using the gill slits to remove and concentrate organic particles.

Table 7.1

# Some of the Most Important Characteristics of the Major Animal Phyla

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| Phylum  | Representative Groups                                | Distinguishing Features                                       | General Habitat                  |  |
|---|--|---|----------------------------------|--|
| Porifera (sponges)  | Sponges  | Collar cells (choanocytes)                                    | Benthic                          |  |
| Cnidaria (cnidarians)   | Jellyfishes, sea anemones, corals                    | Nematocysts   | Benthic, pelagic                 |  |
| Ctenophora (comb jellies)   | Comb jellies   | Ciliary combs, colloblasts                                    | Mostly pelagic                   |  |
| Platyhelminthes (flatworms)   | Turbellarians, flukes, tapeworms                     | Flattened body  | Mostly benthic, many parasitic   |  |
| Nemertea (ribbon worms)   | Ribbon worms   | Long proboscis  | Mostly benthic                   |  |
| Nematoda (nematodes)  | Nematodes, roundworms                                | Body round in cross section                                   | Mostly benthic, many parasitic   |  |
| Annelida (segmented worms)  | Polychaetes, oligochaetes, leeches                   | Segmentation  | Mostly benthic                   |  |
| Sipuncula (peanut worms)  | Peanut worms   | Retractable, long proboscis                                   | Benthic                          |  |
| Echiura (echiurans)   | Echiurans  | Non-retractable proboscis                                     | Benthic                          |  |
| Pogonophora (beard worms)   | Beard worms, vestimentiferans                        | No mouth or digestive system                                  | Benthic                          |  |
| Mollusca (molluscs)   | Snails, clams, oysters, octopuses                    | Foot, mantle, radula (absent in some groups)                  | Benthic, pelagic                 |  |
| Arthropoda (arthropods)   | Crustaceans (crabs, shrimps), insects                | Exoskeleton, jointed legs                                     | Benthic, pelagic, some parasitic |  |
| Ectoprocta (bryozoans)  | Bryozoans  | Lophophore, lace-like colonies                                | Benthic                          |  |
| Phoronida (phoronids)   | Phoronids  | Lophophore, worm-like body                                    | Benthic                          |  |
| Brachiopoda (lamp shells)   | Lamp shells  | Lophophore, clam-like shells                                  | Benthic                          |  |
| Chaetognatha (arrow worms)  | Arrow worms  | Transparent body with fins                                    | Mostly pelagic                   |  |
| Echinodermata (echinoderms)   | Sea stars, brittle stars, sea urchins, sea cucumbers | Tube feet, five-way radial symmetry,<br>water vascular system | Mostly benthic                   |  |
| Hemichordata (hemichordates)  | Acorn worms  | Dorsal, hollow (and ventral) nerve<br>cords, gill slits       | Benthic                          |  |
| Chordata (chordates)  | Tunicates, vertebrates, (fishes, etc.)               | Dorsal, hollow nerve cord, gill slits,<br>notochord           | Benthic, pelagic                 |  |
| Note: Benthic—living on the bottom; pelagic—living in the water column. |  |   |                                  |  |

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| Level of<br>Organization | Symmetry                              | Segmentation | Digestive Tract      | Respiratory<br>Exchange | Circulatory<br>System  |
|--------------------------|---------------------------------------|--------------|----------------------|-------------------------|------------------------|
| Cellular                 | Asymmetrical                          | No           | None                 | Body surface            | None                   |
| Tissue                   | Radial                                | No           | Incomplete           | Body surface            | None                   |
|                          | Radial                                | No           | Incomplete           | Body surface            | None                   |
|                          | Bilateral                             | No           | Incomplete or absent | Body surface            | None                   |
|                          | Bilateral                             | No           | Complete             | Body surface            | Closed                 |
|                          | Bilateral                             | No           | Complete             | Body surface            | None                   |
|                          | Bilateral                             | Yes          | Complete             | Gills                   | Closed                 |
|                          | Bilateral                             | No           | Complete             | Body surface            | None                   |
|                          | Bilateral                             | No           | Complete             | Body surface            | Closed                 |
|                          | Bilateral                             | Reduced      | None                 | Body surface            | Closed                 |
| ystem —                  | Bilateral                             | No           | Complete             | Gills                   | Open or closed         |
| Organ system             | Bilateral                             | Yes          | Complete             | Gills (in crustaceans)  | Open                   |
| 0                        | Bilateral                             | No           | Complete             | Body surface            | None                   |
|                          | Bilateral                             | No           | Complete             | Body surface            | Closed                 |
|                          | Bilateral                             | No           | Complete             | Body surface            | Open                   |
|                          | Bilateral                             | No           | Complete             | Body surface            | None                   |
|                          | Radial (adults)<br>Bilateral (larvae) | No           | Complete             | Body surface            | None                   |
|                          | Bilateral                             | Reduced      | Complete             | Body surface            | Part closed, part open |
|                          | Bilateral                             | Reduced      | Complete             | Gills, lungs            | Closed                 |

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# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

# **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. If bilateral symmetry were to evolve among cnidarians, in which group or groups would you expect it to occur? Why?
- 2. Cephalopods, the squids, octopuses, and allies, show a much higher degree of structural and behavioral complexity than the other groups of molluscs. What factors triggered the evolution of these changes? A rich fossil record among cephalopods shows that once they were very common and even dominant in some marine environments. Now there are only about 650 living species of cephalopods, far fewer than gastropods. In the end, were cephalopods successful? What do you think happened along the way?
- 3. A new class of echinoderms, the sea daisies or concentricycloids, was discovered in 1986. They are deepwater animals living on sunken wood. They are flat and round, looking very much like a small sea star without arms. They also lack a gut. Without ever having seen them, why do you think they were classified as echinoderms, not as members of a new phylum? Any hypotheses as to how they feed or move around?

# **For Further Reading**

Some of the recommended readings listed below may be available online. These are indicated by this symbol ., and will contain live links when you visit this page in the Online Learning Center.

## **General Interest**

- Conniff, R., 2000. Jelly bellies. *National Geographic*, vol. 197, no. 6, June, pp. 82–101. Jellyfishes are efficient predators that are eaten by relatively few predators.
- Douglas, K., 2000. Pee is for particular. New Scientist, vol. 166, no. 2233, 8 April, pp. 40–41. Lobsters use urine for individual recognition.

- Foale, S. and M. Norman, 2000. Australia's rock stars. *Natural History*, vol. 109, no. 3, April, pp. 77–79. Cuttlefishes use amazing color changes during mating behavior.
- Holloway, M., 2000. Cuttlefish say it with skin. *Natural History*, vol. 109, no. 3, April, pp. 70–76. Color changes are used for communication and disguise in cuttlefishes.
- Paine, S., 2000. Slime scene. New Scientist, vol. 165, no. 2229, 11 March, pp. 34–37. Mucus trails left valuable information on the lives of fossil invertebrates.
- Wray, G. A. and R. A. Raff, 1998/1999. Body builders of the sea. *Natural History*, vol. 107, no. 9, December/January, pp. 38–47. Echinoderms have evolved many body shapes from a basic radial symmetry.

## In Depth

- Aguinaldo, A. M. A. and J. A. Lake, 1998. Evolution of the multicellular animals. *American Zoologist*, vol. 38, pp. 878–887.
- Carlon, D. B., 1999. The evolution of mating systems in tropical reef corals. *Trends in Ecology and Evolution*, vol. 14, pp. 491–495.
- Gill, J. M. and R. Coma, 1998. Benthic suspension feeders: Their paramount role in littoral marine food webs. *Trends in Ecology and Evolution*, vol. 13, pp. 316–321.
- Moore, J. and P. Willmer, 1997. Convergent evolution in invertebrates. *Biological Reviews*, vol. 72, pp. 1–60.
- Nielsen, C., 1998. Origin and evolution of animal life cycles. *Biological Reviews*, vol. 73, pp. 125–155.
- Pechenik, J. A., 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Biology Progress Series*, vol. 177, pp. 269–297.
- Schmidt-Rhaesa, A., U. Ehlers, T. Bartolomaeus, C. Lemburg and J. R. Garey, 1998. The phylogenetic position of the Arthropoda. *Journal of Morphology*, vol. 238, pp. 263–285.
- Tegner, M. J., L. V. Basch and P. K. Dayton, 1996. Near extinction of an exploited marine invertebrate. *Trends in Ecology and Evolution*, vol. 11, pp. 278–280.

# See It in Motion

Video footage of the following animals and their behaviors can be found for this chapter on the Online Learning Center:

- Spiny lobster (Honduras)
- Featherduster worms (Belize)
- Sea urchin (Diadema) at night (Belize)

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- Jellyfish (Ripley's Aquarium of the Smokies, Tennessee)
- Giant cuttlefish changing color (Solomon Islands)
- Burrowing sea cucumber (Solomon Islands)
- Feeding octopus (Palau)
- Hairy chiton (Florida)

# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Phylum Porifera
- Phylum Cnidaria
- Coral reefs

- Phylum Ctenophora
- Phylum Annelida
- Class Polychaeta
- Class Bivalvia
- Class Cephalopoda
- Subphylum Chelicerata
- Subphylum Crustacea
- Phylum Echinodermata
- Subphylum Urochordata

# Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

II. Life in the Marine Environment 8. Marine Fish

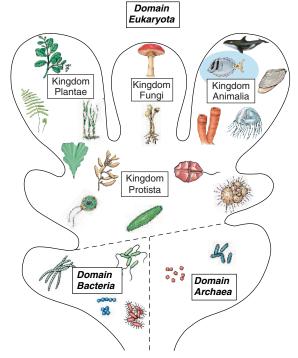
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# Marine Fishes





A school of squirrelfish (Holocentrus) hiding under coral during the day.



F ishes were the first vertebrates, appearing more than 500 million years ago. The first fishes probably evolved from an invertebrate chordate not much different from the lancelets or the tadpole larvae of sea squirts that still inhabit the oceans.

Fishes soon made their presence felt and have had a tremendous impact on the marine environment. They feed on nearly all types of marine organisms. Some of the organisms discussed in Chapters 5 through 7, from bacteria to crustaceans, use fishes as their home. Many other animals eat them.

Fishes are the most economically important marine organisms, and marine fishes are a vital source of protein for millions of people. Some are ground up as fertilizer or chicken feed. Leather, glue, vitamins, and other products are obtained from them. Many marine fishes are chased by sportfishing enthusiasts. Others are kept as pets and have brought the wonders of ocean life into many homes.

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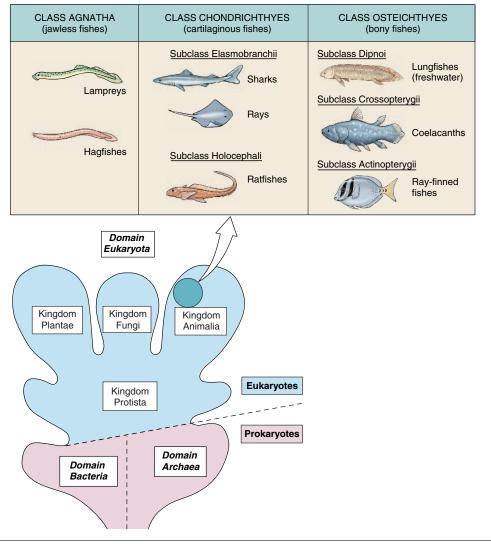


FIGURE 8.1 Classification scheme of fishes.

# VERTEBRATES: AN INTRODUCTION

Vertebrates (subphylum Vertebrata) share the four fundamental characteristics of the phylum Chordata with invertebrate chordates like lancelets and sea squirts. Vertebrates differ from these other chordates in having a **backbone**, also called the **vertebral column** or **spine**, which is a dorsal row of hollow skeletal elements, usually bone, called **vertebrae**. The vertebrae enclose and protect the **nerve cord**, also called the **spinal cord**, which ends in a complex brain that is protected by a skull made of cartilage or bone. Vertebrates also are characterized by a bilaterally symmetrical body and the presence of an endoskeleton.

Vertebrates are chordates with a backbone that encloses a nerve cord, or spinal cord.

## **TYPES OF FISHES**

Fishes are the oldest and structurally the simplest of all living vertebrates. They also are the most abundant vertebrates in terms of both species and individuals. The estimated 27,000 species of fishes make up about half of all species of vertebrates on earth. Most species of fishes, about 58%, are marine. Fishes are divided into three major groups (Fig. 8.1).

## Jawless Fishes

The most primitive fishes living today are the **jawless fishes** (class **Agnatha**). Because they lack jaws, they feed by suction with the aid of a round, muscular mouth and rows of teeth. The body is cylindrical



and elongate like that of eels or snakes (Fig. 8.2). They lack the paired fins and scales of most fishes.

Hagfishes, or slime eels (Myxine, Eptatretus), are jawless fishes that feed mostly on dead or dying fishes. They sometimes bore into their prey and eat them from the inside out. Hagfishes live in burrows they dig in muddy bottoms, mostly at moderate depths in cold waters. Only about 20 species are known. They reach a maximum length of approximately 80 cm (2.6 ft). Their skin is used in the manufacture of leather goods, but they are mostly known for attacking bait or fishes on fishing lines and in nets or traps.

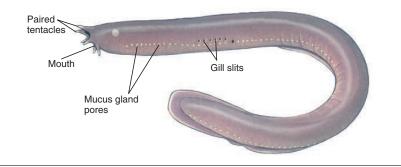
Lampreys (*Petromyzon*), found in most temperate regions, are primarily freshwater fishes. They breed in rivers and lakes, but some move to the sea as adults. They attach to other fishes and suck their blood or feed on bottom invertebrates. There are roughly 30 species of lampreys.

Hagfishes and lampreys lack jaws and are the most primitive living fishes.

# **Cartilaginous Fishes**

The cartilaginous fishes (class Chondrichthyes) are a fascinating and ancient group that includes the sharks, rays, skates, and ratfishes. Cartilaginous fishes have a skeleton made of cartilage, a material that is lighter and more flexible than bone. Though the skeleton of jawless fishes is also cartilaginous, sharks and related fishes feature some significant advances. They possess movable jaws that are usually armed with well-developed teeth (Fig. 8.3). The mouth is almost always ventral, that is, underneath the head. Another important development is the presence of paired lateral fins for efficient swimming. Cartilaginous fishes have rough, sandpaper-like skin because of the presence of tiny placoid scales. They have the same composition as teeth, and each consists of a pointed tip that is directed backward (see Fig. 8.8a).

Sharks, rays, skates, and ratfishes are characterized by a cartilaginous skeleton and a rough skin covered by minute, placoid scales. They also have movable jaws and paired fins.



**FIGURE 8.2** The Pacific hagfish (*Eptatretus stouti*) has 4 pairs of sensory tentacles around the mouth and 12 pairs of gill slits. Hagfishes are also known as slime eels because of the abundant mucus produced by glands on the skin. Notice the absence of paired fins.



**FIGURE 8.3** Shark jaws have several rows of triangular teeth. Individual teeth often have even smaller serrations, or denticles, along their edges. A tiger shark may grow and discard 24,000 teeth in a 10-year period! These are the jaws of a sandtiger shark (*Carcharias taurus*). The small holes in the skin between the eye and the nostrils are the ampullae of Lorenzini (see p. 168).

## Sharks

Sharks are cartilaginous fishes magnificently adapted for fast swimming and predatory feeding. They are often described as "mysterious," "evil," or "formidable" evidence of our fascination with sharks.

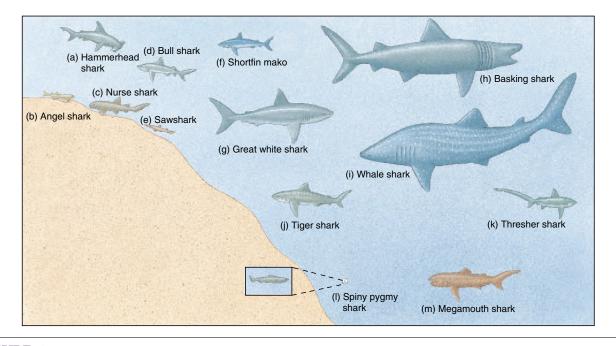
Sharks are sometimes referred to as "living fossils" because many of them are similar to species that swam the seas over 100 million years ago. Their fusiform, or spindle-shaped, bodies, tapering from the rounded middle toward each end, slip easily through the water. The tail, or **caudal**  The four basic characteristics of chordates:

- 1. A single dorsal, hollow nerve cord
- 2. Gill, or pharyngeal, slits
- 3. A notochord
- 4. A post-anal tail
- Chapter 7, p. 146

**Fish** Used for a single individual or for more than one individual of the same kind.

**Fishes** Used to refer to more than one kind of fish.





**FIGURE 8.4** Sharks live practically everywhere in the ocean. Some of those mentioned in the text include (*a*) hammerhead shark (*Sphyrna zygaena*), (*b*) angel shark (*Squatina*), (*c*) nurse shark (*Ginglymostoma cirratum*), (*d*) bull shark (*Carcharbinus leucas*), (*e*) sawshark (*Pristiophorus*), (*f*) shortfin mako shark (*Isurus oxyrinchus*), (*g*) great white shark (*Carcharodon carcharias*), (*b*) basking shark (*Cetorbinus maximus*), (*i*) whale shark (*Rbiniodon typus*), (*j*) tiger shark (*Galeocerdo cuvier*), (*k*) thresher shark (*Alopias vulpinus*), (*l*) spiny pygmy shark (*Squaliolus laticaudus*), and (*m*) megamouth shark (*Megachasma pelagios*).

fin, is well developed and powerful. The tail is usually heterocercal, meaning that the upper lobe is usually longer than the lower lobe (see Fig. 8.8*a*). The upper surface of the body typically features two dorsal fins, the first of which is typically larger and nearly triangular. The paired **pectoral fins** are large and pointed in most species. Five to seven gill slits are present on each side of the body.

Most sharks swim continuously, forcing water through the mouth, over the gills, and out through the gill slits (see Fig. 8.16*a*). When caught in fishing nets, they cannot force the water in and therefore "drown." Not all sharks need to swim, however. Nurse sharks (*Ginglymostoma*) and several other sharks rest on the bottom during the day (Fig. 8.4*c*). Their gills can obtain enough oxygen without swimming.

The powerful jaws of sharks have rows of numerous sharp, often triangular teeth (Fig. 8.3). The teeth are embedded in a tough, fibrous membrane that covers the jaws. A lost or broken tooth is replaced by another, which slowly shifts forward from the row behind it as if on a conveyor belt. Not all the nearly 350 living species of sharks conform to these specifications. Hammerhead sharks (*Sphyrna*), for example, have flattened heads with eyes and nostrils at the tip of bizarre lateral extensions (Fig. 8.4*a*). The head serves as a sort of rudder. The wide head also separates the eyes and nostrils, which improves the shark's sensory perception. The head of sawsharks (*Pristiophorus*) extends in a long, flat blade armed with teeth along the edges. The upper lobe of the tail is very long in the thresher sharks (*Alopias*; Fig. 8.4*k*). They use the tail to herd and stun schooling fishes, which they then eat.

The size of fully grown adults also varies. The spiny pygmy shark (*Squaliolus laticaudus*; Fig. 8.41) grows to no longer than 25 cm (almost 10 in). At the other extreme, the whale shark (*Rhiniodon typus*; Figs. 8.4i and 10.6) is the largest of all fishes. This huge animal, found in tropical waters around the world, may be as long as 18 m (60 ft), though specimens longer than 12 m (40 ft) are rare. Whale sharks pose no danger to swimmers; they are **filter feeders** that feed on plankton. Another giant, second in size only to the whale shark, is the basking shark (*Ce-torhinus maximus;* Fig. 8.4*h*), also a plankton eater. There are reports of basking sharks 15 m (50 ft) long, but most do not exceed 10 m (33 ft). Another very large shark is considered the most dangerous of all—the great white shark (*Carcharodon carcharias;* Fig. 8.4*g*). Individuals may exceed 6 m (20 ft) in length.

Sharks are found throughout the oceans at practically all depths. They are more prevalent, however, in tropical coastal waters. Sharks are primarily marine, but a few species travel far up rivers. The bull shark (*Carcharhinus leucas;* Fig. 8.4*d*) may be permanently established in some rivers and lakes in the tropics. Several sharks, including some rare species, are restricted to deep water (Fig. 8.5*b*).

Shark meat is eaten around the world. Many people have tried shark without knowing it: It is often illegally sold as "regular" fish or scallops. Sharks are still fished for their oil, once used extensively in all kinds of products, and for their skin, which is processed into a leather called



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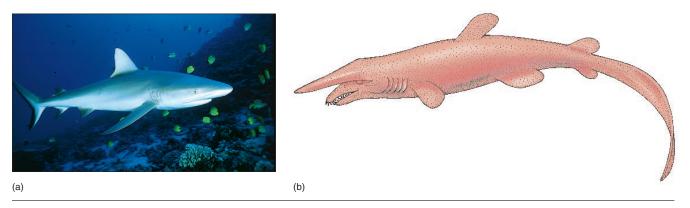


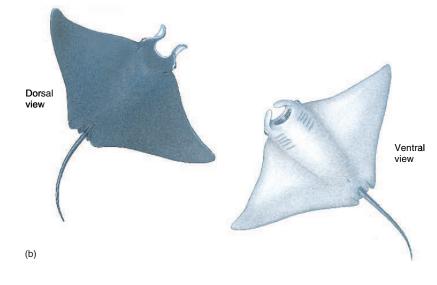
FIGURE 8.5 (a) The gray reef shark (*Carcharhinus amblyrhynchos*) is common in shallow waters of the tropical Pacific and Indian oceans. (b) The bizarre goblin shark (*Mitsukurina owstoni*) is restricted to deep water.



(a)

**FIGURE 8.6** Rays and skates have a flattened body and ventral gill slits. Common examples are (*a*) the yellow stingray (*Urolophus jamaicensis*) and (*b*) the manta ray (*Manta birostris*).

shagreen. The skin is also used for sandpaper. Much more valuable are their fins, used for soup in the Orient. Sharks are caught, their fins cut off (a practice known as shark finning), and the wounded animals sometimes dumped in the sea to die. The belief that shark cartilage may be a "joint nutrient" that may help in the treatment of arthritis has led to even more fishing pressure. Our appetite for shark has led to disastrous overfishing. So many sharks are being caught that the number of these slow-growing and slow-reproducing fishes has sharply declined in many parts of the world. As a result, more stringent management of shark fishing, which includes banning shark finning, has been implemented in the United States.



#### Rays and Skates

The 450 to 550 species of rays and skates have flattened bodies and for the most part live on the bottom (Fig. 8.6). Fishes that live on the bottom are called demersal. Some sharks, like angel sharks (Squatina) and sawsharks, also have flattened bodies (Fig. 8.4b and e). To complicate things, some true rays, like the guitarfishes (Rhinobatos), have a body that looks very much like a shark's. Only rays, skates, and related fishes, however, have their gill slits (always five pairs) on the underside of the bodythat is, located ventrally (Fig. 8.6b)-rather than on the sides. The pectoral fins are flat and greatly expanded, looking almost like wings. They are typically fused with

the head. The eyes are usually on top of the head.

The tropical sawfishes (*Pristis*) look very much like sawsharks but have ventral gill slits and are therefore grouped with the rays and skates. They feed by swimming through schools of fish and swinging their blades back and forth to disable their prey. They are known to grow up to 11 m (36 ft) long.

Many species of **stingrays** (Fig. 8.6*a*) and their relatives—the eagle, bat, and cow-nosed rays—have a whip-like tail usually equipped with stinging spines at the base for defense. Poison glands produce venom that can cause serious wounds to anyone who steps or falls on them. Abdominal wounds from stingrays,





Most sharks are harmless-at least to humans. Nevertheless, 25 species of sharks are known to have attacked humans, and at least 12 more are suspected of doing so. Three are particularly dangerous: the great white, tiger, and bull sharks (Fig. 8.4). There was a record number of 85 reported shark attacks (12 fatal) worldwide in 2000 and 76 (5 fatal) in 2001. The average for the 1990s was 54 (12.7 fatal). Several hypotheses have been proposed to explain this recent increase. Perhaps more tourists are visiting less spoiled areas or sharks are following an increasing number of whales migrating along coasts. Even so, shark attacks are rare. The chances of being attacked by a shark are lower than those of being hit by lightning.

Many shark attacks, however, have been documented over the years: A U.S. naval officer was killed by massive bites while swimming in the Virgin Islands in 1963, an abalone diver in Southern California was last seen protruding from the mouth of a shark, parts of arms and legs were found in the stomach of a tiger shark caught after a man had been mortally wounded in Australia, and a series of attacks by tiger sharks occurred in Hawai'i. One of the authors knew a young man whose promising life ended horribly in the jaws of a tiger shark off Western Samoa.

World War II exposed the crews of torpedoed ships and downed airplanes to shark attacks. Many grim stories about bleeding bodies surrounded by sharks began to spread. They prompted research on the aggressive behavior of sharks and the circumstances leading to shark attacks.

Great white sharks typically inflict a massive wound on their prey (such as seals and sea lions) and then release it. The sharks wait until the bleeding prey is too weak to resist, then move in for the kill. White shark attacks on humans wearing wet suits may be cases of mistaken identity. Sometimes people are able to escape when sharks release them after the first bite. It has been discovered that before attacking, the small but dangerous gray reef shark performs a distinct aggressive display-a warning unrelated to feeding. Displaying sharks may attack if someone approaches.

So far there is no guaranteed shark repellent. Copper acetate was used during World War II as a shark repellent but was eventually found to be ineffective. A black chemical dye was used, but this helped only by obscuring the shark's vision. A repellent based on a poison obtained from a flatfish seems more promising. Chain mail suits offer effective protection from sharks but are too expensive and cumbersome for widespread use. For someone like a downed flyer or shipwrecked sailor, perhaps the best protection is a black plastic bag large enough to float inside.

How can you decrease the risk of an attack? First, do not swim, dive, or surf in an area known to be frequented by dangerous sharks. Seal and sea lion colonies and coastal garbage dumps attract them. Blood, urine, and feces also attract sharks. Avoid murky water. Many sharks are more active at night, so avoid night swims. Sharks should not be provoked in any way. Even resting nurse sharks can turn and bite. Leave the water if fish suddenly appear in large numbers and behave erratically, which may be an indication that sharks are around. If you see a large shark, get out of the water with as little splashing as possible.

Actually, we threaten the survival of sharks more than they threaten us. They reproduce slowly, and their numbers are being depleted by overfishing in many areas. This attitude toward sharks may be shortsighted, because they play an important role in marine communities. When large sharks were netted off South Africa, for example, the number of species of small sharks, which are eaten by large sharks, increased. As an apparent result, the number of bluefish, a commercially important species, decreased. Some people catch shark only for the shark's fins or jaws. Others practice shark hunting for sport, leaving the meat to waste. A magnificent predator, the shark may soon be exterminated by human beings, the bloodiest predators of them all.

which often occur when handling rays caught in nets, may result in death. Many stingrays cover themselves with sand, becoming nearly invisible. They feed on clams, crabs, small fishes, and other small animals that live in sediment; stingrays have been known to damage valuable shellfish beds. They expose their food by excavating sediment with their pectoral fins. Their teeth are modified into grinding plates that crush their prey.

Electric rays (Torpedo) have special organs on each side of the head that produce electricity. They can deliver shocks of up to 200 volts that can stun the fishes they eat and discourage predators. The ancient Greeks and Romans used the shocks of electric rays to cure headaches and other ailments, the original shock treatment.

Not all rays spend their lives on the bottom. Eagle rays (Aetobatus) and the spectacular manta and devil rays (Manta, Mobula) "fly" through the water, using their pectoral fins like wings. Eagle rays return to the bottom to feed. Mantas feed in midwater on plankton. They have been observed leaping out of the water. The manta ray (Manta birostris; Fig. 8.6b) grows into a majestic giant. One individual was found to be almost 7 m (23 ft) wide.

Skates (Raja) are similar to rays in appearance and feeding habits, but they lack a whip-like tail and stinging spines. Some have electric organs. Skates lay egg cases, whereas rays give birth to live young. Skates can be extremely abundant, and the larger species are fished for food in some parts of the world.

### Ratfishes

About 30 species of strange-looking, mostly deep-water cartilaginous fishes are grouped separately because of their unique features. The ratfishes, or chimaeras (Fig. 8.7), for instance, have only one pair of gill slits covered by a flap of skin. Some have a long rat-like tail. They feed on bottom-dwelling crustaceans and molluscs.

## **Bony Fishes**

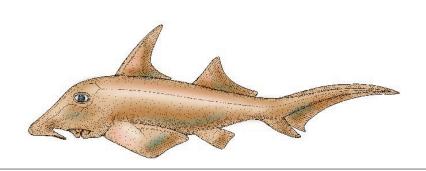
The great majority of fishes are **bony** fishes (class Osteichthyes). As the name implies, they have a skeleton made at least partially of bone. There are approximately 26,000 species of bony fishesabout 96% of all fishes and almost half of all vertebrates. Between 75 and 100 new species are described every year. A little more than half of all bony fishes live in the ocean, where they are by far the dominant vertebrates.

The composition of the skeleton is not the only distinguishing feature of bony fishes. In contrast to the tiny, pointed placoid scales of cartilaginous fishes, bony fishes usually have cycloid or ctenoid scales, which are thin, flexible, and overlapping (Fig. 8.8b). Cycloid scales are smooth, whereas ctenoid scales have many tiny spines along their exposed borders. The scales are made of bone and are covered by a thin layer of skin (see Fig. 8.19), as well as protective mucus. Some bony fishes, however, lack scales altogether. A flap of bony plates and tissue known as the operculum, or gill cover, protects the gills.

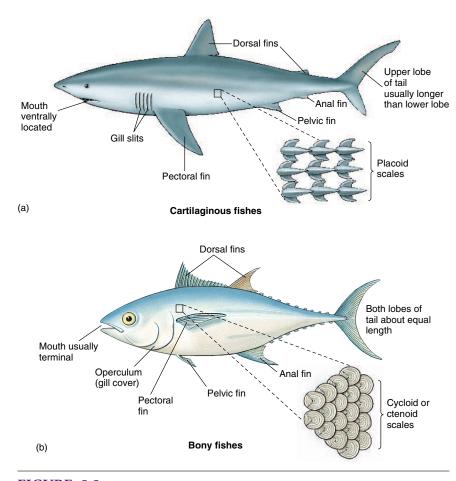
The upper and lower lobes of the tail, the caudal fin, are generally the same size (Fig. 8.8*b*). The fins of bony fishes generally consist of thin membranes that are supported by bony spines, or **fin rays**, in contrast to the stiff, fleshy fins of cartilaginous fishes. Fin rays may consist of rigid spines that act as a rudder or are used for protection. Some are flexible and used for propulsion and added maneuverability.

Whereas cartilaginous fishes have a ventral mouth, the mouth of most bony fishes is terminal, that is, located at the anterior end. Bony fishes have jaws with much more freedom of movement than those of sharks. The teeth are generally attached to the jawbones. Though they are usually replaced, the new teeth do not move forward in rows as those in sharks.

Another important characteristic is the presence in many bony fishes of a **swim bladder**, a gas-filled sac just above the stomach and intestine (see Fig. 8.12*b*). It allows the fish to adjust its buoyancy to keep from sinking or rising (see "Increased Buoyancy," p. 334). This is a significant development that compensates for the relatively heavy bony skeleton.



**FIGURE 8.7** The elephant fish (*Callorhinchus*), an example of a ratfish, or chimaera. The elephant fish, which is caught commercially for food in the Southern Hemisphere, receives its name because of a snout that hangs down like an elephant's trunk.



**FIGURE 8.8** The most important external differences between cartilaginous (*a*) and bony (*b*) fishes (also see Fig. 8.12).

Bony fishes are the largest group of living vertebrates. In addition to their bony skeleton, they typically have gills covered by an operculum, highly maneuverable fins, protrusible jaws, and usually a swim bladder.

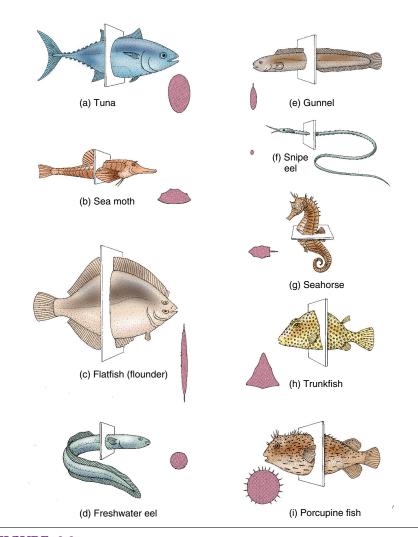
As we shall see in the next section, bony fishes are extraordinarily diverse in shape, size, color, feeding habits, reproductive patterns, and behavior. They have adapted to nearly every type of marine environment. All land vertebrates evolved from early bony fishes.

## **BIOLOGY OF FISHES**

Discovering how fishes, cartilaginous and bony alike, have conquered the demands of the aquatic environment so successfully has been a challenge to many investigators. The scientific study of fishes is called **ichthyology.** 

## **Body Shape**

The body shape of a fish is directly related to its lifestyle. Fast swimmers like sharks, tunas (Thunnus, Euthynnus), mackerels (Scomber, Scomberomorus), and marlins (Makaira) have a streamlined body shape that helps them move through the water (Figs. 8.8 and 8.9a; also see "Swimming Machines," p. 340). Laterally compressed bodies are good for leisurely swimming around coral reefs, kelp beds, or rocky reefs, but are still efficient enough to allow for bursts of speed to escape from enemies or capture food. This body form is seen in many inshore fishes like snappers (Lutjanus), wrasses (Labroides, Thalassoma), damselfishes (Amphiprion, Pomacentrus), and butterflyfishes (Chaetodon; see Fig. 8.28). Many demersal fishes, like rays, skates, and sea moths (Pegasus; Fig. 8.9b), are flattened from top to bottom. Flatfishes such as flounders (Platichthys), soles (Solea), and halibuts (Hippoglossus) are flat and beautifully adapted to live on the bottom, but their bodies are actually laterally compressed (Fig. 8.9c). They lie on one side, with both eyes on top. They begin life with one eye on each side like other fishes, but as they develop one eye migrates up to lie next to the other one. Distinctly elongate bodies are characteristic of moray eels (Gymnothorax), trumpetfishes (Aulostomus), and pipefishes (Sygnathus), among others. Eel-like fishes often live in narrow spaces in rocks, coral reefs, or



**FIGURE 8.9** Body shape among bony fishes varies as an adaptation to habitat. It is streamlined and fusiform for fast swimming as in tunas (*Thunnus; a*), flattened from top to bottom in bottom-dwellers such as the sea moth (*Pegasus; b*), or flattened sideways in bottom-dwellers such as the flounder (*Platichthys; c*). Fishes living among vegetation or rocks have eel-like bodies as in the freshwater eel (*Anguilla; d*), ribbon-shaped as in the gunnel (*Pholis; e*), or thread-like as in the snipe eel (*Nemichthys; f*). Slow swimmers feature bodies that are elongate on a vertical plane as in the seahorse (*Hippocampus; g*), triangular and truncate as in the trunkfish (*Ostracion; b*), or round as in the porcupine fish (*Diodon; i*).

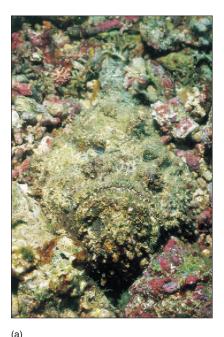
among vegetation (Fig. 8.9*d–f*). Many bony fishes, like seahorses (*Hippocampus*; Fig. 8.9*g*) depart from these generalized shapes. Trunkfishes (*Ostracion*) have truncate, or relatively short, bodies (Fig. 8.9*b*).

Body shapes may be especially useful for camouflage. For example, some pipefishes live among the eelgrass they resemble. The long, thin trumpetfishes often hang vertically among gorgonian corals or tube-like sponges, or even sneak behind other fish when approaching prey. An irregular shape is often an excellent means of concealment. Slow-moving bottom fishes such as blennies (*Blennius*) and sculpins (*Oligocottus*) have their outline broken up with irregular growths, particularly on the head, that resemble seaweeds. The body of the stonefish (*Synanceia verrucosa*; Fig. 8.10*a*) resembles a rock so closely that it is almost invisible to both potential prey and humans. Unfortunately for humans, this shallow-water fish from the tropical Pacific and Indian oceans

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(b)



**FIGURE 8.10** The variety of forms and habits among marine bony fishes is spectacular. (*a*) The stonefish (*Synanceia verrucosa*) does look like a stone, thus concealing its deadly venom. (*b*) The queen parrotfish (*Scarus vetula*) and other parrotfishes, so-called because of their beak-like mouths, sleep at night by secreting a loose mucus envelope that surrounds the body. (*c*) A colorful bar-tailed lionfish (*Pterois radiata*) advertises spines that contain a powerful venom that sometimes kills humans.

possesses the most potent venom known in fishes. Stepping on a stonefish is excruciatingly painful and has been known to cause death.

## Coloration

Some bony fishes use color for camouflage, but others, particularly those living in the tropics, are among the most brightly colored animals in the sea. The colored pigments in bony fishes are mostly found in special cells in the skin called chromatophores. These cells are irregular in shape and have branches radiating from the center. The amazing variety of colors and hues observed among marine fishes results from combinations of chromatophores with varying amounts of different pigments. Many fishes can rapidly change color by contracting and expanding the pigment in the chromatophores. Fishes may also have struc**tural colors** that result when a special surface reflects only certain colors of light. Most structural colors in fishes are the consequence of crystals that act like tiny mirrors. The crystals are contained in special chromatophores called **iridophores**. The iridescent, shiny quality of many fishes is produced by structural colors in combination with pigments (Fig. 8.10*b*).

Colors can tell us a lot about fishes. Some change color with their mood or reproductive condition. They may also use color to advertise the fact that they are dangerous, poisonous, or taste bad—a phenomenon known as **warning coloration** (Fig. 8.10*c*). **Cryptic coloration**, blending with the environment to deceive predators or prey, is a common adaptation (Fig. 8.10*a*). Flatfishes and some blennies, sculpins, rockfishes (*Sebastes*), and others can change color to match their surroundings. Another use of color is **disruptive coloration**, the presence of

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color stripes, bars, or spots that help break up the outline of a fish. These and other ingenious uses of color are especially common among coral reef fishes (see Figs. 8.28 and 14.30).

Open-water fishes and many shallowwater predators, on the other hand, are rarely as colorful. Most of them have silver or white bellies in sharp contrast to dark backs (Fig. 8.8). This distinctive color pattern, known as countershading, is a form of disguise in open water (see "Coloration and Camouflage," p. 337). When viewed from below, the light belly blends with the bright light coming from the surface. The dark back blends into the ocean's color as seen from above. Deep-water fishes also use color for concealment. They tend to be black or red, either of which is hard to see in the ocean depths (see "Coloration and Body Shape," p. 365).

## Locomotion

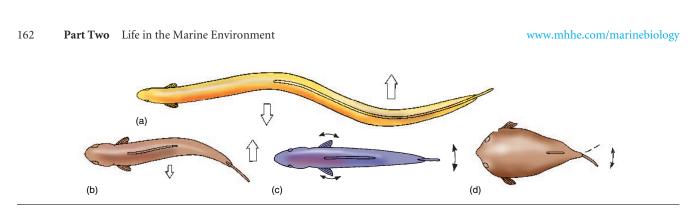
Swimming is obviously a major part of the life of fishes. Fishes swim to obtain food, escape from predators, and find mates. Many cartilaginous fishes must also swim to flush their gills with water to obtain oxygen.

Most fishes swim with a rhythmic side-to-side motion of the body or tail. S-shaped waves of contractions moving from head to tail push against the water and force the body forward. Variations on this theme are illustrated in Figure 8.11.

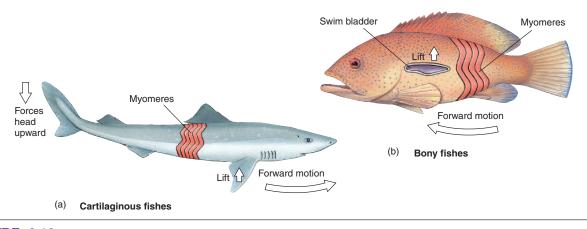
The rhythmic contractions are produced by bands of muscle called **myomeres**, which run along the sides of the body (Fig. 8.12). The distinctive bands of muscle are easily seen in fish fillets. Myomeres are attached to the backbone for support. Muscles make up a large percentage of the body weight of a fish—as much as 75% in tunas and other active swimmers.

Sharks tend to sink because they lack the buoyant swim bladder of bony fishes. To compensate, they have large, stiff pectoral fins that provide lift as do the wings of a plane (Fig. 8.12*a*). The longer upper lobe of the tail tends to tilt the body upward, also generating some lift. The large amount of oil in the huge liver also provides buoyancy because it is less dense than water. In rays and skates, whose wing-like

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**FIGURE 8.11** Locomotion in marine fishes. (*a*) Eels and other elongate fishes swim by undulating their body in lateral waves that travel from head to tail. (*b*) Fast fishes with shorter bodies—like tunas, snappers, and jacks—swim by flexing mainly the caudal (tail) portion of the body. (*c*) Surgeonfishes, parrotfishes, and others swim mainly by moving only the fins, that is, the caudal (tail), pectoral, anal, and/or dorsal fins. (*d*) Trunkfishes and porcupine fishes swim slowly by moving the base of the tail while the rest of the heavy body remains immobile.



**FIGURE 8.12** Cartilaginous and bony fishes use different adaptations to maintain their position in the water. (*a*) Sharks use their fins for lift. (*b*) Many bony fishes have evolved a gas-filled swim bladder to compensate for their heavier bony skeleton. This frees their fins for maneuverability, resulting in a much greater diversity of swimming styles (see Fig. 8.11).

pectoral fins are the main source of both thrust and lift, the tail is greatly reduced.

Because bony fishes have a swim bladder, they do not have to rely on their pectoral fins to provide lift. The pectorals are thus free to serve other purposes. This gives bony fishes great maneuverability. They can turn on a dime! Some can hover in the water or even swim backward, things that sharks cannot do. The other fins of bony fishes also help provide maneuverability. The dorsal and **anal fins** (Fig. 8.8b) are employed as rudders, at least part of the time, to steer and provide stability. The paired **pelvic fins** (Fig. 8.8b) also help the fish turn, balance, and "brake."

The flexibility of their fins has allowed many fishes to depart from the standard undulating style of swimming. Some emphasize sheer speed (see "Swimming Machines," p. 340). Many fishes, particularly those living around coral reefs, rocks, or kelp beds, swim mainly by moving their fins rather than their bodies, especially for the precise movements needed in feeding. Their tails are used almost solely as rudders. Wrasses, surgeonfishes (Acanthurus), and parrotfishes (Scarus, Sparisoma), which all live on coral reefs, and the California sheephead (Semicossyphus pulcher), common in kelp beds, swim mainly with their pectoral fins. Triggerfishes (Balistes) undulate their dorsal and anal fins to swim. This style is perfect for hovering over the bottom while hunting for crabs and sea urchins. Flying fishes (Cypselurus) have greatly expanded pectoral fins that they use to glide through the air (see Fig. 15.20). A large

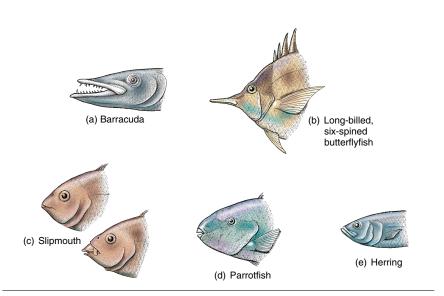
variety of bottom fishes (gobies, sculpins, and many others) crawl or rest on the bottom on their pectoral and/or pelvic fins (Fig. 8.9b). Clingfishes (*Gobiesox*) are small fishes that have their pelvic fins modified into part of a sucker that allows them to attach to rocks. Remoras, or sharksuckers (*Echeneis*), attach to sharks, whales, turtles, and many types of large fishes using a large sucker on top of their heads. This sucker is derived from part of the dorsal fin.

Locomotion of fishes usually involves sideways undulations of the body and tail. In contrast to those of sharks, the more flexible fins and tail of bony fishes do not have a role in buoyancy control and, as a result, have become highly maneuverable and important in locomotion.

## Feeding

Sharks are carnivores, but in contrast to typical carnivores, which capture smaller prey, some sharks feed by taking bites from prey larger than themselves. For this they use their formidable jaws coupled with shaking of the head. A few sharks are not particular; almost anything can be found in a shark's stomach. A tiger shark (Galeocerdo cuvier; Fig. 8.4) that was caught off South Africa was found to contain the front half of a crocodile, the hind leg of a sheep, three gulls, and two cans of peas, among other goodies. Nurse sharks feed mostly on bottom invertebrates, including lobsters and sea urchins. Some deep-water sharks subsist mainly on squids. Cookie-cutter sharks (Isistius) are small deep-water sharks that attack larger fishes and dolphins and cut out chunks of flesh with their razor-sharp teeth and sucking lips. Even the rubber sonar domes of nuclear submarines have not escaped their bites. It has been suggested that these sharks use bioluminescence to imitate squids in order to lure their prey.

Several species of cartilaginous fishes are filter feeders: the whale shark, the basking shark, the manta and devil rays, and the megamouth shark (Megachasma pelagios: Fig. 8.4m), a gigantic deep-water shark discovered off the Hawaiian Islands in 1976 and more recently in Southern California and several other locations around the world. Like other filter-feeding fishes, basking sharks filter the water with their gill rakers, slender projections on the inner surface of the gill arches (see Fig. 8.17b). Whale sharks have filter plates made of modified placoid scales. The large mouths of the three filter-feeding sharks have many small teeth and, excluding the megamouth, very long gill slits. The width of the spaces between the gill rakers or filter plates determines the size of the food captured. Water is strained through the gill rakers, and the shark swallows the food that is left behind. Whale sharks feed in warm water on small schooling fishes, squids, and planktonic crustaceans. Basking sharks, which live in colder water, feed on plankton by opening their mouths and slowly swimming through the water (Fig. 8.4*b*).



**FIGURE 8.13** The shape of the mouth of bony fishes tells much about their diets. (*a*) The barracuda (*Sphyraena*) uses its large mouth to tear off chunks of prey. Most bony fishes, however, swallow their prey whole. (*b*) Many butterflyfishes (*Chaetodon*) use a long snout and small mouth to feed on very small prey. (*c*) The extremely protrusible mouth of the slipmouth (*Leiognathus*) is used for feeding on relatively small prey. (*d*) Parrotfishes (*Scarus*) use their beak-like mouth to graze on small algae and coral (see Fig. 8.10*b*). (*e*) Herrings (*Clupea*) and other filter feeders typically have large mouths.

Mantas feed on plankton and small fishes, filtering them from the water with their gill rakers. Two fleshy, horn-shaped projections on the sides of the manta's mouth help channel food into the cavernous mouth (Fig. 8.6b).

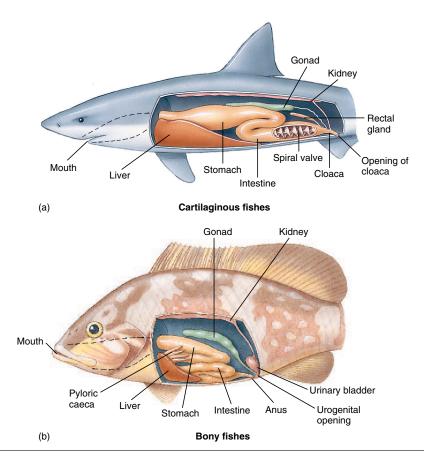
Bony fishes are very diverse in the ways they feed. Their protrusible jaws allow them much more flexibility in feeding habits than sharks and rays have. Most bony fishes are carnivores; almost no animal in the ocean is immune to being eaten by some bony fish. Bony fishes capture their prey from sediments, the water column, the surface of rocks, or from other organisms, including other fishes, or combinations of these. Some chase their prey; others sit and wait.

Carnivorous bony fishes typically have well-developed teeth for catching, grasping, and holding their prey (Fig. 8.13*a*), which is usually swallowed whole. The roof of the mouth, gill rakers, and pharynx may also have teeth to help hold the prey. Deep-water fishes often have huge mouths and teeth (see Fig. 16.12), and a few capture and swallow prey larger than themselves.

Unusual food preferences have evolved in fishes. Some prefer sponges, infrequently touched by other carnivores. Others prefer sea urchins, sea squirts, or other seemingly unsavory or tough-to-eat food items. Reef corals, skeleton and all, are eaten by several types of fishes including butterflyfishes and parrotfishes, though only living tissue is utilized as food (Figs. 8.13b and 8.28). Many species, however, are non-specialists and capture a wide variety of prey. Some feed on small invertebrates and dead animal material from the bottom. These bottom feeders have a downward-oriented mouth adapted to suck food from the bottom. Frogfishes (Antennarius) and anglerfishes (Gigantactis; see Fig. 16.23a) use a modified spine on the head to lure small fishes.

Fishes that feed primarily on seaweeds and plants are known as grazers. Parrotfishes, for example, graze on small algae growing on hard surfaces. Their front teeth are fused to form a beak-like structure (Fig. 8.13*d*). Some species use the beak to scrape off bits of live coral.

Fishes such as herrings (*Clupea*), sardines (*Sardinops*), anchovies (*Engraulis*),



**FIGURE 8.14** The digestive systems of cartilaginous (*a*) and bony (*b*) fishes display many of the basic features found in all vertebrates.

and menhaden (*Brevoortia*) filter plankton with their gill rakers. They typically strain their food by swimming with their large mouths (Fig. 8.13*e*) open. These plankton feeders are small, in contrast to the huge plankton-feeding sharks. They usually occur in large, often immense, schools (see the photo on page 383). Plankton feeders are the most abundant fishes in the ocean, and they are an important food source for many types of carnivores. They also account for a large share of the world's fish catch (see "Major Food Species," p. 387).

## Digestion

After being swallowed, food passes into the **stomach** (Fig. 8.14) through the pharynx and a short tube called the **esophagus.** The stomach is where the process of chemical digestion usually begins. It is typically J-curved or elongate but may be modified into a grinding structure or even lost altogether. The food passes from the stomach into the intestine. In most bony fishes the anterior portion of the intestine has many slender blind tubes, the pyloric caeca, which secrete digestive enzymes. Other digestive enzymes are secreted by the inner walls of the intestine and the pancreas. Another organ important in digestion is the liver, which secretes bile needed for the breakdown of fats. The liver is particularly large and oil-rich in sharks, sometimes making up as much as 20% of their body weight.

A few fishes lack a stomach and tend to have a portion of the intestine expanded for the digestion of food. Carnivorous fishes have short, straight intestines. Fishes that eat seaweeds, which are hard to digest,

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on the other hand, have coiled intestines, which may be much longer than the fish itself. The intestines of cartilaginous fishes and a few primitive bony fishes contain a spiraling portion called the **spiral valve**, which increases the internal surface area of the intestine (Fig. 8.14*a*). The intestine is responsible for absorbing the nutrients resulting from digestion. These nutrients pass into the circulatory system to be distributed through the body. Undigested material exits through the anus.

## **Circulatory System**

All fishes have a two-chambered heart located below the gills (Fig. 8.15). Deoxygenated blood comes into the first chamber of the heart from the body. The blood is then pumped to the second chamber, from where it is pumped to the gills, where gas exchange takes place. The oxygenated blood is then carried back to the body by blood vessels called arteries. The arteries branch out into thin-walled capillaries that allow oxygen and nutrients to reach every cell. The capillaries then collect into larger blood vessels, veins, that carry deoxygenated blood, along with carbon dioxide, back to the heart to complete the cycle.

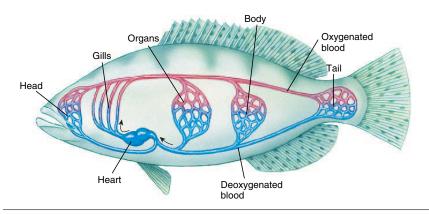
## **Respiratory System**

Fishes obtain oxygen dissolved in water and release carbon dioxide through paired gills. The gills lie in the pharynx, a chamber just behind the mouth that represents the front part of the gut.

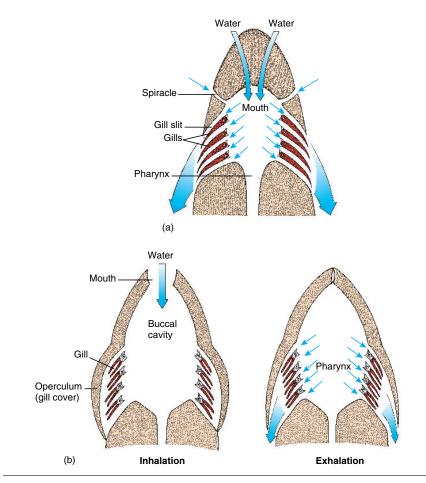
## Irrigation of the Gills

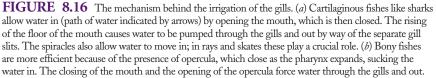
Fishes get the oxygen they need by extracting it from the water. To do this, they must make sure that water flows over the gills, that is, they must irrigate, or ventilate, the gills.

Most sharks swim with their mouths open so they passively irrigate their gills. Some, however, open and close the mouth to force water over the gills (Fig. 8.16*a*). Expansion and contraction of the walls of the pharynx and the gill slits assist in the process. Every gill lies in its own chamber, and each gill chamber opens to the outside by a separate gill slit. The first pair of gill



**FIGURE 8.15** The circulatory system of fishes consists of veins that carry deoxygenated blood (in blue) from the body, a two-chambered heart that pumps blood to the gills for oxygenation, and arteries that carry oxygenated blood (in red) to the rest of the body.





## Chapter 8 Marine Fishes 165

slits of cartilaginous fishes is modified into **spiracles**, a pair of round openings just behind the eyes. The spiracles are located on the dorsal surface of rays and skates (Fig. 8.6b). They allow these fishes, many of which live on the bottom, to take in water even when the ventral mouth is buried in the sediment. Lampreys and other jawless fishes pump water directly in and out through their gill slits during feeding when the passage of water through the mouth is blocked.

Most bony fishes have a more efficient mechanism to bring in water to the gills. The gills on each side share a common gill chamber, which opens to the outside through a single opening. The opening is covered by an operculum (Fig. 8.16b). When the mouth opens, the opercula close and the pharynx expands, sucking water in. The fish does the reverse to pump water out: The mouth closes, the pharynx contracts, and the opercula open. Some fast swimmers simplify things by just opening their mouths to force water into the gills.

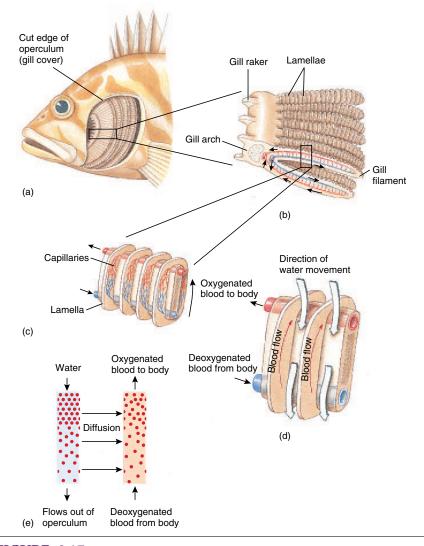
## Structure of the Gills

Fish gills are supported by cartilaginous or bony structures, the gill arches (Fig. 8.17*b*). Each gill arch bears two rows of slender fleshy projections called **gill filaments**. Gill rakers project along the inner surface of the gill arch. They prevent food particles from entering and injuring the gill slits or may be specialized for filtering the water in filter-feeding fishes.

The gill filaments have a rich supply of capillaries (Fig. 8.17*c*), the blood of which gives them a bright red color. Each gill filament contains many rows of thin plates or disks called **lamellae**, which contain capillaries. The lamellae greatly increase the surface area through which gas exchange can take place. The number of lamellae is higher in active swimmers, who need large supplies of oxygen.

**Gas Exchange** The absorption of oxygen to be used in respiration (the breakdown of glucose to release energy) and the elimination of carbon dioxide that results from the same process.

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**FIGURE 8.17** The gills of fishes are very efficient structures for gas exchange. Bony fishes have four pairs of gills (*a*), each containing two rows of numerous gill filaments (b). Lamellae in the gill filaments (*c*) increase the surface area of the gill filaments. (*d*) Diffusion of oxygen from seawater into the blood gets a boost because the water flows across the lamellae in the opposite direction to that of the blood. (*e*) The concentration of oxygen (indicated by dots) is always higher in the water than in the blood. If circulation was not reversed, blood to the body would have less oxygen.

## Gas Exchange

Oxygen dissolved in the water diffuses into the capillaries of the gill filaments to oxygenate the blood. **Diffusion** will take place only if oxygen is more concentrated in the water than in the blood. This is usually true because the blood coming to the gills has already traveled through the rest of the body and is depleted of oxygen (Fig. 8.15). As oxygen diffuses from the water to the blood, the amount of oxygen in the water decreases and that in the blood increases. This could reduce the efficiency of gas exchange, which depends on the water having more oxygen than the blood. Fishes have evolved a clever adaptation called a **countercurrent system of flow** to increase efficiency. The blood in the gills flows in the *opposite* direction to the water passing over them (Fig. 8.17*d*). When the water has passed over the gill and given up much of its oxygen, it meets blood that has just come

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from the body and is "hungry" for what oxygen remains in the water (Fig. 8.17*e*). By the time the blood has flowed most of the way through the gill, picking up oxygen, it encounters water that is just entering the gill chamber and is rich in oxygen. Thus, the oxygen content of the water is always higher than that of the blood. This system makes the gills very efficient at extracting oxygen. Without this countercurrent system, blood returning to the body would have less oxygen.

The blood disposes of its carbon dioxide using the same mechanism. Blood flowing into the gills from the body has a high concentration of carbon dioxide, a product of respiration. It easily diffuses out into the water.

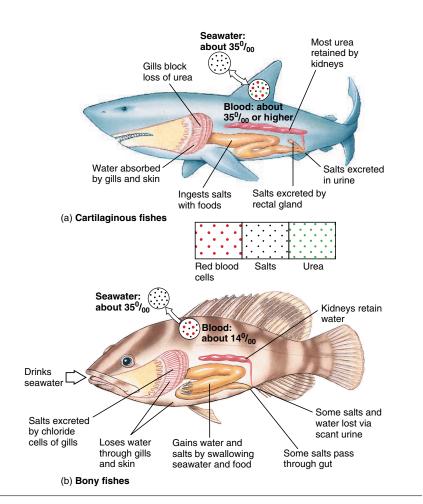
Gas exchange in the gills of fishes is highly efficient. The surface area of gills is greatly increased by lamellae, and the flow of water through them is in a direction opposite to that of blood.

Once oxygen enters the blood it is carried through the body by **hemoglobin**, a red protein that gives blood its characteristic color. Hemoglobin is contained in specialized cells called **erythrocytes**, or **red blood cells**. The hemoglobin releases oxygen to the tissues as it is needed. After it gives off its oxygen, the hemoglobin picks up carbon dioxide from the body and carries it to the gills, where it diffuses into the water.

Muscles use a lot of oxygen during exertion. They have a protein called **myoglobin**, similar to hemoglobin, that can store oxygen. Hard-working muscles tend to have a lot of myoglobin, which makes them dark red. Strong swimmers, such as open-water sharks and tunas, have a high proportion of red, as opposed to white, muscle (see "Swimming: The Need for Speed," p. 338). Many other fishes have concentrations of red muscles at the base of heavily used fins.

## Regulation of the Internal Environment

In contrast to most marine organisms, the blood of marine bony fishes is less salty than seawater (see Fig. 4.14). As a result



**FIGURE 8.18** Marine fishes live in water that is saltier than their body fluids. For this reason, water tends to diffuse out of the body. (*a*) To prevent dehydration, sharks and other cartilaginous fishes concentrate urea, absorb seawater through their gills and skin, and excrete excess salts by way of the urine and feces. A special gland, the rectal gland, also excretes excess salts. Their blood ends up with a solute concentrate urea, which is toxic to them. Instead, their kidneys conserve water, and they drink seawater, excreting excess salts as do cartilaginous fishes, but using different organs. Compare with Fig. 4.14.

they lose water by **osmosis**. Marine bony fishes therefore need to **osmoregulate** to prevent dehydration. To replace lost water, they swallow seawater (Fig. 8.18*b*). Seawater contains excess salts, some of which pass straight through the gut without being absorbed. Salts that are absorbed are excreted by the **kidneys**, the most important excretory organs of vertebrates, and specialized **chloride cells** in the gills. The kidneys conserve water by producing only small amounts of urine.

Cartilaginous fishes use a different approach to salt balance. (Fig. 8.18*a*).

They reduce osmosis by increasing the amount of dissolved molecules, or **solutes**, in their blood, making the blood concentration closer to that of seawater. They do this by retaining a chemical called **urea**, a waste product that results from the breakdown of proteins. The amount of urea in the blood is controlled by the kidneys. As in all vertebrates, the kidneys remove wastes from the blood and eliminate them in the urine. In most animals urea is toxic and is excreted, but sharks and other cartilaginous fishes excrete only small amounts. Urea and re-

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lated compounds are much less toxic to cartilaginous fishes. They retain most of the urea in their blood; their gills help in this process by blocking the loss of urea.

Cartilaginous fishes also absorb water to prevent dehydration, mostly through the gills and from food. Excess salts are excreted by the kidneys, intestine, and a special gland near the anus called the **rectal gland**.

Marine fishes keep a constant internal environment and check water loss through the osmoregulatory activities of the kidneys, gills, and other mechanisms.

# Nervous System and Sensory Organs

Vertebrates have the most complex and advanced nervous systems of any animal group. At the heart of the system is the central nervous system, consisting of the brain and spinal cord. The central nervous system coordinates and integrates all body activities and stores information. The brain is divided into several regions known to serve as centers for particular functions such as olfaction and vision. It is protected by a cartilaginous or bony skull. Nerves connect the central nervous system with various organs of the body and with sense organs that receive information from the surroundings. This information is sent to the brain in the form of nerve impulses.

Most fishes have a highly developed sense of smell, which they use to detect food, mates, and predators, and sometimes to find their way home. Fishes do this

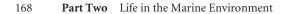
**Diffusion** The movement of molecules from areas of high concentration to areas of low concentration.

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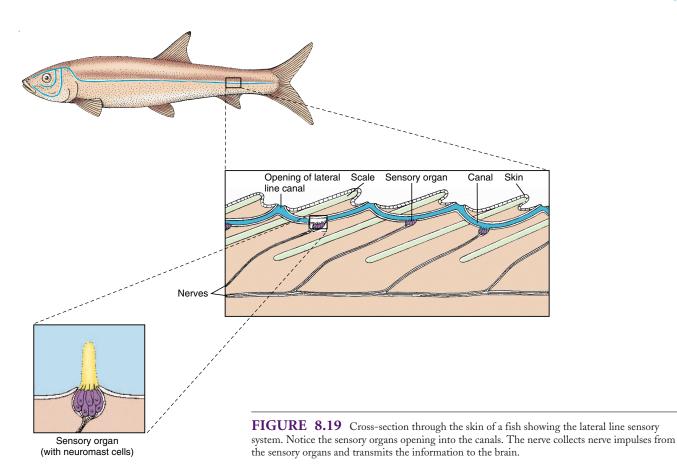
**Osmosis** The diffusion of water across a selectively permeable membrane, such as a cell membrane.

**Osmoregulation** The active control by an organism of its internal *solute* concentration to avoid osmotic problems.

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with special sensory cells located in **olfactory sacs** on both sides of the head. Each sac opens to the outside through one or two openings, the nostrils, or **nares.** 

The sense of smell is particularly well developed in sharks. They can detect blood and other substances in concentrations as low as fractions of one part per million. Salmon (*Oncorbynchus*), which live as adults at sea but reproduce in fresh water, use olfaction to find the stream where they were born years earlier (see "Migrations," p. 171). There is evidence that they accomplish part of this remarkable feat by memorizing the sequence of smells on their way out to sea.

Fishes detect other chemical stimuli with **taste buds** located in the mouth and on the lips, fins, and skin. Taste buds also are found on **barbels**, whisker-like organs near the mouth of many bottom feeders such as marine catfishes (*Arius*). Fishes that have them use their barbels to detect food on the bottom.

Bony fishes appear to rely on vision more than most cartilaginous fishes. Fish eyes are not very different from those of vertebrates that live on land. One important difference, though, is the way they focus. Whereas the eyes of most land vertebrates focus by changing the shape of the lens, the round lens of the fish eye focuses by moving closer or farther away from the subject. This is partially why fish eyes tend to bulge. Many bony fishesparticularly shallow-water species-have color vision, but most cartilaginous fishes have little or none. Some sharks have a distinct nictitating membrane that can be drawn across the eye to reduce brightness and to protect the eye during feeding.

Fishes have a unique sense organ called the **lateral line** that enables them to detect vibrations in the water. The lateral line consists of a system of small canals that run along the head and body (Fig. 8.19). The canals lie in the skin and in the bone or cartilage of the head. They are lined with clusters of sensory cells, or **neuromasts** that are sensitive to vibration. The canals usually open to the surface through pores that are quite visible.

The lateral line system picks up vibrations resulting from the swimming of other animals, as well as water displacements caused by sound waves. It allows fishes to avoid obstacles and predators, detect prey, orient to currents, and keep their position in a school.

Cartilaginous fishes also have sense organs in the head called the **ampullae of Lorenzini** (see Fig. 8.3) that can detect weak electrical fields. This system has been shown to help them locate prey. It may also help in navigation as a sort of electromagnetic compass or perhaps a detector of currents.

Fishes can also perceive sound waves with their **inner ears**, paired hearing organs located to the sides of the brain just behind the eyes. The inner ears are a set of fluid-filled canals that contain sensory II. Life in the Marine Environment 8. Marine Fish

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cells similar to those in the lateral line canals. In some fishes the swim bladder is known to amplify sound by vibrating and transmitting sound waves to the inner ear. The inner ear is also involved in equilibrium and balance. In many fishes changes in position are detected by shifts in the position of calcareous **ear stones**, or **otoliths**, that rest on sensory hairs, a mechanism similar to the **statocysts** of invertebrates.

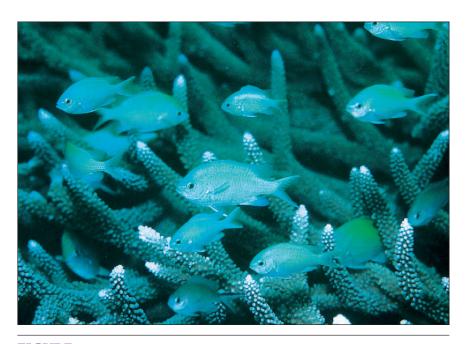
The sense organs of fishes include eyes, olfactory sacs, taste buds, and inner ears, as well as a lateral line and other specialized organs that pick up vibrations or electrical stimuli from the water.

## **Behavior**

The well-developed nervous system of fishes allows them to respond to their environment in complex ways. Among the most important aspects of their response is their behavior, which in general is much more sophisticated than that of invertebrates. Complex behavior dominates nearly every phase in the lives of fishes. They use behavior to adapt to such physical factors as light and currents. Behavior is of key importance in finding food and shelter and avoiding enemies. Fishes also display a fascinating variety of behaviors related to courtship and reproduction. We can give only a glimpse here of some important aspects of fish behavior. Reproductive behavior will be covered in the next section, and some other highlights will be discussed in later chapters.

## Territoriality

Many marine fishes, particularly openwater species, do not reside in any particular area. Others, however, are known to establish **territories**, home areas that they defend against intruders. Some fishes defend territories only during reproduction. Many, however, have more or less permanent territories that they use for feeding and resting or as shelter. It is thought that fishes often guard territories to ensure that they have enough food and other resources. Thus, territoriality is most common in crowded environments like kelp beds and coral reefs, where resources are



**FIGURE 8.20** Some damselfishes, such as species of *Chromis*, live among corals. They dash into the spaces between the coral branches whenever danger approaches.

most likely to be in short supply. Coral reef damselfishes are famous for fiercely defending their territories, often attacking fishes many times their size or even divers.

Fishes use a variety of **aggressive behaviors** to defend their territories. Actual fights are surprisingly rare. Instead, fishes usually prefer to avoid risking injury by bluffing. Raised fins, an open mouth, and rapid darting about are examples of such threatening postures. Territorial defense may also involve sound production. Marine bony fishes may make sound by grinding their teeth or rubbing bones or fin spines on another bone. Some fishes "drum" by pulling muscles on the swim bladder, and this sound is amplified by the air-filled bladder.

Sometimes a solitary individual defends a territory. In other species, like some butterflyfishes, territories are established by a male-female pair. Territories may also be inhabited by groups that belong to the same species. This is the case in damselfishes, which inhabit spaces between the branches of corals (Fig. 8.20), and anemonefishes, or clownfishes (*Amphiprion;* see Fig. 14.35). Members of such groups often divide the territory into subterritories.

## Schooling

Many fishes form well-defined groups, or schools. Some, including herrings, sardines, mullets (Mugil), and some mackerels, school throughout their lives. Others are part-time schoolers, especially as juveniles or during feeding. Most cartilaginous fishes are solitary, but a few, such as hammerhead sharks, mantas, and other rays, sometimes travel in schools. It has been estimated that around 4,000 species, including both marine and freshwater species, school as adults. Schools can be huge, as large as 4,580 million m<sup>3</sup> (161,720 ft<sup>3</sup>) in the Atlantic herring (Clupea harengus). The members of a school are typically all about the same size. The stationary schools that are common around coral reefs, kelp beds, rocks, and shipwrecks, however, may include

**Statocysts** Sense organs of many invertebrates consisting of one or more grains or hard bodies surrounded by sensitive hairs and used to orient the animal with gravity.

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# A FISH CALLED LATIMERIA

In December of 1938 the skipper of a fishing trawler operating in deep water off the Chalumna River in South Africa found a very strange fish in his catch. He took it to Marjorie Courtnay-Latimer, a young curator at the local museum, who recognized the fish as something special. She sent a sketch of the 1.5-m (5-ft) specimen to Dr. J. L. B. Smith at nearby Rhodes University, and history was made.

The fish was a big catch indeed. It was a **coelacanth**, a type of fish thought to have become extinct 60 million years ago. Coelacanths were previously known only from fossils, some at least 400 million years old. They belong to the crossopterygian fishes, a group of fishes that might have given rise to the first land vertebrates. About 350 million years ago a crossopterygian fish with paddle-like bony fins crawled out of the water and changed life on earth forever.

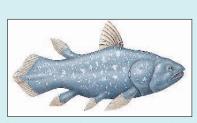
Dr. Smith officially described the fish and named it *Latimeria chalumnae* in honor of its discoverer and the river near which it was caught. Unfortunately, the internal organs of the fish had been discarded by the time Dr. Smith got to it, so nothing was known of its internal structure. A reward was offered for more specimens of this incredible living fossil. It was not until 1952 that a second specimen was caught near the Comoro Islands, between Madagascar and mainland Africa. Ironically, the fish is well known to the natives of the islands. They eat its oily flesh after drying and salting it, and they use its rough skin for sandpaper!

The fish is still very rare. None of the captured specimens has survived more than 20 hours; thus, little is known about their habits. In 1987 a small submersible was used to film and observe a live *Latimeria* in its natural environment for the first time. The fish was observed only at night, at depths of 117 to 200 m (386 to 660 ft). In 2000 divers filmed several live *Latimeria* off the northeastern coast of South Africa. The fish were filmed at a depth of only 104 m (320 ft).

Latimeria is a large fish, up to 1.8 m (6 ft) in length and weighing as much as 98 kg (216 lbs). The body is covered by large blue scales. It feeds on fish and squid. This living fossil is unique in many ways. It has heavy, stalked fins that have bones like land vertebrates. The fish appears to stand on the fins, but not to crawl over the bottom with them as once thought. The pectoral fins can rotate nearly 180 degrees, allowing the fish to slowly swim over the bottom, sometimes standing on its head or with its belly up.

Much remains to be discovered about this fascinating creature. Jelly-filled organs on the head may be used to detect electrical fields and thus help in prey location. Little is known about its reproduction. Females bear live young, and the huge eggs (about 9 cm, or 3.5 in, in diameter) develop in the reproductive tract.

Latimeria remains a priceless catch, and several aquaria around the world would like very much to capture live specimens. As its value in dollars soars, so do



The coelacanth (*Latimeria chalumnae*), a living fossil.



Live Indonesian coelacanth (*Latimeria menadoensis*).

the concerns about the 200 individuals that may still survive in the Comoros. International trade has now been officially outlawed.

In 1997 Latimeria surprised everybody by turning up in a fish market in Sulawesi, one of the islands of Indonesia, almost 10,000 km (6,200 miles) from the Comoros! A live specimen was taken off the same island in 1998. Though very similar in appearance to the Indian Ocean specimens, DNA evidence showed that the Indonesian coelacanth belonged to a different species than that in the Indian Ocean. The discoverer, Dr. Mark Erdmann, and the Indonesian team that had studied the specimen, planned to formally describe the new species in a scientific publication. But a group headed by French scientists went ahead, and without Erdmann's knowledge, officially described the Indonesian coelacanth as a new species, Latimeria menadoensis, in a French scientific publication.

Are there any new coelacanths waiting to be discovered somewhere else? Only time and alert fishers will tell.

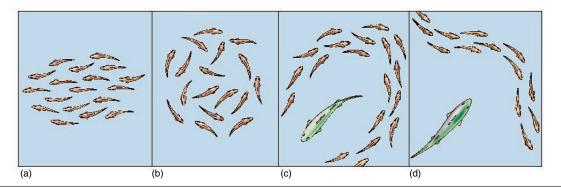
members of different sizes or even different species.

Schools function as well-coordinated units, though they appear to have no leaders (Fig. 8.21). The individual fishes tend to keep a constant distance between themselves, turning, stopping, and starting in near perfect unison. Vision has been found to play an important role in the orientation of individuals within a school. In some species, though, blinded fish can school in a coordinated way. These fish probably use the lateral line, olfaction, and sound they emit to keep track of each other. The tight coordination of schooling fishes may break down when they are feeding or attacked by a predator.

Why do fishes school? One explanation is that schooling offers protection against predation. Predators may be confused if, for instance, the school circles the predator (Fig. 8.21*c*) or splits into several groups. It is also difficult for a predator to aim for just one fish in a cloud of shifting, darting individuals (Fig. 8.21*d*). On the other hand, some predators, such as jacks (*Caranx*), are more efficient when they attack schools of prey rather than individuals. It also has been suggested that schooling increases the swimming efficiency of the fish because the fish in front form an eddy that reduces water resistance for those behind. There is experimental evidence, however, that this is not always the case and that fish do not always align in a hydrodynamically efficient way. In at least some fishes, schooling is advantageous in feeding or mating. There is probably no single reason that fishes school, and the reasons probably vary from species to species.

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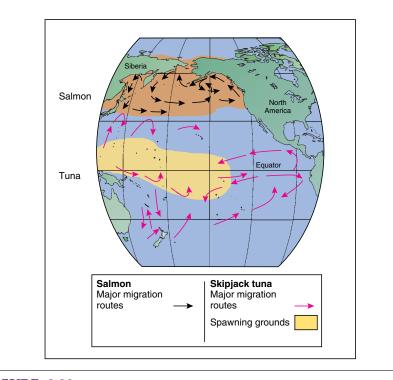
**FIGURE 8.21** Fishes follow different recognizable patterns when schooling. Some common patterns include (*a*) traveling, (*b*) feeding on plankton, (*c*) encirclement of a predator, and (*d*) streaming to avoid a predator.

### Migrations

Another fascinating aspect of the behavior of marine fishes is **migration**, regular mass movements from one place to another once a day, once a year, or once in a lifetime. Schools of parrotfishes and other fishes migrate onshore and offshore to feed. Many open-water fishes migrate several hundred meters up and down the water column every day (see "Vertical Migration," p. 339). The most spectacular migrations, however, are the transoceanic journeys made by tunas, salmon, and other fishes. We still know little about why fishes migrate, but most migrations seem to be related to feeding or reproduction.

There is little doubt that feeding is the main reason behind the migration of open-water species like tunas. Recaptures of tagged fish have provided much information on how far, how fast, and when tunas migrate (see "Swimming: The Need for Speed," p. 338). Though essentially tropical, some species migrate long distances to feed in temperate waters. Such is the case in the skipjack tuna (*Katsuvonus pelamis*; Fig. 8.22) and other tunas.

Even more amazing are the migrations between the sea and fresh water undertaken by some fishes that are dependent on fresh water for reproduction. **Anadromous** fishes spend most of their lives at sea but migrate to fresh water to breed. Sturgeons (*Acipenser*), whose eggs are eaten as caviar, some lampreys, and smelts (*Osmerus*) are examples. By far the best known anadromous fish, however, is the salmon.



**FIGURE 8.22** The skipjack tuna (*Katsuwonus pelamis*), the leading commercial catch among tunas, undertakes extensive migrations that every year take it almost halfway across the globe. The Pacific salmon (*Oncorhynchus*) migrates to spawn only once in a lifetime. Approximate limits of distribution and migration routes indicated are for all seven species of salmon.

There are seven species of salmon in the Pacific, each known by several common names. They spend their adult lives in the North Pacific, traveling thousands of miles in vast sweeps along the coast, the Aleutian Islands, and the open sea (Fig. 8.22). Some even venture into the Bering Sea and the Arctic Ocean. How they navigate at sea is not known. It has been hypothesized that they use land features at least part of the way. Currents, salinity, temperature, and other water characteristics might provide clues. Other possibilities include orientation to polarized light, the sun, or the earth's magnetic field. 8. Marine Fish

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**FIGURE 8.23** The journey of Pacific salmon such as these sockeye salmon (*Oncorhynchus nerka*) is an arduous one indeed. The fish have to swim far upstream, often leaping over rapids and waterfalls. Many fall prey to hungry predators or to the nets and lines of fishers.

After several years at sea, a period characteristic of each species, salmon mature sexually and start migrating into rivers. They are probably guided at first by the earth's magnetic field. They do not feed once they enter fresh water, living instead on stored fat. Their kidneys must adjust to the change from salt to fresh water. Eventually they reach the exact stream of their birth, sometimes far upstream (Fig. 8.23). The king, or chinook, salmon (*Oncorbynchus tschawytscha*) and chum, or dog, salmon (*O. keta*) reach as far inland as Idaho and the headwaters of the Yukon River.

Salmon find their home streams with remarkable accuracy, the result of a type of chemical memory. They have been found to recognize not only the "smell" of their own stream, but of others they pass along the way. There also is evidence that they respond to chemicals released by other members of their own species. The ability of an animal to find its way back to a home area is known as **homing behavior**.

Salmon spawn on beds of clean gravel in the shallows. The female digs out a shallow nest, or "redd," into which she deposits her eggs. The eggs are fertilized by the male and covered with gravel. After defending the nest for a while, the salmon die.

After hatching, the young salmon may return to sea immediately, as in the pink, or humpback, salmon (*O. gorbuscha*). The young of other species remain in fresh water for a time, as long as five years for the sockeye, or red, salmon (*O. nerka*). The kokanee salmon, a race of this last species, is landlocked and does not migrate to sea at all.

One of the biggest hazards that Pacific salmon must endure during their migration, however, is the rapid destruction of their natural environment by humans. Migration routes have been blocked by dams, spawning grounds filled with silt as a result of logging and cattle grazing, and rivers polluted by pesticides (which, among other toxic effects, are suspected of disrupting salmon's sense of smell), fertilizers, and animal waste. So serious is the problem that sharp restrictions have been imposed on the commercial harvest of salmon along the Pacific coast of the United States. Some species, like the sockeye, king, and chum salmon, have been declared endangered in some rivers. Around 11 to 15 million salmon once spawned in the Columbia river system in

the northwestern United States. The number is now around 1 million, thanks mostly to an unexpected increase in the number of king, or chinook, salmon in 2001. Most of these, however, were born in hatcheries. Only the remaining quarter of a million can make it back to their old, natural spawning grounds.

The Atlantic salmon (*Salmo salar*) breeds on both sides of the North Atlantic. It migrates across the ocean, mostly off Greenland, before returning to rivers from New England to Portugal. Atlantic salmon may survive after spawning; some females are known to have made as many as four round-trips to their homes. Like their Pacific cousins, populations of the Atlantic salmon in the wild are in serious decline.

**Catadromous** fishes have a migratory pattern opposite that of salmon. They breed at sea and migrate into rivers to grow and mature. Several catadromous fishes are known, but the longest migration of any of them is that of freshwater eels (*Anguilla*). There are at least 16 species including the American (*A. rostrata*) and European (*A. anguilla*) eels.

Both American and European eels spawn in the Sargasso Sea at depths of at least 400 to 700 m (1,300 to 2,300 ft) and then die (Fig. 8.24). The eggs hatch into tiny, transparent larvae that gradually develop into elongate, leaf-shaped leptocephalus larvae. The larvae of the American eel drift in the plankton for at least a year before metamorphosis. The juveniles then move into rivers along the Atlantic coast of North America. The leptocephalus larvae of the European eel are believed to spend at least an extra two or three years drifting in the Gulf Stream to reach rivers throughout western Europe. Adults of both species eventually grow to more than 1 m (40 in) in length. Both juveniles and adults are highly valued as food, particularly in Europe. After 10 to 15 years in fresh water, adults turn silver and their eyes become larger. Soon after this, they head out to sea.

The migration of eels back to the Sargasso Sea is not completely understood. How do they navigate to reach such a distant spot? There is experimental evidence that they use the earth's magnetic field as a cue for navigation. It has been assumed

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### Chapter 8 Marine Fishes 173

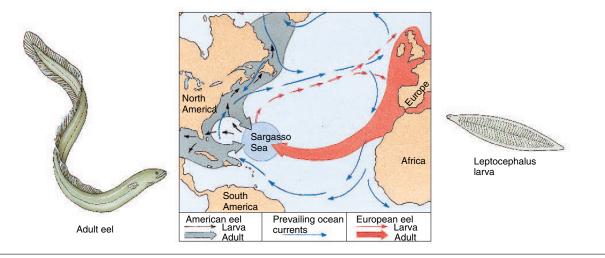


FIGURE 8.24 Two species of freshwater eels, the American (*Anguilla rostrata*) and European (*A. anguilla*) eels, breed in the Sargasso Sea and migrate to rivers in North America and Europe. The return trip of larvae is not precisely known, so the arrows indicate only the most likely routes.

that European eels follow favorable currents that take them first along the coast of northwest Africa (Fig. 8.24), much like the Portuguese navigators of old (see "Tall Ships and Surface Currents," p. 59).

Some biologists once suggested that the adults of the European eel did not return to the Sargasso Sea at all but died at sea. According to this view, American and European eels were really the same species. Larvae that remained too long at sea simply ended up drifting to Europe. We now know that this is not true. The American and European eels are distinct species. They spawn at different, though overlapping, periods and locations in the Sargasso Sea.

# Reproduction and Life History

Marine fishes have evolved an enormous variety of ways to produce offspring. Reproduction is a complex enterprise involving, in particular, adaptations of the reproductive system and the behavior that brings the two sexes together and ensures successful spawning.

## Reproductive System

The reproductive system of fishes is relatively simple. The sexes are usually separate. Both sexes have paired gonads located in the body cavity (see Fig. 8.14). In cartilaginous fishes, ducts lead from the ovaries and testes into the **cloaca**, a common passage for the digestive, excretory, and reproductive systems (see Fig. 8.14*a*). The cloaca opens to the outside. Jawless and bony fishes, on the other hand, have a separate opening for urine and gametes, the **urogenital opening**, which is located just behind the anus (see Fig. 8.14*b*).

In many marine fishes the gonads produce gametes only at certain times. The timing of gamete production is crucial. Both sexes must be ready to spawn at the same time. Spawning, as well as larval development, must take place during the period with the most favorable conditions. The exact timing of reproduction is especially critical for fishes that make long migrations to breed.

The timing of reproduction is controlled for the most part by **sex hormones**. Sex hormones are produced in the gonads and released in small amounts into the blood. They stimulate the maturation of gametes and may cause changes in color, shape, and behavior before breeding.

The release of sex hormones is triggered by environmental factors such as day length, temperature, and the availability of food. Fishes can be artificially induced to spawn when these environmental factors are controlled or when hormones are injected. This discovery is being used by scientists interested in increasing the reproductive potential of fishes grown for food (see "Mariculture," p. 397).

A few marine fishes are **hermaphrodites.** Though able to fertilize their own eggs, these fishes usually breed with one or more other individuals, ensuring fertilization between different individuals. Hermaphroditism also is found among several deep-water fishes, an adaptation to the depths of the ocean where it may be difficult to find members of the opposite sex (see "Sex in the Deep Sea," p. 370).

A variation of hermaphroditism among fishes is **sex reversal**, or **sequential hermaphroditism**, in which individuals begin life as males but eventually change into females, or females change into males. These changes are controlled by sex hormones. Sex reversal occurs in several

**Sargasso Sea** Area of the Atlantic Ocean north of the West Indies that is characterized by masses of drifting Sargasso weed, a brown seaweed.

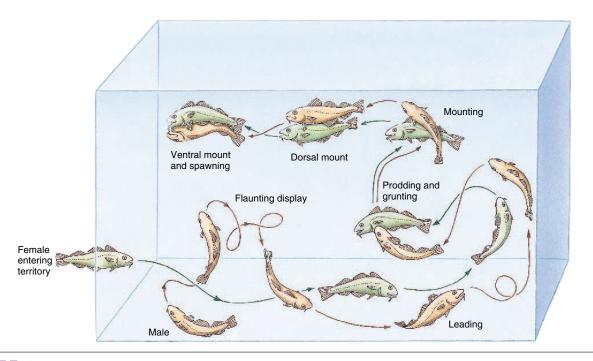
Chapter 6, p. 108

**Hormones** Molecules that act as chemical messengers within the body. *Chapter 4, p. 70* 

**Hermaphrodites** Individuals that have both male and female gonads.

Chapter 7, p. 134

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**FIGURE 8.25** The Atlantic cod (*Gadus morbua*), once one of the most important food fishes in the world, spawns in large aggregations in the North Atlantic. The two sexes do not spawn indiscriminately but follow a strictly choreographed series of behaviors. The male establishes a territory, and the action starts after an interested female enters his territory. Most of the display is made by the male, which uses fully spread fins, grunting sounds, and a series of swimming behaviors. If the female does not follow the male, he has to start all over again to try to attract another female. The spawning of gametes into the water thus climaxes a series of behaviors that includes visual, sound, and tactile signals.

groups of marine fishes, but it is most prevalent among sea basses and groupers (*Serranus, Epinephelus*), parrotfishes, and wrasses. Some rather complicated reproductive strategies have been discovered among these fishes.

In at least some species of anemonefishes (Amphiprion), all individuals begin as males. Each sea anemone is inhabited by a single large female that mates only with a large, dominant male. All the other fishes that live on the anemone are small non-breeding males. If the female disappears or is experimentally removed, her mate changes into a female and the largest of the non-breeding males becomes the new dominant male. The new female can start spawning as soon as 26 days after her sex change! Males of some wrasses form harems of many females. If the male disappears, the largest, dominant female immediately begins to act like a male and within a relatively short period of time changes color and transforms into one that is capable of producing sperm.

### **Reproductive Behavior**

Potential mates must get together at the right time to breed. Many species migrate and congregate in specific breeding grounds, as in the salmon and freshwater eels previously discussed. Sharks are usually loners but may come together during the breeding season. Many of them appear to stop feeding at spawning time.

Many bony fishes change color to advertise their readiness to breed. Most salmon undergo dramatic changes. Both sexes of the sockeye salmon turn from silver to bright red, giving rise to another of its common names, the red salmon. In male sockeye and pink, or humpback, salmon, the jaws grow into vicious-looking hooks. Males of the latter species also develop a large hump. Color changes also can be observed in tropical fishes. Many male wrasses, colorful all the time, appear even more spectacular before breeding.

The first step in reproduction is **courtship**, a series of behaviors that serves to attract mates. These behaviors

involve an exchange of active displays such as "dances," special postures that display colors, and swimming upside down (Fig. 8.25). Each species has its own unique courtship behavior. This is thought to help keep fishes from mistakenly mating with members of the wrong species.

Reproduction in fishes involves many adaptations that help individuals get together for mating. These include migrations, displaying particular colors as sex signals, and courtship behavior.

Some fishes have **internal fertilization** of the eggs, in which the sperm is directly transferred from males to females through the act of **copulation. External fertilization**, the release of gametes into the water, or **spawning**, is more common in fishes, however.

Internal fertilization occurs mainly in cartilaginous fishes. Unfortunately, not much is known about their sex life. Male sharks, rays, and skates have a pair of II. Life in the Marine Environment 8. Marine Fish

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copulatory organs called **claspers** located along the inner edge of the pelvic fins (Fig. 8.26). The typical approach of a romantic male shark consists of biting his potential mate on the back. The male copulates by inserting his claspers into the female's cloaca. He bites and hangs from her or partly coils around her middle. Some skates mate after the male bites the female's pectoral fins. He presses his ventral surface against hers and inserts the claspers.

Bony fishes exhibit an almost infinite array of ways to spawn. Open-water fishes (sardines, tunas, jacks, and others) and those living around coral reefs and other inshore environments (such as surgeonfishes, parrotfishes, and wrasses) spawn directly into the water after courtship (Fig. 8.27). Females typically release many eggs. In the Atlantic cod (*Gadus morhua*), for example, a female 1 m (40 in) long can release up to five million eggs. The Atlantic tarpon (*Megalops atlanticus*) releases more than 100 million eggs every time it spawns!

Some fishes, like butterflyfishes, spawn in pairs (Fig. 8.28), others in groups. Individual males may establish territories or aggregate into groups. Groups of males may be approached by single females or by females in groups. Usually males seek out the females and entice them to spawn via courtship. Two individuals may pair only during spawning time, as in butterflyfishes, or may establish long-lasting bonds.

Eggs fertilized in the water column drift in currents and develop as part of the plankton. Most eggs contain oil droplets and are buoyant. Other eggs sink to the bottom. Herrings deposit their eggs on the surface of seagrasses, seaweeds, and rocks. Lampreys and salmon bury their eggs after spawning. The California grunion (*Leuresthes tenuis*) buries its eggs on sandy beaches during high tides; they will not hatch until the next high tide (see Fig. 3.25).

Most of the eggs that are released into the plankton will never survive. Fishes and other marine animals that spawn into the plankton are broadcast spawners that release as many eggs as possible to ensure that at least some hatch and make it to adulthood. Eggs re-



**FIGURE 8.26** Fertilization in cartilaginous fishes is internal, so males must possess some type of copulatory organ. This is the function of the claspers, which are located on the inner edge of the pelvic fins. They are provided with a groove for the passage of sperm. Only one clasper is inserted into the female at a time. These are the claspers of a scalloped hammerhead shark (*Sphyrna lewini*).



FIGURE 8.27 Males and females of the rainbow wrasse (*Thalassoma lucasanum*) from the Gulf of California swarm to release sperm and eggs.

quire a lot of energy to produce because they must contain enough yolk to nourish the young until they hatch and can feed.

Fishes that spawn fewer and larger eggs have evolved ways to take care of

them. In many damselfishes, males establish and defend breeding sites or nests (Fig. 8.29) in holes among rocks or coral, empty mollusc shells, and other shelters even discarded tires. After spawning, the





**FIGURE 8.28** Butterflyfishes are among the most colorful of coral reef fishes. Adults of some species occur in male and female pairs. (*a*) In the oval butterflyfish (*Chaetodon trifasciatus*) pairs establish territories around coral colonies. These fish use their tiny mouths (see Fig. 8.13*b*) to feed on coral. (*b*) Experiments using transparent plastic cages provide valuable information on the behavior of butterflyfishes. Here, a caged oval butterflyfish elicits an aggressive response from an individual chevron butterflyfish (*Chaetodon trifascialis*), an indication that the caged fish has intruded in the territory of the latter. This technique can be used to map the boundaries of butterflyfish territories. Territorial butterflyfishes that live in pairs, like *C. trifasciatus*, fight with other pairs, but fighting occurs only between individuals of the same sex in each pair. Therefore, by using a caged fish of known sex, experimenters can determine the sex of the wild fish, which is normally impossible in the field.



FIGURE 8.29 The Clarion damselfish (*Stegastes redemptus*), like many other damselfishes, establishes and actively defends breeding sites where females lay their eggs. This female is guarding her nest.

eggs are retained in the nest and guarded by the males; females leave after spawning. Males are promiscuous and will guard eggs they have fertilized from different females. Nests also are guarded by males in some gobies, blennies, and sculpins. In the Antarctic plunderfish (*Harpagifer bispinis*), the female prepares a breeding site and guards it for four to five months after spawning. If she disappears or is removed, her job is taken over by another plunderfish, usually a male.

Some fishes go even further and physically carry the eggs after they have been fertilized. Male pipefishes carry the eggs attached in neat rows to their bellies. A male seahorse literally becomes pregnant after the female deposits eggs in a special pouch on his belly! In some cardinalfishes, marine catfishes, and other groups, males brood the fertilized eggs in their mouths (see Fig. 4.21*b*).

### Early Development

Most fishes spawn eggs and are known as oviparous. In oviparous sharks, skates, and other cartilaginous fishes, the embryo is enclosed by a large, leathery egg case (the "mermaid's purse" of skates) that drops to the bottom after spawning (Fig. 8.30). About 43% of all cartilaginous fishes are oviparous. The egg cases are rather large and often have thin extensions that attach



FIGURE 8.30 An egg of the swell shark (*Cephaloscyllium ventriosum*) containing a one-monthold embryo.

them to surfaces. Only a few are laid at a time. The eggs have a large amount of yolk in a **yolk sac** that is attached to the embryo's belly. Yolk provides energy for several months of development, a long time by fish standards. As a result, the pup is well developed when it finally hatches. In some cartilaginous fishes the female retains the eggs inside her reproductive tract for additional protection. The eggs develop inside the female, which gives birth to live young. Such fishes are known as **ovoviviparous**. Most ovoviviparous fishes are cartilaginous. A total of

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300 embryos, still in egg cases, were found ready to emerge inside the reproductive tract of a female whale shark. Some rockfishes are among the few marine bony fishes that can be classified as ovoviviparous. Most bony fishes are oviparous and spawn their eggs for external fertilization.

In some ovoviviparous sharks, the embryos rely on other sources of nutrition once they have consumed the yolk. In the sandtiger shark (*Carcharias taurus* see Fig. 8.3) only two pups, which are large (up to 1 m or 3.3 ft) and active, are born. Each survived in one of the two branches of its mother's reproductive tract by eating its brothers and sisters. When that source of food is gone, they are known to consume unfertilized eggs produced by their mother's ovaries! Some sharks and rays have embryos that actually absorb nutrients from the walls of the mother's reproductive tract. This is truly remarkable because it is very similar to the development of the embryo in mammals. These sharks are said to be **viviparous.** Not only are they live-bearers, but nutrition for development before birth is provided by direct contact with the reproductive tract of the female. The surfperches (*Embiotoca*), which are bony fishes, are also viviparous. Their young have large fins that absorb nutrients from the walls of the mother's uterus.

Development of the embryo proceeds rather quickly in most bony fishes. The transparent outer envelope of the eggs, the chorion, is thin, allowing oxygen to diffuse through. The eggs are usually spherical.

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The embryo is supplied with nutrientrich yolk. After one or more days of development, the eggs hatch into free-swimming larvae, or fry. When they first hatch, the larvae still carry the yolk in a yolk sac. The yolk is eventually consumed, and the larvae begin feeding in the plankton. Many larvae, like the leptocephalus larvae of eels (Fig. 8.24), do not resemble their parents at all and undergo metamorphosis to a juvenile stage that resembles the adult. The larvae of flatfishes have eyes on both sides of the head, but during metamorphosis to the juvenile stage they migrate to one side.

Most marine fishes are oviparous and release eggs into the water. Internal fertilization leads to ovoviviparous or viviparous conditions in some, especially cartilaginous fishes.



# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

## **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. Hagfishes and lampreys are the only living representatives of a very ancient group. Why do you suppose there are still some of these jawless fishes around?
- 2. A deep-water shark, new to science, is collected for the first time. The specimen is studied in detail, but its stomach is empty. How could you get a rough idea of its feeding habits?

The specimen is a female, and its reproductive tract is found to contain 20 eggs. Can you tell the type of development characteristic of this species?

3. Individuals of some species of bony fishes change sex, some to maintain more males than females, others more females than males. What are the advantages and disadvantages of each situation? Are there any advantages and disadvantages in having an equal number of males and females?

# For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol **2**, and will contain live links when you visit this page in the Online Learning Center.

## **General Interest**

Benchley, P., 2000. Great white sharks. National Geographic, vol. 197, no. 4, April, pp. 2–29. The largest carnivorous shark is not the fearless, brutal hunter we once thought.

- Crystall, B., 2000. Monstrous mucus. *New Scientist*, vol. 165, no. 2229, 11 March, pp. 38–41. Hagfishes produce huge amounts of mucus as a defensive tool.
- Franklin, H. B., 2001. The most important fish in the sea. *Discover*, vol. 22, no. 9, September, pp. 44–51. The Atlantic menhaden is more than an important catch.
- Klimley, P., 1999. Sharks beware. *American Scientist*, vol. 87, no. 6, November–December, pp. 488–491. Slow reproductive rates make sharks particularly vulnerable to overfishing.
- Levin, P. S. and M. H. Schiewe, 2001. Preserving salmon biodiversity. *American Scientist*, vol. 89, no. 3, May–June, pp. 220–227. The loss of genetic biodiversity appears to be a more serious threat to the survival of the Pacific salmon.
- Levine, J., 1999. In living colors. *Natural History*, vol. 108, no. 7, September, pp. 40–47. The many colors of coral reef fishes actually result from the combination of three primary colors (red, yellow, and blue) plus black or white.
- Pain, S., 2000. Squawk, burble and pop. *New Scientist*, vol. 166, no. 2233, 8 April, pp. 42–45. Sound is a common behavior among reef fishes.
- Thompson, K. S., 1999. The Coelacanth: Act three. *American Scientist*, vol. 87, no. 3, May–June, pp. 213–215. The discovery, and rediscovery, of *Latimeria* follow the twists and turns of a detective story.
- Watson, B., 2000. You gotta remember, eels are weird. *Smithsonian*, vol. 30, no. 11, February, pp. 124–133. The Atlantic eel follows a long and perilous migratory route from the Sargasso Sea to North Atlantic rivers.

### In Depth

- Findley, J. S. and M. T. Findley, 2001. Global, regional, and local patterns in species richness and abundance of butterfly fishes. *Ecological Monographs*, vol. 71, pp. 69–91.
- Griem, J. N. and K. L. M. Martin, 2000. Wave action: The environmental trigger for hatching in the California grunion *Leuresthes tenuis* (Teleostei: Atherinopsidae). *Marine Biology*, vol. 137, pp. 177–181.
- Grutter, A. S., 1997. Effect of the removal of cleaner fish on the abundance and species composition of reef fish. *Oecologia*, vol. 111, pp. 137–143.
- Hixon, M. A., 1997. Effect of reef fishes on corals and algae. In: *Life and Death of Coral Reefs* (C. Birkeland, ed.), pp. 230–248. Chapman & Hall, New York.
- Wolfgang, M. J., J. M. Anderson, M. A. Grosenbaugh, D. K. Yue and M. S. Triantafyllou, 1999. Near-body flow dynamics in swimming fish. *Journal of Experimental Biology*, vol. 202, pp. 2303–2327.

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## See It in Motion

Video footage of the following animals and their behaviors can be found for this chapter on the Online Learning Center.

- School of chevron barracudas (Solomon Islands)
- Smooth trunkfish (Belize)
- Spotted moray eel (Belize)
- Clownfish in sea anemone (Papua New Guinea)
- Blue-spotted ray (Fiji)
- Young whitetip sharks resting in a hole in the reef (Red Sea)
- Creole wrasses feeding on plankton (Honduras)
- Eagle ray (Belize)
- Nurse shark (Dry Tortugas)
- Peacock flounder changing color and pattern to match bottom (Honduras)
- Southern stingray (Belize)
- Whitetip shark (Fiji)
- Yellow stingray (Dry Tortugas)
- · Surgeonfishes being cleaned and changing color (Red Sea)
- Feeding whale shark (Gulf of California)

## Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- General chordate references
- Systematics and characteristics of the craniates
- Class Myxini
- Class Cephalaspidomorphi
- Subclass Elasmobranchii
- · Dissection guides for elasmobranchs
- Class Osteichthyes
- Primitive bony fish
- Teleosts
- Fisheries
- Dissection guides for teleosts
- · Fisheries and conservation issues concerning teleosts

## **Quiz Yourself**

Take the online quiz for this chapter to test your knowledge.

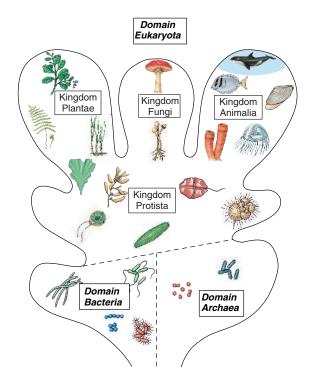
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# Marine Reptiles, Birds, and Mammals





Humpback whale (*Megaptera novaeangliae*): mother with calf "under wing," Maui, Hawai'i.



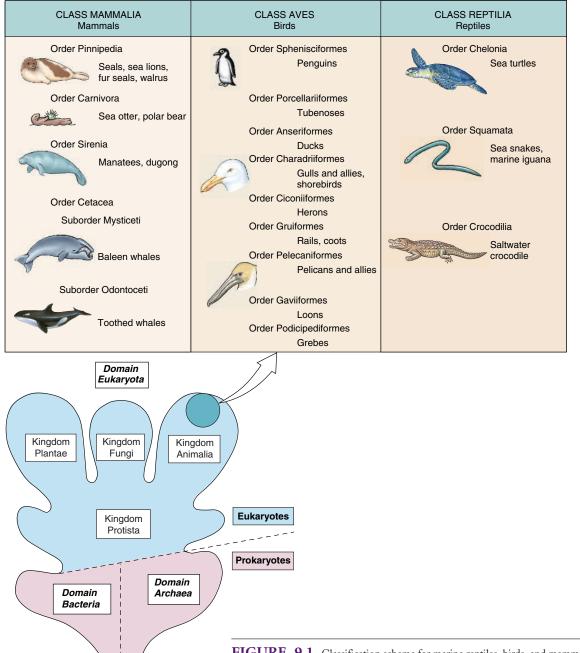
ertebrates originated in the ocean and have thrived there ever since. Roughly 350 million years ago, vertebrates invaded the land as well, an event that changed life on earth forever. Descended from bony fishes, land vertebrates had to adapt to the harsher conditions ashore. They lost the structural support that water provides and had to develop ways of crawling or walking to get around. They evolved two pairs of limbs. Because of this, land-dwelling

vertebrates—even snakes—are called **tetrapods**, meaning "four-footed."

Living on land also means having to breathe air. Tetrapods evolved **lungs**, which are internal air sacs that allow absorption of oxygen directly from air. Tetrapods also had to evolve ways to keep from drying out. The delicate egg is especially vulnerable, and the first land tetrapods, the **amphibians** (class **Amphibia**), never really solved this problem. Represented today by frogs, salamanders, and their relatives, amphibians must keep themselves moist, and most lay their eggs in water. None of them are strictly marine.

Other groups of tetrapods solved the problem of water loss and truly adapted to life on land. **Reptiles** (class **Reptilia**; Fig. 9.1) evolved from now-extinct amphibians and for a long time were the dominant land vertebrates The **birds** (class **Aves**) and **mammals** (class **Mammalia**) both evolved from different groups of now-extinct reptiles.

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Having adapted to the land, various groups of reptiles, birds, and mammals turned around and reinvaded the ocean. This chapter deals with these marine tetrapods. Some, like sea turtles, have not fully made the transition and still return to land to lay their eggs. Others, like the humpback whales shown on page 179, spend their entire lives at sea. They have adapted so completely to a marine existence that their streamlined bodies look almost fish-like. This fishlike appearance, however, belies the fact that they evolved from animals that once, about 55 million years ago, walked on land (see "The Whales That Walked to Sea," p. 192). Their embryos even have the four limbs that characterize all land vertebrates (see Fig. 9.16).

The marine animals to be covered in this chapter include some of the most

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fascinating and awesome creatures on the planet. Unfortunately, many are in danger of disappearing forever because of our own greed. Some already have become extinct.

## MARINE REPTILES

There are around 7,000 living species of reptiles, including lizards, snakes, turtles, and crocodiles. Their dry skin is covered with scales to prevent water loss. Their eggs have a leathery shell that prevents them from drying out so that reptiles can lay their eggs on land. Like most fishes, reptiles are poikilotherms and ectotherms, commonly called "coldblooded." Like other poikilotherms, their metabolic rate-and therefore activity level-varies with temperature: They get sluggish in the cold. This tends to keep them out of cold regions, especially on land because the air temperature fluctuates more widely than does the ocean temperature.

Reptiles are air-breathing, ectothermic ("coldblooded"), poikilothermic vertebrates. Their skin is covered with dry scales and nearly all lay their eggs on land.

Reptiles first appeared more than 300 million years ago, and several different groups have invaded the seas. Many are long gone, like the ichthyosaurs (see Fig. 9.14) that thrived during the socalled Age of Reptiles. Only a few reptiles still roam the seas. Some are rare and endangered; others, however, are common and widely distributed.

## Sea Turtles

Sea turtles belong to an ancient group of reptiles. Their bodies are enclosed by an armor-like shell, or carapace, that is fused to the backbone. Unlike land tortoises and turtles, sea turtles cannot retract their heads into the shell. Their legs, particularly the larger forelimbs, are modified into flippers for swimming.

There are only nine species of sea turtles, which live primarily in warm waters. Green turtles (*Chelonia mydas*, see



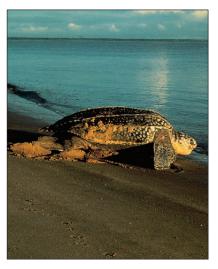
**FIGURE 9.2** (*a*) The hawksbill turtle (*Eretmochelys imbricata*) takes its name from the shape of its jaw (see Fig. 4.15). It is the source of tortoiseshell. (*b*) The largest of all sea turtles, the leatherback turtle (*Dermochelys coriacea*), sometimes ventures into cold waters as far north as Newfoundland and Alaska.

photo on page 182) were once found in coastal waters throughout the tropics. Their shells may grow to 1 m (40 in) in length. They feed mostly on seagrasses and seaweeds. Like all turtles, green turtles lack teeth, but they have strong biting jaws. The hawksbill turtle (*Eretmochelys imbricata;* Fig. 9.2*a*) is smaller, and the shell is reddish brown with yellow streaks. It uses its beak-like mouth to feed on encrusting animals (sponges, sea squirts, barnacles) and seaweeds.

The largest sea turtle is the leatherback (*Dermochelys coriacea*; Fig. 9.2*b*). Individuals may attain a length of 2 m (7 ft) and weigh at least 540 kg (1,200 lb). Instead of a solid shell, they have a series of small bones buried in the dark skin, forming distinct longitudinal ridges. Leatherbacks are an open-water, deep-diving species and are rarely seen except on nesting beaches. Their diet consists largely of jellyfishes.

All sea turtles must return to land to reproduce. They migrate long distances to lay their eggs on remote sandy beaches, and were doing so millions of years before humans appeared on the scene. Green turtles still gather to nest on beaches on the east coast of Central America, Northern Australia, Southeast Asia, Ascension Island (in the middle of the South Atlantic), and a few other locations. Marine biologists have tagged adult sea turtles at Ascension and have found

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(b)

that the turtles regularly cross 2,200 km (1,360 mi) of open water to their feeding grounds along the coast of Brazil, a journey that takes a little more than two months (see world map in Appendix B). Though we are still not sure how they find their way, evidence suggests that they do it by sensing wave motion and the earth's magnetic field.

Most of what we know about the reproduction of sea turtles is based on the green turtle. They return to their nesting areas every two to four years, often against prevailing currents. Evidence that females return to the beaches where they were born has been obtained by analyzing the **DNA** of breeding populations at separate Caribbean and Atlantic sites. The DNA of turtles breeding in one area differs from the DNA of turtles breeding at

**Poikilotherms** Organisms that have a body temperature that varies with that of the environment.

**Ectotherms** Organisms that lose metabolic heat to the environment without it affecting the body temperature. *Chapter 4, p. 80* 

**DNA** A complex molecule that contains a cell's genetic information.

Chapter 4, p. 70

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## THE ENDANGERED SEA TURTLES

Humans are by far the most formidable and destructive enemies of sea turtles. Many nesting areas have been turned into resorts or public beaches. Females searching for nesting beaches avoid lights because dark areas along the horizon indicate land, and lights along a beach look like a starry horizon. Artificial lighting also disorients baby turtles after hatching so they do not head to sea and therefore die. Turtles drown in fishing nets, especially drift nets, and choke to death after swallowing plastic bags they think are jellyfishes. Turtles have been used as food for centuries. Their eggs are taken by the bucketful, and are located by pushing a stick into the sand until it comes out yellow. The eggs are eaten or fed to pigs or cattle. Turtle eggs, particularly those of leatherbacks, are said to be an aphrodisiac, a myth that probably arose because adult turtles can be seen copulating for long periods at sea.

Sea turtles can live for months without food or water. In the days before refrigeration, sailors kept them alive aboard ship as a source of fresh meat, storing them on their backs for months. Coming ashore by the thousands, females were an easy catch. They were, and still are, immobilized by turning them on their backs to be gathered later without giving them a chance to lay their eggs. The green turtle is especially esteemed for its meat, and its cartilage is used to make turtle soup. Some people consider the oily leatherback meat a delicacy.

The polished shell of the hawksbill is the source of valuable **tortoiseshell** used to make jewelry, combs, and other articles (see Fig. 18.15), particularly in Japan. Sea turtle leather, which is soft and durable, is much prized for shoes, handbags, and wallets. Leather articles from illegally slaughtered animals still make their way into the United States from Mexico and other countries. The oil of many sea turtles is also of commercial value. Even baby sea turtles are valuable; they are stuffed and sold as souvenirs.

The green turtle, once very common, has disappeared in many areas as the result of relentless overexploitation for eggs and meat. It is the most widely distributed and most common of all sea turtles, but only an estimated half a million individuals are left worldwide.



Green sea turtle (Chelonia mydas).

All sea turtle species are classified as **threatened** worldwide because their numbers are low (see Table 18.1, p. 422). For example, only about 4,000 nesting leatherback turtles remain in the Pacific Ocean. Sea turtles are not protected at all in many countries, and in those where they are, enforcement is difficult. Shrimp nets are estimated to kill up to 4,000 sea turtles a year in Southeast Asia. Many more become entangled in gill and drift nets and die asphyxiated. It is impossible to protect all coasts and nesting grounds from fishers and egg hunters. Stricter worldwide enforcement of conservation practices, the control of pollution, the regulation of trade in sea turtle products, and the restocking of former nesting areas might help save them.

All six species of sea turtles in the United States are protected under the Endangered Species Act of 1973. Three of these species are classified as threatened. Three other species are classified as **endangered** and as such in great danger of disappearing: the leatherback, hawksbill, and Kemp's (or Atlantic) ridley (*Lepidochelys kempii*). Shrimp nets in the Gulf of Mexico have been especially deadly to the Kemp's ridley turtle, once very common but now so rare that only a few hundred breeding females remain. It is the most endangered of all sea turtles. After a lengthy struggle, the U.S. government mandated that shrimp nets be fitted with turtle exclusion devices, or TEDs, that allow sea turtles to escape once caught in the nets.

other sites. It thus appears that turtles keep returning to the same place generation after generation.

Copulating pairs of sea turtles are often seen offshore, but only females venture ashore, usually at night. Therefore biologists have mostly tagged females, because turtles can be tagged most easily on land. The females congregate on the beach, and each proceeds to excavate a hole in the sand using both pairs of flippers (Fig. 9.3). They lay between 100 and 160 large, leathery eggs in this nest. The female covers the eggs with sand before she returns to the sea. She may make several trips ashore during the breeding season, laying eggs each time.

The eggs hatch after about 60 days of incubation in the sand. The baby turtles must then dig themselves out of the sand and crawl all the way back to the water, protected by darkness if they're lucky. Green turtles and other sea turtles have many enemies. The eggs are often eaten by dogs, ghost crabs, wild pigs, and other animals. The hatchlings are easy prey for land crabs and birds, especially during the day. Even more young turtles are lost in the water, where they are taken by a variety of fishes and seabirds.

#### Sea Snakes

Approximately 55 species of **sea snakes** are found in the tropical Indian and Pacific oceans (Fig. 9.4). Their bodies are laterally flattened, and the tail paddleshaped for swimming. Most are 1 to 1.3 m (3 to 4 ft) long. Practically all sea snakes lead a totally marine existence. They mate in the ocean and are **ovoviviparous**, giving birth to live young. A few species, however, still come ashore to lay their eggs.

Like all snakes, sea snakes are carnivores. Most feed on bottom fish, a few specializing in fish eggs. They are closely

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**FIGURE 9.3** Egg laying in green turtles (*Chelonia mydas*) culminates a long and hazardous trip by females. It is at this time that they are most vulnerable to egg collectors. This photograph was taken on Sipadan Island, one of the Turtle Islands off the northeastern coast of Borneo, Malaysia.

related to cobras and their allies, the most venomous of all snakes. Sea snakes are among the most common of all venomous snakes, and their bites can be fatal to humans. Fortunately, they are rarely aggressive, and the mouth is too small to get a good bite. Most casualties, swimmers accidentally stepping on them and fishers removing them from nets, have been reported in Southeast Asia. Sea snakes are also victims of overexploitation. They are hunted for their skins, and some species have become rare.

## **Other Marine Reptiles**

An unusual lizard is among the unique inhabitants of the Galápagos Islands, which lie off the Pacific coast of South America. The **marine iguana** (*Amblyrbynchus cristatus;* Fig. 9.5) spends most of its time basking in large groups on rocks along the coast, warming up after swimming in the cold water. It eats seaweeds and can dive as deep as 10 m (33 ft) to graze.



**FIGURE 9.4** Sea snakes are found from the Indian Ocean coast of South Africa to the Pacific coast of tropical America, where they occur from the Gulf of California to Ecuador. They sometimes occur under floating debris, feeding on the fish it attracts. The conspicuous coloration of sea snakes may be a warning to potential predators because many fishes learn to associate the bright colors with danger. There are no sea snakes in the Atlantic, but a sea-level canal across Central America may allow their migration into the Caribbean.

The other marine reptile is the **salt-water crocodile** (*Crocodylus porosus;* see Fig. 17.17), which inhabits mangrove swamps and estuaries in the Eastern Indian Ocean, Australia, and some of the Western Pacific islands. They live mostly on the coast but are known to venture into the open sea. There is a record of an individual 10 m (33 ft) long, but they are rarely over 6 m (20 ft). They are among the most aggressive of all marine animals and are known to attack and eat people. Where they occur, they are more feared than sharks.

Marine reptiles include the sea turtles, sea snakes, the marine iguana, and the saltwater crocodile.

## **SEABIRDS**

Birds have some significant advantages over reptiles, including the ability to fly. Birds are **homeotherms**, commonly referred to as "warm-blooded." They are also **endotherms.** This has allowed them to live in a wide variety of environments. Their bodies are covered with waterproof feathers that help conserve body heat. Waterproofing is provided by oil from a gland above the base of the tail. The birds preen by rubbing the oil into their feathers with their beaks. Flight is made

**Ovoviviparous Animals** Animals in which the eggs develop and hatch in the reproductive tract of females.

Chapter 8, p. 176

**Homeotherms** Organisms able to keep body temperature more or less constant regardless of the temperature of the environment.

**Endotherms** Organisms that retain some metabolic heat, which raises their body temperature.

Chapter 4, p. 81

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**FIGURE 9.5** The marine iguana of the Galápagos Islands (*Amblyrhynchus cristatus*) is probably one of the ugliest creatures of the sea, with the face of a dragon and peeling skin. In the water, however, these iguanas are elegant swimmers. They swim by undulating the body and the laterally flattened tail, the tip of which is shown on the bottom left.

easier by their light, hollow bones. Furthermore, their eggs have hard shells that are more resistant to water loss than those of reptiles.

Birds are endothermic ("warm-blooded"), homeothermic vertebrates that have feathers and light bones as adaptations for flight.

Seabirds are those birds that spend a significant part of their lives at sea and feed on marine organisms. Seabirds nest on land. Most breed in large colonies, mate as lifelong pairs, and take care of their young. True seabirds have webbed feet for swimming.

Seabirds descended from several different groups of land birds. As a result, they differ widely in their flying skills, feeding mechanisms, and ability to live away from land.

#### Seabirds are birds that nest on land but feed entirely or partially at sea.

Though comprising only about 3% of the estimated 9,700 species of birds, seabirds are distributed from pole to pole, and their impact on marine life is significant. Most are predators of fish, squid, and bottom invertebrates, but some feed on plankton. Seabirds have amazing appetites. They need a lot of food to supply the energy required to maintain their body temperatures.

## Penguins

**Penguins** (Fig. 9.6*a*) are the seabirds most fully adapted for life at sea. They are flightless, with wings modified into stubby "flippers" that allow them to "fly" underwater. Their bones are denser than those of other birds to reduce buoyancy and make diving easier.



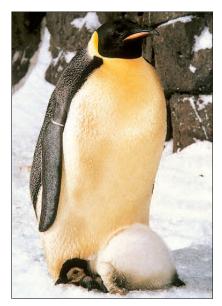




FIGURE 9.6 (a) An emperor penguin (Aptenodytes forsteri) and chick. The emperor is the largest living penguin, with a height of up to 115 cm (45 in). (b) The brown booby (Sula leucogaster) nests in the Caribbean and Gulf of California. It is a regular visitor to the Gulf of Mexico. (c) The gannet (Morus bassanus) is the largest seabird in the North Atlantic. It nests in large colonies on offshore islands such as Bonaventure Island in Quebec, Canada, where around 50,000 birds breed every year.



(b)



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Penguins are spectacular swimmers, propelling their streamlined bodies with powerful strokes of the wings (see Fig. 9.14). They can also jump out of the water and sometimes cover long distances by alternately swimming and jumping. On land it is another story: They are clumsy and awkward. They are nearsighted, having eyes that are adapted for underwater vision.

Penguins are also adapted for cold temperatures. Protection against low temperatures is provided by a layer of fat under the skin. The dense, waterproof feathers trap air that, warmed by body heat, protects against the cold like a down coat. All but one of the 18 species of penguins live primarily in Antarctica and other cold regions of the Southern Hemisphere. The exception is the Galápagos penguin (*Spheniscus mendiculus*), which lives right on the Equator. Even so, this penguin is confined to regions that are bathed by cold currents.

The larger penguins, like the imposing emperor penguin (*Aptenodytes forsteri*; Fig. 9.6*a*), hunt for fish and squid. The Adélie (*Pygoscelis adeliae*) and other small penguins feed mostly on **krill**. Penguins have strong beaks, a characteristic of seabirds that feed on fish and large plankton like krill (Fig. 9.7*b*). Some species migrate seasonally between feeding grounds at sea and nesting areas on land or ice. They establish breeding colonies, which in Adélies may number more than a million pairs.

Breeding season and number of eggs laid vary from species to species. Emperor penguins mate for life. The male incubates a single large egg during the dark Antarctic winter. The female leaves to feed as soon as she lays the egg. The male, standing on ice, must keep the egg warm by holding it on top of his feet and against his body for 64 days. Males huddle together to protect themselves from the cold and the dreadful winter storms.

You may wonder why the penguins lay their eggs at the coldest time of the year. Reproduction is timed so that the egg hatches during the productive Antarctic summer, when food is most plentiful. When the egg hatches, the female finally returns and regurgitates food for the fuzzy chick. After that, both parFIGURE 9.7 The shape of a seabird's beak is related to the kind of food it eats and the bird's feeding style. (a) In tubenoses such as petrels (*Pterodroma*), the beak is relatively short, heavy, and hooked—an ideal shape for holding and tearing prey that is too big to be swallowed whole. Such a beak is best suited for shallow feeding because its size and shape interfere with fast pursuit underwater. (b) The beak is heavy but more streamlined in the penguin (*Aptenodytes* and others), the razorbill (*Alka*), and other seabirds that dive deeper to feed on crustaceans and other prey. (c) Boobies (*Sula*), terms (*Sterna*), and other plunge divers have a straight and narrow beak for feeding on fish that are swallowed whole. (d) Skimmers (*Rynchops*) are the only birds with a lower part of the beak that is longer than the upper, which permits feeding while flying. Shorebirds that feed on mudflats have a long, thin beak that allows them to get to prey buried in the mud (see Fig. 12.12).

ents take turns feeding the chick. While the parents feed, the fast-growing young are herded into groups guarded by a few adult "babysitters." Returning parents identify their chick among thousands by its voice and appearance. The parents continue to feed the chick for five and a half months, until it is strong enough to feed itself at sea.

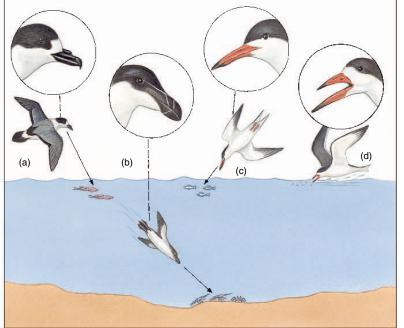
#### Tubenoses

The **tubenoses** comprise a large group of seabirds with distinctive tube-like nostrils and heavy beaks that are usually curved at the tip (Fig. 9.7*a*). They spend months and even years on the open sea. Like other seabirds and sea turtles, they have **salt glands** that get rid of excess salts; these empty into the nostrils. Tubenoses include

the albatrosses (*Diomedea*), shearwaters (*Puffinus*), and petrels (*Pterodroma*).

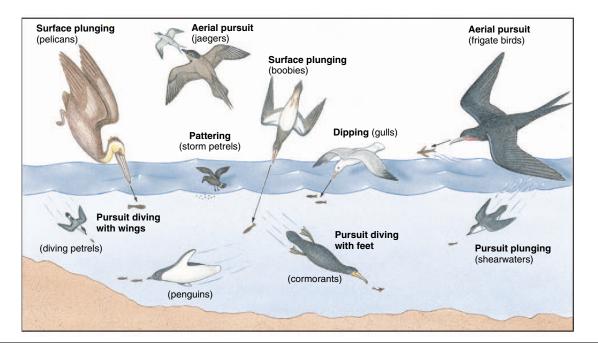
Tubenoses are very skillful fliers. Most catch fish at the sea surface (Fig. 9.7*a*), though some scavenge on dead birds or whales. The whalebirds, or prions (*Pachyptila*), feed on krill and other plankton. Albatrosses are magnificent gliders with huge wings that hardly ever seem to flap. Wandering albatrosses (*D. exulans*) and royal albatrosses (*D. epomophora*) have wingspans of up to 3.4 m (11 ft), the longest of any bird alive.

Krill Planktonic, shrimp-like crustaceans. *Chapter 7, p. 137; Figure 17.12* 



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**FIGURE 9.8** Feeding strategies vary widely among seabirds. Pelicans (*Pelecanus*) and boobies (*Sula*) plunge into the water, jaegers (*Stercorarius*) pursue other seabirds and force them to regurgitate food, and frigate birds (*Fregata*) take fish from the surface and steal fish from other seabirds. Gulls (*Larus*) rarely dive from the air, and storm petrels (*Oceanodroma*) simply flutter over the waves. Divers such as cormorants (*Phalacrocorax*) pursue prey underwater, swimming with their wings or feet. Mudflat shorebirds also follow various strategies (see Fig. 12.13).

Male and female tubenoses remain faithful to each other and perform elaborate courtship and greeting behaviors. Most nest on remote islands, on cliffs that are inaccessible to predators. Incubation and care of the single chick takes eight months, and even longer in some species. Tubenoses make some of the most spectacular migrations of any animal. Many breed on islands around Antarctica, then migrate across the open ocean to summer feeding grounds near the Arctic. The wandering albatross gets its name from the fact that it spends two years or more traveling around the Southern Hemisphere before returning to nesting sites near Antarctica. Some nonbreeding individuals wander off and pay visits as far away as California and the Mediterranean!

## **Pelicans and Allies**

Several quite different-looking seabirds are grouped together because they have webbing between all four toes. They are relatively large fish-eaters of wide distribution.

Pelicans (Pelecanus) have a unique pouch below their large beaks. Some species, like the brown pelican (P. occidentalis; see Fig. 18.9), catch their food by plunging into the water and catching fish in the pouch (Fig. 9.8). The brown pelican was once common along the coasts of the United States but was decimated by pesticide pollution (see "Toxic Chemicals," p. 415). It has made a comeback as a result of restrictions on the manufacture and use of the pesticide DDT. Cormorants (Phalacrocorax) are black, long-necked seabirds that dive and pursue their prey. They can be easily identified by their low flights over water and the fact that they float low in the water, with only the neck above the surface. Frigate birds (Fregata) have narrow wings and a long, forked tail. They soar majestically along the coast, forcing other seabirds to regurgitate fish in midair or catching prey from the surface (Fig. 9.8). These agile pirates seldom enter the water, not even to rest, because their feathers are not very waterproof.

Pelicans and related species nest in large colonies along the coast. They build

messy nests of twigs and anything else they can find. The excrement of millions of boobies (Fig. 9.6*b*), cormorants, pelicans, and other seabirds accumulates as **guano**. Guano deposits are particularly thick in dry coastal regions and islands near very productive waters, such as the coasts of Perú, Chile, and southwest Africa. These deposits are mined for fertilizer (see "Of Fish and Seabirds, Fishers and Chickens," p. 393).

## **Gulls and Allies**

**Gulls** (*Larus*) and their kin make up the largest variety of seabirds. Common and widespread, gulls are predators and scavengers happy to eat just about anything (Fig. 9.8). They are very successful in the company of humans and congregate near piers, garbage dumps, or anywhere else we throw refuse. Jaegers (*Stercorarius*) and skuas (*Catharacta*) are gull-like predators that steal fish from other birds (Fig. 9.8). They nest near the rookeries of penguins and other seabirds and eat their eggs and young.

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**Terns** (*Sterna*) are graceful flyers that hover over their prey before plunging for it. Their slender beaks are specialized to catch small fish, which they swallow whole (Fig. 9.7c). The Arctic tern (*S. paradisaea*) is another amazing wanderer. It breeds in the Arctic during the northern summer, travels 16,000 km (10,000 mi) to Antarctica for the southern summer, and then returns to the Arctic.

Also related to gulls are several coldwater diving seabirds. Puffins (Fratercula) have heavy beaks that make them look like misplaced parrots. The related razorbill (Alca torda) is a black and white bird reminiscent of penguins (Fig. 9.7b). In fact, these birds may fill the role of penguins, which are absent in the Northern Hemisphere. Like penguins, they use their wings to swim underwater. Their extinct cousin, the great auk (Pinguinus impennis), looked and acted like a penguin. Great auks once lived in great numbers in the North Atlantic but were slaughtered for their eggs, meat, and feathers. The last great auk died in 1844.

## Shorebirds

Usually included among the seabirds are many species of wading **shorebirds** that do not have webbed feet. Because they do not swim much, they are not really seabirds in the strict sense. Many live in inland waters, as well as the sea. Some are common in estuaries and coastal marshes. Plovers, sandpipers, and similar birds are related to gulls (see Fig. 9.1). Many other shorebirds may live on the coast: rails, coots, herons, egrets, and even ducks. The distribution and significance of shorebirds in estuaries will be discussed in Chapter 12.

## MARINE MAMMALS

About 200 million years ago another major group of air-breathing vertebrates, the mammals (class Mammalia), evolved from now-extinct reptiles. For a long time the mammals were overshadowed by the dinosaurs, which were reptiles. About 65 million years ago, however, the dinosaurs disappeared. It was then that mammals thrived, taking the place of the dinosaurs. There are now roughly 4,600 species of mammals, including humans. Fishes, reptiles, and birds each outnumber mammals in number of species.

Like birds, mammals have the advantage of being endotherms, or "warmblooded," and homeotherms. The skin of mammals, however, has hair instead of feathers to retain body heat. With few exceptions, mammals are **viviparous**. The embryo receives nutrients and oxygen through the **placenta**, a membrane that connects it to the womb. It is also known as the afterbirth. The newborn is fed by milk secreted by the mother's **mammary glands**. Instead of releasing millions of eggs, mammals produce few—but well-cared-for—young.

And then there is the brain. It is larger in relation to body size and far more complex than that of other vertebrates, allowing the storage and processing of more information. This accounts in part for the amazing adaptability of mammals. They live anywhere there is air to breathe and food to eat. This, of course, includes the ocean.

### Types of Marine Mammals

There is something fascinating about mammals that live at sea like fishes. At least five different groups of land mammals succeeded in invading the oceans. They have followed different paths in adapting to the marine environment. Some are so fish-like that we have to remind ourselves that they have hair and bear live young nourished by their mother's milk.

#### Seals, Sea Lions, and Walruses

Seals and related forms are marine mammals that have paddle-shaped flippers for swimming but still need to rest and breed on land. They make up one of the 19 or 20 major groups, or orders, of mammals, the **pinnipeds** (order **Pinnipedia**; see Fig. 9.1). Pinnipeds evolved from an early form of terrestrial carnivore (order Carnivora), which includes cats, dogs, bears, and their kin. The similarities are so close that many scientists classify them with the carnivores. Pinnipeds are predators, feeding mostly on fish and squid. Their streamlined bodies are adapted for swimming (Fig. 9.9). Most pinnipeds live in cold water. To keep warm they have a thick layer of fat under their skin called **blubber**. Besides acting as insulation, it serves as a food reserve and helps provide buoyancy. Pinnipeds also have bristly hair for added protection against the cold. Many of them are quite large, which also helps conserve body heat because large animals have less surface area for their size than small animals, and therefore lose less body heat (see Fig. 4.17).

Pinnipeds, which include seals and their relatives, are marine mammals with flippers and blubber that need to breed on land.

The largest group of pinnipeds, including some 19 species, is the seals. Seals are distinguished by having rear flippers that cannot be moved forward (Fig. 9.9*b*). On land they must move by pulling themselves along with their front flippers. They swim with powerful strokes of the rear flippers.

Harbor seals (Phoca vitulina) (Fig. 9.9b) are common in both the North Atlantic and North Pacific. Elephant seals (Mirounga; Fig. 9.10a) are the largest pinnipeds. Males, or bulls, reach 6 m (20 ft) in length and can weigh as much as 3,600 kg (4 tons). One unusual seal is the crabeater seal (Lobodon carcinophagus), which actually feeds on Antarctic krill. These seals strain krill from the water with their intricately cusped, sieve-like teeth. Unlike most seals, monk seals (Monachus) live in warm regions. The Mediterranean (M. monachus) and Hawaiian (M. schauinslandi) monk seals are now endangered. A third species, the Caribbean monk seal (M. tropicalis), was last seen in 1952.

Seals have been hunted for their skin and meat, and for the oil extracted from their blubber. The Marine Mammal Protection Act of 1972 extends protection to all marine mammals and restricts the sale

**Viviparous Animals** Live-bearing animals whose embryos develop within their mothers' bodies and are nourished by the maternal bloodstream.

Chapter 8, p. 177



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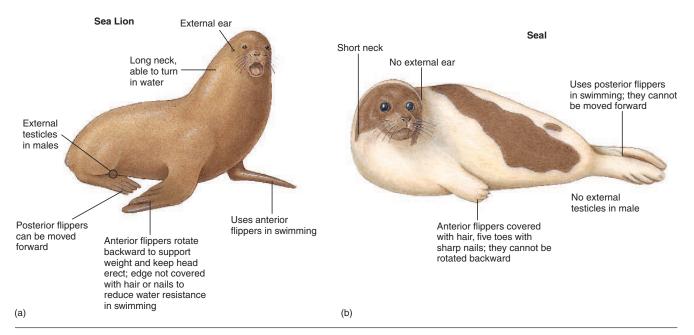


FIGURE 9.9 Though they differ in some structural features and the ways in which they swim and move on land, sea lions (a) and seals (b) are now thought to have evolved from the same group of land carnivores.





**FIGURE 9.10** Seals. (*a*) The northern elephant seal (*Mirounga angustirostris*), so-called because of the huge proboscis of the male, was almost exterminated for its blubber. By 1890 only about 100 remained, but because of protection and a drop in the use of its blubber it rapidly recovered, and there are now more than 100,000 of them in California and Baja California. (*b*) The New Zealand fur seal (*Arctocephalus forsteri*), like the other fur seals, is characterized by its thick underfur. (*c*) Female harp seals (*Phoca groenlandica*), one seen here peeking through the ice, give birth to white, furry pups on the floating Arctic ice. Pups must grow fast and shed their white coats before the drifting ice melts. In eastern Canada the clubbing of young pups to harvest their white fur provoked worldwide protests, and Canada banned the sale of the fur. Unemployment caused by the collapse of fisheries, however, prompted the government to reverse itself and the hunt has resumed.

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of their products in the United States. For some seals, this protection has not been enough (see Table 18.1, p. 422).

Sea lions, or eared seals, are similar to seals, except that they have external ears (Fig. 9.9a). They can also move their rear flippers forward, so they can use all four limbs to walk or run on land. The front flippers can be rotated backward to support the body, permitting the animal to sit on land with its neck and head raised. Sea lions are graceful and agile swimmers, relying mostly on their broad front flippers. Adult males are much bigger than females, or cows, and have a massive head with a hairy mane (see Fig. 9.32a). The head of sea lions looks dog-like, whereas the head of seals has much softer outlines, making it look more like a cat's (Fig. 9.9).

There are five species of sea lions, plus nine species of the related fur seals. The most familiar of all is the California sea lion (Zalophus californianus; see Fig. 9.33) of the Pacific coast of North America and the Galápagos Islands. These sea lions are the trained barking circus "seals" that do tricks for a fish or two. Fur seals (Fig. 9.10b), like the northern fur seal (Callorhinus ursinus), were once almost exterminated for their thick fur. They are now mostly protected around the world, though some species are still hunted. Sea lions were luckier because they lack the underfur of their cousins. Still, both sea lions and fur seals may run afoul of fishers. They sometimes drown in nets or are shot because of their notorious ability to steal fish.

The walrus (Odobenus rosmarus; Fig. 9.11) is a large pinniped with a pair of distinctive tusks protruding down from the mouth. It feeds mostly on bottom invertebrates, particularly clams. It was once thought that the walrus used its tusks to dig up food, but there is no evidence for this. Instead, these pinnipeds apparently suck up their food as they move along the bottom. The stiff whiskers of the snout probably act as feelers. The tusks are used for defense, and to hold or anchor to ice.

#### Sea Otters and Polar Bears

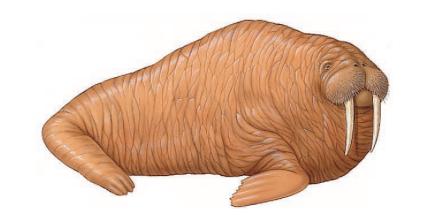
Though there is doubt about the pinnipeds, the **sea otter** (*Enhydra lutris*; Fig. 9.12) is definitely a member of the order **Carnivora**. The sea otter is the smallest marine mammal; an average male weighs 25 to

**FIGURE 9.11** Walruses (*Odobenus rosmarus*) typically inhabit the edge of pack ice in the Arctic. They migrate as far south as the Aleutian Islands and Hudson Bay, Canada. They also crowd onto beaches on isolated islands that they use as resting places. The walrus is still hunted legally by native Alaskans and Siberians.

**FIGURE 9.12** Sea otters (*Enhydra lutris*) are remarkable for their use of a tool—a rock for crushing shells. They carry a flat rock in side "pockets" of loose skin and fur. The sea otter floats on its back at the surface, places the rock on its chest, and crushes its toughest prey against it. Some have been observed carrying and using beer bottles as tools!

35 kg (60 to 80 lb). It also differs from other marine mammals in lacking a layer of blubber. Insulation from the cold is provided by air trapped in its dense fur. This splendid, dark brown fur unfortunately attracted hunters. Sea otters were slaughtered to near extinction until they became protected by an international agreement in 1911. The sea otter was then able to slowly expand from the few individuals that had managed to survive in some remote locations. Their numbers, however, have leveled off and the species is still endangered (see Table 18.1, p. 422).

Sea otters are playful and intelligent animals. They spend most or all of their time in the water, including breeding and giving birth. The furry pup is constantly groomed and nursed by its mother. Sea otters require 7 to 9 kg (15 to 20 lb) of



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food every day, so they spend a lot of time looking for it. They satisfy their ravenous appetites with sea urchins, abalone, mussels, crabs, other invertebrates, and even fishes. They live in or around kelp beds from the Pacific coast of Siberia to central California. Sea otters help protect kelp beds from sea urchins (see "Kelp Communities," p. 290).

The **polar bear** (*Ursus maritimus*) is the second member of the order Carnivora that inhabits the marine environment. Polar bears are semiaquatic animals that spend a good part of their lives on drifting ice in the Arctic. They feed primarily on seals, which they stalk and capture as the seals surface to breathe or rest.

#### Manatees and Dugongs

It is hard to believe that relatives of the elephant live at sea. **Manatees** and the **dugong** are also known as **sea cows**, or **sirenians** (order **Sirenia**). They have a pair of front flippers but no rear limbs (Fig. 9.13). They swim with up-and-down strokes of the paddle-shaped, horizontal tail. The round, tapered body is well padded with blubber. They have wrinkled skin with a few scattered hairs. The group is named after the sea nymphs or mermaids (*sirenas* in Spanish) whose songs drove sailors crazy!

Sirenians are gentle, peaceful creatures. They usually live in groups. They are the only strict vegetarians among marine mammals. Their large lips are used to feed on seagrasses and other aquatic vegetation. All sirenians are large. Dugongs may reach 3 m (10 ft) in length and 420 kg (930 lb) in weight. Manatees reach 4.5 m (almost 15 ft) and 600 kg (1,320 lb) in weight. The largest sirenian of all was the now-extinct Steller's sea cow, which supposedly grew to 7.5 m (25 ft) long (see Fig. 18.13).

Humans have exploited sirenians for their meat (which supposedly tastes like veal), skin, and oil-rich blubber. Like elephants and other large mammals, they reproduce slowly, typically one calf every three years. Only four species remain, and all are in danger of extinction (see Table 18.1, p. 420). Three species of manatees (*Trichechus*) live in the Atlantic Ocean; one is restricted to the Amazon, and the others inhabit shallow coastal FIGURE 9.13 It has been estimated that approximately 1,000 West Indian manatees

**FIGURE 7.13** It has been estimated that approximately 1,000 West Indian manatees (*Trichechus manatus*) remain along the coasts and rivers of Florida. Some concentrate in the warmwater effluents of power plants. They are strictly protected, but collisions with boats take their toll. Manatees have been considered as a possible way to control weeds that sometimes block waterways. Some people have suggested raising them for food.

waters and rivers from Florida to West Africa. The dugong (*Dugong dugon*) is strictly marine and survives from East Africa to some of the western Pacific islands. Its numbers are critically low throughout most of its range.

### Whales, Dolphins, and Porpoises

The largest group of marine mammals is the **cetaceans** (order **Cetacea**), the **whales**, **dolphins**, and **porpoises**. No group of marine animals has captured our imaginations like the dolphins and whales. They have inspired countless legends and works of art and literature (see "Oceans and Cultures," p. 430). The rescue of whales stranded on a beach or the birth of a killer whale in an oceanarium brings out strong emotions in all of us.

Of all marine mammals, the cetaceans, together with the sirenians, have made the most complete transition to aquatic life. Whereas most other marine mammals return to land at least part of the time, these two groups spend their entire lives in the water. The bodies of cetaceans are streamlined and look remarkably fishlike (Fig. 9.14). This is a dramatic example of **convergent evolution**, where different species develop similar structures because they have similar lifestyles. Though they superficially resemble fishes, cetaceans breathe air and will drown if trapped below the surface. They are "warmblooded," have hair (though scanty), and produce milk for their young.

Cetaceans have a pair of front flippers (Fig. 9.15), but the rear pair of limbs has disappeared. Actually, the rear limbs are present in the embryo but fail to develop (Fig. 9.16). In adults they remain only as small, useless bones. Like fishes, many cetaceans have a dorsal fin. The muscular tail ends in a pair of finlike, horizontal flukes. Blubber (see Fig. 4.2) provides insulation and buoyancy; body hair is practically absent. Cetacean nostrils differ from those of other mammals. Rather than being on the front of the head, they are on top, forming a single or double opening called the **blowhole** (Fig. 9.15).

There are around 90 species of cetaceans. They are all marine except for five species of freshwater dolphins. Cetaceans are divided into two groups: (1) the toothless, filter-feeding whales and (2) the toothed, carnivorous whales, a group that includes the dolphins and porpoises.

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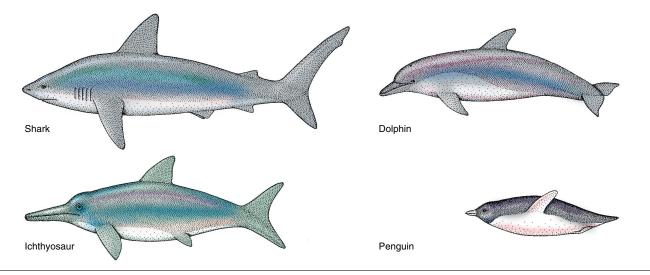
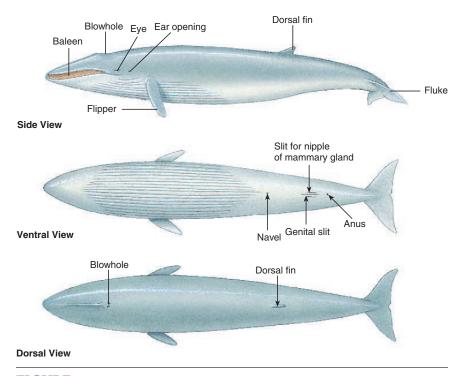


FIGURE 9.14 Streamlining to reduce water resistance evolved independently in different groups of fast-swimming marine animals: sharks, ichthyosaurs (reptiles that became extinct about 65 million years ago), dolphins, and penguins. Notice that dolphins lack posterior fins and that their flukes are horizontal, not vertical like the tail (caudal fin) of fishes (see Fig. 9.24).



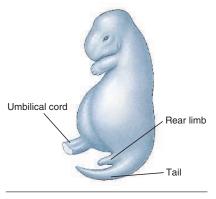


FIGURE 9.16 The fetus of a whitesided dolphin (*Lagenorhynchus*) shows two distinct pairs of limbs; the rear pair will eventually disappear. The umbilical cord connects the fetus with the placenta.

**FIGURE 9.15** External morphology of the blue whale (*Balaenoptera musculus*). A female is shown; males have a genital slit halfway between the anus and navel, and they lack mammary slits.

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## THE WHALES THAT WALKED TO SEA

It should be obvious that cetaceans are mammals. Their streamlined bodies, absence of hind legs, and the presence of a fluke and blowhole cannot disguise their affinities with land-dwelling mammals. Unlike the cases of sea otters and pinnipeds, however, it is not easy to suggest what the first whales looked like. Extinct but already fully marine cetaceans are known from the fossil record. How was the gap between a walking mammal and a swimming whale bridged? Missing until recently were fossils clearly intermediate, or transitional, between land mammals and cetaceans.

Very exciting discoveries have finally allowed scientists to reconstruct the most likely origins of cetaceans. It all started in 1979 when a team looking for fossils in North Pakistan found what proved to be the oldest known fossil whale. The fossil was officially described as Pakicetus in honor of the country where the discovery was made. Pakicetus was found embedded in rocks formed from river deposits that were 52 million years old. The river was actually not far from the shores of the former Tethys Sea (see "Continental Drift and the Changing Oceans," p. 33).

The fossil consists of a complete skull of an archeocyte, an extinct group of ancestors of modern cetaceans. Though limited to a skull, the Pakicetus fossil provides precious details on the origin of cetaceans. The skull is cetacean-like but its jawbones lack the enlarged space that is filled with fat or oil and used for receiving underwater sound in modern whales (see "Echolocation," p. 201). Pakicetus probably detected sound through the ear opening as in land mammals. The skull also lacks a blowhole, another adaptation for diving in cetaceans. Other features, however, show experts that Pakicetus is a transitional form between a group of extinct flesh-eating mammals, the mesonychids, and cetaceans. It has been suggested that Pakicetus fed on fish in shallow water and was not yet adapted for life in the open ocean. It probably bred and gave birth on land.

Another major discovery was made in Egypt in 1989. Several skeletons of another early whale, Basilosaurus, were found in sediments left by the Tethys Sea and now exposed in the Sahara Desert. This whale lived around 40 million years ago, 12 million years after Pakicetus. Many incomplete skeletons were found but they included, for the first time in an archeocyte, a complete hind leg that features feet with three tiny toes! The legs are small, far too small to have supported the 50-foot long Basilosaurus on land. Basilosaurus was undoubtedly a fully marine whale with possibly non-functional, or vestigial, hind legs.

Ambulocetus natans, the walking whale that swam.

Another remarkable find was reported in 1994, also from Pakistan. The now extinct whale, Ambulocetus natans ("the walking whale that swam"), lived in the Tethys Sea 49 millon years ago. It lived around 3 millon years after Pakicetus but 9 million years before Basilosaurus. The fossil luckily includes a good portion of the hind legs. The legs were strong and ended in long feet very much like those of a modern pinniped. The legs were certainly functional both on land and sea. The whale still retained a tail and lacked a fluke, the major means of locomotion in modern cetaceans. The structure of the backbone shows, however, that Ambulocetus swam like modern whales by moving the rear portion of its body up and down, even if a fluke was missing. The large hind legs were used for propulsion in water. On land, where it probably bred and gave birth, Ambulocetus may have moved around very much like a sea lion. It was undoubtedly a whale that linked life on land with life at sea.

Even more exciting are recent findings in Pakistan, reported in 2001, of yet other fossil skeletons. These fossils link early cetaceans with ungulates, the group that includes animals such as cattle, sheep, pigs, and hippos. Some of the oldest bones (at least 50 million years old) were from land-living, wolf-like, hoofed animals. The finding of these fossil whales is one of the most exciting recent discoveries in marine biology. Once an important discovery is made, it is only the beginning. It spurs new interest and nearly always leads to more new questions than answers.

The toothless whales are better known as the baleen whales. Instead of teeth they have rows of flexible, fibrous plates named **baleen** that hang from the upper jaws (Fig. 9.17). Baleen is made of keratin, the same material as our hair and nails. The inner edge of each plate consists of hair-like bristles that overlap and form a dense mat in the roof of the mouth. The whale filter feeds by taking a big mouthful of water and squeezing it out through the bristles. The whale then

licks off the food that is left behind on the bristles and swallows it.

Baleen whales are cetaceans that filter feed with baleen plates.

Baleen whales are not only the largest whales, they are among the largest animals that have ever lived on earth. There are 11 species of these majestic creatures. They were once common in all the oceans, but overhunting has

brought many species to the brink of extinction. The blue whale (Balaenoptera musculus), which is actually blue-gray, is the largest of all (Fig. 9.18). Males average 25 m (80 ft), and there is a record of a female 33.5 m (110 ft) long. How do you weigh a blue whale? Very carefullythey average 80,000 to 130,000 kg (90 to 140 tons), but the record is an estimated 178,000 kg (200 tons)!

The blue whale, the fin whale (B. physalus; Fig. 9.18), and the minke whale

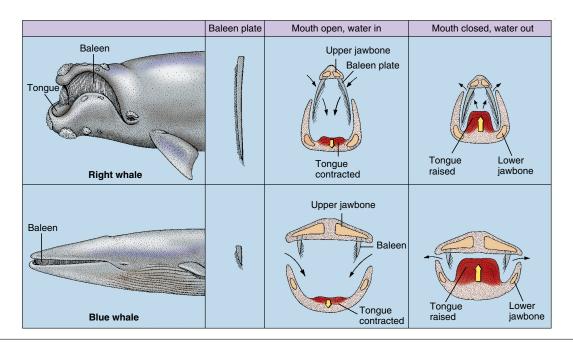




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**FIGURE 9.17** The filtering apparatus of whales consists of vertical baleen plates. The number and length of plates vary in different species, up to an average of 360 on each side in the sei whale (*Balaenoptera borealis*). The plates vary from 30 cm (1 ft) long in the minke whale (*B. acutorostrata*) to 4.5 m (15 ft) in the bowhead whale (*B. mysticetus*). The baleen, also called whalebone, was once used to make corset stays, backings for billiard tables, and buggy whips. Water is filtered as the mouth closes and the tongue (yellow arrow) pushes up, forcing the water out through the baleen.

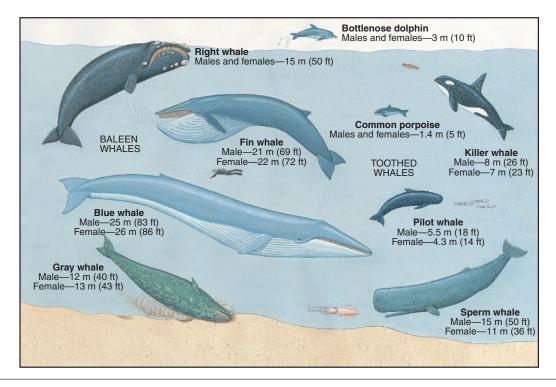


FIGURE 9.18 Representative baleen and toothed whales.

## Table 9.1 Diet of Great Whales

| Whale<br>Species | Bottom<br>Invertebrates<br>(%) | Large<br>Zooplankton<br>(%) | Small<br>Squids<br>(%) | Large<br>Squids<br>(%) | Small<br>Pelagic<br>Fishes (%) | Mesopelagic<br>Fishes*<br>(%) | Miscellaneous<br>Fishes<br>(%) |
|------------------|--------------------------------|-----------------------------|------------------------|------------------------|--------------------------------|-------------------------------|--------------------------------|
| Blue             | —                              | 100                         | _                      | _                      |                                | —                             |                                |
| Bowhead          | 20                             | 80                          | —                      | —                      | —                              | —                             | —                              |
| Bryde's          | —                              | 40                          | —                      | —                      | 20                             | 20                            | 20                             |
| Fin              | —                              | 80                          | 5                      | —                      | 5                              | 5                             | 5                              |
| Gray             | 90                             | 5                           | —                      | —                      | —                              | 5                             | —                              |
| Humpback         | —                              | 55                          | —                      | —                      | 15                             | —                             | 30                             |
| Minke            | —                              | 65                          | —                      | —                      | 30                             | —                             | 5                              |
| Northern Right   | —                              | 100                         | —                      | —                      | —                              | —                             | —                              |
| Southern Right   | —                              | 100                         | —                      | —                      | —                              | —                             | —                              |
| Sei              | —                              | 80                          | 5                      | —                      | 5                              | 5                             | 5                              |
| Sperm            | 5                              |                             | 10                     | 60                     | 5                              | 5                             | 15                             |

Source: Adapted from D. Pauly, et al., 1998, ICES Journal of Marine Science, 55:467-481.

(B. acutorostrata)-together with two other related species-are known as the rorquals. They and the humpback whale (Megaptera novaeangliae; see photo on page 179), which is often included among the rorquals, feed by gulping up schools of fish and swarms of krill. The lower part of the throat expands when feeding; hence the distinctive accordion-like grooves on the underside of these whales. Humpback whales often herd fish by blowing curtains of bubbles around them. Krill is the most important part of the rorqual diet, especially in the Southern Hemisphere, but fishes such as herring and mackerel are also eaten (Table 9.1).

The right whales (*Eubalaena*, *Caper-aea*) and the bowhead whale (*Balaena mysticetus*) feed by swimming along the surface with their huge mouths open (Fig. 9.18). They have the largest baleen plates of the whales but the finest bristles (Fig. 9.17). This allows them to filter small plankton like copepods and some krill (Table 9.1).

Gray whales (*Eschrichtius robustus*) are primarily bottom feeders. When examined, their stomachs contain mostly **amphipods** that inhabit soft bottoms (Table 9.1). Grays stir up the bottom with their pointed snouts and then filter the sediment (Fig. 9.18), leaving characteristic pits on the bottom. Most appear to feed on their right sides because the baleen on this side is more worn. Some, however, are "left-handed" and feed on the left side. A 10-week-old female kept in captivity in San Diego, California, ate over 815 kg (1,800 lb) of squid every day, gaining weight at the rate of 1 kg (2.2 lb) an hour!

The roughly 80 remaining species of cetaceans are toothed whales that lack baleen. Their teeth are adapted for a diet of fish, squid, and other prey. They use the teeth only to catch and hold prey, not to chew it. Food is swallowed whole. As in all cetaceans, food is ground up in one of the three compartments of the stomach. The blowhole has one opening, as opposed to two in the baleen whales.

The toothed whales, which include the dolphins and porpoises, lack baleen and feed on fish, squid, and other prey.

The largest toothed whale is the sperm whale (*Physeter catodon*), the unmistakable blunt-nosed giant of *Moby Dick* fame (Fig. 9.18). Together, the sperm and baleen whales are often called the **great whales.** There is growing evidence that sperm whales, though toothed, are more closely related to baleen whales than to other toothed whales. The sperm whale is now the most numerous of the great whales, even though it was the mainstay of the whaling industry for centuries (see Table 9.2, p. 196). The largest on record weighed 38,000 kg (42 tons).

Sperm whales are fond of squid, including the giant deep-sea ones. Undigested squid beaks and other debris accumulate in the gut as large globs of sticky material known as **ambergris**. Believe it or not, ambergris is an ingredient in fine perfumes. Sperm whales also eat a wide variety of fishes (including sharks), lobsters, and other marine animals (Table 9.1).

The other toothed whales are much smaller than the great whales. One is the killer whale, or orca (*Orcinus orca*; see Figs. 9.18 and 10.7), a magnificent black and white predator with a taste for seals, penguins, fishes, sea otters, and even other whales. They use their flukes to stun their prey when feeding on schools of herring—more efficient than chasing individual fish. Killer whales are most

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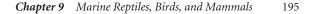
common in cold water but are found around the world. A few are kept in captivity. Killer whales have a nasty reputation, but there are no confirmed cases of them attacking humans in the wild.

Though they are all whales, most of the small toothed whales are called dolphins or porpoises. Technically, porpoises comprise only a small group of blunt-nosed whales (Fig. 9.18), but in some places the name "porpoise" is given to some of the dolphins. Most of the small whales, however, are called dolphins and some people prefer to call all of them dolphins.

The many species of dolphins typically possess a distinctive snout, or beak, and a perpetual "smile." Playful, highly social, and easily trained, dolphins easily win people's hearts. They often travel in large groups called **pods**, herds, or schools. They like to catch rides along the bows of boats (Fig. 9.19a) or even around great whales. The bottlenose dolphin (Tursiops truncatus) is the dolphin seen in marine parks and oceanaria around the world. The spinner dolphin (Stenella longirostris; Fig. 9.19b) is so named because of its spectacular twisting jumps in the air. It is one of the species of dolphins that get caught in the nets of tuna fishers. This happens because the tuna and dolphins eat the same fish and often occur together.

Dolphins are not the only cetaceans to be threatened. Whale hunting, or whaling, is an old tradition with a rich history. Native Americans hunted gray whales in prehistoric times; Eskimos still legally hunt them. Basques may have hunted them off Newfoundland before Columbus. It was not until the 1600s, however, that Europeans started to substantially exploit the great whales in the North Atlantic. Americans, who eventually dominated worldwide whaling, began hunting off New England by the late 1600s. Whales were harpooned from small open boats (Fig. 9.20), a technique whalers learned from the natives. It was a rewarding fishery, though not one exploited primarily for food. Blubber provided "train oil" that was used to make soap and as lamp oil. Baleen was used to make stays for corsets and other goods. Meat and other valuable products also were obtained from the huge animals. Whaling efforts rapidly increased after

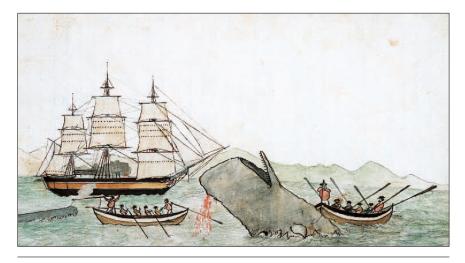






(b)

**FIGURE 9.19** Dolphins often ride the bow wave of boats (*a*) or even that of whales. They ride without beating their tails, obtaining thrust from the pressure wave in front of the ship. (*b*) This spinner dolphin (*Stenella longirostris*) from the Eastern Pacific was photographed swimming alongside a ship.



**FIGURE 9.20** Sperm whales being harpooned in the South Pacific by the crew of the *Acushnet*, an American whale ship from Fairhaven, Massachusetts. This watercolor painting is part of the sea journal of an 1845 to 1847 voyage. Herman Melville, the author of *Moby Dick*, sailed as a seaman on the *Acushnet* from 1841 to 1842.

fast steamships and the devastating explosive harpoon were introduced in the 1800s. The largest and fastest whales, like the blue whale and the fin whale, were then at the mercy of whalers.

**Amphipods** Small crustaceans whose bodies are compressed from side to side. *Chapter 7, p. 136; Figure 7.30* 

## Table 9.2

Estimated Numbers of Great Whales before Exploitation and during the Late 1990s

| Whale Species          | Status     | Estimated Pre-Exploitation Number | Estimated Number in the Late 1990s |
|------------------------|------------|-----------------------------------|------------------------------------|
| Blue                   | Endangered | 160,000-240,000                   | 5,000                              |
| Bowhead                | Endangered | 52,000-60,000                     | 8,200                              |
| Bryde's                | Protected  | 100,000                           | 66,000–86,000                      |
| Fin                    | Endangered | 300,000-650,000                   | 123,000                            |
| Gray (eastern Pacific) | Protected  | 15,000-20,000                     | 26,000                             |
| Gray (western Pacific) | Endangered | 1,500-10,000                      | 100-200                            |
| Gray (Atlantic)        | Extinct    | Unknown                           | 0                                  |
| Humpback               | Endangered | 150,000                           | 25,000                             |
| Minke                  | Hunted     | 350,000                           | 850,000                            |
| Northern right         | Endangered | Unknown                           | 870-1,700                          |
| Southern right         | Endangered | 100,000                           | 1,500                              |
| Sei                    | Endangered | 100,000                           | 55,000                             |
| Sperm                  | Endangered | >2,000,000                        | >1,000,000                         |

Source: International Whaling Commission (IWC) and others.

Whales are long-lived mammals with a very low reproductive rate. The great whales generally give birth to one welldeveloped calf that has been carried by the mother for a year or more (see "Biology of Marine Mammals," p. 198). Females usually don't become pregnant for one or two years after giving birth. As a result of this low reproductive potential, whale stocks could not stand the intense whaling pressure, and many of the fisheries collapsed. Almost all great whales are now classified as endangered (Table 9.2).

The first to be seriously depleted was the slow-swimming North Atlantic right whale (Eubalaena glacialis), the "right" species to be killed, according to whalers, because it floated after being harpooned. By the early 1900s whaling had moved to the rich feeding grounds around Antarctica. This location proved to be a real bonanza. Whaling nations developed factory ships able to process whole carcasses. The Antarctic fishery reached its peak in the 1930s. The whales received a reprieve during World War II, but it was too late for saving the fisheries. It is estimated that more than a million whales were taken from Antarctica alone.

Blue whales, the largest of them all, were especially sought. A large specimen yielded more than 9,000 gallons of oil. It has been estimated that over 200,000 blue whales were taken worldwide between 1924 and 1971, close to 30,000 during the 1930–31 whaling season alone. Catches climbed way above the optimal yield level. Catch per whaler-day's effort declined every year after 1936. As many as 80% of all blue whales caught by 1963 were sexually immature, so that there were even fewer individuals in the ocean able to perpetuate the species.

Fin whales, the second largest of all whales, became the next major target as blue whales became more and more scarce. The 1950s and early 1960s saw annual catches of 20,000 to 32,000 fin whales per year, mostly from Antarctica. As their stocks dwindled, whalers shifted their target again in the mid-1960s, this time to the smaller sei whale (*Balaenoptera borealis*). The sei whale averages a length of around 13 m (44 ft), whereas the fin whale averages 20 m (65 ft).

Intense whaling has led to the near extermination of most species of great whales. Practically all of these species are now endangered.

The abrupt disappearance of the more commercially valuable whales, one after the other, meant lower profits for the whaling industry. In 1946, 20 whaling nations established the International Whaling Commission (IWC) in an attempt to regulate whale hunting to stop overfishing. It collected data on the number of whales, though the numbers came mostly from the whalers themselves. It set annual quotas for the number of whales to be killed each year, quotas that unfortunately were non-binding and could not be enforced. Furthermore, some whaling nations did not belong to the IWC. Saving the whaling industry was considered more important than saving the whales. The blue whale was not completely protected by the IWC until the 1965-66 season, long after its numbers had been drastically reduced; by then blue whales were so hard to find that the fishery for them was no longer a profitable fishery. Even under the protection of the IWC, blue whales were hunted at least until 1971 by the fleets of countries that did not belong to the IWC.

Under mounting pressure from conservationists, the IWC gradually banned the hunting of other whales. Demand for whale products, mostly oil used in the manufacture of margarine and lubricants, was reduced because substitutes had been found for most of them. Whale meat, however, continued to be used as pet food and is still valued as human food, mostly in Japan. The lower quotas of the

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IWC were unfortunately not always accepted by all nations.

The United States Congress separately passed the Marine Mammal Protection Act of 1972, which bans the hunting of all marine mammals in U.S. waters (except in the traditional fisheries of Alaskan natives; see Fig. 4.2) and the importation of marine mammal products. By 1974 the IWC had protected the blue, gray, humpback, and right whales around the world, but only after their stocks were no longer economically viable. Sperm, minke, fin, and sei whales were still hunted in large numbers, but worldwide catches began to dwindle. Catches of these whales fell from 64,418 in 1965 to 38,892 in 1975 and to 6,623 in 1985. A moratorium on all commercial whaling was finally declared by the IWC in 1985, a move long sought by conservationist groups. The former Soviet Union halted all whaling in 1987. Japan, Iceland, and Norway, however, opted in 1988 to continue hunting minke, fin, and sei whales, as allowed by the IWC under the controversial title of "scientific whaling." Iceland eventually quit the IWC.

In 1994 IWC members signed an agreement that created a vast sanctuary for all whales in the waters around Antarctica. This area is the main feeding ground for 80% of the surviving great whales. Japan voted against the agreement and independently decided to continue hunting whales in Antarctica. Starting with the 1997-98 season Japan took 440 minkes from Antarctica and 100 from the North Pacific each season. The 2002 season saw Japan expand its North Pacific catch to include 150 minke, 50 Bryde's (Balaenoptera edeni), 10 sperm, and for the first time since 1987, 50 sei whales. In 1997 Norway announced its resumption of commercial whaling of minkes in the North Sea in defiance of the IWC (Fig. 9.21). Norway allowed the killing of 671 whales during the 1998-99 season. Meanwhile, hunting of smaller cetaceans not protected by the IWC, like the Dall porpoise (Phocoenoides dalli), has increased in an attempt to find substitutes for whale meat.

Nobody knows when the great whales will again roam the oceans in numbers approaching those before the



FIGURE 9.21 A harpooned minke whale (*Balaenoptera acutorostrata*) being hauled on board a Norwegian whaling ship in the North Sea.

start of large-scale whaling. Some experts are afraid that a few critically endangered species will never recover completely. Small-scale whaling remains part of the traditional fisheries of the native inhabitants of the Arctic region from Greenland to Siberia and in the Lesser Antilles in the Caribbean. One of the whales hunted in the Arctic, the bowhead, and another in the Lesser Antilles, the humpback, are endangered. Other smaller whales—the killer whale, narwhal (*Monodon monoceros*), and beluga (*Delphinapterus leucas*) are also hunted in the Arctic.

Recovery is under way in other species. The California gray whale, protected since 1947, has made a phenomenal comeback (Fig. 9.22). It was removed from the endangered species list in 1994. In 1997 the IWC allowed the killing of 600 gray whales by native hunters in Siberia and 20 by the Makah Indian tribe in the state of Washington. Only one, however, was killed in 1999. Even the blue whale, whose reproduction is severely limited by its restriction to small populations scattered around the world, is making a comeback of sorts. It has returned to the southern reaches of the Arctic Ocean

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**FIGURE 9.22** California gray whales (*Eschrichtius robustus*) are once again a common sight along their long migration routes from Alaska to Mexico (see Fig. 9.31). This species was removed from the endangered species list in 1994.

north of Norway, a region where they flourished before their near extermination by whalers. Sightings in California waters have increased sharply. Their numbers in Antarctica, however, are even lower than first estimates: around 500 animals, or only 0.2% of those feeding there before whaling began.

Dolphins, not protected by the IWC, are also at great risk (see Table 18.1, p. 422). They have replaced the larger whales as the most threatened of all cetaceans. As many as 28 species of small cetaceans are in immediate danger of extinction. Only 200 to 500 vaquitas, or "little cows" (Phocoena sinus), are left. This shy, shovel-nosed porpoise, known only from the northern Gulf of California, remained unknown to science until 1958. Everywhere, fishers are depleting stocks of fish and squid on which dolphins feed. Dolphins themselves are being hunted for human food. It is becoming popular in countries like Perú, where dolphin meat is cheaper than beef or chicken.

Tuna fishers using giant purse seine nets (see Fig. 17.6b) trap and drown the many dolphins that often swim above schools of tuna, mostly yellowfin tuna (Thunnus albacares) in the Eastern Pacific. Fishers often find their catch after spotting dolphins, which is known as "setting on tuna." During the early 1970s an estimated 200,000 dolphins died annually, mostly in the hands of American fishing fleets. The slaughter induced such public outrage that the United States, through the Marine Mammal Protection Act of 1972, called for a reduction in the accidental deaths of dolphins. It imposed a quota of 20,500 for the number of dolphins that could be killed by American fleets. The use of special nets was enforced, and observers were placed on board vessels to verify compliance with the ruling. By 1990 it was estimated that the number of dolphins killed by the United States tuna fleet, by then operating in "dolphin-safe" western Pacific waters, had reached zero. Environmentalists won a major victory when in 1990 the three biggest tuna packers in the United States pledged not to buy or sell fish that was caught using methods that injure or kill dolphins. Tuna cans began to display "dolphin-safe" labels, and imported tuna caught without the use of dolphin-safe methods were banned from sale in the United States. In 1997 the ban was lifted from some countries, notably Mexico, where fishers improved their methods.

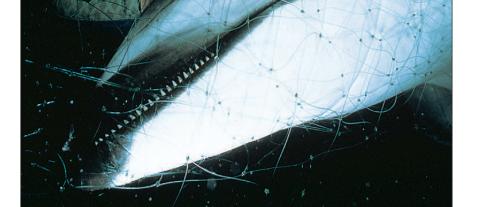
Dolphins, however, continue to drown in purse seine nets, mostly in the tropical Eastern Pacific at the hands of unregulated fishing fleets. The number of dolphins in the Eastern Pacific has noticeably decreased, particularly among the coastal spotted (*Stenella attenuata*) and eastern spinner (see Fig. 9.19*b*) dolphins.

Dolphins have also been entangled and killed by the thousands in huge **drift nets** (see Fig. 17.6e), which also threaten sharks, sea turtles, seals, seabirds, and other marine life (Fig. 9.23). The nets, in some cases as large as 60 km (37 mi) long and 15 m (50 ft) deep, have been used to catch fish and squid, but they actually catch practically anything that tries to swim by. Not only do they deplete valuable commercial fisheries like albacore tuna and salmon, but they trap FIGURE 9.23 This Pacific white-sided dolphin (*Lagenorbynchus obliquidens*) drowned after getting caught in a drift net in the North Pacific.

many noncommercial species. These "walls of death" also are very wasteful because a large percentage of the catch drops out during hauling. Their use in the North Pacific salmon fishery has been particularly deadly to the Dall porpoise. Hundreds of fishing boats outfitted for drift netting have been used to catch tuna in the South Pacific with potentially disastrous results. International pressure persuaded Japan, which had the largest fleet of drift-net boats in the Pacific, and Taiwan to end the use of driftnet fishing in 1993.

## Biology of Marine Mammals

It is surprising how little we know about marine mammals. Most are difficult or impossible to keep in captivity or even to observe for long periods at sea. Some whales and dolphins are rarely seen, so what little we know about them comes from captive or stranded individuals and information gathered over the years by whalers. What we do know about marine mammals, however, is simply fascinating.

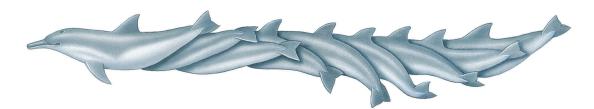


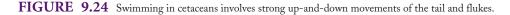
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|                   | Surfacing and blowing | Start of dive | End of dive |
|-------------------|-----------------------|---------------|-------------|
| Blue whale        |                       |               |             |
| Fin whale         |                       |               |             |
| Gray whale        |                       |               | -           |
| Right whale       | <b>\$</b> <i>P</i>    |               | Y           |
| Sperm whale       |                       |               | Y           |
| Humpback<br>whale |                       |               | T           |

FIGURE 9.25 Great whales can be identified from a distance by their blowing pattern, their outline on the surface, and the way they dive.

#### Swimming and Diving

Streamlining of the body for swimming is a hallmark of marine mammals. Seals, sea lions, and other pinnipeds swim mostly by paddling with their flippers. Sirenians and cetaceans, in contrast, move their tails and flukes up and down (Fig. 9.24). Fishes, you will recall, move their tails from side to side (see Fig. 8.11). Cetaceans turn mostly by up-and-down movements of the tail and flukes. Sea lions have been timed at speeds of 35 kph (22 mph). Blue and killer whales can reach speeds of 50 kph (30 mph). A group of common dolphins (*Delphinus*  *delphis*) was recorded bowriding at a speed of 64 kph (40 mph)!

Cetaceans have the advantage of having the blowhole on top of the head. This allows them to breathe even though most of the body is underwater. It also means, by the way, that cetaceans can eat and swallow without drowning. To avoid inhaling water, marine mammals take very quick breaths. A fin whale can empty and refill its lungs in less than 2 seconds, half the time we take, even though the whale breathes in 3,000 times more air! When swimming fast, many pinnipeds and dolphins jump clear out of the water to take a breath. In the large whales the moisture in their warm breath condenses when it hits the air. Together with a little mucus and seawater, this water vapor forms the characteristic **spout**, or **blow** (see Fig. 1.20). The spout can be seen at great distances and its height and angle used to identify the whale (Fig. 9.25). The blue whale, for instance, has a spout some 6 to 12 m (20 to 40 ft) high.

To keep warm in cold water, the great whales depend on a thick layer of blubber (see Fig. 4.2). Feeding, however, leaves their huge mouths exposed to low temperatures, a major problem in the very cold polar waters where they normally II. Life in the Marine Environment 9. Marine Reptiles, Birds, and Mammals

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THE OTHER "BIG BANG THEORY"

It is widely known that toothed whales use sound for echolocation and to communicate with each other. Recently a different use of sound waves by these cetaceans has been suggested.

This new hypothesis developed as a possible explanation for the feeding habits of sperm whales, the largest of the toothed whales. Squids taken from the stomach of captured and stranded whales often show no tooth marks or scars of any kind. In fact, live squids have been known to swim out of the stomachs of freshly caught whales! It seems that sperm whales have a way of catching squids—including giant squids—without using their teeth, even if their teeth are actually of little help because they are present only in the lower jaw. Another puzzle is explaining how sperm whales weighing 36,000 kg (40 tons) or more and averaging speeds of just 2 to 4 knots catch squids that can swim at 30 knots.

How about the possibility that whales and dolphins may use powerful blasts of sound to catch their food? This ingenious hypothesis has been dubbed a second "big bang theory," the original being the well-known view proposed to explain the origin of our universe (see "The Structure of the Earth," p. 22). Catching prey whole and still alive could be explained if the whale stuns its prey with a blast of sound and then simply swallows it whole.

Some indirect evidence is provided by the now-extinct ancestors of toothed whales. Fossils of the earliest known toothed whales

have long snouts armed with many piercing teeth (see "The Whales That Walked to Sea," p. 192). Like those of a barracuda, the teeth were probably used to catch small fish and other prey. The long snout, however, has disappeared in most modern cetaceans, and the teeth have become wider and shorter. Have modern toothed whales evolved a new technique to catch their food, or has their food source changed?

Sonic hunting may involve a beam of low-frequency sound waves powerful enough to stun a fish or squid. Although the sophisticated sound-producing mechanism of cetaceans is not fully understood, it is thought to be capable of emitting the required sound waves. It has been suggested that sonic hunting evolved as a byproduct of echolocation in the early toothed whales.

It is not easy to obtain the necessary evidence to support this hypothesis. Loud noises can indeed stun fish, but it is difficult to reproduce the exact sounds produced by cetaceans. Dolphins living in the wild have produced gun-like bangs that can be heard by humans. Unfortunately, undertaking detailed studies of sonic hunting in the wild presents many complications. Captive dolphins do not produce loud noises, which is not surprising because the echo of the noise off the tank walls would be very painful to them. The function of big bangs in whales is but one of the many surprising adaptations of cetaceans waiting to be explored.

feed. It has been recently discovered that a network of blood vessels in their tongues actually reduces heat loss by transferring heat from warm blood into vessels that carry it back to the body core.

Marine mammals have mastered the art of diving, and most make prolonged dives to considerable depths for food. There is a wide range in diving ability. Sea otters can dive for only 4 or 5 minutes, to depths of perhaps 55 m (180 ft). Pinnipeds normally dive for up to 30 minutes, and maximum depths are roughly 150 to 250 m (490 to 820 ft). Female northern elephant seals (Mirounga angustirostris), however, are capable of continuous deep dives of up to 400 m (1,300 ft). One individual was recorded diving to a depth of 1,500 m (5,000 ft). The Weddell seal (Leptonychotes weddelli) has been recorded diving for as long as 1 hour 13 minutes and as deep as 575 m (1,900 ft).

The plankton-feeding habits of baleen whales do not require them to dive too deeply for their food, and they seldom venture below 100 m (300 ft). Toothed whales, however, are excellent divers. Dolphins are known to dive as deep as 300 m (990 ft). The champion diver is the sperm whale, which can stay under for at least an hour. They are known to dive to 2,250 m (7,380 ft) and can probably go much deeper.

The long, deep dives of marine mammals require several crucial adaptations. For one thing, they must be able to go a long time without breathing. This involves more than just holding their breath, for they must keep their vital organs supplied with oxygen. To get as much oxygen as possible before dives, pinnipeds and cetaceans hold their breath for 15 to 30 seconds, then rapidly exhale and take a new breath. As much as 90% of the oxygen contained in the lungs is exchanged during each breath, in contrast to 20% in humans.

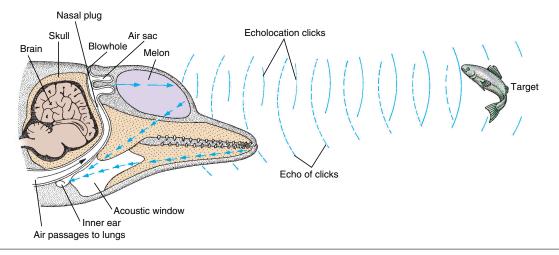
Not only do diving marine mammals breathe more air faster than other mammals, they are better at absorbing the oxygen from the air and storing it in their blood. They have relatively more blood than non-diving mammals. Their blood also contains a higher concentration of erythrocytes, or red blood cells, and these cells carry more **hemoglobin**. Furthermore, their muscles are extra rich in **myoglobin**, which means that the muscles themselves can store a lot of oxygen.

Marine mammals have adaptations that reduce oxygen consumption in addition to increasing supply. When they dive, the heart rate slows dramatically. In the northern elephant seal, for example, the heart rate decreases from about 85 beats per minute to about 12. Blood flow to non-essential parts of the body, like the extremities and the intestine, is reduced, but it is maintained to vital organs like the brain and heart. Thus, oxygen is made available where it is needed most when oxygen supply is cut off during a dive.

Another potential problem faced by air-breathing, diving animals (including human divers) results from the presence of large amounts of nitrogen (70% of total volume) in the air. Nitrogen dissolves much better at high pressures, like those experienced at depth. The blood of scuba divers picks up nitrogen while they are below the surface. If the pressure is suddenly released, some of the nitrogen will not stay dissolved and will form tiny bubbles in the bloodstream. You can see a

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**FIGURE 9.26** Dolphins echolocate by emitting bursts of sound waves, or clicks, by pushing air through internal air passages. Two muscular nasal plugs act as valves, closing and opening the passages. Flaps of tissue on the plugs probably also produce sound by vibrating in the moving air. The clicks are focused into a beam by the melon. To cover a wider area the dolphin moves its head from side to side. The melon is also known to receive the echoes and transmit them to the ears, but most are received by the lower jaw.

similar phenomenon when you open a bottle of soda pop. As long as the top is on, the contents are under pressure. The carbonation, actually carbon dioxide gas, remains dissolved. When you open the bottle the pressure is released and bubbles form. When nitrogen bubbles form in the blood after diving, they can lodge in the joints or block the flow of blood to the brain and other organs. This produces a horribly painful condition known as the **bends.** To avoid the bends, human divers must be very careful about how deep they go, how long they stay underwater, and how fast they come up.

Marine mammals dive deeper and stay down longer than human divers, so why don't they get the bends? The answer is that they have adaptations that prevent nitrogen from dissolving in the blood in the first place. Human lungs work pretty much the same while scuba diving underwater as on land. When marine mammals dive, on the other hand, their lungs actually collapse. They have a flexible rib cage that gets pushed in by the pressure of the water. This squeezes the air out of peripheral areas of the lungs where it readily dissolves into the blood. Air is moved instead into the central spaces of the lungs, where little nitrogen is absorbed. Some pinnipeds actually exhale before they dive, further reducing the amount of air—and therefore nitrogen—in the lungs.

Adaptations for deep, prolonged dives in marine mammals include efficient exchange of air on the surface, storage of more oxygen in the blood and muscles, reduction of the blood supply to the extremities, and collapsible lungs to prevent the bends.

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#### Echolocation

Marine mammals depend little on the sense of smell, which is so important to their terrestrial cousins. Their vision is excellent, but they have developed another sensory system, **echolocation**, based on hearing. Echolocation is nature's version of sonar. Most if not all toothed whales, including dolphins and porpoises, and some pinnipeds are known to echolocate. At least some baleen whales may use echolocation. Echolocation is not exclusive to marine mammals. Bats, for example, use it to find insects and other prey while flying at night.

Toothed whales echolocate by emitting sound waves, which travel about five times faster in water than in air, and listen for the echoes that are reflected back from surrounding objects (Fig. 9.26). The echoes are then analyzed by the brain. The time it takes the echoes to return tells the animals how far away the object is.

Many marine mammals echolocate by analyzing the echo of sound waves they emit. Echolocation is used to find prey and orient to the surroundings.

The sounds used in echolocation consist of short bursts of sharp **clicks** that are repeated at different frequencies. Low-frequency clicks have a high penetrating power and can travel long distances. They reflect from large features and are used to obtain information on the surrounding topography. Low-frequency sound waves may also be used in some toothed whales to stun their prey (see "The Other 'Big Bang Theory,'" p. 200). To discriminate more detail and locate nearby prey, high-frequency clicks that

Hemoglobin A blood protein that transports oxygen in many animals; in vertebrates it is contained in erythrocytes, or red blood cells. Myoglobin A muscle protein in many animals that stores oxygen.

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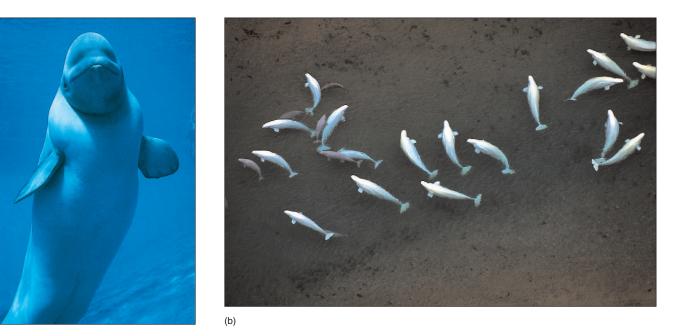




FIGURE 9.27 (a) The beluga (*Delphinapterus leucas*) is a white Arctic whale (beluga means "white one" in Russian) with a conspicuous melon. (b) In their natural environment belugas live in small groups.

are inaudible to humans are used. Experiments have shown that blindfolded bottlenose dolphins can discriminate between objects of slightly different size or made of different types of materials and even detect wires.

We are not completely sure how echolocation operates in marine mammals. The process is rather complicated (Fig. 9.26). The clicks, squeaks, and whistles of cetaceans are produced as air is forced through the air passages and several associated air sacs while the blowhole is closed. The frequency of the clicks is changed, or modulated, by contracting and relaxing muscles along the air passages and sacs. A fatty structure on the forehead of toothed whales, the melon, appears to focus and direct the sound waves. The melon gives these whales their characteristic rounded foreheads. To accommodate the melon, the skull is modified to form a pointed, dishshaped face. The skull is also asymmetric, the right side being slightly different from the left side. Belugas (Fig. 9.27) have a bulging forehead that changes shape as the melon, moved by muscles,

focuses the sound. The huge forehead of the sperm whale is filled in part with a massive melon called the **spermaceti organ**. Whalers originally thought this was the sperm sac of the whale, hence the peculiar name. This organ is filled with a waxy oil, **spermaceti**, once much sought for making candles and still used as a lubricant for precision instruments. The actual function of the spermaceti organ is a controversial issue. It has also been suggested that the deep-diving sperm whale might also use the spermaceti organ to regulate buoyancy or to absorb excess nitrogen.

In toothed whales incoming sound waves are received primarily by the lower jaw (Fig. 9.26). The ear canal that connects the outside with the inner ear is reduced or blocked in most cetaceans. The jawbones, filled with fat or oil, transmit sound to the two very sensitive inner ears. Each ear receives sound independently. The ears are protected by a bony case and embedded in an oily mixture that insulates the ear but allows sound waves to pass from the jaws. Sound information is sent to the brain, which forms a mental "picture" of the target or surroundings. In fact, sight and sound information seem to be handled similarly by the brain. Captive dolphins can recognize by echolocation objects they have seen and recognize by sight those they have previously echolocated.

#### Behavior

Echolocation is just one indication of the amazing mental capabilities of marine mammals. The mammalian brain has evolved as an association center for complex behaviors in which learning, not instinct, dominates. In contrast to fishes, birds, and other vertebrates, mammals rely mostly on past experience, stored and processed by the brain, to respond to changes in the environment (see "How Intelligent *Are* Cetaceans?," p. 203).

Most marine mammals are highly social animals that live in groups at least part of the time. Many pinnipeds live in huge colonies during the breeding season. Most cetaceans spend their entire lives in highly organized pods of a few (Fig. 9.27b) to thousands of individuals. Some pods include smaller subgroups organized by age Castro–Huber: Marine Biology, Fourth Edition II. Life in the Marine Environment 9. Marine Reptiles, Birds, and Mammals © The McGraw–Hill Companies, 2003

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## HOW INTELLIGENT ARE CETACEANS?

We often hear that whales, dolphins, and porpoises are as intelligent as humans, maybe even more so. Are they really that smart? There is no question that cetaceans are among the most intelligent of animals. Dolphins, killer whales, and pilot whales in captivity quickly learn tricks. The military has trained bottlenose dolphins to find bombs and missile heads and to work as underwater spies.

This type of learning, however, is called **conditioning**. The animal simply learns that when it performs a particular behavior it gets a reward, usually a fish. Many animals, including rats, birds, and even invertebrates, can be conditioned to perform tricks. We certainly don't think of these animals as our mental rivals.

Unlike most other animals, however, dolphins quickly learn by observation and may spontaneously imitate human activities. One tame dolphin watched a diver cleaning an underwater viewing window, seized a feather in its beak, and began imitating the diver—complete with sound effects! Dolphins have also been seen imitating seals, turtles, and even water-skiers.

Given the seeming intelligence of cetaceans, people are always tempted to compare them with humans and other animals. Studies on discrimination and problem-solving skills in the bottlenose dolphin, for instance, have concluded that its intelligence lies "somewhere between that of a dog and a chimpanzee."

Such comparisons are unfair. It is important to realize that intelligence is a very human concept and that we evaluate it in human terms. After all, not many people would consider themselves stupid because they couldn't locate and identify a fish by its echo. Why should we judge cetaceans by their ability to solve human problems?

Both humans and cetaceans have large brains with an expanded and distinctively folded surface, the **cortex**. The cortex is the dominant association center of the brain, where abilities such as memory and sensory perception are centered. Cetaceans have larger brains than ours, but the ratio of brain to body weight is higher in humans. Again, direct comparisons are misleading. In cetaceans it is mainly the portions of the brain associated with hearing and the processing of sound information that are expanded. The enlarged portions of our brain deal largely with vision and hand-eye coordination. Cetaceans and humans almost certainly perceive the world in very different ways. Their world is largely one of sounds, ours one of sights.

Contrary to what is depicted in movies and on television, the notion of "talking" to dolphins is also misleading. Though they produce a rich repertoire of complex sounds, they lack vocal cords and their brains probably process sound differently from ours. Bottlenose dolphins have been trained to make sounds through the blowhole that sound something like human sounds, but this is a far cry from human speech. By the same token, humans



Bottlenose dolphins participating in research to test acoustic communication. The devices on their heads, which are held in place by suction cups, light up every time a dolphin whistles.

cannot make whale sounds. We will probably never be able to carry on an unaided conversation with cetaceans.

As in chimps, captive bottlenose dolphins have been taught American Sign Language. These dolphins have learned to communicate with trainers who use sign language to ask simple questions. Dolphins answer back by pushing a "yes" or "no" paddle. They have even been known to give spontaneous responses not taught by the trainers. Evidence also indicates that these dolphins can distinguish between commands that differ from each other only by their word order, a truly remarkable achievement. Nevertheless, dolphins do not seem to have a real language like ours. Unlike humans, dolphins probably cannot convey very complex messages.

Observations of cetaceans in the wild have provided some insights on their learning abilities. Several bottlenose dolphins off Western Australia, for instance, have been observed carrying large cone-shaped sponges over their beaks. They supposedly use the sponges for protection against stingrays and other hazards on the bottom as they search for fish to eat. This is the first record of the use of tools among wild cetaceans.

Instead of "intelligence," some people prefer to speak of "awareness." In any case, cetaceans probably have a very different awareness and perception of their environment than do humans. Maybe one day we will come to understand cetaceans on their terms instead of ours, and perhaps we will discover a mental sophistication rivaling our own.

and sex. To keep in contact, many of their highly complex and sophisticated behaviors are directed toward members of their own species.

Sounds, or **vocalizations**, play a prominent role in communication. Sea lions and fur seals communicate by loud

barks and whimpers; seals use more sedate grunts, whistles, and chirps. The vocalizations of pinnipeds are especially important in maintaining territories during reproduction (see "Reproduction," p. 207). Females and their pups or calves recognize each other by their "voices." Cetaceans produce a rich variety of vocalizations that are different from the sounds used for echolocation. Both types of sounds can be produced simultaneously, providing further evidence of the complexity of sound production in marine mammals. Social vocalizations are

low-frequency sounds that humans can hear. The variety of sounds is amazing and includes grunts, barks, squeaks, chirps, and even "moos." Different sounds are associated with various moods and are used in social and sexual signaling. Whistles, emitted in a multitude of variations and tones, are characteristic of each species. Some of these sounds serve as a "signature," allowing individuals of the same species to recognize one another. Among the more than 70 calls that have been identified among killer whales, some are present in all individuals, whereas others are "dialects" that identify certain pods.

Sounds are also used to maintain the distance between individuals and have an important role in the structure of the pod. Particular sounds are emitted during breeding, feeding, alarms, and birth. Mother gray whales grunt to stay in contact with their calves. Fin whales make a low-pitched sound thought to be involved in long-distance communication. Right whales have at least six distinct calls, each related to a specific function.

The humpback whale is renowned for its soulful songs. They are sung by breeding males to attract females by advertising their readiness to mate. The songs consist of phrases and themes repeated in a regular pattern for a half hour or longer. They may be repeated over and over for days! The songs change over time. Males also start each breeding season with the song they were singing at the end of the previous breeding season. New songs learned from immigrants have been shown to gain instant popularity among native whales. Researchers record and catalogue songs to help track whales in their annual migrations.

Communication among cetaceans is not restricted to vocalizations. Researchers have described a variety of postures and movements that may indicate the animal's mood. Dolphins clap their jaws or turn around with their mouths open as a threat. The loud cracking sound made when some marine mammals flap their flukes or flippers on the surface is thought to be a warning signal.

Cetaceans are noted for their play behavior, seemingly pleasurable activities with no serious goal. Many species, in-

FIGURE 9.28 A humpback whale (Megaptera novaeangliae) performing a full spinning breach.

cluding the great whales and killer whales, play with food or floating objects like logs, kelp, and feathers, throwing them up in the air or holding and pushing them with their snouts. Individuals may swim head down or on their backs apparently just for the fun of it. Dolphins play with rings of air bubbles they create. Dolphins also like to surf, and pilot (Globicephala) and right whales go sailing with their flukes out of the water to catch the wind. Sex play, the rubbing and touching of the genital opening, is also common.

The sight of a great whale breaching, leaping up in the air and loudly crashing on the surface, is awesome (Fig. 9.28). Breaching has been variously interpreted as a warning signal, as a way of scanning the surface or the shoreline, as a means of getting rid of external parasites or an ardent lover, and simply as fun. After a deep dive, sperm whales may breach, fall on their backs, and make a splash that can be heard 4 km (2.5 mi) and seen 28 km (17.4 mi) away! Many whales stick their

heads out of the water to spy on their surroundings (Fig. 9.29a).

The complex behavior of cetaceans is evident in other ways. When one individual is in trouble, others may come to assist (Fig. 9.29b). Members of a pod refuse to leave a wounded or dying comrade. Whalers knew that a harpooned whale was a lure for others, who are drawn from miles around. Dolphins will carry injured individuals to the surface to breathe (Fig. 9.29c), and there are records of females carrying the body of a stillborn calf until it rots.

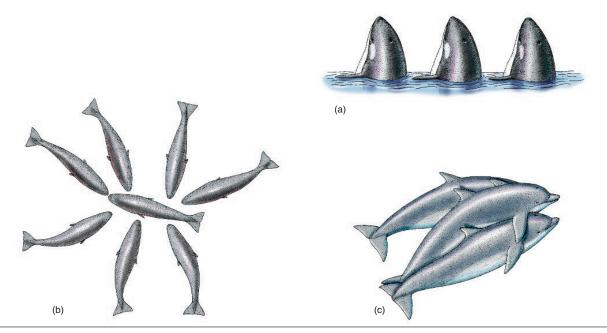
Many toothed whales work together when they hunt, some in coordinated pairs. Sometimes whales take turns feeding while their partners herd a school of fish. An individual may investigate something strange lying ahead while the rest of the group waits for the "report" of the scout. Studies of animals in the wild show that dolphins belong to a complex society, one in which long-term partnerships of members of the same sex play an



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**FIGURE 9.29** Whale watchers may be rewarded with examples of the complex behavior of whales: (*a*) "spying" behavior in killer whales (*Orcinus orca*) in the wild, (*b*) sperm whales (*Physeter macrocephalus*) surrounding an injured member of a pod, (*c*) two bottlenose dolphins (*Tursiops truncatus*) carrying a stunned companion to the surface to breathe.

important role in sexual behavior, parental care, and other aspects of daily life. Social behavior in cetaceans may ultimately show many parallels with social behavior in large-brained mammals such as apes and humans.

Marine mammals, particularly cetaceans, use a rich variety of vocalizations and tactile and visual signals to communicate with each other. Play behavior and mutual assistance are additional evidence of the complexity of their behavior.

The relationship between dolphins and humans is a controversial one. Some people swear of experiencing spiritual inspiration while swimming among dolphins during the "dolphin encounters" offered by some resort hotels. Dolphins trained for military purposes by the former Soviet navy are being used to treat children suffering from behavioral disorders. Others see this as outright exploitation of the captive animals. It has been suggested that stress among captive dolphins reduces their life span. Though exaggerations abound, there are authenticated cases of dolphins approaching human swimmers who appeared to be in trouble. For more than a century, fishers in southern Brazil have established a unique partnership with dolphins. The dolphins detect fish and deliver them to fishers waiting with nets. Fishers have learned to interpret cues given by the dolphins about the location and abundance of fish. Generations of dolphins have learned that a row of fishers holding a net in shallow water means an easy catch for themselves, even if it has to be shared with funny-looking, two-legged mammals.

One of the mysteries of the behavior of whales and dolphins is the stranding, or beaching, of individuals, sometimes dozens, on beaches (Fig. 9.30). The animals refuse to move, and efforts to move them into deeper water usually fail. Even if they are pulled out to sea, they often beach themselves again. The whales die because their internal organs collapse without the support of the water. Stranding has been described in many species, but some, such as pilot and sperm whales, strand themselves more often than others. It appears that whales become stranded when they follow one or more members of their group that have become



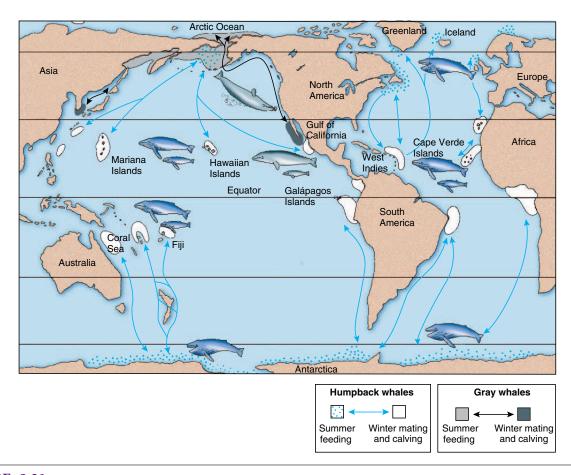
FIGURE 9.30 These pilot whales (*Globicephala melas*) stranded themselves on a beach in Cape Cod, Massachusetts. Only two of the 55 stranded whales survived.

disoriented by a storm, illness, or injury. This indicates the strong cohesiveness and herd instinct of the group.

#### Migrations

Many pinnipeds and cetaceans make seasonal migrations, often traveling thousands of miles from feeding grounds to breeding areas. Most toothed whales, on the other hand, do not migrate at all, though they may move about in search of food.

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**FIGURE 9.31** Migration routes of humpback (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*). Both species tend to migrate and breed close to shore, where they were easily hunted. Both species are on the comeback. The gray whale was removed from the endangered species list in 1994. The western Pacific population of grays that may still breed south of Korea also appears to be making a comeback. Gray whales used to live in the North Atlantic until exterminated in the last century. Also see Fig. 9.22.

The migrations of the great whales are by far the most remarkable. Many baleen whales congregate to feed during the summer in the productive waters of the polar regions of both hemispheres, where huge concentrations of diatoms and krill thrive in the long days. During the winter they migrate to warmer waters to breed. The seasons are reversed in the Northern and Southern Hemispheres, so when some humpback whales are wintering in the Hawaiian Islands or the West Indies, other humpbacks living in the Southern Hemisphere are feeding around Antarctica during the southern summer (Fig. 9.31).

Most great whales migrate from winter breeding areas in the tropics to summer feeding areas in colder waters.

The migratory route of the gray whale is the best known of any of the great whales (Fig. 9.31). From the end of May to late September the whales feed in shallow water in the northern Bering, Beaufort, and East Siberian seas. They begin moving south in late September when ice begins to form. By November they begin crossing through the eastern Aleutian Islands. They eat less while on the move, burning off close to a quarter of their body weight. The whales cover about 185 km (115 mi) per day. They travel alone or in small groups along the coast of the Gulf of Alaska and down the western coast of North America en route to the Baja California Peninsula in Mexico (Fig. 9.22). Migrating individuals often show spying behavior, pushing their heads out of the water. This raises the possibility that they navigate by using memorized landmarks. They reach Oregon around late November or early December and San Francisco by mid-December. Females generally migrate earlier. By late February pregnant females are the first to appear in shallow, quiet lagoons in southern Baja California and the

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(a)

**FIGURE 9.32** (a) A male Steller sea lion (*Eumetopias jubatus*) guarding his harem on a rocky island off the coast of Alaska. Steller sea lions are the largest of the eared seals; males may weigh nearly 900 kg (1 ton). (b) A harem of female California sea lions (*Zalophus californianus*) on Santa Barbara Island, Southern California. The harem (center) is being guarded by a large, darker bull (top left). Large female elephant seals (*Mirounga angustirostris*) rest near the harem, oblivious to the occasional fights between the bull and rival males around the harem.

(b)

southern mainland coast of the Gulf of California. It is here that females give birth and males mate with non-pregnant females.

The northbound migration begins by March, after the birth of the 700- to 1,400-kg (1,500- to 3,000-lb) calves. Females mate every two years, and the first to migrate north are the newly pregnant females that did not give birth. They will return 12 months later to give birth. Mothers with calves leave last. On the way north the whales tend to stay farther from the coast and move slower, an average of 80 km (50 mi) per day, because of the newborn calves and unfavorable currents. The last whales leave the coast off Washington state by early May. They start reaching their feeding areas by late May, completing an amazing eight-month trip of up to 18,000 km (11,200 mi), the longest migration of any mammal.

There is still much to be learned about the migrations of the gray whale and other whales. It has been found, for instance, that some isolated groups of gray whales along the migratory route do not migrate at all. This is the case in a group that resides in the Queen Charlotte Islands off the coast of British Columbia. Scientists are using novel ways to investigate the migration of whales. Attaching small radio transmitters to whales and tracking their movements by satellite promises to uncover intriguing details. Gray whales are known to avoid cities by moving away from the coast. Females and young may slow down their migration back to the Arctic by taking shelter in kelp forests to avoid killer whales. Analysis of the DNA of humpback whale populations in the Hawaiian Islands suggests that, as in the green turtle, individuals always return to the feeding grounds of their mothers. Another vexing question is how whales navigate. It has been suggested that they use the earth's magnetic field, a possibility that implies that they must carry some type of internal compass to orient themselves.

#### Reproduction

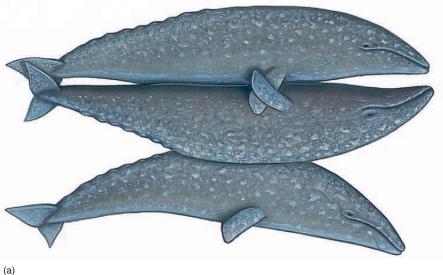
The reproductive system of marine mammals is similar to that of land mammals. They have some unique adaptations to life in the water, however. To keep the body streamlined, male cetaceans and most other marine mammals have an internal penis and testes. The penis, which in blue whales is over 3 m (10 ft) long, is kept rigid by a bone. It is extruded just before copulation through the **genital slit**, an opening anterior to the anus (see Fig. 9.15).

Pinnipeds breed on land or ice, some migrating long distances to isolated islands to do so. In most species of seals each adult male breeds with only one female. Camcorders attached to animals in the wild (see "Eyes (and Ears) in the Ocean," p. 11) have shown that male harbor seals make rumbling noises, quiver their necks, and release a stream of air bubbles, perhaps a display to attract females. In sea lions, fur seals, and elephant seals, however, a male breeds with many females. During the breeding season the males of these species, who are much bigger and heavier than females, come ashore and establish breeding territories. They stop eating and defend their territories by constant, violent fighting. They herd harems of as many as 50 females onto their territories and keep other males away (Fig. 9.32). Only the strongest males can hold territories and breed. The others gather into bachelor groups and spend much of their time trying to sneak into harems for a quick copulation. Defending the harem is exhausting work, and dominant males "burn out" after a year or two, making way for newcomers. It nevertheless pays off in the huge number of offspring they leave compared with the males that never reach dominance, even though the subordinate males live longer!

FIGURE 9.33 A California sea lion (Zalophus californianus) with nursing pup.

Female pinnipeds give birth to their pups on shore. They seem to be indifferent to the birth process but soon establish a close relationship with the pup (Fig. 9.33). Because females continue to go to sea to feed, they must learn to recognize their own pups out of all the others by sound and smell. The pups generally cannot swim at birth. They are nursed for periods of four days to two years, depending on the species. Most pinnipeds have two pairs of mammary glands that produce a fat-rich milk ideal for the rapid development of the pup's blubber.

A female pinniped can become pregnant only during a brief period after ovulation, the release of an egg by her ovaries. This occurs just days or weeks after the birth of her pup. Females of most species return to the breeding grounds only once a year. By contrast, gestation, the length of time it takes the embryo to develop, is less than a year. This difference would cause the pup to be born too early, before the mother returns to the breeding ground. To prevent this, the newly formed embryo stops developing and remains dormant in the female's womb, the uterus. After a delay of as long as four months, the embryo finally attaches to the inner wall of the uterus and continues its normal development. This phenomenon, known as delayed implantation, allows pinnipeds to prolong the embryo's development so that the timing of birth coincides with the female's arrival at the safety of shore.



Delayed implantation allows pinnipeds to time the birth of pups with the arrival of pregnant females in breeding areas.

Our knowledge of the reproductive behavior of cetaceans in their natural environment is limited. We do know that cetaceans are intensely sexual animals. Sex play is an important component of the behavior of captive dolphins. Like humans, they appear to use sex not only for procreation, but for pleasure as well. Sexual behavior appears to have a role in the establishment and maintenance of bonds among all individuals, not just potential mates. The sexes are typically segregated within the pod, and males perform elaborate courtship displays to catch the attention of potentially receptive females. Fights among rival males are common, but cooperation also occurs sometimes. Gray whales are known to copulate with the help of a third party, another male that helps support the female (Fig. 9.34a). Group matings have been observed in humpback and white whales. Considerable touching and rubbing is known to precede copulation (Fig. 9.34b). Actual copulation lasts less than a minute but is repeated frequently.

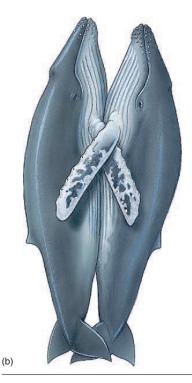
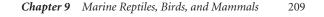


FIGURE 9.34 Mating behavior in great whales. (a) Gray whales (Eschrichtius robustus) often mate with the help of a third party, another male that props the female against the mating male. Actual copulation is reported to last for just 30 to 60 seconds. (b) Courtship in humpback whales (Megaptera novaeangliae) includes rolling, slapping of the flukes, and pairs surfacing vertically face to face.



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**FIGURE 9.35** A Commerson's dolphin (*Cephalorhynchus commersoni*) giving birth in captivity. Not much is known about this dolphin, which is found only in southern South America.

Gestation lasts for 11 or 12 months in most cetaceans. An exception is the sperm whale, which has a gestation period of 16 months. Development in most species of large baleen whales is relatively fast for a mammal of their size. It is synchronized with the annual migration to warm waters. It is remarkable that it takes 9 months for a 3-kg (7-lb) human baby to develop, but a 2,700-kg (3-ton) blue whale calf needs only about 11 months!

The calves of probably all cetaceans are born tail-first (Fig. 9.35). This allows

them to remain attached to the placenta, which provides oxygenated blood from the mother, for as long as possible to prevent oxygen deprivation. The calf immediately swims to the surface. In captive dolphins, the mother or an attending female may help the calf to the surface. Fat-rich milk is responsible for the rapid growth of calves, particularly in the great whales. They are born without their full complement of blubber and must gain weight before migrating with their mothers to feeding grounds in polar waters. It has been estimated that a typical blue whale calf gains 90 kg (200 lb) in weight and 4 cm (1.5 in) in length every day for the first seven months of its life! The mother's milk is produced by two mammary glands with nipples located on both sides of the genital slit (see Fig. 9.15). The milk is squirted into the calf's mouth, which allows the calf to drink underwater. In at least some of the great whales, females do not seem to feed much while they are nursing. The calves are not weaned until they arrive at the feeding grounds. In some species they continue to nurse for more than a year after birth.

The relationship between mother and calf during the nursing period is very close. Frequent contact and vocalizations are used in communication. Mother whales are known to defend their calves when there is danger. There is a report of a female gray whale lifting her calf onto her flipper to save it from the attacks of killer whales. The bond between mother and calf probably lasts for several years. Captive young dolphins are known to return to their mothers for comfort in times of danger or stress.

Cetaceans reach sexual maturity relatively early, at age 5 to 10 in great whales. Most females, however, give birth to only a single calf—occasionally twins—every two or three years. This low birthrate, coupled with extensive hunting, may have already sealed the fate of some of the great whales.

Great whales have been estimated to live at least 30 to 40 years on average. Humpbacks are known to live at least 50 years, bowheads 150 years. Castro–Huber: Marine Biology, Fourth Edition II. Life in the Marine Environment 9. Marine Reptiles, Birds, and Mammals © The McGraw–Hill Companies, 2003



## interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

## **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

## Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

## **Critical Thinking**

- 1. Sea turtles have disappeared from many regions, and one way of trying to save them is to reintroduce them to areas where they have been wiped out. This is done by reburying eggs or by releasing newborn baby turtles on beaches. Why are eggs reburied or baby turtles released instead of fully grown individuals?
- 2. Most seabirds are specialists that feed on particular types of fish and other prey. In some cases this may reduce the chances of competing with other species of seabirds for limited resources. Sometimes, however, we find two or more species of seabirds feeding on the same type of fish. What type of mechanisms might have evolved to prevent direct competition?
- 3. Cetaceans give birth to few well-developed calves at wellspaced intervals. They also feed and protect the calves for long periods. This is in sharp contrast to most fishes, in which many eggs are spawned and the parents spend no time feeding and protecting the offspring. What do you think is the best strategy? Has this effort paid off in the great whales?

## For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol ., and will contain live links when you visit this page in the Online Learning Center.

## **General Interest**

- Chadwick, D. H., 1999. Listening to humpbacks. *National Geographic*, vol. 196, no. 1, July, pp. 110–129. Marine biologists study the migration patterns and social behavior of humpback whales in the Pacific.
- Chadwick, D. H., 2001. Pursuing the minke. *National Geographic*, vol. 199, no. 4, April, pp. 58–71. The most abundant baleen whale, minkes are increasingly being pursued by whalers.

- Chadwick, D. H., 2001. Evolution of whales. National Geographic, vol. 2000, no. 5, November, pp. 64–77. New discoveries have helped us understand how cetaceans evolved from landdwelling mammals.
- Geber, L. R., D. P. DeMaster and S. P. Roberts, 2000. Measuring success in conservation. *American Scientist*, vol. 88, no. 4, July–August, pp. 316–324. Populations of some whales are on the increase while others are not. Perhaps some of the species may not need help from conservation efforts after all.
- Hrynyshyn, J., 2000. The old man of the sea. *New Scientist*, vol. 168, no. 2265, 18 November, pp. 44–46. Some of the few surviving bowhead whales have been shown to be at least 200 years old.
- Kemper, S., 1999. The 'sea canary' sings the blues. Smithsonian, vol. 30, no. 8, November, pp. 86–96. PCBs and other problems threaten endangered populations of beluga whales.
- Levy, S., 1999. What's wrong with the right whale? New Scientist, vol. 164, no. 2211, 6 November, pp. 38–42.Right whales get tangled up in fishing gear or collide with ships.
- Martin, G., 1999. The great white's ways. *Discover*, vol. 20, no. 6, June, pp. 54–61. Video cameras attached to elephant seals help scientists find out when and where great white sharks attack.
- McClintock, J., 2000. Baywatch. *Discover*, vol. 21, no. 3, March, pp. 64–69. A long-running study of dolphins in the wild reveals complex social relationships.
- Motani, R., 2000. Ruler of the Jurassic seas. *Scientific American*, vol. 283, no. 6, December, pp. 52–59. Ichthyosaurs, fish-like reptiles, ruled the seas for 155 million years.
- Nevitt, G., 1999. Foraging by seabirds on an olfactory landscape. *American Scientist*, vol. 87, no. 1, January–February, pp. 46–53. Response to particular odors helps petrels and albatrosses find food in the ocean surface.
- Pitman, R. L. and S. J. Chivers, 1998/1999. Terror in black and white. *Natural History*, vol. 107, no. 9, December/January, pp. 26–29. Killer whales attack a pod of sperm whales off the coast of California.
- Safina, C., 2001. Albatross wanderings. *Audubon*, vol. 103, no. 1, January–February, pp. 70–77. Albatrosses travel thousands of miles over the North Pacific to feed their chicks.

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### In Depth

- Bowen, W. D., 1997. Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series*, vol. 158, pp. 267–274.
- Claphan, P. J., S. B. Young and R. L. Brownell, 1999. Baleen whales: Conservation issues and the status of the most endangered species. *Mammal Review*, vol. 29, pp. 35–60.
- Pauly, D., A. W. Trites, E. Capuli and V. Christensen, 1998. Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science*, vol. 55, pp. 467–481.
- Schreer, J. F., K. M. Kovacs and R. J. O'Hara Hines, 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs*, vol. 71, pp. 137–162.
- Watt, J., D. B. Siniff and J. A. Estes, 2000. Interdecadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. *Oecologia*, vol. 124, pp. 289–298.
- Whitehead, H., 1998. Cultural selection and genetic diversity in matrilineal whales. *Science*, vol. 282, pp. 1708–1711.

## See It in Motion

Video footage of the following animals and their behaviors can be found for this chapter on the Online Learning Center:

- Egret eating (South Carolina)
- Humpback whale slapping pectoral fin (Alaska)
- Humpback whale spouting, diving (Alaska)

#### • Marine iguana (Galápagos Islands)

- Sea otter (Alaska)
- Sea lions (Gulf of California)
- Hawksbill turtle (Belize)
- Manatees (Florida)

## Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Class Reptilia
- Marine turtles
- Order Crocodilia
- Suborder Serpentes
- · Conservation issues concerning reptiles
- Class Aves
- Marine birds
- Conservation issues concerning birds
- Class Mammalia
- Marine mammals
- Resources from the sea

## **Quiz Yourself**

Take the online quiz for this chapter to test your knowledge.

III. Structure and Function of Marine Ecosystems

10. An Introduction to Ecology © The McGraw–Hill Companies, 2003

# An Introduction to Ecology



**E** verywhere you look in the ocean there are living things. How many and what kind of organisms there are depend on where you go—that is, on the specific nature of the **habitat**. Every habitat has distinct characteristics that determine which organisms live there and which do not. The amount of light, for example, determines whether algae and plants can grow. The type of bottom, the temperature and salinity of the water, waves, tides, currents, and many other aspects of the environment profoundly affect marine life. Some of these physical and chemical features were introduced in Chapters 2 and 3.

Equally important are the ways that organisms affect each other. They eat each other, crowd each other out, and even cooperate. Living things interact in complex and fascinating ways. Part Two of this book, Chapters 4 through 9, introduced the organisms that live in the sea. This part, Part Three, looks a little more carefully at how these organisms live and interact. We will explore the different habitats that make up the ocean world, from the water's edge to the darkest depths. We will consider the special physical and chemical features of each habitat, how the organisms have adapted to each environment, and how they affect each other.

Before examining each individual habitat, here in Chapter 10 we briefly examine a few basic principles that apply to all habitats. No matter where you go, for instance, algae and plants need light and animals need food. These are just two examples, though fundamental ones, of the interactions among organisms and their environment. The study of these inter-



Photosynthesizing seaweed, filter-feeding sponge, grazing chiton (black), predatory sea star and nudibranch (yellow), and other organisms on an Alaskan rocky shore.

actions is called **ecology**. It is important to realize that ecology is a science, the branch of biology that studies how and why organisms interact with each other and with their environment. Contrary to the way the term is often used in the media, ecology is not the same as defending the environment, as important as that may be.

# THE ORGANIZATION OF COMMUNITIES

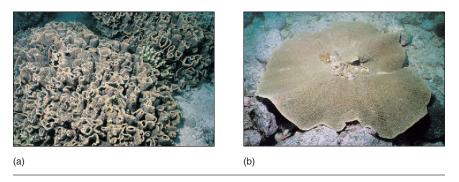
The nature of life in a particular habitat is determined to a large extent by the nonliving, or abiotic, part of the environment, that is, the environment's physical and chemical features such as salinity or bottom type. Each environment makes different demands, and the organisms that live there must adapt to those demands.

Individual organisms can adapt to their environments to some extent through changes in their behavior, metabolism, pattern of growth, and other characteristics

Habitat The natural environment where an organism lives. *Chapter 2, p. 21* 

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#### 216 **Part Three** Structure and Function of Marine Ecosystems



**FIGURE 10.1** These two corals belong to the same species (*Turbinaria mesenterina*). (a) The "normal" growth form occurs in relatively shallow water, where there is plenty of light. (b) In deeper water, with less light, the coral grows in a flattened shape. This flat shape, like that of a solar panel, is an adaptation that increases the coral's ability to capture the sunlight it needs to grow (see "Light and Temperature," p. 303).

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FIGURE 10.2 All species are capable of undergoing population explosions.
(a) When a single-celled dinoflagellate divides, for example, it leaves two daughter cells. Each daughter cell, in turn, produces two new daughter cells, which also divide, and so on. At each generation the number of cells doubles, and the population grows at an everincreasing rate. If this population growth were to continue unchecked, the combined weight of the dinoflagellates would soon exceed the weight of the universe! Imagine the growth potential of organisms that can produce thousands of young instead of just two.
(b) A graph of the number of cells at each generation produces a J-shaped curve, which is typical of populations undergoing unrestrained growth.

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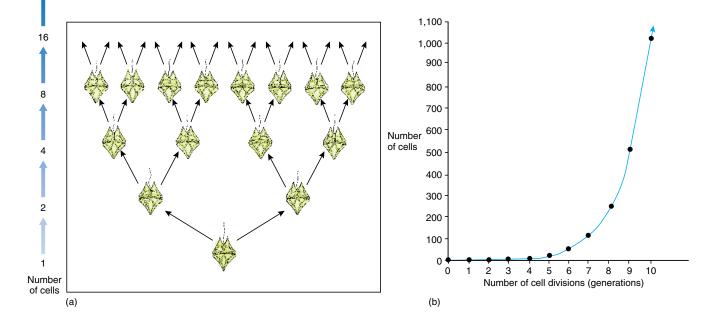
(Fig. 10.1). Over generations, species adapt through **natural selection** for characteristics that are advantageous in their particular habitat, a process known as **evolutionary adaptation**. The chapters that follow highlight some of the remarkable evolutionary adaptations of marine species.

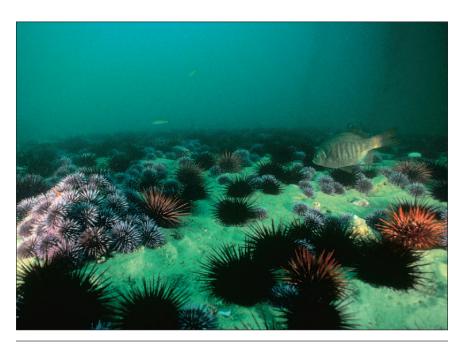
Organisms are also affected by other organisms—the living, or **biotic**, environment. Biological **populations** interact in complex ways that make the organisms in a **community** dependent on each other. Organisms adapt to biotic factors just as they do to abiotic ones.

The nature of a community is determined by both biotic, or living, and abiotic, or non-living, factors.

## How Populations Grow

When the conditions are right, organisms can produce many more offspring than it takes to just replace themselves. If every individual has more than one offspring or each pair has more than two—the total number of offspring increases every generation (Fig. 10.2). The population grows





**FIGURE 10.3** The purple and red sea urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*) of the Pacific coast of North America sometimes undergo population explosions, as do many other species of urchins. These outbreaks can have dramatic effects on the rest of the community.

faster and faster, and there is a population "explosion." Were its reproduction left unchecked, any species could grow to cover the earth in a relatively short time.

Fortunately, we are not up to our necks in dinoflagellates. Though many organisms occasionally undergo dramatic population explosions (Fig. 10.3), reproduction obviously does not continue unchecked forever. Many factors can control, or regulate, the growth of populations. For one thing, explosive population growth can occur only under favorable conditions. When the abiotic environment changes, the population may stop growing or even decline. Some environmental fluctuations are regular and predictable, like the seasons. The growth of algae in temperate and polar regions, for example, often slows dramatically in the winter because there is less light for photosynthesis. Other changes, like a sudden storm or a drifting log that smashes organisms on a rocky shore, are not so predictable. Predictable or not, large or small, changes in the environment can slow the growth of or even wipe out populations.

There are also mechanisms that limit population growth even if the non-living environment doesn't fluctuate. Some animals slow down or stop reproduction when their habitat becomes too crowded. Others fight among themselves or even cannibalize each other. Natural enemies may be attracted when the population gets large, and diseases often spread faster under crowded conditions. Large populations can pollute the environment with their own wastes.

As more and more individuals join the population, they use up their **resources**, the things they need to live and

**Natural Selection** The production of more offspring by the best-adapted individuals in a population.

Chapter 4, p. 84

**Population** A group of individuals of the same species that live together. **Community** All the different populations of organisms that live in the same place.

Chapter 4, p. 76

reproduce, like food, **nutrients**, and living space. Eventually there are just not enough resources to support any more individuals and the population levels off (Fig. 10.4). The largest population size that can be sustained by the available resources is called the **carrying capacity**.

Organisms use many different resources. A lack of any of these will slow or prevent growth and reproduction. A dinoflagellate living in the open ocean, for example, can be limited by a lack of nitrate  $(NO_3^{-1})$ , even if it has plenty of light, water, carbon dioxide (CO<sub>2</sub>), and other nutrients. During the winter in polar regions, there may be plenty of nitrate but not enough light. Seaweeds on a rocky shore, on the other hand, might have plenty of light and nutrients but be unable to grow because there is no space left. A **limiting resource** is one whose short supply restricts the growth of a population.

Because of the drain of resources or other effects of crowding, populations do not grow forever. As the population becomes more crowded, its *growth rate* goes down. In this sense the population is **selfregulating;** that is, its growth rate depends on its own numbers. Whereas non-living factors such as the weather can affect populations of any size, self-regulation acts only when the population is large.

Populations are capable of explosive growth. Population growth is usually limited, however, by either the non-living environment or by the activities of the organisms themselves.

As resources are depleted, there are not enough to go around. Each individual has to vie with other organisms for what resources remain. **Competition** is

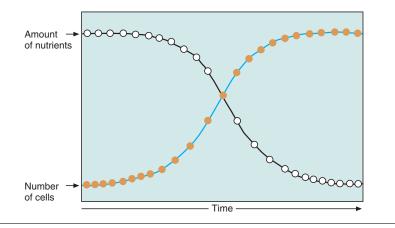
**Ecosystem** A community, or interacting communities, plus the physical environment in a large, more or less self-contained area.

#### Chapter 4, p. 77

**Nutrients** Raw materials other than carbon dioxide and water that are needed by primary producers for primary production.

Chapter 4, p. 74

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**FIGURE 10.4** The kind of explosive population growth shown in Figure 10.2 would never go on forever. As the dinoflagellates get more and more numerous, they use up the nutrients and other resources that they need to grow and reproduce. Curves like this are often observed in laboratory experiments, but in the real world they are rarely so smooth.



**FIGURE 10.5** A short supply of any resource can lead to competition. Hermit crabs rely on abandoned snail shells for protection. They must move into new shells as they grow or as their old shells get worn, and sometimes there aren't enough shells to go around. These European hermit crabs (*Pagurus bernhardus*) both want the same shell and are fighting over it.

the interaction that results when a resource is in short supply and one organism uses the resource at the expense of another (Fig. 10.5). When members of the same species compete it is called **intraspecific competition**.

Those who compete successfully survive to replace themselves by reproducing. The poorer competitors do not reproduce as successfully and eventually disappear. In this way nature favors the members of the population that are best suited to the environment. Because of this natural selection, the population as a whole is, on average, a little better adapted each generation. In other words, the population **evolves**. www.mhhe.com/marinebiology

## Ways That Species Interact

Species do not live in a vacuum, isolated from other species. Members of different species may have strong effects on each other. Species can interact in many ways, all of which influence the organization of communities.

### Competition

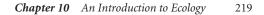
Organisms must compete for resources not only with members of their own species, but with members of other species. Competition between species is known as **interspecific competition**.

When two species use the same resource and the resource is scarce, the species must compete just as if they were members of the same population. One of the two species almost always turns out to be a little better in the competition. If two species eat exactly the same food, for example, one of the two will be better at catching it. Unless something interferes, the inferior competitor loses out and the competitively superior species takes over. When one species eliminates another by outcompeting it, **competitive exclusion** is said to occur.

Competition between species results when both species have the same limiting resource. In competitive exclusion, one species wins the competition and eliminates the other from the community.

Sometimes a competitively superior species is prevented from excluding poorer competitors. The superior species might have natural enemies that keep it from taking over, for example. This gives the lesser competitors a chance. Furthermore, which species is superior might depend on the conditions. In summer, for example, one species might do better, but the other species might dominate in winter. As long as the conditions are variable, neither species will be able to exclude the other. Thus, there may be a shifting balance between competing species.

Species can also avoid excluding each other if they manage to share the limiting resource, with each species specializing on just part of the resource. For example, two species of fish that eat seaweeds





**FIGURE 10.6** The whale shark (*Rhiniodon typus*) feeds by straining plankton from huge mouthfuls of water. It has probably evolved a huge mouth and lost the large teeth of most other sharks not to avoid competition with other sharks but as adaptations for efficient plankton feeding.

might divide the resource by specializing on different kinds of seaweed. Animals that eat exactly the same thing might live in different places or feed at different times, staying out of each other's way. Ecologists call this sharing of a resource by specialization **resource partitioning**.

Species that might otherwise competitively exclude each other sometimes coexist by resource partitioning, or dividing the resource.

Resource partitioning allows species to coexist when they might otherwise exclude each other, but it does have its price. By specializing, each species gives up some of the resource. The fish that specializes on just one kind of seaweed, for example, will have less food available than if it ate all types. With fewer resources available, the size of the population tends to be smaller. On the other hand, the species might be able to use the resource more efficiently by being a specialist than if it were a "jack-of-all-trades." Different species of shorebirds, for example, have specialized bill shapes that make them more efficient at feeding upon particular types of mudflat animals (see Fig. 12.12) and may also reduce competition. Not all specializations, however, are a result of interspecific competition (Fig. 10.6).



**FIGURE 10.7** A killer whale (*Orcinus orca*) attacks a southern elephant seal (*Mirounga leonina*). Killer whales are one of the ocean's most widely distributed predators.

To be successful in the long run, a species must find the right balance between specialization and generalization. There is no one best answer to the problem—just look at all the different kinds of organisms. Each species has its own special role, or **ecological niche**, in the community. A species' niche is defined by the combination of virtually every aspect of its lifestyle: what it eats, where it lives, when and how it reproduces, how it behaves, and so on.

The role a species plays in the community is called its ecological niche. The niche includes feeding habits, habitat, and all the other aspects of the species' lifestyle.

### Eating Each Other

Species don't always compete for resources. Sometimes they use each other as the resource. In other words, they eat each other (Fig. 10.7). **Predation** is the act of one organism eating another. The organism that does the eating is the **predator**, and the organism that gets eaten is the **prey**. The term "predator" is often reserved for **carnivores**, animals that eat other animals. A special case of predation occurs when organisms eat algae or plants. This is usually called **herbivory** rather than predation, and the organism doing the eating is called an **herbivore.** No matter what you call it, the alga or plant gets eaten just the same.

Predation obviously affects the individual organism that gets eaten. It also affects the prey population as a whole by reducing the number of prey. If the predators don't eat too much, reproduction by the prey population can replace the individuals that have been eaten. If predation is intense, however, it can greatly reduce the prey population.

The interaction between predator and prey is not a one-way street. After all, the predator depends on the prey for its food supply. If bad weather or disease wipes out the prey, the predators suffer as well. Prey populations can also decline if there are too many predators or the predators eat too much. In this case the predator population soon starts to decline, having used up its food supply.

**Evolution** A change in the genetic makeup of a population, usually resulting when natural selection favors some individual characteristics over others.

Chapter 4, p. 84

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FIGURE 10.8 The sargasso fish (*Histrio histrio*) is beautifully adapted to blend in with the fronds of floating sargasso weed (*Sargassum*) in which it lives. Presumably its camouflage makes it harder for predators to see the fish.

Predation, which occurs when an animal eats another organism, affects the numbers of both predator and prey.

The most successful individual predators catch more food, and therefore tend to survive longer, grow faster, and produce more offspring. Natural selection, therefore, favors the most efficient predators in the population. Each generation will be a little better at capturing its food.

A tremendous variety of predatory strategies have evolved. Sharks and tunas are highly efficient killing machines, swift and powerful. Other predators sneak up on their prey, catching them unaware. Predators such as anglerfishes go a step further and lure their prey. Many snails can drill through the shells of their prey, and many sea stars evert their stomachs to digest prey outside their bodies (see "Feeding and Digestion," p. 145). Many predators eat only part of the prey, leaving the rest alive to continue growing. In the following chapters we will examine some of the many ways that predators catch their prey.

Just as natural selection favors the best predators, it also favors the prey individuals that are most successful at getting away. Organisms have evolved at least as many ways to escape from predators as there are predators. Some are fast and elusive, others use camouflage (Fig. 10.8). Organisms may have protective spines, shells, or other defensive structures. Many seaweeds and animals protect themselves with distasteful or even poisonous chemicals.



**FIGURE 10.9** Some barnacles live only on the skin of whales. Because they do not appear to affect their host at all, most such barnacles are considered to be commensals.

Some organisms use their defenses against predators only when they need them. Certain barnacles, for example, normally grow upright, but when predatory snails are around they grow bent over. This makes it more difficult for the snails to get through the covering plates on the barnacles' upper surface to eat them. Some algae that use chemical defenses only produce the nasty chemicals after they have been damaged. Thus, they don't waste energy making the chemicals when they are not needed. Defense mechanisms that are used only in response to predators are called **inducible defenses**.

Thus, there is a continual "arms race" between predators and their prey. The predator keeps getting better at catching the prey and overcoming its defenses. In response, the prey becomes more adept at escaping or develops better defenses. This interplay, with each species evolving in response to the other, is known as **coevolution**.

### Living Together

Coevolution becomes even more important when species interact more intimately. Members of different species may live in very close association, even with one inside another (see "From Snack to Servant: How Complex Cells Arose," p. 77). Such close relationships are examples of **symbiosis**, which literally means "living together." The smaller partner in the symbiosis is usually called the **symbiont** and the larger one the **host**, though sometimes the distinction is unclear.

Biologists traditionally divide symbiosis into different categories according to whether the organisms involved benefit or suffer from the relationship. In commensal relationships, one species obtains shelter, food, or some other benefit without affecting the other species one way or the other. For example, certain barnacles live only on whales (Fig. 10.9). The barnacles get a place to live and a free ride. They feed by filtering the water, and as far as we can tell the whale is neither harmed nor helped by the barnacles. There are many other examples of symbiotic organisms that live on, or even in, a host without apparently either hurting or helping it (see Fig. 7.33).

On the other hand, sometimes the symbiont benefits at the expense of the host (Fig. 10.10). This is called **parasitism**. The giant tapeworms that live in the guts of whales (see "Flatworms," p. 124) are considered parasites because they derive food and shelter from their whale hosts and may weaken them. Marine parasites are very common. In fact, few marine species escape having at least one type of parasite.

Not all symbiotic relationships are one-sided. In **mutualism**, both partners benefit from the relationship. In many

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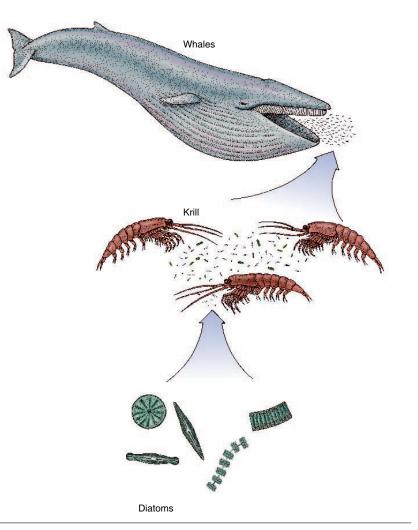
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**FIGURE 10.10** The isopod (*Anilocra*) just below the eye of this coney (*Cephalopholis fulva*) is a blood-sucking parasite of fishes.

places, small cleaner fishes and shrimps have mutualistic relationships with larger fishes known as **cleaning associations** (see "Cleaning Associations," p. 224).

In the case of cleaning associations, both partners can get by without the other if they have to. Sometimes the partners depend on each other. The colorful crab shown on page 117, for example, is found nowhere else but on its host coral. The coral supplies not only shelter but also food, by producing the mucus that the crab eats. Even though the coral isn't really dependent on the crab, it benefits because the crab helps chase away sea stars and other coral predators.



**FIGURE 10.11** This three-step food chain is typical of Antarctic waters. The main primary producers are diatoms, which capture sunlight to fix carbon. The energy is transferred from the diatoms to the krill that eat them, and then to blue whales that eat the krill. Though only part of a complex food web (see Fig. 10.12), this simple food chain accounted for a great deal of the total productivity of Antarctic waters until whales were hunted nearly to extinction.

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The coral provides an example of an even closer relationship, one in which neither partner can live without the other. The tiny **zooxanthellae** that live within its tissues help the coral make its calcium carbonate (CaCO<sub>3</sub>) skeleton. The zooxanthellae also make food for the coral by photosynthesis. The zooxanthellae, in turn, get both nutrients and a place to live.

In symbiosis, members of different species live in close association. Symbiosis includes parasitism, in which the symbiont harms the host, commensalism, in which the host is not affected, and mutualism, in which both partners benefit.

In practice, it may be very difficult to tell whether the partners in a symbiotic relationship are helped or harmed. Some biologists prefer to emphasize the movement of energy or of food or other materials between the partners, without reference to possible harm or benefit.

# THE FLOW OF ENERGY AND MATERIALS

All living things use energy to make and maintain the complex chemicals necessary for life. **Autotrophs** get this energy from the non-living environment, usually in the form of sunlight. They use the energy to make their own food from simple molecules like carbon dioxide, water, and nutrients. As the autotrophs grow and reproduce they become food for **heterotrophs** (Fig. 10.11). When one organism eats another, both the organic material and the energy stored in it are passed from one to the other. Thus, energy and chemical

**Zooxanthellae** Photosynthetic dinoflagellates that live in animal tissues. *Chapter 5, p. 99* 

Autotrophs Organisms that can use energy (usually solar energy) to make organic matter.

**Heterotrophs** Organisms that cannot make their own food and must eat the organic matter produced by autotrophs.

Chapter 4, p. 72

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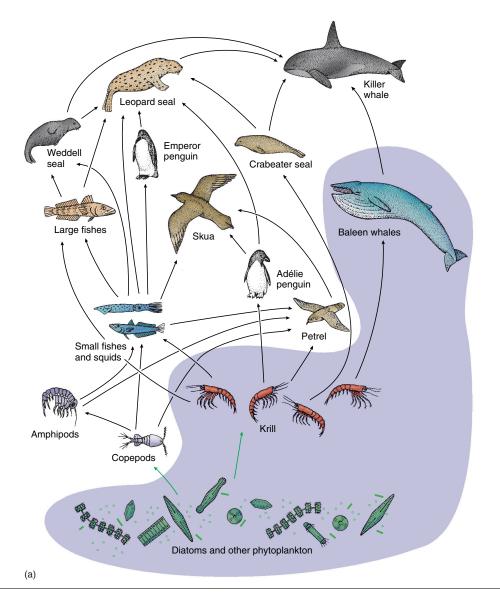


FIGURE 10.12 (a) A simplified Antarctic food web. The simple diatom-krill-whale chain illustrated in Figure 10.11 is an important part of this food web (blue shading). (Continued)

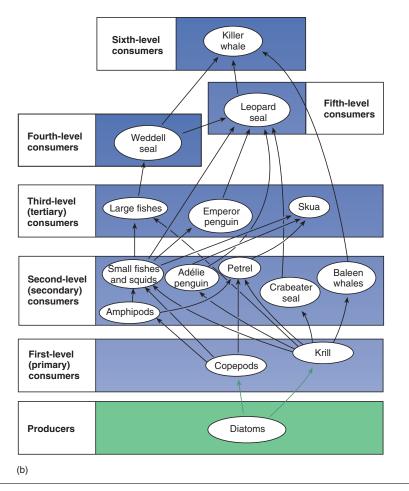
substances flow from the non-living part of the ecosystem to organisms and from organism to organism. The pathways taken by energy and materials tell us a lot about how an ecosystem works.

# **Trophic Structure**

The flow of energy and matter through an ecosystem can be traced by observing the nutritional, or **trophic**, relationships

among its organisms: who makes the food and who eats it. The organisms can be divided into two broad components: **primary producers**, the autotrophs that make the food, and **consumers**, the heterotrophs that eat it. Not all consumers feed directly on producers. Many animals eat other animals rather than primary producers. Thus, the transfer of energy through the system usually takes place in several steps known as a **food chain** (see Fig. 10.11). Each of the steps in the food chain is known as a **trophic level.** 

Most ecosystems have a number of different primary producers. Furthermore, many animals eat more than just one kind of food, and many change their diet as they get older and larger (see Fig. 15.23). For these reasons, trophic structure is usually a complex, interwoven **food web** (Fig. 10.12) instead of a simple, straightline food chain. Such food webs are often



**FIGURE 10.12** (*b*) The organisms in the food web can be grouped into categories according to their trophic level. The same organism, however, may feed at different levels. Petrels, for example, act as second-level consumers when they eat copepods but as third-level consumers when they eat amphipods. In this simplified diagram they are shown as second-level consumers. The food web shown here is longer than most; three or four levels are more common.

difficult for biologists to unravel and understand, but their complexity is one reason for the tremendous diversity of life.

Energy and materials are passed from one trophic level to another along a food chain or food web. The first level is occupied by primary producers, the other levels by consumers.

### **Trophic Levels**

Food chains and food webs are a little easier to understand if we consider how many steps, or trophic levels, through which the energy has traveled. The first step in the flow of energy, and therefore the first trophic level, is occupied by the primary producers that originally capture the energy and store it in organic compounds. Diatoms are the main primary producers in the food web illustrated in Figure 10.12. Consumers that feed directly on the producers are called **firstlevel**, or **primary**, **consumers**, and occupy the next trophic level. At the level above that are **second-level**, or **secondary**, **consumers**, predators that eat the primary consumers. Feeding on the secondary consumers are the **third-level**, or **tertiary**, **consumers**, and so on. Each trophic level relies on the level below for sustenance. At the end of the food web are **top predators** such as the killer whales in Figures 10.7 and 10.12.

The concept of trophic levels helps us understand how energy flows through ecosystems, but the organisms themselves are not especially concerned about which level they feed at. Predators commonly feed on prey from different trophic levels, for example.

### The Trophic Pyramid

Instead of being passed on to the next higher level, much of the energy contained in a particular trophic level is used up by the activities of the organisms. Energy and organic matter are also lost as waste. Depending on the ecosystem, between about 5% and 20% of the energy in one trophic level is passed on to the next; an average is about 10%. Suppose, for example, that the diatoms in the Antarctic food chain illustrated in Figure 10.11 contain a total of 10 million calories of energy. According to the 10% rule, only about 1 million calories will make it to the primary consumers, the krill, and the whales will get only about 100,000 calories. The trophic structure of ecosystems can be represented by a pyramid of energy (Fig. 10.13), with less energy contained in each succeeding level.

Because there is less energy available at each level, there are also fewer individual organisms. Thus, there are fewer primary consumers than producers, and fewer secondary than primary consumers. Often, though not always, the trophic pyramid can be pictured in terms of numbers of individuals as well as energy and is then called the **pyramid of numbers** (see "Standing Stock," p. 226). The pyramid can also be expressed in terms of the total weight of tissue, or

**Primary Production** The conversion of carbon dioxide into organic matter by autotrophs, that is, the production of food. *Chapter 4, p. 73* 

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# CLEANING ASSOCIATIONS

Marine organisms have developed some novel approaches to the art of survival while getting along with neighbors—especially big, hungry ones. The fishes and shrimps that specialize in **cleaning associations** are a good example. These small, colorful marine animals make a living by picking parasites and diseased tissue off larger fishes. Although especially common in very crowded environments such as coral reefs, cleaning associations have evolved in many other subtidal communities.

Several species of wrasses, butterflyfishes, gobies, and other fishes display cleaning behavior. The banded coral shrimp (*Stenopus hispidus*) is among the most well known of the cleaning shrimps. This cleaning behavior can be either a full-time or part-time job. Some cleaners do it all their lives, others only as juveniles.

To attract customers, cleaners set up a "cleaning station," usually marked by prominent features like a large sponge or a conspicuous coral head or rock. The cleaners also advertise their services with characteristic bright colors and distinctive stripes. Hosts, as the larger fishes are known, congregate at the cleaning stations: Getting cleaned of parasites and dead skin is a popular service. The host fishes learn where the stations are and will continue to congregate there even if the cleaners are experimentally removed.

Many of the hosts are carnivores that can easily swallow a cleaner in one gulp. They are, however, willing to cooperate and forgo an easy meal in exchange for being cleaned. To signal their good intentions, many host fishes swim unusually slowly, hovering in midwater. Some change color, or assume unusual postures: "standing" head up, tail up, or with the body turned at an angle. Cleaner fishes approach the host and inspect it by swimming close to the host. Some of them "dance" as part of the ritual, perhaps to remind the host that they are cleaners and not food. Cleaner shrimps use their antennae, tapping the host. Once the cleaning starts, the hosts remain still to allow the cleaners to pick at their skin and fins. They often open their gill covers to allow the cleaner to inspect and clean their gills. The cleaner can even swim inside the mouth without mishap, at least most of the time.

Cheating and

communication lapses

between hosts and



A cleaning wrasse (*Labroides*) doing its job on a moray eel (*Gymnothorax*).

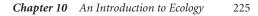
cleaners are surprisingly rare. This probably indicates that the arrangement benefits both parties. Hosts that confuse cleaning stations with fast-food stands might suffer from parasites. The experimental removal of cleaners, however, does not seem to harm resident fishes, so this benefit to the hosts is uncertain. The cleaners benefit from a steady supply of food, with little competition from other species. The benefits of this must outweigh the risks, even for part-time cleaners that can feed on something else. Furthermore, being recognized as a cleaner reduces the chances of being eaten by another fish.

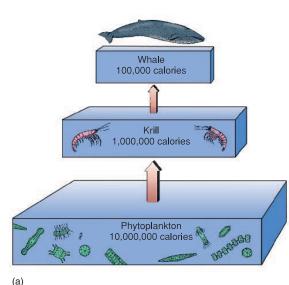
There is one species, however, that takes advantage of the system. A small Caribbean fish, a blenny, has a color pattern that closely imitates, or mimics, a local cleaner wrasse. It also mimics the behavior of the cleaner, tricking host fishes into approaching the blenny in search of a cleaning. The fake cleaner gives them a nasty surprise, biting off a piece of skin and darting to safety with its illgotten meal!

biomass, produced by the organisms at each level. In this case, the trophic pyramid is called the **pyramid of biomass**. To support a given biomass of primary consumers, primary producers must make about 10 times as much living tissue. To support 1,000 grams of copepods, for example, about 10,000 grams of phytoplankton must be eaten. In turn, only about onetenth of the primary consumer's biomass will make it to the secondary consumers.

On the average, only about 10% of the energy and organic matter in one trophic level is passed to the next higher level.

At each step in the food web some organic matter is lost rather than being eaten by higher-level consumers. This material is not lost to the ecosystem, however. Bacteria, fungi, and other decomposers break down this non-living organic matter into its original components: carbon dioxide, water, and nutrients. Some of this organic matter is excreted as waste, is spilled during feeding, or leaks out of cells through diffusion. This material dissolves in the water, so it is known as dissolved organic matter (DOM). There is also a lot of dead organic matter in solid form, such as decaying seaweeds, cast-off seagrass and mangrove leaves, discarded exoskeletons, and dead bodies. This material is called **detritus**. Detritus is an important energy pathway in marine ecosystems because many marine organisms feed on it. Large populations of microscopic decomposers live in association with detritus, and detritus feeders often derive as much or more nutrition from these decomposers as from the detritus itself. Similarly, many organisms eat the microorganisms that decompose DOM. Thus, decomposers play a vital role in the ocean by channeling dead organic matter back into the food web.





(u)

**FIGURE 10.13** (*a*) Although the figure varies, an average of 90% of the energy that primary producers capture in photosynthesis is lost at each step up the food chain. (*b*) This relationship is often depicted as a pyramid representing the amount of energy, the numbers of individuals, or the biomass at each trophic level. Regardless of its form, the idea remains the same: It takes a lot of energy, numbers, and biomass at the bottom to support just a little at the top.

Waste organic matter that is dissolved in the water is called dissolved organic matter (DOM). Detritus consists of non-living, solid organic matter. Decomposers help channel DOM and detritus back into the food web.

If it were not for decomposers, waste products and dead bodies would accumulate instead of rotting away. Not only would this make quite a mess, nutrients would remain locked up in the organic matter. When decomposers break down organic matter, the nutrients incorporated into the organic matter during primary production are released, making the nutrients available again to photosynthetic organisms. This process is known as nutrient regeneration. Without it, nutrients would not be recycled and made available to autotrophs, and primary production would be greatly limited.

### Measuring Primary Productivity

Because primary production supplies the food at the base of the trophic pyramid, it is useful to know how much production occurs in a given area. The rate of primary production, or **productivity**, is expressed as the amount of carbon fixed under a square meter of sea surface in a day or in a year (Fig. 10.14). It includes the production of both phytoplankton in the water column and producers that live on the bottom.

To measure primary production, biologists determine either the amount of raw materials used up in photosynthesis or the amount of end products given off. **Photosynthesis** produces oxygen  $(O_2)$  and consumes carbon dioxide  $(CO_2)$ , so photosynthesis can be estimated by measuring how much oxygen is produced or carbon dioxide used up in a given period of time.

Primary production was traditionally measured by placing water samples in bottles and determining the amount of oxygen produced. Usually two bottles were used: a clear one and one that is opaque—painted black, covered with foil, or made of dark glass. To understand the need for this "light-dark bottle" technique, you must remember that all organisms, including phytoplankton, constantly use up energy to stay alive. To provide this energy primary producers must perform **respiration**, using up oxygen, even

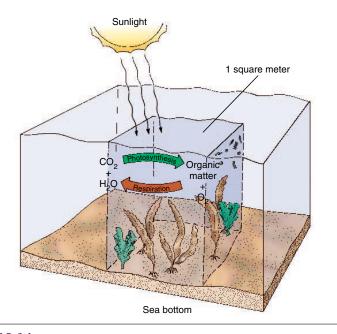
**Photosynthesis**  $CO_2 + H_2O + sun$ energy  $\rightarrow$  glucose +  $O_2$ *Chapter 4, p. 71* 

**Respiration** Glucose  $+ O_2 \rightarrow CO_2 + H_2O + energy$ *Chapter 4, p. 72* 

(b)

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**FIGURE 10.14** To describe primary productivity, marine biologists figure out how much carbon ends up being fixed, or converted from carbon dioxide to organic material, in the water column under 1 m<sup>2</sup> of sea surface in a given time. Primary productivity is thus expressed in units of grams of carbon per square meter per day or year ( $gC/m^2/day$  or  $gC/m^2/year$ ).

while they are photosynthesizing. A water sample will also contain heterotrophs that consume oxygen in respiration. Thus, changes in oxygen in the light bottle reflect the amount produced by photosynthesis minus the amount taken up by respiration (Fig. 10.15). To measure photosynthesis, the amount used by respiration must be known. Respiration is estimated from the amount of oxygen consumed in the dark bottle. There is no light in the dark bottle so there can be no photosynthesis. Any change in the oxygen level must be due to respiration. The oxygen produced in the light bottle is then corrected for the rate of respiration, and the net rate of photosynthesis is calculated.

A more modern method measures the amount of carbon dioxide used by phytoplankton. This method uses an **isotope** of carbon (<sup>14</sup>C) that can be measured very accurately. The principle is the same as when oxygen is measured.

The rate of primary production is usually measured in light and dark bottles. Changes in the oxygen or carbon dioxide level in the light bottle indicate both photosynthesis and respiration, whereas changes in the dark bottle reflect only respiration.

In the ocean the amount of primary production varies dramatically from one environment to the other (Table 10.1). Some marine environments are as productive as any on earth. Others are biological deserts, with productivity as low as any desert on land. Productivity in the ocean depends largely on the physical characteristics of the environment, in particular on the amount of light and nutrients that are available. These characteristics will be explored in the following chapters.

#### Standing Stock

The total amount of phytoplankton in the water, or the **standing stock**, or **standing crop**, of phytoplankton, is related to the primary productivity, but the two are not the same thing. The standing stock refers to how much phytoplankton

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is already in the water. Primary productivity refers to the amount of new organic material being created. In a lawn, for example, the standing stock would correspond to the length of the grass. The primary productivity would be the amount of clippings produced if the lawn were mowed every day to keep it the same length.

This difference between primary productivity and standing stock explains why the trophic pyramid is not always reflected in a pyramid of numbers (see "The Trophic Pyramid," p. 223). A lawn that is growing very fast will produce a lot of clippings even if it is kept short. In other words, it can have high productivity but low standing stock. In the ocean, it often happens that when primary producers are growing very fast they are also eaten very fast. With lots of food available, the population of herbivores grows, keeping the number of primary producers low. As a result, the pyramid of numbers is turned upside down, with more herbivores than primary producers. The pyramid of biomass refers to the productivity, not the standing stock, so like the pyramid of energy the pyramid of biomass always holds true.

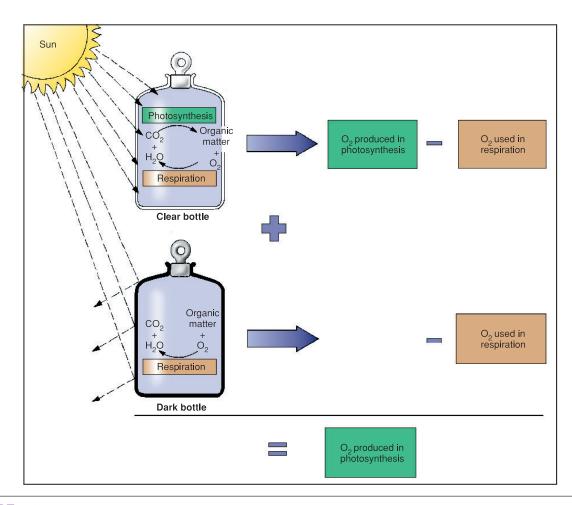
Phytoplankton contain **chlorophyll**, so the amount of chlorophyll in the water is a good indication of the amount of phytoplankton. Indeed, the most common way to measure the phytoplankton standing stock is to measure the concentration of chlorophyll in the water.

The standing stock of phytoplankton is the total amount of phytoplankton in the water column. Standing stock is usually determined by measuring the chlorophyll concentration.

Chlorophyll can be measured by chemically extracting it from the water, but this is time-consuming and expensive. Instead, an instrument called a fluorometer is usually used. Under certain kinds of light, chlorophyll emits a glow, or fluorescence; the amount of chlorophyll can be determined by measuring this fluorescence.

Phytoplankton standing stock can also be measured from space. Satellites equipped with special cameras take color

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**FIGURE 10.15** To measure primary production, scientists put water samples into both light and dark bottles. In the light bottle both photosynthesis and respiration take place. In the dark bottle there can be only respiration. The production from photosynthesis alone is determined by combining the results in the two bottles.

pictures of the sea surface and beam the images down to earth. Using computers, scientists carefully analyze the photos, paying special attention to the characteristic green color of chlorophyll. Phytoplankton standing stock can be estimated over vast areas of the sea surface (Fig. 10.16) by applying various correction factors, taking account of the weather at the time the photo was taken, and relating the results to actual chlorophyll measurements made from ships. Satellites are the only means for assessing the large-scale distribution of phytoplankton; ships can measure standing stock at only one place at a time.

# Cycles of Essential Nutrients

Once the energy that is stored in organic compounds is used in metabolism or given off as heat, it is lost to the system forever. Unlike energy, the *materials* that make up organic matter can be used over and over in a repeating cycle. These materials, like carbon, nitrogen, and phosphorus, originally come from the atmosphere, the earth's interior, or the weathering of rocks. Starting out as simple inorganic molecules, they are converted into other forms and incorporated into the tissues of autotrophs. When this organic material is broken down by digestion, respiration, and decomposition, the raw materials are released back to the environment, and the cycle begins again.

**Isotopes** Different atomic forms of an element.

Chapter 2, p. 35

**Chlorophyll** A green pigment that absorbs light energy for photosynthesis. *Chapter 4, p. 72* 

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# Table 10.1

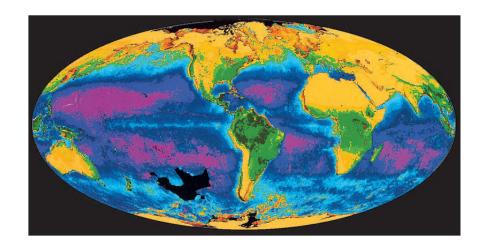
Typical Rates of Primary Production in Various Marine Environments\*

| Environment                  | Rate of Production<br>(grams of carbon fixed/m <sup>2</sup> /yr) |
|------------------------------|--|
| Pelagic Environments         |  |
| Arctic Ocean                 | < 1-100  |
| Southern Ocean (Antarctica)  | 40–260   |
| Subpolar seas                | 50-110   |
| Temperate seas (oceanic)     | 70–180   |
| Temperate seas (coastal)     | 110–220  |
| Central ocean gyres**        | 4–40   |
| Equatorial upwelling areas** | 70–180   |
| Coastal upwelling areas**    | 110-370  |
| <b>Benthic Environments</b>  |  |
| Salt marshes                 | 260-700  |
| Mangrove forests             | 370–450  |
| Seagrass beds                | 550-1,100  |
| Kelp beds                    | 640–1,800  |
| Coral reefs                  | 1,500–3,700  |
| Terrestrial Environments     |  |
| Extreme deserts              | 0-4  |
| Temperate farmlands          | 550-700  |
| Tropical rain forests        | 460–1,600  |
|                              |  |

\*Production rates can be much higher at certain times or in specific locations, especially at high latitudes. Values for some selected terrestrial environments are given for comparison.

\*\*See Chapter 15.

**FIGURE 10.16** A global view of the distribution of primary producers on earth. The parts of the ocean with the highest amounts of phytoplankton pigment are shown in red and yellow; dark blue and violet represent areas with the lowest phytoplankton concentration. Note that phytoplankton are scarce over much of the ocean's surface. On land, desert and ice areas are shown in yellow, while the most productive forests are in dark green.



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The carbon cycle provides a good example of this process (Fig. 10.17). The carbon that forms the backbone of all organic molecules starts in the atmosphere as carbon dioxide, then dissolves in the ocean. This inorganic carbon is converted into organic compounds by photosynthesis. Respiration by consumers, decomposers, and the producers themselves breaks down the organic compounds and makes the carbon dioxide available to producers again. Some carbon is also deposited as calcium carbonate in biogenous sediments and coral reefs. Under certain conditions, some of this calcium carbonate dissolves back into the water.

Nitrogen, like carbon dioxide, is present in the atmosphere. Atmospheric nitrogen, however, is in the form of nitrogen gas (N<sub>2</sub>), which most organisms are unable to use. A few types of cyanobacteria, other bacteria, and archaea are able to convert nitrogen gas into forms that can be used by algae, plants, and other photosynthetic organisms. This conversion process is known as **nitrogen fixation**, and the organisms that perform it are called **nitrogen fixers**. Without nitrogen fixers, algae and plants would be unable to obtain the nitrogen they need to grow and reproduce.

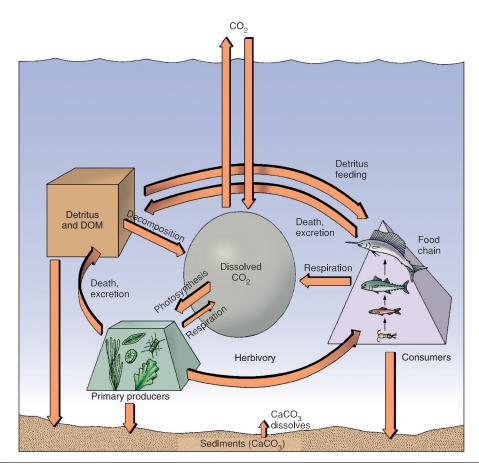


FIGURE 10.17 The carbon cycle in the ocean. Carbon dioxide  $(CO_2)$  from the atmosphere dissolves in the ocean. In photosynthesis, primary producers convert carbon dioxide into organic matter, which is then passed to animals and other consumers in the food chain. Both producers and consumers release carbon dioxide as a product of their respiration. The rest of the carbon fixed by autotrophs is eventually either excreted as waste or ends up in the form of dead bodies. This non-living organic matter forms detritus and dissolved organic matter (DOM). Bacteria and other decomposers break down this organic matter, releasing carbon dioxide and starting the cycle anew.

Nitrogen fixation is the conversion of atmospheric nitrogen gas into a form that organisms can use. It is performed by certain cyanobacteria, other bacteria, and archaea.

Once nitrogen has been fixed, it cycles within the ecosystem as part of the **nitrogen cycle** (Fig. 10.18). There are several nutrient forms of nitrogen, the most important of which is **nitrate**  $(NO_3^{-1})$ . Nitrate and other nitrogen compounds are taken up during primary production and regenerated by decomposition. Most of the nitrogen-containing nutrients used in primary production

come from this recycling of nitrogen compounds, not the original fixation of nitrogen.

The other raw materials needed by organisms, like phosphorus and silicon, undergo similar cycles. The tremendous abundance and diversity of living things depend on this recycling. Without it, the living world would soon run out of raw materials, and life on earth would be scarce indeed.

The living world depends on the recycling of materials such as carbon, nitrogen, and phosphorus. Decomposition is a vital part of this cycle.

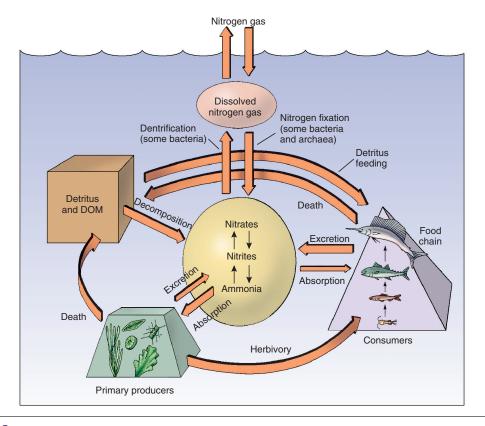
# ECOLOGICAL ZONATION OF THE MARINE ENVIRONMENT

It has already been noted that, because physical and chemical conditions change from place to place, different parts of the

**Biogenous Sediment** Made of the skeletons and shells of marine organisms. *Chapter 2, p. 33* 

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**FIGURE 10.18** The nitrogen cycle in the ocean. The atmosphere is rich in nitrogen gas  $(N_2)$ , which cannot be used by most organisms. Some cyanobacteria, other bacteria, and archaea convert  $N_2$  into usable forms of nitrogen by the process of nitrogen fixation. There are several different forms of usable nitrogen; various bacteria and archaea convert nitrogen from one usable form to another. Primary producers take up the usable nitrogen may be excreted as waste by producers and consumers or regenerated by decomposing bacteria.

ocean harbor very distinct communities. For convenience, marine biologists categorize communities according to where and how the organisms live. Perhaps the simplest classification relates to the lifestyle of the organism: whether it lives on the bottom or up in the water column. **Benthic organisms**, or the **benthos**, are those that live on or buried in the bottom (Fig. 10.19). Some benthic organisms are **sessile**, or attached to one place; others move around. **Pelagic** organisms, on the other hand, live up in the water column, away from the bottom.

Pelagic organisms are further subdivided according to how well they can swim. Some marine organisms swim only weakly or not at all. These organisms, called **plankton**, are at the mercy of the currents and are carried from place to place. The term "plankton" comes from the Greek word for "drifters." Planktonic algae and other autotrophs are collectively called the **phytoplankton** and are the most important primary producers in many marine ecosystems. The heterotrophic plankton are called the **zooplankton**.

Animals that can swim well enough to oppose the currents are called the **nekton.** Most nektonic animals are vertebrates, mainly fishes and marine mammals. There are a few nektonic invertebrates, however, such as squids. Not all nekton are pelagic. The ray in Figure 10.19, for example, is part of the nekton because it can swim. It is not considered pelagic, however, because it spends most of its time on or just above the bottom rather than up in the water column.

Another way to classify marine communities is by the part of the ocean in which they live. Zonation in benthic organisms, for example, relates to depth and the continental shelf (Fig. 10.20). Right at the boundary between land and sea is the shallowest part of the shelf, the intertidal zone. sometimes called the littoral zone. This is the area between the tides that is exposed to the air when the tide is out but underwater at high tide. The intertidal zone makes up only a small fraction of the continental shelf. Most of the shelf is never exposed to the air, even at the lowest of low tides. Benthic organisms that inhabit the continental shelf beyond the intertidal live in the subtidal zone, sometimes called the sublittoral zone. Away from the shelf the benthic environment is subdivided by

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|--------------------------------|-----------------------------|------------------------|-------------------|
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### Chapter 10 An Introduction to Ecology 231

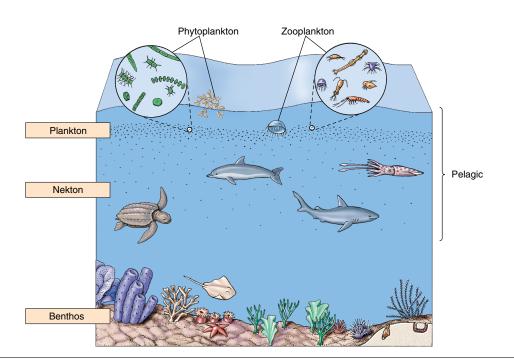
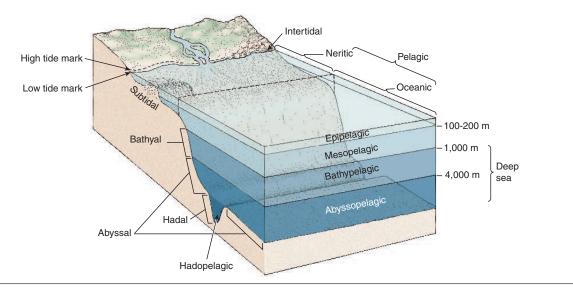
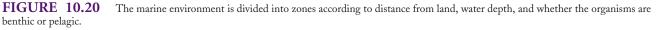


FIGURE 10.19 Three major groups, the benthos, nekton, and plankton, result when marine organisms are classified by lifestyle.





depth into the **bathyal**, **abyssal**, and **hadal** zones. For the sake of simplicity, we shall lump these different zones together and call them the "deep-sea floor."

The pelagic environment, too, is divided with reference to the continental shelf. The pelagic environment that lies over the shelf is called the **neritic zone**. Pelagic waters beyond the **shelf break** are the **oceanic zone**.

Besides being divided into the neritic and oceanic zones, the pelagic is divided **Shelf Break** The increase in steepness that marks the outer edge of the continental shelf.

Chapter 2, p. 35

III. Structure and Function10. Aof Marine EcosystemsEcol

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# BIODIVERSITY: ALL CREATURES GREAT AND SMALL

From bacteria to baleen whales, our planet is home to tens of millions of different life forms at least; biologists can only guess at the true number of species. The richness and variety of life is referred to as **biological diversity**, or just **biodiversity**. In recent years, the subject of biodiversity has been the focus of discussion not only in scientific circles but in the news media and the highest levels of government and international affairs. The reason for this attention, unfortunately, is that the earth's biodiversity is disappearing. Extinction is a natural event that has gone on since life first appeared on earth, but pollution, habitat destruction, overexploitation, and other human folly are now driving species extinct at a rate unprecedented in the history of life. At the rate things are going, most kinds of living things will disappear forever from the face of the earth, many before we even know they are there.

When it comes to conservation, the emphasis of decision makers, conservation organizations, and the general public has traditionally been on organisms that we find beautiful or emotionally compelling. Bald eagles, whales, and redwood trees evoke strong positive reactions in most people; microscopic worms and bottomdwelling fungi do not. Worms, fungi, and millions of other seemingly insignificant species are at least as vital to earth's survival—and therefore to our own—as are the larger organisms that we happen to find attractive. There is a growing recognition of the need to protect the earth's biodiversity, to reverse or at least slow the process of mass extinction. What is new about this recent attention is the focus on maintaining the total *number* of species, rather than on saving particular ones.

So why should we care about how many different *kinds* of organisms there are, as long as the ones we care about are still around? For one thing, no organism lives in isolation from its environment and the other living things in it. Creatures like whales, pandas, sea turtles, and tigers that capture our imagination cannot survive without countless other species. Organisms are bound together in complex food webs, nutrient cycles, symbioses, and other ecological interactions. The loss of even the "lowliest" of species could have profound effects on many others. Biologists simply do not understand ecosystems well enough to predict what these effects might be.

Another reason to conserve biodiversity is that it represents a hidden treasure trove. Most pharmaceuticals are derived from natural chemicals in organisms, but only a tiny fraction of species have been tested. The wild plants from which our farm plants were derived contain genes for pest resistance, faster growth, and higher quality that could be used to improve our food crops or develop new ones. New materials—a substitute for petroleum, perhaps, or industrial chemicals or better fibers for clothing—also remain undiscovered. There are so many different kinds of organisms, however, that scientists have not had time to even identify most of them, much less evaluate their usefulness. The next species that goes extinct might hold the cure for cancer, a solution to hunger, or maybe just the makings of an elegant new perfume—a secret that will be lost forever.

There is also recent evidence that having a lot of different species is a good thing in and of itself. A diverse community, one with a lot of species, seems to be more efficient at using the available resources than one that is less diverse. Thus, the diverse community produces more food and oxygen, breaks down waste faster, and is more likely to survive a natural disaster. The loss of species may be placing ecosystems in greater and greater jeopardy, not only because of the value of particular individual species but also because having a lot of species, whichever ones they are, is important. Humans, having become a largely urban species, sometimes forget that our survival still depends on natural ecosystems to produce oxygen, clean water, and much of our food and materials; to process our wastes; and even to maintain our climate.

What can be done? Some scientists fear that it is already too late, that the planet is irreversibly headed for disaster. Others are more optimistic, and all agree that we should at least try to maintain the earth's biodiversity. Governments and decision makers have begun to listen. At the 1992 Earth Summit in Rio de Janeiro, world leaders from nearly all countries gathered to discuss the critical environmental issues that threaten the planet, and therefore the wellbeing of people. A major result of the conference was an international convention, or agreement, to protect the earth's biodiversity. Participants agreed that protecting diversity requires finding ways for poor countries to develop without destroying their natural biodiversity, a concept dubbed "sustainable development." This, in turn, will require developed countries to make a major commitment to scientific research and to provide technical assistance. Some important steps have already been taken, such as setting up global programs to monitor the health of the oceans, assist sustainable development projects, and reduce pollution. Will these steps be enough? Do they represent the long-term commitment to change that is needed to ensure our survival, or just a passing fad? Only time will tell.

vertically into depth zones that correspond to the amount of light. In the shallowest, the **epipelagic zone**, there is plenty of light for photosynthesis, at least for part of the year. Given a supply of nutrients, phytoplankton thrive, producing food for the rest of the ecosystem. The epipelagic usually extends down to a depth of 100 to 200 m (350 to 650 ft). Because this is approximately the depth of the continental shelf, nearly all neritic waters lie in the epipelagic.

Other pelagic zones lie in the deep oceanic waters beyond the shelf. Below the epipelagic lies the **mesopelagic zone**. There is not enough light in the mesopelagic to support photosynthesis, so primary producers cannot grow. There is, however, enough light to see by. On even the brightest day, the mesopelagic is an area of twilight. This twilight zone typically extends to a depth of around 1,000 m (3,000 ft).

No sunlight at all penetrates to the deepest parts of the ocean, the **bathypelagic, abyssopelagic,** and **hadopelagic** zones. Although each of these zones supports a different community of animals, they share many similarities. We refer to all these zones together as the "deep-sea" environment.



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# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

# **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. Two species of sea urchins live practically side by side on sandy bottoms. The two species appear to have the same diet: drift seaweeds and other bits of organic matter. They are able to live in the same environment without competing with each other. How might they be able to share their habitat and food resources?
- 2. It is not always easy to categorize a particular case of symbiosis. Suppose a certain species of snail is always found living on a certain coral. No one has found evidence that the snail harms the coral, so the relationship is classified as an example of commensalism. How would you go about testing this hypothesis? What kinds of observations might lead to the conclusion that the snail is a parasite, or that it has a mutualistic relationship with the coral?

# For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol (, and will contain live links when you visit this page in the Online Learning Center.

### **General Interest**

- Eldredge, N., 1998. Life in the balance. *Natural History*, vol. 107, no 5, June, pp. 42–55. Biodiversity has concrete benefits to humankind, but steps are urgently needed to preserve them.
- Marine biodiversity. *Oceanus*, vol. 38, nos. 2 and 3, Fall/Winter 1995 and Spring 1996. A series of articles on marine biodiversity including that in bacteria, plankton, and marine mammals as well as in several marine environments.
- Nybakken, J. W. and S. K. Webster, 1998. Life in the ocean. Scientific American Presents, vol. 9, no. 3, Fall, pp. 74–87. An excellent summary of the ecology of the seas and life in different environments.

- Polovina, J., 1994. The case of the missing lobsters. *Natural History*, vol. 103, no. 2, February, pp. 50–59. What does the atmospheric pressure over the Aleutian Islands have to do with lobster catches in Hawai'i? This article demonstrates the complex links that exist between organisms and their environment.
- Zimmer, C., 2000. Do parasites rule the world? *Discover*,
   vol. 21, no. 8, August, pp. 80–85. Parasites are more than a nuisance. They may be one of the most powerful forces shaping the evolution of life on earth.

## In Depth

- Abrams, P. A., 2000. The evolution of predator-prey interactions: Theory and evidence. *Annual Review of Ecology and Systematics*, vol. 31, pp. 79–105.
- Benitez-Nelson, C. R., 2000. The biogeochemical cycling of phosphorus in marine systems. *Earth-Science Reviews*, vol. 51, nos. 1–4, pp. 109–135.
- Carlton, J. T., J. B. Geller, M. L. Reaka-Kudla and E. A. Norse, 1999. Historical extinctions in the sea. *Annual Review of Ecology and Systematics*, vol. 30, pp. 515–538.
- Côté, I. M., 2000. Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology: An Annual Review*, vol. 38, pp. 311–355.

# See It in Motion

Video footage of the following animals and their behaviors can be found for this chapter on the Online Learning Center:

- Gray angelfish feeding on invertebrates (Belize)
- Clownfish in anemone—an example of mutualism (Papua New Guinea)
- Giant cuttlefish changing color (Solomon Islands)
- Whale shark with remoras attached (Gulf of California)
- Parasitic isopods on a fish (Bonaire, West Indies)
- · Whale shark feeding on copepods (Gulf of California)

# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- General ecology sites
- Animal population ecology
- Population growth

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- Life histories
- Field methods for studies of populations
- Community ecology
- Field methods for studies of ecosystems
- Food webs
- Nutrient cycling

# Biodiversity

- Endangered species
- Species preservation

# Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

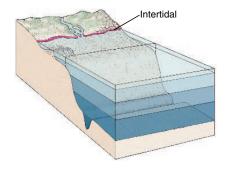
III. Structure and Function 11. Between the Tides of Marine Ecosystems

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# Between the Tides







Rocky shore, Washington state.

f all the vast ocean, the narrow fringe that is the intertidal zone is by far the best known to marine biologists and laypersons alike. The reason is simple: The intertidal is the only part of the marine world that we can experience firsthand without leaving our own natural element. We don't need a boat to visit the shore, and, at least at low tide, we can see it without a face mask and move through it without swim fins. Perhaps more important from the scientist's point of view, we can work in the intertidal without cumbersome and expensive equipment and can easily return to the exact same place time after time.

Intertidal communities are among the most studied and best understood of all marine communities. Although the intertidal zone constitutes only a tiny fraction of the marine environment, lessons learned in the intertidal have added immensely to our knowledge of marine ecology, and indeed of ecology in general.

The intertidal, sometimes called the **littoral zone**, is defined as the part of the sea floor that lies between the highest high and the lowest low tides. It is unique among marine environments in that it is regularly exposed to the air. Organisms that live in the intertidal must have a way to cope with this exposure, even if it means giving up characteristics that would be advantageous below the tides. Being out of the water and exposed to air is called **emersion**—the opposite of **immersion**, or being submerged.

The effects of the tide, and thus the nature of the **community**, depend to a great extent on the type of bottom. The

**Community** All the different populations of organisms that live in a defined area.

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bottom, that is, the material on or in which an organism lives, is called the **substrate**. Hard, rocky bottoms are a very different **habitat** from soft bottoms made of mud or sand. In Chapter 11 we consider intertidal communities on both kinds of substrate, beginning with the rocky intertidal. The major coastal communities of North America are shown on the map in Appendix C.

The intertidal zone is the shoreline between the high and low tide marks. It is the only part of the marine world that faces regular exposure to air, or emersion. Intertidal communities differ greatly depending upon whether they have rocky or soft bottoms.

# ROCKY SHORE COMMUNITIES

Rocky shores generally occur on steep coasts without large amounts of sediment. Such areas have often been recently uplifted or are still rising as a result of geological events. These uplifted coasts have not had much time to erode or accumulate sediments. The west coast of the Americas, for example, is largely rocky because its active margin has been uplifted by geological processes. Eastern Canada and New England were covered by huge sheets of ice during the last ice age (see "Climate and Changes in Sea Level," p. 35). The ice sheets scraped the sediments from the continental shelf, exposing the bare rock underneath. Under the tremendous weight of the ice, the coast actually sank partially down into the mantle. When the ice melted, the coast slowly rose, or rebounded, leaving a coastline of exposed rock. Sea level, however, began to rise, and eventually the rise in sea level overtook the rebound of the coast. The sea flooded the rocky coast, forming the beautiful, deeply sculptured shoreline seen north of Cape Cod. This area is the only part of the Atlantic coast of North America that has much rocky shore. The southern Atlantic and Gulf coasts of North America are slowly sinking, or subsiding, weighed down by the huge amounts of sediment that are accumulating on the passive continental



FIGURE 11.1 Lava flows are creating new rocky shorelines on the island of Hawai'i.

**margin.** Rocky areas are largely absent from these coasts.

Not all rocky shores are formed by uplift. Waves and currents can carry sediments away, leaving bare rock behind. Similarly, outcrops of hard, erosionresistant rock may be left behind after softer surrounding rocks erode away. Much of the coast of the island of Hawai'i is rocky because it is geologically very young. Formed by successive flows of lava into the sea, the coast hasn't had time to accumulate sediment. In fact, the coast is still being formed by the periodic eruptions of the Kilauea volcano (Fig. 11.1).

Rocky shores usually occur on recently uplifted or geologically young coasts or on coasts where erosion is removing sediments and soft rock. In North America, rocky shores are common on the west coast and on the east coast north of Cape Cod.

It is difficult to burrow through rock, though rock-boring clams (*Zirfaea, Penitella*) can do it in soft rock like sandstone. Most rocky intertidal organisms live right on the rock's surface. Animals that live on the surface of the substrate be it rock, sand, mud, or anything else are called **epifauna**. Some epifauna move about over the rocks, but many are **sessile** and stay put, attaching to the rock.

Living on the rock's surface, the organisms in the rocky intertidal are fully exposed to the elements. This subjects them to great physical stress.

### Exposure at Low Tide

Low tide presents many problems for the organisms of the rocky intertidal. Left high and dry, they are exposed to the air, a much harsher environment than the water. This exposure is more of a problem for organisms that live high in the intertidal. The upper part of the intertidal zone is only immersed at the peak of high tide and then only briefly. The very upper edge may not be submerged every day, but only during exceptionally high **spring tides.** The highest part of the "intertidal," in fact, is almost never immersed. It is kept wet by wave splash.

Organisms that live low in the intertidal, on the other hand, are submerged most of the time and only have to cope with emersion for short periods or, at the lowermost edge, only at the most extreme low tides. The higher the organisms live in the intertidal, then, the more time they have to spend out of the water.

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**FIGURE 11.2** These periwinkles (*Littorina cincta*) get through low tide by clustering in a moist, shady crevice. They also seal against the rock to retain moisture.



**FIGURE 11.3** When the tide goes out, a little bit of the ocean stays in this small tide pool in New Zealand. Organisms like these chitons (*Sypharochiton pelliserpentis*) and snails (*Diloma atrovirens*) move to such pools to stay moist. Even in tide pools, however, life can be tough. The water undergoes drastic changes in salinity, oxygen content, and temperature.

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Emersion time, or time spent out of the water, gets longer the higher in the intertidal you go.

### Water Loss

Marine organisms tend to dry out, or **desiccate**, when they are out of the water. To survive in the intertidal, an organism must be able to prevent desiccation, tolerate it, or both. Most intertidal organisms cope with the problem of drying out in one of two basic ways: They either run and hide or they "clam up."

The run-and-hide strategy is simple enough. When the tide goes out, the organism goes somewhere wet and waits for the tide to come back in. It is not unusual to see shore crabs, hermit crabs, snails, and other denizens of rocky shores huddled in moist, shady cavities or crevices in the rocks (Fig. 11.2). **Tide pools**, depressions in the rocks that hold seawater after the tide goes out, are favorite places to hide (Fig. 11.3). Some areas are kept

**Habitat** The natural environment where an organism lives.

Chapter 2, p. 21

Active Continental Margin One that is colliding with another plate, and therefore has a lot of geological activity.

Chapter 2, p. 36; Figure 2.20

**Passive Continental Margin** One that is on the "trailing edge" of a continent and has little geological activity.

Chapter 2, p. 37; Figure 2.20

**Mantle** One of the three main internal layers of the earth. The mantle lies under the *crust*, the outermost layer, and over the *core*, the innermost layer.

Chapter 2, p. 23; Figure 2.3

**Spring Tides** Tides with a large range that occur around times of the full or new moon.

Neap Tides Tides with a small range that occur when the moon is in quarter. **Tidal Range** The difference in height between a high tide and the next low tide.

Chapter 3, p. 59

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FIGURE 11.4 Mussels (*Mytilus californianus*) form dense clumps that retain moisture. This can help protect the mussels themselves and provides a place to live for a variety of smaller organisms.

moist by spray from waves or by water that slowly leaks out of tide pools. The hiding place may even be provided by other organisms (Fig. 11.4).

Seaweeds and sessile animals cannot run, but many are able to hide. Instead of moving to moist areas when the tide goes out, they live in moist areas all the time (Fig. 11.5). This may be because the larvae settle only in moist, shady places or because larvae that settle elsewhere dry out and die.

Organisms that use the "clam-up" strategy have some sort of protective covering, like a shell, that they can close to hold in water. Some, like barnacles and mussels, are completely enclosed and can seal in moisture simply by closing their shell. Others, like limpets, have an opening that cannot be completely shut. These organisms typically clamp themselves tightly to the rock to seal the opening. Some use mucus to make a better seal. They may also carve out shallow depressions, or "home scars," in the rock that make the seal more effective. They do this by scraping the rock with their shell or their radula, slowly wearing the rock away.

Some organisms use a combination of strategies. The periwinkles (*Littorina*) shown in Figure 11.2, for example, clamp themselves to the rocks to seal in moisture. They can also seal off the opening



FIGURE 11.5 These seaweeds can't move to moist depressions at low tide, so they live there permanently. They don't grow on the surrounding rock because it dries out.

of their shell by closing the **operculum**, a stiff plate that fits the opening like a door. Periwinkles are still not immune to desiccation, however, so at low tide they congregate in moist, shady places, especially on hot, sunny days.

Finally, some intertidal organisms use neither the run-and-hide nor the "clam-up" approach. Instead, they simply allow themselves to dry out. Some intertidal **chitons** can survive the loss of 75% of the water in their tissues. Some intertidal seaweeds, such as rockweeds (*Fucus*; see Fig. 6.5), can withstand a water loss of as much as 90%, becoming almost completely dry and practically crunchy. They quickly recover when the tide comes in and wets their tissues.

Some intertidal organisms avoid drying out by moving to or living in wet spots. Others can close a shell to retain water. Still others are able to dry out and then recover after the tide returns.

### Temperature and Salinity

Emersion creates problems for marine organisms other than desiccation. Sea temperatures are relatively constant and mild because of the high **heat capacity** of water, but air temperatures can be much more extreme. At low tide, intertidal organisms are at the mercy of the sun's heat www.mhhe.com/marinebiology

and the freezing cold of winter. Because tide pools are shallow, they too experience extreme temperatures, though usually not as extreme as air temperatures.

Most intertidal organisms can tolerate a wide temperature range. Tide-pool fishes, for example, are much more tolerant of extreme temperatures than their relatives that live below the tides. Certain species of periwinkle that live high in the intertidal show remarkable heat tolerance. One is known to survive temperatures as high as 49°C (120°F) under laboratory conditions.

Organisms deal with temperature extremes in ways besides simply being tough. Those that move to moist hiding places to avoid drying out, for example, also avoid high temperatures because such places tend to be cool as well as damp. Some snails, especially in the tropics, have pronounced ridges on their shells. Like the fins on a car radiator, these ridges help the snail lose excess heat.

The color of a snail's shell can also help it tolerate high temperatures. Snails that are regularly subjected to extreme high temperatures tend to be light in color. The light color helps reflect sunlight to keep the snail cool. On Atlantic shores, for example, the dog whelk or dog winkle (Nucella lapillus), has two color forms: white-shelled and brown-shelled. On shores exposed to heavy wave action, brown whelks predominate. On sheltered shores the white form is most common. The difference appears to be related to temperature. Brown whelks absorb more heat than white ones and die in temperatures that don't seem to harm the white snails. On the exposed coasts where brown snails live, there are dense mussel beds, which stay moist (Fig. 11.4) and relatively cool. Wave spray also helps cool the snails. Sheltered coasts have few mussels and little wave spray so they are hotter, and white whelks have an advantage.

Salinity also fluctuates widely in the intertidal. When it rains, exposed intertidal organisms have to endure fresh water, which is fatal to most marine organisms. Many simply keep the fresh water out by closing their shells—another benefit of the "clam-up" strategy. Even so, rainstorms during low tide sometimes cause the mass mortality of intertidal organisms. Castro–Huber: Marine Biology, Fourth Edition III. Structure and Function 11. Between the Tides of Marine Ecosystems

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Chapter 11 Between the Tides

### Tide-pool residents, too, face extreme variation in salinity. At low tide, pools may be diluted by rain, lowering the salinity. On hot, dry days, salinity rises because of evaporation. To cope, tide-pool organisms can usually withstand a wide range of salinity, as well as temperature. They may also burrow or reduce their activity to ride out the extreme salinity and wait for high tide.

The intertidal faces more extremes of temperature and salinity than other marine environments because it is exposed to the air. Intertidal organisms have evolved various mechanisms to avoid or endure these extremes.

### **Restriction of Feeding**

Because little sediment accumulates in the rocky intertidal, **deposit feeders** are rare. Most of the sessile animals are **filter feeders**. They are unable to feed when the tide is out. For one thing, they have to be under the water to filter it. Furthermore, many of them "clam up" during low tide to avoid water loss and can't extend their filtering or pumping apparatuses with their shells closed.

Even animals that are not filter feeders have trouble feeding at low tide. Many mobile animals in the rocky intertidal are grazers that scrape algae, bacteria, and other food from the rocks. Others are predators and move over the rocks in search of prey. At low tide these animals seek shelter or clamp to the rocks to avoid water loss. This prevents them from moving around to find food.

Being unable to feed when the tide is out is not much of a problem for animals that live low in the intertidal; they still have plenty of time to feed since they are immersed for most of the day. Higher in the intertidal, however, animals may not be underwater long enough to get adequate feeding time. This may cause them to grow more slowly than they would with more time to feed. It may even prevent them from living in the high intertidal at all.

Many intertidal animals are unable to feed when exposed at low tide. This may prevent them from living higher on the shore than they do.

### The Power of the Sea

Even when the tide is in, life in the intertidal is not necessarily easy. Ocean waves expend tremendous energy as they crash on the shore. Anyone who has been knocked around by the surf appreciates how much energy waves can carry. Rocky intertidal organisms are exposed to the full power of the sea (see the photo on page 43).

### The Distribution of Wave Energy Along the Shore

The impact of the waves varies along the shoreline. Some areas are sheltered from the surf, others are fully exposed. Enclosed bays, for example, are usually protected from wave action, which is why they are used for harbors. It is not always so easy to predict which areas will be sheltered and which exposed, however. To understand the distribution of wave energy along the shore, we must learn a little more about the behavior of waves.

Recall from Chapter 3 (see "Waves," p. 55) that when a wave enters shallow water it "feels" the bottom and slows down. Thus, the same wave will travel faster in deep than in shallow water.

Waves almost never approach the shore straight on, but instead come in at an angle (Fig. 11.6). As a result, one "end" of the wave reaches shallow water before the other. The end in shallow water slows down, but the end in deep water continues to travel at its original speed. As a result, the wave bends, just as a two-wheeled cart will turn to one side if



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**FIGURE 11.6** Like nearly all waves, these waves are approaching the coast at an angle. As a result, they refract, or bend toward the coast. By the time the waves break they have bent until the surf is almost parallel to shore.

the wheel on that side sticks. This bending of the wave, called **refraction**, causes the waves to become nearly parallel to the shore (Fig. 11.7). They never quite get perfectly parallel, however.

Refraction can produce especially complicated wave patterns when the coast is not a straight line. In particular,

**Radula** A rasping ribbon of small teeth that is possessed by most molluscs. *Chapter 7, p. 130; Figure 7.19 inset* 

Chitons Molluscs whose shells consist of eight overlapping plates on their upper, or dorsal, surface. *Chapter 7, p. 133* 

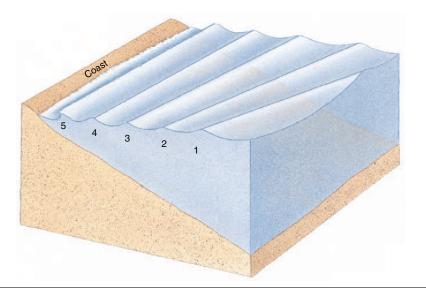
**Heat Capacity** The amount of heat energy require to raise the temperature of a substance; also its ability to hold heat. Water has one of the highest heat capacities of any natural substance. *Chapter 3, p. 45* 

**Deposit Feeders** Animals that eat organic matter that settles to the bottom. *Chapter 7, p. 126; Figure 7.16* 

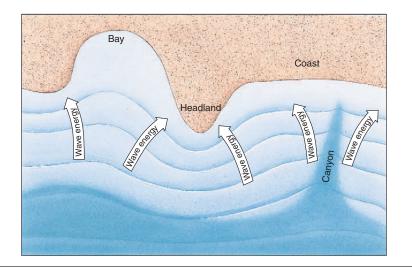
Filter Feeders Animals that actively filter food particles from the water. They are a common type of *suspension feeder*. *Chapter 7, p. 118; Figure 7.16* 

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**FIGURE 11.7** Wave refraction. Wave crests, which appear as dark lines in Figure 11.6, can be represented by lines on a diagram. In this diagram the lines indicate the crest of a single wave at successive times. At time 1, the entire wave is in deep water. At time 2, the left end of the wave, which is closer to shore, has entered shallow water and slows down, but the right end is still in deep water. As a result, the wave bends to the left, becoming more parallel to the shore. This process continues so that the wave is nearly, but not quite, parallel to shore when it breaks (time 5).



**FIGURE 11.8** Both the coastline and bottom affect wave refraction. For example, an incoming wave first hits shallow water straight out from a headland. This part of the wave slows, lagging behind the sections on either side. As a result the wave wraps around the headland, which gets most of the wave shock. Just the opposite occurs in bays or over submarine canyons: The central part of the wave is in the deepest water, and the wave turns off to both sides. This deflects wave energy away from the bay or the shore behind the canyon.

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wave action tends to focus at headlands (Fig. 11.8). Bays, even if they are not physically sheltered from incoming waves, tend to get less wave energy.

Incoming waves refract, or bend, to become more parallel to the shore. This increases wave impact at headlands and decreases it in bays.

Offshore bottom features can influence the effect of waves on the coast. Submarine canyons, for example, may cause wave refraction. Also, waves often break on reefs or sand bars and expend their energy before they reach the shore.

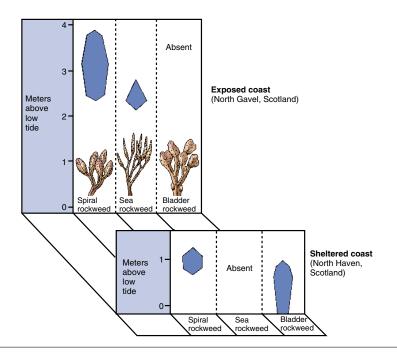
The result of all this is that there is tremendous variation in the intensity of wave impact, or **wave shock**, from place to place along the shore. Exposure to waves strongly affects intertidal organisms (Fig. 11.9).

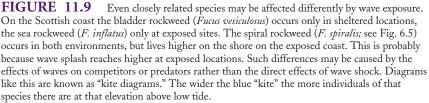
### Coping with Wave Shock

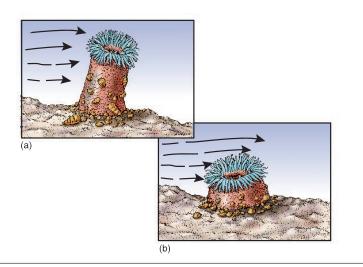
Some intertidal organisms simply can't withstand wave shock and are found only in sheltered locations. They are often rather delicate or unable to keep a firm grip on the rocks. Because sediment tends to accumulate in the sheltered spots where they live, these organisms are often better at coping with sedimentation than those that live on exposed shores.

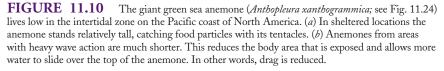
Organisms that are exposed to the force of the waves need some way to cope with wave shock. Sessile organisms anchor themselves firmly to the rocks to keep from being washed away. Seaweeds use their holdfasts or simply encrust on rocks. Barnacles secure themselves with a glue so strong that several companies have tried to duplicate it, without success. Mussels hold on with their byssal threads, strong fibers made of protein that the mussel produces with a special gland in its foot. It is these threads that form the mussel's "beard." Though we usually think of them as stationary, mussels can slowly move from place to place by putting out new threads and detaching old ones.

Mobile animals may also cling strongly to the rocks. Limpets and chitons, for example, use their muscular foot like a powerful suction cup. Gobies (*Gobius*) and clingfishes (*Gobiesox*), which are common









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tide-pool fishes, also have suction cups, formed by modified pelvic fins. The fishes don't stick as strongly as limpets, but unlike limpets they can always swim home if they are dislodged. Intertidal fishes also tend to lack **swim bladders**, so they sink and stay on the bottom.

There are always those who prefer to hide from trouble. Many intertidal animals move to sheltered spots when wave action gets too strong. This is especially true of highly mobile animals like shore crabs (Pachygrapsus, Grapsus). In fact, there may be a trade-off between being able to move fast and having a strong grip on the rocks. Holding on tightly tends to slow an animal down. Many intertidal snails are easier to knock from the rocks when they are moving around than when they stop and clamp down. Not surprisingly, they usually stop and hold on when wave action is heavy. This, of course, prevents them from feeding, which prevents some species from living in highly exposed areas.

Intertidal organisms have other adaptations that help them withstand wave shock. Animals in exposed locations tend to have thicker shells than those in sheltered ones. A compact shape can help reduce the impact of the waves (Fig. 11.10). Many intertidal animals, including barnacles, mussels, limpets, and chitons, have low profiles close to the rocks. Colonies of the tube worm Phragmatopoma californica provide another example of the importance of shape. These colonies are not especially strong and are easily crushed if stepped upon, but they can withstand considerable wave shock because water flows easily over their domed surface. Some organisms, especially seaweeds, are flexible and can "go with the flow" (Fig. 11.11). There may also be some safety in numbers (Fig. 11.12).

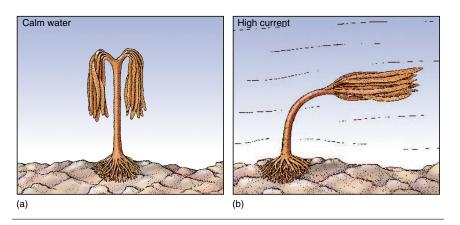
**Holdfast** A structure used by many seaweeds to anchor themselves to the bottom.

Chapter 6, p. 106; Figure 6.1

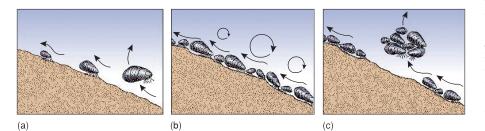
Swim Bladder A gas-filled sac that provides bony fishes with buoyancy.

Chapter 8, p. 159; Figure 8.12

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**FIGURE 11.11** Organisms like this brown alga, the kelp *Eisenia arborea*, survive waves by being flexible. (*a*) In calm water the plant stands upright. (*b*) When a wave hits, the plant bends over and the fronds fold up. This streamlines the plant and reduces water resistance.



**FIGURE 11.12** Intertidal animals may get some protection from wave shock by growing in dense groups. (a) When mussels (*Mytilus*), for example, grow as isolated individuals, they get the full impact of the waves. Small individuals, which are closer to the rock, may be able to hang on but larger mussels, with more exposed surface area, can be torn away. (b) When the mussels grow in dense clusters, the waves do not get a direct shot at any of them but slide over the tops. Eddies created as the water flows over the mussels may also keep plankton near the mussels, increasing their food supply, and the dense clumps retain moisture. (c) If the clumps get *too* dense, however, many of the mussels attach to other mussels instead of to the rock. Waves can cause more strain than the mussels on the bottom can bear, and entire clumps may be ripped away. This opens up space for other organisms, including other mussels.

Organisms on exposed coasts deal with wave shock in several ways, including strong attachments, thickened shells, low profiles, and flexibility.

Even the firmest grip on the rocks is of little help if the wave smashes a drifting log or something into the rocks, crushing whatever happens to live there. Waves can also turn rocks over, even large boulders. When this happens the organisms on top of the rock may be smashed or buried, and sunlight for the algae is blocked. The underside of the rock supports different organisms than the top, and these fare no better. Once nestled comfortably under the rock, they are suddenly exposed to the sun and waves, not to mention hungry predators. When waves overturn a rock, therefore, the organisms on both top and bottom usually die. People can have the same effect. If you happen to look under rocks at the shore, don't forget to turn them back over the way you found them.

Not only does wave action vary from place to place, but organisms differ in how they are affected by waves. The result of this is that sheltered and exposed areas www.mhhe.com/marinebiology

have very distinct communities. The marine communities in quiet bays are much different from those at unprotected headlands. The effect of wave action can also be seen on a smaller scale: The organisms in a sheltered crevice usually differ from those on exposed rocks nearby.

### The Battle for Space

For organisms that have adapted to its physical extremes, the rocky intertidal can be a good place to live. The shallow coastal waters provide lots of light and nutrients, the basic requirements for photosynthesis. The vigorous plant and algal growth that results produces abundant food for animals. Furthermore, high tide bathes the intertidal in planktonrich water, and the waves and tides bring in even more food in the form of drifting seaweeds and detritus (Fig. 11.13). In general, food is not a limiting resource for sessile intertidal animals, though high on the shore they might not be underwater long enough to eat it.

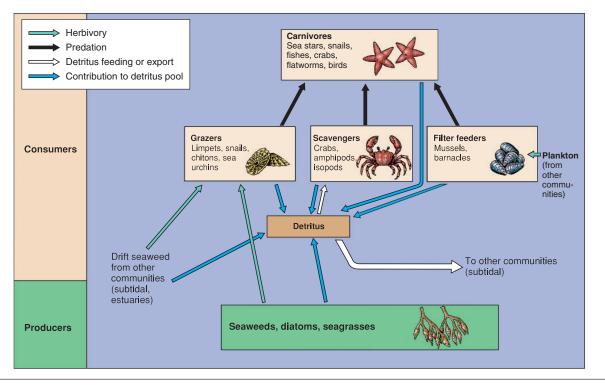
In even the most sheltered areas, intertidal organisms will drift away or be smashed on the rocks if they aren't attached to the substrate. Sessile organisms need a permanent place to hold on to. Unfortunately, there is often not enough room to go around. In fact, it is the availability of space that most often limits rocky intertidal populations. Nearly all the space in the intertidal is occupied (Fig. 11.14), and colonizers quickly take over what open space there is. Space is so scarce that organisms may attach to each other instead of directly to the rock.

Intertidal populations are usually limited by space, not food or nutrients.

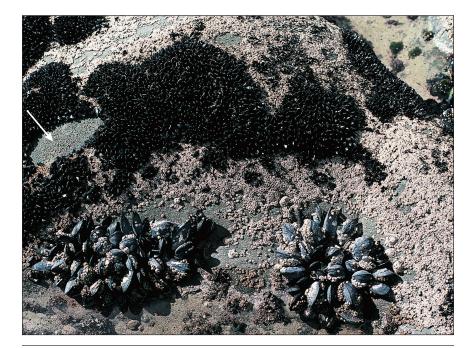
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It should come as no surprise that competition for space is a dominant biological factor in the rocky intertidal. There are many ways to compete for space. One way is to be the first to get to open spots. For intertidal organisms, this means having an effective means of **dispersal;** that is, organisms that depend on being the first to occupy new patches of open space must be good at getting themselves or their offspring from place to place. Most rocky intertidal species

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### FIGURE 11.13 A generalized food web on a rocky shore.



**FIGURE 11.14** Most organisms in the intertidal zone live attached to the rocks, and most of the available space is occupied. This little patch of rock supports two species of mussels and two of barnacles, plus limpets and sea anemones. What little open space there is doesn't last for long: A small bare patch (arrow) has already been colonized by newly settled barnacles.

disperse via their larvae, which settle on the rocks to colonize open space. Having taken over the space, the organism must be either good at holding on to it or able to rapidly reproduce and disperse its young to the next opening. Both strategies are used in the intertidal.

Rather than colonizing open patches, some intertidal organisms take over space that is already occupied. Barnacles, for instance, undercut their neighbors, loosening them from the rock. Owl limpets

**Photosynthesis**  $CO_2 + H_2O + sun$ energy  $\rightarrow$  glucose +  $O_2$ . *Chapter 4, p. 71* 

**Detritus** Particles of dead organic matter.

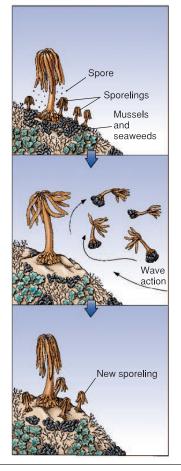
Chapter 10, p. 224

**Limiting Resource** A resource that is so scarce that it restricts the growth of a population.

Chapter 10, p. 217

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**FIGURE 11.15** The sea palm (*Postelsia palmaeformis*; see Fig. 6.7) is a kelp that takes advantage of wave action to compete for space. Adults literally drip spores, which develop into young sporelings near the parent. When the space below is occupied, the sporelings grow on these competitors, which are eventually pulled from the rocks. This clears the way for a new generation of young sea palms.

(*Lottia gigantea*) keep a territory for themselves by bulldozing out intruders. Less forceful methods may also work. Many intertidal organisms simply grow over their competitors, making them vulnerable to waves (Fig. 11.15), smothering them, or, in the case of seaweeds, blocking precious sunlight. Some species grow in colonies, gradually increasing the amount of space they hold as they reproduce.

Two species of mussel provide an example of how competition and physical factors can interact. On the west coast of North America the blue mussel (*Mytilus*)



FIGURE 11.16 Intertidal organisms often form distinct bands, or zones, at different heights on the shore.

galloprovincialis) is found mainly in sheltered locations, whereas the California mussel (M. californianus) is found on the open coast. As you might expect, the California mussel has a thicker shell and attaches more strongly to the rocks than the blue mussel. On the other hand, the blue mussel does just fine on open coasts as long as the California mussel is absent. The blue mussel is apparently rare on open coasts not because it can't take the waves but because it cannot compete with the California mussel. The California mussel, with its thicker shell, crushes the blue mussel when the two grow together. On the other hand, the blue mussel is able to live in calm bays because it can tolerate a lot of silt, unlike the California mussel. These two mussels provide just one example of how physical and biological factors can interact to determine the distribution of organisms.

### Vertical Zonation

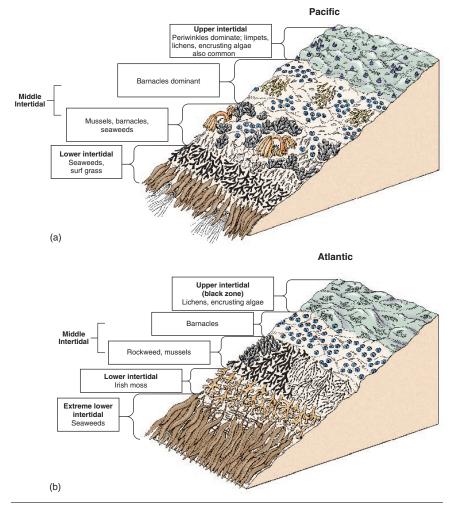
The particular organisms that make up rocky intertidal communities vary from place to place. There is, however, one feature that is remarkably universal. Nearly everywhere, the community is divided into distinct bands, or **zones**, at characteristic heights in the intertidal (Figs. 11.16 and 11.17). Thus, a given species is usually not found throughout the intertidal, but only within a particular vertical range. Biologists call this pattern of banding **vertical zonation**.

When the shore consists of an evenly sloping rock face, the zones are often sharply defined belts that can be easily distinguished by the colors of the organisms (Fig. 11.16). Many shores are much more uneven, with scattered boulders, channels, and gullies. Zonation may not be as obvious in such areas, but it usually exists nonetheless.

Marine biologists have spent a tremendous amount of time and energy studying the causes of vertical zonation. Though there is still much to be learned, we now know that zonation results from the complex interaction of physical and biological factors. A general rule is that the upper limit at which a species occurs is usually determined mainly by physical factors, whereas the lower limit is usually determined by biological factors, especially predation and competition.

Most rocky shores have a distinct pattern of vertical zonation. The upper limit of a zone is often set by physical factors, the lower limit by biological ones.

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**FIGURE 11.17** Generalized patterns of zonation on rocky shores on the (*a*) Pacific and (*b*) Atlantic coasts of North America. At any particular place on the coast the exact pattern will probably be different. Only organisms that characteristically dominate the various zones are shown. Hundreds of other species live in the intertidal.

This rule is a useful place to begin when trying to understand the causes of vertical zonation. As with all generalizations, however, there are exceptions. For example, zonation can be produced if the larvae of a species settle only at a particular height on the shore. One cannot just *assume* that the upper limit of a certain species is set by physical factors. Instead, this hypothesis must be *tested* by experiment (see "Transplantation, Removal, and Caging Experiments," p. 246). Furthermore, different factors often interact to determine the limits, and sometimes the line between physical and biological factors is fuzzy. As noted previously, for example, some filter feeders do not live high in the intertidal because they are not submerged long enough to feed. Is this upper limit due to a physical factor—emersion by the tide—or a biological one—feeding?

Rocky shores around the world frequently show a pattern of vertical zonation that is quite similar in its general nature but highly variable in its particulars. Biologists studying a certain area sometimes name the zones after the dominant organism, as in the "limpet zone" or the "mussel zone." These zones

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actually contain a variety of organisms. The mussel zone, for example, is also home to worms, crabs, snails, seaweeds, and many other species. Also, the specific organisms found in the intertidal vary from place to place. On the east coast of North America, for example, the mussel zone is often replaced by a rockweed zone.

Instead of naming the zones after animals and seaweeds, we will simply divide the intertidal into the upper, middle, and lower zones. These names may not be especially informative or creative, but at least they apply everywhere! Bear in mind that the following sections are general descriptions of "typical" intertidal communities and don't apply exactly to any particular place. Furthermore, the boundaries between zones are not absolute; some species occur in more than one zone. The next time you go to the shore, think about how these descriptions apply. Perhaps more importantly, think about how the place you visit is different. What factors might cause the differences?

### The Upper Intertidal

Seldom submerged, the inhabitants of the upper intertidal zone must be well adapted to withstand exposure to air. This zone actually lies mostly above the high tide mark, and the organisms are wetted mainly by wave splash and spray. It is often called the "splash zone." On exposed, stormy coasts with more wave splash, the upper intertidal extends further above the high tide line than on sheltered coasts.

In most places, **lichens** (*Verrucaria*) form black, tar-like blotches on rocks in the upper intertidal. The fungus part of the lichen soaks up water like a sponge, storing it for long dry periods. Dark green mats of cyanobacteria (*Calothrix*) are abundant. They are protected from drying out by a jelly-like coating and have

Lichens Close, *mutualistic* associations between fungi and microscopic algae; mutualism is a type of *symbiosis*.

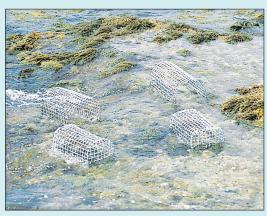
Chapter 5, p. 102, and Chapter 10, pp. 220–221

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## TRANSPLANTATION, REMOVAL And Caging Experiments



These cages in the intertidal zone in California were used to test for the effects of spiny lobsters (*Panulirus interruptus*). The lower cages have closed ends and keep the lobsters out. The upper cages have open ends so that the lobsters can move in and out. They are a control for any effects of the cages themselves, other than keeping out lobsters.

A general principle in the intertidal is that physical factors, especially drying in air, usually determine how high in the intertidal a particular organism can live. Biological factors such as competition and predation set the lower limit. Where does this principle come from? How can you tell why a certain species of barnacle or seaweed is found only in a particular zone, not higher or lower?

Like most scientific questions, this one is best answered by performing experiments—altering natural conditions to see what happens. In the intertidal, three general types of experiments have been particularly effective. In one of these, organisms are **transplanted** from one place to another to see whether they can survive under the new conditions. In one such experiment barnacles were grown on panels that could be placed at various heights on intertidal pier pilings. The barnacles soon died if they were moved higher than they normally lived. Measurements of their body fluids showed that they had lost a lot of water, so the cause of death was probably drying out at low tide. The experiment showed that the barnacles cannot survive the conditions above their normal range. Thus their upper limit is set by a physical factor—desiccation.

Transplantation can also tell us when physical factors are not important. When barnacles are transplanted lower in the intertidal than they normally live, they do just fine. The same is true of many other intertidal species, including certain mussels, snails, and seaweeds. In fact, some species actually grow faster when moved below their normal range. Their lower limit, therefore, is not set by the physical environment.

If organisms can live lower in the intertidal, why don't they? Experiments suggest that other organisms, either competitors or predators, often set a species' lower boundary. In **removal experiments**, one species is removed from an area, which is then compared to an untouched **control** area. A classic experiment examined competition between rock barnacles (*Semibalanus balanoides*) and little gray barnacles (*Chthamalus stellatus*), which normally live higher on the shore (see Fig. 11.18). Rocks with newly settled juveniles of both species were collected and placed at different heights. The rock barnacles were removed from some of the rocks, while other rocks were not disturbed.

High in the intertidal, little gray barnacles survived better than rock barnacles. They apparently tolerate drying better. Lower in the intertidal, where the rock barnacles can survive, little gray barnacles



This dark patch of mussels was protected by a closed cage, which has been removed. Protected from lobsters, mussels have taken over the space inside the cage. The surrounding rock is dominated by red algae (as are areas inside open-ended cages, not visible in this photo). The conclusion is that mussels would dominate the community if not eaten by lobsters.

can't compete. They do quite well as long as the rock barnacles are removed, but when the two species grow together the bigger, fastergrowing rock barnacles crush, undercut, or smother the little gray barnacles. Thus, the lower limit of little gray barnacles is determined by a biological factor: competition.

Removal experiments have also shown the importance of grazing and predation. When limpets are removed from test areas, for example, a profusion of seaweeds usually results. While limpets are present the algae cannot establish themselves because limpets scrape young algae off the rocks. If the seaweeds get a foothold, however, they are often able to persist because adult seaweeds can stand up to these grazers. Another removal experiment, involving a sea star, is summarized in Figure 11.20.

It may be time-consuming, difficult, or downright impossible to remove all the organisms of interest from an area, or they may move back into an area too soon after removal. Instead, caging experiments can be used to keep them out. On the Channel Islands off the coast of Southern California, the intertidal is covered by a nearly unbroken carpet of seaweeds. When marine biologists discovered that large numbers of spiny lobsters (Panulirus interruptus) moved into the intertidal during nighttime high tides, they wondered what effect the lobsters were having. They installed plastic cages to keep the lobsters out. Just to make sure that the seaweed wasn't affected by the shade of the cages, they also installed control cages that had roofs but no ends, allowing lobsters to enter unimpeded. Seaweeds continued to flourish in these control areas, and in adjacent open areas, but within the fully enclosed cages the seaweeds were soon replaced by mussels. This demonstrated that seaweeds were able to dominate because the lobsters ate the mussels, which are superior competitors.

Caging experiments don't have to use actual cages, just some sort of barrier to keep the animals out. Plastic rings or strips of artificial turf, for example, will keep out sea stars, limpets, and snails, which can't crawl over the turf. Cages can also be used to hold animals inside an area, rather than keep them out, to determine their effects.

Transplantation, removal, and caging experiments have been extraordinarily effective in unraveling the web of physical and biological interactions in the intertidal zone. So effective, in fact, that they have become an important tool for ecologists not only in the intertidal, but in many other environments. Castro–Huber: Marine Biology, Fourth Edition III. Structure and Function 11. Between the Tides of Marine Ecosystems

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the advantage of being able to fix nitrogen from the air. Small tufts of a filamentous green alga (*Ulothrix*), which are also resistant to drying out, may spring up here and there. Various other green (*Prasiola, Enteromorpha*), brown (*Pelvetia*), and red (*Porphyra, Bangia*) algae are occasionally found in the upper intertidal, usually in moist spots or tide pools.

Large numbers of periwinkles graze on the algae, scraping it from the rocks with their radulas. Periwinkles are so abundant that the upper intertidal is often called the "*Littorina* zone" after the scientific name of the snails. Not all of the many species of periwinkles live high in the intertidal, but those that do are well adapted to it. They can breathe air like land snails and live out of water for months. They can also tolerate extreme temperatures. They do have limits, however, and may have to seek shelter on hot days (Fig. 11.2).

Limpets (*Colisella, Acmaea, Lottia*) may also be found in the high intertidal. Like periwinkles, limpets are hardy grazers. Shore crabs occasionally venture into the upper intertidal, scurrying over the rocks. They mostly eat algae that they scrape off the rocks with their claws, but they may also eat animal matter, dead or alive. Sea lice or sea roaches (*Ligia*; see Fig. 7.31), breathe air and live above the water's edge, moving into the upper intertidal at low tide.

Most of the upper intertidal lies above the high tide line and is kept wet by wave splash. The dominant primary producers are lichens and cyanobacteria. Periwinkles are the most common animals.

Few marine predators can reach the upper intertidal. Shore crabs occasionally eat periwinkles and limpets. From time to time predatory snails, such as unicorn shells (*Acanthina*), may venture into the splash zone to do the same. On the other hand, the upper intertidal is visited by predators from land. Birds, such as oystercatchers (*Haematopus*), may eat large numbers of limpets and snails. Raccoons, rats, and other land animals are also known to enjoy these tasty molluscs, as do people in most of the world.

### The Middle Intertidal

Unlike the upper intertidal, which is affected only by wave splash and the highest spring tides, the middle intertidal is submerged and uncovered by the tides on a regular basis. A diurnal tide exposes the organisms once a day, a semidiurnal tide twice. If the tide is mixed, the lower of the two successive high tides may not submerge the high part of the zone, and the higher of the two lows may not expose the bottom part. Thus, even in places with a semidiurnal tide, some parts of the intertidal may be submerged or exposed only once a day. With so much variation in the time spent out of the water, different heights within the middle intertidal may support very different kinds of marine life. In other words, the middle intertidal is often made up of several separate vertical zones.

The upper boundary of the middle intertidal is almost always marked by a band of acorn barnacles. In many places at least two separate species of barnacles, such as little gray (*Chthamalus*) and rock barnacles (*Balanus*, *Semibalanus*), form distinct bands, with little gray barnacles living higher up.

Experiments (see "Transplantation, Removal, and Caging Experiments," p. 246) have shown that this zonation results from a combination of the barnacles' larval settlement pattern, how well they tolerate desiccation, and competition and predation (Fig. 11.18). The larvae of both species settle over a wider range than that occupied by adults. The upper limit of both species appears to result from emersion, because larvae that settle too high in Chapter 11 Between the Tides 247

the intertidal die. Little gray barnacles tolerate drying better than rock barnacles and can therefore live higher on the shore. At lower levels, where the rock barnacles can survive, they outcompete the little gray barnacles. Adult little gray barnacles, then, live perched in a narrow band above their competitors where they can survive emersion.

The lower limit of rock barnacles, like that of little gray barnacles, is determined by biological factors, in this case both predation and competition. Whelks are major predators of barnacles (Fig. 11.19). These snails use their radula to drill holes in barnacles' shells. They also secrete chemicals that soften the shells. If protected from the snails by wire cages, rock barnacles flourish below their normal limit. Unprotected barnacles, however, suffer heavy losses to snail predation. The only thing that saves the rock barnacles is that the dog whelks do most of their feeding during high tide. When emersed they lose a lot of water if they move around in search of barnacles, and to avoid dessication at low tide they cease feeding or move lower in the intertidal. In the upper intertidal, the snails don't have enough time at high tide to eat the barnacles. Sea stars, which also eat barnacles, have the same problem as the snails. Rock barnacles may also face competition from mussels. In some places, in fact, the lower limit of barnacles is set not by dog whelk predation but by competition with mussels. Like the little gray barnacles, the rock barnacles persist in a narrow zone between the level where they die of "thirst" and the level where their enemies can reach them.

Nitrogen Fixation Conversion of nitrogen gas  $(N_2)$  into nitrogen compounds that can be used by primary producers as nutrients.

Chapter 10, p. 228

**Primary Producers** Organisms that manufacture organic matter from CO<sub>2</sub>, usually by photosynthesis. *Chapter 4, p. 73*  **Diurnal Tide** A tidal pattern with one high and one low tide each day. **Semidiurnal Tide** A tidal pattern with two high and two low tides each day. **Mixed Tide** A tidal pattern in which two successive high tides are of different heights.

Chapter 3, p. 62; Figure 3.29

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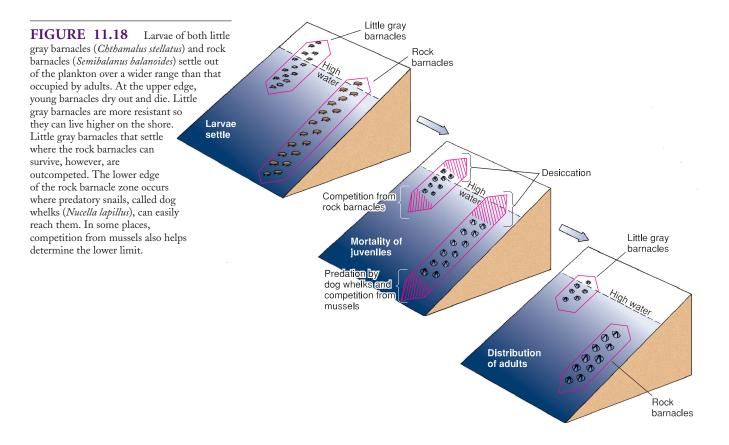




FIGURE 11.19 A dog whelk (*Nucella lapillus*) preying on rock barnacles (*Semibalanus balanoides*) on a rocky shore in Maine. In moist conditions like these the whelk is able to feed at low tide, but its activity will cease if the rock drys out. Acorn barnacles usually occupy the top of the middle intertidal. Their upper limit is determined by how high they can live without drying out. Their lower limit is set by competition with other barnacles or mussels or by snail or sea star predators.

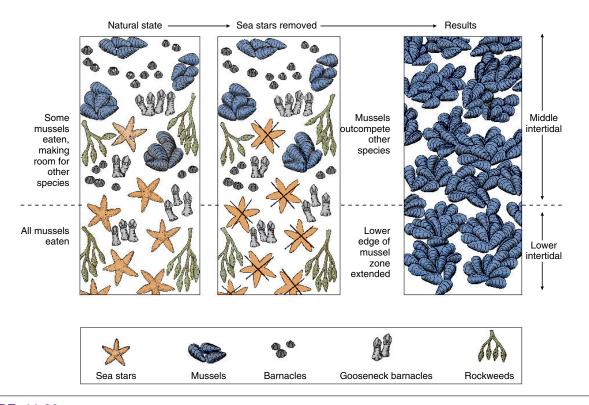
Many other organisms live in the middle intertidal among or below the barnacles. Which organisms are present, how many there are, and where they occur all depend on the unique combination of physical and biological factors at that site. The pattern of the tides, steepness of the shore, exposure to waves, and the local weather all exert a profound influence. Predation, competition, and larval settlement patterns are almost always involved. If you consider all the possible ways in which these factors might interact, you may get some idea of how complicated the story can be.

Depending on all these factors, mussels (*Mytilus*), gooseneck barnacles (*Pol-* licipes), and brown seaweeds, particularly rockweeds (Fucus, Pelvetia), often dominate the middle intertidal below the barnacles. Many rockweeds have air bladders called **pneumatocysts** that float their fronds closer to the light. They may form a luxuriant thicket, or algal turf, that shelters many small animals. Mussels are especially common on stormy, exposed shores. They cannot live as high on the shore as barnacles, because they dry out and also because at high levels they do not spend enough time underwater to filter feed. At levels where they can live, however, mussels are the dominant competitors, smothering or crowding out other organisms.

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Sea stars (*Pisaster, Asterias*) are voracious predators of mussels. Contrary to popular belief, sea stars do not force open the mussel's shell to eat it. Instead, they insert their stomachs into the shell, and begin digesting the mussel from the inside. Only a tiny crack in the shell is needed. The ochre sea star (*Pisaster*)

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**FIGURE 11.20** Removing predatory sea stars—or keeping them out with cages—shows how they affect the middle intertidal community. Below a certain level the sea stars can easily reach the mussels, their favorite food, and eat them all. Above this level the sea stars cannot eat all the mussels, but they eat enough to make space available for other species. When there are no sea stars around, the mussels are able to live lower, and they monopolize the available space by overgrowing and crowding out other species.

*ochraceus*), for example, can insert its stomach through a crack only 0.2 mm (0.008 in) wide. The shell opens after the mussel is weakened.

Sea stars don't tolerate dessication very well and need to be underwater to search for food, though they may finish a meal after the tide goes out. In the lower part of the middle intertidal this is no problem, and sea stars take a heavy toll on mussels. Thus, mussels are found only above the level of heavy sea star predation. As with other intertidal species, the lower limit of mussels is set by a biological factor: predation by sea stars.

Mussels are the dominant competitors for space on many rocky shores. Their upper limit is set by desiccation and filter feeding time, their lower limit by predatory sea stars.

In some places spiny lobsters (Panulirus) instead of sea stars are the main predators of mussels (see "Transplantation, Removal, and Caging Experiments," p. 246). The lobsters can almost eliminate the mussels from the intertidal zone altogether.

Sea stars and other mussel predators can have a strong effect, even above the level where they completely wipe out the mussels. They venture into the mussel bed during high tide and eat some of the mussels before retreating with the tide. This opens up space for other organisms-such as acorn barnacles, gooseneck barnacles, and seaweeds-that would otherwise be crowded out. The sea stars also eat dog whelks, doing the barnacles another favor. If the barnacles can live long enough, they get too big for the dog whelks to eat. By reducing the number of dog whelks, the sea stars give the barnacles a better chance to grow before a whelk tries to eat them.

The sea stars are absent from areas with extremely strong wave action. In such areas, or if the predators are experimentally removed (Fig. 11.20), the mussels take over. They outcompete other organisms and form dense beds. Thus, many of the species in the middle intertidal would be crowded out if the sea stars did not keep the number of mussels down.

Note that many intertidal species are more abundant than the sea stars, but the sea stars are of central importance in the community. Removing them would profoundly affect the other species. This demonstrates a common feature of biological communities: Just because a species is relatively uncommon does not mean that it is unimportant. Though not the most abundant species, certain predators such as sea stars are important because they determine the structure of the community. Predators that have effects on their communities that are proportionately much greater than their abundance are known as keystone predators.

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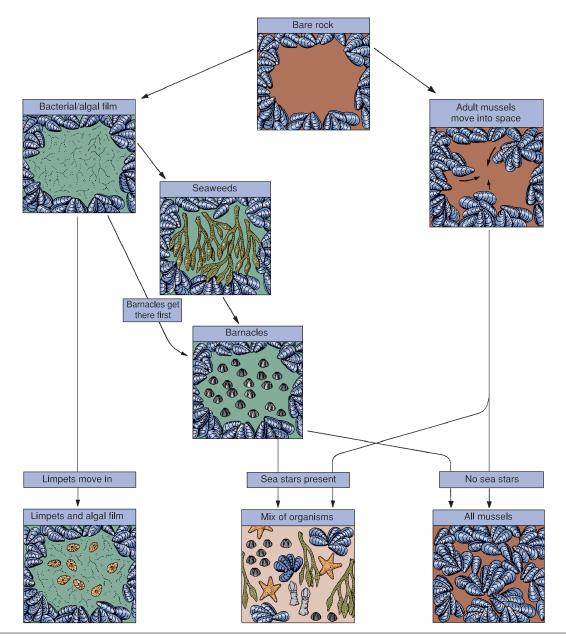


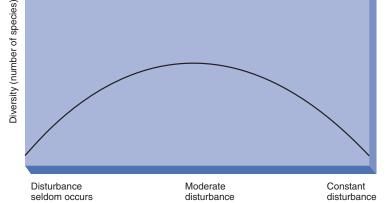
FIGURE 11.21 Ecological succession following the clearing of a patch in a mussel bed. The pathway taken and the end result depend on the size of the patch, when it opens up, and just plain luck—which organisms get there first.

Natural disturbances can have effects similar to those of predation. When mussel beds get too dense, clumps of mussels can be torn away by waves (Fig. 11.12), exposing the bare rock. Drifting logs that batter the rocks and, in cold places, scouring ice and severe freezes have the same effect of opening up new space. This prevents mussels from monopolizing the available space, allowing other organisms to persist.

When a patch of space is cleared, new organisms often move into the patch and get replaced by others in a regular sequence (Fig. 11.21). The term **ecological succession** is used to refer to such regular patterns of regrowth. In the rocky intertidal the first stage is usually a thin film of

bacteria and microscopic algae, such as diatoms, that covers the rock. This film may condition the rock surface, since the settling larvae of some species prefer surfaces with this film to bare rock. Seaweeds often move in next, followed by barnacles and finally mussels, the dominant competitor. The final stage in an ecological succession is called the **climax community**.





**FIGURE 11.22** Other things being equal, the number of species depends on how often disturbances occur. In this context, predation on the dominant competitors counts as a disturbance. When disturbance is rare, the dominant competitors take over and exclude other species. Intermediate levels of disturbance prevent this and give other species a chance. Thus, the number of species is highest when disturbance is moderate. If disturbance happens too often, most species cannot get a foothold and the number of species drops.

The typical steps of ecological succession in the middle intertidal of many rocky shores are, first, a bacterial and algal film, then seaweeds, barnacles, and finally the climax mussel community.

The actual pattern of succession may deviate from the "typical" pattern for many reasons. For example, grazers such as limpets and chitons may remove newly settled animal larvae and seaweed spores. If grazers move into a patch early on, the succession may never get past the bacterial and algal film stage. Predators and other disturbances help determine whether the final stage is a solid mussel bed or a mixture of species.

Furthermore, steps in the succession may be skipped. For example, seaweeds may never be able to colonize a patch if barnacle larvae get there first (Fig. 11.14). The time of year that the patch is created is important. If the patch opens up when barnacle larvae are abundant and seaweed spores are rare, the barnacles have the upper hand. Thus, there is an element of random chance, or "luck," in the development of the community. Stages may also be skipped if the bare patch is small. A small patch cleared in the middle of a mussel bed may be taken over by other mussels that move in from the sides before the succession gets started.

Without predation and other disturbances, the best competitors take over and many species disappear from the area. Disturbances can prevent this. Mussels, for instance, are often unable to completely cover middle intertidal rocks because sea stars eat them or waves tear them away. This gives other species a chance. Disturbance can thus increase the number of species that live in an area, that is, the diversity, by interfering with competitive exclusion. The rocky intertidal in some places can be thought of as a mosaic of patches that were cleared at different times and are therefore in different stages of succession. Because each patch supports a separate set of organisms, the number of species in the area as a whole increases. On the other hand, if predation and other disturbances happen too often, the community will keep getting knocked back to the starting point. It will never get a chance to develop, and not many species will be able to live there. The highest diversity occurs when there is enough disturbance to prevent the dominant competitors from taking over, but not so much that the community is unable to develop (Fig. 11.22).

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Species diversity in the intertidal is strongly affected by predation and other disturbances. Without such disturbances, a few dominant competitors, especially mussels, take over. Occasional disturbance removes the mussels and gives other species a chance. Too much disturbance removes most species.

#### •

### The Lower Intertidal

The lower intertidal is immersed most of the time. This makes it easy for predators like sea stars and dog whelks to feed, so mussels and barnacles are rare. The lower intertidal is dominated by seaweeds, which form a thick turf on the rocks. These seaweeds, including species of red, green, and brown algae, cannot tolerate drying out, but in the lower intertidal they grow in profusion. Not surprisingly, grazing and competition are also important in the lower intertidal. Light, as well as space, is an important resource. Seaweeds often compete by overgrowing each other, blocking the light.

The lower intertidal is dominated by red, green, and brown seaweeds.

A good example of the importance of the interaction of competition and grazing comes from the coast of New England. Two common seaweeds there are a green alga, *Enteromorpha*, sometimes called the green thread alga, and a red alga (not a moss), called Irish moss (*Chondrus crispus*). When the two seaweeds grow together in tide pools, *Enteromorpha* dominates by overgrowing the Irish moss (Fig. 11.23). Surprisingly, however, Irish moss is the most common seaweed in many tide pools.

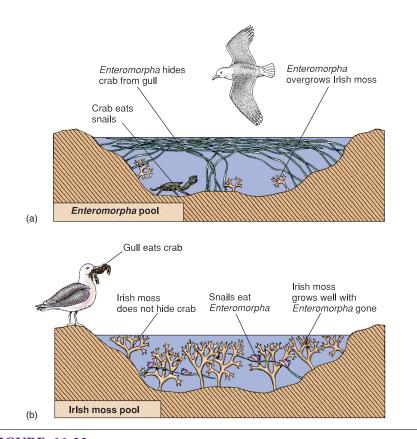
The reason for this is that grazing sometimes prevents *Enteromorpha* from taking over. A common grazer in the area is the common periwinkle (*Littorina littorea*), which is closely related to the

**Competitive Exclusion** The elimination of one species by another as a result of competition.

Chapter 10, p. 218

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**FIGURE 11.23** Biological interactions determine what type of seaweed predominates in New England tide pools. Unless something interferes, both types of pool are self-sustaining. As with the chicken and the egg, you might ask yourself which part of each system comes first.

periwinkles that live in the upper intertidal. Although *Enteromorpha* is one of its favorite foods, the snail hardly touches Irish moss. If a tide pool has a lot of snails, they eat the *Enteromorpha* and make way for Irish moss. The importance of the periwinkles has been shown in transplantation and removal experiments. If snails are transplanted into an *Enteromorpha* pool, *Enteromorpha* quickly disappears and Irish moss takes over. On the other hand, *Enteromorpha* soon moves in after periwinkles are removed from an Irish moss pool.

The story doesn't end there. If the periwinkles like *Enteromorpha* so much, you might think that they would move into *Enteromorpha* pools, but they don't. For one thing, large periwinkles do not move around a lot and prefer to stay in one tide pool. Young periwinkles are eaten by green crabs (*Carcinus maenas*), which also live in tide pools. The crabs, in turn, are eaten by gulls (*Larus*). *Enteromorpha* provides cover for the crabs, protecting them from gulls. The crabs then eat young periwinkles, preventing *them* from colonizing the pool. In Irish moss pools, on the other hand, the crabs lack cover and are eaten by gulls. Without the crabs, young periwinkles can survive in the tide pools. Thus both types of tide pools perpetuate themselves.

The lower intertidal supports many other seaweeds besides *Enteromorpha* and Irish moss. These range from delicate reds and greens to large, tough kelps (*Egregia, Laminaria*; see Fig. 13.20). The kelps mark the lower limit of the intertidal and continue down into the **subtidal zone**. Thus, there is no precise boundary between the lower reaches of the intertidal and the upper edge of the subtidal. **Coralline red algae** (*Corallina*,

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*Lithothamnion*) can also be abundant. Surf grass (*Phyllospadix*), a flowering plant, is common in the lower intertidal on the Pacific coast of North America (see Figs. 6.13*c* and *e*).

A host of small animals live among the seaweeds, hiding from predators and staying moist during very low tides. Sea urchins (*Strongylocentrotus, Echinometra*; see Fig. 13.19) are common grazers on the seaweeds. Also present in the lower intertidal are sea anemones (*Anthopleura, Metridium*; Fig. 11.24), polychaete worms (*Spirorbis, Phragmatopoma*), snails (*Tegula, Nucella*), sea slugs (*Aplysia, Dendronotus*), and many others.

Most intertidal fishes live in the lower intertidal or in tide pools. Gobies, clingfishes, sculpins (*Oligocottus*), pricklebacks (*Cebidichthys*), and gunnels (*Xererpes*) are among the most common. These are all small fishes that are adapted to the environmental extremes of the intertidal. Most are carnivorous.

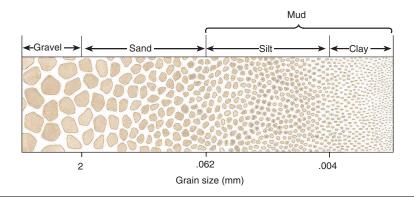
# SOFT-BOTTOM INTERTIDAL COMMUNITIES

Any bottom that is composed of sediment, as opposed to rock, is considered to be a **soft bottom**. The dividing line isn't always clear. Boulder fields are usually thought of as rocky, but how small the rocks have to be before the bottom is considered soft is not precisely defined. In this text we refer to a bottom as soft if organisms are able to burrow in it easily.

Soft bottoms occur where large amounts of sediment have accumulated. In North America, soft bottoms dominate on the east coast south of Cape Cod and virtually all of the Gulf coast (see map in Appendix C). The rocky west coast is often interrupted by sandy beaches and mudflats, especially in and near river mouths. The kind of sediment that accumulates in an area and whether sediment is deposited at all depends on how much water motion there is, as well as on the source of the sediment. In turn, the type of sediment strongly influences the community.



**FIGURE 11.24** The giant green sea anemone (*Anthopleura xanthogrammica*) from the Pacific coast of North America catches small prey with its tentacles but also gets nutrition from symbiotic algae, or zooxanthellae, in its tissues.



**FIGURE 11.25** Sediments are classified by the size of the particles. Sand is relatively coarse; clay is very fine. Together, silt and clay are called mud.

#### The Shifting Sediments

Soft bottoms are unstable and constantly shift in response to waves, tides, and currents. Thus, soft-bottom organisms do not have a solid place for attachment. Very few seaweeds have adapted to this. Seagrasses are the most common large plants on soft bottoms, and they live only in certain places. Under the right conditions, however, seagrasses can form thick beds in the intertidal. In this chapter we deal only with intertidal soft-bottom communities that lack seagrasses. Seagrass communities are discussed in Chapter 13 (see "Seagrass Beds," p. 286).

The animals that live on soft bottoms also lack solid attachment sites. Though a few of them are epifauna and live on the sediment surface, most burrow in the sediment for protection and to keep from being washed away. Animals that burrow in the substrate are called **infauna** because they live *in* the sediment.

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The kind of sediment on the bottom, especially the size of the grains, is one of the most important physical factors affecting soft-bottom communities. Most people use the terms "sand," "silt," "clay," and "mud" without much thought. To a geologist these terms refer to sediments with specific particle sizes (Fig. 11.25).

Careful analysis is needed to determine grain size precisely, but a "quick and dirty" test will literally give you a feel for the different sediment types. Rub a pinch of sediment or soil between your fingers. Any grittiness is caused by sand. Silt and clay, which together are called mud, feel smooth. The finest sand also corresponds to the smallest particles that you can see. To tell silt and clay apart, rub a little between your teeth. The silt feels gritty, but the clay is still smooth.

The terms "sand," "silt," and "clay" refer to sediments of particular grain sizes. Sand is the coarsest, followed by silt and then clay. "Mud" refers to silt and clay together.

Actually, most sediments are made up of a mixture of different particle sizes. The terms for the sediments refer to the most common grain size. Sand, for instance, has mostly sand-sized grains, but it may also have small amounts of mud or a few large rocks.

The sediment composition is directly related to the degree of water motion. Imagine or, better yet, actually perform the following experiment. Take a handful of sediment or soil that contains a wide range of particle sizes, from large pebbles down to clay. Put it in a container with some water and shake it up. As soon as you stop shaking, the pebbles will sink to the bottom. As the water gradually stops moving, first the coarse sand and then finer particles

**Subtidal Zone** The part of the continental shelf that is never exposed by low tide.

Chapter 10, p. 230; Figure 10.20

**Coralline Red Algae** Red algae that deposit calcium carbonate (CaCO<sub>3</sub>) in their tissues.

Chapter 6, p. 110; Figure 6.10

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will begin to sink. Very fine material will remain suspended for a long time, making the water look muddy. You might have to let the container sit still for weeks before the finest clay settles out completely. If the container is stirred even gently, the fine material will never settle out.

This demonstrates a general rule: Fine sediments remain suspended with even a small amount of water motion, whereas coarse sediments settle out unless there is considerable flow. Bottom sediments thus reflect the prevailing conditions at the site. Calm, sheltered areas have muddy bottoms because fine sediments can settle out. Particles of organic matter sink at about the same rate as clay particles, so the two tend to settle out together; clay sediments are therefore rich in organics. Places that experience waves and currents have coarser bottom sediments. If the water motion is strong enough, it may carry away all the loose material, leaving bare rock or large boulders.

Fine sediments are found in calm areas such as bays and lagoons. Coarser sediments are found in areas that are affected by waves and currents.

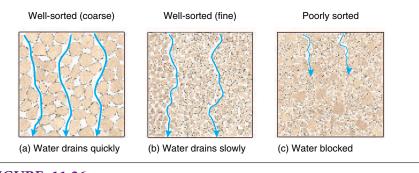
In the experiment described, all the particles would eventually settle out if the container were kept still. If there was a constant flow of water through the container, however, the fine material would be carried away and only certain particles, the coarse ones, would remain. The coarse particles would have been sorted out from the fine ones.

#### Living in the Sediment

Living in sediment has advantages in the intertidal. Soft bottoms stay wet after the tide is out, so the problem of desiccation is not as critical as in the rocky intertidal. This depends on the grain size, however. Coarse sands drain, and therefore dry out, quite rapidly (Fig. 11.26). Partially because of this, coarse sand beaches have relatively little animal life.

#### Oxygen Availability

The amount of organic matter in bottom sediments is particularly important to deposit feeders. Because there are relatively



**FIGURE 11.26** "Sorting" refers to the uniformity of the grain size in the sediment. In well-sorted sediments (*a* and *b*) the grains are all about the same size. There is a lot of space between the grains, so water can flow through. The grain size, as well as sorting, affects how well water circulates; larger grains have larger spaces and are thus more porous. Poorly sorted sediments (*c*) have many different-sized grains. The smaller grains fill in the spaces between the larger ones, making water flow especially difficult.

few primary producers, detritus is the main source of food for soft-bottom animal communities. Deposit feeders extract this organic matter from the sediments. The amount of detritus depends on grain size (see Fig. 13.12). Coarse sands contain very little organic matter. This is why we think of sand as clean. Silt and clay, on the other hand, are usually rich in detritus, which is why they are often smelly.

The grain size also affects the amount of oxygen that is available in the sediments. Oxygen in sediments is used up by the **respiration** of animals and, more importantly, decay bacteria. Below the sediment surface there is no light and therefore no photosynthesis, so the infauna depend on the circulation of water through the sediments to replenish the oxygen supply. Grain size and the degree of sorting strongly affect how porous a sediment is (Fig. 11.26). Any backyard gardener knows that water flows more easily through sand than clay. Water circulation through fine sediments is greatly restricted.

Muddy bottoms, then, have a double problem. First, they have more organic material to decay and use up oxygen. Second, the flow of water that brings in new oxygen is reduced. Except for the upper few centimeters of mud the **interstitial water**, or water between the grains, is deficient in oxygen. If you go very far down at all, in fact, the oxygen is completely used up. Sediments with absolutely no oxygen are said to be **anoxic**.

Anoxic conditions are no problem at all for many bacteria. The bacteria are ca-

pable of anaerobic respiration, in which they break down organic matter without oxygen. A noxious gas called **hydrogen sulfide (H<sub>2</sub>S)** is produced as a by-product. If you have ever had to unclog the drain of your kitchen sink, you have probably run into hydrogen sulfide. It turns things black and smells like rotten eggs. In the sediments, just as in your drain, hydrogen sulfide is produced when bacteria continue to decompose organic material after all the oxygen has been used up. A distinct black layer appears where anoxic conditions begin in the sediments (Fig. 11.27).

The decay of organic matter in the sediments uses up oxygen. Because of this, the interstitial water beneath the sediment surface is often depleted of oxygen, especially in fine sediments.

The infauna, unlike bacteria, must adapt to the short supply of oxygen, especially in muddy bottoms. Many animals avoid the problem by pumping oxygenrich water from the sediment surface with siphons or through their burrows (see Fig. 12.11). Such animals are never actually exposed to low oxygen levels, although the sediments around them may be oxygen deficient.

Other animals are completely buried and have adapted to low-oxygen environments. They often have special **hemoglobins** and other adaptations to extract as much as possible of what little oxygen there is in the interstitial water. Some are sluggish, which reduces their consumption of oxygen. They may even have a Castro–Huber: Marine Biology, Fourth Edition III. Structure and Function 11. Between the Tides of Marine Ecosystems

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**FIGURE 11.27** The black layer in the sediments shows where the oxygen has been completely depleted and hydrogen sulfide (H<sub>2</sub>S) is produced by anaerobic bacteria.

limited capability to carry out anaerobic respiration. A few animals, in fact, have symbiotic bacteria that help them live in low-oxygen sediments. Even so, hydrogen sulfide is highly toxic, and anoxic sediments have little animal life.

#### Getting Around

Soft-bottom animals use a variety of methods to burrow through the sediments. Clams (Macoma, Donax) and cockles (Cardium) take advantage of being able to change the shape of their muscular feet. First, they make the foot thin and reach forward with it (Fig. 11.28). Then, the end of the foot thickens and acts as an anchor while they pull the rest of the body along. Many soft-bodied animals do something similar, using their bodies the way clams use the foot (Fig. 11.29). Heart urchins (Lovenia, Echinocardium; see Fig. 13.7) burrow or plough through the sediment with their spines and tube feet. The many crustaceans that live on soft bottoms-such as amphipods (Talitrus, Corophium); sand,

or mole, crabs (*Emerita*); and ghost (*Callianassa*) and mud (*Upogebia*) shrimps—use their jointed appendages to dig.

Quite a few deposit feeders solve two problems at once by eating their way through the sediment. Sea cucumbers, certain worms, and other animals use the same inchworm style of locomotion as do the clams and worms described previously, with one important exception. Rather than push through the sediments, they push the sediments *through them.* They digest the organic matter and leave the rest of the sediment behind (fig. 11.30).

**Respiration** Glucose  $+ O_2 \rightarrow CO_2 + H_2O + energy.$ *Chapter 4, p. 72* 

**Hemoglobin** Red protein in the blood of vertebrates and some invertebrates that transports oxygen.

Chapter 8, p. 166

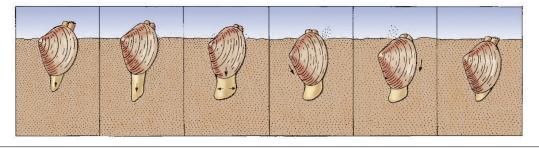
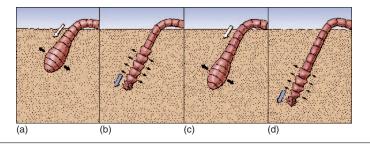


FIGURE 11.28 Burrowing in clams and cockles. The foot does all the work. The clam first pushes its foot down through the sediment. Then the clam expands the end of the foot, which anchors the clam as it pulls its body down.



**FIGURE 11.29** Burrowing in the lugworm (*Arenicola*). (*a*) The worm expands the end of its body (black arrows). The expanded end acts as an anchor and the rest of the body is pulled along behind (white arrow). (*b*) The worm then flares its segments (black arrows), which prevents it from sliding backward when it pushes its proboscis forward (blue arrow). As the process is repeated (*c* and *d*), the worm moves forward through the sediment.



FIGURE 11.30 After digesting out the organic matter, this sea cucumber (*Holothuria edulis*) has deposited a pile of undigested sand pellets.

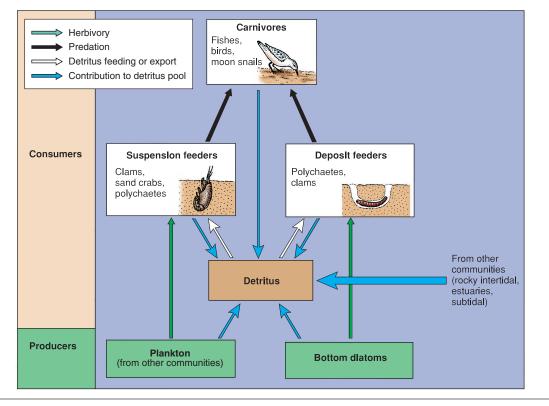


FIGURE 11.31 A generalized food web on a sandy beach.

Some soft-bottom animals are so small that instead of burrowing through the sediments they move between the grains. These animals are collectively called the **meiofauna**. There are many different types of animals in the meiofauna, but most have independently evolved a worm-like shape (see "Life in Mud and Sand," p. 283).

#### Feeding

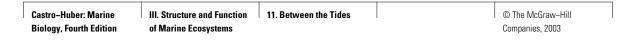
As already noted, detritus is the main source of food in the soft-bottom intertidal (Fig. 11.31). **Diatoms** at the sediment surface sometimes form mats that can be very productive. Diatoms generally do not account for much production, however. In any case, most animals don't distinguish between the diatoms and detritus. **Plankton** brought in by the tides also make a small contribution to the food supply. Many different methods of deposit feeding have evolved. One of the more common methods has already been described: Animals such as sea cucumbers and various worms take in sediment as they burrow, digest the detritus and small organisms, and leave the rest of the sediment in their wake. This technique is more common in mud bottoms than sand, probably because mud contains more organic matter. Sand is also abrasive and hard on the digestive system.

Sand dollars (*Mellita, Dendraster*; see Figs. 7.45*b* and 13.8) are more selective. They use their tube feet to pick up organic particles. Sand dollars burrow near the sediment surface, where detritus is still accumulating and is therefore more abundant. The bent-nosed clam (*Macoma*; see Fig. 12.11*f*) also concentrates on the upper layer of sediment. It uses a long siphon to suck up food particles

from the surface. Other animals catch particles as they settle out and are thus on the line between suspension feeding and deposit feeding. Some polychaete worms (*Terebella*) have long, sticky tentacles that they spread out on the bottom to gather food (see Fig. 13.11). Other polychaetes produce a mucus net that they use instead of tentacles.

There are also suspension feeders that don't wait for the detritus to settle. An olive shell (*Olivella*) from Central America makes a mucus net, but instead of spreading the net on the bottom the snail holds the net up in the water to filter food. Sand, or mole, crabs use a somewhat similar method. They have a pair of large, bushy antennae that they hold up into the water to trap food. By quickly burying and uncovering themselves, they combine feeding and locomotion. When the tide is coming in and they want to

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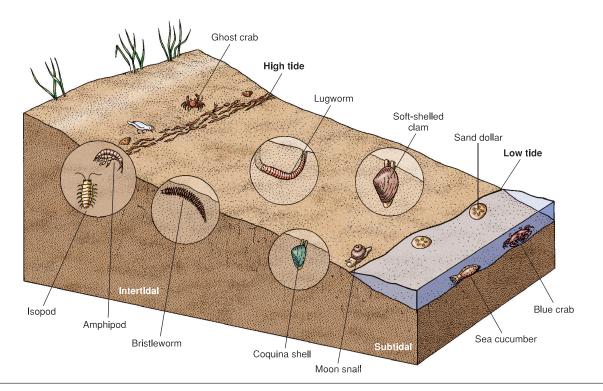


FIGURE 11.32 Typical zonation pattern on sandy beaches of the Atlantic coast of North America.

move up the beach, they uncover just before a wave hits, ride the wave up, and raise their antennae. Then they burrow to keep from being washed back down. As the tide recedes, they do the opposite, burrowing before the wave arrives, then popping out to ride the backwash down the beach.

Soft bottoms also have their share of predators. Moon snails (*Polinices*) burrow through the upper sediments looking for clams. When the snails find a clam, they drill a hole in the clam's shell and eat it. Several polychaetes and other worms are also important predators. Birds can be major predators during low tide (see Fig. 12.12). At high tide, fishes can come in. Fishes often don't eat an entire animal. Instead they just nip off clam siphons or other bits that stick out.

#### Zonation

Because the organisms live in the sediments and can't be seen, zonation on soft bottoms is not as obvious as in the rocky intertidal. Zonation does exist, however, especially on sandy beaches (Fig. 11.32). Water drains rapidly from the sand and, because the beach slopes, the upper part is drier than the lower part.

The upper beach is inhabited by beach hoppers, or sand fleas, which are really amphipods, and by isopods. In warmer areas, these small crustaceans are replaced by ghost (*Ocypode*) and fiddler crabs (*Uca*; see "Fiddler on the Mud," p. 269) that scurry about catching smaller animals, scavenging bits of dead meat, and gathering detritus. Polychaetes, clams, and other animals appear lower on the beach. Zonation is even less obvious in muddy areas. The bottom in such places is flat, and fine sediments retain water. The habitat therefore does not change very markedly between the high- and low-water marks.

**Diatoms** Single-celled, photosynthetic organisms that have a shell, or test, made of silica.

Chapter 5, p. 96; Figure 5.5

**Plankton** Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents. *Chapter 10, p. 230; Figure 10.19*  III. Structure and Function 11. Bet of Marine Ecosystems

11. Between the Tides

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## interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

### **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

### Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

### **Critical Thinking**

- 1. There are marked differences in the type of organisms found at four different locations at the same tidal height along a rocky shore. What might account for this? Offer at least three possible explanations.
- 2. Most marine biologists hypothesize that space, not food, limits populations in the rocky intertidal. What kind of experiments could be performed to test this hypothesis?

### For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol ., and will contain live links when you visit this page in the Online Learning Center.

#### **General Interest**

- Chadwick, D. H., 1997. What good is a tidepool? *Audubon*, vol. 99, no. 3, May–June 1997, pp. 50–59. Tide pools are a microcosm of the oceans and a great place to learn about nature.
- Horn, M. H. and R. N. Gibson, 1988. Intertidal fishes. *Scientific American*, vol. 258, no. 1, January, pp. 64–70. The ways in which fishes have adapted to the rigorous demands of the intertidal are described.
- Leggett, W. C. and K. T. Frank, 1990. The spawning of the capelin. *Scientific American*, vol. 262, no. 5, May, pp. 102–107. This small fish spawns on beaches on the Atlantic coast of North America. The emergence of the offspring is dependent on weather as well as tides.
- Mangin, K., 1990. A pox on the rocks. *Natural History*, vol. 99, no. 6, June, pp. 50–53. In Mexico a recently discovered hydroid, a relative of jellyfishes, kills young barnacles. This makes way for seaweeds and limpets.
- Robles, C., 1996. Turf battles in the tidal zone. *Natural History*, vol. 105, no. 7, July, pp. 24–27. Spiny lobsters gobble up mussels during their nighttime forays into the intertidal zone. This makes way for a luxurious carpet of seaweeds.

- Winston, J. E., 1990. Intertidal space wars. *Sea Frontiers*, vol. 36, no. 1, January/February, pp. 46–51. An examination of the battle for space among intertidal invertebrates.
- Wolcott, T. G. and D. L. Wolcott, 1990. Wet behind the gills. *Natural History*, vol. 99, no. 10, October, pp. 46–55. Land and shore crabs carry salt water with them in order to breathe.

#### In Depth

- Booth, D. J. and D. M. Brosnan, 1995. The role of recruitment dynamics in rocky shore and coral reef fish communities. *Advances in Ecological Research*, vol. 26, pp. 309–385.
- McLachlan, A. and E. Jaramillo, 1995. Zonation on sandy beaches. *Oceanography and Marine Biology: An Annual Review*, vol. 33, pp. 305–335.
- Menge, B. A. and G. M. Branch, 2001. Rocky intertidal communities. In: *Marine Community Ecology* (M. D. Bertness, S. D. Gaines, and M. E. Hay, eds.), pp. 221–251. Sinauer, Sunderland, Mass.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco and R. T. Paine. Challenges in the quest for keystones. *BioScience*, vol. 46, pp. 609–620.

### See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

- Surgeonfishes being cleaned and changing color (Red Sea)
- Typical Florida coast, showing sand and worm reef (Florida)
- Hairy chiton (Florida)
- Ghost crab (South Carolina)

### Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Rocky shore communities
- Beaches and mudflats
- Waves, tides, and currents
- Shallow subtidal communities
- The coast and the continental shelf

### Quiz Yourself

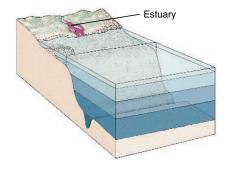
Take the online quiz for this chapter to test your knowledge.

III. Structure and Function of Marine Ecosystems 12. Estuaries: Where Rivers Meet the Seas © The McGraw–Hill Companies, 2003

# Estuaries: Where Rivers Meet the Sea







Drowned river valley estuary (left) Oregon.

unique environment develops where fresh water from rivers enters the sea. **Estuaries** are semi-enclosed areas where fresh water and seawater meet and mix. They therefore represent a close interaction between land and sea. Estuaries are typically inhabited by fewer species than rocky shores. Nevertheless, they are among the most productive environments on earth. Salt-marsh grasses or mangroves thrive along the shore. Seaweeds and cyanobacteria may be common among salt-marsh grasses or on mudflats. A multitude of worms, clams, and shrimps burrow in the

muddy bottom. Snails and crabs crawl along the shore. Fishes swim in the murky, plankton-rich water.

Estuaries also rank among the environments most affected by humans. Most natural harbors are estuaries, and many of the world's great cities—New York, London, and Tokyo among others developed along them. The environmental consequences of human intrusion in estuaries have been disastrous. Estuaries are dredged or filled and transformed into marinas, seaports, industrial parks, cities, and garbage dumps. Countless have been obliterated, and many surviving ones are endangered (see "Modification and Destruction of Habitats," p. 407).

### ORIGINS AND TYPES OF ESTUARIES

Estuaries are scattered along the shores of all the oceans and vary widely in origin, type, and size. They may be called lagoons, sloughs, or even bays, but all share the mixing of fresh water with the sea in a partially enclosed section of the coast. Some oceanographers go as far as classifying



**FIGURE 12.1** Satellite view of the bar-built estuary (arrow) that is formed by the Cape Hatteras barrier islands along the coast of North Carolina in the eastern United States.

enclosed, low-salinity seas, such as the Baltic and Black seas, as estuaries.

Estuaries are partially enclosed coastal regions where fresh water from rivers meets and mixes with seawater.

Many estuaries were formed when sea level rose because of the melting of ice at the end of the last ice age, about 18,000 years ago. The sea invaded lowlands and river mouths in the process. These estuaries are called **drowned river** valleys or coastal plain estuaries (see the photo on page 259). They are the most common type of estuary. Examples are Chesapeake Bay and the mouths of the Delaware and St. Lawrence rivers on the east coast of North America and the mouth of the River Thames in England.

A second type of estuary is the **barbuilt estuary.** Here the accumulation of sediments along the coast builds up **sand** 



**FIGURE 12.2** Milford Sound, on the southwestern coast of New Zealand's South Island, is a fjord. It is a finger-like inlet surrounded by sheer walls that rise 1,200 m (3,900 ft) above sea level and plunge to depths of 500 m (1,640 ft). Its entrance is only 55 m (180 ft) deep. As in other fjords, the shallow entrance restricts the exchange of water between the fjord and the open sea, resulting in stagnant, oxygen-depleted, deep water.

bars and barrier islands (see "Sand on the Run, or What to Do with Our Shrinking Beaches," p. 424) that act as a wall between the ocean and fresh water from rivers. Bar-built estuaries are found, for instance, along the Texas coast of the Gulf of Mexico, the section of the North Carolina coast protected by the Outer Banks and Hatteras barrier islands (Fig. 12.1), and along the North Sea coast of the Netherlands and Germany.

Other estuaries, such as San Francisco Bay in California, were created not because sea level rose but because the land sank, or **subsided**, as the result of movements of the crust. These are known as **tectonic estuaries**.

Another type of estuary was created when retreating glaciers cut deep, often spectacular, valleys along the coast. The valleys were partially submerged when sea level rose, and rivers now flow into them. These estuaries, or **fjords**, are common in southeastern Alaska, British Columbia, Norway, southwestern Chile, and the South Island of New Zealand (Fig. 12.2). Estuaries can be classified into four basic groups based on their origins: drowned river valleys, bar-built, tectonic, and glacier-carved estuaries, or fjords.

Broad, well-developed estuaries are particularly common in regions with flat coastal plains and wide continental shelves, a feature typical of **passive margins**. This is the case along the Atlantic coast of North America. The opposite is true for the steep coasts and narrow continental shelves of the Pacific coast of North America and other **active margins**. Here narrow river mouths carved along the steep coast have restricted the formation of estuaries.

### PHYSICAL CHARACTERISTICS OF ESTUARIES

Influenced by the tides and the mixing of fresh and salt water, estuaries have a unique combination of physical and

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chemical characteristics. These factors govern the lives of the organisms that live there.

#### Salinity

The salinity of estuaries fluctuates dramatically both from place to place and from time to time. When seawater, averaging about 35‰ salinity, mixes with fresh water (nearly 0‰) the mixture has a salinity somewhere in between. The more fresh water that is mixed in, the lower the salinity. Salinity therefore decreases as one moves upstream (Fig. 12.3).

Salinity also varies with depth in the estuary. The salty seawater is more dense and stays on the bottom (see "Salinity, Temperature, and Density," p. 48). It flows in along the bottom in what is frequently known as a **salt wedge.** Meanwhile, the fresher, less dense water from the river flows out on the surface.

The salt wedge moves back and forth with the daily rhythm of the tides (Fig. 12.4). It moves up the estuary on the rising tide, then recedes as the tide falls. This means that organisms that stay in one place are faced with dramatic fluctuations in salinity. They are submerged under the salt wedge at high tide and under lowsalinity water at low tide. If the area has a **diurnal tide**, the organisms are subjected to two shifts in salinity every day: one as the tide moves upstream and a second as it retreats. In an estuary with **semidiurnal tides**, salinity changes four times a day.

Estuaries are subject to wide fluctuations in salinity.

The behavior of water masses in estuaries is not always this simple. The shape of the estuary and its bottom, the wind, evaporation of water from the surface, and changes in the tide all influence the distribution of salinity. Also of importance are seasonal variations in freshwater runoff from rivers as a result of droughts, rains, or snowmelt. Currents are especially important. Because most estuaries are long and narrow, the tide doesn't just rise, it rushes in, often creating strong **tidal currents**. In a few places the tide actually comes in as a nearly vertical wall of water known as a **tidal bore**. Such strong water movements greatly affect the pattern of salinity in an estuary.

of similar salinity and are known as isohalines.

FIGURE 12.3

Another factor that affects circulation in estuaries is the **Coriolis effect**. North of the Equator, the fresh water that flows from rivers toward the sea is deflected toward the right. South of the Equator, the flow is to the left. This means that in estuaries located in the Northern Hemisphere marine organisms can penetrate farther upstream on the left side when one faces seaward. In the Southern Hemisphere they extend up the right side.

In regions of little freshwater runoff and high evaporation, the salinity of the water increases. An example is Laguna Madre, a shallow bar-built estuary with limited access to the open ocean that parallels the Texas coast for 185 km (115 mi). The average salinity is over 50‰ in some areas, and it may reach 100‰ or more during dry spells. These high-salinity estuaries are called **negative estuaries**.

#### Substrate

Rivers carry large amounts of sediment and other materials, including pollutants, into most estuaries. Sand and other coarse material settle out in the upper reaches of the estuary when the river current slows. The fine, muddy particles, however, are carried further down the estuary. There many of them settle out when the current slows even more, though the finest particles may be carried far out to sea. Therefore, the **substrate**, or type of bottom, of most estuaries is soft mud.

**Plate Tectonics** The process in which large sections of the earth's crust move about.

#### Chapter 2, p. 24

**Passive Continental Margin** One that is on the "trailing edge" of a continent and has little geological activity.

Chapter 2, p. 37; Figure 2.20

Active Margin One that is colliding with another plate and therefore has a lot of geological activity.

Chapter 2, p. 36; Figure 2.20

**Diurnal Tide** A tidal pattern with one high and one low tide each day.

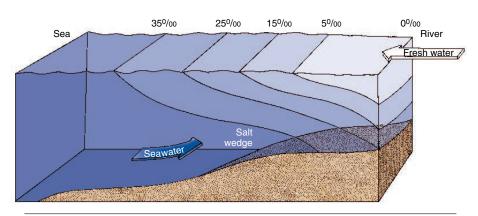
**Semidiurnal Tide** A tidal pattern with two high and two low tides each day.

**Mixed Semidiurnal Tide** A tidal pattern in which two successive high tides are of different heights.

Chapter 3, p. 62; Figure 3.29

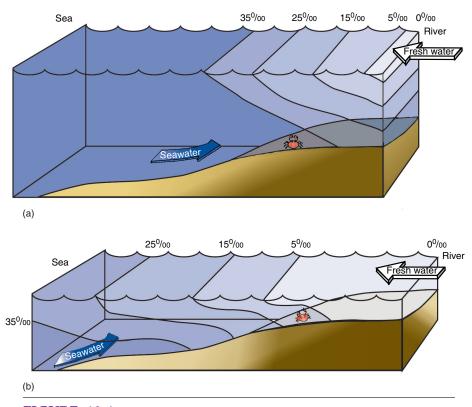
**Coriolis Effect** As a result of the earth's rotation, anything that moves large distances on the earth's surface tends to bend to the right in the Northern Hemisphere and to the left in the Southern Hemisphere.

Chapter 3, p. 52



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Profile of an idealized estuary. The lines across the estuary connect points



**FIGURE 12.4** The salt wedge in a typical estuary moves in and out with the tide. (*a*) At high tide the crab is covered by water with a salinity of 35‰. (*b*) At low tide it is covered by water with a low salinity, between 5‰ and 15‰.

Mud, which is actually a combination of silt and clay (see Fig. 11.25), is rich in organic material. As in other organic-rich sediments, respiration by decay bacteria uses up oxygen in the interstitial water, the water between sediment particles. Water cannot easily flow through the fine sediments to replenish the oxygen supply. As a result, the sediments in estuaries are often devoid of oxygen, or are anoxic, below the first few centimeters (see Fig. 11.27). They have the black color and rotten-egg smell typical of anoxic sediments, in which hydrogen sulfide (H<sub>2</sub>S), which is toxic to most organisms, accumulates. Anoxic sediments are not completely devoid of life. Anaerobic bacteria, which do not need oxygen to carry out respiration, thrive under these conditions.

In estuaries that have unimpeded tidal flow, which includes most shallow ones, there is plenty of oxygen dissolved in the water. Some deep-water estuaries such as fjords (Fig. 12.2), however, have a shallow "sill" at the entrance that restricts water circulation. Low-salinity water flows out unimpeded on the surface. The sill, however, prevents seawater from flowing in along the bottom. The stagnant deep water may become depleted in oxygen because of bacterial respiration associated with the decomposition of organic matter that sinks and accumulates on the bottom.

Fine, muddy sediments brought into estuaries by rivers settle out in the relatively quiet waters. Bacterial respiration in these organic-rich sediments depletes the oxygen in them.

### **Other Physical Factors**

Besides extreme salinity fluctuations and muddy substrates, other physical factors help make estuaries one of the harshest of all marine environments. Water tempera-

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ture in estuaries, except fjords, varies markedly because of their shallow depths and large surface area. Organisms that are exposed at low tide may have to face even more drastic daily and seasonal temperature fluctuations.

There is a large amount of suspended sediment in estuaries, greatly reducing the water clarity. This allows very little light to penetrate through the water column. The particulate material in the water can also clog the feeding surfaces of some filter feeders and even kill some organisms, such as some sponges, that are sensitive to sediment.

### ESTUARIES AS ECOSYSTEMS

To the uninitiated, an estuary may at first look like a wasteland. This impression is far from the truth. Estuaries are tremendously productive and are home to large numbers of organisms, many of which are of commercial importance. Estuaries also provide vital breeding and feeding grounds for many birds, fishes, and other animals. Estuarine ecosystems consist of several distinct communities, each with its own characteristic assemblage of organisms.

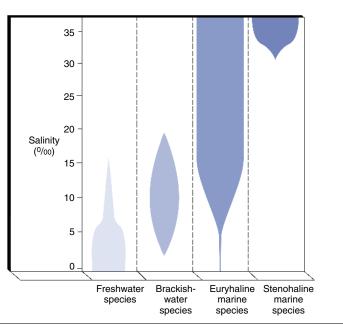
#### Living in an Estuary

Life in an estuary revolves largely around the need to adapt to extremes in salinity, temperature, and other physical factors. Though other marine environments may be more extreme—they may be colder or more saline, for instance—none changes so rapidly or in so many ways as an estuary. Living in an estuary is not easy, so relatively few species have successfully adapted to estuarine conditions.

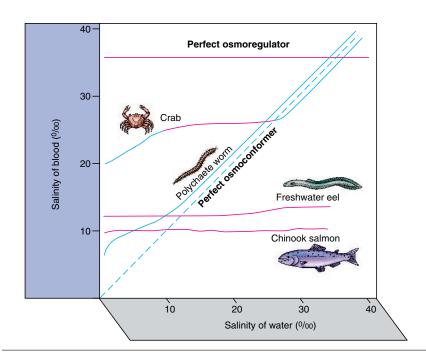
#### Coping with Salinity

Maintaining the proper salt and water balance of cells and body fluids is one of the greatest challenges facing estuarine organisms (see "Regulation of Salt and Water Balance," p. 79). Most estuarine organisms are marine species that have developed the ability to tolerate low salinities (Fig. 12.5). How far they can move up the estuary depends on just how tolerant they are. Most

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**FIGURE 12.5** Types of species living in an idealized estuary in relation to salinity. The width of the bars represents the relative number of species.



**FIGURE 12.6** The concentration of salts and other solutes, known as *salinity*, in the body fluids of estuarine animals responds in various ways to the salinity of the surrounding water. In a perfect osmoconformer, the salinity of the blood exactly matches that of the water. In a perfect osmoregulator, blood salinity stays the same no matter what the water salinity is. We have drawn the line for an imaginary perfect osmoregulator at 35‰. The salmon and freshwater eel are nearly perfect osmoregulators even though their bloods are more dilute. The important point is not the actual salinity of the blood but the fact that it remains relatively constant. Notice that some organisms, like the crab in the diagram, can only osmoregulate within a certain range of salinity; they are osmoconformers outside this range.

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estuarine organisms are **euryhaline** species, that is, they tolerate a wide range of salinities. They evolved from marine species. The relatively few **stenohaline** species, species that tolerate only a narrow range of salinities, may be either freshwater or marine; most are limited to the upper or lower ends of the estuary and rarely penetrate into the estuary proper. There are also some **brackish-water** species, those that are adapted to live in intermediate salinities. Some of these species are stenohaline; others are euryhaline.

Because of their marine background, most estuarine organisms face the problem of the water in estuaries being diluted with fresh water. Those having an internal salt concentration higher than that of the surrounding water tend to take on water through **osmosis**. Some animals adapt by simple changes in behavior. They may hide in their mud burrows, close their shells, or swim away if the salinity drops. These strategies are not widespread in estuaries, however, and most organisms rely on more complex but reliable mechanisms.

Soft-bodied estuarine animals, such as many molluscs and polychaete worms, often maintain osmotic balance simply by allowing their body fluids to change with the salinity of the water. They are called osmoconformers (Fig. 12.6). Many crabs and fishes, as well as some molluscs and polychaetes, are instead osmoregulators. They keep the salt concentration of their body fluids more or less constant regardless of the water salinity. They get rid of excess water and, via active transport, absorb some solutes from the surrounding water to compensate for those lost in the elimination of water. The kidneys, gills, and other structures accomplish this.

**Osmosis** The movement of water from high to low concentrations across a membrane.

Active Transport The transfer of substances across membranes by a cell against a *concentration gradient*.

Chapter 4, p. 79



FIGURE 12.7 Cordgrass (*Spartina*) is an important component of salt marshes on both the Atlantic and Pacific coasts of North America and other temperate shores around the world.

Organisms in estuaries have adapted to salinity fluctuations in various ways. Osmoconformers let the salinity of their body fluids vary with that of the water. Osmoregulators keep the salt concentration of their body fluids constant.

Bony fishes that inhabit estuaries also need to osmoregulate since their blood is less salty than seawater (see Fig. 4.14 and "Regulation of the Internal Environment," p. 166). Salmon and freshwater eels migrate back and forth between rivers and the sea and still maintain a stable internal environment thanks to the active transport of solutes by their kidneys and gills.

Few animals can be neatly classified as perfect osmoconformers or perfect osmoregulators. Many invertebrates, for instance, osmoregulate at low salinities and osmoconform at higher salinities. Even efficient osmoregulators such as salmon and freshwater eels do not keep *exactly* the same concentration of salts and other solutes in their blood as salinity changes.

Estuarine plants must also handle salinity variations. Grasses and other salt-



**FIGURE 12.8** Several species of pickle weed (*Salicornia*) are common succulent plants in salt marshes around the world.

marsh plants are land plants that have developed high salt tolerance. Some of these plants actively absorb salts and concentrate harmless solutes like sugars to match the outside concentrations and prevent water from leaving their tissues. Notice that this is opposite to the situation in marine organisms that live in estuaries, which have to adapt to reduced, not increased, salinities.

Cordgrasses (*Spartina*; Fig. 12.7), other salt-marsh plants, and some mangroves excrete excess salts by way of salt glands in their leaves. Some estuarine plants, such as pickle weed (*Salicornia*), accumulate large amounts of water to dilute the salts they take up (Fig. 12.8). Fleshy plants such as these are known as **succulents**.

#### Adapting to the Mud

As we learned in Chapter 11 (see "Living in the Sediment," p. 254) living in mud has its problems. There is nothing to hold on to, so most animals either burrow or live in permanent tubes beneath the sediment surface. Clams do well because they can extend their siphons through the mud to get water for food and oxygen. Because it is difficult to move through mud, the inhabitants tend to be stationary or slow-moving. Living in mud, however, has a benefit: Salinity fluctuations are less drastic than in the water column.

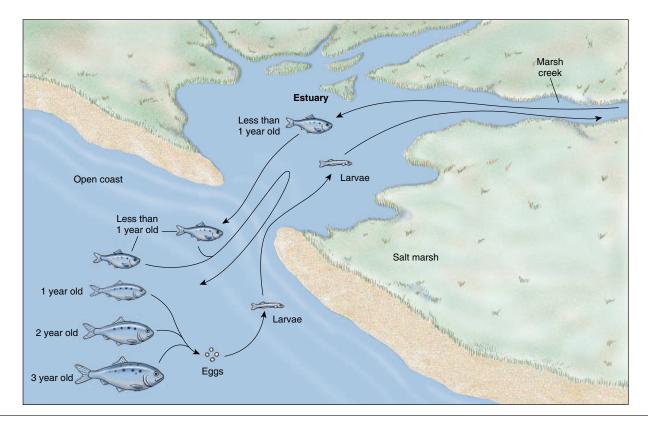
The depletion of oxygen caused by the decay of organic matter in the mud presents another challenge. This is no problem to burrowers that pump oxygenrich water into their burrows. Burrowers without this luxury have special adaptations to low-oxygen environments. Some have blood that contains **hemoglobin**. Furthermore, the hemoglobin itself has a particularly high affinity for oxygen: It can hold and carry oxygen even when only minute quantities are available. Some clams and a few other mud-dwellers can even survive without oxygen for days.

### Types of Estuarine Communities

Several distinct communities are associated with estuaries. One consists of the **plankton**, fishes, and other open-water organisms that come in and leave with the tide. Several other communities are permanent parts of the ecosystem.

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**FIGURE 12.9** The menhaden (*Brevoortia*) is one of the most important commercial fishes along the Atlantic and Gulf coasts of the United States. Adult fish (1 to 3 years old) spawn offshore and the larvae drift with the tides and currents into estuaries, moving into shallow areas in the salt marshes to grow.

Estuarine communities consist of relatively few species. These species, however, are typically represented by many individuals. A surprising number of estuarine species, particularly those inhabiting temperate estuaries, are widely distributed around the world. Many have been introduced by humans.

#### Open Water

The type and abundance of plankton inhabiting estuaries vary tremendously with the currents, salinity, and temperature. The murky water restricts the penetration of light and may limit **primary production** by phytoplankton. Most of the phytoplankton and zooplankton in small estuaries are marine species flushed in and out by the tides. Larger, more stable estuaries may also have their own, strictly estuarine, species.

One reason many of the world's great cities developed around estuaries is

the rich supply of fish and shellfish in or near estuaries. Many species of commercially important fishes and shrimps use estuaries as nurseries for their young, taking advantage of the abundant food and relative safety from predators. About 90% of the marine commercial catch in the northern Gulf of Mexico, for example, is of species that depend on estuaries at some point in their lives. A rich variety of fishes live in most estuaries. Many are the juveniles of marine species that breed at sea but use estuaries as nurseries. A significant number is of enormous commercial importance worldwide. Examples are the menhaden (Fig. 12.9), anchovies, mullets, croakers, and many species of flatfishes. Some fishes move through the estuary during their migrations. Migrating fishes are

**Hemoglobin** Red protein in the blood of vertebrates and some invertebrates that transports oxygen.

Chapter 8, p. 166

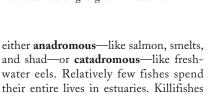
**Plankton** Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.

Chapter 10, p. 230; Figure 10.19

**Primary Production** The conversion of carbon from an inorganic form, carbon dioxide, into organic matter by autotrophs—that is, the production of food.

Chapter 4, p. 73

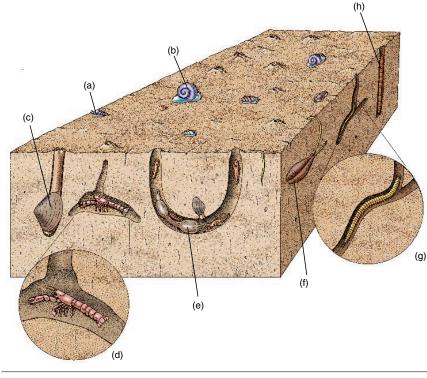
**FIGURE 12.10** The California horn snail (*Cerithidea californica*), a deposit feeder, is extremely abundant on mudflats. The green alga is *Enteromorpha*, which tolerates wide fluctuations in salinity and temperature as well as pollution. It can be found on rocky shores as well as along the shores of estuaries. It thrives during the long, sunny days of summer, when it can turn mudflats into bright-green "meadows."



(*Fundulus*) are one example. Shrimps and crabs are often common in estuaries, and many commercially valuable species use estuaries as nurseries.

#### Mudflats

The bottoms of estuaries that become exposed at low tide often form **mudflats** (see Fig. 12.14). Mudflats are especially extensive in estuaries where there is a large tidal range difference between high and low tide and a gently sloping bottom. It all looks pretty much the same, but the mudflat can vary widely in the size of particles. Sand may accumulate to create sand flats near river mouths and in the tidal creeks that form as the tide changes. In the calmer central part the mudflat contains more fine, silty material.



**FIGURE 12.11** Some representative inhabitants of mudflats in temperate estuaries include (a) mud snails (*Hydrobia*), (b) moon snails (*Polinices*), (c) the soft-shelled clam (*Mya arenaria*), (d) ghost shrimps (*Callianassa*), (e) the fat innkeeper (*Urechis caupo*) and guests, (f) bent-nosed, or small, clams (*Macoma*), (g) sandworms (*Nereis*), and (b) bamboo worms (*Clymenella*). Many mudflat organisms also can be found in muddy bottoms outside estuaries (also see Fig. 13.6).

Mudflat communities in estuaries are similar to those on muddy shores (see "Soft-Bottom Intertidal Communities," p. 252). Low tides expose organisms to desiccation, wide variations in temperature, and predation, just as in any other intertidal community. In estuaries, however, mudflat organisms must also withstand regular variations in salinity.

The presence of **primary producers** is usually not very evident on mudflats. A few hardy seaweeds—such as the green algae *Enteromorpha* (Fig. 12.10) and *Ulva*, the sea lettuce, and the red alga *Gracilaria*—manage to grow on bits of shell. These and other primary producers may be particularly common during the warmer months. Large numbers of benthic diatoms grow on the mud and often undergo extensive blooms, forming golden-brown patches. In tide pools left by the receding tides these patches become coated with oxygen bubbles as intense photosynthesis takes place in the sunlight.

Bacteria are extremely abundant on mudflats. They decompose the huge amounts of organic matter brought in by rivers and tides. When the oxygen is used up by decay, some bacteria produce hydrogen sulfide. This, in turn, is used by **sulfur bacteria**, **chemosynthetic bacteria** that derive energy by breaking down sulfur compounds such as hydrogen sulfide. Diatoms and bacteria, including photosynthetic bacteria, actually account for most of the primary production in mudflats.

The dominant animals on mudflats burrow in the sediment and are known as **infauna** (Fig. 12.11). Though there are not many species of these burrowing animals, they often occur in immense numbers. At low tide their presence may be revealed only by small sediment mounds topped by a hole or piles of feces and other refuse. They feed on the abundant

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**detritus** in the sediment and water. Most of the food for these animals is brought in by the rivers and tides and is not actually produced on the mudflat. Very few mudflat animals can be classified as **epifauna**, those that either live *on* the sediment surface or are attached to a surface as **sessile** forms.

Mudflat inhabitants that feed on detritus are **deposit** and **suspension feeders**. Deposit feeders are more common than suspension feeders on mudflats and other muddy bottoms (see Fig. 13.12). Many suspension feeders, which include filter feeders, are actually excluded, or eliminated, by deposit feeders on these soft bottoms. They are at a disadvantage because their filtering mechanisms tend to get clogged by the higher amounts of detritus that rain on soft bottoms. Suspension feeders, on the other hand, are more common where the sediment is more sandy. The wider interstitial spaces between these larger sand particles hold less of the detritus that feeds deposit feeders. Suspension feeders, many of which stay in one place while filtering the water, are better adapted to live in sandy sediments than deposit feeders, who find softer sediments easier to dig into. The disturbance of sediments caused by deposit feeders further helps in the exclusion of suspension feeders by clogging filtering surfaces and burying newly settled larvae.

The dominant producers on mudflats are diatoms and bacteria. Most of the animals are burrowing deposit and suspension feeders that feed on detritus.

Protozoans, nematodes, and many other minute animals that compose the meiofauna (see "Life in Mud and Sand," p. 283) also thrive on detritus. The meiofauna are also known as interstitial animals. The larger burrowing animals, or infauna, include many polychaetes (see Figs. 11.29 and 12.11). Most are deposit feeders. Other polychaetes are suspension feeders that filter water or extrude tentacles to collect the detritus that falls from the water column. Yet another detritus-feeding strategy among some polychaetes is to switch back and forth between suspension and deposit feeding, depending on the amount of suspended material in the water.

Bivalves often abound on mudflats. Many are filter feeders that are also found on muddy and sandy shores outside estuaries (see Fig. 11.28). Examples from temperate waters are the quahog, or hard clam (*Mercenaria mercenaria*), the softshelled clam (*Mya arenaria;* Fig. 12.11c), and razor clams (*Ensis*). Some of these are of considerable commercial importance. Bent-nosed, or small, clams (*Macoma;* Fig. 12.11f) are deposit feeders that use their long incurrent siphons to vacuum the surface.

The ghost (*Callianassa*; Fig. 12.11*d*) and mud (*Upogebia*) shrimps make elaborate burrows that, as a side effect, help oxygenate the sediment. These shrimps feed on detritus that they filter from the water and sift from the mud. Fiddler crabs (*Uca*) also live in burrows but are active on the mudflats at low tide (see "Fiddler on the Mud," p. 269). They process the mud and extract the detritus, which they eat.

On the Pacific coast of North America the fat innkeeper (*Urechis caupo*), an echiuran worm, secretes a funnel-shaped net of mucus. It pumps water through this net to filter out food (Fig. 12.11*e*). It gets its common name because it shares its U-shaped burrow with a polychaete (*Hesperonoe adventor*), a crab (*Scleroplax* granulata), one or more fish (*Clevelandia* ios), and other guests.

Some animals live on the surface of the mud or move in and out with the tide. These include deposit feeders such as mud snails (*Cerithidea*, *Hydrobia*;

Anadromous Fishes Those that migrate from the sea to spawn in fresh water. *Chapter 8, p. 171* 

**Catadromous Fishes** Those that migrate from fresh water to spawn at sea. *Chapter 8, p. 172* 

**Chemosynthetic Bacteria** *Autotrophic bacteria* that use energy contained in inorganic chemicals rather than sunlight to make organic matter.

Chapter 5, p. 95

**Detritus** Particles of dead organic matter. *Chapter 10, p. 224*  Figs. 12.10 and 12.11*a*), amphipods, and shrimps. Carnivores include polychaete worms (*Nereis*; Fig. 12.11*g*), moon snails (*Polinices*; Fig. 12.11*b*) and other predatory snails (*Busycon*), and swimming crabs (*Callinectes*).

By far the most important predators in the mudflat community are fishes and birds. Fishes invade mudflats at high tide, whereas birds congregate at low tide to feed. Estuaries are important stopover and wintering areas for many species of migratory birds. The open spaces offer them safety from natural enemies, and food is plentiful. The most significant predators in mudflats are wading shorebirds (Figs. 12.12 and 12.13). These include the willet, godwits, dowitchers, and many species of plovers and sandpipers. They feed on polychaetes, ghost shrimps and other small crustaceans, clams, and mud snails. Oystercatchers specialize on clams and other bivalves.

These many birds do not all exploit the same type of prey. The varying lengths of their bills may represent a specialization in prey because different types of prey live at different depths in the mud (Fig. 12.12). In addition, shorebirds use different strategies to locate their food. Birds such as sandpipers rely mostly on their bills, probing in the mud as they walk around (Fig. 12.13*a*). Others, like plovers, use their eyesight to detect slight movements on the surface of the mud (Fig. 12.13*b*). Some biologists think that these differences in feeding habits are an example of **resource partitioning**.

**Deposit Feeders** Animals that feed on organic matter that settles in the sediment.

Chapter 7, p. 126; Figure 7.16

**Suspension Feeders** Animals, including *filter feeders*, that feed on particles suspended in the water column.

Chapter 7, p. 118; Figure 7.16

**Resource Partitioning** The sharing of a resource by two or more species to avoid competition.

Chapter 10, p. 219

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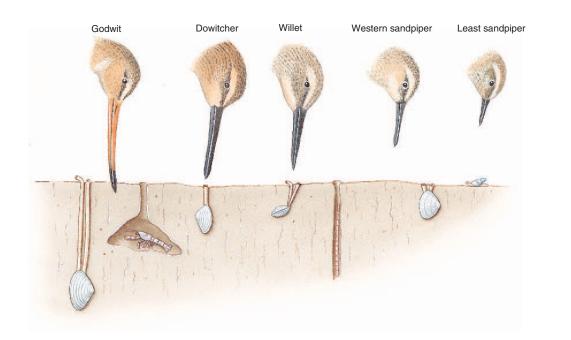


FIGURE 12.12 Differences in the bill length of wading shorebirds from the west coast of North America allow them to feed on particular mudflat animals.

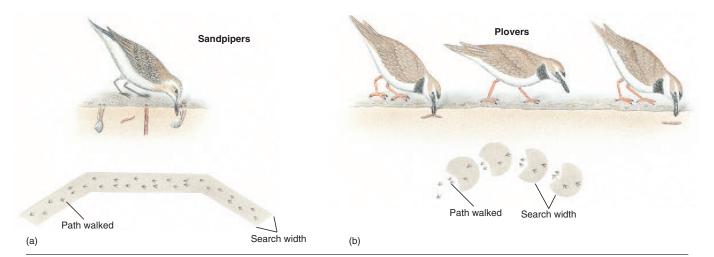


FIGURE 12.13 Feeding behavior also varies among shorebirds. (*a*) Sandpipers use their bills to search for food and follow a roughly straight path. (*b*) Plovers rely mostly on their vision, turning their heads sideways as they move.

Herons and egrets compose yet another group of wading birds. They specialize in catching fishes, shrimps, and other small swimming prey. Birds that feed by swimming or diving in the estuary, such as ducks, terns, and gulls, are often seen resting on mudflats.

#### Salt Marshes

Estuaries in temperate and subarctic regions are usually bordered by extensive grassy areas that extend inland from the mudflats. These areas are partially flooded at high tide and are known as salt, or tidal, marshes (Fig. 12.14). Sometimes they are grouped with coastal environments flooded at high tide and with freshwater marshes and collectively called wetlands. Though mostly associated with estuaries, salt marshes can also develop along sheltered open coasts. Castro-Huber: MarineIII. Structure and Function12. Estuaries: Where Rivers© The McGraw-HillBiology, Fourth Editionof Marine EcosystemsMeet the SeasCompanies, 2003

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What lives in mud, literally feeds on mud, and finds mates by calling and waving across the mud? But, of course—fiddler crabs, creatures remarkable in many ways but best known as the ultimate experts in mud.

The many species of fiddler crabs (Uca) are inhabitants of mud and sand flats in estuaries and other sheltered coasts. They are found mostly in the tropics and subtropics, but some species are found as far as Southern California and Boston Harbor. Fiddlers are deposit feeders. They feed at low tide, using their pincers to scoop mud up into feeding appendages close to the mouth. The detritus in the mud is extracted with the help of brush-like mouthparts. Water is pumped from the gill chambers into the mouth to make the lighter detritus float and thus help separate it from the mud. The detritus is swallowed, and the clean mud is spat out on the substrate in neat little balls.

Fiddlers are active at low tide and retreat into their burrows at high tide. Each burrow has an entrance (revealed by the neat little balls of mud around it) that the occupant can plug when the tide comes in. At the next low tide, crabs emerge from home to feed and do whatever healthy, active fiddlers like to do. The tidal cycle means everything to them. Tides are so crucial that if crabs are taken away and isolated in an environment of constant light and temperature, they will continue to be active at the times that correspond to low tide and sit quietly when they were expected to be at home! Not only activity patterns but color changes that normally take place in their natural environment (darker color during the day, lighter at night) continue to be observed in isolation. These patterns are examples of **biological clocks**, repeated rhythms that are synchronized with time. In the case of fiddlers, activity patterns and color changes are synchronized with tides, which depend on lunar cycles, and also with day-night changes, which depend on the sun.

Fiddlers also have an interesting sex life. Males feature one tremendously enlarged claw, either right or left. It is brightly colored or highlighted with markings in many species. Females have a much smaller pair of claws, which is used in feeding, as is the case of the males' small pincer. Males use their big claw to advertise their sex-to tell females they mean business and to threaten any other males that may be in their way. They wave the claw at low tide on territories established around their burrows. In one species, males build a mud shelter around the burrow to heighten the effect. Claw-waving gets so heated sometimes that a whole mudflat seems to move up and down with hundreds of displaying males. Males entice any interested females into their burrows, and a female may visit a few pads before deciding on a particular one. Males often fight for prospective mates. They fight very carefully: A lost claw means disaster. It takes many molts to regenerate one that is big enough to get the crab back in action, and crabs whose claws are too small or that don't have the right moves can get pretty lonely!

In those areas coinhabited by several species of fiddlers, waving is used to prevent a male from attracting females of the wrong species. Some species wave up and down, others sideways. The angle and frequency of waving also vary, and bowing, fancy steps, and other body movements may form part of the ritual. Some beat the claw on the ground, and males of many species even produce sound by vibrating a joint of the large claw. It pays to advertise!



Signaling in a male fiddler crab (Uca).

They develop as long as disturbance from wave action is minimal to allow the accumulation of muddy sediments. Tidal creeks, freshwater streams, and shallow pools frequently cut through the marsh.

Salt marshes are particularly extensive along the Atlantic and Gulf coasts of North America (Fig. 2.22). The broad estuaries and shallow bays of these gently sloping coastlines provide optimal conditions for the development of salt marshes. The Pacific coast of North America, on the other hand, is generally steeper, and most of the estuaries have formed along narrow river valleys. This has resulted in the development of less extensive salt marshes. In the Northern Hemisphere salt marshes tend to be more extensive on the left side than on the right side of estuaries since the freshwater flow from rivers is stronger on the right side as a result of the Coriolis effect.

Salt marshes are subject to the same extremes in salinity, temperature, and tides that affect mudflats. They also have a muddy bottom, but it is held together by the roots of marsh plants and thus is more stable. Salt-marsh communities are dominated by a few hardy grasses and other salt-tolerant land plants. These plants thrive in the marsh, though the environment is too harsh for most other land plants. There is a pronounced zonation of plants in salt marshes. The location of a given zone is related to the height relative to the tide, but it varies according to geographical location, type of substrate, and other factors. For instance, soil salinity may become particularly high at intermediate heights as a result of higher evaporation in marshes closer to hot, dry

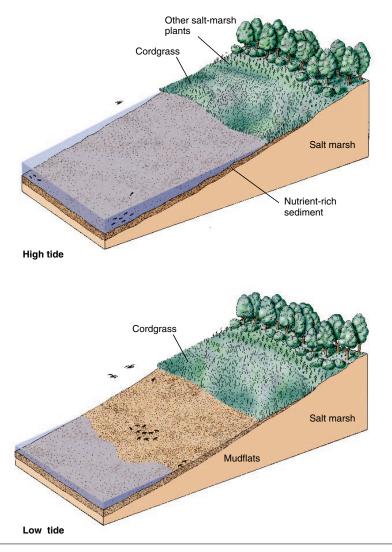


FIGURE 12.14 The daily tides play a crucial role in salt marshes. They help circulate detritus and nutrients and expose mudflat organisms to predation by shorebirds and other animals.

regions. This may result in areas bare of vegetation.

Cordgrasses (Spartina alterniflora on the Atlantic coast; S. foliosa on the Pacific coast; see Fig. 12.7) are typically the most common plants along the seaward limit of the salt marsh, where it meets the mudflats (Fig. 12.14). These grasses invariably occupy the fringe above the mean low-tide level. Plants do better here because the soil is well-drained and therefore richer in oxygen and less salty. The tops of their tall leaves remain exposed to the air even when the bottom is covered at high tide. The plants have extensive horizontal stems that stretch out underground. The leaves and roots develop from the stems. Roots just below the soil may take in oxygen from the air.

Cordgrass may gradually invade mudflats because the plants slow down the tidal flow and thus increase the amount of sediment trapped among the roots. The landward extension of the salt marsh is eventually limited by the height of the highest tide.

In addition to providing a significant portion of the high primary production of estuarine communities (see "Feeding Interactions Among Estuarine

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Organisms," p. 274), salt-marsh plants like cordgrass help stabilize soils by decreasing the effects of wave action. A species of cordgrass from the Atlantic coast of North America, *Spartina alterniflora*, has been introduced in many parts of the world for the protection of shorelines, sometimes with negative effects (see "Biological Invasions: The Uninvited Guests," p. 420).

Cordgrass gives way to other plants in the higher parts of the marsh. On the Atlantic coast (Fig. 12.15), a second species of cordgrass (S. patens) dominates, but rushes (Juncus), pickle weed, and several other plants often form distinct zones. The higher levels of salt marshes on the Pacific coast are usually dominated by pickle weed (see Fig. 12.8). The landward limit of salt marshes is a transition zone with adjacent terrestrial, or land, communities. It is characterized by a large variety of plants resistant to salt spray, such as salt grasses (Distichlis) and several species of pickle weed. It appears that in most salt marshes zonation is determined not only by the effects of flooding by tides but by the combined effect of other factors. They include competition for space among salt-marsh plants, increase in soil salinity as a result of increased temperatures, and even the effect of burrowing animals.

The muddy salt-marsh substrate is home to bacteria, diatoms, and thick mats of filamentous green algae and cyanobacteria. Bacteria play a crucial role by decomposing the large amounts of dead plant material produced in the salt marsh. These bacteria and the partially broken-down organic matter are a major source of the detritus that feeds many of the inhabitants of the estuary. Some bacteria are **nitrogen fixers** that enrich the sediment.

Salt marshes are dominated by grasses and other marsh plants. Bacteria in the mud decompose dead plant material and contribute a large portion of the detritus in the estuary.

Some burrowing animals of mudflats also inhabit the salt marshes. In addition, nematodes, small crustaceans, larvae of land insects, and other small invertebrates live among the algal mats and decaying

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**FIGURE 12.15** A salt marsh near Atlantic Beach, North Carolina. As in other Atlantic marshes, cordgrass (*Spartina alterniflora*) occupies the edge of the marsh that is flooded the most by seawater. It is replaced higher up in the marsh by the salt-marsh hay (*Spartina patens*), a shorter and finer grass that may form extensive meadows. It grows where the marsh is flooded only at high tide. Many of these marshes have been filled in and destroyed.



**FIGURE 12.16** The Atlantic horse, or ribbed, mussel (*Geukensia demissa*) is adapted to live half buried in mud in salt marshes. Like rocky shore mussels, it closes its valves at low tide to prevent dessication and opens them at high tide to feed.

marsh plants. Crabs are conspicuous inhabitants of salt marshes. Fiddler crabs build burrows along the mudflat edges, where they increase the oxygenation of soils. Other marsh crabs (*Sesarma, Hemigrapsus*) are scavengers that eat dead organic matter. Some of these species live in burrows.

Marsh plants provide shelter and food to many marine and land animals. Coffee bean snails (Melampus) and marsh periwinkles (Littorina, Littoraria) are airbreathing snails that feed on detritus and minute algae that grow on marsh plants. They move up the plants as the high tide moves in. Though they are air-breathers, they lay their eggs in the water and the larvae that hatch develop in the plankton. The horse, or ribbed, mussel (Geukensia demissa) is a suspension feeder that lives half buried in the mud among the cordgrass (Fig. 12.16). Killifishes and juvenile silversides (Menidia) are examples of fishes that inhabit tidal creeks and pools in the marsh at low tide. They move into the salt-marsh grass at high tide to escape predators such as crabs and larger fishes, which enter the creeks with the rising tide. Crustaceans and small fishes retreat to pools or tidal creeks at low tide. Rails and American coots are among the birds that feed and nest here. Many other land birds and mammals, from ospreys to raccoons, are common visitors.

#### Mangrove Forests

Though not limited to estuaries, mangrove forests are in many ways the tropical equivalents of salt marshes, although they coexist in many places. Mangroves are flowering land plants adapted to live in the intertidal (see "Flowering Plants," p. 114). These shrubs and trees may form thick forests. The forests are often called mangals to distinguish them from mangroves, the actual plants themselves (see Figs. 6.14 and 6.15). Mangroves are typical of tropical and subtropical regions, where they replace the temperate salt marshes (Fig. 12.17 and map in Appendix C). It has been estimated that from 60% to 75% of all tropical shores are fringed with mangroves, a figure that suggests their tremendous importance.

Mangrove forests, or mangals, are the tropical equivalents of salt marshes. They are dominated by mangroves, which are bushes or trees adapted to be partially immersed at high tide.

Mangroves grow on protected coasts where muddy sediments accumulate. Though mangroves grow in estuaries, they are not restricted to river mouths. As in salt-marsh plants, the various species of mangroves have different tolerances to immersion by high tide. Partly as a result of these differences in tolerance, they show a distinctive zonation in the intertidal, from a marine to a progressively terrestrial environment.

Mangroves need fresh water for growth. Since they live at the sea edge, mangroves must get rid of salts from the water that is taken in by the roots. Most salts are actually not taken in by the roots, and salt glands on the leaves of some species excrete salts.

The red mangrove (*Rhizophora man-gle*) is the most common species of mangrove along the shores of southern Florida, the Caribbean, and the Gulfs of California and Mexico. It lives right on the shore (Fig. 12.18) and is easily identified by its peculiar prop roots, which branch downward and support the treelike stilts (see Fig. 6.14). Flexible aerial roots drop down from the higher branches, helping extend the tree laterally. The trees can be as high as 9 m (30 ft). Under optimal conditions they form dense forests noted for their high primary production.

Nitrogen Fixation Conversion of nitrogen gas (N<sub>2</sub>) into nitrogen compounds that can be used by primary producers as nutrients.

Chapter 10, p. 228

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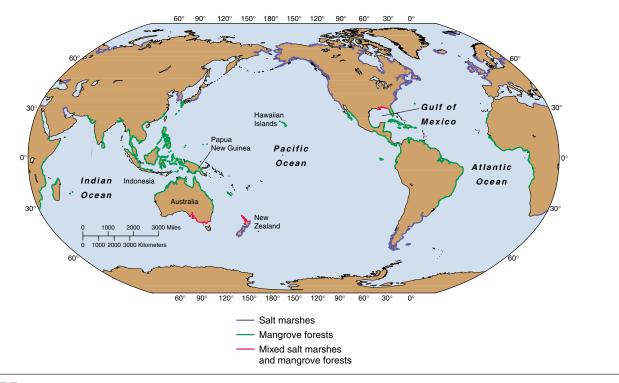


FIGURE 12.17 The world distribution of salt marshes and mangrove forests. Mangroves replace salt marshes in tropical regions. The two overlap in such areas as the Gulf of Mexico, southern Australia, and New Zealand. Mangroves were introduced by humans to the Hawaiian Islands.



**FIGURE 12.18** Aerial view of a mangrove forest on the southern coast of Puerto Rico. The outer seaward edge of the forest is dominated by the red mangrove (*Rhizophora mangle*). As in Florida and most of the Western Hemisphere, the coastal red mangrove is followed by a broad belt of black mangrove (*Avicennia germinans*). Farther inland is the white mangrove (*Laguncularia racemosa*).

Other species of Rhizophora are found on tropical coasts around the world. Along the Caribbean and Atlantic coasts of the Western Hemisphere, the black mangrove (Avicennia germinans) and the white mangrove (Laguncularia racemosa) live inland from the red mangrove (Fig. 12.18). Black mangrove seedlings can survive the high salinity of the water that remains standing after high tide flooding. As a result, the black mangrove grows higher in the intertidal than the red mangrove. The black mangrove, like other mangroves from the tropical Pacific Ocean, develops pneumatophores, conspicuous, unbranched extensions of the shallow roots that grow upward from the oxygenpoor mud to help aerate the plant tissues (Fig. 12.19). White mangrove seedlings cannot tolerate well flooding by seawater, and as a consequence, the white mangrove is only found along the landward edge of the mangrove forest. Its leaves have two clearly visible salt glands at the base for

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FIGURE 12.19 Pneumatophores, the vertical extensions of shallow roots, obtain additional oxygen in mangroves such as *Sonneratia alba*. Here in Palau, western Pacific, this species is found along the seaward fringe of mangrove forests.

the excretion of salts. Salts are also excreted by the leaves of the black mangrove.

Most species of mangroves are found along the shores of the western Pacific and the Indian oceans. Mangrove forests may reach as far inland as 320 km (200 mi) in southern New Guinea and some islands in Indonesia, where the influence of the tides extends far up estuaries.

Many marine and land animals live in mangrove forests. Crabs are particularly common in mangrove forests. Many, such as species of *Sesarma* and *Cardisoma*, feed on the abundant leaf litter that accumulates below the mangrove trees. These crabs spend most of their lives on land, but when eggs are ready to hatch, females must release the larvae at sea. Several species of fiddler crabs (see "Fiddler on the Mud," p. 269) excavate burrows in the mud. As in temperate mudflats and salt marshes, burrowing crabs help oxygenate the sediment. Mudskippers (*Periophthalmus*; Fig. 12.20) are unique



FIGURE 12.20 A mudskipper (*Periophthalmus*) from the mudflats of mangrove forests in New Guinea. Its protruding eyes are adapted to see in air. Each eye can be retracted into a moist pocket to keep it from drying out.

fishes found in Indian Ocean and western Pacific mangrove forests. They have burrows in the mud but spend most of their time out of the water, skipping over the mud and crawling up mangrove roots to catch insects and crabs. Their gills get oxygen not from the water, but from air trapped in their mouth. Many organisms attach to, or take shelter among, the submerged mangrove roots (Fig. 12.21). Large sponges living on the roots have been found to provide significant amounts of nitrogen to mangrove plants. They also help protect roots from burrowing isopods, which may cause considerable damage. The muddy bottom around mangroves is inhabited by a variety of deposit and suspension feeders, as on temperate mudflats. These include polychaetes, mud shrimps, and clams. The channels that cross mangrove forests are rich nurseries for many species of shrimps, spiny lobsters, and fishes. Birds make their homes in the branches and feed on fishes, crabs, and other prey. Snakes, frogs, lizards, bats, and other land animals also live in mangrove forests.

Large amounts of detritus accumulate as leaves and other dead plant material are broken down by bacteria even though considerable amounts of leaves are eaten by crabs and some of the plant material is exported to other ecosystems. This makes the mud among the roots black and oxygen-poor, much like that in salt marshes. Oxygen-poor sediments

#### Chapter 12 Estuaries: Where Rivers Meet the Sea 273



FIGURE 12.21 Seaweeds, sponges, oysters, sea anemones, barnacles, sea squirts, and many other types of organisms live attached to the roots of the red mangrove (*Rhizophora mangle*).

and the effect of toxic substances released by the leaves are reasons why life in muddy bottoms in mangrove forests is not as abundant as in similar bottoms elsewhere.

As sediment and detritus accumulate among the roots, mangroves gradually extend the coastline seaward, actually creating new land. When enough material has accumulated, the mangroves may be replaced by land plants. Thus, mangrove forests can be considered a stage of **ecological succession** between marine and terrestrial communities.

**Ecological Succession** Successive changes of communities brought about by modifications of the biological and physical environment.

Chapter 11, p. 250

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**FIGURE 12.22** An oyster reef formed by the eastern oyster (*Crassostrea virginica*) near Beaufort, North Carolina, exposed at low tide.

#### Other Estuarine Communities

The muddy bottoms below low-tide levels are sometimes covered by beds, or meadows, of grass-like flowering plants known as **seagrasses**. They include eel grass (*Zostera*; see Fig. 6.13*b*), which is restricted to temperate waters, and turtle grass (*Thalassia testudinum*; see Fig. 6.13*d*), a warmwater species often found around mangrove forests. The roots of seagrasses help stabilize the sediment, and their leaves provide shelter to many organisms, as well as an additional source of detritus. Seagrass beds are not restricted to estuaries and are discussed in more detail in Chapter 13 (see "Seagrass Beds," p. 286).

Oysters (Ostrea, Crassostrea) may form extensive beds on the muddy bottoms of estuaries in temperate waters. These **oyster reefs** gradually develop as successive generations of oysters grow on the shells of their predecessors (Fig. 12.22). They provide a complex three-dimensional surface for many organisms. The oysterreef community includes seaweeds, sponges, tube worms, barnacles, and other organisms that attach to the hard shells. Other animals take shelter among or even inside the shells. A similar estuarine community develops in association with mussel (*Mytilus*) beds, though the mussels require a hard substrate for attachment.

### Feeding Interactions Among Estuarine Organisms

Though relatively few species live in estuaries when compared to rocky shores, they reap the benefits of living in a very productive ecosystem. They are adapted to exploit the abundant food resources of the estuary. The generalized food webs shown in Figure 12.23 summarize the feeding relationships among different organisms in estuarine ecosystems.

Why do estuaries show a high primary production? There are several reasons. Nutrients brought in by the tide and rivers, together with those generated by nitrogen-fixing organisms and the decomposition of detritus, are used by plants and algae, the primary producers. Primary production is especially high in the communities that surround estuaries. The dense stands of cordgrass and other salt-marsh plants (or mangroves in the tropics), as well as seagrasses, thrive in the high concentration of nutrients. The diatoms and seaweeds in the mud and the phytoplankwww.mhhe.com/marinebiology

ton in the water also contribute significantly to primary production.

Detritus also tends to sink to the bottom. Bottom water, which has a higher salinity and density than shallower water, thus acts as a nutrient trap in deep estuaries. Some phytoplankton are known to migrate to deep water at night to take in nutrients and move up to shallow water the next day to carry out photosynthesis in the light!

Primary production by estuary plants and other organisms varies geographically and seasonally, as does their relative contribution to the ecosystem as a whole. Estimates of primary production range from 130 to nearly 6,000 grams dry wt/m<sup>2</sup>/year for cordgrasses in salt marshes on the Atlantic coast of the United States. See Table 10.1 (p. 228) for a summary of the typical rates of primary production for salt marshes, mangroves, and seagrass beds.

The organic material manufactured by plants and algae is made available to consumers mainly in the form of detritus. A distinctive feature of estuarine ecosystems is that most of the animals feed on dead organic matter. Except for insects, geese, and some land animals on the fringes, there are relatively few herbivores that actually graze on salt-marsh plants. Many detritus feeders obtain more energy from the bacteria and other decomposers in the detritus than from the dead organic matter itself. They excrete any detritus that remains undigested, however, and return it to the detritus pool. The surplus detritus is exported to the open ocean and neighboring ecosystems in a process known as outwelling. The exported detritus serves as a valuable source of food and nutrients to other ecosystems. The amount of exported detritus varies among estuaries, and some are actually net importers. Nonetheless, outwelling is an important role of estuaries, an additional reason that they must be preserved and protected.

Estuaries include plant-dominated communities with very high primary production. A significant amount of the food manufactured by these plants is made available to consumers by way of detritus.





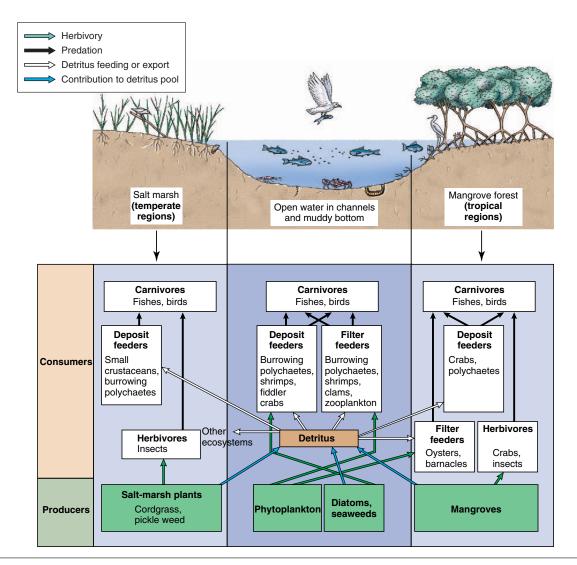


FIGURE 12.23 Generalized food webs in estuarine ecosystems. Salt marshes (left) occur in temperate regions, mangroves (right) in the tropics.

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## interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

### Do-It-Yourself Summary

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

### Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

### **Critical Thinking**

- 1. A proposal is made to deepen the entrance and main channel of an estuary. What do you think will happen to the salt marshes that surround the channel? What do you predict will happen to the primary production of the estuary as a whole?
- 2. Some of the organic material manufactured in estuarine communities is exported to other ecosystems. What type of ecosystems receive this material? How is this material transported?

### For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol  $\square$ , and will contain live links when you visit this page in the Online Learning Center.

### **General Interest**

- Boyle, R. H., 1999. Bringing back the Chesapeake. *Audubon*, vol. 101, no. 3, May–June, pp. 78–84. Estuaries such as Chesapeake Bay face many environmental problems, from bacterial blooms to pollution.
- Cole, J. 1997. The magic of mangroves. *Audubon*, vol. 99, no. 2, March–April, pp. 46–53. Mangrove forests are a habitat for many forms of life.
- Glenn, E. P., J. J. Brown and J. W. O'Leary, 1998. Irrigating crops with seawater. *Scientific American*, vol. 279, no. 2, August, pp. 76–81. Some salt-marsh plants may be cultivated and used as animal feed or for human consumption.
- Rapport, D. J. and W. G. Whitford, 1999. How ecosystems respond to stress. *BioScience*, vol. 49, no. 3, March, pp. 193–203. An estuary is compared to two terrestrial ecosystems, all three of which are impacted by humans.

#### In Depth

Ellison, A. M., E. J. Farnsworth and R. E. Merkt, 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography Letters*, vol. 8, pp. 95–115.

- Ellison, A. M. and E. J. Farnsworth, 2001. Mangrove communities. In: *Marine Community Ecology* (M. D. Bertness, S. D. Gaines and M. E. Hay, eds.), pp. 423–442. Sinauer, Sunderland, Mass.
- Hauxwell, J., J. McClelland, P. J. Behr and I. Valiella, 1998. Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. *Estuaries*, vol. 21, pp. 347–360.
- Irlandi, E. A. and M. A. Crawford, 1997. Habitat linkages: the effect of subtidal salt-marshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia*, vol. 110, pp. 231–236.
- Lee, S. Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research*, vol. 49, pp. 335–343.
- Micheli, F. and C. H. Peterson, 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology*, vol. 13, pp. 869–881.
- Pennings, S. C. and M. D. Bertness, 2001. Salt marsh communities. In: *Marine Community Ecology* (M. D. Bertness, S. D. Gaines and M. E. Hay, eds.), pp. 289–316. Sinauer, Sunderland, Mass.

### See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

- Fiddler crabs (South Carolina)
- Seagrass bed with blue tangs feeding (Belize)
- Salt marsh and estuary (South Carolina)
- Periwinkles on cord grass (North Carolina)
- Shore birds feeding in salt marsh (South Carolina)
- Black mangrove pneumatophores and flower (Bermuda)
- Red mangrove (Bermuda)

### Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Estuaries
- Beaches and mudflats

## Quiz Yourself

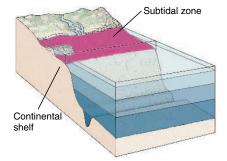
Take the online quiz for this chapter to test your knowledge.

III. Structure and Function of Marine Ecosystems 13. Life on the Continental Shelf © The McGraw–Hill Companies, 2003

# Life on the Continental Shelf







Subtidal rocky bottom with giant kelp (Macrocystis pyrifera) in California.

The submerged edge of the continents, the **continental shelf**, was once considered the beginning of the unknown blue sea. But when the shelf came under scrutiny during the last century, the unknown began to give up its secrets. We have learned even more in just the last few years because the use of scuba and underwater habitats has allowed firsthand study and observation (Fig. 13.1). Biologically, the shelf is the richest part of the ocean. It includes the world's most important fishing grounds, which yield about 90% of the total global catch. Oil and minerals have been found on the shelf, and nations have extended their international borders to protect their newfound, or yet-to-be found, resources. The continental shelf, being close to shore, is also profoundly affected by pollution and other activities of humans on land.

Chapter 13 looks at life on the continental shelf, paying particular attention to the bottom organisms. Life in the water column above the shelf is discussed in Chapter 15, and the shelf's fisheries in Chapter 17. Coral reefs, important shelf communities in the tropics, are covered separately in Chapter 14.

### PHYSICAL CHARACTERISTICS OF THE SUBTIDAL ENVIRONMENT

The part of the continental shelf that is never exposed at low tide constitutes the **subtidal zone** of the marine environment. The subtidal zone, which is sometimes called the **sublittoral zone**, extends from the low tide level on shore to the **shelf break**, the outer edge of the continental shelf where depth suddenly

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**FIGURE 13.1** Scuba diving has dramatically expanded the possibilities for the study of the subtidal environment by marine biologists.

increases (see Fig. 10.20). The depth of the shelf break varies, but averages around 150 m (490 ft). The width of the shelf is also highly variable. It ranges from less than 1 km (0.6 mi) to over 750 km (470 mi), with an average of approximately 80 km (48 mi). The **benthos** of the continental shelf live in the subtidal zone, whereas the **plankton** and **nekton** of the water column over it inhabit the **neritic zone** (see Fig. 10.19).

The subtidal zone consists of the bottom of the ocean from the low tide level to the shelf break, the outer edge of the continental shelf.

The physical factors that affect subtidal organisms are linked to two of the shelf's fundamental characteristics: its relatively shallow water and its proximity to land. Because the bottom is shallow, temperature varies more from place to place in the subtidal zone than on the deeper bottom beyond the shelf. This is significant because temperature is one of the most important factors influencing the distribution of marine organisms. The kinds of organisms found in the subtidal change dramatically from the Equator to the poles. There are also *more*, not just different, species in the tropics than in temperate or polar waters. The bottom below the Arctic and Antarctic ice, however, is far from being a desert (see "Under the Antarctic Ice," p. 279). The benthos in deep water change much less because the temperature there is uniformly cold and does not vary as much as in shallow water.

The bottom in shallow water is also much more affected by waves and currents than in deep water. The rise and fall of tides can produce particularly strong tidal currents on the shelf, especially in bays and narrow straits. Wind waves can affect the bottom even at depths of 200 m (650 ft). Water motion, or turbulence, tends to stir up the water column and prevents stratification. Thus, except for seasonal variations in temperate waters, the temperature and salinity of the water at the bottom are not much different from those at the surface. More importantly, nutrients do not concentrate in the bottom layer and become unavailable to primary producers at the surface, as they do in deep water (see "Nutrients," p. 344). Nutrients are also

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brought in by rivers, often as by-products of the highly productive salt marshes or mangrove forests that fringe the shore. As a result, the water over the continental shelf is far more productive and plankton-rich than the open ocean, so there is much more food available. The high concentration of phytoplankton, plus decaying organic matter brought in by rivers, gives coastal water a greenish tint, as opposed to the deep blue of open-ocean water.

Rivers, obviously, also bring in large amounts of fresh water. Freshwater runoff dilutes the seawater, reducing its salinity. The effects of large rivers such as the Mississippi and the Amazon extend many miles offshore. Away from the influence of rivers, however, the salinity of coastal water is about the same as that beyond the shelf.

The combination of proximity to land and shallow water greatly influences sedimentation, the settling of sediment particles from the water. Most of the sediment on the shelf is lithogenous, and rivers bring in huge quantities of sediment from the continents. Water motion sorts out the particles by size and density, especially on the shallower parts of the shelf. Large-grained material such as gravel and sand settles out even in areas with strong waves and currents. On the other hand, turbulence keeps fine particles such as silt and clay in suspension. Fine particles are deposited only in quiet areas or in deeper water, where turbulence does not reach the bottom.

The abundant phytoplankton and the sediment that is brought in by rivers and stirred up by waves and currents make shelf water murkier than that in the open ocean. Light does not penetrate as deeply, which reduces the depth at which plants and other primary producers—both phytoplankton and attached seaweeds—can carry out photosynthesis and grow.

The type of substrate, depth, turbulence, temperature, salinity, and light are among the most important physical factors that influence life on the continental shelf. Castro–Huber: Marine Biology, Fourth Edition III. Structure and Function of Marine Ecosystems 13. Life on the Continental Shelf © The McGraw–Hill Companies, 2003

### UNDER THE ANTARCTIC ICE

Antarctica, one of the last unspoiled wildernesses on earth, is for many of us a vision of awesome whales, smiling seals, and frolicking penguins. Life on the Antarctic shelf is as fascinating and pristine as in the cold waters above it.

Ice is a major physical factor for shelf organisms in the Antarctic. A layer of ice several meters thick forms during winter, freezing and eventually crushing any organisms living on the bottom. Winds and currents push the ice, scouring the bottom and crushing even more organisms. Ice may also form around the organisms to depths of 30 m (100 ft) or more. The ice, less dense than the water, often floats to the surface, carrying with it these trapped, often frozen, organisms. Except for these effects of winter ice at shallow depths, however, the physical environment in Antarctic waters is remarkably constant. Year-round low temperatures mean that life processes, including growth, proceed at a slow pace in Antarctica. In contrast to the Arctic region, there is no runoff from rivers in Antarctica. Another important difference from the Arctic is the absence of disturbance from the feeding of large mammals such as the gray whale and the walrus in Antarctica.

Though kelps are present on several of the offshore islands, they are surprisingly absent in mainland Antarctica. Here they are replaced by *Desmarestia* and a few other brown seaweeds. These are not considered kelps, though they may be large.

Sessile organisms are rare at the shelf's shallower depths because of the scouring effect of winter ice. Below this depth, however, benthic invertebrates are plentiful. The invertebrate fauna of Antarctica is rich, colorful, and highly diverse. Many of the invertebrate species are unique to Antarctica. They evolved there over a long period of isolation from the continental shelves of other continents.

The nutrient-rich waters result in very high primary production when sunlight becomes available during the long days of summer. Rich blooms of phytoplankton (diatoms even grow in the ice) provide food for the many suspension feeders. Sponges in particular are so common that they cover most of the bottom in many places.

Sponges are not only represented by many different species, but by a multitude of growth forms. Huge volcano-like sponges may grow 2 m (close to 7 ft) or more in height. These large individuals are probably hundreds of years old. Others are fan-shaped or resemble bushes or branching corals. These and other sponges provide refuge and perches for many fishes and other mobile animals, much as kelps or corals do elsewhere. Sponges are so common that the bottom below 30 m (100 ft) or so is nothing but a thick mat of siliceous, or glass, sponge spicules—truly a glass bottom.



A tree-like soft coral, a yellow sponge, scallops, and other benthic invertebrates from Antarctica.

Glass spicules may play an amazing role in some Antarctic sponges that harbor symbiotic algae. The green algae may provide some nutrients to the sponges but must obtain light in order to carry out photosynthesis. How these symbiotic algae survive deep inside sponges that live in water covered by a thick sheet of ice is something that puzzles marine biologists. The answer seems to be in the glass spicules. They efficiently transmit to the algae what little light reaches the sponges, a real network of fiber-optic cables!

Other invertebrates abound: sea anemones, soft corals, sea stars, nudibranchs, and sea urchins. Many of these, like sponges, are suspension feeders, whereas many feed on the sponges. To protect themselves against predators, many sponges produce toxic substances. These chemical defenses are especially common in those sponges with bright colors. Others are predators of sponge feeders and help keep the slowgrowing sponges from being wiped out. Not all of these subtidal invertebrates are unique to Antarctica. Some are found elsewhere, but in progressively deeper water as one gets closer to the Equator.

Antarctic fishes are remarkable in their own right because they can remain active at temperatures that are close to the freezing point of seawater. Many have a chemical "antifreeze" in their blood. The cold water holds so much dissolved oxygen that some, like the icefishes, have colorless blood that lacks hemoglobin.

The wonders of life in Antarctica, both below and above the ice, are unfortunately being threatened. Cruise-ship tourists, oil and sewage pollution, leftover garbage, the potential exploitation of oil and mineral resources, and an ozone hole over the continent (see "Living in a Greenhouse: Our Warming Earth," p. 410) may eventually overwhelm our most desolate continent and harm its unique life.

### THE CONTINENTAL SHELF AS AN ECOSYSTEM

The type of substrate is very important in determining which particular organisms inhabit the floor of the continental shelf. It also dictates how they are sampled by marine biologists (Fig. 13.2). In fact, sub-tidal communities are often classified according to the type of substrate. The most

Benthos Organisms that live on the bottom. Plankton Those that drift with the currents. Nekton Those able to swim against the currents.

Chapter 10, p. 230; Figure 10.19

**Stratification** Separation of the water column into layers, with the densest, coldest water at the bottom, which prevents the mixing of the nutrient-rich

deep water with the less dense, warmer upper layer.

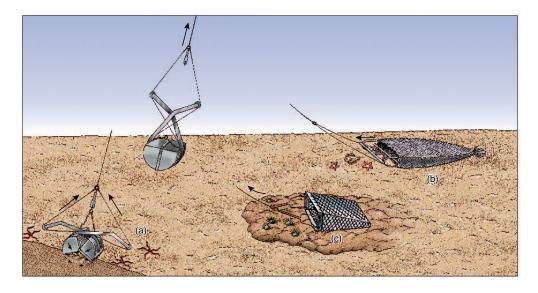
Chapter 3, p. 63; Figure 3.31

Lithogenous Sediment Sediment that comes from the physical or chemical breakdown of rocks on land. Biogenous Sediment Sediment composed of the skeletons and shells of marine organisms.

Chapter 2, p. 33

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**FIGURE 13.2** Though scuba diving is an excellent method for sampling and studying subtidal environments, its use is limited to shallow depths. (a) Soft bottoms at greater depths can be sampled by using grabs such as the Van Veem bottom grab. The grab is lowered from the surface and its jaws close as the dredge is retrieved. (b) Different types of bottom trawls are used to collect the larger inhabitants of soft bottoms. They are similar to the bottom trawls used by fishers (see Fig. 17.6c). (c) Dredges with heavy metal frames are used to scrape organisms off rocky bottoms.



common of these are communities associated with soft bottoms. Hard-bottom, or rocky-bottom, communities constitute the second type.

### Soft-Bottom Subtidal Communities

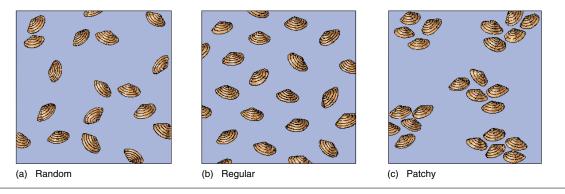
Sandy and muddy substrates dominate the world's continental shelves. Large areas covered by soft sediments stretch from the shore to the edge of the shelf. Even along rocky shores, rocks eventually give way to sand or mud in deeper water. The organisms that inhabit these often flat and seemingly homogeneous bottoms (Fig. 13.3) are not necessarily distributed by chance. It has long been recognized that these organisms form distinct communities whose distribution is greatly influenced by such factors as the particle size and stability of the sediment, light, and temperature.

The shelf's soft-bottom communities share many traits with the communities of sandy beaches and mudflats covered in Chapters 11 and 12. In all of these communities there is a predominance of **infauna**, benthic animals that burrow or dig in the sediment. There are also some **epifauna**, animals that live on top of the sediment. Because there is nothing to hold on to, **sessile**, or attached, forms are virtually absent.



FIGURE 13.3 Conspicuous life on shallow sandy bottoms includes occasional clumps of seaweeds that manage to grow on small rocks or shells and large predators like flatfishes.

Most of the continental shelf is covered by mud or sand. The subtidal communities in these areas are dominated by infauna. The number of species living on subtidal soft bottoms is usually higher than the number of species on soft bottoms in the intertidal zone. This is largely because the physical conditions below the low tide mark are somewhat less demanding.



**FIGURE 13.4** The spacing, or distribution, of organisms can be classified into three basic types: (*a*) *random*, in which animals are scattered with no particular pattern, (*b*) *regular*, where they are spaced at even intervals, and (*c*) *patchy*, or *clumped*, where they cluster together. Many marine species show a patchy distribution. Can you think of a reason why organisms such as clams might show a regular distribution?

Desiccation is not a problem. Furthermore, there are none of the drastic temperature changes caused by exposure at low tide or the salinity variations of estuarine mudflats. This stable environment allows a wider variety of organisms to live in the subtidal.

The close relationship between particle size and the distribution of organisms is particularly evident in the infauna, which for the most part are very selective as to where they live. Different species may also partition their environment and thus reduce competition by living at different depths in the substrate. Because only the upper layer of sediment contains enough oxygen, however, the depth at which the infauna can live is limited. In organic-rich mud, oxygen is quickly used up by decomposition. In contrast, sand usually contains less organic matter. It is also more porous, so water can circulate through the sediment and replenish the oxygen (see Fig. 11.26). Thus, the infauna can burrow deeper in sand than in mud. Even in mud, however, the presence of burrows aids circulation, helping organisms obtain oxygen.

Soft substrates often contain patches of different types of sediment. As a result, the distribution of organisms along the bottom is typically **patchy**, that is, the organisms occur in distinct clumps or patches (Fig. 13.4). Some species have a patchy distribution because their planktonic larvae select a particular environment on which to settle and undergo **metamorphosis.** Some larvae are known to postpone metamorphosis and "taste" the bottom until they find a certain type of substrate. Metamorphosis may be triggered by specific chemical, physical, and biological factors (Fig. 13.5). The larvae of some species can sense adults and prefer to settle near them. This may cause the species to be distributed in clumps even if there is a uniform bottom. The arrival of new individuals to a population, either by settling larvae or by migrating juveniles or adults, is known as **recruitment.** 

Many marine biologists now think that the establishment of subtidal and other marine communities is influenced by a random, or chance, element. This view maintains that whenever an empty space becomes available on the substrate because of the death of adults or disturbances caused by, say, a feeding ray larvae will settle on a "first come, first served" basis. In other words, there is an element of unpredictability, or luck, associated with the development of communities: It depends on what kinds of larvae happen to be in the neighborhood.

#### Unvegetated Soft-Bottom Communities

The great majority of the shelf's softbottom communities lack significant amounts of seaweeds or seagrasses. They are therefore known as **unvegetated** communities. The absence of large seaweeds and plants is the defining feature of these communities. Sea lettuce (*Ulva*) and other green algae such as *Entero-morpha* may grow in the shallows, but only on hard surfaces such as rocks and shell fragments. The main primary producers are diatoms and a few other microscopic algae and bacteria that grow on sand or mud particles in shallow water. This almost complete absence of seaweeds and plants means that, as on sandy beaches, the primary production by benthic **primary producers** is practically nil. Nearly all of the primary production is by phytoplankton that are not part of the bottom communities.

Because there is little primary production by benthic organisms, **detritus** is a very important food source for many inhabitants. Detritus is brought in by currents from estuaries, rocky shores, and other more productive coastal communities. It is also present as feces, dead individuals, and other debris from the plankton and nekton in the water column.

**Metamorphosis** The transformation of one stage of a life cycle into another, as when a larva changes into a juvenile.

Chapter 7, p. 120

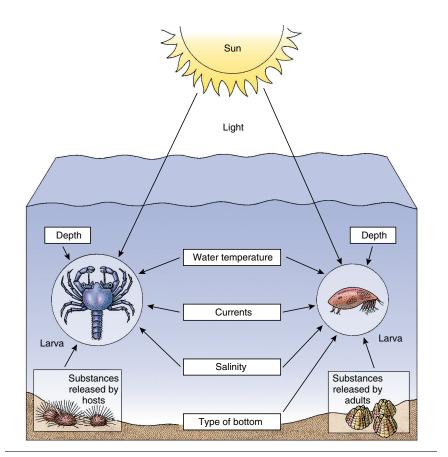
**Primary Producers** Organisms that can create organic matter from  $CO_2$ , usually by photosynthesis.

Chapter 4, p. 73

**Detritus** Particles of dead organic matter. *Chapter 10, p. 224* 

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**FIGURE 13.5** Many factors are known to influence the settlement and metamorphosis of planktonic larvae. The larva illustrated on the left, a megalopa, belongs to a crab (*Echinoecus pentagonus*) that as an adult lives on tropical sea urchins. The larva on the right is the cypris larva of a barnacle (see Fig. 7.37). Many barnacle larvae settle near adults of their species.

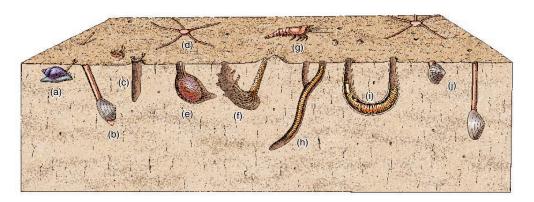
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Detritus is also generated by the bottom inhabitants themselves as they die.

The detritus is used by bacteria and by the many types of microscopic animals that live between the sediment particles, the **interstitial** animals, or **meiofauna** (see "Life in Mud and Sand," p. 283).

Larger benthic invertebrates also feed on detritus. They are mostly burrowing **deposit feeders** (Fig. 13.6). Polychaetes are the most diverse group of deposit feeders in the soft sediments of the shelf. Trumpet (*Pectinaria*; Fig. 13.6f) and bamboo worms (*Clymenella*; see Fig. 12.11*b*) are deposit-feeding polychaetes that inhabit tubes they build from sediment particles. Lugworms (*Arenicola*) and others live in burrows. These polychaetes and other worms eat detritus and other organic matter by collecting it with their tentacles or by ingesting sediment and extracting food from it.

Some sea urchins are uniquely adapted to live as deposit feeders on soft bottoms. Heart urchins (*Spatangus*) have abandoned the round shape of most urchins, becoming more streamlined with shorter spines that lie flat (Figs. 13.6e and 13.7). Sand dollars (*Dendraster*) are almost completely flat and have very short spines (Figs. 13.8 and 7.45b). They typically feed on detritus and use mucus to carry particles to the mouth. Other deposit feeders among the



**FIGURE 13.6** The infauna and epifauna of subtidal soft bottoms in different parts of the world include (*a*) snails such as whelks (*Nassarius*), (*b*) clams (the soft-shelled clam *Mya arenaria*), (*c*) amphipods (the tube-building *Haploops*), (*d*) brittle stars (*Ophiura*), (*e*) heart urchins (*Spatangus*, *Lovenia*), (*f*) trumpet worms (*Pectinaria*), (*g*) shrimps (*Crangon*), (*b*) sandworms (*Nereis*), (*i*) parchment worms (*Chaetopterus*), and (*j*) cockles (*Cardium*) (also see Fig. 12.11 for a sample of mudflat inhabitants).

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### LIFE IN MUD AND SAND

The space between sediment particles is largely invisible to us, but it is an active and important part of the marine environment. This microscopic world, which extends from sandy beaches and estuaries to deep water, is inhabited by highly specialized **interstitial** organisms, often called the **meiofauna**.

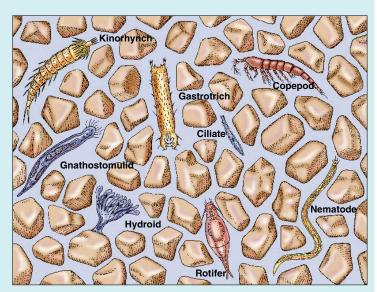
Some meiofauna glide freely among the sediment particles, whereas others attach to them. Though detritus is probably the most important source of food, many meiofauna are predators and scavengers. There also are grazers who eat the diatoms and other tiny algae that live in the upper few millimeters of the sediment. The meiofauna, in turn, are part of the diet of many deposit feeders.

The underground world of the meiofauna is packed with bizarre creatures. There are protozoans, wiggling nematodes, tiny attached hydroids that capture their food with snake-like tentacles, and vacuum-cleaning worms. Some members are just miniature versions of flatworms, polychaetes, copepods, and other more familiar animals that live elsewhere. Many, however, are uniquely adapted to the interstitial habitat, and some are found nowhere else. This is the case in **gnathostomulids** (phylum **Gnathostomulida;** see "How to Discover a New Phylum," p. 129).

Only about 150 species of **kinorhynchs** (phylum **Kinorhyncha**) are known, and all are restricted to marine mud and sand. Their bodies are divided into a series of segments armed with spines. The head, which is also surrounded by spines, can be retracted into the body.

**Gastrotrichs** (phylum **Gastrotricha**) use suction to eat detritus and smaller members of the meiofauna. They have short, hair-like cilia on the head and the ventral surface of the body. About half the over 450 known species are marine. Though they look much like protozoans, gastrotrichs have many cells and true tissues and organ systems.

**Rotifers** (phylum **Rotifera**) are a group of nearly 2,000 species, of which only about 100 are marine. Of these, several species are part of the meiofauna. They are known as "wheel animals" because of a crown of cilia on their heads. This structure is used in locomotion and feeding.



Examples of the meiofauna in sand.

The **archiannelids** are segmented worms (phylum **Annelida**) that are very common members of the meiofauna. They are simple in structure and minute in size. Unlike polychaetes, the group of segmented worms in which they are often included, archiannelids typically lack distinct segments, parapodia, or bristles.

**Oligochaetes** are segmented worms that are widely distributed on land and in fresh water. They include the earthworms and related forms. Oligochaetes are less common at sea. They are present in the meiofauna, however, especially in polluted bays and harbors.

Collecting and extracting live meiofauna is not particularly complicated. The easiest procedure is to take moist mud or sand and let it stagnate in a container for an hour or so. The meiofauna will move to the top layer of sand as they run out of oxygen. Samples are taken close to the sediment surface with an eyedropper and observed under a dissecting or, even better, a compound microscope. The show is about to begin.

infauna include echiurans (Fig. 13.9), peanut worms, sea cucumbers, and ghost shrimps (*Callianassa*; see Fig. 12.11*d*).

The infauna also include invertebrates that are **suspension feeders** that eat drifting detritus and plankton from the water column. Many of these suspension feeders are **filter feeders**, and actively filter the water to obtain suspended particles. Soft-bottom suspension feeders include many types of clams (Fig. 13.6b and j): razor clams, the quahog (Mercenaria mercenaria), cockles, the soft-shelled clam (Mya arenaria), and others. Most clams are filter feeders, but some—such as the bent-nosed, or small, clams and a few others—are deposit feeders. They collect detritus and micro-scopic organisms with their siphons or specialized appendages (Fig. 13.10). Also among the filter feeders are amphipods (Fig. 13.6c) and polychaetes such as parchment worms (Fig. 13.6i) and terebellids (Fig. 13.11).

**Deposit Feeders** Animals that feed on organic matter that settles in the sediment.

Chapter 7, p. 126; Figure 7.16

**Suspension Feeders** Animals, including *filter feeders*, that feed on particles suspended in the water column.

Chapter 7, p. 118; Figure 7.16



**FIGURE 13.7** Like all heart urchins, *Spatangus purpureus* is specialized for living in sediments. Heart urchins burrow below the surface (see Fig. 13.6e) and use modified tube feet for feeding. This photo was taken in the Mediterranean Sea at night, when the urchin emerged from the sediment.

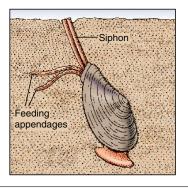


FIGURE 13.8 These sand dollars (*Dendraster excentricus*) form dense beds on sandy bottoms along the California coast. They lie partially buried in the sand, angled into the current.

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FIGURE 13.9 *Thalassema mellita* is a deposit-feeding echiuran that inhabits soft bottoms in the Gulf of Mexico and on the Atlantic coast of North America. It uses a spoon-shaped proboscis to feed.



**FIGURE 13.10** The file yoldia (*Yoldia limatula*) inhabits mud and muddy sand from shallow water to depths of 30 m (100 ft) in the North Atlantic. The siphon brings water in, but is not used for feeding as in most other clams. Instead, this clam uses two grooved, tentacle-like appendages to feed. Each groove contains cilia that bring small organisms to the mouth.



FIGURE 13.11 *Terebella* is a polychaete worm that burrows in soft bottoms. Its long tentacles are extended over the bottom for suspension feeding.

|   | More turbulence            | Less turbulence            |
|---|----------------------------|----------------------------|
| Size of<br>sediment<br>particles        | Sand                       | Mud                        |
| Oxygen and<br>detritus<br>concentration | More oxygen, less detritus | Less oxygen, more detritus |
| Type of<br>animals                      | Suspension feeders         | Depositifeeders            |

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**FIGURE 13.12** The distribution of suspension and deposit feeders in soft bottoms is largely influenced by the size of the sediment particles. This relationship, however, is not clear-cut. Animals already established in the sediment, for instance, influence colonization by others.

The distribution of burrowing deposit and suspension feeders is influenced by several factors. Already mentioned in the previous section is the type of substrate. Deposit feeders tend to predominate in muddy sediments because more detritus is retained in the smaller interstitial spaces between mud particles (Fig. 13.12). Suspension feeders, on the other hand, are more common on sandy bottoms. The types of organisms present also affect the establishment of others. Deposit feeders, for instance, are known to exclude suspension feeders. The constant reworking of the sediment by deposit feeders makes the bottom loose and unstable. These conditions facilitate the clogging of the filtering surfaces of suspension feeders and the burying of their newly settled larvae. Deposit feeders and other members of the infauna that move sediment while burrowing or feeding are called bioturbators. They uncover and oxygenate deeper sediments and bury those on the surface. Sea cucumbers (see Fig. 11.30), echiurans (Fig. 13.9), and peanut worms are important bioturbators.

Many tube builders are deposit feeders, but they help stabilize the substrate, making it more suitable for suspension feeders. Their tubes may also interfere with the activities of burrowing deposit feeders. The tubes also slow down the flow of water over the sediment, which decreases the rate of particle suspension. The modification of the environment by deposit feeders, especially of bioturbators, and the effects of tubes are examples of how some species can indirectly influence the recruitment and survival of others.

Many of the epifaunal invertebrates are deposit feeders. These include most amphipods and other small crustaceans, as well as many species of brittle stars (Fig. 13.6d). Many of these brittle stars use their tube feet to collect detritus from the bottom. Other brittle stars are suspension feeders that raise their arms up into the water to catch suspended particles with their tube feet. Still others are scavengers and feed on dead animals. Shrimps, including commercially valuable species (Penaeus), can be very abundant (Fig. 13.6g). Shrimps and many large crustaceans are mostly scavengers that feed on dead organic matter. Suspension feeders such as sea pens (Stylatula; Fig. 13.13) and sea pansies (Renilla) can often be found in dense stands.

FIGURE 13.13 Sea pens are suspension-feeding cnidarians. Each individual is a colony that includes numerous minute polyps and a fleshy stalk that is anchored in soft substrates. This is *Stylatula elongata* from the Pacific coast of North America.

Most soft-bottom subtidal communities lack large seaweeds and plants. They are mostly inhabited by deposit and suspension feeders.

Some members of the soft-bottom epifauna are predators. They may burrow through the sediment to get their prey or catch it on the surface. As in other communities, predators are important in regulating the number and type of bottom inhabitants. They remove individuals and cause disturbances in the sediment that allow recolonization by different types of organisms. Some only nip off the siphons instead of eating the entire animal. Snails such as whelks (Nassarius; Fig. 13.6a) and moon snails (Polinices; see Fig. 12.11b) feed on clams by drilling a hole in the shell and rasping away the flesh. Sea stars (Astropecten; Fig. 13.14) prey on clams, brittle stars, polychaetes, and other animals. Predatory amphipods influence subtidal communities by preying on the settling larvae of other species. Crabs are

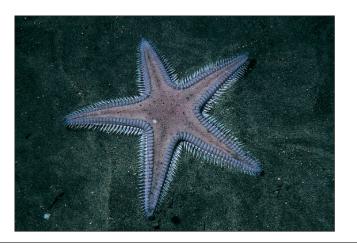


FIGURE 13.14 Sea stars such as *Astropecten* prey on clams and other burrowing invertebrates.

common predators and scavengers on soft bottoms. Examples are the blue crab (*Callinectes sapidus*) and other swimming crabs, the lady crab (*Ovalipes ocellatus*), and many species that partially bury themselves in the sand or mud. Other predatory crabs, hermit crabs, lobsters, and octopuses take shelter on rocky bottoms but move to soft bottoms to feed.

Many fishes are also noteworthy predators. Most bottom-dwelling, or demersal, fishes in these soft-bottom communities are carnivores. Rays and skates scoop up clams, crabs, and other infauna and epifauna. Flatfishes such as flounders, halibuts, soles, and turbots lie camouflaged or covered on the bottom and forage for a wide variety of prey. Pelagic fishes and squids also feed on the inhabitants of the shelf's soft bottoms. A very large predator indeed is the gray whale (Eschrichtius robustus), which filters the sediment for amphipods and other small animals (see Fig. 9.18). Large predators such as whales, walruses, and rays have important effects on soft-bottom communities. Not only do they remove their prey, in the process of feeding they dig pits in the bottom, killing large numbers of infauna that aren't eaten and changing the characteristics of the sediment.

#### Seagrass Beds

Soft bottoms along the coast are occasionally carpeted by **seagrasses**. These are flowering plants, grass-like in appearance but unrelated to true grasses, that have become established in the marine environment (see "Flowering Plants," p. 114). Seagrass beds develop best in sheltered, shallow water along the coast. They are also found in estuaries and in association with mangrove forests (see "Other Estuarine Communities," p. 274).

Only 50 to 60 species of seagrasses are known. Most are tropical and subtropical, but several species are common in colder waters. Most seagrasses are restricted to muddy and sandy areas below the low tide level. Different species of seagrasses vary in maximum depth, but all are limited by the penetration of light through the water column.

Turtle grass (Thalassia testudinum; see Fig. 6.13d) is the most common seagrass in the tropical and subtropical Atlantic, the Caribbean, and the Gulf of Mexico. Extensive meadows are found to depths of about 10 m (33 ft), but turtle grass can grow deeper in clear water. Another seagrass, manatee grass (Syringodium filiforme; see Fig. 6.13a) is often found together with turtle grass. Eelgrass (Zostera marina; see Fig. 6.13b) is widely distributed in temperate and cold waters of the Pacific and North Atlantic. It is most common in shallow water, sometimes exposed at low tide (Fig. 13.15), but has been found at depths of up to 30 m (100 ft). Posidonia oceanica is an important species in the Mediterranean. Most species, however, are found in the Indo-West Pacific region.

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FIGURE 13.15 An extensive eelgrass (*Zostera marina*) bed on the Pacific coast of Baja California, Mexico.

Seagrasses can grow into thick, luxuriant beds, which often consist of more than one species of seagrass and many species of seaweeds. Their roots and a network of underground stems (see Fig. 4.19*a*) keep them anchored in the face of turbulence. The roots and stems also help stabilize the soft bottom, and the leaves cut down wave action and currents. This decrease in turbulence causes more and finer sediment to be deposited, which in turn affects colonization by other organisms. It also improves water clarity because less sediment remains suspended in the water column.

Seagrass beds contain a very high plant **biomass**, as high as 1 kg/dry wt/m<sup>2</sup> for turtle grass. With such a high density of photosynthesizing plants, seagrass beds have a higher primary production than anywhere else on soft bottoms. In fact, they rank among the most productive communities in the entire ocean. Values as high as 8 gC/m<sup>2</sup>/day have been recorded for seagrasses alone. Part of the reason for such high primary production is the fact that seagrasses have true roots, unlike seaweeds, and are therefore able to absorb nutrients from the sediment. Phytoplankton and seaweeds, by contrast, must depend on nutrients dissolved in the water column. Some typical rates of primary production in seagrass beds and

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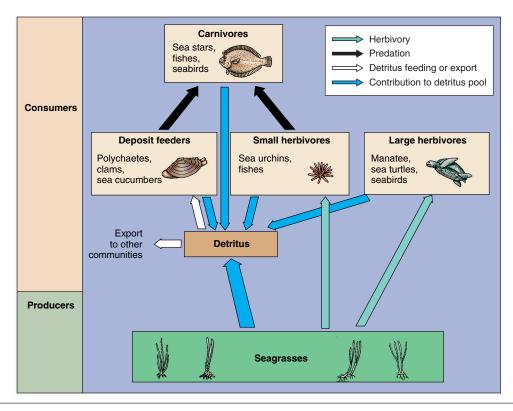


FIGURE 13.16 Generalized food web in a seagrass community. As in estuaries (see Fig. 12.23), detritus generated from dead plants is an important source of food for many animals.

other marine environments are summarized in Table 10.1 (p. 228).

Many small algae grow on the surface of seagrass leaves. These algae, known as **epiphytes**, further increase primary production in seagrass communities. Microscopic diatoms are particularly abundant. Some epiphytic cyanobacteria also carry out **nitrogen fixation** and release nutrients in the form of nitrogen compounds.

The number of grazers, or herbivores, varies with geographical location. Herbivores, not many of which eat seagrass leaves, directly consume much less than half of seagrass primary production. Herbivores that do eat seagrasses include sea turtles, manatees, sea urchins (*Diadema, Lytechinus*), and some parrotfishes (*Sparisoma*). Seagrasses are also important in the diet of some birds, such as ducks and geese in the Arctic and other regions.

Animals take advantage of the high primary production of seagrasses in several ways, even when they do not actually eat the seagrasses themselves (Fig. 13.16). Many feed on the large amounts of decaying leaves and seaweeds. Depositfeeding polychaetes, clams, and sea cucumbers live in or on the detritus-rich sediment. Detritus is also exported to other communities, such as the unvegetated soft bottoms of deeper water.

The dense seagrasses also offer shelter to many animals that do not feed on detritus. More animals live in or on the sediments in seagrass beds than in unvegetated sediments nearby. A variety of small sessile or crawling animals live on the leaves: hydroids, snails, tiny tube-dwelling polychaetes, amphipods, shrimps, and the like (Fig. 13.17). Larger animals live among the plants. Turtle-grass beds in the western Atlantic, for instance, support a rich fauna (Fig. 13.18). This includes a pen shell (Pinna carnea), which is a filter-feeding bivalve, and carnivores such as fishes and the West Indian sea star (Oreaster reticulatus). Seagrass beds also serve as

nurseries for commercially valuable species such as the Atlantic bay scallop (*Argopecten irradians*) and shrimps.

Highly productive seagrass communities are restricted to soft bottoms in shallow, sheltered water. The plants are not heavily grazed but produce a lot of detritus that is used by deposit feeders and exported to other communities.

**Pelagic** Pertaining to the water column away from the bottom or other structure.

Chapter 10, p. 230; Figure 10.19.

**Biomass** The total weight of living organisms.

Chapter 10, p. 224

Nitrogen Fixation Conversion of nitrogen gas  $(N_2)$  into nitrogen compounds that can be used by primary producers as nutrients.

Chapter 10, p. 228

**FIGURE 13.17** Eelgrass (*Zostera marina*) leaves are often inhabited by sessile, or attached, organisms. These include (*a*) green and other algae such as *Enteromorpha*, (*b*) the trumpet-stalked jellyfish (*Haliclystus*), a non-swimming jellyfish, (*c*) colonial sea squirts, (*d*) tube-dwelling polychaetes (*Spirorbis*), and (*e*) bryozoans.



FIGURE 13.18 The Queen conch (*Strombus gigas*) is a large snail commonly associated with turtle-grass beds in Florida and the Caribbean. It is highly prized as food.

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### Hard-Bottom Subtidal Communities

Hard bottoms make up a relatively small portion of the continental shelf. Usually they are just the submerged extensions of rocky shores. There are also some subtidal rocky outcrops of varying size. In some cases a significant component of the hard substrate is provided by **calcareous algae**, the tubes of polychaete worms, and oyster shells (see Fig. 12.22). These three-dimensionally complex hard bottoms are often called reefs, but they should not be confused with the coral reefs of warm waters.

#### **Rocky Bottoms**

Unlike those in the intertidal, the communities that develop on subtidal rocky bottoms are never subject to desiccation. This means that a wider variety of organisms can live there than in the intertidal.

Rocky-bottom communities in shallow water are rich and productive. Seaweeds are the most conspicuous inhabitants of hard substrates in shallower water, especially on flat or gently sloping bottoms. They occur in an awesome array of colors, growth forms, textures, and sizes. Most are brown and red seaweeds. They can be filamentous (*Chordaria, Ceramium*), branched (*Agardhiella, Desmarestia*), thin and leafy (*Porphyra, Gigartina*), or **encrusting** (*Lithothamnion*). Many of these species can also be found in the intertidal.

Subtidal seaweeds may have different growth forms at different times of their lives (see Fig. 6.11). Practically all have a **holdfast** (see Fig. 13.20) to anchor them to the substrate.

As in the intertidal, one of the main problems for seaweeds and sessile animals in the subtidal is to find a place to attach. Every bit of space is occupied, even if it seems clean to our naked eye. Thus, there is intense competition for living space on the rocks. Different species of seaweed have different competitive abilities. They also vary in their tolerance to wave action, grazing by sea urchins and other herbivores, temperature, light, and the stability of the substrate. The effect of light is

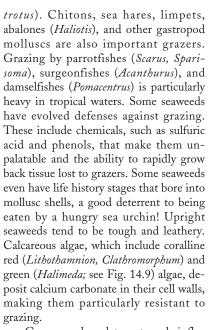
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particularly intriguing. As depth increases, the amount of light available for photosynthesis decreases, making it harder for seaweeds to live there. Some species are better adapted to deep water than others, however. Several can live at depths of over 200 m (650 ft) in clear water. Deep-water seaweeds have increased levels of chlorophyll and other pigments (see Table 5.1, p. 92) that capture light energy. These adaptations can be found in all groups of seaweeds and are not restricted to the red algae, once thought to be the best adapted to deep water. In any case, depth zonation is not determined by light alone. It is affected by grazing, competition for space, temperature, and other factors.

Seaweeds also vary in their life history strategies. Some are **perennial** and are found year-round, whereas others are found only at certain times. Though some grow fast and are short-lived, others grow slowly and are sturdy and longlived. Fast growers are typically the first to colonize surfaces recently disturbed by grazers, turbulence, or other phenomena. Some seaweeds use both strategies by alternating a fast-growing, short-lived stage with a slow-growing, perennial one. Both stages belong to the same species but look and function differently.

Seaweeds must compete for space not only with each other, but also with a huge assortment of sessile animals. Invertebrates tend to dominate on steeply sloping bottoms and vertical walls, where light limits seaweed growth. Hard substrates provide a good place for organisms to attach, but are much harder to burrow through than sand or mud. As a result, hard-bottom communities tend to have a rich epifauna and a poor infauna, the reverse of soft-bottom communities. Sponges, hydroids, sea anemones, soft corals, bryozoans, tube-dwelling polychaetes, barnacles, and sea squirts are among the most frequently found groups. Many form thin colonies that outcompete other species simply by growing over them. A few, such as the rock-boring clam (Pholas), live embedded in rocks.

Grazers on subtidal rocky bottoms are usually small, slow-moving invertebrates. Perhaps most important are sea urchins (*Arbacia, Diadema, Strongylocen*-



new surfaces where other sessile organisms can settle.

Grazers and predators strongly influence the composition of hard-bottom communities. They remove residents from the rocks, opening up space for other organisms. Sea urchins (Fig. 13.19) feed not only on seaweeds, but also on some of the flimsier attached invertebrates as well. Carnivores, including sea stars, nudibranchs, and other gastropods, also feed on invertebrates. The patches cleared by grazers and carnivores are colonized by settling larvae and seaweed spores. Because these planktonic stages are often seasonal, patches formed at different times are colonized by different species. This increases the total number of species in a given area.

**Encrusting Seaweeds** Those that grow as a thin layer over rocks, such as some of the *coralline algae*.

Chapter 6, p. 110

Sunlight penetrates through the water column to depths that depend on water transparency. Not all colors of light penetrate to equal depths. In clear ocean water, blue light penetrates the deepest, red the least.

Chapter 3, p. 51; Figure 3.12



of North America, are important in influencing the composition of hard-bottom subtidal

communities. They graze on seaweeds and on some of the encrusting animals and thus uncover

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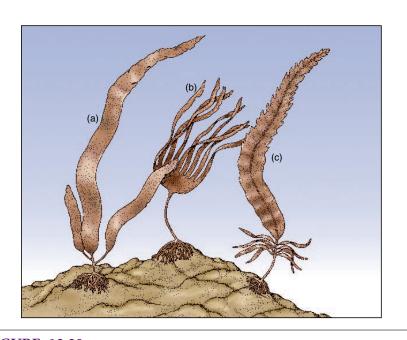
Carnivores such as crabs, lobsters, and many types of fishes prey on grazers. Other carnivores feed on smaller carnivores or even on the external parasites of other fishes (see "Cleaning Associations," p. 224). These predators act as a check on the grazers, helping maintain a relatively stable situation. This balance can be easily upset, however. For example, explosive increases in sea urchin populations have been reported in several subtidal communities (see p. 294), as have mass mortalities. Like all biological communities, subtidal communities are constantly changing.

The species composition of rocky-bottom subtidal communities is influenced by factors such as light, competition for space, grazing, and predation.

### Kelp Communities

Kelp communities are among the most fascinating and important, not to mention beautiful, types of marine communities. Kelps are a group of large brown seaweeds that live in relatively cold water and are restricted to temperate and subpolar regions. They are true giants compared with other subtidal seaweeds or seagrasses, creating luxuriant forests (see Fig. 4.3) that are home to a vast assortment of organisms.

There are several species of kelp. In the North Atlantic and on the Asiatic coast of the North Pacific, various species of Laminaria (Fig. 13.20a and b) predominate. Their simple or cleft blades may be 3 m (10 ft) long. The giant kelp (Macrocystis) dominates kelp communities on the Pacific coasts of North and South America and other parts of the Southern Hemisphere (Fig. 13.21). Each kelp individual is attached to the rocky bottom by a large holdfast (see Fig. 6.1). Several long stipes, intertwined to form a trunk-like foundation, grow from a single holdfast. The fronds, leaf-like blades, grow from the stipes. A single stipe, can reach 20 to 30 m (65 to 100 ft) or more. In some Southern Hemisphere communities, Ecklonia, rather than Macrocystis is the main species. Kelp communities on the Pacific coast of North America are



**FIGURE 13.20** Examples of North Atlantic kelps include (*a*) hollow-stemmed kelp (*Laminaria longicruris*), (*b*) horsetail kelp (*L. digitata*), and (*c*) edible kelp (*Alaria escuelenta*). The hollow-stemmed kelp reaches lengths of 12 m (40 ft) in deeper water.

particularly diverse. A number of species, including the bullwhip kelp (*Nereocystis*), the elk kelp (*Pelagophycus*; Fig. 13.22), *Alaria*, and *Pterygophora*, may be important or even replace *Macrocystis*. The bullwhip kelp consists of many blades, each up to 5 m (16 ft) long, that hang below the surface suspended by a gas-filled **pneumatocyst** located at the end of a long stipe. *Alaria* (Fig. 13.20c), which like many other species of kelp is edible, is also important in the North Atlantic.

Large, dense patches of kelp are known as **kelp beds**. They are called **kelp forests** when the fronds float on the surface in a thick mat (Fig. 13.23). This floating **canopy** is characteristic of Pacific kelp forests dominated by giant and bullwhip kelps. *Ecklonia* and some species of *Laminaria* and *Alaria* also form a canopy.

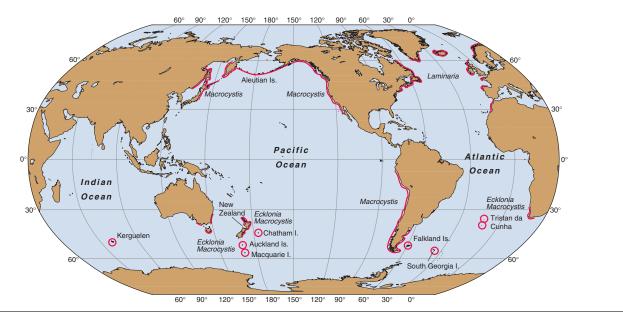
Physical factors have a major influence on kelp communities. Temperature is of particular importance because kelps are restricted to cold water. This is partially because kelps don't do well in warm water and partially because warm waters tend to lack the rich supply of nutrients that kelps need (see "Patterns of Production," p. 343). This dependence on cold water is reflected in the geographic distribution of kelps (Fig. 13.21). The surface waters of the oceans flow in great clockwise gyres in the Northern Hemisphere and counterclockwise gyres in the Southern Hemisphere (see Fig. 3.19). The currents that flow toward the poles on the western sides of the oceans carry warm water from equatorial regions. Because of this, kelps are restricted to high latitudes on the western sides of the oceans. On the other hand, kelps extend well down eastern shores, where cold, nutrient-rich currents flow down from high latitudes.

All but a few species of kelp are limited to hard surfaces, which may include substrates such as worm tubes and the holdfasts of other seaweeds. Given a suitable place to attach, kelps will grow in water as deep as light allows. This can be quite deep, up to 40 m (130 ft) in some species. Their fronds float at the surface, basking in sunlight, while their stipes connect them to the bottom far below.

Kelps are actually quite fragile for their giant size; in fact, they are fragile largely *because* of their size. The fronds cause a lot of drag, but the long, thin stipe breaks easily, and the kelp is often

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**FIGURE 13.21** The geographical distribution of kelps is greatly affected by surface temperatures, which are influenced by the surface circulation of the ocean. Currents along the west sides of the continents transport cold water from polar regions; on the east sides warm water is transported away from the Equator. As a result, kelps extend farther toward the Equator along the west sides of the continents than on the east sides. The opposite is true for reef-building corals, which require warm water (also see Fig. 14.10).



**FIGURE 13.22** The elk kelp (*Pelagophycus porra*) grows on the outer, deeper edges of some giant kelp beds (see Fig. 13.25). It has two impressive, antler-like branches from which large blades hang at the mercy of the currents.

torn from the bottom. Drifting kelp cause more damage by tangling up with other fronds. Kelps don't do well where there is heavy wave action, and storms can be disastrous. Though they must extend their blades to the surface, many species prefer to attach to the bottom in relatively deep water, where wave action is reduced. Thus, the very adaptations that allow these species of kelp to live in deep water, large size and floating fronds, also tend to restrict them there.

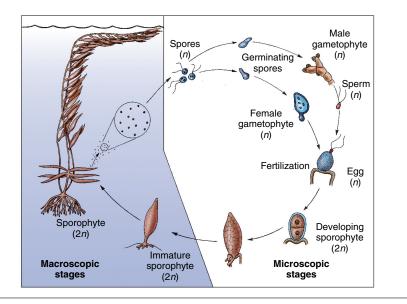
Kelps can grow very fast, with the giant kelp growing as fast as 50 cm/day (20 in/day). Not surprisingly, kelp communities are also very productive. Primary production values of 1,000 gC/m<sup>2</sup>/year (where gC is grams of carbon fixed) have been measured in *Ecklonia* in Australia and South Africa, up to around 1,500 gC/m<sup>2</sup>/year in California giant kelp, and close to 2,000 gC/m<sup>2</sup>/year in *Laminaria* in the North Atlantic (also see Table 10.1, p. 228).

Kelp communities are restricted to hard substrates in cold, nutrient-rich water.

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FIGURE 13.23 Giant kelp (*Macrocystis pyrifera*) forest at Cedros Island, Baja California, Mexico.



**FIGURE 13.24** The life history of the giant kelp (*Macrocystis*) and other kelps includes a large spore-producing sporophyte. Spores settle on the bottom and develop into minute male or female gametophytes. Each gametophyte releases male or female gametes which, after fertilization, develop into the sporophyte, thus completing the cycle (also see Fig. 6.11*a*).

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The large kelps we see are only one stage in their life history. All kelps go through two stages: a large sporeproducing **sporophyte** and a microscopic **gametophyte**, which produces male and female gametes (Fig. 13.24). The sporophyte is the organism we see.

In some kelps the sporophyte is an annual. In contrast, the giant kelp and others are perennial and can live for several years. These long-lived kelps often lose fronds to grazers, storms, and waves. They are able to grow them back because, unlike many seaweeds, growth takes place at the holdfast as well as the end of the stipes.

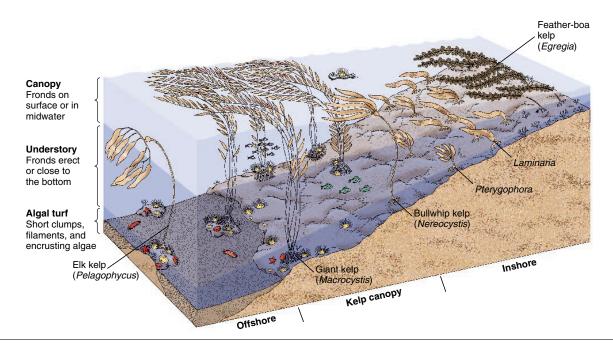
Pacific kelp communities are arranged in distinct depth zones, each made up of species that grow at a characteristic height above the bottom (Fig. 13.25). This structure results from the interaction of several physical and biological factors. The floating canopy of the giant kelp, for instance, develops only where the water is deep enough to reduce wave action but shallow enough for light to reach the bottom, permitting growth from the holdfasts. Other kelps may contribute to the surface canopy. These include the bullwhip kelp, found closer inshore, and the feather-boa kelp (Egregia), which lives in shallower water subject to wave action. Pelagophycus forms a midwater canopy under the giant kelp canopy.

The dense canopy of kelp forests cuts down the amount of light underneath. Diving under the canopy is like walking into a dense forest on land: It takes a few moments for your eyes to adjust to the dim light. The kelps that live there also have to adapt to the reduced light level, but life under the canopy is surprisingly rich and varied. Smaller kelps exploit the **understory**, the area below the canopy. They include *Laminaria*, *Pterygophora*, and other kelps that have either erect fronds that stand above the bottom or fronds that lie right on it.

A variety of shorter algae, mostly red algae, live on the bottom under the two overlying layers, even when light is greatly reduced. Both branching and encrusting coralline algae are common. Some seaweeds are more abundant in shallow water, where increased wave action reduces the canopy.



### *Chapter 13 Life on the Continental Shelf* 293



**FIGURE 13.25** Distribution of the major types of kelps and other seaweeds in a generalized giant kelp (*Macrocystis*) forest on the Pacific coast of North America. The complex distribution of algae results from the effects of factors such as light, type of substrate, wave action, depth, number and type of grazers, and even time of year because some of the seaweeds are annuals.

North Atlantic kelp beds are dominated by species of *Laminaria* that typically do not form a canopy. They are similar to Pacific kelp forests, however, in that they include many species of seaweeds and are arranged in depth zones.

The complex three-dimensional structure of kelp communities is exploited by many different animals. An amazing assortment of polychaetes, small crustaceans, brittle stars, and other small invertebrates live on the kelp holdfasts, particularly those of the giant kelp. Tube-dwelling polychaetes, lace-like bryozoans, and other sessile organisms are common on the blades and stipes. Like the animals that live associated with the holdfast, they are mostly suspension feeders. One conspicuous inhabitant of the blades is a bryozoan (Membranipora) that forms thin, lace-like colonies. Their calcareous encrustations weigh the blades down and cover photosynthetic tissues, but their effect appears to be minimal. The rocky bottoms around kelps are inhabited by sponges, sea squirts, lobsters, crabs, hermit crabs, sea stars, (see Fig. 7.43a), abalones (see Fig. 7.21b), and octopuses, among others.

Fishes are very common in kelp communities. They use the food resources and shelter provided by the kelp community in many different ways thus occupying many different ecological niches. For instance, the fishes often use the available resources by feeding and taking shelter in different areas within the forest. Some species feed close to the bottom. In the Pacific kelp beds, bottom feeders include many species of rockfishes (Sebastes) and the kelp bass (Paralabrax clathratus). The California sheephead (Semicossyphus pulcher) uses its dog-like teeth to crush sea urchins, crabs, and other bottom invertebrates. Surfperches (Rhacochilus, Brachyistius) and others may feed in different parts of the canopy, around the holdfasts, or in the open water among the kelp. Topsmelt (Atherinops) are plankton feeders that take advantage of large swarms of opossum shrimps, or mysids, and other planktonic animals found around kelps. Fishes may define additional ecological niches by being active at different times of the day or night.

Small algae are grazed by snails, crabs, sea urchins, and fishes, but surprisingly few grazers eat the large kelps. One large kelp grazer, the Steller's sea cow, is now extinct (see Fig. 18.13). Isopods (*Phycolimnoria*) are small crustaceans that burrow into the holdfast, weakening it. A few fishes graze on kelps, but they do not appear to cause much mortality. Instead of feeding on the attached, actively growing individuals, animals use most of the huge production of kelps in the form of drift kelp, pieces that break loose and sink to the bottom or are washed ashore. As with seagrasses, salt-marsh plants, and mangroves, much of this detritus is exported to other communities.

Kelp beds form a multistoried, complex environment. Drift kelp and understory seaweeds are a major food source but not the live kelp themselves.

**Ecological Niche** The combination of what a species eats, where it lives, how it behaves, and all the other aspects of its lifestyle.

Chapter 10, p. 219

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Sea urchins are by far the most important grazers in kelp communities. Of special importance are the red (Strongylocentrotus franciscanus) and purple (S. purpuratus) sea urchins on the Pacific coast of North America and the green sea urchin (S. droebachiensis; see Fig. 7.45a) in both the North Atlantic and Pacific oceans. Sea urchin populations sometimes "explode". These explosions have had devastating impacts on kelp communities in several different parts of the world. Sea urchins normally feed on drift kelp. During population explosions, or "plagues," however, the urchins eat live kelps and other seaweeds (see Fig. 10.3). When the sea urchins eat the holdfasts or stipes, the kelps break loose, float away, and die. The sea urchins may even climb up the kelp, weighing down the fronds and allowing other urchins to reach them. The urchins may completely clear large areas, which are then known as "urchin barrens" or "urchin deserts." Encrusting coralline algae are virtually the only seaweeds left on these barrens.

The reasons for such outbreaks of urchins remain unclear. In the North Pacific a probable cause is the decline in sea otters (Enhydra lutris; see Fig. 9.12), an urchin predator that has disappeared from most of its former range. In a study of several islands in the Aleutian chain, Alaska, kelp forests were found to be healthy where sea otters were common. In contrast, there were many sea urchins and few kelps on islands where sea otters were absent. These results, however, do not explain the situation in Southern California, where sea otters were wiped out more than 150 years ago, but the destruction of kelps by sea urchins was not observed until the 1950s. Heavy fishing on other urchin predators, including lobsters, crabs, and fishes, probably plays a role in urchin outbreaks in many places.

In the 1990s declines in the kelp forests of the Aleutian Islands, probably because of increased grazing by sea urchins, followed reductions in sea otter populations. There is evidence that otter populations have declined because of predation by killer whales, which normally prefer seals and sea lions. Seals and sea lions have become increasingly scarce since the late 1980s, probably because overfishing has reduced their food supply. Overfishing thus may have affected kelp forests by way of a chain of events that includes seals and sea lions, killer whales, sea otters, and sea urchins.

Another possibility is that a decrease in the amount of drift algae might have caused the urchins to switch to feeding on live kelps. Sewage pollution, temperature increases, and a decrease in nutrients are factors that may have caused the availability of drift kelp to drop. Some of these factors may also stimulate the growth and survival of sea urchins. Some organic compounds released in sewage, for example, are used as nutrients by juvenile sea urchins.

The harvesting of Pacific abalones for food has also been proposed as a possible cause of sea urchin plagues. These large molluscs compete with sea urchins for shelter in rock crevices. Removal of the abalones may provide more space for urchins.

It is also possible that fluctuations in the number of sea urchins are caused by the higher survival of their planktonic larvae, perhaps the result of more favorable temperatures or more abundant food. It is likely that a combination of factors causes urchin plagues. To some extent, "plagues" may really be natural fluctuations in population size.

Weather is a complicating factor. A strong **El Niño** in 1983 produced severe storms and unusually warm currents, which caused high kelp mortality. The 1997–98 El Niño was similarly destructive. A **La Niña** that followed the 1997–98 El Niño, however, brought cold, nutrientrich currents to the California coast, stimulating the recovery of kelp forests.

Kelp communities may be severely disrupted by strong wave action, grazing by sea urchins, warm currents, and pollution.

•

The recovery of Southern California kelp forests has progressed well in some areas. It has been aided in part by transplanting healthy kelps tied to blocks into depleted areas (see "Restoration of Habitats," p. 425). As an experiment, a few sea otters were transplanted to one of the Channel Islands off Southern California. Most transplanted animals disappeared, however, so the experiment was discontinued. The red sea urchin is now being harvested for human food in growing numbers. Will these measures have an effect? Nobody really knows. One thing is for sure: Some kelp forests have not recovered and perhaps never will.

Evidence from other parts of the world seems to indicate that catastrophic disturbances of kelp communities are eventually followed by a recovery, all in recurring cycles. Sea urchins and kelps are apparently kept in a delicate balance that can be tipped one way or the other by factors such as climate fluctuation, effects of nutrient pollution on the survival of urchin larvae, and the removal of urchin predators. The dynamics of kelp communities remains one of the fascinating questions in marine biology. It will ultimately be explained by the complex interplay of the biological and physical factors that govern kelp communities.

El Niño A warming of the surface water in the Eastern Pacific, part of large-scale changes in atmospheric and ocean current patterns, or *ENSO*. La Niña A cooling trend of the surface water in the Eastern Pacific. *Chapter 15, pp. 351–354*  III. Structure and Function of Marine Ecosystems 13. Life on the Continental Shelf © The McGraw–Hill Companies, 2003



# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

## **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

## Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

## **Critical Thinking**

- 1. Eelgrass communities in Europe and the eastern coast of North America were severely affected by a still unknown disease. The so-called eelgrass blight, or wasting disease, of the 1930s caused many eelgrass beds to disappear. What changes would you expect to take place if an eelgrass community vanishes from a given area? Consider changes to the substrate, the benthos, and other types of marine animals. Are there any possible changes among animals living on land? What type of community do you think replaced the eelgrass communities after they disappeared?
- 2. The life history of kelps consists of a very large sporophyte and a tiny gametophyte. Sea lettuce and some other seaweeds, however, have a gametophyte that is as big as their sporophyte (see Fig. 6.11*a*). Do you see any advantages for kelps having such an inconspicuous, puny gametophyte?

## **For Further Reading**

### **General Interest**

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### In Depth

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- Micheli, F., 1997. Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. *Ecological Monographs*, vol. 67, pp. 203–224.
- Witman, J. D. and P. K. Dayton, 2001. Rocky subtidal communities. In: *Marine Community Ecology* (M. D. Bertness, S. D. Gaines and M. E. Hay, eds.), pp. 339–366. Sinauer, Sunderland, Mass.

## See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center.

- Oyster reef in estuary (South Carolina)
- · Seagrass bed with blue tangs feeding (Belize)

## Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Shallow subtidal communities
- The coast and the continental shelf
- Kelp forests

## Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

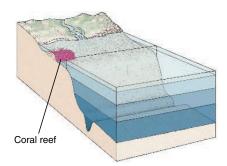
III. Structure and Function 14. Coral Reefs of Marine Ecosystems

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# Coral Reefs







A coral reef in Indonesia.

here is something special about coral reefs. The warm, clear water, spectacular colors, and multitude of living things captivate almost everyone who sees a reef. Coral reefs rival that other great tropical community, the rain forest, in their beauty, richness, and complexity. Tropical rain forests and coral reefs are also similar in that the basic physical structure of both communities is produced by organisms. Both reef-building corals and the giant trees of a rain forest create a three-dimensional framework that

is home to an incredible assortment of organisms. Coral reefs are such massive structures, in fact, that they must be considered not only biological communities but geological structures, the largest geological features built by organisms.

A few organisms other than corals, like oysters, polychaete worms, and red algae can form reefs (see Fig. 12.22). Such reefs are important in some places, but they are minor features compared to coral reefs. Chapter 14 looks exclusively at coral reefs.

## THE ORGANISMS THAT BUILD REEFS

Coral reefs are made of vast amounts of **calcium carbonate (CaCO<sub>3</sub>)**, limestone, that is deposited by living things. Of the thousands of species in coral reef communities, only a fraction produce the limestone that builds the reef. The most important of these reefbuilding organisms, as you might guess, are corals. 298 **Part Three** Structure and Function of Marine Ecosystems

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## **Reef Corals**

Corals are **cnidarians.** Nearly all are in the class Anthozoa, making them closely related to sea anemones. Unlike many other cnidarians, they lack a **medusa** stage and live only as **polyps.** In reef-building corals, which are sometimes called **hermatypic** corals, the polyps produce calcium carbonate skeletons. Billions of these tiny skeletons build a massive reef.

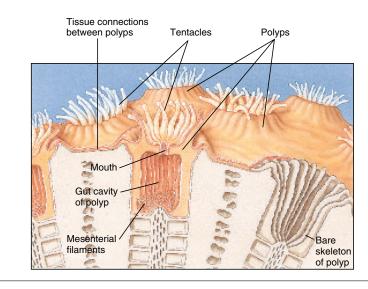
There are a few kinds of reef-building corals that are not anthozoans. Fire corals (*Millepora*), for example, are hydrozoans, more closely related to jellyfishes than sea anemones. They do have a medusa stage during their life cycle, but like other reefbuilding corals they grow on the reef in colonies of polyps that have limestone skeletons. They are called "fire corals" because their powerful nematocysts cause a burning sensation if you touch them.

Not all corals help build reefs. Nearly all soft corals (order Alcyonacea) lack a hard skeleton and, although they are abundant on coral reefs (see Fig. 14.28), they don't help build them. Black corals (order Antipatharia) and **gorgonians** (order Gorgonacea), including sea fans (see Fig. 7.9) and sea whips, are hard but their skeletons are made mostly of protein and contribute little to reef formation. These non-reef-building, or ahermatypic, corals are common in other habitats as well as coral reef. Precious corals live mostly in deep-water habitats rather than coral reefs, though they do have a calcareous skeleton. Precious corals are gorgonians.

Reef-building corals are the primary architects of coral reefs.

### The Coral Polyp

You have to look closely to see the little polyps that build coral reefs. Coral polyps are not only small but deceptively simple in appearance. They look much like little sea anemones, consisting of an upright cylinder of tissue with a ring of tentacles on top (Figs. 14.1 and 14.2*b*). Like anemones and other cnidarians, they use their nematocyst-armed tentacles to capture food, especially zooplankton. The tentacles surround the mouth, the only opening to the sac-like gut.



**FIGURE 14.1** Cutaway view of one of the polyps in a coral colony and of the calcium carbonate skeleton underneath. The polyps are interconnected by a very thin layer of tissue.





FIGURE 14.2 Coral polyps. (a) A few corals, like the mushroom coral (*Fungia*) from the Indo-West Pacific, consist of a single polyp. Most are colonies of many individual polyps. (b) In some of these, like the large-cupped boulder coral (*Montastrea cavernosa*) from the Caribbean, each polyp has its own individual cup, called a corallite. (c) In coral colonies like the brain coral (*Diploria*) from the Caribbean, meandering lines of polyps lie in a common corallite.

Most reef-building corals are colonies of many polyps, all connected by a thin sheet of tissue. The colony starts when a planktonic coral larva, called a **planula**, settles on a hard surface. Coral larvae generally do not settle on soft bottoms. Immediately after settling, the larva transforms, or **metamorphoses**, into a polyp. This single "founder" polyp, if it







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survives, divides over and over to form the colony. Thus, all the polyps in a coral colony are genetically identical copies, or clones, of the founder polyp. The digestive systems of the polyps usually remain connected, and they share a common nervous system (Fig. 14.3). A few reefbuilding corals consist of only a single polyp (Fig. 14.2*a*). III. Structure and Function 14. Coral Reefs of Marine Ecosystems

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### Chapter 14 Coral Reefs 299



Corals are amazingly adaptable animals. They come in all shapes and sizes and have many ways to feed themselves. It should come as no surprise, then, that they also have more than one way to reproduce.

In one way, growth and reproduction are the same thing in corals. The coral colony grows as its individual polyps divide to form new polyps. Thus, the colony grows as the polyps reproduce. The process crosses the fine line between growth and reproduction when a piece of coral breaks off and continues to grow. It is now a separate colony, though it is a genetically identical clone of its "parent." Certain species of coral may depend heavily on this form of reproduction and may even be adapted to break easily. After a reef is damaged by a severe storm, an important part of its recovery is the growth of pieces of shattered coral colonies.

Corals can also reproduce sexually. Like other animals, they produce eggs and sperm, which fuse and eventually develop into planula larvae, the characteristic larvae of cnidarians. Some corals are hermaphrodites, and make both eggs and sperm, whereas other species have separate sexes. The method of fertilization also varies among corals. In some, whether or not they are hermaphrodites, the egg is fertilized and develops inside the polyp. Most corals, however, are broadcast spawners and release the eggs and sperm into the water.

One of the most spectacular findings about coral reefs in recent years was the discovery of annual mass spawning of corals on the Great Barrier Reef. For a few nights a year between October and early December, a whole variety of coral species spawns at once. The event takes place just after a full moon. At a given place, the time of mass spawning can usually be predicted down to the night. It may seem surprising that this was only recently discovered—the first scientific report appeared in 1984—but no one was really looking! Since its discovery on the Great Barrier Reef, mass spawning has also been found to occur on a number of other reefs around the world.

The eggs and sperm may be released directly into the water or enclosed in little bundles that are released through the mouth. Depending on the coral species, the bundles may contain both eggs and sperm, or only one or the other. The bundles float to the surface and break up, allowing the eggs and sperm to mix.

Nobody knows why the corals all spawn together. Maybe the egg predators get so full that most of the eggs go uneaten. Maybe it has something to do with the tides. There may be an explanation that no one has thought of. Another interesting thing is that although the mass spawning





The release of sperm and egg bundles during the mass coral spawning on the Great Barrier Reef. Photographs courtesy of the Great Barrier Reef Marine Park Authority.

happens on some reefs it does not occur on others. Is there something different about these reefs? The answers to these questions are likely to occupy coral reef biologists for some time to come.

## Most corals are colonies of many identical polyps.

Coral polyps lie in a cup-like skeleton of calcium carbonate that they make themselves. Over the years a series of polyps, each laying down a new layer of calcium carbonate, builds up the skeleton (Fig. 14.4). The skeleton forms the bulk of the colony (Fig. 14.5), which can take many different shapes (Fig. 14.6). The actual living tissue is only a thin layer on the surface. It is the calcium carbonate coral skeletons, growing upward and outward with the coral, that create the framework of the reef.

Nearly all reef-building corals contain symbiotic **zooxanthellae** (Fig. 14.7). In fact, hermatypic corals are sometimes defined as those with zooxanthellae rather than as those that build reefs. **Cnidarians** Animals in the phylum Cnidaria; they have radial symmetry, tissue-level organization, and tentacles with *nematocysts*, specialized stinging structures.

Life stages of cnidarians: **Polyp** The sessile, sac-like stage, with the mouth and tentacles on top.

Medusa The swimming, bell-like stage, with the mouth and tentacles underneath.

Chapter 7, p. 120

**Plankton** Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.

Chapter 10, p. 230; Figure 10.19

**Zooxanthellae** Dinoflagellates (single-celled, photosynthetic algae) that live within animal tissues.

### Chapter 5, p. 99

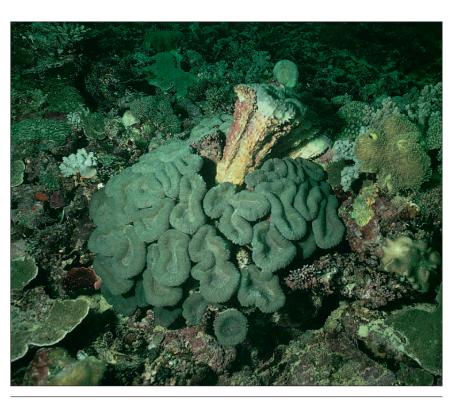
**Symbiosis** The living together in close association of two different species, often divided into *parasitism*, where one species benefits at the expense of the other; *commensalism*, where one species benefits without affecting the other; and *mutualism*, where both species benefit.

Chapter 10, p. 220

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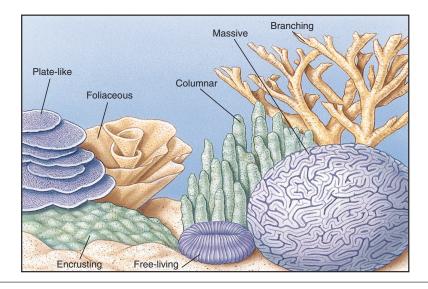
**FIGURE 14.3** The polyps in a coral colony are interconnected. If you touch an extended polyp, it will contract, and so will its neighbors, followed by their neighbors, and so on, so that a wave of contraction passes over the colony. In this colony of the coral *Goniopora lobata* the wave of contraction is moving up from the bottom.

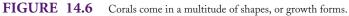


**FIGURE 14.4** This coral (*Lobophyllia hemprichii*) shows particularly well how corals build up their skeleton. Each of the irregular rings is a single polyp that has built up a column of calcium carbonate skeleton.



**FIGURE 14.5** The calcium carbonate skeleton makes up most of a coral colony. A live colony (*Pocillopora verrucosa*) is shown on the right. On the left is a colony with the living tissue removed. You can see that the main difference is the color; the live part is only a thin layer of tissue on the surface. The "corals" sold in shell and aquarium shops are actually only the skeletons of live corals that were taken from the reef and bleached. Some reefs have been devastated by the collectors who supply these shops in order to feed their families.





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FIGURE 14.7 The microscopic, golden-brown zooxanthellae that pack these polyp tentacles help corals build reefs. They also occur in sea anemones, giant clams, and other animals.

A few reef-building corals, however, lack zooxanthellae. There are also some deepwater corals without zooxanthellae that slowly build up calcium carbonate mounds on the ocean floor. These mounds are technically not reefs, though they are often referred to as such.

Without zooxanthellae corals produce their skeletons very slowly, not nearly fast enough to build a reef. The zooxanthellae enable the coral to deposit calcium carbonate much faster. It is the zooxanthellae as much as the corals that construct the reef framework; without them there would be no coral reefs.

### Coral Nutrition

Zooxanthellae also provide vital nourishment to the coral. They perform **photosynthesis** and pass some of the organic matter they make on to the coral. Thus, the zooxanthellae feed the coral from the inside. Many corals can survive and grow without eating, as long as the zooxanthellae have enough light.

Almost all reef-building corals contain symbiotic zooxanthellae. The zooxanthellae nourish the corals and help them produce their skeletons. Although corals get much of their nutrition from their zooxanthellae, most eat when they get the chance. They prey voraciously on zooplankton. The billions of coral polyps on a reef, along with all the other hungry reef organisms, are very efficient at removing zooplankton brought in by currents. Indeed, the reef has been called a "wall of mouths."

Coral polyps catch zooplankton with their tentacles or in sheets of mucus that they secrete on the colony surface. Tiny, hair-like cilia gather the mucus into threads and pass them along to the mouth. Some corals hardly use their tentacles and rely on the mucus method. A few corals have even lost their tentacles altogether.

Corals have still other ways of feeding themselves. There are a number of long, coiled tubes called **mesenterial filaments** attached to the wall of the gut (Fig. 14.1). The mesenterial filaments secrete digestive enzymes. The polyp can extrude the filaments through the mouth or body wall to digest and absorb food particles outside the body. Corals also use the mesenterial filaments to digest organic matter from the sediments. In addition, corals are among the relatively few animals that can absorb **dissolved organic matter (DOM)** (see "The Trophic Pyramid," p. 223).

Corals nourish themselves in a remarkable number of ways. Zooxanthellae are the most important source of nutrition. Corals can also capture zooplankton with tentacles or mucus nets, digest organic material outside the body with mesenterial filaments, or absorb dissolved organic matter (DOM) from the water.

### **Other Reef Builders**

Although they are the chief architects, corals cannot build a reef alone. Many other organisms help make a coral reef. The most important of these are algae, which are essential to reef growth. In fact, some marine biologists think that coral reefs should be called "algal reefs" or, to be fair to both, "biotic reefs." One reason for this is that zooxanthellae, which are algae, are essential to the growth of corals. There are other algae,

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however, that also have key roles in building the reef. Like corals, **coralline red algae** produce a "skeleton" of calcium carbonate. Encrusting coralline algae (*Porolithon, Lithothamnion*) grow in rockhard sheets over the surface of the reef. They deposit considerable amounts of calcium carbonate, sometimes more than corals, and thus contribute to reef growth. Coralline algae are more important on Pacific reefs than Atlantic ones.

Encrusting coralline algae not only help build the reef, they also help keep it from washing away. The stony pavement formed by these algae is tough enough to withstand waves that would smash even the most rugged corals. The algae form a distinct ridge on the outer edge of many reefs, especially in the Pacific. This **algal ridge** absorbs the force of the waves and prevents erosion from destroying the reef.

Encrusting algae do yet another job that is vital to reef growth. Coral skeletons and fragments create an open network, full of spaces, that traps coarse carbonate sediments (Fig. 14.8). Sediment, especially fine sediment, damages corals when it settles directly on them, but the buildup of coarse sediment in the reef framework is an essential part of reef growth. The structure of a reef is formed as much by the accumulation of calcareous sediment as by the growth of corals. Encrusting algae grow over the sediment as it builds up, cementing the sediment in place. Thus, encrusting coralline algae are the glue that holds the reef together. Some invertebrates, notably sponges and bryozoans, also form encrusting growths that help bind the sediments.

Encrusting coralline algae help build the reef by depositing calcium carbonate, by resisting wave erosion, and by cementing sediments.

•

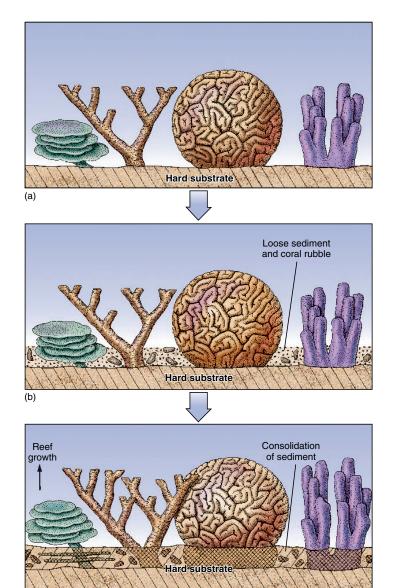
**Photosynthesis**  $CO_2 + H_2O +$ sun energy  $\rightarrow$  glucose +  $O_2$ 

Chapter 4, p. 71

**Bryozoans** Small, colonial, encrusting animals that make delicate, often lace-like, skeletons.

Chapter 7, p. 139; Figure 7.40

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**FIGURE 14.8** Reef growth involves several processes. (*a*) The framework is made when reef-building corals settle and grow on some hard surface, usually a preexisting reef. (*b*) The spaces in this framework are partially filled in by coarse carbonate sediments. (*c*) When the sediments are glued together by encrusting organisms, new reef "rock" is formed and the reef has grown. On a real reef all three steps go on at the same time. Reefs are not actually completely solid as depicted here but are porous, with many holes and crevices that serve as home to a host of organisms.

Nearly all the sediment that accumulates to help form the reef comes from coral fragments, or **coral rubble**, and the shells or skeletons of other organisms. In other words, nearly all the sediment is **biogenous**. Probably the most important

(c)

of all the sediment-forming organisms is a calcareous green alga called *Halimeda* (Fig. 14.9). *Halimeda* deposits calcium carbonate within its tissues to provide support and to discourage grazers—a mouthful of limestone is pretty unappe-

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FIGURE 14.9 This calcareous green alga (*Halimeda*) is one of the main sedimentforming organisms on most reefs. About 95% of the plant's weight is calcium carbonate, and there is only a thin layer of live tissue on the outside. When the tissue dies the segments separate, each leaving a piece of limestone.

tizing. The remnants of *Halimeda* accumulate on reefs in huge amounts, to be bound together by encrusting organisms.

Many other organisms make calcium carbonate sediments and thus contribute to the growth of the reef. The shells of **forams**, snails, clams, and other molluscs are very important. Sea urchins, bryozoans, crustaceans, sponges, bacteria and a host of other organisms add or help bind carbonate sediments. Reef growth is truly a team effort.

The accumulation of calcium carbonate sediments plays an important role in reef growth. A calcareous green alga, Halimeda, and coral rubble account for most of the sediment, but many other organisms also contribute.

## **Conditions for Reef Growth**

Other organisms may be important, but coral reefs do not develop without corals. Corals have very particular requirements that determine where reefs develop. Reefs are rare on soft bottoms, for example, because coral larvae need to settle on a hard surface.

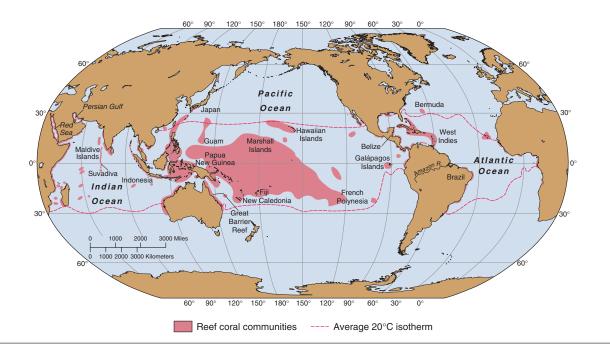


FIGURE 14.10 The geographic distribution of reef-building corals, like that of kelps, is related to temperature. Reef corals require warm water, however, whereas kelps need cold water. Compare the distribution of reefs with that of kelps shown in Figure 13.21. Note the effects of warm surface currents: Reefs extend farther north and south on the east sides of continents than on the west sides.

### Light and Temperature

Corals can grow only in shallow water, where light can penetrate, because the zooxanthellae on which they depend need light. Calcareons algae also require sunlight. Particular types of coral and algae have different depth limits-some can live deeper than others-but reefs rarely develop in water deeper than about 50 m (165 ft). Because of this, coral reefs are found only on the continental shelves, around islands, or on top of seamounts. Many types of coral live in deep water and do not need light, but these corals do not contain zooxanthellae or build reefs. Corals also prefer clear waters, since water clouded with sediment or plankton does not allow light to penetrate very well.

Reef-building corals are limited to warm water and can grow and reproduce only if the average water temperature is above about 20°C (68°F). Most reefs grow in considerably warmer areas. Figure 14.10 illustrates the relationship between coral reefs and water temperature. Corals need light and warm temperatures, so reefs grow only in shallow, warm waters.

Water that is *too* warm is also bad for corals. The upper temperature limit varies, but is usually around 30° to 35°C (86° to 95°F). The first outward sign of heat stress, or stress of other kinds, is **bleaching**, in which the coral expels its zooxanthellae (see Fig. 18.3). It is called bleaching because the golden-brown or greenish zooxanthellae give the coral most of its color; without them, the coral is almost white. Corals also slough off large amounts of slimy mucus when stressed. If the warm conditions last too long or the temperature gets too high the coral dies.

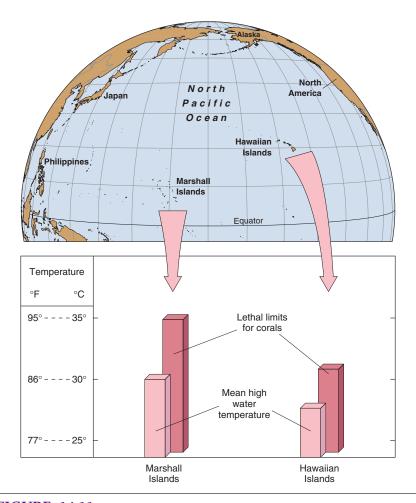
The exact temperature range preferred by corals differs from place to place because corals from a particular location adapt to the normal temperatures there (Fig. 14.11). Corals from places with very warm water, for example, are able to tolerate higher temperatures. In some places, corals must adapt to drastic fluctuations in temperature. For instance, reefs grow in parts of the Persian Gulf where the water temperature ranges from  $16^{\circ}$  to  $40^{\circ}$ C ( $60^{\circ}$  to  $104^{\circ}$ F).

The upper temperature tolerances of corals are usually not far above the normal temperature range at the place where they live. Corals suffer when exposed to temperatures outside this normal range. This sometimes happens during extreme low tides, when shallow pools on the reef may be cut off from circulation. Heated by the sun, the water can warm up to fatal temperatures. By discharging heated water, electric power plants can also kill corals.

El Niño (see "The El Niño-Southern Oscillation Phenomenon," p. 351), brings unusually warm water to many parts of the ocean. Widespread coral bleaching

Foraminiferans (Forams) Protozoans, often microscopic, with a calcium carbonate shell. *Chapter 5, p. 101; Figure 5.10* 

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**FIGURE 14.11** The upper temperature limit that corals can stand is related to the temperature at their home sites. For example, the water in the Marshall Islands is warmer on average than that in Hawai'i. During the hottest months of the year the average high temperature is several degrees higher in the Marshalls. Corals from the Marshalls can tolerate correspondingly higher temperatures. Why do you think the highest temperature that the corals can tolerate would be higher than the average high temperature at their location?

and mortality also occur during El Niño events. During the unusually strong El Niño of 1997–98, severe bleaching occurred on many reefs around the world, probably as a direct result of the unusually warm water. In some places, including the Caribbean and parts of the Great Barrier Reef, bleaching did not kill many corals, and reefs quickly recovered after the water cooled. In other areas, such as the Indian Ocean, Southeast Asia, and the far western Pacific, many corals died after bleaching and some reefs were severely damaged. Some of these may be recovering as new coral larvae settle and grow, but it is too early to tell.

High water temperatures have led to several other major, though more localized, bleaching events since the 1997–98 El Niño. It is possible that such events occurred in the past but were not reported because many reefs are in remote locations that were rarely observed by scientists. Today, scientists continually monitor seawater temperatures by satellite and can immediately report bleaching when it occurs via the Internet. It is also possible that the high water temperatures and coral bleaching of the past several years are just nor-

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FIGURE 14.12 Corals often flourish where there is plenty of wave action. The water motion keeps sediment from settling on the corals and brings in food, oxygen, and nutrients.

mal, random fluctuations. Both El Niño and coral bleaching are natural events that have occurred for millenia. Increasingly, however, coral reef scientists are concerned that warm-water episodes and bleaching events are becoming more frequent, and more intense, as a result of global climate change (see "Living in a Greenhouse: Our Warming Earth," p. 410). If so, this threatens coral reefs around the globe, especially because they are already faced with many other human-induced stresses (see "Coral Reefs," p. 408).

### Sediments, Salinity, and Pollution

Fine sediment like silt is very harmful to corals. It clouds the water, cutting down light for the zooxanthellae. Even a thin layer of sediment on the colony surface smothers the coral. To remove the sediment, corals use mucus opposite to the way in which they use it to feed. Instead of being brought to the mouth, the mucus is sloughed off, carrying sediment with it. Even with this defense, corals generally don't do well in places where there is a lot of sediment, unless there is enough wave or current action to wash the sediment away (Fig. 14.12). Reefs tend to be poorly developed, for example, near river mouths. This is not only because of the sediment brought in by rivers but because corals are also quite sensitive to reduced salinity caused by the freshwater input. Human activities like mining, logging, construction, and dredging can greatly increase the amount of sediment and freshwater runoff. These factors may have very harmful effects on local reefs.

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Corals are also sensitive to pollution of many kinds. Even low concentrations of chemicals like pesticides and industrial wastes can harm them. The larvae are especially sensitive. In high concentrations, nutrients also can be harmful to reef growth. Humans release tremendous amounts of nutrients in sewage and in fertilizers that are washed from farmland and carried to the sea. The nutrients may harm the corals directly by interfering with the formation of their skeletons. More importantly, increased nutrients can alter the ecological balance of the community. Most coral reefs grow in water that is naturally low in nutrients. In such nutrient-poor water, seaweeds do not grow very rapidly and are kept under control by grazers. This allows corals to compete successfully for space and light. When nutrients are added, seaweeds may grow much faster and shade and choke out the slow-growing corals. This is a particular problem when, as is often the case, grazing fishes have been removed by fishing (see "Grazing," p. 318).

Corals are very sensitive to fine sediment, fresh water, and pollution, including pollution by high nutrient levels.

### The Kane'ohe Bay Story

One of the best-known examples of the harmful effects of nutrient enrichment occurred in a partially enclosed bay in the Hawaiian Islands. Kane'ohe Bay, located on the northeast shore of the island of O'ahu, once had some of the most luxuriant reefs in Hawai'i. Until the 1930s the area around the bay was sparsely populated. In the years leading up to World War II, with the military buildup of O'ahu, the population began to increase. This increase continued after the war as the shores of the bay were developed for residential use.

The sewage from this expanding population was dumped right into the bay. By 1978 about 20,000 m<sup>3</sup> (over 5 million gallons) of sewage were being dumped into the bay every day. Long before then, by the mid-1960s in fact, marine biologists began to notice disturbing changes in the middle part of the bay. Loaded with nutrients, the sewage acted as a fertilizer for seaweeds. A green alga, the bubble alga (*Dictyosphaeria cavernosa*), found the conditions particularly to its liking and grew at a tremendous rate, literally covering the bottom in many parts of the bay. Bubble algae began to overgrow and smother the corals. Phytoplankton also multiplied with the increase in nutrients, clouding the water. Kane'ohe Bay's reefs began to die. Such accelerated algal growth due to nutrient input is called **eutrophication** (see "Eutrophication," p. 410).

For a time it appeared that the story had a happy ending. As the once beautiful reefs smothered, scientists and the general public began to cry out. It took a while, but in 1978 public pressure finally managed to greatly reduce the discharge of sewage into the bay, and the sewage was diverted offshore. The result was dramatic. Bubble algae died back in much of the bay, and the bay's corals began to recover much faster than anyone had expected. By the early 1980s, bubble algae were fairly scarce and corals had started to grow again. The reefs were not what they once were, but they seemed to be on track to recover.

Then the ghost of pollution past reared its ugly head. In November 1982, Hurricane Iwa struck Kane'ohe Bay. During the years of pollution a layer of the coral skeleton had weakened, becoming fragile and crumbly. When the hurricane hit, this weak layer collapsed and many reefs were severely damaged. Fortunately, the corals were already beginning to recover, and the broken pieces were able to grow back. If the hurricane had hit during the years of pollution, the reefs of Kane'ohe Bay—and the benefits of fishing, tourism, and recreation—might have disappeared forever.

The rapid recovery of Kane'ohe Bay's reefs that was seen during the early 1980s did not continue. By 1990 the recovery seemed to have leveled off. Some areas even began to decline again, with bubble algae once more becoming abundant. There are a number of possible explanations for this. Even though most sewage is now discharged outside the bay, some nutrients continue to enter from boats, the septic tanks and cesspools of private homes, and other sources. Not only that, nutrients from the old sewage outfalls

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were stored in the sediments, and are still being released even after 30 years. There is also evidence that fishing has reduced populations of fishes that graze on bubble algae. Furthermore, the grazing fishes that remain prefer to eat other species of seaweed that have been introduced from outside Hawai'i, and have shifted away from eating bubble algae. Thus, bubble algae may be abundant because they are not being eaten as fast as they once were. Another introduced seaweed, which like bubble algae is not a preferred food of herbivorous fishes, has also started to proliferate and smother corals in the bay (Fig. 14.13). It will be much harder to restore the coral gardens of Kane'ohe Bay than it was to destroy them.

The Kane'ohe Bay story is far from unique. Most of the world's tropical coasts are undergoing increasing development and population growth. As a result, more and more nutrients are ending up in the waters that support coral reefs, and there are many reports of reefs being threatened by eutrophication. On the other hand, new research is showing that the effects of added nutrients on coral reefs are much more complicated than we once thought. A few experiments have indicated that algal growth is not nutrientlimited on at least some reefs. There are even suggestions that in some cases added nutrients may be good for the zooxanthellae and help corals grow faster. The bulk of the evidence, however, is that eutrophication is damaging, especially when populations of algal grazers are reduced. Many reef biologists consider it one of the most serious threats to the world's coral reefs.

## KINDS OF CORAL REEFS

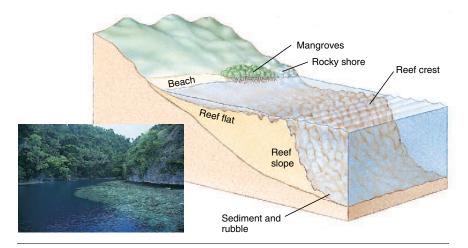
Coral reefs are usually divided into three main categories: **fringing reefs**, **barrier reefs**, and **atolls**. Some reefs do not fit neatly into any particular category, and some fall between two categories. Still, the division of reefs into the three major types works well for the most part.

The three main types of reefs are fringing reefs, barrier reefs, and atolls.

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**FIGURE 14.13** The red alga *Kappaphycus striatum*, introduced to Kane'ohe Bay from the Philippines, has gotten out of control. The arrow shows one of many clumps of *K. striata* in this picture that are growing over and smothering reef corals.



**FIGURE 14.14** Typical structure of a fringing reef. Fringing reefs, like this one in the Bismarck Archipelago in the southwest Pacific (photo), can grow right up to the shore.

## Fringing Reefs

Fringing reefs are the simplest and most common kind of reef. They develop near shore throughout the tropics, wherever there is some kind of hard surface for the settlement of coral larvae. Rocky shorelines provide the best conditions for fringing reefs. Fringing reefs also grow on soft bottoms if there is even a small hard patch that lets the corals get a foothold. Once they get started, the corals create their own hard bottom and the reef slowly expands.

As their name implies, fringing reefs grow in a narrow band or fringe along the shore (Fig. 14.14). Occurring close to land, they are especially vulnerable to

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sediment, freshwater runoff, and human disturbance. Under the right conditions, however, fringing reefs can be impressive. In fact, the longest reef in the world (though not the one with the largest coral area) is not the famous Great Barrier Reef in Australia but a fringing reef that runs some 4,000 km (2,500 mi) along the coast of the Red Sea. Part of the reason that this reef is so well developed is that the climate is dry and there are no streams to bring in sediment and fresh water.

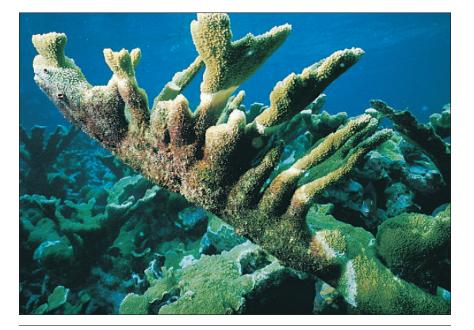
The typical structure of a fringing reef is shown in Figure 14.14. Depending on the place, the shore may be steep and rocky or have mangroves or a beach. The reef itself consists of an inner reef flat and an outer reef slope. The reef flat is the widest part of the reef. It is shallow, sometimes exposed at low tide (Fig. 14.15), and slopes very gently toward the sea. Being closest to land, it is the part of the reef most strongly affected by sediments and freshwater runoff. The bottom is primarily sand, mud, or coral rubble. There are some living corals, but neither as many colonies nor as many different kinds as on the reef slope. Seaweeds, seagrasses, and soft corals may also occupy the reef flat, sometimes in dense beds.

The reef slope can be quite steep, nearly vertical in fact. It is the part of the reef with the densest cover (Fig. 14.16) and the most species of coral, because the slope is away from shore and therefore away from the effects of sediment and fresh water. Also, the waves that bathe the slope provide good circulation, bring in nutrients and zooplankton, and wash away fine sediments. The reef crest is the shallow edge of the reef slope. The crest usually has even more luxuriant coral growth than the rest of the reef slope. If there is intense wave action, however, the crest may consist of an algal ridge, with the richest coral growth just below. Because there is less light in deep water, the deepest part of the reef slope usually has less live coral and fewer coral species.

Fringing reefs grow close to shore and consist of an inner reef flat and an outer reef slope. III. Structure and Function 14. Coral Reefs of Marine Ecosystems © The McGraw–Hill Companies, 2003



**FIGURE 14.15** The upward growth of most reefs is limited by the tides. When extreme low tides occur, shallow areas like this reef flat on the Great Barrier Reef are exposed. If the corals are only exposed for a short time, they can survive, but they will die if exposed for too long. It is this occasional exposure at extreme low tides that keeps reef flats flat because all the corals above a certain depth are killed. Photograph courtesy of the Great Barrier Reef Marine Park Authority.



**FIGURE 14.16** The elkhorn coral (*Acropora palmata*) is a dominant coral on the reef slopes of fringing reefs in the Caribbean and Florida. Its broad branches rise parallel to the surface to collect light. This colony suffers from a disease known as white-band disease (see "Coral Reefs," p. 408).

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Large amounts of sediment and coral rubble tumble down the reef slope and settle at the base. As this material builds up, reef organisms may begin to grow on it, depending on the water depth and other factors. Thus, the reef can grow outward, as well as upward. Beyond the base of the slope, the bottom is usually fairly flat and composed of sand or mud. On many Caribbean reefs, turtle grass (*Thalassia testudinum*) dominates the bottom beyond the slope.

## **Barrier Reefs**

The distinction between barrier reefs and fringing reefs is sometimes unclear because the two types grade into one another. Like fringing reefs, barrier reefs lie along the coast, but barrier reefs occur considerably farther from shore, occasionally as far as 100 km (60 mi) or more. Barrier reefs are separated from the shore-which may also have a fringing reef-by a relatively deep lagoon (Fig. 14.17). Largely protected from waves and currents, the lagoon usually has a soft sediment bottom. Inside the lagoon, coral formations variously known as patch reefs, coral knolls, or pinnacles depending upon their size and shape may grow up nearly to the surface.

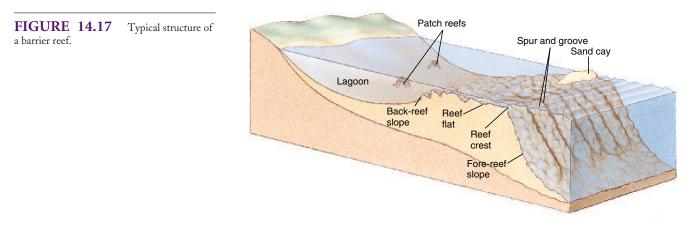
The barrier reef consists of a **back-reef slope**, a reef flat, and a **fore-reef slope**, which corresponds to the reef slope of a fringing reef and has a reef crest (Fig. 14.17). The back-reef slope may be gentle or as steep as the fore-reef slope. It is protected from waves by the rest of the reef, but waves wash large amounts of sediment from the reef down the slope. As a result, coral growth is often not as vigorous on the back-reef slope as on the fore-reef slope. This is not always true; some back-reef slopes, especially gentle ones, have luxuriant coral growth (Fig. 14.18).

The reef flat, like that on fringing reefs, is a shallow, nearly flat platform. Sand and coral rubble patches are interspersed with seagrass or seaweed beds, soft corals, and patches of dense coral cover. Waves and currents may pile up sand to form small sand islands called **sand cays** or, in the United States, **keys**.

The richest coral growth is usually at the outer reef crest. There may be a

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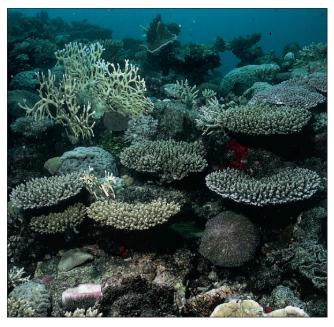


FIGURE 14.18 A rich back-reef slope on a Pacific barrier reef.



FIGURE 14.19 A portion of the spur-and-groove formations at Enewetak, an atoll in the Marshall Islands, at low tide.

well-developed algal ridge if the reef is exposed to wave action, with coral growth most luxuriant just below the crest. Exposed fore-reef areas often have a series of finger-like projections alternating with sand channels (Figs. 14.17 and 14.19). There is still debate about what causes these formations, known as **spurand-groove** formations or **buttresses**. The wind, waves, or both, are definitely involved, because spur-and-groove formations develop primarily on reef slopes that are exposed to consistent strong winds. These formations are found on atolls and some fringing reefs as well as barrier reefs.

Fore-reef slopes vary from relatively gentle to nearly vertical. The steepness depends on the action of wind and waves, the amount of sediment flowing down the slope, the depth and nature of the bottom at the reef base, and other factors. As with other types of reefs, the abundance and diversity of corals on the fore-reef slope generally decreases with depth. The growth form of the corals also changes down the slope. At the crest, under the pounding of the waves, the corals are mostly stout and compact; many are massive (see Fig. 14.6). Below the crest there is great variety in form. Whether they form branches, columns, or whorls, corals in this zone often grow vertically upward. This may be an adaptation for competition. Corals that grow upward like skyscrapers rather than outward need less space to attach. They are also less likely to be shaded, and if they spread out at the top, can shade out other corals. Deeper on the reef slope, corals tend to grow in flat sheets, which probably helps them collect more light (see Fig. 10.1). The largest and most famous barrier reef is the Great Barrier Reef. It runs more than 2,000 km (1,200 mi) along the northeastern coast of Australia, varying in width between about 15 and 350 km (10 to 200 mi) and covering an area of over 225,000 km<sup>2</sup> (80,000 mi<sup>2</sup>). Though not the longest reef in the world, it covers such a large area and is so complex and well developed that it is generally regarded as the largest reef structure. Actually, the Great Barrier Reef is not a single reef but a system of more than 2,500 smaller reefs, lagoons, channels, islands, and sand cays (Fig. 14.20).

The largest barrier reef in the Caribbean lies off the coast of Belize, Central America. Other major barrier reefs include the Florida Reef Tract and barrier reefs associated with the islands of New Caledonia, New Guinea, and Fiji in the Pacific. There are many other smaller barrier reefs, especially in the Pacific. Like the Great Barrier Reef, these usually are not single reefs but complex systems of smaller reefs.

## **Atolls**

An atoll is a ring of reef, and often islands or sand cays, surrounding a central lagoon (Figs. 14.21 and 14.22). The vast majority of atolls occur in the Indo-West Pacific region, that is, the tropical Indian and western Pacific oceans. Atolls are rare in the Caribbean and the rest of the tropical Atlantic Ocean. Unlike fringing and barrier reefs, atolls can be found far from land, rising up from depths of thousands of meters or more. With practically no land around, there is no river-borne silt and very little freshwater runoff. Bathed in pure blue ocean water, atolls display spectacular coral growth and breathtaking water clarity. They are a diver's dream.

### Atoll Structure

Atolls range in size from small rings less than a mile across to systems well over 30 km (20 mi) in diameter. The two largest atolls are Suvadiva, in the Maldive Islands in the Indian Ocean, and Kwajalein, one of the Marshall Islands in the central Pacific. These atolls cover areas of



**FIGURE 14.20** The Great Barrier Reef is a complicated system of thousands of small reefs, sand cays, and lagoons. Shown here are four reefs that are part of the Great Barrier Reef Marine Park. Photograph courtesy of the Great Barrier Reef Marine Park Authority.



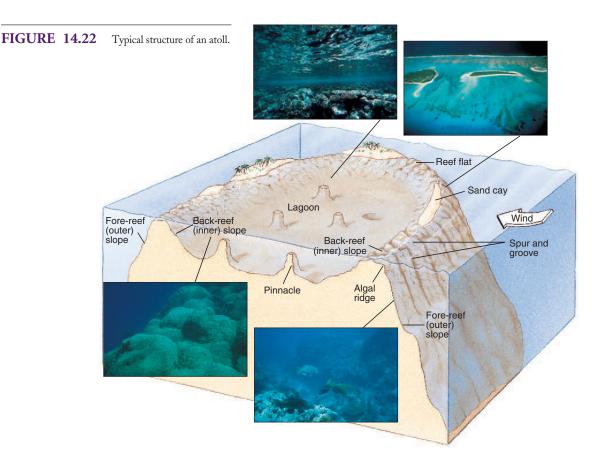
FIGURE 14.21 Fulanga atoll, in the South Pacific nation of Fiji.

more than  $1,200 \text{ km}^2$  (700 mi<sup>2</sup>). Atolls may include a dozen or more islands and be home to thousands of people.

An atoll's reef flat is much like the reef flat on a fringing or barrier reef: a flat, shallow area. Unlike those of barrier reefs, however, the atoll's reef flat is rarely more than a kilometer or so wide. The fore-reef and back-reef slopes can now be thought of as outer and inner slopes, respectively, since they extend all the way around the ring-shaped atoll.

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The reef crest of an atoll is strongly influenced by wind and waves. Because most atolls lie in the zone of the trade winds, the wind usually comes from a consistent direction. Consequently, the wind affects various parts of the atoll in different ways. Encrusting coralline algae, which can endure the constant pounding of the waves, build a distinct algal ridge on the reef crest of the windward side of the atoll, the side that faces the prevailing wind. On the few Caribbean atolls, the coralline algae may be replaced by especially wave-resistant corals. The leeward, or sheltered, side of the atoll has no algal ridge. Spur-and-groove formations, too, develop only on the windward side.

The fore-reef, or outer, slope is nearly vertical, though there is usually a series of ledges and overhangs. The reef wall continues down to great depths. The water may be hundreds, even thousands, of meters deep just a stone's throw from the reef. The lagoon, on the other hand, is relatively shallow, usually about 60 m (195 ft) deep. The bottom of a lagoon is very uneven, with many depressions and coral pinnacles. Some pinnacles rise almost to the surface, where they may form "mini-atolls," small rings of coral within the lagoon.

Atolls are rings of reef, with steep outer slopes, that enclose a shallow lagoon.

### How Atolls Grow

When atolls were discovered, scientists were at a loss to explain them. It was known that corals can grow only in shallow water, yet atolls grow right in the middle of the ocean, out of very deep water. Therefore, the atoll could not have grown up from the ocean floor. If the reefs grew on some kind of shallow structure that was already there, like a seamount, why is there no sign of it? The islands on atolls are simple sand cays that have been built by the accumulation of reef sediments and would not exist without the reef. They are *products* of the reef and could not provide the original **substrate** for reef growth. Finally, why do atolls always form rings?

The puzzle of atoll formation was solved by Charles Darwin in the midnineteenth century. Darwin is most famous, of course, for proposing the theory of evolution by natural selection, but his theory of atoll formation is also an important contribution to science.

Darwin reasoned that atolls could be explained by reef growth on a subsiding island. The atoll gets its start when a deep-sea volcano erupts to build a volcanic island. Corals soon colonize the shores of the new island, and a fringing reef develops (Fig. 14.23*a*). As with most fringing reefs, coral growth is most vigorous at the outer edge of the reef. The inner reef is strongly affected by sediment and runoff from the island. Fringing reef

Island

(a)

(c)

Atoll

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FIGURE 14.23 (a) An atoll begins as a fringing reef around a volcanic island. (b) As the island slowly sinks, the reef flat gets wider and deeper and eventually becomes a lagoon. At this stage the fringing reef has become a barrier reef. (c) Eventually the island sinks altogether, leaving only a ring of living growing reef—an atoll.

Surprisingly, Darwin's explanation of how atolls are created was pretty much ignored for a century while scientists proposed various other hypotheses. None of these alternative hypotheses held up. Finally scientists found conclusive evidence that Darwin was right. Unlike other hypotheses for atoll formation, Darwin's hypothesis predicted that, below the thick calcium carbonate cap formed by the reef, there should be volcanic rockthe original island. In the 1950s the United States Geological Survey drilled several deep holes on Enewetak atoll in the Marshall Islands. These cores revealed exactly what Darwin predicted: volcanic rock far beneath the calcium carbonate of the reef. The thickness of the carbonate cap is impressive. The volcanic island that underlies Enewetak is covered by more than 1,400 m (4,600 ft) of calcium carbonate!

Scientists now believe almost unanimously that Darwin's hypothesis of atoll formation is correct. There are, of course, a few details to be added to the picture, in particular the effects of changes in sea level (see "Climate and Changes in Sea Level," p. 35). When sea level is low, atolls may be left above the surface. The corals die and the reef is eroded by the wind and rain. If sea level rises rapidly, the atoll may be drowned, unable to grow in deep water. In either case, corals recolonize the atoll when the sea level returns to "normal".

Calcium carbonate

Original island

Barrier reef

Lagoon

(b)

## THE ECOLOGY OF CORAL REEFS

Coral reefs may be impressive to geologists, but to the biologist they are simply awesome. They are easily the richest and most complex of all marine ecosystems. Literally thousands of species may live on a reef. How do all these different species live? How do they affect each other? What is their role in the reef ecosystem? These and countless other questions fascinate coral reef biologists. Our ability to answer the questions, however, is surprisingly limited. This is partly because reefs are so complicated. Just keeping track of all the different organisms is hard enough; the task of figuring out what they all *do* is mind-boggling. Furthermore, until the last quarter of a century or so most marine biologists lived and worked in the temperate regions of the Northern Hemisphere, far from the

The **trade winds**, the steadiest winds on earth, blow from latitudes of about 30° toward the Equator.

Chapter 3, p. 53; Figure 3.17

**Substrate** The bottom or other surface upon or in which an organism lives. **Subsidence** The slow sinking into the *mantle* of a part of the earth's crust that contains a landmass.

Chapter 11, p. 236

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nearest reef. As a result, relatively few biologists studied reefs. Tremendous progress has been made in recent years, but there is still much to learn. The rest of this chapter summarizes what *is* known about the ecology of coral reefs and points out some of the important questions that remain.

## The Trophic Structure of Coral Reefs

The tropical waters where coral reefs are found are usually poor in nutrients (see "Patterns of Production," p. 343) and therefore have very little phytoplankton or **primary production.** In these barren waters, coral reefs are oases of abundant life. How can such rich communities grow when the surrounding sea is so unproductive?

A good part of the answer lies in the mutualistic relationship between corals and their zooxanthellae. We have already learned what the zooxanthellae do for the coral: They provide food and help make the calcium carbonate skeleton. In return the zooxanthellae get not only a place to live, but also a steady supply of nutrients such as nitrogen and phosphorus. Most of the coral's nitrogen and phosphorus waste products are not released into the water. Instead, they are taken up and used as nutrients by the zooxanthellae. Using sunlight, the zooxanthellae incorporate the nutrients into organic compounds, which are passed on to the coral. When the coral breaks down the organic matter, the nutrients are released and the whole process begins again (Fig. 14.24). The nutrients are recycled, used over and over, so that far fewer nutrients are needed than would otherwise be the case. Nutrient recycling is thought to be one of the main reasons that reefs can grow in nutrient-poor tropical waters.

Nutrient recycling occurs not just between corals and their zooxanthellae, but among all the members of the coral reef community. Sponges, sea squirts, giant clams, and other reef invertebrates have symbiotic algae and recycle nutrients just as corals do. Recycling also takes place outside the bodies of reef organisms. When fishes graze on seaweeds, for

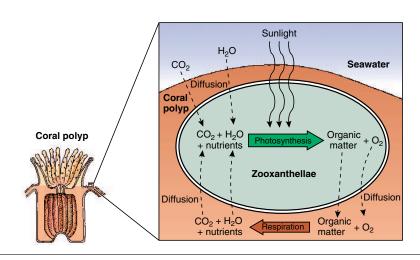


FIGURE 14.24 Carbon dioxide and nutrients are continually recycled between a coral polyp and its zooxanthellae.

example, they excrete nitrogen, phosphorus, and other nutrients as waste. These nutrients are quickly taken up by other algae. Many corals provide shelter to schools of small fish (see Fig. 8.20). The fish leave the coral at night to feed and return during the day. The waste products of the fish can be an important source of nutrients and help the coral grow faster. In this way nutrients are cycled from whatever the fish feed on to the coral. Nutrients pass through the community again and again in this cycle of feeding and excretion.

Coral reef communities use nutrients very efficiently as a result of recycling. The recycling is not perfect, however, and some nutrients are lost, carried away by the currents. Thus, the reef still needs a continual supply of new nutrients. Recycling alone is not enough to account for the high productivity of reefs.

The reef is able to provide some of its own nutrients. Coral reefs are now known to have among the highest rates of **nitrogen fixation** of any natural community. The main nitrogen fixers are cyanobacteria, especially a free-living one called *Calothrix* and another group that lives symbiotically in sponges. There is evidence that corals, too, have symbionts that can fix nitrogen, providing nutrients for the zooxanthellae. Just what the symbionts are is not known. All these nitrogen fixers provide a substantial source of nitrogen nutrients. Nitrogen, therefore, probably does not limit coral reef communities, though not all reef biologists agree about this.

Ocean currents bring in additional nitrogen and, more importantly, phosphorus and other nutrients that are not produced on the reef. Corals, bacteria, algae, and other organisms can absorb nutrients directly from the water. Even though the water is low in nutrients, if enough water washes over the reef the nutrients add up. In business terms, this is a low-margin, high-volume proposition. More importantly, the water carries zooplankton, a rich source of nutrients. When zooplankton are captured by the "wall of mouths," the nutrients in the zooplankton are passed on to the reef community. In fact, many biologists think that corals eat zooplankton not so much to feed themselves as to get nutrients for their zooxanthellae.

Coral reefs are very productive even though the surrounding ocean water lacks nutrients because nutrients are recycled extensively, nitrogen is fixed on the reef, and the zooplankton and nutrients that occur in the water are used efficiently.

The production and efficient use of nutrients by coral reef communities result in high primary productivity. This is reflected in the overall richness of the

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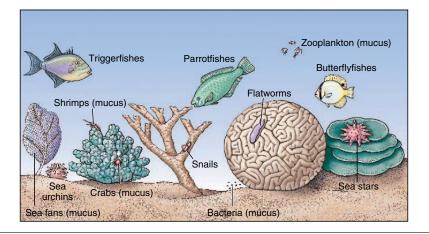


FIGURE 14.25 A number of animals eat coral directly, and many others feed on the mucus that corals produce. The primary production of coral zooxanthellae is thus passed on to coral feeders, and then to the animals that eat them.

community. Scientists don't really know, however, just how much primary production there is on coral reefs, or even which particular organisms are the most important producers. There is no doubt that zooxanthellae are very important, but because they live inside corals, it is very hard to measure exactly how much organic matter they produce. For a time it was thought that very few animals eat coral, since there is so little live tissue on a coral colony. It was therefore believed that, even though zooxanthellae produce a lot of organic matter, most of it was consumed by the coral and not much was passed on to the rest of the community. As biologists looked closer, however, they found more and more animals that eat corals or the mucus they shed (Fig. 14.25). Primary production by coral zooxanthellae therefore may be important not only to corals but to the community at large. Exactly how much production corals and their zooxanthellae contribute is still unknown.

Seaweeds are also important primary producers on the reef (Fig. 14.26), especially the small, fleshy or filamentous types that are called **turf algae** because they often grow in a short, thick turf on the reef flat. A great many fishes, sea urchins, snails, and other animals graze on these seaweeds. The turf algae may perform more photosynthesis on the reef than the zooxanthellae, but biologists are not sure. Zooxanthellae and turf algae are probably the most important primary producers on coral reefs.

Cyanobacteria, some other bacteria, and coralline algae are also primary producers on coral reefs. They probably account for less primary production than do zooxanthellae and turf algae.

## **Coral Reef Communities**

With so many species on coral reefs, the interactions among them are exceedingly complex. What is known about these interactions is fascinating; what remains to be learned will be even more so.

### Competition

Space is at a premium on coral reefs, as it is in the rocky intertidal (see "The Battle for Space," p. 242). Corals, seaweeds, and many others need a hard place on which to anchor themselves. Corals and seaweeds need not just space but space in the sunlight. The reef is crowded, and most of the available space is taken. As a result the sessile organisms, those that stay in one place, must compete for space.

Sessile coral reef organisms must compete for space. Corals and seaweeds compete for light as well.

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Corals compete for the space they need in different ways. The fast-growing ones tend to grow upward and then branch out, cutting their neighbors off from the light. Other corals take a more direct approach and actually attack their neighbors (Fig. 14.27). Some use their mesenterial filaments for this. When they contact another coral, they extrude the filaments and digest away the tissue of the other coral. Still other corals develop special long tentacles, called sweeper tentacles, that are loaded with nematocysts and sting neighboring colonies. Corals differ in their aggressive abilities. The most aggressive corals tend to be slowgrowing, massive types, whereas the less aggressive forms are usually fast-growing, upright, and branching. Both strategies have their advantages, and both kinds of corals thrive on the reef.

The two main ways in which corals compete for space are by overgrowing or directly attacking their neighbors.

Corals compete for space and light not only with each other, but also with seaweeds and sessile invertebrates. Like corals, encrusting algae have to produce a calcium carbonate skeleton and therefore grow relatively slowly. They tend to be found in places where corals don't do well because of sedimentation, wave action, or predation.

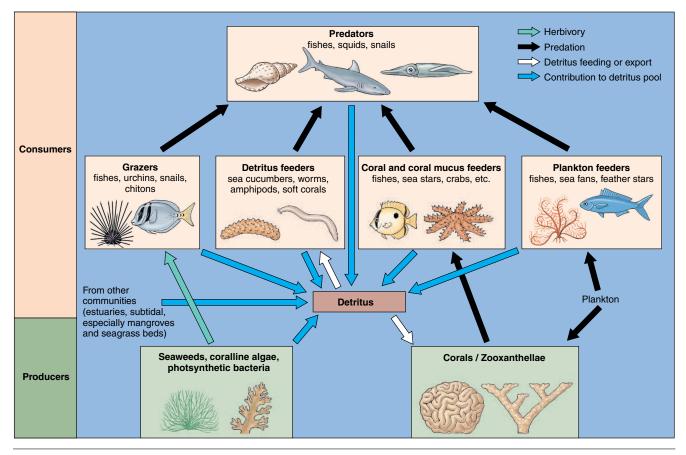
Under the right conditions seaweeds, except for encrusting forms, can grow much faster than either corals or encrusting algae. Even with the nitrogen fixation and nutrient cycling that occur on reefs, seaweeds are probably somewhat nutrientlimited most of the time. Hence they grow

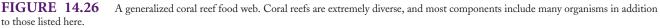
**Primary Production** The conversion of carbon from an inorganic form, carbon dioxide, into organic matter by autotrophs, that is, the production of food. *Chapter 4, p. 73* 

Nitrogen Fixation Conversion of nitrogen gas  $(N_2)$  into nitrogen compounds that can be used by primary producers as nutrients.

Chapter 10, p. 228







**FIGURE 14.27** When different species of coral come in contact, they attack each other. The pink band separating the brown (*Porites lutea*) and blue (*Mycedium elephantotus*) corals is a dead zone where the blue coral has killed the brown one in the process of overgrowing it. The width of the pink band corresponds to the length of the blue coral's tentacles. To the upper left of the brown coral is a soft coral (*Sarcophyton*), which may be attacking the brown coral by releasing poison. The brown coral seems to be stuck between a rock and a soft place!

fairly slowly. The reef also has an abundance of hungry grazers that eat the seaweeds. The combination of nutrient limitation and grazing keeps the seaweeds in check. If the nutrient levels increase or the grazers are removed, seaweeds may rapidly take over, overgrowing and choking out corals and other organisms.

Soft corals are also important competitors for space on reefs, and in some places they make up almost half the living tissue (Fig. 14.28). Like most seaweeds, soft corals lack a calcium carbonate skeleton and are able to grow faster than hard corals. Some soft corals contain sharp little calcium carbonate needles, or spicules, that discourage predation. Many of them also contain various chemicals that are toxic or taste bad to predators. Because of these defense mechanisms, only a few specialized predators eat soft corals. The defensive chemicals can also be released into the water, where they kill hard corals that come too close (Fig. 14.27). Another III. Structure and Function 14. Coral Reefs of Marine Ecosystems

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FIGURE 14.28 Soft corals can form dense patches. This photo is from New Guinea.



**FIGURE 14.29** Diving on a coral reef is like taking a swim in a tropical fish aquarium brightly colored fishes seem to be everywhere. The competitive relationships among the various species of fishes are poorly understood.

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competitive advantage enjoyed by some soft corals is that they are not completely sessile. Though they stay in one place most of the time, they can move about slowly. This helps them invade and occupy available space on the reef.

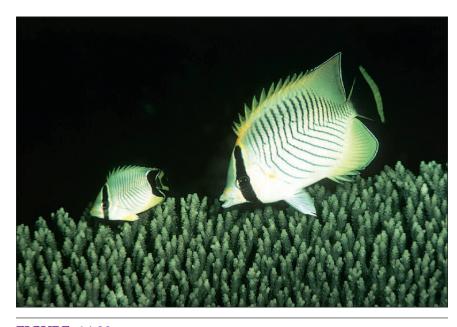
Soft corals are important competitors for space on reefs. They grow rapidly, are resistant to predators, and can occasionally move about.

With all these competitive weapons at their disposal, why don't soft corals take over? Not much is known about how soft corals compete with reef-building corals and other reef organisms or what determines the winner. Many soft corals appear to have shorter lives than reefbuilding corals although some may live for decades. They are also more easily torn away by storm waves. They have symbiotic zooxanthellae like reef-building corals, but are much less efficient photosynthesizers. They also seem to depend on very favorable physical conditions. It is not known how these factors interact to determine when and where soft corals compete successfully for space on the reef.

Like soft corals, sponges often have spicules and nasty chemicals that protect them from predators. They can be important users of space on reefs, much more so in the Caribbean than in the Pacific and Indian oceans. Part of the reason for this seems to be that there are far fewer species of coral in the Caribbean than in the Indo-West Pacific. This is a result of geological history. During the most recent series of ice ages, the sea surface was cooler. Corals survived in the heart of the Indo-West Pacific region, around Indonesia and New Guinea, but many coral species became extinct in other parts of the ocean. When the ice age ended, corals spread out again across the Pacific, recolonizing areas where they had died out. The Caribbean, however, was not recolonized because the Isthmus of Panamá blocked their dispersal. It is thought that the Caribbean contains only those coral species that managed to survive the ice ages there.

Coral reef fishes are another group in which competition may be important. Along with corals, fishes are probably the most conspicuous and abundant animals on the reef (Fig. 14.29). Many of

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**FIGURE 14.30** The chevron butterflyfish (*Chaetodon trifascialis*) is one of many reef animals that feed on corals without killing the entire coral colony. Its mouth is adapted for nipping off individual coral polyps (also see Fig. 8.28).

these fishes share similar diets; for example, many species eat coral, many graze on algae, and many are carnivores. Different species of fishes of the same feeding type at least potentially compete with each other.

There is much debate about how competition affects coral reef fishes. One hypothesis is that competition is relatively unimportant, and that the abundances of individual species are determined mainly by how many of their larvae settle out from the plankton. With favorable currents and other conditions, many larvae will be available to settle out and the species becomes abundant. If the supply of larvae is low, for example if currents carry the larvae away from the reef, the species becomes rare. This is called a presettlement hypothesis because it holds that the nature of reef fish communities is determined by the availability of different species' larvae before the larvae settle.

An alternative, **post-settlement**, hypothesis is that for most species there are plenty of larvae available to settle out on the reef. The species that survive and become abundant are those that compete successfully for space, food, and other resources after the larvae settle, that is, as juveniles and adults. This hypothesis holds that so many different fish species can live on the reef because each does something a little different from other species, thereby avoiding competition and the risk of **competitive exclusion**. In other words, each species has its own particular **ecological niche**. According to this view, the structure of the fish community on a reef is determined by the range of resources available on that reef, and the fish communities of reefs vary because different reefs offer different resources.

It is still not clear whether the supply of larvae for settlement or post-settlement competition is more important in structuring reef fish communities. Their relative importance probably varies from species to species and from reef to reef, and other factors such as predation and natural disturbances may also be significant factors.

There are two schools of thought about what controls the structure of reef fish communities. One holds that reef fish abundances are determined by how many larvae are available to settle out from the plankton. The other asserts

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**FIGURE 14.31** The crown-of-thorns sea star (*Acanthaster planci*) is an important and controversial coral predator.

that there is an ample supply of larvae for most species, and that reef fish communities are structured by competition among juveniles and adults after the larvae settle out.

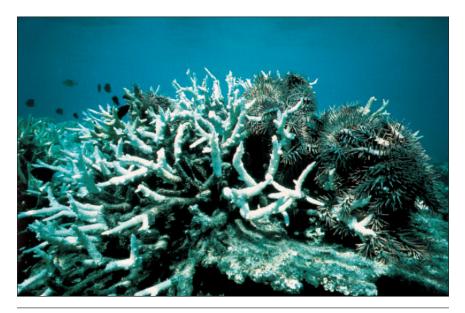
### Predation on Corals

As in other communities, predation and grazing are important in structuring coral reef communities. A variety of animals eat corals, but instead of killing the coral and eating it entirely, most coral predators eat individual polyps or bite off pieces here and there (Fig. 14.30). The coral colony as a whole survives and can grow back the portion that was eaten. In this respect, coral predation is similar to grazing by herbivores.

Coral predation can strongly affect both the number and the type of corals that live on a reef, as well as how fast the reef as a whole grows. In Kane'ohe Bay, for example, a butterflyfish (*Chaetodon unimaculatus*) slows the growth of a particular coral (*Montipora verrucosa*) that it likes to eat. When the coral is protected from the fish by a cage, it grows much faster. If it were not for the fish, this fastgrowing coral would probably dominate other corals in the bay. Coral-eating snails (*Coralliophila, Drupella*) have similar effects on some reefs.

### The Crown-of-Thorns Sea Star

Another example of the effect of coral predators is the case of the **crownof-thorns sea star** (*Acanthaster planci*; Fig. 14.31). The crown-of-thorns feeds by pushing its stomach out through the mouth, covering all or part of the coral



**FIGURE 14.32** An outbreak of crown-of-thorns sea stars (*Acanthaster planci*) in Australia. The white branches of this colony of staghorn coral (*Acropora*) show the bare calcium carbonate skeleton left behind after being fed upon by several sea stars. Photograph courtesy of the Great Barrier Reef Marine Park Authority.

colony with the stomach, and digesting away the live coral tissue. The crown-ofthorns has distinct preferences for certain types of coral and avoids others—some corals must taste bad. Other corals harbor symbiotic crabs (see the photo on p. 117), shrimps, and fishes that discourage the sea stars by pinching and biting their **tube feet.** 

The crown-of-thorns has had a major impact on some reefs. Beginning in the late 1950s, people began to notice large numbers, sometimes thousands, of the sea star on reefs scattered across the Pacific (Fig. 14.32). The sea stars in these large aggregations move in a mass across the reef, consuming almost every coral in their path. Reefs recover in 10 to 15 years, though it may take longer for slow-growing coral species to grow back.

The first response to the problem was panic. Coral reefs are valuable resources: They support fisheries, tourism, and recreation. Reefs also protect many coastlines from wave erosion. With the crown-of-thorns apparently threatening reefs, people decided to take action and control the sea star. The first attempt backfired. With limited knowledge of the animal's biology, some people cut the sea stars into pieces and dumped them back in the sea. Because sea stars can regenerate, the pieces grew into new sea stars! More sophisticated methods, such as poisoning the sea stars, were tried, but these methods were time consuming and expensive, did not work that well, and sometimes did more harm than good. Fortunately, the outbreaks mysteriously went away by themselves. Did the sea stars starve? Did they move away? No one knows. Crown-of-thorns outbreaks are still appearing, and disappearing, without explanation.

The cause of these outbreaks has been the cause of considerable, sometimes emotional, controversy. At first it

**Competitive Exclusion** The elimination of one species by another as a result of competition.

Chapter 10, p. 218

**Ecological Niche** The combination of what a species eats, where it lives, how it behaves, and all the other aspects of its lifestyle.

Chapter 10, p. 219

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seemed obvious that they were unnatural and that humans were to blame. After all, the plagues had never occurred before. Or had they? Some biologists pointed out that people began using scuba only a short time before the sea star plagues were noticed. Even if the plagues had been occurring for a long time, there were no scientists around to see them. Geologists found fossil evidence of crown-of-thorns outbreaks dating back thousands of years, and in some places there are old stories and other historical evidence for past outbreaks. The outbreaks, then, may be a natural part of the reef ecosystem and have nothing to do with humans. A leading hypothesis is that in unusually wet years river runoff naturally brings more nutrients into the sea than normal. According to this hypothesis, the extra nutrients increase the growth of phytoplankton that are food for sea star larvae. It may also be that periodic population explosions are a natural part of the sea star's biology.

The evidence for past outbreaks of the crown-of-thorns, however, is hotly disputed. Some scientists are convinced that the plagues are the result of some human activity that has altered the ecological balance of reefs. Even if outbreaks did occur in the past, they seem to be happening more often. One possibility is that the plagues are indeed caused by nutrients boosting the larvae's phytoplankton food supply, but that the nutrients come not from natural sources but from fertilizers and sewage. Another hypothesis is that fishers have caught too many fishes that eat young sea stars, allowing more to survive to adulthood. Some biologists have suggested that plagues occur because shell collectors have removed the

**Tube Feet** Water-filled tubes, possessed only by echinoderms, many of which end in a sucker and can be extended and contracted to grip things and to move around.

Chapter 7, p. 142

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triton shell, a large snail that preys on adult crown-of-thorns. Others argue that even without shell collectors the triton shell has always been naturally rare and unlikely to control sea star populations. They also point out that crown-of-thorns outbreaks continue to occur in areas where collecting triton shells has been banned for years.

Thus, the issue of what causes crown-of-thorns plagues remains unsolved. The question has practical implications for the management and protection of reefs. If the plagues are caused by humans and threaten reefs, then we should probably do something to stop them. On the other hand, the "plagues" may be a natural, potentially important, part of the ecosystem. We might do more harm than good by interfering in a system that we don't understand. The managers of the Great Barrier Reef have taken a middle road. They have developed an effective method to kill sea stars by injecting them with a poison. They use the poison, however, only if a crown-of-thorns outbreak is threatening a particularly valuable part of the reef, for example, a popular dive spot or the site of scientific research. Otherwise, they allow the outbreak to run its course.

The crown-of-thorns sea star has undergone population explosions on many Pacific reefs. There is still debate about what causes the outbreaks and what should be done about them.

## • Grazing

Grazing on algae by herbivores is at least as important in coral reef ecosystems as is predation on corals. Many fishes, especially surgeonfishes (*Acanthurus*), parrotfishes (*Scarus, Sparisoma*; see Fig. 6.10*a*), and damselfishes (*Pomacentrus, Dascyllus*; see Fig. 8.20) graze intensively on reefs. Among the invertebrates, sea urchins (*Diadema, Echinometra*) are especially important. There are also many **microherbivores**, small invertebrates like snails, **chitons**, crustaceans, and polychaete worms that eat algae.

Many seaweeds grow rapidly and have the potential to outcompete and overgrow corals. Under natural conditions they are kept in check by grazers,



FIGURE 14.33 The long-spined black sea urchin (*Diadema antillarum*) is one of the most important grazers on Caribbean reefs. Closely related species are found on reefs in other parts of the world.

and to some extent by nutrient limitation. Caging experiments (see "Transplantation, Removal, and Caging Experiments," p. 246) have been used to demonstrate the importance of grazers. For example, seaweeds are abundant on sand flats next to many Caribbean reefs but relatively scarce on the reef itself. To test the hypothesis that reef fishes were responsible for this, biologists transplanted seaweeds from the sand flat to the reef. If left unprotected, they were soon eaten by fishes. When protected by cages, they grew even faster than on the sand flat! The seaweeds are perfectly capable of living on the reef, therefore, but are rare there because they get eaten. Caging experiments on the Great Barrier Reef have had similar results.

If grazers are removed, seaweeds can flourish and take over space from corals and other organisms. In many parts of the Caribbean, for example, grazing reef fishes have become less common because of fishing. When this happened another important grazer, a sea urchin (Diadema antillarum; Fig. 14.33) became more common. The urchin apparently benefited from the reduced competition. For years, the urchin seems to have picked up the slack for the fishes and seaweed populations remained more or less stable. In 1983, however, a disease wiped out populations of the urchin over much of the Caribbean. Seaweeds, released from grazing pressure, became much more abundant on many reefs, at the expense of corals. In Jamaica they took over many reefs almost completely, and the formerly www.mhhe.com/marinebiology

rich coral reefs are now more seaweed bed than coral reef.

Many reef scientists fear that such changes are becoming more and more common as fishing pressure on reefs escalates because of increasing populations and demand for tasty reef fish. There is often a double whammy. Coastal development often leads not only to more intensive fishing, but also to greater release of nutrients from sewage and agricultural fertilizer. Thus, seaweed growth may be artificially enhanced by eutrophication at the same time that the grazers that keep the seaweeds under control are removed. There is increasing evidence that this is a global threat to coral reefs.

Grazers help prevent fast-growing seaweeds from overgrowing other sessile organisms on the reef.

In addition to controlling how many seaweeds there are, grazers affect which particular types of algae live on the reef and where. Coralline algae, for example, are abundant because the calcium carbonate in their tissues discourages grazers. Other seaweeds produce noxious chemicals that are poisonous or taste bad; these seaweeds also tend to be abundant. Such chemical defenses, however, appear to be somewhat less common on coral reefs than in temperate communities. The tasty seaweeds are most heavily grazed and thus tend to be rare. Even so, they generally grow rapidly and are an important food source.

Damselfishes provide some interesting examples of the effects of grazing on reefs. Many damselfishes graze on seaweeds inside territories that they vigorously defend, chasing away other fishes that happen to venture inside. Many such damselfishes actually "farm" their territories. They weed out unpalatable algae, pulling them up and carrying them outside the territory. What is left in the territory is a dense mat of tasty seaweeds, usually fine, filamentous types. Protected by the damselfish, these algae grow very rapidly and outcompete corals and coralline algae. Outside the territory, parrotfishes and surgeonfishes gobble up the algae, clearing space for other organisms. Thus, the community inside the III. Structure and Function 14. Coral Reefs of Marine Ecosystems

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## "MUST HAVE BEEN SOMETHING I ATE"

Ahhhhh! You're relaxing on a warm tropical night after a delicious fish dinner. The palm trees sway, a warm tropical breeze blows and suddenly your bowels begin to churn. Before long your lips burn and tingle, and your hands and feet feel like pins and needles. You go into the kitchen for a drink, but the cool water feels warm. The cool floor and the cold compress you put on your forehead are also warm to the touch: The sensations of hot and cold are reversed. As you stagger to the bathroom, your arms and legs are heavy and weak. Now feeling really sick, you mumble, "Must have been something I ate."

You're right. What you have is a case of **ciguatera**—tropical fish poisoning. Maybe it will comfort you to know that you're not alone. Tens, perhaps hundreds of thousands, of people get ciguatera every year. And relax, you probably won't die, though you might be a little sick (if you're unlucky, *very* sick) for months or even years. Don't count on a cure, though there are various folk remedies, and some treatments might help you feel a little better. There are also reports that the intravenous administration of an inexpensive sugar called mannitol can help, but this remains unconfirmed.

So what *is* ciguatera, anyway? The disease has been known for hundreds of years. The name comes from the Spanish word for a Caribbean snail: You can also get ciguatera from eating molluscs, and perhaps sea urchins, though fish dinners are the most common cause. It is probably most common in the top predatory fishes on the reef, like jacks, barracudas, and groupers, but it can also be caused by eating herbivorous fishes like parrotfishes and surgeonfishes. A particular kind of fish may be perfectly safe in most places, but poisonous in particular spots. To make matters even more confusing, ciguatera may disappear from one area and pop up in another. All of which makes things difficult for lovers of fresh reef fish.

Ciguatera is caused by toxic dinoflagellates that live on the reef. Herbivorous fishes eat the dinoflagellates, and the poison is passed on to the predatory fishes that eat them. As blooms of the dinoflagellates arise and die out, ciguatera comes and goes in the area. Predatory fishes range over larger areas and eat many fish, which may all contain small amounts of the toxin. Thus, they are most likely to cause ciguatera. Herbivorous fishes probably carry the toxin only when they feed in an area with a bloom.

The big problem is trying to tell when a fish carries the poison. You could just avoid reef fish altogether, but if you are in the tropics that means missing out on a lot of tasty meals. One way to tell if a fish is carrying ciguatera is to feed a bit to a cat: Cats are highly sensitive to ciguatera. If any mongooses are handy, they're good tasters too. Of course, this isn't exactly kind to the animals, who usually die if the food is affected by ciguatera. There has been research on a number of chemical tests, but none of them are yet in widespread use. Many of these tests are expensive or complicated, and not really suitable for routinely testing seafood. Another problem is that there are actually several different dinoflagellate toxins that can cause ciguatera, and it is difficult to test for all of them. We aren't even sure we know what they all are. Until a reliable test is developed, you'll have to go hungry or take your chances.

territory is very different from that outside. One interesting point is that cyano bacteria, which are nitrogen fixers, are much more common inside damselfish territories than outside. Thus, damselfishes may indirectly have an important role in the nutrient balance of the reef.

Herbivores obviously affect coral reef algae, but they may have indirect effects on animals as well. Many reef grazers scrape their food off the reef with some kind of specialized hard structure. Parrotfishes, for instance, get their name because their fused teeth form a parrotlike beak (see Fig. 8.13*d*). Sea urchins use their **Aristotle's lantern** to scrape surfaces. If grazing is intense, as it often is, the surface of the reef flat may be scoured smooth; the marks made by herbivores are often visible. In the process of scraping off the seaweeds that are their food, herbivores incidentally remove settling larvae and other small animals. It may be very difficult for new coral colonies to establish themselves, for instance, unless the larva happens to settle in a crevice or other protected spot. If this kind of grazing pressure is intense enough it can erode the reef.

### Living Together

Among the vast number of species that live on coral reefs, many have evolved special symbiotic relationships. There are far too many cases of symbiosis on the reef to describe here. In fact, coral reefs probably have more different symbiotic relationships than any habitat on earth. The few examples discussed here will give you some idea of how fascinating these relationships are. Symbiotic relationships are very important in coral reef communities. Coral reefs probably have more examples of symbiosis than any other biological community.

Chitons Molluscs whose shells consist of eight overlapping plates on their upper, or dorsal, surface. *Chapter 7, p. 133* 



**Aristotle's Lantern** A complicated set of calcium carbonate (CaCo<sub>3</sub>) teeth and associated muscles that is found in sea urchins.

Chapter 7, p. 144

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We have already seen how mutualism between corals and their zooxanthellae is the essential feature of reef formation. Many other organisms also have photosynthetic symbionts. Sea anemones, snails, and giant clams (*Tridacna*) all harbor zooxanthellae. The "deal" between the two partners is the same as in corals: The zooxanthellae get nutrients and a place to live, and the host gets food. Giant clams grow so large (Fig. 14.34) because their zooxanthellae provide a constant food supply.

There are primary producers other than zooxanthellae that live inside reef animals. As mentioned previously, some sponges have cyanobacteria that fix nitrogen in addition to performing photosynthesis. Certain sea squirts house a photosynthetic bacterium called *Prochloron*. *Prochloron* is especially interesting because some scientists think it is similar to the symbiotic organisms that eventually became the chloroplasts of plants (see "From Snack to Servant: How Complex Cells Arose," p. 77).

Another important example of mutualism on the reef is the relationship between corals and the crabs, shrimps, and fishes that help protect them from the crown-of-thorns sea star and other predators. Most corals host a number of symbionts, especially crustaceans. Some of these are only casual symbionts and can live as well off the coral as on it. Others are much more specialized and are found only on their host coral. These are called obligate symbionts. Some of the obligate symbionts are parasites and harm the coral, some are commensals and apparently do not affect the coral one way or the other, and some are mutualists that benefit the coral. It is often hard to tell which is which, because for most symbionts the nature of the relationship between coral and symbiont is not well understood. Those who study such organisms must frequently revise their ideas as more information is obtained. The crabs that protect their coral from predators, for instance, were once thought to be parasites.



FIGURE 14.34 The giant clam (*Tridacna gigas*) does not deserve its reputation as a killer: Stories of people getting trapped in them and drowning are myths. Symbiotic zooxanthellae give the upper surface its blue and green colors, and provide food that allows the clam to get so big. The clam also filter feeds. The hole visible on the clam's fleshy upper surface is one of the siphons through which the clam pumps water for feeding and to obtain oxygen. The giant clam does not occur in the Caribbean.

Anemonefishes (Amphiprion; Fig. 14.35) have an interesting relationship with several kinds of sea anemone. The anemones inhabited by anemonefishes have a powerful sting and are capable of killing the fish. The fish have a protective mucus, however, that keeps the anemone from stinging. It is not known whether the mucus is produced by the fish themselves, by the anemone, or by both. When anemonefishes are newly introduced to an anemone, they typically rub against and nip the anemone's tentacles. They may be coating themselves with the anemone's mucus. To understand why this is an advantage, you have to remember that anemones have no eyes and www.mhhe.com/marinebiology



FIGURE 14.35 An orange-fin anemonefish (*Amphiprion chrysopterus*) and its sea anemone host.

no brain, but lots of tentacles. If the anemone simply stung everything it touched, it would end up stinging itself every time the tentacles bumped into each other. The anemone recognizes itself by the "taste" of its own mucus. When one tentacle touches another, the anemone detects the mucus coating on the tentacles and refrains from stinging. Anemonefishes may be taking advantage of this. On the other hand, there is evidence that the fishes' own mucus protects them against the anemone.

Anemonefishes are protected by the anemone's stinging tentacles and brood their eggs under the anemone. In at least some cases the relationship is mutually beneficial because the anemonefish drive away other fishes that eat anemones. Anemonefishes kept in aquaria will sometimes feed their host, but this behavior does not seem to be important in nature. It is also possible that the fishes benefit their hosts in ways that are not yet understood. III. Structure and Function 14. Coral Reefs of Marine Ecosystems

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# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

## **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

## Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

## **Critical Thinking**

- 1. What factors might account for the fact that the vast majority of atolls occur in the Indian and Pacific oceans and that atolls are rare in the Atlantic?
- 2. Scientists predict that the ocean will get warmer and the sea level will rise as a result of an intensified greenhouse effect (see "Living in a Greenhouse: Our Warming Earth," p. 410). How might this affect coral reefs?
- 3. There are only a few reefs off the northeast coast of Brazil (see map in Fig. 14.10), even though it lies in the tropics. How would you explain this?

## For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol \_\_\_\_\_, and will contain live links when you visit this page in the Online Learning center.

### **General Interest**

- Chadwick, D. H., 2001. Kingdom of coral: Australia's Great Barrier Reef. *National Geographic*, vol. 199, no. 1, pp. 30–57. A fabulous tour of the earth's largest reef area.
- Doubilet, D., 1999. Coral Eden. National Geographic, vol. 95, no. 1, January, pp. 2–29. Superb photos of coral reef diversity.
- Levine, J. S., 1993. Dusk and dawn are rush hours on the coral reef. *Smithsonian*, vol. 24, no. 7, October, pp. 104–115. The change from day to night brings a changing of the guard on coral reefs.
- Marshall, J., 1998. Why are reef fish so colorful? Scientific American Presents, vol. 9, no. 3, Fall 1998, pp. 54–57. The often gaudy colors of reef fish serve to attract mates, fend off rivals, and deter predators.
- Pain, S., 1997. Swimming for dear life. *New Scientist*, vol. 155, no. 2099, 13 September, pp. 28–32. The tiny larvae of coral reef fishes are champion swimmers. They have to be.

- Ross, J. F., 1998. The miracle of the reef. *Smithsonian*, vol. 28, no. 11, February, pp. 86–96. Scientists study mass coral spawning on reefs in Florida.
- Sale, P. F., G. E. Forester and P. S. Levin, 1994. Reef fish management. *Research and Exploration*, vol. 10, no. 2, Spring, pp. 224–235. Coral reef fisheries are an important food source in many countries, but many have been decimated by overfishing. Unfortunately, management of reef fisheries is not well understood.

## In Depth

- Birkeland, C. (Editor), 1997. *Life and Death of Coral Reefs.* Chapman & Hall, New York. 536 pp.
- Booth, D. J. and D. M. Brosnan, 1995. The role of recruitment dynamics in rocky shore and coral reef fish communities. *Advances in Marine Biology*, vol. 26, pp. 309–385.
- Miller, M. W., 1998. Coral/seaweed competition and the control of reef community structure within and between latitudes. *Oceanography and Marine Biology: An Annual Review*, vol. 36, pp. 65–69.
- Munday, P. L. and G. P. Jones, 1998. The implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review*, vol. 36, pp. 373–411.
- Wilkinson, C. (Editor). *Status of Coral Reefs of the World:* 2000, Australian Institute of Marine Science, Townsville. 363 pp.

## See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

- Staghorn coral (Honduras)
- Gray angelfish feeding (Belize)
- Clownfish in anemone (Papua New Guinea)
- Giant clam (Papua New Guinea)
- Giant clam siphons (Papua New Guinea)
- Saddleback butterflyfishes feeding on coral polyps (Solomon Islands)
- Branching reef corals (Acropora) (Solomon Islands)
- Bleached reef corals (Solomon Islands)
- Soft coral (Palau)
- Reef corals (Palau)
- Retraction of soft coral polyps (Palau)
- Blue tangs feeding on algae (Bonaire, West Indies)
- Bigeye trevally (Solomon Islands)
- Crown-of-thorns sea star (Fiji)

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- Coral spawning (Solomon Islands)
- Octopus eating a clam (Palau)
- Relative of reef-building corals, feeding on plankton (Belize)

## Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Coral reefs
- Class Anthozoa

- Color bleaching
- Mangroves
- Community ecology
- Competition
- Parasitism, predation, and herbivory
- BiodiversityFood webs

## Quiz Yourself

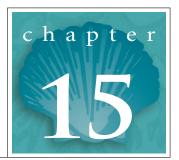
Take the online quiz for this chapter to test your knowledge.

III. Structure and Function 15. Life of Marine Ecosystems

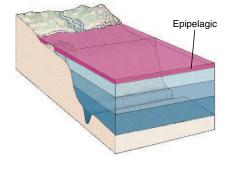
15. Life Near the Surface

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# Life Near the Surface







A violet snail (*Janthina janthina*), covered with gooseneck barnacles, eats a Portuguese man-of-war (*Physalia physalis*).

he ocean," for most of us, conjures up images of beaches and cliffs, breaking surf, or quiet bays. Such familiar inshore waters, however, make up only a small fraction of the world ocean. The rest is the vast open sea, the **pelagic realm**. Though distant and unfamiliar, the open ocean affects us all. It regulates our climate, conditions our atmosphere, and provides food and many other resources. It is hard for most of us to really grasp how vast the pelagic is. The pelagic holds practically all the liquid water on earth, the water planet.

As we learned in Chapter 10, the pelagic environment is the water column itself, away from the bottom or the shore. Pelagic organisms live suspended in their liquid medium. With very few exceptions, the pelagic lacks the solid physical structure provided by either the bottom and other geological features or by large organisms like corals and kelps. There is no place for attachment, no bottom for burrowing, nothing to hide behind. Imagine spending your life floating weightless in the air, never touching the ground. This is what the pelagic realm is like for the organisms that live there. Pelagic organisms face very different problems from those that live near shore or on the bottom.

Chapter 15 deals with the surface layers of the pelagic environment, the **epipelagic**, or upper pelagic, realm. The epipelagic is often defined as the zone from the surface down to a given depth, commonly 200 m (650 ft). Being the shallowest part of the pelagic realm, the epipelagic is generally the warmest, and of course the best lit. The epipelagic is therefore similar to the **photic zone**, the

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zone from the surface to the depth where there is no longer enough light for organisms to grow by photosynthesis. The depth of the photic zone varies, depending on water clarity and the amount of sunlight. In practice the epipelagic and photic zones are usually much the same, and their differences will not be stressed in this chapter.

The epipelagic is divided into two main components. Epipelagic waters that lie over the continental shelf are referred to as **coastal**, or **neritic** (see Fig. 10.20). The coastal environment is only a small part of the epipelagic, but it is important to humans because it lies relatively close to shore and supports most of the world's marine fisheries production (see "Major Fishing Areas," p. 386). The surface waters beyond the continental shelf are known as the **oceanic** part of the epipelagic.

The epipelagic realm is the layer of the ocean from the surface to a depth of 200 m. It is divided into coastal, or neritic, waters, which lie over the continental shelf, and oceanic waters, which lie beyond the shelf. The epipelagic is similar to the photic zone, the layer from the surface to the depth where light limits photosynthesis.

## THE ORGANISMS OF THE EPIPELAGIC

Like nearly all ecosystems, the pelagic realm is fueled by energy from the sun that is captured in photosynthesis. Epipelagic ecosystems differ from shallowwater ones in that nearly all the **primary production** takes place within the epipelagic system itself. Coastal ecosystems often receive large amounts of food from elsewhere. The intertidal zone, for example, gets drifting seaweeds from offshore, and rivers carry organic material into estuaries. The pelagic realm, far from the shore and bottom, gets almost no outside input of organic matter.

On the other hand, the epipelagic supplies food to other communities. Large amounts of organic matter sink out of the epipelagic to feed the organisms that live below (see Chapter 16). Ocean currents carry epipelagic **plankton** into shallow water, where it is consumed by a



(a)

profusion of filter feeders. Epipelagic fishes and zooplankton provide food not only to other marine communities, but also to land-dwelling birds and mammals, including humans.

Because there is no bottom where organic-rich sediments can build up, the epipelagic lacks **deposit feeders**. **Suspension feeders**, on the other hand, abound. After all, the food is suspended in the water column. There are also many large predators, like fishes, squids, and marine mammals.

## The Plankton: A New Understanding

For more than a century the main way that scientists studied the plankton was to catch them by towing nets through the water (Fig. 15.1), or sometimes by pumping water through a filter. To understand how this reliance on plankton nets affected our understanding of the epipelagic, imagine if our only way to study flying organisms was with nets. If our nets were too small or too slow, we might never know there were birds. Nets with too coarse a mesh would leave us completely ignorant of mosquitoes. Imagine if there were organisms with the

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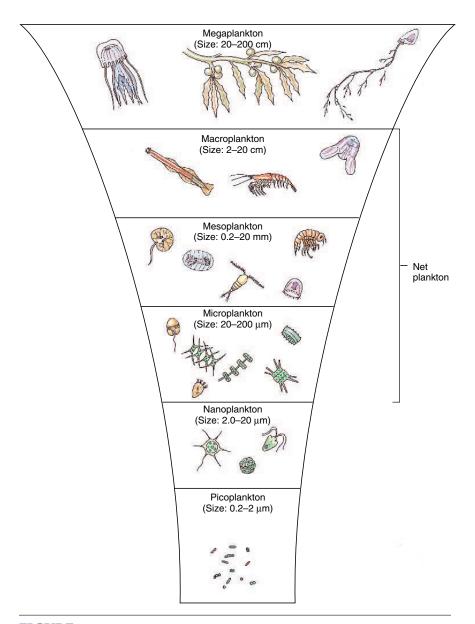
(b)

FIGURE 15.1 (a) A typical phytoplankton net is relatively small and has very fine netting that prevents many microscopic plankton from passing through. (b) A bongo net, so called because of the two rings that hold the mouth of the net open, is used to sample zooplankton. Zooplankton nets are usually larger and have coarser mesh than phytoplankton nets. The coarse mesh lets phytoplankton pass through but retains zooplankton, which are larger.

consistency of clouds that slipped through any net! Similar misunderstandings and more have resulted from oceanographers' dependence on plankton nets to study the epipelagic.

Within the last few decades, new techniques, including better microscopes, underwater photography, satellites, chemical procedures, and, yes, even improved nets and filters, have revolutionized scientific understanding of the epipelagic zone. New discoveries have raised even more questions, and it has become clear that we don't understand the plankton as well as we once thought.

Of particular importance was the discovery of vast numbers of plankton that are too small to be caught in standard plankton nets. These are known as picoplankton or nanoplankton depending on their size (Fig. 15.2). Most of the picoplankton consists of archaea and bacteria. The larger net plankton, so called because they can be collected with nets, are also subdivided on the basis of size into the micro-, meso-, macro-, and megaplankton (Fig. 15.2), but these categories are not stressed in this book. Categorizing the plankton by size should not be confused with the division between phytoplankton-plankton that perform photosynthesis-and zooplankton. The



**FIGURE 15.2** Plankton are often separated into categories based on their size (also see Appendix A).

phytoplankton, for example, include species of all size classes from the picoplankton to the megaplankton.

## The Phytoplankton

Large primary producers like seaweeds and seagrasses are largely absent from the epipelagic because they have no place to attach. Floating seaweeds are important in a few places, such as the Sargasso Sea (see Fig. 8.24), but in most of the epipelagic the only primary producers are singlecelled or simple chains of cells. These tiny organisms make up the phytoplankton, which occur virtually everywhere in the epipelagic, often in huge numbers. Phytoplankton perform more than 95% of the photosynthesis in the ocean. This amounts to nearly half the world's primary production, and produces nearly half the oxygen in our atmosphere in the process.

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Because the net phytoplankton are relatively easy to catch, their importance has long been known. Most important among these are the **diatoms** (Fig. 15.3) and the **dinoflagellates**. Before the discovery of the nanoplankton and picoplankton, it was thought that diatoms dominated the phytoplankton and accounted for most photosynthesis in the epipelagic. Although we now know this is not true, diatoms are still extremely important. They are especially common in temperate and polar regions and other nutrient-rich waters. They are abundant both near the coast and in the open ocean.

Dinoflagellates are another major group of net phytoplankton. Like diatoms, they are important in both coastal and oceanic waters, but they tend to prefer warm areas. In the tropics they may replace diatoms as the most abundant members of the net phytoplankton. Dinoflagellates may be better able to

**Primary Production** The conversion of carbon dioxide  $(CO_2)$  into organic matter by autotrophs; that is, the production of food.

Chapter 4, p. 73

**Plankton** Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents. *Chapter 10, p. 230; Figure 10.19* 

**Deposit Feeders** Animals that eat organic matter that settles to the bottom. *Chapter 7, p. 126; Figure 7.16* 

Suspension Feeders Animals, including *filter feeders*, that eat particles suspended in the water column. *Chapter 7, p. 118; Figure 7.16* 

Archaea Single-celled, *prokaryotic* organisms once thought to be bacteria but now known to be as different from bacteria as from humans.

Chapter 5, p. 96

**Dinoflagellates** Single-celled organisms that use two flagella to swim.



Chapter 5, p. 97



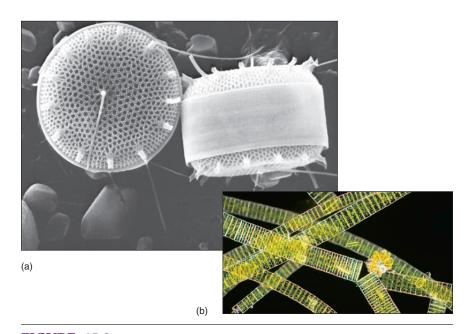
From time to time, especially near the coast, the sea surface becomes bright red literally overnight. This phenomenon, called a **red tide**, has occurred for thousands of years. The Old Testament (*Exodus* 7:20–21) may contain the earliest known reference to a red tide when it describes the waters of the Nile turning to blood. The Red Sea is named after the red tides that often occur there.

The term "red tide" is here to stay, but it is somewhat confusing. For one thing, red tides have nothing to do with the tide. They are massive blooms of phytoplankton. At the peak of a red tide there may be thousands, even tens or hundreds of thousands, of cells in a single drop! Furthermore, red tides are not always red. The sea may instead turn orange, brown, or bright green. In fact, the name "red tide" is applied to harmful phytoplankton blooms even if they don't discolor the water. In recent years the term "brown tide" has been used in some places for blooms of a particular type of phytoplankton called chrysophytes, but the basic phenomenon is the same.

Red tides are different from ordinary phytoplankton blooms like the spring bloom that occurs in cold waters (see "Seasonal Patterns," p. 347). The spring bloom includes many different phytoplankton species and is quite predictable, occurring in response to increased light or nutrient levels. In a red tide, on the other hand, only a single species typically blooms. Furthermore, we don't know what causes red tides so they are unpredictable. Red tides occur all over the world. Only around 6% of all phytoplankton species are known to cause red tides. This may not sound like much, but it is still around 200 species at least, probably more. About half of red tide organisms are dinoflagellates, but many other organisms including cyanobacteria, diatoms, chrysophytes, and several other groups can cause red tides.

These exceptional phytoplankton blooms are often nothing more than oceanographic oddities, but sometimes they cause serious problems. Such **harmful algal blooms (HABs)** are receiving increasing attention from both scientists and society at large. Of course, what is harmful depends on your point of view. If you are on a beach vacation, a foul brown foam caused by a bloom may be nothing more than an annoying reason to cut the vacation short. To the motel owner depending on your business it is a disaster.

Some blooms, however, are more than just a nuisance. They are deadly. About a third of red tide organisms produce poisons, some of which are among the most powerful toxins known. Under normal circumstances there are too few of the organisms around to worry about, but when they bloom they can cause serious problems. Mussels, clams, crabs, and other shellfish often tolerate the toxins by storing them away in the digestive gland, kidney, liver, or other tissues. People who eat the shellfish may suffer nausea, diarrhea, vomiting, numbness and tingling, loss of balance and memory, slurred speech, shooting pains, and paralysis. The most severe cases are



**FIGURE 15.3** Diatoms have sculptured shells, or frustules, made of silica. (*a*) *Thalassiosira allenii* (top and side views) consists of a single cell. (*b*) *Fragillaria* is a diatom that forms chains of cells. Each division in the long green filaments is an individual cell (also see Fig. 5.5).

grow under low-nutrient conditions than diatoms. Given nutrients, on the other hand, dinoflagellates may **bloom**, that is, grow explosively into huge numbers, sometimes causing **red tides** (see "Red Tides and Harmful Algal Blooms," above).

Because they are so small and hard to catch, and even to see under a microscope, the importance of picoplankton and nanoplankton has only recently been appreciated. As a result, they are generally not as well known as the diatoms and dinoflagellates. They are, however, much more abundant. They also contribute most of the epipelagic's photosynthesis, 90% or more in many places. They are especially important in tropical areas.

**Cyanobacteria** are very important primary producers in the phytoplankton. One group *(Trichodesmium)* grows in filamentous colonies and can be caught in nets. It can become very abundant, sometimes forming red tides. Singlecelled cyanobacteria are also important

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fatal. A recent estimate indicates that every year toxic algae cause 100,000 to 200,000 cases of serious poisoning, including ciguatera (see "Must Have Been Something I Ate," p. 319). These lead to 10,000 to 20,000 deaths and a similar number of cases of paralysis and other serious consequences. This is much higher than earlier estimates, which numbered in the hundreds of deaths, so the problem is worse than previously realized. You don't have to eat the shellfish to suffer. Swimming or boating in affected water, even breathing sea spray that is blown ashore, can cause sore throats, eye irritation, and skin complaints. There is even evidence that some of the toxins are carcinogenic.

The effects of HABs aren't confined to humans. HABs sometimes turn the surface into a sea of dead fish, creating another health hazard. In recent years a dinoflagellate called *Pfiesteria* has been a particular problem along parts of the U.S. east and Gulf coasts (see "Dinoflagellates," p. 97), but many other HAB organisms cause fish kills. Whales and sea birds that eat fish have also been killed. Even herbivores have been affected. Though they eat aquatic vegetation, manatees in Florida have been killed by red tides on several occasions. They are exposed just by being in the water, and perhaps by breathing in toxic spray at the surface. In 1996 about 150 manatees, or 10% of the small surviving population, were killed by red tides.

Not all harmful effects of red tides are due to toxins. Fish kills can also happen if the masses of phytoplankton suddenly die, even if they are not poisonous. Their decomposition depletes the oxygen in the water, and the fish suffocate. Blooms of certain diatoms can kill fish because the diatoms have spines that damage the fishes' gills. Though quite controversial, it has been suggested that phytoplankton may harbor the bacteria that cause cholera, a deadly disease, and that phytoplankton blooms are implicated in cholera epidemics. There are even concerns that HABs may affect global climate.

Red tides cost hundreds of millions of dollars in losses to tourism and, especially, fisheries. Valuable shellfish fisheries are often closed as a result of red tides, or during seasons when red tides are most likely. Even perfectly safe seafood may be rendered nearly worthless when the public perceives it as dangerous to eat. Fish farms and other aquaculture facilities are especially vulnerable because the fish or other seafood can't swim away and because they are usually held in high densities. Single HABs have wiped out entire local industries. The cost of HABs is estimated at \$49 million annually just in the United States, and is many times higher globally.

HABs have been around since biblical times, and probably much longer. There is fossil evidence of HABs from more than 100 million years ago. Scientists are concerned, however, that they seem to be becoming more common. It is hard to be sure, because it may just be that people are paying more attention. With more people living on the coast, it is more likely someone will get sick because of an HAB, and scientific advances make it more likely that we will be able to tell why they got sick. Where a bloom might go unnoticed in a lonely, undeveloped bay, it is devastatingly obvious once an aquaculture industry has been established.

Nevertheless, there is good evidence that, at least in some places, HABs are increasing due to human activity. The best-known examples are Hong Kong Harbor and the Seto Sea in Japan. In these places HABs steadily became more common as the population and water pollution increased. In the Japanese example the case is even stronger: HABs declined again after pollution control measures were introduced.

If humans are causing more HABs, the most likely cause is eutrophication, increased algal growth due to nutrient pollution. This increased growth might come in the form of more frequent red tides, and some of these red tides will be HABs. Furthermore, there might be more HABs than would be expected if eutrophication simply promoted the growth of all phytoplankton. In other words, eu-



A bloom of a dinoflagellate called *Noctiluca* caused this red tide. The organism is bioluminescent, and blooms like this produce spectacular blue-green light at night. This photo was taken in Mexico.

trophication might selectively favor harmful algae. The reason for this is that humans don't add the same nutrients to the ocean that nature does. We tend to add a lot of nitrogen (N), and much less phosphorus (P) and silicon (Si). Dams can also cut off the supply of silicon. Most marine systems are nitrogen-limited, and when we add nitrogen the phytoplankton tend to grow until they run out of something else. In particular, diatoms might run out of silicate, which they need to make their shells. This shifts the balance in favor of dinoflagellates. While some diatoms produce toxins, dinoflagellates are much more likely to do so. Not only that, some dinoflagellates produce more toxin when their supply of phosphorus runs low, which is likely to happen if we pump in nitrogen and not phosphorus.

HABs are also spreading to new places. Ships can carry HAB organisms in their ballast water. A single ship was estimated to be carrying more than 300 million toxic dinoflagellate cysts! It is not known how many of these survive, but there is strong evidence that HAB organisms in Australia and New Zealand, for example, have been introduced in ballast water. Natural movements of red tide organisms, though, are probably more important. The closure of shell-fish beds in Canada and New England, for example, began when a hurricane carried in a seed population of toxic dinoflagellates. Red tide toxins have been turning up in shellfish there ever since. The effects of such natural events are often amplified because we are using the marine environment more intensively than ever before.

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| Table 15      | The Major G                               | roups of Ma | arine Phytoplankton |   |   |
|---------------|---|-------------|---------------------|---|---|
| Size Category | Group                                     | Kingdom     | Coastal or Oceanic  | Latitude/Temperature  | Notes   |
| Net plankton  | Diatoms                                   | Protista    | Both                | Everywhere, but most<br>common in temperate<br>and polar waters | Important primary producers   |
|               | Dinoflagellates                           | Protista    | Both                | Everywhere, but most<br>common in warm waters                   | Common red tide<br>organisms  |
|               | Colonial cyanobacteria<br>(Trichodesmium) | Bacteria    | Oceanic             | Mainly tropical   | Can fix atmospheric<br>nitrogen; causes red<br>tides in the Red Sea |
| Nanoplankton  | Coccolithophorids                         | Protista    | Oceanic             | Everywhere, but most<br>common in tropical waters               | Important primary<br>producers in nutrient-<br>poor waters          |
|               | Cryptomonads                              | Protista    | Coastal             | Everywhere  | Very important primary<br>producers; poorly<br>known                |
|               | Silicoflagellates                         | Protista    | Coastal             | Temperate and polar waters                                      | Sometimes form blooms   |
| Picoplankton  | Unicellular cyanobacteria                 | Bacteria    | Both                | Everywhere  | Dominant primary<br>producers                                       |
|               | Various protists                          | Protista    | Not Known           | Not Known   | Presence of many groups<br>recently discovered                      |

in the photosynthetic picoplankton. A very poorly known group called prochlorophytes, which are sometimes classified as separate from cyanobacteria, are probably the most abundant and may account for as much as half of the ocean's total primary production. Prochlorophytes are tiny, even for bacteria, and their importance as primary producers in the ocean has only become apparent within the last two decades. Previously they were known only as symbionts of certain animals (see "From Snack to Servant: How Complex Cells Arose," p. 77) and thought to be quite rare. Another group of single-celled cyanobacteria (Synechococcus) is also very abundant in all but polar waters. Cyanobacteria are particularly important in nutrient-poor waters, possibly because they can fix nitrogen.

Bacteria are considered to dominate the photosynthetic picoplankton, but protists may be more important than we thought. The presence of characteristic nucleic acids in seawater reveals that there are a number of different groups of photosynthetic protists in the picoplankton, including three new groups related to dinoflagellates (see "Tiny Cells, Big Surprises," p. 99) The organisms themselves have not yet been isolated and their contribution to total primary production is unknown.

Protists are, however, known to dominate the nanoplankton, and many of them are photosynthetic. **Coccolithophorids** are one of the more abundant groups, and probably the best known. They do best in the open ocean but also occur in coastal waters.

In coastal areas another group of minute phytoplankton known as **cryptomonads** are very plentiful. They appear to be very important in the economy of the seas, especially in coastal waters, but not much is known about them. **Silicoflagellates** (see Fig. 5.8) occasionally bloom and become important primary producers. There are several other groups of protistan nanoplankton that appear to be important primary producers in the epipelagic. Although most diatoms and dinoflagellates belong to the net plankton, a few unusually small species are part of the nanoplankton. Phytoplankton are the main primary producers in the epipelagic. The most abundant phytoplankton are cyanobacteria and various groups of protistan nanoplankton, including coccolithophorids, cryptomonads, and silicoflagellates. Among the larger net phytoplankton, diatoms and dinoflagellates are dominant. Several new groups of protistan picoplankton have been discovered but their importance as primary producers is not known.

Table 15.1 shows the major groups of marine phytoplankton. Various other groups may form blooms, but only rarely, and such groups are of secondary importance in the overall economy of the seas.

# The Zooplankton

Phytoplankton form the base of the food web. The solar energy that they capture and store in organic matter is passed on to the other creatures of the epipelagic, from minute zooplankton to gigantic whales. The first step in the flow of

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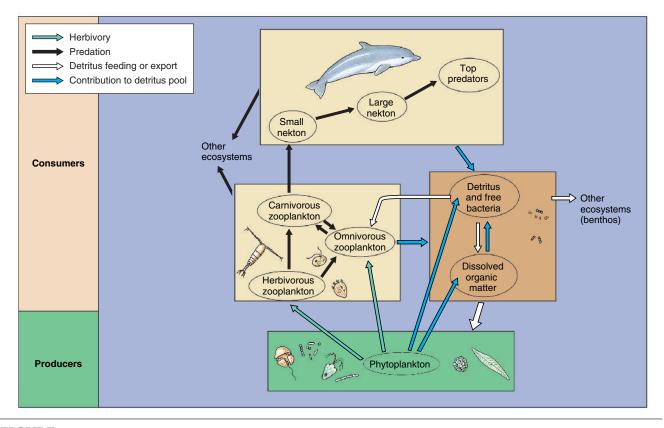


FIGURE 15.4 A simplified epipelagic food web.

energy through the food web occurs when **herbivores** eat the phytoplankton. Herbivores are the vital link between the primary producers, the phytoplankton, and the rest of the community. Large epipelagic animals cannot feed directly on the tiny phytoplankton. They rely instead on herbivorous zooplankton, which can. Zooplankton are by far the most important herbivores in the epipelagic. Thus, a fundamental part of the epipelagic food web is the flow of energy from phytoplankton to herbivorous zooplankton.

Very few zooplankton are strict herbivores. The ones that do eat phytoplankton also eat other zooplankton occasionally. Most zooplankton species are primarily carnivorous and hardly eat phytoplankton at all. These carnivores may feed directly on herbivorous zooplankton and thus reap the production of phytoplankton with only one intermediate step, or **trophic level**, in the food web. They may also eat other carnivores, adding links to the food web (Fig. 15.4).

## Protozoan Zooplankton

The tiny picoplankton and nanoplankton are too small for most multicellular animals to catch and eat. Protozoans, however, can catch them. When it was discovered that pico- and nanoplankton are the most abundant phytoplankton, the importance of protozoans was also recognized. Without protozoans, much of the primary production in the epipelagic would go unutilized. The most important of these protozoans are various flagellates, protozoans that move around by means of flagella. Ciliates, foraminiferans (Fig. 15.5), and radiolarians (see "Protozoans: The Animal-like Protists," p. 100) are also important protozoan grazers. Many grazing protozoans are also capable of photosynthesis, so they also act as members of the phytoplankton.

## Copepods

Small crustaceans, especially **copepods** (Fig. 15.6) dominate the net zooplankton. Copepods are the most abundant members of the net zooplankton practically everywhere in the ocean, typically

Nitrogen Fixation The conversion of nitrogen gas  $(N_2)$  into nitrogen compounds that can be used by primary producers as nutrients.

Chapter 10, p. 228

**Protozoans** Single-celled organisms that are animal-like in that they ingest food and usually can move around. *Chapter 5, p. 100* 

**Copepods** Tiny crustaceans that are often planktonic.

Chapter 7, p. 135

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**FIGURE 15.5** A planktonic foramaniferan (*Orbulina universa*) captures a copepod on its long, sticky pseudopodia. The copepod will be drawn to the surface of the foram's shell, where it will be digested. The shell is 0.5 mm (0.02 in) in diameter.



**FIGURE 15.6** An epipelagic copepod. The orange balls attached to the tail are eggs (also see Fig. 7.28).

numbering 70% or more of the community. This probably makes them the most numerous group of animals on earth.

Nearly all epipelagic copepods eat at least some phytoplankton. It was once thought that they filter feed by continuously pumping a stream of water past their mouthparts. According to this view, water flows through a sieve formed by the bristles on the mouthparts and antennae (Fig. 15.7*a*). The copepod blindly catches whatever particles, phytoplankton or otherwise, happen to be the right size to snag in the bristles.

Feeding experiments and close-up photography, however, have shown that

copepods can actively select the particles they capture. At least some copepods can sense individual phytoplankton cells, using both "smell" and sight. Then they use their limbs like paddles to draw in a stream of water that carries the cell closer. The cell is actively caught in the bristles like a butterfly in a net, and the phytoplankton cell is eaten.

Copepods are also major carnivores. Though most copepods eat at least some phytoplankton, many also eat other zooplankton, including other copepods, when they can. A few copepods are exclusively carnivorous. These generally catch their prey by seizing it with their claw-like appendages (Fig. 15.7*b*).

## Other Crustaceans

Other crustaceans are also important members of the zooplankton. One major group is the shrimp-like **krill**. Though not as abundant around the world as copepods, krill may aggregate into huge, dense swarms. Preferring cold oceanic waters, krill sometimes dominate the zooplankton in polar seas. They are very efficient filter feeders, capturing particles with their bristly appendages. Phytoplankton, especially diatoms, are a favorite food. Krill also eat **detritus**, including fecal pellets, the solid waste excreted by other zooplankton. Small zooplankton are also eaten.

Copepods are so small that most large animals cannot catch them. Krill, by contrast, are relatively big, up to 6 cm (2.5 in) in Antarctic krill (*Euphausia superba*; see Fig. 17.12). Fishes, seabirds, and even the great whales eat them (see Fig. 10.12).

Copepods and krill are by far the most abundant crustaceans in the zooplankton, but there are many other crustaceans, both herbivorous and carnivorous. At certain times and places, one of these crustacean groups may be very abundant. Amphipods and most other planktonic crustaceans are small, like copepods. A few larger crustaceans, some similar to krill, are also found in the net zooplankton. These include a number of decapods—crabs, shrimps, and their relatives (see "Shrimps, Lobsters, and Crabs," p. 137). The decapods are almost exclusively carnivorous. Copepods, krill, and other crustaceans dominate the net zooplankton. Copepods are the main herbivores in the epipelagic and are by far the most abundant group of zooplankton.

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## Non-Crustacean Zooplankton

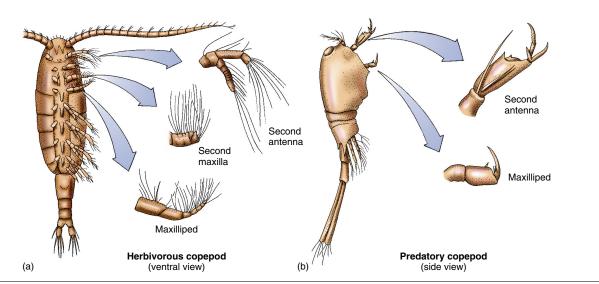
Many groups of animals other than crustaceans are found in the zooplankton. Among the most important of the noncrustacean herbivores are the transparent, planktonic **salps** (Fig. 15.8), relatives of the sea squirts, or tunicates, that live on the bottom (see "Tunicates," p. 147). Salps filter out phytoplankton by pumping water through a sieve-like sac or a fine mucus net.

Larvaceans (Fig. 15.9) are also relatives of sea squirts, though they hardly look it-unless, that is, you look at their larvae. Sea squirt larvae, which are also known as tadpole larvae, are very similar to larvaceans (see Fig. 7.48b). Larvaceans float inside a "house" they make of mucus. By beating its tail, the larvacean pumps water in through passages in the house (Fig. 15.9). Food particles are caught in a complicated mucus net that is secreted inside the house. At least some larvaceans also secrete a net outside the house that can extend as much as 2 m (6 ft). The use of sticky mucus nets allows larvaceans to capture extremely small food particles. They are among the few animals that can catch pico- and nanoplankton. Larvaceans are therefore important in linking primary production by pico- and nanoplankton to the rest of the epipelagic community. The same is true of some salps.

The openings through which water enters the house filter out particles too large for the larvacean to eat. As the larvacean feeds, these filters eventually get clogged. Some species can reverse the water flow, clearing the filters. If the filters get too clogged or a predator threatens, the larvacean simply abandons the house and swims away. It can produce a new house within minutes and resume feeding. When disturbed, some species can build and discard houses every 10 minutes! Even under normal circumstances, most species change houses every four hours or so. When larvaceans are abundant, their discarded houses are an important source of detritus.

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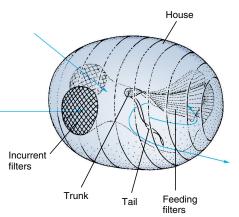
**FIGURE 15.7** (*a*) The mouthparts and appendages of copepods that feed mainly on phytoplankton, such as *Calanus*, have many long bristles. (*b*) Copepods that prey on other zooplankton, such as *Corycaeus*, have appendages with fewer and shorter bristles. Their appendages are better adapted for grasping.

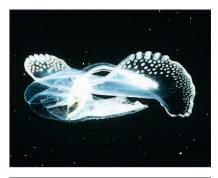


FIGURE 15.8 A pelagic salp, *Thetys* vagina. These gelatinous animals feed by filtering phytoplankton out of the seawater. Like larvaceans (Fig. 15.9), some of them are able to capture bacteria and other very tiny plankton.

A group of molluscs called **pteropods** also includes phytoplankton grazers. Pteropods are small snails in which the foot has been modified to form a pair of "wings" that they flap to stay afloat (Fig. 15.10). Some feed by capturing phytoplankton, including picoplankton and nanoplankton, in mucus nets or threads; others are carnivorous.

Larvaceans, salps, and some pteropods feed with mucus nets or threads. They are among the few zooplankton that eat nanoplankton. Discarded larvacean houses can be an important source of detritus in the epipelagic. FIGURE 15.9 A larvacean spends most of its time inside a mucus "house." By beating its tail, the larvacean draws water into the house (blue arrows) through two intake filters. Food particles are caught on the mucus feeding net, and the filtered water flows outward.





**FIGURE 15.10** In pteropods the foot is typically expanded into "wings," which the animal uses to swim. They have a shell like most other molluscs, but it is greatly reduced.

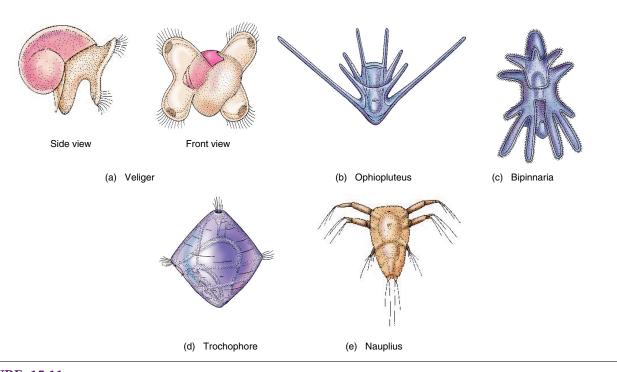
Krill Planktonic, shrimplike crustaceans. Chapter 7, p. 137



**Detritus** Particles of dead organic matter. *Chapter 10, p. 224* 

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**FIGURE 15.11** There is tremendous variety in the larvae found in the meroplankton. Some examples are (a) the veliger of molluscs, (b) the ophiopluteus of brittle stars, (c) the bipinnaria of sea stars, (d) the trochophore of polychaete worms and some molluscs, and (e) the nauplius of many crustaceans.

Arrow worms, or chaetognaths, are extremely important predators in the zooplankton. They feed mostly on copepods. This may not be because they actually prefer copepods but because there are so many copepods around. Arrow worms consume an assortment of other prey when it is available. They can be very abundant, and they have a significant role in epipelagic food webs.

Not all carnivorous zooplankton are tiny. Jellyfishes and **siphonophores**, for example, can be quite large but are weak swimmers and drift with the currents as part of the plankton. Jellyfishes are carnivorous, and many eat small fishes as well as zooplankton. The somewhat similar **comb jellies** (see Fig. 15.18*b*) are also carnivorous. The ocean sunfish *(Mola mola)*, which can grow to 2,300 kg (5,000 lb), swims so weakly that it is sometimes considered to be a member of the zooplankton.

## Meroplankton

The zooplankton discussed to this point, with the exception of a few jellyfishes, spend their whole lives in the plankton and are called **holoplankton**. In addition to these permanent members of the zooplankton, there are a vast number of organisms that have planktonic larvae. These animals—whether from estuaries, the rocky intertidal, kelp beds, coral reefs, or even the deep sea—release their eggs or young into the water column, and the young spend the early part of their lives in the plankton. Such temporary members of the plankton are called **meroplankton**. Coastal waters are particularly rich in meroplankton.

Invertebrates often have a particular type of larva that is characteristic of the group (Fig. 15.11). Some invertebrates have a whole series of different larval stages (see Fig. 7.37). Nearly all marine fishes also have planktonic larvae.

The meroplankton are the larval stages of invertebrates and fishes that spend only part of their lives in the zooplankton.

Small larvae tend to feed predominantly on phytoplankton; larger ones eat zooplankton. If there is a series of stages, as in crustaceans, the larvae may feed on phytoplankton initially and later switch to zooplankton. Fish larvae, too, often change from herbivores to carnivores as they grow.

## The Nekton

Plankton are by far the most abundant organisms in the sea, and they form the foundation of the food chain in the epipelagic. Most of us, however, are much more familiar with the **nekton**, the large, strong swimmers. Fishes, marine mammals, and squids are the most abundant nekton. Turtles, sea snakes, and penguins are also included.

Practically all nekton are carnivorous. **Planktivorous** nekton, those that eat plankton, include small fishes like herrings, sardines, and anchovies. They also include the world's largest fishes, the whale shark (*Rhiniodon typus*) and basking shark (*Cetorhinus maximus*). The largest nekton of all, baleen whales, also eat plankton, mostly krill. Seals, penguins, squids, and an assortment of fishes including salmon, tunas, and flying fishes eat krill as well. Castro–Huber: Marine Biology, Fourth Edition III. Structure and Function 15. Life Near the Surface of Marine Ecosystems

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Fishes like lanternfishes that stay in deeper water during the day and swim up into the epipelagic at night (see "Vertical Migration and the Deep Scattering Layer," p. 364) consume large amounts of zooplankton. These fishes are important foods for some large epipelagic nekton, such as tunas and dolphins, that dive into deeper waters to feed.

Most species of nekton, however, eat other nekton rather than plankton. Fishes, squids, and large crustaceans are the main foods. Epipelagic predators are usually not fussy and will eat many different prey, provided they are the right size. In general, the larger the predator, the larger the prey, though there are exceptions like baleen whales and whale sharks. Thus, small fishes like herrings have small prey: zooplankton. Bigger fishes eat these small fishes, and in turn are eaten by even bigger predators. At the top of the food chain are the largest predators of all, the top predators, or top carnivores, which eat the largest prey. The sperm whale (Physeter catodon), the largest of all nekton except the baleen whales, eats giant squid that can be more than 10 m (33 ft) long. There are other top predators that eat massive prey. Among predators, killer whales (Orcinus orca) are second in size only to the sperm whale. They not only eat porpoises and seals (see Fig. 10.7), but may attack and kill baleen whales. Large sharks such as the great white (Carcharodon carcharias) and makos (Isurus) eat seals, billfishes like marlins and sailfishes, and even other sharks.

Nearly all the nekton are predators. A few eat plankton, but most species eat other, usually smaller, nekton.

# LIVING IN THE EPIPELAGIC

Every environment places special demands on the organisms that live there, and the epipelagic is no exception. The adaptations of epipelagic organisms largely center around two main needs: the need to stay in the epipelagic and the need to eat and avoid being eaten.

# **Staying Afloat**

To live in the epipelagic, organisms must stay in the epipelagic. All epipelagic organisms face a fundamental problem: Cells and tissue are denser than water. Shells and skeletons are even more dense. As a result, organisms sink unless they have some adaptation that prevents it. This is not much of a problem for organisms that live on the bottom or in deep water, since they don't need to float anyway. On the other hand, organisms that live near the surface must keep from sinking to stay in their habitat.

Phytoplankton have to stay in relatively shallow water to get enough light for photosynthesis. Once a phytoplankton cell sinks or is carried by water movement out of the photic zone it is doomed, unless it can somehow get back into the sunlit layer. Animals, too, whether zooplankton or nekton, must be able to stay near the surface. This is not because these animals need sunlight but because their food is found in the shallow waters.

There are two basic ways that organisms that can't swim can keep themselves from sinking out of the epipelagic. One of these is to increase their water resistance so that they sink slower. The other is to make themselves more buoyant so that they tend not to sink in the first place. Buoyancy also benefits organisms that swim because it allows them to stay at a given depth without working as hard. This applies not only to the nekton, who by definition are strong swimmers, but also to zooplankton and even some phytoplankton, like dinoflagellates. They swim up and down in the water column even though they cannot swim strongly

Organisms must avoid sinking to stay in the epipelagic. This is achieved by increasing water resistance and increasing buoyancy.

enough to move against the currents.

## Increased Resistance

How fast an organism of a given weight sinks depends on how much water resistance, or **drag**, it encounters. The drag depends mainly on the surface area of the organism: The higher the surface area, the higher the resistance and the slower the organism sinks. This is probably one reason that plankton are usually small: Small organisms have much more surface area for a given volume than large ones (see "Surface-to-Volume Ratio," p. 81) and therefore relatively more drag. Other things being equal, small organisms sink slower than large ones.

An organism's shape can also increase its surface area, and therefore make it sink slower. Clearly, the parachute-like shape of many jellyfishes helps slow sinking. Many planktonic organisms have extremely flat shapes (Fig. 15.12). You can see how this helps slow sinking with a simple experiment. Take two sheets of paper, both of the same weight. Crumple one sheet into a tight ball. Drop both the flat sheet and the ball from the same height. The flat sheet will take much longer to hit the ground because it offers much more wind resistance. Exactly the same principle applies in the water. A flat shape has another advantage for phytoplankton. Note how the flat sheet of

Arrow Worms or Chaetognaths Small, worm-like predators with fins along the body and spines on the head.

Chapter 7, p. 141

**Siphonophores** Drifting colonial cnidarians in which different members of the colony are specialized for different tasks.

Chapter 7, p. 121

**Comb Jellies** or **Ctenophores** Radially symmetrical animals that resemble jellyfishes but have eight rows of cilia and no *nematocysts*.

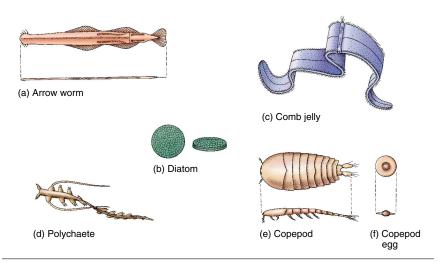
Chapter 7, p. 123



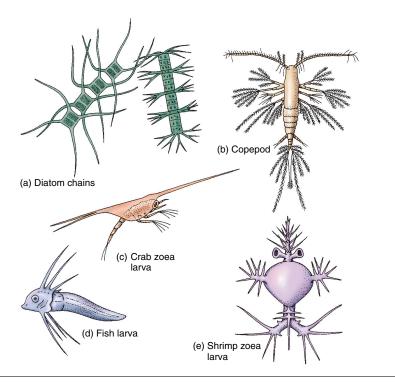
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**FIGURE 15.12** Some planktonic organisms that have flat shapes include (*a*) arrow worms (*Sagitta*), (*b*) many diatoms, (*c*) *Cestum*, a highly modified comb jelly, (*d*) *Tomopteris*, a planktonic polychaete worm, (*e*) certain copepods, such as *Sapphirina*, and (*f*) some copepod eggs.



**FIGURE 15.13** Some planktonic organisms have long spines or projections. They may also form chains. Examples are (a) diatoms, (b) copepods like *Augaptilus*, (c) zoea larvae of porcellanid crabs, (d) fish larvae (*Lophius*), and (e) zoea larvae of *Sergestes*, a shrimp.

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paper zigzagged from side to side as it fell. Flat phytoplankton cells do the same thing. The back-and-forth motion keeps seawater flowing over the cell's surface, renewing the layer of water with which the cell exchanges gases, nutrients, and waste products.

Long projections or spines are another common adaptation that increases surface area in planktonic organisms (Fig. 15.13). Spines have the added advantage of making the organism harder to eat. Many phytoplankton form chains, another adaptation that helps slow sinking. Chains sink slower than the individual cells would if the chain were broken up.

Swimming organisms rarely have spines or other features that increase surface area, since this would increase water resistance and make swimming harder. They usually have adaptations that *reduce* drag, making it easer to move through the water.

## Increased Buoyancy

The second way that epipelagic organisms can stay near the surface is to have special adaptations that make them more buoyant. Unlike adaptations that help the organism resist sinking, buoyancy reduces the tendency to sink in the first place.

One common adaptation that provides extra buoyancy is to store lipids, such as oils or fats, in the body. Being less dense than water, lipids tend to float. Many plankton-notably diatoms, copepods, and fish eggs and larvae-contain droplets of oil. Many adult epipelagic fishes also gain buoyancy by storing large amounts of lipid. This is especially true in sharks, tunas and their relatives, and other species in which the swim bladder is poorly developed or missing altogether. Epipelagic sharks, for example, have enlarged livers with a very high oil content. Whales, seals, and other marine mammals also have a great deal of buoyant fat in a thick layer of blubber under the skin (see Fig. 4.2).

Oils and fats are a good way to increase buoyancy because they serve other functions at the same time. Lipids are the most efficient way to store energy, for instance. In marine mammals the blubber provides insulation from the cold ocean water as well as buoyancy. Insulation is especially important to warm-blooded animals because they must burn up energy to maintain their body temperatures (see "Temperature," p. 80).

Pockets of gas are another adaptation that provides buoyancy. Cyanobacteria, for example, have tiny gas bubbles, or vacuoles, inside their cells. They are able to change the number and buoyancy of the vacuoles. This allows them to regulate their depth; they can increase buoyancy to move up in the water column or decrease it to sink. Some other plankton, especially large ones, also have special gas-filled floats. Such floats are especially common in organisms that live right at the sea surface, as is described in the next section. Similarly, most epipelagic bony fishes have internal swim bladders that give buoyancy.

A gas-filled bladder or float provides much more buoyancy than, for example, lipid, but it has a major disadvantage. Gas expands and contracts as the animal moves up and down in the water column and the pressure changes. When the volume of gas changes, so does the amount of buoyancy. To control its buoyancy, a fish must be able to regulate the amount of gas in the swim bladder. Most fishes can do this, but the actual mechanism varies. Some fishes simply pump gas in and out of the bladder through a special duct. These fishes can adjust fairly rapidly to changes in pressure. Other fishes regulate the amount of gas in their swim bladders much more slowly and cannot cope well with changes in depth. Many fishers have pulled up fish with bulging eyes or with the stomach protruding out of the mouth (see Fig. 3.14). This happens when the swim bladder blows up like a balloon as the fish is brought to the surface and the gas inside expands. In normal life the fish would never come to the surface, or it would surface much more slowly than it did on the end of the line.

The swim bladder is often poorly developed or absent in active fishes that frequently change depth, such as tunas. It never evolved in sharks. Such fishes must compensate for the loss of buoyancy. In addition to their large oily livers, sharks have large, stiff fins and asymmetrical tails that provide lift as long as the shark

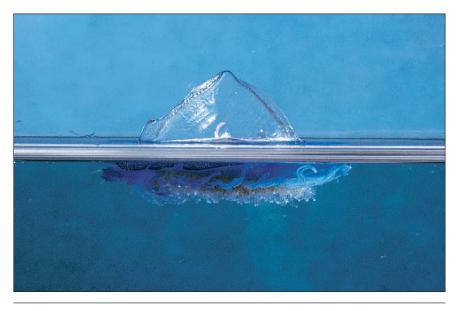


FIGURE 15.14 The by-the-wind sailor (Velella).

is swimming (see Fig. 8.12). Members of the tuna family also rely on stiff, almost wing-like fins and constant swimming to provide lift.

Yet another way to gain buoyancy is to control the composition of the body fluids. The basic idea is that by excluding heavy ions, like sulfate  $(SO_4^{-2})$  and magnesium  $(Mg^{+2})$ , and replacing them with lighter ones, especially ammonium  $(NH_4^+)$  and chloride  $(Cl^-)$ , organisms can reduce their density and become more buoyant. Certain dinoflagellates do this. So do various zooplankton, including salps, comb jellies, and some squids.

Mechanisms that increase the buoyancy of epipelagic organisms include the storage of lipids, gas-filled floats, and the substitution of light ions for heavy ones in internal fluids.

## The Floaters

The plankton include an unusual and highly specialized group of organisms that live right at the very surface of the ocean. Marine biologists usually refer to these surface-dwelling organisms as **neuston**.

All plankton need to keep from sinking, but the neuston have to go one step further and actually float. The most common method of doing this is to have some sort of gas-filled structure to provide buoyancy. There are many variations on this seemingly simple theme.

Organisms living at the surface constitute the neuston.

The upper surface of the by-thewind sailor (Velella), a colonial, jellyfishlike cnidarian, is specialized as a float (Fig. 15.14). The float protrudes into the air and acts like a sail, pushing the colony along in the wind. The Portuguese manof-war (Physalia), a siphonophore, is famous for its powerful sting (see "The Case of the Killer Cnidarians," p. 125). Like the by-the-wind sailor, part of the colony acts as a sail (see the photo on p. 323). Several other species of cnidarians live at the sea surface. Some of these can even control the buoyancy of their floats and sink below the surface for shelter during storms.

Despite their powerful stinging cells, these relatives of jellyfishes have enemies. The violet shell *(Janthina)* makes a raft of

Swim Bladder A gas-filled sac that lies inside the body cavity of most bony fishes. *Chapter 8, p. 159; Figure 8.12* 

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## **Bart Three** Structure and Function of Marine Ecosystems

mucus filled with bubbles from which it hangs upside down. These inch-long snails drift about, eating Portuguese men-of-war and other delicacies when they find them. Another mollusc, a sea slug called *Glaucus*, stays afloat by swallowing a bubble of air. It feeds on the by-the-wind sailor and its relative, the small, disk-shaped *Porpita* (Fig. 15.15). *Porpita*'s stinging cells, still capable of firing, end up in the flaps that protrude from the sea slug's back and will sting animals that disturb the sea slug. Thus, *Porpita* provides not only food but protection for the sea slug.

One unusual inhabitant of the surface does not have a gas-filled float. In fact, it doesn't actually float at all. The water strider *(Halobates)*, the only insect that lives in the open ocean, skims over the water surface (Fig. 15.16). It is closely related to the water striders that are common in lakes and ponds. The water strider isn't marine in the strict sense because it cannot swim and drowns if it falls through the surface. Still, it manages to live all over the oceans.

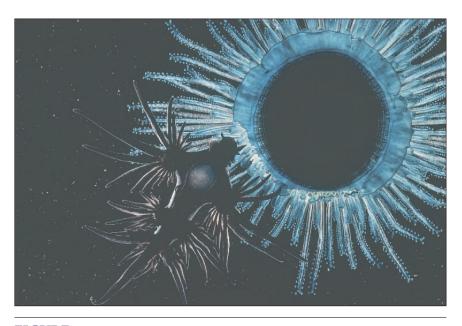
# **Predators and Their Prey**

Many of the adaptations of epipelagic animals, or for that matter any animals, are related to the need to find food and at the same time avoid being eaten. In comparison with other marine environments, the need to adapt to predation, whether as predator or prey, is especially important in the epipelagic.

## Sense Organs

Predators and their prey play a continual game of hide-and-seek. The predator tries to find its prey and attack before the victim has a chance to react, while the prey wants as much warning of approaching enemies as possible. Most animals in the epipelagic therefore have highly developed sense organs to help them detect their prey and enemies.

The epipelagic has plenty of light to see by, at least during the day, so it should come as no surprise that vision is important to many epipelagic animals. Many zooplankton have well-developed eyes. Most can't actually see images, but



**FIGURE 15.15** The pelagic sea slug (*Glaucus*) feeding on *Porpita*, a relative of jellyfishes. The sea slug not only gets a meal but uses *Porpita*'s stinging cells for defense.

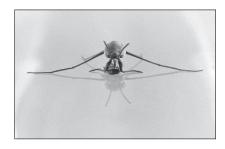


FIGURE 15.16 The marine water strider *(Halobates sericeus)* relies on greatly elongated legs and the water's surface tension to skate on the surface.

even so they can detect motion, shapes, and shadows. Copepods and other zooplankton may use vision to locate their prey. There is some evidence that vision also helps them avoid predators.

Squids, fishes, and marine mammals all have good eyesight. Vision is especially important to nekton in the epipelagic because there are no solid structures that can be used for concealment. In other environments, animals can hide in the sediments, under rocks, or behind seaweeds. There are no such hiding places in the epipelagic. The large, welldeveloped eyes of most epipelagic fishes (Fig 15.17) and other nekton are used not only to find prey and watch for predators, but also to find mates and stay together in schools.

Fishes have another remote sensing system: the lateral line. Like all fishes, those in the epipelagic are extremely sensitive to vibrations in the water. The lateral line almost certainly plays a major role in schooling behavior (see "Schooling," p. 169). It also alerts the fish to predators. Fishes react instantly to the lunge of an enemy even if they don't see it. Most predatory fishes-including sharks, tunas, and billfishes-also have well-developed hearing and are strongly attracted to splashes on the surface and irregular vibrations in the water, the kinds of vibrations made by an injured fish. Another remote sensing system, echolocation, is found in dolphins and some other cetaceans. This sophisticated built-in sonar allows them to locate their prey at a distance (see "Echolocation," p. 201).

Epipelagic animals have well-developed sense organs, especially vision, the lateral lines and hearing of fishes, and echolocation in cetaceans.

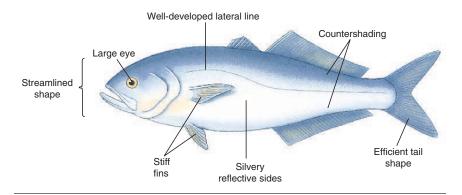


FIGURE 15.17 Typical adaptations of epipelagic fishes.







**FIGURE 15.18** Many species of zooplankton are transparent or nearly so. Examples include (*a*) hyperiid amphipods, which have two giant eyes that cover most of the head, (*b*) comb jellies, and (*c*) squids. These photos have been taken to make the organisms more visible than they really are.

## Coloration and Camouflage

Just because there are no hiding places doesn't mean that epipelagic organisms cannot conceal themselves. Indeed, **protective coloration**, or camouflage, is nearly universal among epipelagic organisms, or at least those large enough to see. This is not surprising in a world where the hunters rely so heavily on vision to find their victims, and the prey use vision to get away.

One way to be inconspicuous in the vast watery world of the epipelagic is to be transparent. This adaptation is seen in a variety of zooplankton, some of which are almost perfectly clear (Fig 15.18).

Gelatinous zooplankton like some jellyfishes, salps, larvaceans, and comb jellies are probably the best at being invisible. Many other groups of zooplankton are at least partially transparent, with perhaps only the eyes, a few spots of pigment, or the internal organs visible. Some nearly transparent zooplankton have a faint bluish tinge, possibly helping them blend in with the surroundings.

A very common form of protective coloration, particularly in nekton, is countershading, where the back (dorsal surface) is dark, usually green, blue, or black, and the belly (ventral surface) is white or silver. Countershading is particularly well suited to the epipelagic. To a predator looking down, the ocean depths are a dark blue. Viewed from above, the dark back of a countershaded fish blends in against the dark background. Looking up, on the other hand, the predator sees the bright light filtering down from above and the silvery-white sea surface. Against this bright background a dark object stands out like a sore thumb, but the silvery-white undersides of epipelagic nekton reflect light and match the bright surface. Laterally compressed bodies, also common, reduce the size of the silhouette whether viewed from above or below (Fig 15.19).

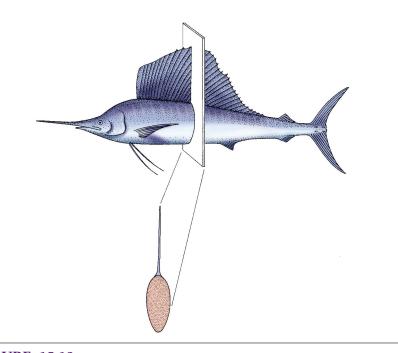
Countershading, in which the dorsal surface is dark and the ventral surface is white or silver, is a widespread adaptation among epipelagic nekton. Countershaded organisms blend in against the background whether they are viewed from above or below.

Most epipelagic fishes have silvery sides that reflect light. This helps them blend in when viewed from the side as well as from below. It is also common for them to have vertical bars or irregular patterns that help break up their outline in the dappled underwater light.

Lateral Line A system of canals on the head and sides of fishes that helps them detect vibrations in the water.

Chapter 8, p. 168; Figure 8.19

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**FIGURE 15.19** Like many epipelagic fishes, the sailfish (*Istiophorus platypterus*) has a laterally compressed body; that is, it is high and narrow when viewed in cross section.



**FIGURE 15.20** Flying fishes (*Cypselurus*) can't actually fly, but their expanded pectoral fins allow them to glide for long distances.

Flying fishes (*Cypselurus*) have evolved a distinctive defense that is not exactly camouflage but does make them hard to see, at least temporarily. When threatened, flying fishes burst out of the water and glide through the air on their greatly enlarged pectoral fins (Fig 15.20). To a predator, the flying fish seems to have disappeared, because it is difficult to see past the surface into the air. This strategy is only partly effective, however, and flying fishes are a favorite food of many epipelagic predators.

## Swimming: The Need for Speed

Protective coloration or not, the keen senses of epipelagic predators enable them to find their prey. When this happens the prey's only hope is to flee, because there are no hiding places. Whether the prey gets away or the predator gets a meal depends on which swims faster. The emphasis is on sheer speed, as opposed to maneuverability, or being able to burrow in the bottom or hide in crevices in the rocks. It is no coincidence that the epipelagic contains the world's most powerful swimmers (see "Swimming Machines," p. 340).

While plankton often have adaptations to increase drag in order to slow their rate of sinking, nekton, who must work to move through the water, have adaptations to *reduce* drag. Practically all epipelagic nekton have streamlined bodies that make swimming easier and more efficient (see Fig 9.14). They rarely have bulging eyes, long spines, or other projections that would increase resistance and slow them down. Instead, their bodies are sleek and compact. They often have

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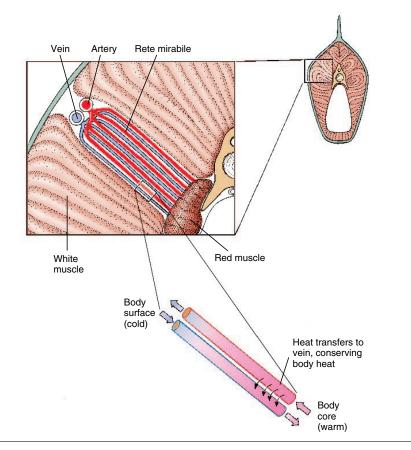
smooth body surfaces to help them slide through the water. Epipelagic fishes usually have small scales, or none at all, and dolphins and whales have lost nearly all their hair. Fishes produce mucus that actually lubricates the body surface, allowing them to slip through the water even more easily.

Epipelagic nekton are also firm and muscular, another adaptation for swimming. The force produced by these muscles is delivered almost entirely by the tail. Epipelagic fishes rarely swim with their pectoral fins, which are used only for steering and lift. Most epipelagic fishes have a tail that is high and narrow. Studies have shown this shape to be the most efficient for high-speed swimming.

Typical bony fishes have fins that consist of movable spines connected by a thin membrane. This feature makes them dexterous and flexible. By contrast, the fins of epipelagic bony fishes tend to be stiff, which gives them the strength to provide maneuverability and lift at high speed. These stiff fins are not much good for hovering, swimming backward, poking into holes and crevices, or other activities that require tight maneuvers at slow speed. Epipelagic fishes don't do such things often anyway.

Epipelagic nekton not only have a lot of muscle, but their muscles are strong and efficient, as you might expect. Fishes have two kinds of muscle, red and white-the equivalent of the light and dark meat on a turkey. Red muscle gets its color from a high concentration of myoglobin and therefore can store a lot of oxygen. It is best suited for long, sustained effort. White muscle, on the other hand, provides short bursts of power. Epipelagic fishes use their red muscle for sustained cruising and they typically have more red muscle than coastal fishes, which don't usually spend as much time in high-speed swimming. Epipelagic fishes still have white muscle that kicks in when they need an extra burst of speed.

Typical epipelagic nekton have sharp eyesight, countershading, streamlined bodies, well-developed and efficient muscles, and high, relatively narrow tails.



**FIGURE 15.21** In "warm-blooded" epipelagic fishes, small veins and arteries are arranged in such a way that heat generated by muscular activity at the body core is carried back to the core in returning blood. The veins and arteries are packed into a complex network known as the rete mirabile, or "wonderful net."

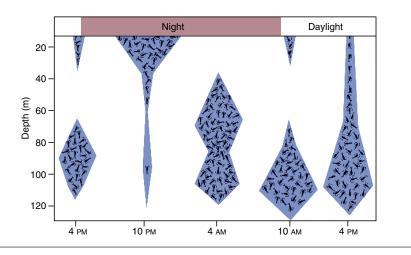


FIGURE 15.22 The depth distribution at different times of day of a vertically migrating copepod.

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Muscle tends to work more efficiently at warm temperatures. Epipelagic sharks, tunas, and billfishes have evolved a system to conserve the heat generated by their muscles and keep their internal temperature above that of the surrounding water. In fact, these fishes can almost be considered "warm-blooded." In most fishes, heat generated in the muscles is carried by the blood to the skin and then lost to the water. "Warmblooded" fishes have a special arrangement of the blood vessels known as the rete mirabile, or "wonderful net." In this arrangement (Fig 15.21), body heat being carried outward in the blood is transferred to inward-flowing blood and taken back into the body. This mechanism greatly reduces heat loss. The fish's core temperature remains well above that of the surrounding water, while the skin remains nearly the same temperature as the water.

## Vertical Migration

The surface layers of the ocean contain by far the most food in the pelagic realm. They can be a dangerous place, however, with voracious predators zooming around and nowhere to hide. Some zooplankton solve this apparent dilemma by spending only part of their time near the surface and retreating to safer territory when not feeding. These animals undertake vertical migration. During the day they live at considerable depth, usually at least 200 m (650 ft) or so (Fig. 15.22). At these depths there is not much light, so the zooplankton are relatively safe from the many predators that use vision. At night, the zooplankton swim up into the surface layers to feed on phytoplankton and other zooplankton. Experiments in deep tanks have shown that zooplankton vertically migrate only if predatory fish are also in the tank; they stop migrating when the fish are removed.

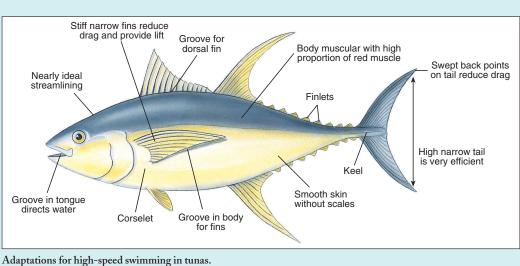
Myoglobin A red muscle protein in vertebrates that stores oxygen. *Chapter 8, p. 166* 

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Tunas, mackerels, and Stiff narrow fins reduce billfishes swim continudrag and provide lift Groove for ously. Feeding, courtship, dorsal fin reproduction, and even "rest" are carried out while Nearly ideal in constant motion. As a streamlining 117 result, practically every aspect of the body form and function of these swimming machines is adapted to enhance their ability to swim. The swimming feats Groove in tongue directs water

of tunas and billfishes are nothing short of amazing. They routinely cover vast distances in their annual migrations. One northern bluefin tuna (Thunnus thynnus) was tagged southeast of Japan



SWIMMING MACHINES

and recaptured off the Pacific coast of Baja California, Mexico. It swam a distance of 10,800 km (6,700 mi). Most other tunas and billfishes also make long-distance migrations.

These long journeys are made in an impressively short time. Tagged northern bluefin have crossed the Atlantic in 119 days, averaging a straight-line distance of over 65 km (40 mi) per day. The fish actually cover a much greater distance because they constantly change direction, dashing here and there in search of food. Some tunas could cross the Atlantic in less than two months at their slow*est* cruising speed if they took a direct route.

Tunas and billfishes are primarily endurance swimmers, adapted for sustained high-speed cruising, but they are also accomplished sprinters and can make blistering high-speed bursts. The fastest fish of all is the Indo-Pacific sailfish (Istiophorus platypterus; see Fig. 1.17), which can exceed 110 km/hr (70 mph) for short periods. No other fish can match this, but most tunas and billfishes are fast swimmers. Several large species can reach 75 km/hr (50 mph); some smaller species are just as fast for their size. Most are so fast that they can easily outdistance most of their prev. Their phenomenal speed has probably evolved not so much to catch prey-they could do that at slower speeds-as to compete with schoolmates. The first one to the prey, after all, gets the meal.

Many of the adaptations of these fishes serve to reduce water resistance. Interestingly enough, several of these hydrodynamic adaptations resemble features designed to improve the aerodynamics of high-speed aircraft. Though human engineers are new to the game, tunas and their relatives evolved their "high-tech" designs long ago.

Tunas, mackerels, and billfishes have made streamlining into an art form. Their bodies are sleek and compact. The body shapes of tunas, in fact, are nearly ideal from an engineering point of view. Most species lack scales over most of the body, making it smooth and slippery. The eyes lie flush with the body and do not protrude at all. They are also covered with a slick, transparent lid that reduces drag. The fins are stiff, smooth, and narrow, which also helps cut drag. When not in use, the fins are tucked into special grooves or

## Vertically migrating zooplankton stay below the photic zone during the day. At night they migrate to the surface to feed.

These daily movements require a great deal of energy. For an organism that is 2 mm long, a 200-m migration is the rough equivalent of a 200-km (120-mi) swim for a human! This is a long way to go to avoid predators when

many other zooplankton manage to withstand predation without migrating. Various explanations for vertical migrations in addition to escaping predation have been proposed. Zooplankton may be able to slow their metabolism and conserve energy by spending part of their time in the deep water, which is cold and reduces their body temperature. This is somewhat like sleep or hibernation. It has also been suggested that

zooplankton migrate to avoid the toxins produced by some phytoplankton. The phytoplankton produce more toxins during the day, when they are actively photosynthesizing. Many species of nekton, mainly fishes and some large shrimps, also make vertical migrations. These animals generally migrate to much greater depths than zooplankton (see "Vertical Migration and the Deep Scattering Layer," p. 364).

depressions so that they lie flush with the body and don't break up its smooth contours. Airplanes retract their landing gear while in flight for the same reason.

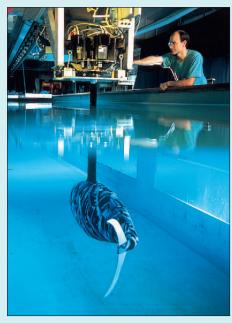
These fishes have even more complex adaptations to improve their hydrodynamics. The long bill of marlins, sailfishes, and swordfish *(Xiphias gladius)* probably helps them slip through the water. Many supersonic aircraft have a similar needle at the nose.

Most tunas and billfishes have a series of keels and finlets near the tail. Although most of their scales have been lost, tunas and mackerels retain a patch of coarse scales near the head called the **corselet**. The keels, finlets, and corselet help direct the flow of water over the body surface in such a way as to reduce resistance. Again, supersonic jets have similar features.

Because they are always swimming, tunas simply have to open their mouths and water is forced in and over their gills. Accordingly, they have lost most of the muscles that other fishes use to suck in water and push it past the gills. In fact, tunas must swim to breathe. They also must keep swimming to keep from sinking, since most have largely or completely lost the swim bladder.

One potential problem is that opening the mouth to breathe detracts from the streamlining of these fishes and tends to slow them down. Some tunas have specialized grooves in their tongue. These grooves are thought to help channel water through the mouth and out the gill slits to reduce water resistance.

There are adaptations that increase the amount of forward thrust as well as those to reduce drag. Again, these fishes are the envy of engineers. Their high, narrow tails with swept-back tips are almost perfectly adapted to provide propulsion with the least possible effort. Perhaps most important of all to these and other fast swimmers is their ability to sense and make use of swirls and eddies in the water. They can slide past eddies that would slow them down and then gain extra thrust by "pushing off" the eddies. The race car driver who "slipstreams" and then "slingshots" past a leading car uses much the same principles, but not nearly as well. Scientists and engineers are beginning to study this ability of fishes in the hope of designing more efficient propulsion systems for ships.



RoboTuna, a robot designed to mimic the northern bluefin tuna, may lead to the development of more efficient ships.

The muscles of these fishes and the mechanism that maintains a warm body temperature are also highly efficient. A bluefin tuna in water of 7°C (45°F) can maintain a core temperature of over 25°C (77°F). This warm body temperature may help not only the muscles, but the brain and eyes work better. The billfishes have gone one step further. They have evolved special "heaters" of modified muscle tissue that warm the eyes and brain, maintaining peak performance of these critical organs.

# EPIPELAGIC FOOD WEBS

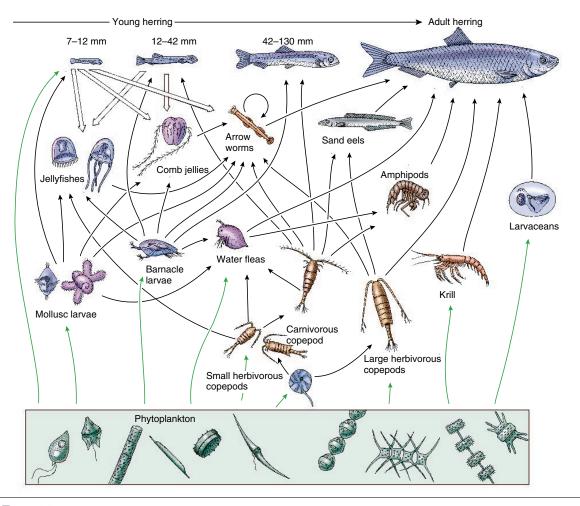
Epipelagic food webs are of great interest, especially because epipelagic fisheries provide food and employment to millions (see "Food from the Sea," p. 383). Species that are caught commercially can be understood and managed only if we understand the rest of the food web on which they depend.

# Trophic Levels and Energy Flow

The trophic structure of the epipelagic is extremely complex. The epipelagic contains a vast number of different species. The feeding habits of most of them are poorly known, if at all. It's hard to describe the trophic structure of a community if you don't even know what many of the animals eat! Another difficulty in understanding epipelagic food webs is that most of the animals are **omnivores** and eat a variety of foods. This means that they often eat prey from different trophic levels. Zooplankton such as copepods often eat both phytoplankton and zooplankton; thus, they function as both herbivores and carnivores. Nekton, too, consume prey at different levels on the food web. A tuna, for example, may act as a secondary consumer when it eats krill, as a third-level

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**FIGURE 15.23** The North Sea herring *(Clupea harengus)* eats different foods at different stages of its life. Its larval stages are eaten by predators that do not feed on adult herring (open arrows). Many, if not most, epipelagic animals have similarly complex feeding relationships. Illustrations of food webs are usually greatly simplified and gloss over such complexities. For example, how would this partial food web fit into the scheme shown in Figure 15.4?

consumer when it eats a sardine that ate zooplankton, and as a fourth-level consumer when it eats a mackerel that ate a flying fish that ate zooplankton. This makes it difficult to assign many animals to a particular trophic level.

Yet another complication is that most epipelagic animals consume different prey at different times in their lives. Many eat different food as larvae than they eat as adults, and even the larvae often switch from phytoplankton to zooplankton. Even after they leave the larval stage, many fishes eat different prey as they grow larger (Fig. 15.23). The basic flow of energy in the epipelagic can be depicted as phytoplankton  $\rightarrow$  zooplankton  $\rightarrow$  small nekton  $\rightarrow$  large nekton  $\rightarrow$  top predators. The top predators, of course, are also nekton. This scheme is greatly simplified, and each level contains a mini-web. Within the zooplankton, for example, are herbivores and several levels of carnivores, forming a food web among themselves. There is also an important side branch called the microbial loop, which is described in the next section.

Epipelagic food chains usually have many steps and are generally longer than in other ecosystems. The number of steps varies: Tropical food webs tend to have more levels than those in colder waters. Even in cold waters there may be five or six steps between the primary producers, the phytoplankton, and a top predator. There are exceptions, of course. The diatoms-to-krill-to-whales chain (see Fig. 10.11), for example, is among the shortest of food chains.

Epipelagic food chains tend to be long and complex because they contain many species and many epipelagic animals feed at different trophic levels. Castro–Huber: Marine Biology, Fourth Edition III. Structure and Function 15. Life Near the Surface of Marine Ecosystems

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The epipelagic is an exception to the rule of thumb that only about 10% of the energy contained in one trophic level is passed on to the next (see "The Trophic Pyramid," p. 223). Epipelagic herbivores convert more than 20% of the energy derived from phytoplankton into growth. Epipelagic carnivores, too, are more than 10% efficient, though not as efficient as the herbivores.

Even with their high efficiency, the length of epipelagic food webs means that most of the energy fixed by phytoplankton is lost before it reaches the top carnivores. After all, even an efficiency of 20% means that 80% of the energy is lost in just one step. Large animals that feed directly on plankton have an advantage in that they have more food available than do predators that eat other high-level carnivores. By feeding directly at low trophic levels, they eliminate many intermediate steps. It is no accident that the largest epipelagic nekton, baleen whales and whale sharks, and the most abundant epipelagic fishes, like anchovies and herrings, eat plankton.

Until a few years ago, most of the primary production in the epipelagic was thought to flow through the simplified food chain of phytoplankton  $\rightarrow$ zooplankton  $\rightarrow$  nekton. "Phytoplankton" and "zooplankton" referred to the relatively large net plankton. When oceanographers discovered vast numbers of picoplankton and nanoplankton in the ocean, they wondered what all these tiny creatures were doing. The answer has greatly changed our understanding of epipelagic food webs.

The ocean contains vast amounts of dissolved organic matter (DOM), organic material that exists not as particles but in dissolved form. Much of the DOM simply leaks out of phytoplankton cells. Zooplankton spill a lot of DOM when they eat and excrete it as waste. The largest source of DOM, however, results from the activities of viruses. There are tens of millions of viruses per milliliter in the ocean that infect large numbers of organisms, particularly microbes. The viruses subvert the cellular machinery of the microorganisms so that it makes many more viruses, until eventually the host cell bursts. This bursting, or **lysis**, releases the rest of the cell's contents along with the viruses.

We may not think of such material as food in the ordinary sense, but it still contains large amounts of energy. Calorie counters who like sugar in their coffee are familiar with this fact. Very few animals, however, are able to use DOM as an energy source. Though some phytoplankton may be able to use it, it was once thought that the huge pool of energy in DOM went largely unused.

# The Microbial Loop

We now know that the DOM in the ocean isn't just sitting there, but is part of a major energy pathway called the microbial loop (Fig. 15.24). The microbial loop starts with phytoplankton of all sizes. As much as *half* the organic matter manufactured by these primary producers becomes DOM. The DOM is not lost to the food web, as was once thought, but is used by bacteria and probably archaea. These microbes are so small that most animals can't eat them either, but instead they are eaten by tiny protozoans in the nanoplankton. The energy from DOM is finally passed up the rest of the food chain when net zooplankton eat the protozoans.

The "microbial loop," in simplified form, refers to the flow of energy through the series phytoplankton  $\rightarrow DOM \rightarrow bacteria \rightarrow$ protozoans  $\rightarrow$  zooplankton. Without the microbial loop, the energy in DOM would go largely unused. As much as half the primary production in the epipelagic is channeled through the microbial loop.

Another important role of protozoan grazers is in channeling the production of primary producers in the nanoplankton up the food chain. Again, these nanoplankton are too small for most zooplankton to eat.

Detritus—particulate rather than dissolved organic matter—is also important in the epipelagic, as in other marine food webs. Two important sources of detritus have already been mentioned: fecal pellets and abandoned larvacean houses. Larvacean houses and other accumulations of mucus can be very abundant and support rich populations of bacteria. They are often called **marine snow** because they look something like underwater snowflakes.

Many zooplankton and small fishes eat marine snow. Much of the detritus, however, sinks out of the epipelagic zone to deeper zones before epipelagic organisms can use it. Furthermore, as previously noted, the epipelagic does not get much detritus from other systems.

# **Patterns of Production**

Epipelagic food webs are complex indeed, but they all share one simple feature: Primary production by phytoplankton, be they pico-, nano-, or net plankton, is the base. All other organisms, from the smallest zooplankton to the largest predators, depend on this primary production. Some parts of the epipelagic rank among the most productive ecosystems on earth (see Table 10.1, p. 228). There are also large areas that are among the least productive, the "deserts" of the ocean. The abundance of animals, from zooplankton to whales, generally follows the pattern of primary production (Fig. 15.25). It is therefore essential to understand the factors that control the amount of primary production by phytoplankton.

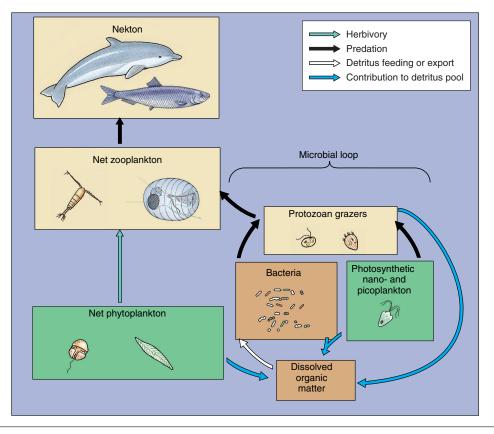
Phytoplankton need two main things to perform photosynthesis. First, they need sunlight, the ultimate source of energy for the ecosystem. Second, they need a supply of essential nutrients. Without sunlight and nutrients, phytoplankton cannot grow and produce the food that fuels the food web.

**Viruses** Particles composed of nucleic acids and proteins that are not usually considered to be alive.

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**FIGURE 15.24** An updated view of epipelagic food webs. The left side of the diagram shows the flow of energy from the net phytoplankton to the nekton. This part of epipelagic food webs has been known for decades. The right side of the diagram shows the more recently discovered microbial loop. Much of the flow from organisms into dissolved organic matter (blue arrows) is caused by viruses.

## Light Limitation

The epipelagic represents the sunlit layer of the ocean, but there still may not always be enough light for photosynthesis. In other words, primary production may be light-limited. There is no light at night, of course, so phytoplankton must get enough light during the day to allow them to grow. At high latitudes, phytoplankton may be light-limited during winter, when the days are short and the sunlight weak. In winter, phytoplankton at these latitudes store less energy in photosynthesis than they burn up in respiration. In tropical and subtropical waters, on the other hand, there is enough light to support photosynthesis throughout the year, at least at the surface.

The total primary production in the water column depends not only on the

intensity of light at the surface, but also on how far down the water column the light penetrates. If only a thin layer at the surface is sufficiently well lit for photosynthesis, there will not be as much production as if the photic zone were deep. The depth of the photic zone varies with the season, being deepest in summer. Photic zone depth also depends on the weather. On cloudy days, light does not penetrate as deeply as on bright, sunny days. Especially important is the amount of sediment and other material in the water. Light does not penetrate as deeply in dirty water, so the photic zone is not as deep as in clear water. The phytoplankton themselves affect the depth of the photic zone. Because they absorb light to perform photosynthesis, the phytoplankton cut down the amount of light available to deeper-living phytoplankton. This

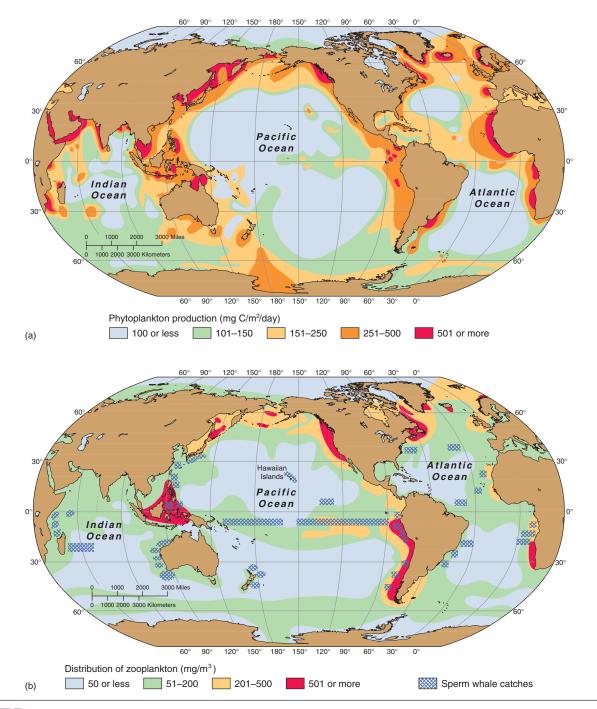
phenomenon, known as **self-shading**, is especially important in highly productive waters, which are rather murky because they contain so much plankton. Conversely, the barren waters of the **central gyres**, in the middle of the ocean basins (see Fig. 3.19), are incredibly clear.

## Nutrients

Nutrients, especially nitrogen, iron, and phosphorus, play a major part in controlling primary production. Even with plenty of light, plants cannot perform photosynthesis if there are not enough nutrients, that is, if primary production becomes **nutrient-limited**. Over most of the ocean the nutrient in shortest supply, that is, the **limiting nutrient**, is nitrogen. **Nitrate (NO<sub>3</sub><sup>-1</sup>)** is the most important source of nitrogen.

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**FIGURE 15.25** (a) The distribution of primary productivity in the oceans. Note the relationship of productivity to current and upwelling systems. Because primary production is the base of the food web, this pattern is reflected at higher levels; for example, in the distribution of zooplankton (b) and of sperm whales, as indicated by whale catches from 1760 to 1926. Some areas with low primary production, such as the Hawaiian Islands, show high catches because of whale migration and the proximity to land bases.

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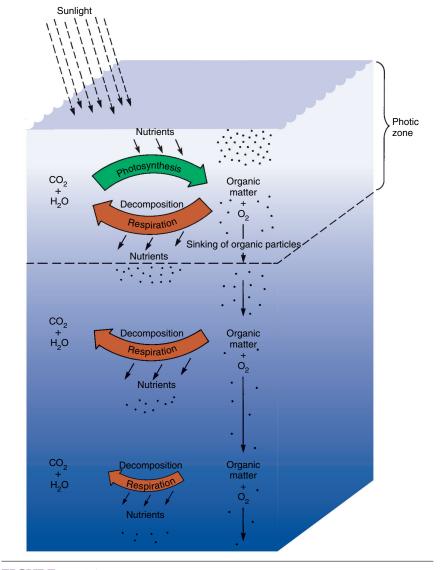
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Large areas of the open ocean, including the Southern Ocean (see Fig. 2.2) and the equatorial Pacific, have sufficient nitrate and instead are limited by iron. This has been demonstrated in dramatic experiments where phytoplankton grow explosively after iron has been added, becoming so abundant that they turn the water pea-soup green. There is a highly controversial proposal to reverse global warming by fertilizing these parts of the ocean with iron, so that the resulting huge phytoplankton blooms would remove carbon dioxide (CO<sub>2</sub>) from the atmosphere (see "Living in a Greenhouse: Our Warming Earth," p. 410). Fertilizing the ocean with iron is more practical than using nitrate because phytoplankton use iron in much smaller amounts. This means that adding relatively small quantities in the right places can greatly stimulate primary production. The possible consequences of this "geoengineering" can only be guessed at, and the risks to the planet are immense.

**Phosphate (PO** $_4^{-3}$ ), a source of phosphorus, and various other nutrients also limit phytoplankton growth in some places or for some groups of organisms. The supply of silicon sometimes limits diatom growth, for example.

Some cyanobacteria can fix free nitrogen  $(N_2)$  and are occasionally a significant source of nitrogen in tropical waters. *Trichodesmium*, one such cyanobacterium, sometimes forms red tides. The vast majority of nutrients in the epipelagic, however, are recycled (see Fig. 10.18). They are used again and again in the cycle of photosynthesis and decomposition. The cycle begins when dissolved nutrients are incorporated into living organic matter by phytoplankton. Later, when the living material dies, the nutrients are **regenerated**, or released, as bacteria decompose the material.

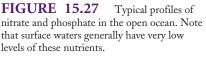
The dependence on recycled nutrients profoundly affects production in the epipelagic. Much of the organic material produced by phytoplankton eventually ends up as detritus: fecal pellets, dead bodies, marine snow, and other organic particles. These organic particles tend to sink, and many sink out of the epipelagic into deeper waters before they break

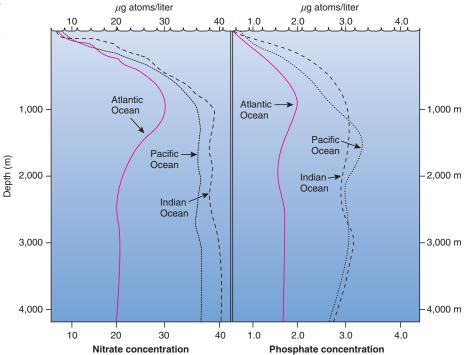


**FIGURE 15.26** The amount of nutrients at different depths is controlled by photosynthesis, respiration, and the sinking of organic particles. During primary production, dissolved nutrients are removed from the water and incorporated into organic matter. Respiration, in this case mainly by bacterial decay, breaks down the organic matter and regenerates the nutrients. The uptake of nutrients can occur only at the surface, where there is light. Because organic particles sink, however, much of the regeneration occurs below the photic zone. This process strips nutrients from the surface layer and carries them into deeper water.

down and decay. The nutrients they contain are released below the photic zone (Fig. 15.26). The net result of this process is that nutrients are removed from the surface and carried to the dark, cold waters below. Thus, surface waters are usually depleted in nutrients, and phytoplankton growth in the epipelagic is often nutrient-limited. Deep water, on the other hand, is usually nutrient-rich, but there is not enough light for photosynthesis and the nutrients cannot be used in primary production. The general nutrient profiles shown in Figure 15.27 are characteristic of most of the pelagic realm.

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Because many organic particles sink out of the epipelagic before the nutrients they contain are regenerated, surface waters are poor in nutrients, and phytoplankton growth is nutrientlimited. Deep waters are high in nutrients because of the rain of organic particles from the surface.

The phytoplankton that support epipelagic food webs, then, have a problem: At the surface there is sunlight but hardly any nutrients, whereas in deep water there are plenty of nutrients but not enough light. Coastal phytoplankton have it somewhat easier than oceanic forms. Coastal areas are relatively shallow, so the bottom traps sinking organic particles and some of the regenerated nutrients are returned to the water column. This is one reason why coastal waters are highly productive. Another reason is that rivers bring in fresh nutrients from land. Even so, coastal waters may have very low surface concentrations of nitrate, phosphate, and other nutrients.

#### •

Coastal waters are usually highly productive because the shallow bottom prevents organic particles and the nutrients they contain from sinking out of the photic zone and because rivers bring in additional nutrients.

For primary production to occur in oceanic areas, the nutrients contained in the deep water must somehow get to the surface. The only effective way for this to happen is for the water itself to move to the surface, carrying the nutrients along with it. This sounds simple enough, but it occurs only at certain times and places. The ocean is usually stratified; that is, the warm surface layers float on the denser water below (see "The Three-Layered Ocean," p. 64). A thermocline, a zone of transition, lies between the warmer, less dense layer on the surface and the colder, denser layer below. Just as energy is needed to push a cork below the surface or lift a weight up from the bottom, it takes energy to push surface water down across the thermocline into the denser water below, mixing it with the deep water, or to bring the dense, nutrient-rich deep water to the surface. Much of the time this simply does not happen, and surface production is often nutrient-limited.

## Seasonal Patterns

One way that deep-water nutrients get to the surface is for the water column to mix, just as shaking a bottle of salad dressing disperses the vinegar (which originally sat on the bottom below the oil) throughout the bottle. On the continental shelf, strong wind and waves may mix the water column all the way to the bottom. Often, however, wind and waves do not mix the water deeply enough to bring nutrients to the surface, especially in the open ocean.

If the surface water gets more dense, however, it loses its tendency to float. In the ocean, this happens at high latitudes when winter cold and winds cool the surface water, making it denser. If the surface water gets denser than the water below, **overturn** occurs (see Fig. 3.32). The thermocline breaks down, the surface water sinks, and nutrient-rich deep water is mixed up to the surface. Overturn depends on very cold conditions and is not usually widespread except in polar waters. Even in the absence of overturn, however, surface cooling can promote mixing. Since the cooler surface water

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becomes less dense, less energy is needed to mix it with the deep water. The mixing of deep nutrients to the surface is assisted by winter storms, which bring strong winds and large waves. Because of overturn and mixing during the winter, polar and temperate waters are highly productive (Fig. 15.25).

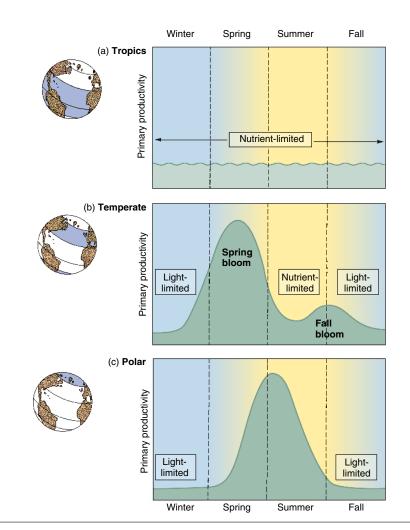
Oceanic waters at high latitudes are highly productive because winter overturn and mixing bring nutrient-rich deep water to the surface.

The productivity figures in Figure 15.25 and Table 10.1 (p. 228) refer to total production during the entire year. This obscures the fact that primary production may vary over the course of the year. In warm temperate and tropical waters such seasonal variation is relatively small. The water column remains stable throughout the year, restricting the transport of deep nutrients up into the photic zone. For this reason, most tropical waters have low but fairly constant levels of production throughout the year (Fig. 15.28*a*).

In temperate waters the effects of the seasons are profound. Overturn and mixing during the winter bring large amounts of nutrients to the surface. The phytoplankton are light-limited in winter, however, and unable to use the nutrients in photosynthesis. Primary production during winter months, therefore, is low at temperate latitudes (Fig. 15.28*b*).

When spring comes, the days get longer and the sunshine becomes more intense. Light is no longer limiting, and there are plenty of nutrients in the surface water because of overturn and mixing during the preceding winter. This combination—sufficient amounts of both light and nutrients—provides ideal conditions for phytoplankton and produces a period of rapid growth called the **spring bloom** (Fig. 15.28*b*). In many temperate areas the spring bloom represents most of the primary production for the entire year.

As the spring bloom develops, two things occur, neither beneficial for phytoplankton growth. First, the increase in sunlight warms the surface water, making it less dense. This increases the stability of the water column, eliminating overturn and greatly reducing the mixing of nutrient-rich deep water to the sur-



**FIGURE 15.28** Generalized seasonal cycles of primary productivity (mg  $C/m^2/day$ ) in (*a*) tropical, (*b*) temperate, and (*c*) polar waters.

face. Second, the phytoplankton rapidly use up nutrients as they photosynthesize and grow. Thus, nutrients are removed from the water at the same time that the supply is blocked. The amount of available nutrients in the water falls, and the phytoplankton become nutrient-limited. Nitrate is usually the nutrient that runs out first.

During most of the summer, primary production is nutrient-limited. The level of production depends on nutrient recycling and the new input of nutrients. If the water column never becomes very stable, some mixing and therefore some production takes place. If the surface water warms considerably and the water column becomes stratified, the input of nutrients by mixing is almost nil and primary production falls. Temperate waters generally have low productivity during the summer months because of stratification.

Production in the autumn depends largely on which comes first: the short days and weak sunlight that bring light limitation, or surface cooling and storms, which increase the mixing of nutrients. If the days are cool and sunny, for example, a strong wind can mix up nutrients while the phytoplankton still have enough light to perform photosynthesis. If so, there will be a burst of production known as the **fall bloom** (Fig. 15.28*b*). If warm, mild conditions persist late into the fall Castro–Huber: Marine Biology, Fourth Edition

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the phytoplankton become light-limited before overturn and mixing begin. Even though production at high latitudes is light-limited during the winter and nutrient-limited during the summer, there is enough production during blooms to give these waters a high total for the year (Fig. 15.25).

At high latitudes, primary production shows a seasonal cycle. During winter production is light-limited, but overturn and wind mixing bring nutrients to the surface. In spring, increased sunlight allows the phytoplankton to use the nutrients and a spring bloom occurs. During summer production is nutrient-limited because the phytoplankton use up the nutrients and stratification prevents mixing. A fall bloom occurs if stratification breaks down while there is enough light for photosynthesis.

Cold polar waters may not become stratified at all and may continue to produce at very high levels throughout the short summer when the sun shines most of the day (Fig. 15.28c). Primary production falls as the days shorten and is greatly reduced during the long winter months. Polar waters, which are not nutrient-limited during the summer, can be extremely productive, as is true around Antarctica (see Table 10.1, p. 228). The Arctic Ocean, on the other hand, lies at such a high latitude and is so extensively covered by ice that it is generally lightlimited and unproductive in spite of overturn and mixing.

## Upwelling and Productivity

Overturn and mixing caused by the cooling of surface waters are not the only processes that transport nutrients up into the photic zone. At certain times and places large amounts of nutrient-rich deep water move up to the surface. This phenomenon, known as **upwelling**, is caused indirectly by the **Coriolis effect**.

The water column can be thought of as a column of thin layers, almost like a stack of paper. The wind pushes the top layer, which begins to move. Because of the Coriolis effect, this uppermost layer of water moves  $45^{\circ}$  to the right of the wind direction in the Northern Hemisphere or to the left in the Southern Hemisphere (see "Surface Currents," **FIGURE 15.29** When a steady wind blows over the sea surface, the uppermost layer moves at 45° from the wind direction. Each deeper layer moves farther to the right in the Northern Hemisphere, shown here, or to the left in the Southern Hemisphere. When the direction of the current at each depth is plotted, the result is a spiral, called the Ekman spiral. The net result of this process is that the affected layer of water, called the Ekman layer, is transported at right angles to the wind direction (also see Fig. 3.18).

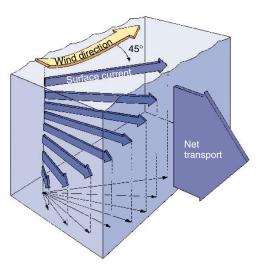
p. 53). The top layer pushes on the layer below, and again the Coriolis effect comes into play: The second layer moves not in the same direction as the top one, but slightly to the right, and slightly slower. This process passes down through the water column, each layer being pushed by the sheet above and pushing the one below. The direction that the water moves changes down the water column in a spiral (Fig. 15.29), called the **Ekman spiral** after the Swedish oceanographer who discovered it.

The effect of the wind decreases with depth, so that progressively deeper layers move slower and slower. Eventually, at a depth of at most a few hundred meters, the wind is not felt at all. The upper part of the water column that is affected by the wind is called the **Ekman layer**. Though each microlayer moves in a different direction, taken as a whole the Ekman layer moves at 90° from the wind direction. This process is called **Ekman transport**.

Winds blowing over the sea surface produce Ekman transport, in which the upper part of the water column moves perpendicular to the wind direction, to the right in the Northern Hemisphere and the left in the Southern Hemisphere.

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In coastal waters Ekman transport can produce extremely intense upwelling. In some places, mainly the eastern sides of the ocean basins, prevailing winds



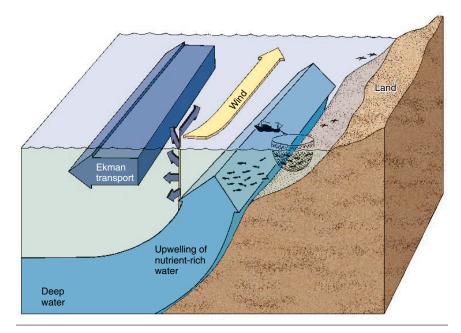
blow parallel to the coast so that Ekman transport carries the surface layer offshore. Cold deep water moves up to replace it (Fig. 15.30), producing intense **coastal upwelling.** Coastal upwelling carries huge amounts of nutrients into the photic zone, and major coastal upwelling areas (Fig. 15.31) are among the most productive waters of the epipelagic (Fig. 15.25). These coastal areas are therefore among the sea's richest fishing grounds (see Fig. 17.4).

On some coasts, like the Pacific coast of South America, upwelling is fairly steady and takes place over a large geographic area. On other coasts, like that of California, upwelling tends to occur as localized, short-lived events (Fig. 15.32). If the wind is strong for a few days, strong upwelling occurs, only to fade away when the wind dies and spring up somewhere else. Even on the Pacific coast of South America, upwelling is usually most intense in small, localized patches.

**Coriolis Effect** As a result of the earth's rotation, anything that moves large distances on the earth's surface tends to bend to the right in the Northern Hemisphere and to the left in the Southern Hemisphere.

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**FIGURE 15.30** When prevailing winds blow in the right direction along the coast, Ekman transport carries surface water offshore. Deep water rises into the photic zone, carrying nutrients with it. This is called coastal upwelling. Is the example in this figure from the Northern or Southern Hemisphere?

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Upwelling also tends to be seasonal, occurring mainly during the time of year when winds are strong and blow in the right direction along the coast. Such seasonality is most pronounced on the coast of Somalia, in eastern Africa (Fig. 15.31). This area is dominated by **monsoons**, strong winds that blow northward in summer and southward in winter. The summer monsoon causes very intense coastal upwelling, which dies when the winds change to the winter monsoon. When the upwelling stops, production falls dramatically.

Coastal winds are not the only source of upwelling. The Coriolis effect also produces **equatorial upwelling**, especially in the Pacific. Note that the direction of the Coriolis effect changes from right to left at the Equator. Thus, the north equatorial currents transport surface water to the right (north), whereas the south equatorial currents transport water to the left (south; Fig. 15.33). In equatorial regions the sea surface is being pulled apart, or diverging, and deep water moves up to

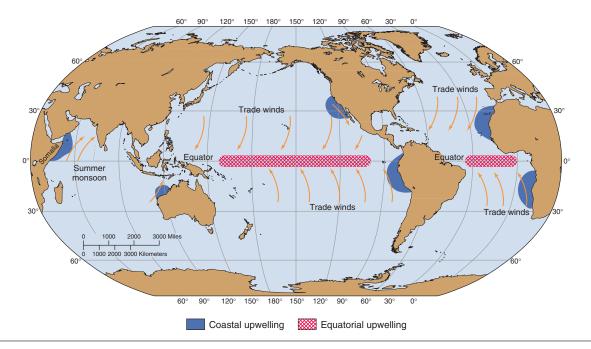
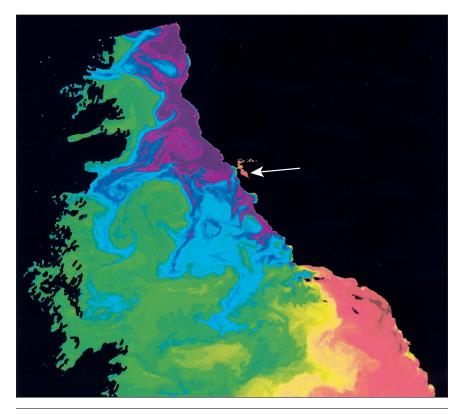
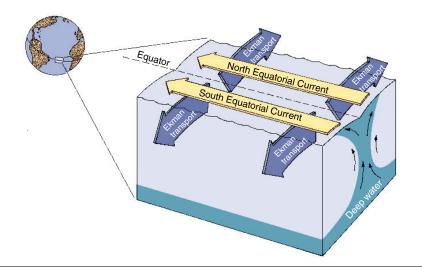


FIGURE 15.31 The major coastal upwelling areas of the world in relation to the prevailing winds. These areas are among the most productive parts of the ocean (see Fig. 15.25).



**FIGURE 15.32** This satellite image shows summer upwelling along the California and southern Oregon coast. The red area in the lower right is warm surface water off Southern California. The purple water to the north is very cold deep water that has upwelled along the coast. Water farther offshore (green) is warmer. The small red patch near the center of the image (arrow) is San Francisco Bay. The black area to the left was obscured by clouds from the satellite's view and the black area on the right is land.



**FIGURE 15.33** The Coriolis effect influences the equatorial currents differently on opposite sides of the equator. Surface water therefore moves away from the Equator. To replace it, deep water moves up into the sunlit zone. This is called equatorial upwelling (see Fig. 15.25).

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fill the void. Equatorial upwelling is not as intense as coastal upwelling, but it still raises primary production significantly and occurs over much larger areas.

Upwelling brings nutrients to the surface and results in high primary production. Coastal upwelling is very intense. It occurs when winds cause the Ekman transport of surface water offshore. Equatorial upwelling is caused by the divergence of equatorial surface currents.

## Geographic Patterns

Water depth and temperature, prevailing winds, and surface currents all affect the ocean's productivity, as we have seen in the previous sections. The geographic distribution of productivity (Fig. 15.25) reflects these factors. Coastal waters are highly productive because the shallow bottom prevents nutrients from sinking out of the photic zone and because wind and waves mix the water column. Coastal areas that experience upwelling are especially productive. Equatorial waters, too, are productive because of upwelling, but not as productive as coastal upwelling zones. Polar and cold temperate regions have high productivity because overturn and upwelling bring nutrients up into the sunlit layer.

None of the processes that bring nutrients to the surface operate in the vast central gyres. These lie in relatively warm latitudes, so the surface waters never cool enough for overturn or mixing. Far from both the coast and the equatorial currents, the central gyres never experience upwelling either. The gyre regions are permanently limited by nutrients; with the exception of the light-limited Arctic Ocean, they have the lowest productivity in the epipelagic. In fact, the central gyres are among the least productive ecosystems on earth (see Table 10.1, p. 228).

# The El Niño—Southern Oscillation Phenomenon

The interplay of winds, currents, and upwelling affects not only the ocean's primary production, but fisheries, climate, and ultimately human welfare. This is brought home most strongly

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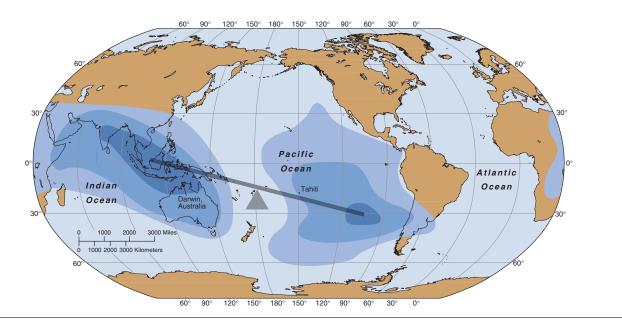


FIGURE 15.34 In the Southern Oscillation, atmospheric pressure "seesaws" between two gigantic systems half a world apart. When the pressure is unusually high in the western Pacific, it tends to be unusually low over the Indian Ocean, and vice versa. The shaded areas represent the linked zones of atmospheric pressure.

when normal patterns suddenly change, as in the phenomenon known as the El Niño—Southern Oscillation (ENSO). In recent years ENSO, often simply called El Niño, has received widespread attention not only from marine scientists but also, because of its impact on humans, from economists, politicians, and the general public.

The term "El Niño" originally referred to a change in the surface currents along the coasts of Perú and Chile. For much of the year the winds along this coast blow from south to north, producing strong upwelling. The upwelling brings nutrients to the surface, making these waters one of the world's richest fishing grounds. Every year, usually in December, the trade winds slack off, upwelling decreases, and the water gets warmer. Local residents have been familiar with this event for centuries because it signals the end of the peak fishing season. Because this change in currents comes around Christmas, they called it El Niño, or "The Child." Every few years, however, the change is much more pronounced than usual. The surface water gets much warmer, and upwelling ceases completely. Primary production drops to

almost nothing, and the fishes that normally teem in these waters disappear. Fisheries along the Perú-Chile coast are devastated, and seabirds die in huge numbers (see "Of Fish and Seabirds, Fishers and Chickens," p. 393).

The "Southern Oscillation" part of ENSO has also been known for a long time. Like El Niño, the Southern Oscillation was first noted because of its impact on humans. People in India depend on the summer monsoon winds to bring rain for their crops. Sometimes the monsoons fail, producing famine and hardship. Beginning in 1904, a British administrator named Gilbert Walker set out to predict when the monsoons would fail by analyzing weather records from around the world. He never achieved his goal, but he did discover a major atmospheric phenomenon that he named the Southern Oscillation.

The Southern Oscillation refers to a long-distance linkage in atmospheric pressure, or barometric pressure as it is called in weather reports. When the pressure is high over the Pacific Ocean, it tends to be low over the Indian Ocean, and vice versa (Fig. 15.34). Over a period of months or years, the air pressure swings back and forth like a giant seesaw that extends halfway around the world. The changes in atmospheric pressure bring dramatic changes in wind and rainfall, including the failure of the summer monsoon.

In the late 1950s it became apparent that El Niño and the Southern Oscillation were two sides of the same coin: Instead of being isolated phenomena that take place in a particular region, they are part of a complex interaction of ocean and atmosphere that links the entire planet. El Niño corresponds closely to dramatic changes in the atmospheric Southern Oscillation. Scientists usually use the term "ENSO" to signify that El Niño and the Southern Oscillation are two aspects of the same global phenomenon.

When the strongest El Niño in at least a century occurred during 1982 and 1983, it became clear that El Niño has profound global effects on weather, wildlife, and society. The 1982–83 El Niño brought extreme weather to much of the planet—storms and floods in some places, in others drought, forest fires, and heat waves. These extreme conditions served to focus scientific and public attention on trying to understand and deal with El Niño.

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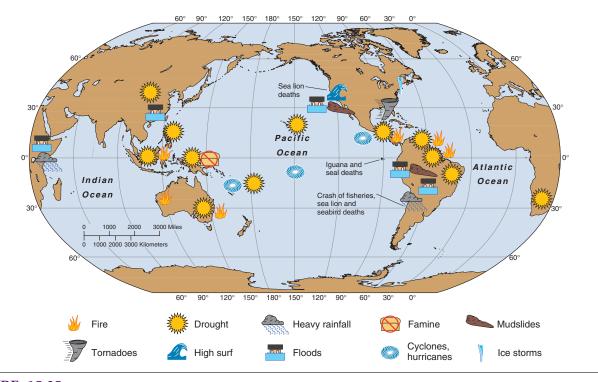


FIGURE 15.35 Some of the worldwide events linked to the 1997–98 El Niño event. This is just a sampling; many other places were affected.

In the ensuing years scientists carefully analyzed information from the 1982–83 El Niño. Milder El Niño events followed in 1986–87 and 1991–95, providing additional information and allowing scientists to test some of their hypotheses. Based on what they learned, scientists developed a Pacific-wide system of oceanographic and atmospheric monitoring equipment in the hope of getting early warning of new ENSO events. The system was soon put to the test. In late 1996 there were early signs, and by early 1997 the prediction was official: Another El Niño was on its way.

The prediction turned out to be accurate, with a vengeance. The 1997–98 El Niño was even stronger than the 1982–83 El Niño, and arguably the strongest in history. Its severity caught even the scientists who predicted it by surprise, and the devastating effects were felt over much of the globe (Fig. 15.35). In Perú, Chile, and Ecuador the 1997–98 El Niño brought not only a failure to fisheries but torrential rain and flooding. Southern California, parts of East Africa,

and southern China also suffered severe floods, bringing devastation and in some places disease. At the other extreme, Indonesia, New Guinea, Australia, southern Africa, Central America, and the Amazon basin suffered droughts. In some places the opposing effects of flooding and drought occurred over very short distances. Bolivia, for example, had drought in highland areas, but floods in the lowlands. The inland areas of southern and central Mexico were also afflicted by drought, but the Pacific coast was lashed by hurricanes. The Caribbean and southeastern United States enjoyed a mild hurricane season because El Niño caused changes in jet stream winds, as in past El Niño's. The 1997-98 El Niño, however, brought such drastic weather changes that swarms of killer tornados struck central Florida, where they are usually uncommon. Worldwide, several thousand people at least were killed in floods and storms.

El Niño is also blamed for many secondary effects. Crop and livestock losses were enormous, bringing hardship to farmers, especially in poorer countries, and in some places famine. In financial terms the losses amounted to hundreds of millions of dollars, and financial markets were affected widely as prices rose because of reduced supply. The fisheries crash in Perú and Chile had similar effects: Much of the catch is processed into animal food and farmers as far away as Ireland faced higher feed prices. Fires, often lit by farmers using the opportunity to clear land, raged out of control in drought-stricken Indonesia and the Amazon basin. Thousands of square miles of rain forest were destroyed. The fires in Indonesia were so bad that much of Southeast Asia endured months of haze and air pollution, and an accompanying increase in respiratory ailments. The thick smoke was even responsible for several plane crashes. Mass coral bleaching occurred on many reefs around the world (see "Conditions for Reef Growth," p. 302).

Disease outbreaks from water contamination sometimes followed storms and floods. Warmer temperatures led to increases in mosquito-borne diseases such

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as malaria, encephalitis, and dengue fever. In North America, outbreaks of bubonic plague and an often fatal respiratory disease known as hantavirus are associated with severe El Niños. This is because the growth in vegetation after the high rainfall provides more food for rats and mice, which spread the diseases. There were even more unusual problems. After its floods were over, for example, Kenya suffered a plague of a kind of beetle that, when crushed, releases a poison that causes burning, itching, and blindness.

The effects of El Niño are not necessarily all bad, or at least not bad for everyone. Cyclone activity was down in Hong Kong and the Philippines, like hurricanes in the Caribbean. Farmers lucky enough to escape El Niño's wrath enjoyed higher prices for their crops. In Chile and the southwestern United States, heavy rains filled dams and replenished water supplies. Heavy snowfall brought great skiing, to the delight of skiers and profit of resort owners and employees. Deserts bloomed when the rains brought spectacular displays of wildflowers. Indeed, El Niño's periodic soakings may be a vital part of desert ecology. El Niño brought a relatively mild winter to much of the northern United States and Europe, and millions of dollars of savings on heating bills. While the normal fisheries in Perú

and Chile crash during severe El Niño events, warm-water species like dolphin fish and tunas appear in record numbers. Salmon fishers in Oregon even caught striped marlin, normally confined to the subtropics.

The effects of ENSO are harmful not so much in and of themselves as because they are extreme changes in the normal pattern. Heavy rains where such rains are rare may cause floods, while the lack of heavy rain causes drought and famine in places that depend on it. Indeed, scientists now realize that El Niño is not really an abnormal occurrence, but simply one extreme of a regular weather cycle. La Niña, the other extreme, brings weather conditions that are roughly the opposite of El Niño's. Places that experience drought during El Niño, for example, can expect wet weather during La Niña years. After a mild hurricane season during the 1997-98 El Niño, Central America and the Caribbean suffered devastating hurricanes in the La Niña that followed. Another major cycle, the North Atlantic Oscillation, has been found to profoundly influence Europe's weather.

Estimates of loss and damages from the record-breaking El Niño of 1997–98 range upward of \$20 billion, but it could have been much worse. Because scientists could predict El Niño the world had advance warning and time to prepare. Authorities in many countries intensified their disaster preparedness efforts and built up food reserves. Industry and especially agriculture adjusted their planning. Cattle ranchers in Australia, for example, reduced their herds, cutting the losses from the subsequent drought. In southern Africa farmers cut back their normal crop of corn and planted more droughtresistant plants. Every El Niño is different, however, and in a given place the exact effects are hard to predict. In 1997-98, for example, authorities in parts of East Africa expected drought based on past El Niños. Instead, they had terrible floods. Nonetheless, the scientific ability to predict when El Niño is on the way has produced huge benefits for society.

As profound as the effects of El Niño are, it is important to recognize that not every unusual occurrence or spell of bad weather is caused by El Niño. During the 1997–98 event, some reports blamed El Niño not for anything to do with the weather, but for everything from political scandal to the Super Bowl winner! Weather patterns are naturally variable, and unusual weather sometimes happens whether there is an El Niño around or not. A little bit of skepticism wouldn't hurt the next time you hear that something must be caused by El Niño. III. Structure and Function 15. Life of Marine Ecosystems

15. Life Near the Surface

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# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

# **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. Plankton are unable to swim effectively and drift about at the mercy of the currents. You might think that the currents would scatter planktonic organisms throughout the oceans, but many species are restricted to particular regions. What mechanisms might allow a species to maintain its characteristic distribution?
- 2. Spiny species of diatoms are found both in warm subtropical waters as well as in colder areas. Because warm water is less dense than cold water, would you predict any differences between the spines of warm-water and cold-water individuals? Why?

# For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol ., and will contain live links when you visit this page in the Online Learning Center.

# **General Interest**

- Johnsen, S., 2000. Transparent animals. *Scientific American*, vol. 282, no. 2, February, pp. 80–89. Becoming invisible requires a bag of tricks.
- Leslie, M., 2001. Tales of the sea. *New Scientist*, vol. 169, issue 2275, 27 January, pp. 32–35. Biological detectives deduce which unseen marine microbes live in the ocean, and how, from fragments of their genetic material.
- Morton, O., 1998. The storm in the machine. *New Scientist*, vol. 157, no. 2119, 31 January, pp. 22–27. The North Atlantic Oscillation—sometimes called El Niño's cousin doesn't pack quite the punch of El Niño. Nonetheless, it is a dominant influence on Europe's climate and may even have changed human history.
- Schueller, G., 1999. Testing the waters. *New Scientist*, vol. 164, no. 2206, 2 October, pp. 34–37. An entrepreneur wants to reap a fisheries bounty by fertilizing the equatorial Pacific with iron. Is it worth the risk?

- Whynott, D., 1999. The most expensive fish in the sea. *Discover*, vol, 20, no. 4, April, pp. 80–85. Sushi lovers pay extraordinary prices for bluefin tuna. The source of these expensive meals has a fascinating biology.
- Whynott, D., 2001. Something fishy about this robot. *Smithsonian*, vol. 31, no. 5, August, pp. 54–60. In the hope of designing more efficient vessels, scientists and engineers
- try to copy the bluefin tuna. Wray, G. A., 2001. A world apart. *Natural History*, vol. 110, no. 2, March, pp. 52–63. The larvae of marine invertebrates have many adaptations for life in the plankton.
- Zimmer, C., 1999. The El Niño factor. *Discover*, vol. 20, no. 1, January, pp. 98–104. A survey of the global effects of El Niño and what lies ahead.

# In Depth

- Hutchins, D. A., 1995. Iron and the marine phytoplankton community. *Progress in Phycological Research*, vol. 11, pp. 1–48.
- Kiorboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Advances in Marine Biology*, vol. 29, pp. 1–72.
- Mauchline, J., 1998. The biology of calanoid copepods. *Advances in Marine Biology*, vol. 33, pp. 1–710.
- Rigby, S. and C. V. Milsom, 2000. Origins, evolution, and diversification of zooplankton. *Annual Review of Ecology and Systematics*, vol. 31, pp. 293–313.
- Wilhelm, S. W. and C. A. Suttle, 1999. Viruses and nutrient cycles in the sea. *BioScience*, vol. 49, no. 10, October, pp. 781–788.

# See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

- Moon jellyfish (Ripley's Aquarium of the Smokies, Tennessee)
- Thimble jellyfish (Cayman Islands)

# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Photosynthetic marine organisms
- Adaptations for planktonic life
- Primary productivity
- Dinoflagellates

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www.mhhe.com/marinebiology

- Zooplankton
- Class Scyphozoa
- El Niño
- La Niña
- Food webs

# Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

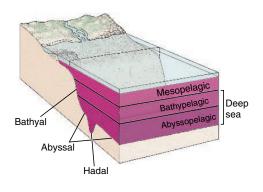
III. Structure and Function 16. The Ocean Depths of Marine Ecosystems

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# The Ocean Depths







Mesopelagic pteropod (Clio polita).

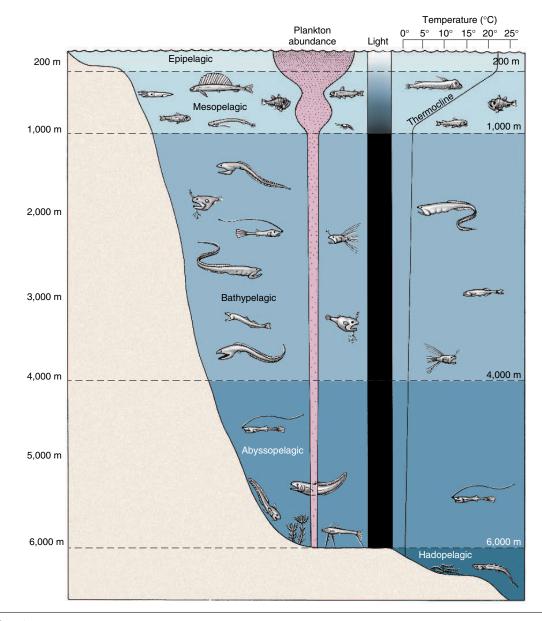
Inner space" it has been called. Dark and cold, inhabited by bizarre, fearsome-looking creatures, it *is* a little reminiscent of the outer space of science fiction movies. Like outer space, humans can venture into this mysterious realm only with the aid of elaborate, specially designed craft. Even then there is an element of risk. But "inner space" is here on earth; it consists of the waters of the sea that lie below the sunlit surface layer. The ocean depths are the least known of all our planet's environments. The ocean depths include a number of distinct habitats. Immediately below the epipelagic lies the **mesopelagic**, or "middle pelagic," **zone** (Fig. 16.1). The epipelagic is roughly equivalent to the **photic zone**, the surface layer down to 150 to 200 m (500 to 650 ft) where there is enough light to support primary production by photosynthesis. In the mesopelagic there is still some dim light, but not enough for photosynthesis. Below the mesopelagic there is no sunlight at all. This inky darkness is the world of the **deep sea**. The term "deep sea" is sometimes used to include the mesopelagic zone, but we use it only for the perpetually dark waters below the mesopelagic.

The waters below the epipelagic can be divided into the mesopelagic zone, where there is some light but not enough for primary production, and the deep sea, where there is no sunlight at all.

Several different habitats are discussed in Chapter 16; each supports a distinct community of organisms. These

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## www.mhhe.com/marinebiology



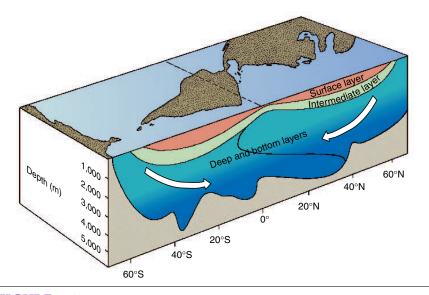


communities share one important feature: the lack of **primary production** of food by **photosynthesis**. Without primary production to support the rest of the food web, most of the communities beneath the photic zone depend for food on organic material produced in the surface layers of the ocean. Some of this surface production sinks into the dark waters below. Without a steady supply of food from above, there could be little life

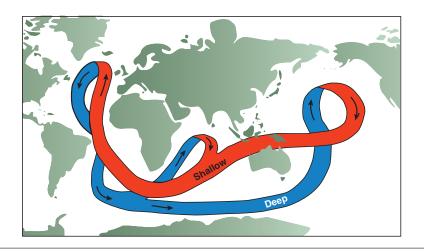
below the sunlit layer of the sea. The only known exception to this principle is discussed in the section "Hot Springs, Cold Seeps, and Dead Bodies" (p. 377).

Because of the dependence on surface production for food, life is much less abundant below the photic zone than in the sunlit surface layer. Most food particles get eaten before they sink into deeper water. With food in short supply, pelagic organisms become more and more scarce at greater depths. There are typically 5 or 10 times fewer organisms at 500 m (1,600 ft), for example, than there are at the surface, and perhaps 10 times fewer again at 4,000 m (13,000 ft).

Deep-water organisms depend on the surface not only for food, but also for oxygen (O<sub>2</sub>). If the ocean were stagnant, the oxygen below the surface would be quickly used up by **respiration** and animal life would be impossible. Fortunately,



**FIGURE 16.2** The deep-water masses in the ocean originate at the surface in the extreme North and South Atlantic, then sink and spread out along the bottom. Water that originates in the Atlantic also spreads into the other ocean basins (see Fig. 16.3).



**FIGURE 16.3** The deep circulation of the oceans is part of a global pattern known as the great ocean conveyor. This circulation constantly replenishes the oxygen supply to the ocean depths. Small variations in the conveyor circulation are thought to produce dramatic changes in weather patterns around the world. Larger changes may even bring on ice ages.

however, there is gradual **thermohaline circulation** to even the deepest parts of the sea, bringing life-giving oxygen. To sink all the way to the deep sea, oxygenrich surface water must become very dense, that is, cold and relatively salty (see "Vertical Motion and the Three-Layered Ocean," p. 63). This takes place at only a few locations and only occasionally. The main places where this surface **overturn**  reaches the bottom are in the Atlantic, south of Greenland and just north of Antarctica (Fig. 16.2). After sinking, the water spreads through the Atlantic and into the other ocean basins. The water eventually rises to the surface and flows back to the Atlantic, where the cycle begins again (Fig. 16.3). This global circulation pattern, called the **great ocean conveyor**, is thought to play a central role in regulating the earth's climate. Furthermore, it constantly replenishes the supply of oxygen to the deep sea. Oxygen may become depleted in some places, but by and large the ocean depths have plenty of oxygen to support life.

## THE TWILIGHT WORLD

The mesopelagic is a world of twilight. In the upper part of the mesopelagic the dim light during the day is enough to see by, perhaps even enough to read a newspaper. There is not, however, enough light to support phytoplankton. As depth increases, of course, the sea gets darker. Eventually, typically at a depth of about 1,000 m (3,300 ft), there is no light at all. The absence of light marks the bottom of the mesopelagic zone, which thus stretches from the bottom of the epipelagic, around 200 m (660 ft) deep, to about 1,000 m deep.

The mesopelagic zone extends from about 200 m to about 1,000 m deep.

**Primary Production** The conversion of carbon dioxide into organic matter by autotrophs, that is, the production of food.

Chapter 4, p. 73

**Photosynthesis**  $CO_2 + H_2O + sun$ energy  $\rightarrow$  glucose +  $O_2$ *Chapter 4, p. 71* 

**Respiration** glucose +  $O_2 \rightarrow CO_2$  +  $H_2O$  + energy

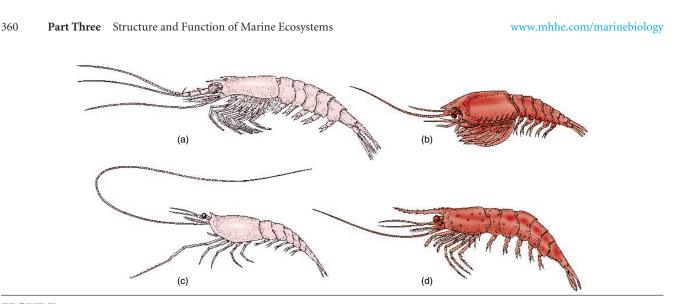
Chapter 4, p. 72

Thermohaline Circulation Ocean circulation that is driven by differences in water density, due to variations in water temperature and salinity, rather than by the wind or tides.

## Chapter 3, p. 64

**Overturn** The sinking of surface water caused by an increase in its density, which results from a decrease in temperature, an increase in salinity, or both.

Chapter 3, p. 64; Figure 3.32



**FIGURE 16.4** Some crustaceans that inhabit the mesopelagic zone include (*a*) krill (*Thysanopoda tricuspidata*), (*b*) mysid, or opossum, shrimps (*Gnathophausia ingens*), and true (decapod) shrimps like (*c*) Sergestes similis and (*d*) Systellaspis debilis.

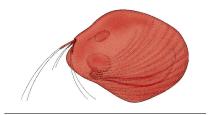
The temperature at a given depth in the mesopelagic generally varies much less than in the epipelagic. The mesopelagic, however, is the zone where the **main thermocline** occurs (Fig. 16.1), so organisms that move up and down in the water column encounter large changes in temperature. Mesopelagic organisms that stay at about the same depth experience more constant temperatures.

# The Animals of the Mesopelagic

Though phytoplankton and other photosynthetic organisms cannot live in the dim light, the mesopelagic supports a rich and varied community of animals, which are often called **midwater** animals.

## Zooplankton

The major groups of animals in the mesopelagic zooplankton are much the same as those in the epipelagic (see "The Organisms of the Epipelagic," p. 324). Krill (Fig. 16.4*a*) and copepods are generally dominant, as they are in surface waters. Several different kinds of shrimps (Fig. 16.4) are also common in the mesopelagic, relatively more so than in the epipelagic. Krill and most mesopelagic shrimps have a common



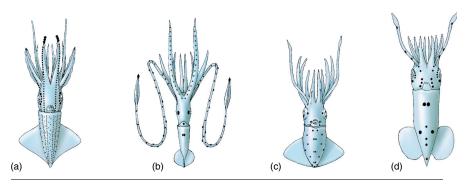
**FIGURE 16.5** A mesopelagic ostracod (*Gigantocypris*). This one is about 1 cm (1/2 in) long. Most ostracods are much smaller.

adaptation of midwater animals: **photophores**, or **light organs**, which are specialized structures that produce light. The function of this "living light," called **bioluminescence**, is discussed later (see "Bioluminescence," p. 365).

A group of crustaceans known as **ostracods** can be very abundant in the mesopelagic. Ostracods have a characteristic shell, or **carapace**, that makes them look like tiny clams with legs (Fig. 16.5). They are crustaceans, however, and unrelated to clams. Like copepods, most ostracods are small, usually only a few millimeters (1/8 in) long. One group (*Gigantocypris*), however, can reach 1 cm (1/2 in). Amphipods and other crustacean groups are also part of the midwater plankton. Arrow worms, or chaetognaths, are important midwater predators. At times they are among the most abundant components of the midwater zooplankton, especially in the upper parts of the mesopelagic. Jellyfishes, siphonophores, comb jellies, larvaceans, and pteropods are also common. Most of the other major groups that are part of the epipelagic zooplankton (see "The Zooplankton," p. 328) are also represented in the mesopelagic, though the particular species are usually different.

Squids (Fig. 16.6) are other prominent members of the midwater community. Some swim only weakly and are therefore considered planktonic, whereas strong-swimming squids are part of the nekton. Mesopelagic squids usually have photophores, which typically are arranged in a different pattern in each species. The vampire squid (Vampyroteuthis; Fig. 16.7) looks something like an octopus but is actually neither a squid nor an octopus. It is in its own separate group. Like true squids, the vampire squid has photophores. There are also a few species of octopuses in the mesopelagic zone. Bioluminescence is not as common in mesopelagic octopuses as in squids, but some species do have photophores. One species was recently discovered to have lightemitting suckers.

# Castro-Huber: MarineIII. Structure and Function16. The Ocean Depths© The McGraw-HillBiology, Fourth Editionof Marine EcosystemsCompanies, 2003



**FIGURE 16.6** Most mesopelagic squids have photophores (shown in black), usually arranged in a different pattern in each species. A few examples are (*a*) *Abraliopsis*, (*b*) *Chiroteuthis*, (*c*) *Thelidioteuthis*, and (*d*) *Pterygioteuthis*.

## Midwater Fishes

Nearly all mesopelagic fishes are quite small, about 2 to 10 cm (1 to 4 in) long, although a very few species get considerably larger. Bristlemouths (Fig. 16.8a) and lanternfishes (Fig. 16.8b) are by far the most abundant fishes in the mesopelagic. These two groups may account for 90% or more of the fishes collected by midwater trawls (Fig. 16.9). The bristlemouths are the most common of all. One species (Cy*clothone signata*) is the most abundant fish on earth, which is both surprising and impressive when you consider the huge schools of fishes like sardines and herrings that live in the epipelagic. Bristlemouths are named for their many sharp teeth. They have rows of photophores on their underside, or ventral surface.

Lanternfishes get their name from the rows of photophores that adorn their heads and bodies. Like squids, each species typically has a distinctive photophore pattern. Lanternfishes have blunt heads, relatively large mouths, and large eyes, probably an adaptation to help them see in the dim light. They are very general in their food habits, eating just about anything they can get down.

The most common mesopelagic, or midwater, organisms are krill, copepods, shrimps, and small fishes like bristlemouths and lanternfishes.

Bristlemouths and lanternfishes are the most numerous, but many other fishes live in the mesopelagic (Fig. 16.8). Marine hatchetfishes look somewhat like the unrelated freshwater hatchetfishes sold in pet shops, except for their large eyes and mouths and ventral photophores. Viperfishes, dragonfishes, barracudinas, sabertooth fishes, lancetfishes, snake mackerels, and cutlassfishes are all long, eel-like fishes with large mouths and eyes. Many of these fishes have photophores, usually in rows along the ventral surface. Most of them are less than 30 cm (about 1 ft) long, but there are a few exceptions. One of the lancetfishes (Alepisaurus ferox; Fig. 16.8f) grows to about 2 m (6.5 ft) and may be the largest mesopelagic fish. The black scabbard fish (Aphanopus carbo; Fig. 16.10), a kind of cutlassfish, can get well over 1 m (3.3 ft) long.

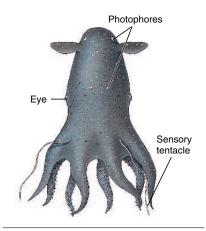
# Adaptations of Midwater Animals

By the standards of the lighted world, many of the animals that live below the photic zone seem bizarre indeed. Though

**Main Thermocline** The layer between about 200 and 1,000 m (650 and 3,300 ft) where the temperature drops rapidly as depth increases. This is a transition zone between the warm surface layers and the cold deep water.

Chapter 3, p. 65; Figure 3.31

Krill Planktonic, shrimplike crustaceans. *Chapter 7, p. 137* 



**FIGURE 16.7** The vampire squid (*Vampyroteuthis infernalis*) is not really a squid. It has arms like a true squid, but two of the arms are modified into long, retractable "feelers" instead of being used to capture prey as in squids. Vampire squid reach a length of only 20 cm (8 in).

they look strange to us, they are well adapted to their unique environment. Species from the same depth often have very similar characteristics even though they are unrelated. On the other hand, closely related species from different depths may differ markedly in appearance and other characteristics.

## Feeding and Food Webs

Most of the food produced in the epipelagic is used there; only about 20% of the surface primary production sinks to the mesopelagic. This means that the mesopelagic is chronically short of food, which is why there are fewer organisms in the mesopelagic than in the epipelagic. The abundance of midwater

| <b>Copepods</b> Tiny crustaceans that are often planktonic. |
|---|
| Chapter 7, p. 135   |
| Arrow Worms or  |
| Chaetognaths Small,   |
| worm-like predators   |
| with fins along the body                                    |
| and spines on the head.                                     |
| Chapter 7, p. 141   |
|   |

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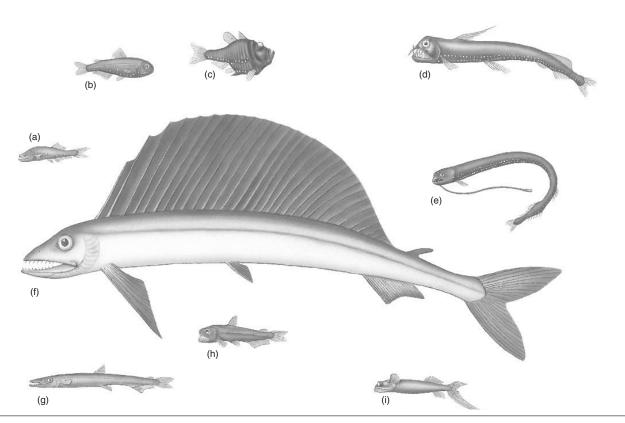


FIGURE 16.8 Some typical mesopelagic fishes: (a) bristlemouth (Cyclothone braueri), (b) lanternfish (Myctophum affine), (c) hatchetfish (Polyipnus laternatus), (d) Pacific viperfish (Chauliodus macouni), (e) dragonfish (Leptostomias gladiator), (f) longnose lancetfish (Alepisaurus ferox), (g) barracudina (Lestidium atlanticum), (b) sabertooth fish (Coccorella atrata), (i) giganturid (Gigantura vorax).





(b)

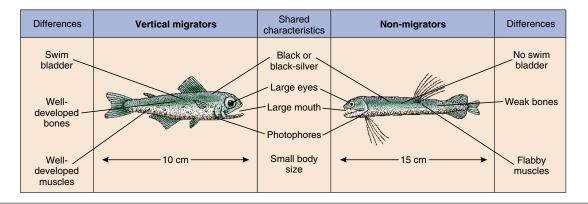
**FIGURE 16.9** Nets called rectangular midwater trawls are commonly used to collect mesopelagic organisms. The net can be opened and closed by remote control when it is at the desired depth. This prevents surface organisms from being caught while the net is being lowered and retrieved. In both (*a*) and (*b*) the mouth of the net is open.



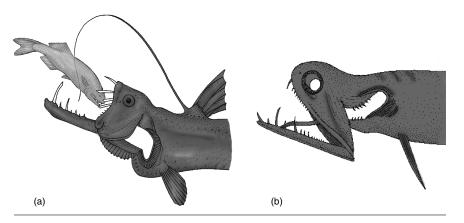
**FIGURE 16.10** A black scabbard fish (*Aphanopus carbo*) being sold by a Madeiran fisherman. The fish, known locally as *espada*, is a relatively rare example of a midwater fish that is caught for food.



#### Chapter 16 The Ocean Depths 363



**FIGURE 16.11** Some adaptations of typical mesopelagic fishes, including some differences between vertical migrators like lanternfishes (left) and non-migrators like dragonfishes (right). Compare these with the adaptations of epipelagic and deep-sea fishes shown in Figures 15.17 and 16.21.



**FIGURE 16.12** (a) The viperfish (Chauliodus) has hinged jaws that can accommodate large prey. (b) The rattrap fish (Malacosteus) has a similar jaw arrangement.

organisms in a particular geographic area is related to the productivity of the waters above. There is more mesopelagic life under highly productive surface waters than under areas with low primary production.

Many of the characteristics of midwater animals are directly related to the lack of food in the mesopelagic. The small size of midwater fishes, for example, is thought to be an adaptation to the limited food supply. Animals need a lot of food to grow large, so there may be an evolutionary advantage to limited growth and small size.

Midwater fishes usually have large mouths, and many have hinged, extendible jaws equipped with fearsome teeth (Figs. 16.11 and 16.12). Because

food is scarce below the photic zone, most fishes cannot afford to be picky. They usually have very broad diets and eat just about anything they can fit into their mouths. The large, protrusible jaws allow them to eat a wide range of prey. The advantage of this is that they don't have to pass up a potential meal because it is too large to eat. Some mesopelagic fishes can even eat prey larger than themselves! The long, sharp teeth help keep prey from escaping.

Common adaptations of midwater fishes include small size, large mouths, hinged, extendible jaws, needle-like teeth, and unspecialized diets. These adaptations result from the limited food supply in the mesopelagic.

Midwater animals fall into two major groups: those that stay in the mesopelagic and those that migrate to the surface at night. The non-migrators include a few species of small zooplankton, mainly copepods and krill, that filter out detritus and the small amount of phytoplankton that sinks out of the photic zone. The fecal pellets of epipelagic copepods and other surface grazers form an important part of the detritus eaten by mesopelagic filter feeders. These pellets sink much faster than individual phytoplankton cells, so they stand a better chance of making it to the mesopelagic before being eaten.

Most non-migrating midwater animals, however, are not zooplankton but fishes, shrimps, and squids. They are sitand-wait predators that lurk in the dim light, gulping down anything that comes within range. With food so hard to come by, these organisms have a number of adaptations that reduce their energy requirements. Instead of energy-consuming muscle, non-migrating midwater fishes have flabby, watery flesh. The amount of energy required to fill and regulate the swim bladder increases with depth

Detritus Particles of dead organic matter. Chapter 10, p. 224

Swim Bladder A gas-filled sac in the body cavity that helps bony fishes control their buoyancy.

Chapter 8, p. 159; Figure 8.12

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because of the increased water pressure, and most of non-migrating midwater fishes have lost the swim bladder as another energy-saving adaptation. To compensate for the loss of the swim bladder, they have developed soft, weak bones and lost defensive structures like spines and scales. These adaptations reduce weight and make them more neutrally buoyant, which allows them to float at a constant depth without wasting energy swimming. Since they don't swim much, they have no need for the streamlining that is so characteristic of epipelagic fishes.

#### Vertical Migration and the Deep Scattering Layer

Rather than staying put and waiting for food to fall from above, most mesopelagic organisms make **vertical migrations**. They swim up at night to feed in the rich surface layers and during the day descend to depths of several hundred meters or more. In the dim light they are probably relatively safe from predators. Some vertical migrators spend the day in a lethargic stupor, conserving energy until their next foray to the surface. Vertical migration is also seen in many zooplankton that live in the deeper parts of the epipelagic (see "Vertical Migration," p. 339).

Vertically migrating fishes differ in several important ways from those that stay in the mesopelagic (Fig. 16.11). Well-developed muscles and bones are needed to make the daily swim up and down the water column. These structures increase the weight of the fish, so these fishes have retained the swim bladder for buoyancy. As they move up and down, they experience dramatic changes in pressure. Vertically migrating fishes can rapidly adjust the volume of gas in the swim bladder to prevent it from collapsing or exploding when they change depth. They are also able to tolerate the temperature changes they experience as they move up and down across the thermocline.

Midwater animals that make vertical migrations have well-developed bones and muscles, wide temperature tolerances, and, in fishes, swim bladders. Non-migratory midwater fishes have soft bones and flabby muscles, and lack swim bladders.



**FIGURE 16.13** Many midwater fishes, like this bristlemouth, have tubular eyes that give them very acute upward vision (in some species the eyes point forward).

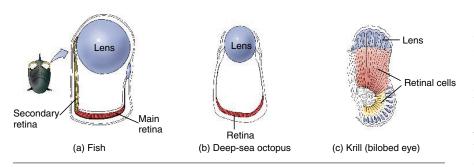
Vertical migration by mesopelagic animals was discovered during World War II, when sonar came into use. Sonar soundings regularly showed a series of sound-reflecting layers, or "false bottoms." The real bottom gives a sharp, clear echo, but these layers, collectively dubbed the deep scattering layer (DSL), give a soft, diffuse echo that makes a shadowy trace on sonar plots. During the day the DSL lies at depths of 300 to 500 m (1,000 to 1,600 ft), but at sunset it rises to the surface. The depth of the DSL is clearly related to light intensity: The DSL stays deeper when there is a full moon than on moonless nights and even moves up and down when clouds pass over the moon.

Net tows have shown that the DSL is composed of fishes—especially lanternfishes—krill, shrimps, copepods, jellyfishes, squids, and other midwater animals. Most of these organisms, though they are found within the DSL, do not contribute to its sound-reflecting properties. Because organisms are made mostly of water, sound passes through them much as it does through seawater, without bouncing off. Air pockets, however, reflect sound quite strongly. The echo of the DSL comes mostly from sound waves bouncing off the swim bladders of the vertically migrating fishes. The deep scattering layer (DSL) is a soundreflecting layer made up of vertically migrating midwater animals. Lanternfishes, krill, shrimps, copepods, jellyfishes, and squids are the dominant organisms of the DSL.

Vertical migration is important in transporting food into deep water. When lanternfishes, krill, and other animals return to the mesopelagic after stuffing themselves near the surface, they carry the products of surface production down with them. This greatly increases the food supply in the mesopelagic. Many non-migratory midwater predators feed heavily on vertically migrating species. Since migrators are more muscular than non-migrators, they provide a much more nutritious meal.

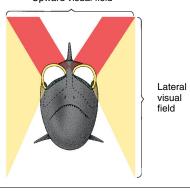
#### Sense Organs

To help them see in the dim light, midwater fishes characteristically have eyes that are not only large but unusually sensitive. Large, light-sensitive eyes also occur in squids, shrimps, and other groups. Some midwater fishes have developed **tubular eyes** (Fig. 16.13), a complex visual system that is almost like having two pairs of eyes. Tubular eyes give very acute vision in the direction that the eyes are pointed,



**FIGURE 16.14** (a) The tubular eye of a midwater fish (*Scopelarchus*). The retina is the part of the eye sensitive to light. The part of the retina at the bottom of the eye, colored red in the diagram, provides good upward vision. The part extending up the side of the eye, colored yellow, provides lateral vision (see Fig. 16.15), which is less acute. Eyes with a similar structure have evolved in (b) octopuses (*Amphitretus pelagicus*) and (c) krill (*Stylocheiron suhmii*).





**FIGURE 16.15** The field of vision of a midwater fish (*Scopelarchus*). The fish has two main visual fields corresponding to the two parts of the retina shown in Figure 16.14*a*.

either upward or forward, but are not good for lateral vision. To compensate, the **retina**, the light-sensitive part of the eye, extends partway up one side of the eye (Fig. 16.14*a*). This allows the fish to see to the side and below (Fig. 16.15). In normal eyes the retina lies only at the back of the eye.

Adaptations very similar to tubular eyes are found in at least one octopus (Amphitretus; Fig. 16.14b) and in the bilobed eyes of some krill (Stylocheiron; Figs. 16.14c and 16.16). One squid, Histioteuthis, has taken a different path to the same apparent end. One eye in these squids is much larger than the other. The squid floats in the water column with the large eye pointed upward and the small eye downward.



**FIGURE 16.16** A midwater krill (*Nematoscelis difficilis*) with bilobed eyes.

Many midwater animals have evolved large, light-sensitive eyes that provide good vision in dim light. Other adaptations include tubular eyes in fishes and bilobed eyes in krill.

#### Coloration and Body Shape

Like their epipelagic counterparts, mesopelagic predators rely heavily on vision. Because midwater prey cannot afford the energetic costs of fast swimming or heavy defensive spines and scales, camouflage is perhaps even more important than in the epipelagic. The basic strategies, however, are very similar: **countershading**, transparency, and reduction of the silhouette. There are many variations on these basic strategies, however, especially in relation to depth and light levels.

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Transparency is particularly common in the shallower and better-lit parts of the mesopelagic. Copepods, jellyfishes, shrimps, bristlemouth fishes, and other animals that live in the upper mesopelagic tend to be transparent, some almost completely so. Deeper in the mesopelagic, fishes tend to be more silvery, and in the deepest, darkest part, black. Zooplankton from the deeper parts of the mesopelagic are typically orange, red, or purple. These colors might be quite conspicuous at the surface, but colors change underwater (see "Transparency," p. 51). Our eyes see them as red at the surface because their skin absorbs most of the colors in sunlight but reflects the red. None of the red light in sunlight penetrates to mesopelagic depths, so the organisms appear an inconspicuous grey or black in their natural habitat.

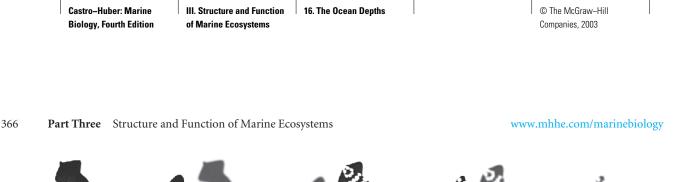
Mesopelagic fishes often have black backs and silvery sides, reminiscent of the countershading of epipelagic animals (see "Coloration and Camouflage," p. 337). In the mesopelagic, however, there is not enough light to reflect off the white or silver belly typical of epipelagic countershading and mask the animal's outline. Even a white object produces a silhouette in twilight. A silhouette makes the animal conspicuous and vulnerable to all those sharp eyes peering up from the depths. To reduce their silhouettes, some mesopelagic fishes, like hatchetfishes, have laterally compressed bodies. This reduces the size of the body outline whether the animal is viewed from above or below.

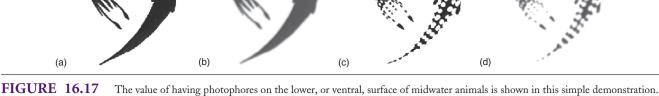
#### Bioluminescence

Most midwater animals have evolved a much more effective way to mask their silhouettes. Their bioluminescent photophores, found mostly on their undersides, produce light that breaks up the silhouette and helps the animal blend in

**Countershading** A pattern of coloration common in open-water nekton in which the back is black or dark blue and the underside white or silver.

Chapter 15, p. 337





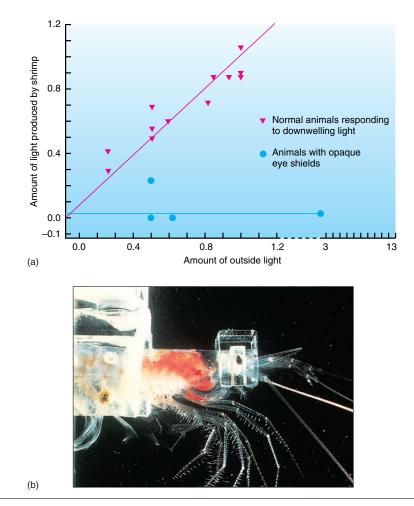
**FIGURE 10.17** The value of having photophores on the lower, or ventral, surface of midwater animals is shown in this simple demonstration. (a and b) Silhouettes of two midwater organisms as they would appear without photophores. (c and d) The same animals with the photophores in white to match the background. The photophores break up the silhouette, making the animal much less visible. This effect is more pronounced when the animals are a little out of focus (b and d), as they are when viewed through the water.

with the background light filtering down from the surface (Fig. 16.17). This adaptation, which functions in a similar manner to countershading, is called **counterillumination.** 

The light produced by midwater animals is closely matched to the background light. Like the natural light at these depths, nearly all midwater bioluminescence is blue-green. Furthermore, many mesopelagic animals can control the brightness of the light they produce to match it to the brightness of the light coming down from above. This has been shown experimentally by placing special blinders on shrimps and other animals. These blinders allow experimenters to control the amount of light the animal sees (Fig. 16.18). When the animal is exposed to bright light, it produces bright bioluminescence; when the light is dim, so is the bioluminescence. When opaque blinders are put on the shrimp so that it sees no light, it turns off its photophores completely. This control of the brightness of the bioluminescence is essential. It is easy to see an animal if it produces light at night or if the light is brighter than the background. On the other hand, the animal creates a silhouette if the light is not bright enough.

Some fishes with tubular eyes have special yellow filters in their eyes. The filters allow the fish to distinguish between natural light and bioluminescence. Thus, these fishes can at least partially defeat the defensive counterillumination of prospective prey.

Most midwater animals are bioluminescent, and midwater organisms have evolved many different ways to produce



**FIGURE 16.18** (*a*) The following experiment showed that a midwater shrimp (*Sergestes similis*; see Fig. 16.4*c*) produces bioluminescence to match the background light intensity. Shrimp having both eyes covered with blinders did not produce any light (lower line), no matter how much outside light there was. Those with clear blinders produced more light as the outside level was increased (upper line). (*b*) The experimental setup, in this case using a control shrimp with clear blinders. Reprinted with permission from J. A. Warner, M. I. Lutz, and J. F. Case, "Cryptic Bioluminescence in a Midwater Shrimp" in *Science*, Vol. 20:1979. Copyright © 1979 American Association for the Advancement of Science.



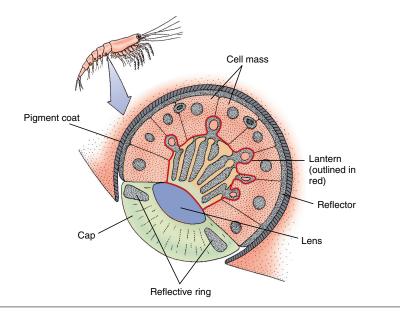


FIGURE 16.19 A cross section of a photophore of a krill.

light. Photophores, as we have seen, are common. In some species the light is produced by the animal's own specialized tissue. In other species, symbiotic bacteria live inside the light organ and produce the light. In either case, the photophore can be quite complex (Fig. 16.19).

Bioluminescence is not always produced by specialized photophores. Many jellyfishes and other gelatinous animals produce light with cells that are scattered over the body surface. Some copepods, ostracods, shrimps, and other animals secrete bioluminescent fluids that they squirt out through special glands, either in addition to or instead of having photophores. Some squids and octopuses even produce bioluminescent ink.

Counterillumination is an important function of bioluminescence in midwater organisms, but not the only one. The pattern of photophores is different among species, and even between sexes, which may mean that bioluminescence is used to communicate and attract mates. Organisms that produce bioluminescent secretions may do so as a defense mechanism in the same way that shallow-water squids and octopuses use their ink. When disturbed, they often produce a burst of light and dart away. This presumably distracts predators and allows the prey to escape. Some use the light to lure prey. In fact, a few species of midwater fishes have photophores that produce red light. The red light is invisible to most other midwater organisms, but these fishes can see it and probably use it to spy, undetected, on potential prey. Some animals have light organs around their eyes that may help them see.

Most midwater animals are bioluminescent. Bioluminescence is used in counterillumination to mask the silhouette, to escape from predators, to attract or see prey, and perhaps in communication and courtship.

#### The Oxygen Minimum Layer

In many places, midwater organisms have to deal with a shortage of oxygen in the water. Oxygen can enter the ocean in two ways: either by gas exchange with the atmosphere (see "Dissolved Gases," p. 51) or as a by-product of photosynthesis. Once a water mass leaves the surface and descends to mesopelagic depths, there is no way for it to gain oxygen. It is removed from contact with the atmosphere, and there is not enough light for photosynthesis. Respiration and bacterial decay, however, continue to use up oxygen (Fig. 16.20). As a result the water be-

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comes depleted in oxygen, often in a fairly well-defined layer around 500 m (1,600 ft) deep known as the **oxygen minimum layer**. The amount of oxygen in the oxygen minimum layer can drop to practically nothing. Below the oxygen minimum layer there is very little food and therefore very little respiration and decomposition, so oxygen is not used up so quickly. Thus, the water below the oxygen minimum layer retains most of the oxygen it had when it left the surface.

Animals live in the oxygen minimum layer despite the lack of oxygen. Fishes, krill, and shrimps that live there usually have large, well-developed gills to help extract what little oxygen there is. They also tend to be relatively inactive, which lowers their oxygen consumption. Many also have complex biochemical adaptations, like **hemoglobin** that functions well at low oxygen concentrations.

# THE WORLD OF PERPETUAL DARKNESS

Below the mesopelagic lies the littleknown world of the deep sea, where sunlight never penetrates. This alien environment is vast indeed. It is the largest habitat on earth and contains about 75% of our planet's liquid water. The deep sea can be divided into several pelagic depth zones. The **bathypelagic zone** includes depths between 1,000 and 4,000 m (3,300 to 13,000 ft), and the **abyssopelagic zone** lies from 4,000 to 6,000 m (13,000 to 20,000 ft). The **hadopelagic**, or **hadal pelagic**, **zone** consists of the waters of the ocean **trenches**, from below 6,000 m to just above the sea floor, as deep as 11,000 m

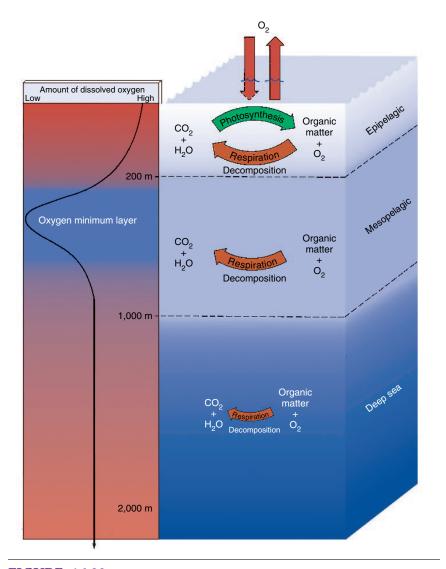
**Hemoglobin** A blood protein that transports oxygen in many animals; in vertebrates it is contained in erythrocytes (red blood cells).

Chapter 8, p. 166

**Trenches** Deep depressions in the sea floor that are formed when two plates collide and one sinks below the other.

Chapter 2, p. 26; Figures 2.11 and 2.12

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**FIGURE 16.20** Surface waters are rich in oxygen, because oxygen both enters from the atmosphere and is released by photosynthesis. In the mesopelagic zone neither the atmosphere nor photosynthesis can contribute oxygen to the water, but there is extensive bacterial decomposition of organic matter sinking from shallow water. This uses up oxygen and results in an oxygen minimum layer. Below the oxygen minimum layer, most of the organic matter has already decayed on its way down, and oxygen remains dissolved in the water. Additional oxygen is brought in by the deep thermohaline circulation (see Figs. 16.2 and 16.3).

(36,000 ft). Each of the depth zones supports a distinct community of animals, but they also have much in common. Here we stress the similarities, rather than the differences, among the depth zones of the deep sea.

The conditions of life in the deep pelagic environment change very little. Not only is it always dark, it is always cold: The temperature remains nearly constant, typically at 1° to 2°C (35°F). Salinity and other chemical properties of the water are also remarkably uniform.

The deep sea also includes the ocean bottom beyond the continental shelf. Bottom-living organisms are covered separately (see "The Deep-Ocean Floor," p. 371).

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The deep sea includes the bathypelagic, from 1,000 to 4,000 m; the abyssopelagic, 4,000 to 6,000 m; and the hadopelagic, 6,000 m to the bottom of trenches. The physical environment in these zones is quite constant. The deep sea also includes the deep-sea floor.

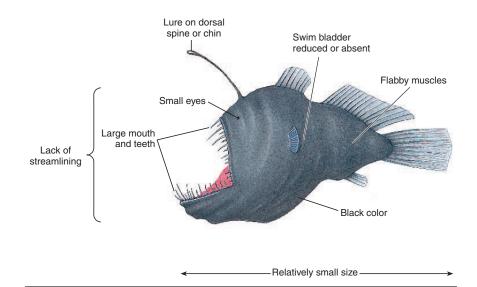
In the darkness of the deep sea there is no need for countershading. Many animals, especially zooplankton, are a drab gray or off-white. Deep-sea fishes are generally black. Shrimps are often bright red, which in the deep sea has the same effect as being black. A few deep-sea fishes are also red.

As in mesopelagic animals, bioluminescence is very common in animals that live in the upper part of the deep sea. Deep-sea animals do not use bioluminescence for counterillumination, however, since there is no sunlight to create a silhouette. They have fewer photophores than midwater species, and the photophores are usually on the head and sides of the body rather than on the ventral surface. In the deep sea the primary uses of bioluminescence are probably in attracting prey and in communication and courtship. Bioluminescence becomes less common in the deeper parts of the deep sea, for reasons that are not understood.

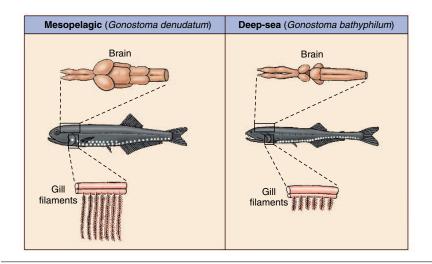
The large, light-sensitive eyes of midwater animals are not needed in the deep sea, where not even dim sunlight penetrates. The deep sea is not *completely* dark, however, because bioluminescence is common. Many deep-sea animals have functional eyes, especially in the upper parts of the deep sea, but the eyes are generally small (Figs. 16.21 and 16.22). Animals from the deepest regions tend to have even smaller eyes or be blind altogether. Deep-sea fishes that are blind are not bioluminescent, one indication that the major function of vision in the deep sea is to see bioluminescence.

## The Lack of Food

Deep-sea organisms may not have to adapt to variations in the physical environment, but they face a continual shortage of food. Very little, only about 5%, of the food produced in the photic zone makes it past all the hungry mouths in



**FIGURE 16.21** Some typical characteristics of deep-sea pelagic fishes. Compare these with the adaptations shown in Figures 15.17 and 16.11.



**FIGURE 16.22** Comparison of typical adaptations in mesopelagic and deep-sea fishes. Shown are closely related bristlemouths from the mesopelagic (*Gonostoma denudatum*) and the deep sea (*G. bathyphilum*). The deep-sea fish has smaller eyes, less muscle, and fewer light organs. It also has less-developed nervous and circulatory systems, as indicated by the smaller brain and gill filaments.

the waters above to reach the deep sea. Deep-sea animals do not make vertical migrations to the rich surface waters, probably because the surface is too far away and the change in pressure too great. With food critically scarce, deepsea animals are few and far between.

Deep-sea fishes, the most common of which are bristlemouths and deep-sea

anglerfishes (Fig. 16.23), are generally small, usually 10 cm (4 in) or less. On average, however, they are larger than mesopelagic fishes. Some deep-sea anglerfishes grow to the size of a football. It is somewhat surprising that deep-sea pelagic fishes tend to be larger than mesopelagic ones, since there is even less food available in the deep sea than in the mesopelagic. It is thought that deep-sea fishes put their energy into growth, reproducing slowly and late in life, while mesopelagic fishes spend less energy on growth and more on reproduction. In addition, the vertically migrating fishes expend a lot of energy in their migrations, which reduces the energy available for growth.

The energy-saving adaptations to food shortage seen in midwater organisms are accentuated in the deep sea. Deep-sea fishes are sluggish and sedentary, even more so than midwater fishes. They have flabby, watery muscles, weak skeletons, no scales, and poorly developed respiratory, circulatory, and nervous systems. Nearly all lack functional swim bladders. It appears that these fishes hang in the water column, expending as little energy as possible, until a meal comes along. Most deep-sea fishes have huge mouths and can consume prey much larger than themselves. This trend reaches its peak in the swallowers (Saccopharynx; Figs. 16.23d and 16.24) and gulpers (Eurypharynx; Fig. 16.23e), which look like swimming mouths. To go along with their large mouths, many species have stomachs that can expand to accommodate the prey once it has been engulfed.

Deep-sea pelagic fishes are typically small and black, with small eyes, large mouths, expandable stomachs, flabby muscles, weak bones, and poorly developed swim bladders. Bristlemouths and anglerfishes are the most common.

Anglerfishes have evolved an unusual method of catching food, from which they get their name. The first spine of their dorsal fin is modified into a long, movable "pole" that they wave in front of their mouths (Figs. 16.21 and 16.23a-c). Dangling from the end of the pole is the bait, a fleshy bit of tissue that resembles a tasty meal. Symbiotic bioluminescent bacteria live in the bait, so it glows enticingly in the dark. The anglerfish gobbles down any unsuspecting victim that comes to the bait. In most species of deep-sea anglerfishes only the females have a pole and bait. Many other deep-sea fishes also attract prey with lures, often on barbels attached to the chin.

# 

**FIGURE 16.23** Some deep-sea fishes: (*a*) deep-sea anglerfish (*Gigantactis macronema*), (*b*) female deep-sea anglerfish with one attached male (*Cryptopsaras couesi*), (*c*) deep-sea devilfish (*Caulophryne acinosa*), (*d*) swallower (*Saccopharynx ampullaceus*), (*e*) gulper (*Eurypharynx pelecanoides*), (*f*) deep-sea bristlemouth (*Gonostoma bathyphilum*).



FIGURE 16.24 The swallower eel's (*Saccopharynx lavenbergi*) gigantic mouth and jaws allow it to take advantage of infrequent large meals.

# Sex in the Deep Sea

Food is not the only thing that is scarce in the deep sea. In such a vast, sparsely populated world, finding a mate can be difficult—even harder than finding food. After all, most deep-sea animals are adapted to eat just about anything they can get, but a mate has to be both the right species and the opposite sex!

Many deep-sea fishes have solved the latter problem by becoming **hermaphrodites.** After all, it would accomplish nothing if two members of the same species finally got together but were both the same sex. If every individual can produce both eggs and sperm, the ability to breed is guaranteed.

Deep-sea organisms probably have also evolved ways to attract mates. Bioluminescence, for example, may send a signal that draws other members of the same species. Many species, as we have seen, have a unique pattern of light organs. Individuals may be able to recognize potential mates by the pattern of light. The lure of female anglerfishes differs between species, so it may also have a role in attracting mates as well as prey. Chemical attraction can be important as well. Male anglerfishes have a very pow-

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erful sense of smell, which they use to locate females. The females apparently release a special chemical that the male can detect and follow. Such special chemicals are called **pheromones.** 

Some anglerfishes (*Cryptopsaras*, *Ceratias*) have evolved a most unusual solution to the problem of finding mates. When a male finally locates a female, who is much larger, he bites into her side, where he remains attached for the rest of his life (Fig. 16.23*b*). In some species the male's modified jaws fuse with the female's tissue. Their circulatory systems join, and the female ends up nourishing the male. This arrangement, sometimes called "male parasitism," ensures that the male is always available to fertilize the female's eggs.

Neither hermaphroditism nor male parasitism seem to be common in deepsea invertebrates. The mechanisms that bring males and females together, if any, are unknown. There is some evidence that they aggregate into breeding groups, perhaps attracted by bioluminescent signals.

Finding mates, a problem for deep-sea animals, is eased by the use of bioluminescent and chemical signals and by the development of hermaphroditism and male parasitism.

# **Living Under Pressure**

Under the weight of the overlying water column, the pressure in the deep sea is tremendous. This is one reason that so little is known about the deep sea. The instruments, camera housings, and submersibles needed to study the deep sea are very expensive because they must be carefully designed and built to withstand the pressure without being crushed. Only a very few submersibles can venture into the deepest trenches, where the pressure may exceed 1,000 atmospheres (14,700 psi; see "Pressure," p. 52). It is just as difficult to bring animals up from the deep sea as it is for us to go down to them. Unable to endure the enormous change in pressure, they nearly always die when brought to the surface. A few scientists have succeeded in retrieving organisms from the deep sea in special pressurized chambers. Much has been learned from such work, but it is frustratingly difficult.

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III. Structure and Function 16. The Ocean Depths of Marine Ecosystems

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It is clear that pressure has important effects on deep-sea organisms. The absence of a functional swim bladder in most deep-sea fishes, for example, is probably due to the high energetic cost of filling the bladder with gas under extreme pressure. Along with the availability of food, pressure seems to be a major factor causing zonation in deep-sea pelagic organisms, that is, dividing the deep sea into bathypelagic, abyssopelagic, and hadopelagic zones.

In shallow-water organisms the enzymes that control metabolism are strongly affected by pressure, and would cease to function at the pressures that prevail in the deep sea. Deep-sea organisms, however, have enzymes that are unusually resistant to the effects of pressure and can function over a wide range of depths. Some also have high concentrations of a chemical that helps to stabilize the enzymes. Such molecular adaptations enable deep-sea organisms to survive under pressures that would kill any surface-dweller.

Nonetheless, pressure probably limits the depth range of most organisms, and the number of species declines going deeper and deeper in the deep sea. The deepest known fish was recorded at a depth of 8,370 m (27,460 ft). Invertebrates, however, have been found in the Mariana Trench, the deepest part of the ocean.

Hydrostatic pressure is great in the deep sea and partially controls the depth distribution of deep-sea organisms. Deep-sea organisms have molecular adaptations that allow their enzymes to function at high pressure.

# THE DEEP-OCEAN FLOOR

The floor of the deep sea shares many characteristics with the pelagic waters immediately above: the absence of sunlight, constant low temperature, and great hydrostatic pressure. Nevertheless, the biological communities of the deep-sea floor are very different from pelagic communities because of one key factor: the presence of the bottom.



FIGURE 16.25 *ABE* (Autonomous Benthic Explorer) is an autonomous underwater vehicle—a submarine robot that functions completely independently, with no cable or wires to the surface. *ABE* is designed to spend long periods on the sea floor, inactive most of the time but "waking up" at regular intervals to cruise over a predefined track on the sea floor taking videos and making measurements. On an acoustic signal from a ship, *ABE* floats to the surface to download its information and recharge its batteries before going back to work in the ocean depths.

Marine biologists have learned a bit more about the benthos, or bottominhabiting organisms, of the deep sea than about deep-water pelagic communities, but much is still unknown. Of the 270 million km<sup>2</sup> (105 million mi<sup>2</sup>) of deep-sea floor, only about 500 m<sup>2</sup>  $(5,400 \text{ ft}^2)$ , the floor area of a large house, have been sampled quantitatively. What we do know has been learned using a variety of techniques. Devices called epibenthic sleds are dragged along the bottom, scooping up organisms, and corers actually bring a chunk of the bottom to the surface. Deep-sea cameras are used to photograph fast-swimming animals such as fishes that are hard to catch in nets. Scientists have even developed a miniature transmitter that can be hidden in bait and used to track the movements of a fish that swallows it. Deep submersibles like Alvin (see Fig. 1.10) have also been very useful, even more so than in the water column. Remote-controlled robots (Fig. 16.25) are used to collect samples, take photos, and perform experiments. In 1995 one such craft succeeded for the first time in reaching the deepest

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part of the ocean. The Japanese-built *Kaiko* descended 10,991 meters (36,061 ft) to the floor of the Challenger Deep in the Mariana Trench. This broke the long-standing record of the submersible *Trieste*, which in 1960 descended to 10,919 meters (35,810 ft), also in the Mariana Trench.

# Feeding in the Deep-Sea Benthos

As you might expect, food shortage is of extreme importance on the floor of the deep sea. Very little of the surface production makes it all the way to the bottom. Benthic organisms, however, have a major advantage over the deep-sea pelagic ones above. In the water column, food particles that are not immediately located and eaten sink away and are lost. Once food reaches the bottom, on the other hand, it stays put until it is found. Thus, although pelagic animals may get first crack at food sinking out of the photic zone, benthic animals have much more time to find and eat it. Food particles that reach the bottom tend to be those that sink fairly rapidly, minimizing the chance that they will be eaten on the way down. Fecal pellets, for example, are an important source of organic matter for the deep-sea benthos.

Still, the rain of organic matter to the sea floor is actually more like a drizzle. Very little food is available to the benthic community. Furthermore, much of the material that reaches the sea floor, like the chitinous remains of crustacean zooplankton, is not immediately digestible. On the sea floor,

Hermaphrodites Individuals with both male and female gonads.

Chapter 7, p. 134

**Enzymes** Proteins that speed up and control chemical reactions in organisms. *Chapter 4, p. 70* 

**Metabolism** The vast set of chemical reactions that sustains life.

Chapter 4, p. 69

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# **BIODIVERSITY IN THE DEEP SEA**

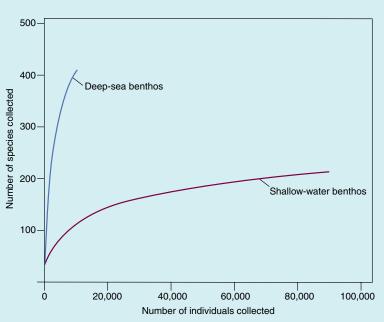
With its immense pressure, near-freezing waters, total lack of sunlight, and chronic food shortage, the deep sea would seem to be one of our planet's least hospitable environments. Indeed, in the nineteenth century the pioneering oceanographer William Forbes (see "The *Challenger* Expedition," p. 5), observing that fewer and fewer organisms were caught in nets as depth increased, hypothesized that no life at all could exist below about 600 m (2,000 ft). This "azoic hypothesis" was quickly proved wrong when other scientists caught animals from deeper depths. Nevertheless, studies do show that the abundance of organisms decreases with depth—organisms are scarce in the deep sea.

Until recently it was thought that in addition to a low abundance of organisms in the deep sea there were relatively few species. Recent studies surprisingly indicate that the opposite is true: The deep sea may be the most diverse environment on earth. Biologists are unable to collect and identify every species that is present in most environments, so they can never know the exact number of species there. They can estimate how many species are present, however, from "species accumulation curves." This involves analyzing how often they find new species as they collect more and more individual organisms. The first organism collected will always be a species new to the study. The second organism could be from the same species, leaving the total number of species collected at one, or it might be a new species, bringing the species total to two. If the number of species-one measure of biodiversity-is small, then

as more and more individuals are collected the number of new species will increase relatively slowly and will soon start to level off near the total number of species that lives in the environment. In highly diverse habitats, ones with many species, the number of species will increase rapidly as more individuals are collected and will take longer to level off.

When this was done on the deep-sea floor, the species curve went through the roof, leading the researchers to estimate that certainly more than 1 million, and possibly more than 10 million, species live on the deep-sea floor, making it as or more diverse than rain forests and coral reefs. This was little short of astonishing because up until then most biologists had thought that no more than a few hundred thousand species lived in the entire ocean!

The estimate that 10 million species may inhabit the deep-sea floor has been controversial, in part because it is extrapolated from samples of only a tiny fraction of the sea floor. Whatever the true number, it is clear that the deep-sea floor is among the most diverse habitats on earth. High biodiversity in other deep-sea habitats is also being revealed. Initial observations of hydrothermal vent communities (see "Hot Springs, Cold Seeps, and Dead Bodies," p. 377)



Species accumulation curves from the deep-sea and shallow-water benthos off the coast of New England.

Source: Etter, R. J. and L. S. Mulineaux, 2001. Deep-Sea Communities. In: Bertness, M. D., S. D. Gaines, and M. E. Hay (Eds.) *Marine Community Ecology*. pp. 367–393. Sinauer Associates, Sunderland, Mass.

indicated that they contained only a few species. With the refinement of sampling techniques and studies of more vents, however, more and more new species have been discovered. More than 400 animal species, many of them small and inconspicuous, have now been found at hydrothermal vents, and the number is steadily rising.

More surprises have come from deep-sea seamounts, which like the rest of the deep sea have hardly been studied. From what little is known, seamounts too appear to have very high biodiversity. Recent samples from only 24 seamounts in the southwest Pacific near Australia produced more than 850 species, and the species accumulation curve was still rising, indicating that many more species would have been found had more samples been taken. What is more, about a third of the species collected were new to science, and probably restricted to small seamount chains or even individual seamounts. Like hydrothermal vents, seamounts seem to be deep-sea islands, each holding a collection of organisms found nowhere else. With some 30,000 seamounts in the deep sea, nearly all unexplored, there must be vast numbers of seamount species yet to be discovered. Clearly, the deep sea is one of the earth's great repositories of biodiversity.

however, bacteria decompose the **chitin** and become food for other organisms.

Most of the deep-sea floor is covered in fine, muddy sediment. The **meiofauna**, tiny animals that live among the sediment particles (see "Life in Mud and Sand," p. 283), graze on bacteria and absorb nutrients from the water between the particles. The meiofauna are the most abundant group of animals on the deep-sea floor. They play a major role in making the energy in bacteria and dissolved organic matter (DOM) available to larger benthic animals.

Suspension feeders are rare among the larger organisms in the deep-sea benthos. Instead, **deposit feeders** dominate. Many of these are **infauna**, burrowing in the sediments. Others, the **epifauna**, rest on the sediment surface.

Polychaete worms are typically the most abundant animals on the deep-sea floor, followed by crustaceans and bivalve molluscs, but there is considerable variation from place to place. Sea cucumbers are sometimes the dominant organisms, for example. Sea cucumbers from the deep sea often have strange, highly modified body forms. Some have developed leg-like appendages that they can use to walk across the sea floor in search of organic-rich sediment. "Herds" of some species have been observed from submersibles. Other species can actually swim above the sea floor by undulating their bodies or squirting jets of water. Other parts of the deep sea are dominated by brittle stars, and sea stars can also be abundant.

The deep-sea benthos is dominated by deposit feeders. The dominant animal groups are the meiofauna, polychaete worms, crustaceans, bivalve molluscs, sea cucumbers, brittle stars, and sea stars.

There are predators in the deep-sea benthos, but they seem to be fairly rare. The main predators on deposit-feeding animals are probably sea stars, brittle stars, and crabs. Members of the nekton, like fishes and squids, are also important predators. Sea spiders, or pycnogonids, prey on other invertebrates by sucking



**FIGURE 16.26** For unknown reasons the deep-sea members of some groups are giants compared to their shallow-water relatives. This is a deep-sea amphipod (*Alicella gigantea*).

out their soft parts. Sea spiders are small in shallow water, but some deep-sea species can be as large as 80 cm (30 in) across. This reversal of the usual trend of small size in deep-sea organisms is also found in other invertebrate groups, especially crustaceans (Fig. 16.26). The reasons for this phenomenon, known as **deep-sea gigantism**, are not known.

The tripod fishes are another interesting group of deep-sea benthic predators. Nearly blind, these fishes sit on the bottom on their elongated fins (Fig. 16.27b), facing into the current and snapping up passing plankton.

The slow rain of food to the bottom is interrupted by an occasional "storm." Large pieces of food that sink rapidly, like the dead bodies of large fishes or whales, are an important source of food to the benthos. Mobile deep-sea animals rapidly congregate around such "baitfalls" (Fig. 16.28). Among the most common of these are crustaceans, especially amphipods (Fig. 16.26), which arrive soon after the bait touches down. Many deepbenthic amphipods are generalists that feed on detritus and perhaps prey on live organisms if nothing else is available. Some, however, seem to specialize as scavengers. They apparently have a welldeveloped sense of smell, which probably helps them find new baitfalls. When caught in traps, these amphipods often have nothing in their guts except the bait, which indicates that they have not fed for some time before. This, and the fact that they have an expandable gut, may mean that they are adapted to capitalize on large but infrequent meals.

**Chitin** Highly resistant carbohydrate found in the skeleton of crustaceans and other structures.

Chapter 4, p. 70

**Suspension Feeders** Animals, including *filter feeders*, that eat particles suspended in the water column.

Chapter 7, p. 118; Figure 7.16

**Deposit Feeders** Animals that eat organic matter that settles to the bottom.

Chapter 7, p. 126; Figure 7.16

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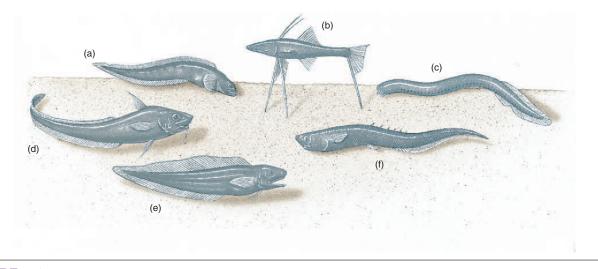


FIGURE 16.27 Some typical deep-sea bottom fishes: (a) eelpout (Zoarces), (b) tripod fish (Bathypterois), (c) hagfish (Eptatretus stouti), (d) grenadier (Lionurus carapinus), (e) brotulid (Bassogigas profundissimus), (f) deep-sea spiny eel (Notacanthus bonapartei).

FIGURE 16.28 A variety of fishes quickly locate large pieces of food on the deep-sea floor. These cusk eels (*Genypterus* blacodes), spiny dogfish sharks (*Centrophorus* squamosus), cutthroat eels (*Diastobranchus* capensis), and snubnose eels (*Simenchelys* parasiticus) have come to a large piece of fish placed at 1,500 m (5,000 ft) on the sea floor near New Zealand.

Various fishes also find freshly placed bait quickly (Fig. 16.28). The most common of these are the grenadiers, or rattails, brotulas and cusk eels, deepsea spiny eels, and hagfishes (Fig. 16.27*c*; also see Fig. 8.2). These bottom scavengers tend to be large, relatively muscular, and active, unlike bathypelagic fishes (Fig. 16.29). They seem to be adapted for cruising along the bottom in search of the occasional bonanza. At depths above 2,000 m, sharks may also show up, quickly putting an end to the feed.

# The Nature of Life in the Deep-Sea Benthos

There is a growing realization that life in the deep sea proceeds at a very different pace than it does at the surface. Most



deep-sea animals seem to grow very slowly, probably because of the lack of food. On the other hand, they live for a long time. Deep-sea clams have been estimated to be 50, 60, or even 100 years old. Perhaps the low temperature and high pressure slow down the processes of life in the deep sea.

It may also be that deep-sea animals need to live a long time to store up enough energy to reproduce. The larvae of deep-sea forms do not spend time in the food-rich photic zone. The chances of making it all the way to the surface and then back to the deep-sea floor are simply too small. Instead, deep-sea animals tend to produce large eggs, with enough yolk to see the larva through its early stages without eating. It takes a lot more energy to produce a large egg than a small one, so deep-sea animals produce only a few eggs. In at least some animals, reproduction may be tied to feeding. In some species of amphipods, individuals caught in baited traps are all sexually immature. Biologists have speculated that they do not reproduce until they manage to find a good meal.

## Bacteria in the Deep Sea

Bacteria play an important role in deepsea benthic food webs. They are eaten by meiofauna and deposit feeders, and they break down indigestible organic matter. Scientific interest in deep-sea bacteria got a major boost as the result of an unplanned "experiment." In late 1968 the crew of Alvin was preparing to make a dive. The submersible was swamped by a wave, its supporting cable broke, and Alvin, hatch open, dropped some 1,540 m (5,000 ft) to the bottom of the sea. The crew escaped, but left their lunch on board. It was to become the most famous lunch in the history of marine biology.

When *Alvin* was recovered 10 months later, scientists discovered that the long-lost lunch, instead of having rotted away, was in amazingly good condition. Though soggy, the sandwiches still looked almost fresh; the bologna was still pink inside. The rest of the lunch apples and a thermos of soup—also looked good enough to eat. Once

#### Chapter 16 The Ocean Depths 375

|                     | Epipelagic   | Mesopelagic<br>(vertical migrators)  | <b>Mesopelagic</b><br>(non-migrators)                                      | Deep Pelagic  | Deep-sea<br>bottom                  |
|---------------------|--|--|--|---|-------------------------------------|
| Appearance          |  |  |  |   |                                     |
| Size                | Wide size range,<br>from tiny to huge                                  | Small  | Small  | Small   | Relatively large                    |
| Shape               | Streamlined shape  | Relatively elongated<br>and/or laterally<br>compressed                     | Relatively elongated<br>and/or laterally<br>compressed                     | No streamlining,<br>often globular in<br>shape              | Very elongated                      |
| Musculature         | Strong muscles, fast<br>swimming                                       | Moderately strong<br>muscles   | Weak, flabby muscles   | Weak, flabby muscles  | Strong muscles                      |
| Eye characteristics | Large eyes   | Very large, sensitive<br>eyes  | Very large, sensitive<br>eyes, sometimes<br>tubular eyes                   | Eyes small or absent  | Small eyes                          |
| Coloration          | Typical counter-<br>shading: dark back<br>and white or silver<br>belly | Black or black with<br>silver sides and<br>belly; counter-<br>illumination | Black or black with<br>silver sides and<br>belly; counter-<br>illumination | Black, occasionally red                                     | Dark brown or black                 |
| Bioluminescence     | Bioluminescence<br>relatively<br>uncommon                              | Bioluminescence<br>common, often<br>used for counter-<br>illumination      | Bioluminescence<br>common, often<br>used for counter-<br>illumination      | Bioluminescence<br>common, often<br>used to attract<br>prey | Only a few groups<br>bioluminescent |

FIGURE 16.29 Comparison of the typical characteristics of fishes from different depth zones in the pelagic realm.

brought to the surface, the food soon spoiled, even though it was refrigerated.

Why was the food preserved in the deep sea? Though the deep sea is cold, so is a refrigerator. Are bacteria absent from the deep sea? Does the pressure somehow inhibit bacterial decay? Is there some other explanation? These questions sparked a flurry of research.

It is now known that bacteria do live in the deep sea, as they do in every other environment on earth. Pressure slows down bacterial growth, however, and most shallow-water bacteria cannot grow at the pressures of the deep sea. Therefore, the bacteria that were already in the lunch probably died when *Alvin* sank. Deep-sea bacteria, however, can tolerate high pressure; some, in fact, cannot grow without it. Even these pressure-loving, or **barophilic**, bacteria, however, grow slower than bacteria from shallower depths.

Many deep-sea bacteria live inside amphipods and other animals; they probably help the animals digest chitin and other detritus. The animals provide transportation, carrying the bacteria to rich food sources. By keeping the animals out, the lunchbox probably prevented these bacteria from getting to the food. There are also free-living bacteria in the deep sea. It may be that these just grow too slowly to have decomposed the lunch. Deep-sea bacteria can take up to 1,000 times longer to decompose organic matter than shallow-water bacteria. It has also been suggested that free-living bacteria in the deep sea are adapted to use nutrients in very low concentrations. If this is the case, they may be overloaded by such rich food as a bologna sandwich, which they would not normally encounter.

Deep-sea sediments also contain large numbers of **chemosynthetic bacteria**, which are probably an important food source for deposit feeders. They may be involved in the formation of mineral deposits known as manganese nodules (see "Ocean Mining," p. 402). Scientists have also learned that chemosynthetic bacteria are gradually digesting the wreck of the *Titanic*!

**Chemosynthetic Bacteria** Autotrophic bacteria that use energy contained in inorganic chemicals rather than sunlight to make organic matter.

Chapter 5, p. 95

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The chambered nautilus (*Nautilus*) is often called a living fossil. All other living cephalopods—the squids, octopuses, and cuttlefishes—have at most only vestiges of the hard outer shell that characterizes most molluscs. Only *Nautilus* retains a large, heavy shell. It is the last surviving relative of a group of organisms that once ruled the seas.

Most of the early animals in the sea lived on the bottom, crawling and scratching for survival. Around 500 million years ago a group of molluscs that looked something like today's limpets developed a new trick: the ability to partially fill their shells with gas. Buoyed by the gas, these ancient ancestors of

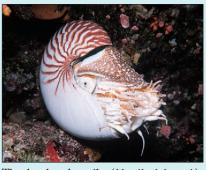
modern cephalopods, called nautiloids, were able to float up off the bottom away from predators. Before long they also developed the ability to move by squirting out water—probably the first form of jet propulsion.

The trick was immensely successful. For 200 million years or so nautiloids and their descendants, especially a group with coiled shells called the ammonites, dominated the ocean. They had the water column more or less to themselves and could drop onto their prey from above.

Then fishes arrived on the scene. To be more accurate, they evolved the swim bladder (fishes had been around for some time). This allowed them to maintain neutral buoyancy and compete with the nautiloids. Fishes had a major advantage: They could swim faster and more efficiently than the nautiloids, with their cumbersome shells. Outcompeted by fishes, most nautiloids went extinct. One group of cephalopods, the squids, became more fish-like. They abandoned the shell and became streamlined, active swimmers. Of all the heavy-shelled cephalopods, only *Nautilus* remains. By studying living *Nautilus*, scientists hope to learn more about their extinct relatives, who left an abundant fossil record and are of great interest to geologists.

*Nautilus* lives in a coiled shell that is partitioned into a series of chambers. The chambers are walled off one by one as the animal grows. The animal lives only in the last chamber. The others are filled with gas and provide buoyancy, without which the heavy shell would drag the animal to the bottom. When the chamber is first partitioned it is filled with seawater. Rather than pumping gas in, *Nautilus* removes all the ions from the water in the chamber. This makes the water more dilute than the animal's blood, so it flows into the bloodstream by osmosis and gas diffuses into the chamber to replace it. After that the chamber is more or less sealed and does not need repeated filling and emptying like a fish's swim bladder. This allows the animal to move rapidly up and down in the water column.

*Nautilus* is found near coral reefs, but it is not really a coral reef animal because it generally lives much deeper than corals, typically between 100 to 500 m (330 to 1,650 ft). In some places it occasion-



The chambered nautilus (Nautilus belauensis).

ally ventures into shallow water for short periods. The upper limit of its normal depth range is set by temperature;



Longitudinal section of a shell of *Nautilus pompilius* showing the gas chambers.

water temperatures above  $25^{\circ}$ C (77°F) are lethal, and those below  $20^{\circ}$ C (68°F) are preferred. If the water is cool enough *Nautilus* is able to live at the surface, and specimens can be maintained in aquaria. The lower depth limit is set by pressure. The shell chambers are sealed, so gas cannot be pumped in to counteract the pressure at great depth. Instead, the animal relies on the strength of its shell, just as a submarine relies on the strength of its hull. When the pressure gets too great, at about 800 m (2,600 ft), the shell is crushed. Actually, water begins to leak into the chambers at much shallower depths, and the animal probably doesn't spend much time at depths of even 500 m (1,650 ft).

Not much is known about the biology of *Nautilus*. It appears to be primarily a scavenger, locating animal remains and the molted shells of lobsters by its sense of smell. Its neutral buoyancy allows it to move up and down the water column looking for a scent trail with very little expenditure of energy. When food is sensed, the animal swims to the food by jet propulsion, squirting water out of a muscular funnel. It may also prey on live hermit crabs and other crustaceans. When not feeding it spends most of its time "asleep" in the cool, deep water conserving energy. Scientists have calculated that a single meal can last a *Nautilus* at least two months!

Interestingly, *Nautilus* can tolerate conditions of almost zero oxygen. It is able to draw on oxygen stored in the chambers of its shell, a trick evolved long before humans invented the scuba tank. The benefits of this ability are not known, since the waters where *Nautilus* lives normally have plenty of oxygen.

Another puzzle is that the vast majority of *Nautilus* caught in traps are males. Maybe females are hard to catch, or perhaps there is a shortage of females. Scientists will continue to study *Nautilus* not only to learn about the animal itself but to try to get a glimpse into the ocean's past.

III. Structure and Function 16. The of Marine Ecosystems

16. The Ocean Depths

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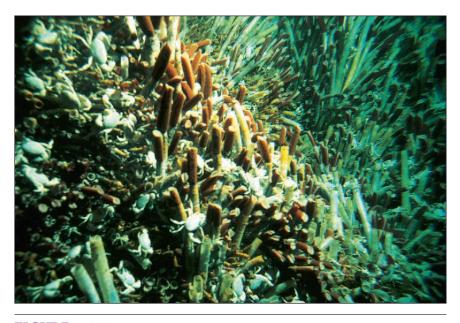
# HOT SPRINGS, COLD SEEPS, AND DEAD BODIES

The year 1977 marked one of the most exciting discoveries in the history of biology, and it wasn't even made by biologists! A group of marine geologists and chemists was using Alvin to look for hydrothermal vents on a section of midocean ridge near the Galápagos Islands in the Eastern Pacific. When the Alvin scientists found the vents, they also found something completely unexpected: a rich, flourishing community unlike anything ever imagined (Fig. 16.30). In the days that followed, more vents were found, each teeming with animals. There were gigantic worms up to 1 m (3.3 ft) long, 30-cm (12-in) clams, dense clusters of mussels, shrimps, crabs, fishes, and a variety of other unexpected life. The vents were like oases of life on the barren deepsea floor.

A series of expeditions was soon mounted to vent areas around the world. With every dive, it seemed, came exciting new discoveries. Nearly all the organisms in the rich communities around the vents were new to science.

Hydrothermal vent communities vary considerably from place to place. Those at mid-ocean ridges in the Eastern Pacific, like the first ones that were discovered, are usually dominated by tubeworms, clams, crabs, and shrimps. In the western Pacific, the dominant organisms are unusual snails and barnacles. Vents on the Mid-Atlantic Ridge are dominated by a shrimp. The relatively cool vents that are found some distance from the mid-ocean ridge (see "The Mid-Ocean Ridge and Hydrothermal Vents," p. 37) support sponges, deep-sea corals and other organisms, but not in the abundance seen at mid-ocean ridge vents.

There is no sunlight to support photosynthesis, and the primary producers in hydrothermal vent communities are chemosynthetic **archaea** and bacteria. Around the mid-ocean ridge, seawater trickles down through cracks and fissures in the earth's crust, and is heated to very



**FIGURE 16.30** A rich, colorful community of animals inhabits deep-sea hydrothermal vents. This photograph was taken at a depth of 2,636 m along the East Pacific Rise.

high temperatures. Rich in sulfide minerals, it emerges at hydrothermal vents to form "black smokers," "chimneys," and other mineral deposits. The hot water also contains large amounts of hydrogen sulfide (H<sub>2</sub>S), which is toxic to most organisms but is an energy-rich molecule. Chemosynthetic microbes that use the energy in hydrogen sulfide and sulfide minerals to make inorganic matter are the base of the food chain. Some of these microbes are extremophiles that can live at temperatures over 110°C (230°F), the highest temperature at which life is known to occur (see "Archaea," p. 96). Thick mats of chemosynthetic archaea and bacteria also grow in the cooler vent areas away from the mid-ocean ridge, using the carbonate minerals that predominate there as an energy source rather than sulfide minerals.

•

Deep-sea hydrothermal vents harbor rich communities. The primary production that supports these communities comes from bacterial chemosynthesis, not photosynthesis.

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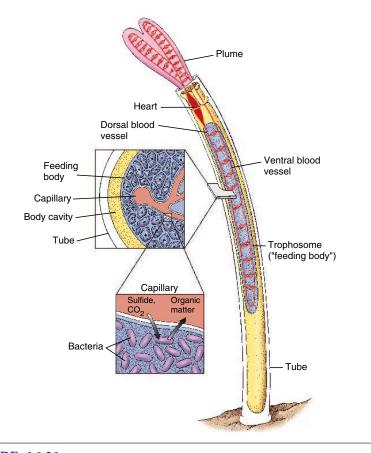
The water near the vents contains huge numbers of archaea and bacteria, so many that they cloud the water. Some vent animals feed by filtering bacteria from the water, but this is not the principal mode of feeding. One of the dominant animals in Eastern Pacific vent communities, the giant tube worm (Riftia), does not filter feed. In fact, it doesn't even have a mouth or digestive tract! Instead, these worms have a highly specialized organ called a trophosome ("feeding body") (Fig. 16.31) that is packed with symbiotic bacteria. The bacteria perform chemosynthesis inside the worm's body and pass much of the organic matter they produce on to the worm. The worm, in turn, supplies the bacteria with raw materials. The bright-red plume acts like a

**Hydrothermal Vents** Undersea hot springs associated with mid-ocean ridges. *Chapter 2, p. 38* 

Archaea Single-celled, prokaryotic organisms once thought to be bacteria but now known to be as different from bacteria as from humans.

Chapter 5, p. 96

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**FIGURE 16.31** The anatomy of the giant hydrothermal-vent tube worm (*Riftia pachyptila*). The plume at the end acts like a gill, except that it exchanges hydrogen sulfide ( $H_2S$ ) as well as carbon dioxide ( $CO_2$ ) and oxygen ( $O_2$ ). The carbon dioxide and sulfide are carried in the blood to the feeding body, where bacteria use them to make organic matter by chemosynthesis.

gill, exchanging not only carbon dioxide and oxygen, but also hydrogen sulfide. The tube worm's blood has special hemoglobin that chemically binds the hydrogen sulfide, protecting the worm from its poisonous effects. The hemoglobin in the worm's blood transports the hydrogen sulfide to the bacteria in the feeding body. Most other vent animals chemically process hydrogen sulfide to avoid being poisoned.

A number of other vent animals, like mussels (*Bathymodiolus*) and large clams (*Calyptogena*), contain symbiotic bacteria, though they can filter-feed as well. Nonsymbiotic microbes are also an important food source. For example, a shrimp (*Rimicaris*) that dominates vent communities on the Mid-Atlantic Ridge scrapes off and eats bits of microbe-covered mineral from the chimneys that form at vents (see Fig. 2.24). The microbes are digested and the remaining mineral eliminated.

These shrimp are unusual in another way. They do not have recognizable eyes but on their upper surface they have two light-sensitive patches. The patches can detect much fainter light than humans can see. Before the discovery that these shrimp could "see," no one suspected that there was any light at all at deep-sea vents. Using a special low-light camera similar to those used to study distant stars, scientists found that there is a faint glow, invisible to the human eye, around the vents. The source of the glow is uncertain, although some of it can be explained by the heat of the emerging water. Biologists speculate that the shrimp use this dim light both to locate

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active vents and to avoid getting cooked by coming too close to the scalding water.

After discovering the variety of animals living at hydrothermal vents, biologists found other communities that were based on chemosynthesis rather than photosynthesis. At a few places, especially on the continental slope and in sediment-rich basins like the Gulf of Mexico, hydrogen sulfide and organic material like oil and natural gas seep out from the sea floor. Gas hydrate deposits (see "Oil and Gas," p. 402) are another rich source of chemical energy. These **cold-water seeps** support biological communities that are very similar to those at deep-sea hot springs.

Communities based on chemosynthesis have even been found on deepsea "graves." As previously discussed, occasional baitfalls like dead whales are an important source of food for deepsea scavengers. When the scavengers are through, the decomposing remains produce hydrogen sulfide and other energy-rich chemicals. Chemosynthetic microbes grow on these chemicals, supporting a community like the ones at vents and seeps.

Unlike the organisms that live on the barren sea floor, those at hot springs, cold seeps, and dead bodies enjoy an energyrich environment, and grow fast and large. On the other hand, their specialized habitats are tiny oases separated by vast distances. These oases are also very unreliable. Hot springs and cold seeps may suddenly "dry up," and hot spring organisms may be suddenly cooked by eruptions of the mid-ocean ridge. The remains of whales and other large organisms rot away, so the communities they support are also short-lived. The species in these communities can only survive if their offspring can "island-hop" to a new oasis. In this regard, the remains of whales, sharks, seals, and other large organisms may be vital stepping stones. They are especially tiny habitats in the expanse of the deep sea, and they don't last long. Compared to hot springs and seeps, however, there are many of them, or at least there were. By hunting the giants of the sea to the brink of extinction, we may have already removed these stepping stones and doomed an entire ecosystem that we have only just discovered.

III. Structure and Function 16. The Ocean Depths of Marine Ecosystems

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# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

# **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. The deep-sea floor has been considered as a potential site for the disposal of toxic and radioactive wastes. What questions about the biology, geology, and chemistry of the deep-sea environment do you think should be answered before such plans are approved?
- 2. How do you think non-migratory midwater fishes, wih their flabby muscles, are able to prey on vertical migrators, which have well-developed muscles?

# For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol **Section**, and will contain live links when you visit this page in the Online Learning Center.

## **General Interest**

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# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- The marine deep-sea zone
- Under sea tectonic and volcanic activity
- Primary productivity
- Food webs

- Phylum Echinodermata
- Class Asteroidea
- Biodiversity
- Phylum Pogonophora

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Take the online quiz for this chapter to test your knowledge.

IV. Humans and the Seas 17. Re

17. Resources from the Sea

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# Resources from the Sea

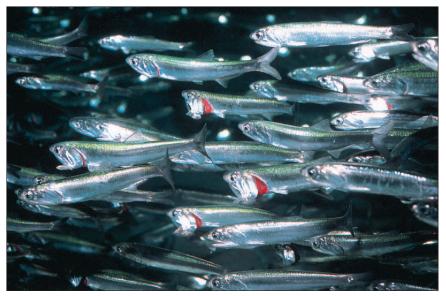


eople have used the many resources that the oceans offer ever since the first humans ventured to the shore. Evidence of the use of marine life as food goes back to prehistoric times and includes fish hooks, seashell artifacts, and mounds of empty mollusc shells. Our exploitation of marine resources is now commonplace and much more sophisticated (Fig. 17.1). Fishers sail across the oceans assisted by satellites, marine chemists extract wonder drugs from the least-expected organisms, genetic engineers develop faster-growing fish, and ocean engineers investigate better ways of harvesting energy from waves and tides.

Chapter 17 examines the resources of the sea and their use by humans. In discussing them we will draw on our knowledge of the sea floor and the chemical and physical features of the ocean (discussed in Part One of the book) and of the types and distribution of marine life (discussed in Parts Two and Three). Also involved are a broad range of other disciplines, ranging from the application of technology to the marketing of new products.

# THE LIVING RESOURCES OF THE SEA

The oceans, which cover most of the surface of the earth, are the planet's largest factory of organic matter. Humans take



Northern anchovy (Engraulis mordax) filter feeding.

advantage of this productivity and harvest many different kinds of marine organisms. Most are harvested for food, but they also provide many other products and materials. Millions of people also use the living resources of the sea in recreational fishing, sport diving, or even by keeping an aquarium at home.

# Food from the Sea

The oceans provide food and also employment for millions of people. Confucius said, "Give a man a fish, and you feed him for a day. Teach him how to fish, and you feed him for life."

Many different types of marine organisms are harvested. Seaweeds and creatures as diverse as jellyfishes, sea cucumbers, sea turtles, and even polychaete worms are part of the diet in many cultures. The vast majority of the harvest, however, consists of fishes, which are known in fisheries terminology as **finfish**. Finfish constitute around 84% of the total world catch. Also harvested are molluscs and crustaceans, which together are called **shellfish**.

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**FIGURE 17.1** The unloading of northern bluefin tuna (*Thunnus thynnus*) from a freezer ship to a modern cannery. The valuable catch was canned for human consumption and the by-products processed into pet food, fertilizer, and chicken feed for sale around the world.

Most of the world's food is grown on land, and food from the sea represents only about 1% of all the food eaten. Still, seafood is one of the world's most important foods. This is because it is rich in protein, which is essential for normal growth. Finfish provides around 16% of the animal protein consumed by people around the world. Dependence on seafood for protein is much higher in most coastal nations, especially poor ones.

The groups of marine organisms that are most widely used as food are fishes, molluscs, and crustaceans. Seafood is important to the world's population because it is a good source of protein.

The world's population reached 4 billion in 1975, 5 billion in 1987, and 6 billion in 1999 (Fig. 17.2). It may reach 10 billion by 2050. The population will grow much faster in the places where it hurts the most: the poor, already crowded countries of the developing

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world. Protein deficiency is already a major cause of disease and death in these countries.

Some people look hopefully to the ocean as a source of food for the earth's growing population. Marine fisheries also provide much-needed employment in developing countries. As we shall see, however, the world's most important fisheries are already overexploited, and some are exhausted. Worldwide catches stabilized despite increasing effort by the late 1980s (Table 17.1) after increasing almost fivefold since 1950. Neither the world fish catch nor the world grain output will be able to catch up with the world's exploding population. The amount of grain and fish per person has already started to decrease. FAO, the Food and Agriculture Organization of the United Nations, has estimated that by 2010 world demand for fish will be 10 to 40 million tons below production. The truth is that the world's oceans have been running out of fish for some time.

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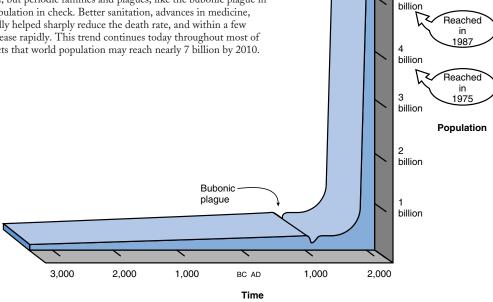
billion

Reached

in

1999

**FIGURE 17.2** The curve that represents the growth of the world human population over the centuries looks like a giant J: Very slow, almost nonexistent population growth is followed by a sudden explosion of very fast growth. This J-shaped curve indicates that the more people there are, the faster the population grows, as was the case with the dinoflagellates shown in Figure 10.2. Growth was slow for millenia because of food shortages and disease. The domestication of plants and animals helped provide more food, but periodic famines and plagues, like the bubonic plague in Europe during the 1300s, kept the population in check. Better sanitation, advances in medicine, and more efficient agriculture eventually helped sharply reduce the death rate, and within a few centuries the population began to increase rapidly. This trend continues today throughout most of the planet. The United Nations projects that world population may reach nearly 7 billion by 2010.



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|  | Commercial Cate<br>ons of Metric To |       | d Fishes, Moll | uscs, and Crus | staceans |       |
|--|-------------------------------------|-------|----------------|----------------|----------|-------|
| Catch  | 1975                                | 1980  | 1985           | 1990           | 1995     | 1999  |
| Herrings, sardines, etc.                           | 13.43                               | 16.14 | 21.10          | 22.32          | 22.01    | 22.71 |
| Miscellaneous marine fishes                        | 7.42                                | 7.97  | 8.41           | 9.82           | 9.80     | 10.72 |
| Cods, haddocks, hakes                              | 11.85                               | 10.75 | 12.46          | 11.58          | 10.73    | 9.40  |
| Jacks, mullets, sauries                            | 6.08                                | 7.30  | 8.31           | 9.78           | 10.79    | 7.71  |
| Rockfishes, basses, congers                        | 5.19                                | 5.30  | 5.21           | 5.80           | 6.85     | 6.83  |
| Tunas, bonitos, billfishes                         | 2.06                                | 2.55  | 3.18           | 4.43           | 4.93     | 5.97  |
| Mackerels  | 4.15                                | 4.03  | 3.83           | 3.54           | 4.69     | 5.11  |
| Flounders and other flatfishes                     | 1.16                                | 1.08  | 1.35           | 1.23           | 0.92     | 0.96  |
| Salmon, smelts                                     | 0.55                                | 0.80  | 1.17           | 1.51           | 1.15     | 0.91  |
| Sharks, rays                                       | 0.59                                | 0.60  | 0.62           | 0.69           | 0.76     | 0.82  |
| Total marine fishes                                | 51.93                               | 55.73 | 64.40          | 69.36          | 71.66    | 70.26 |
| Freshwater fishes                                  | 5.96                                | 6.17  | 8.74           | 12.23          | 5.72     | 6.49  |
| Anadromous and catadromous fishes                  |                                     |       |                |                |          |       |
| (other than salmon)                                | 1.53                                | 1.82  | 2.57           | 3.24           | 1.92     | 1.85  |
| Squids, octopuses                                  | 1.18                                | 1.53  | 1.79           | 2.36           | 2.87     | 3.37  |
| Clams, cockles                                     | 0.94                                | 1.20  | 1.51           | 1.53           | 0.96     | 0.81  |
| Scallops   | 0.29                                | 0.37  | 0.60           | 0.87           | 0.51     | 0.57  |
| Mussels  | 0.53                                | 0.62  | 0.97           | 1.34           | 0.24     | 0.24  |
| Oysters  | 0.85                                | 0.97  | 1.09           | 1.00           | 0.19     | 0.16  |
| Total marine molluscs                              | 4.03                                | 4.91  | 6.18           | 7.73           | 6.27     | 6.79  |
| Shrimps  | 1.33                                | 1.70  | 2.12           | 2.63           | 2.34     | 2.89  |
| Crabs  | 0.75                                | 0.82  | 0.89           | 0.89           | 1.09     | 1.19  |
| Lobsters   | 0.10                                | 0.10  | 0.20           | 0.21           | 0.22     | 0.23  |
| Krill  | 0.04                                | 0.48  | 0.19           | 0.37           | 0.12     | 0.10  |
| Total marine crustaceans                           | 2.35                                | 3.20  | 3.42           | 4.50           | 4.80     | 5.76  |
| World total (all groups,<br>marine and freshwater) | 66.13                               | 72.38 | 86.26          | 97.97          | 91.37    | 92.87 |

Source: Food and Agriculture Organization of the United Nations, FAO Yearbook, Fisheries Statistics.

*Note:* Catches tabulated in groups defined by the Food and Agriculture Organization of the United Nations; figures for catches are rounded to the nearest ten-thousandth and, when added, may not equal totals.

Fishing is one of the oldest human endeavors. Small-scale fisheries that involve simple gear and methods are still practiced around the world, especially in developing countries. These fisheries, in fact, employ most of the world's fishing people. They also provide animal protein to people whose diets are often protein-deficient.

The increased demand for seafood in affluent countries and the continuous ex-

pansion of the world's population have steadily increased the pressure on the food resources of the sea (Fig. 17.3). The application of technology, from the development of more effective gear to the use of satellites to find fish, has greatly increased the efficiency with which we harvest these resources. Nations like China, Japan, South Korea, and the United States have developed high-tech fishing fleets that can remain on the fishing grounds away from the home port for long periods. Factory, or mother, ships process and store the fish taken by smaller fishing boats. The catch is processed, marketed, and sold in a multitude of ways: fresh, frozen, canned, dried and salted, smoked, marinated, as fish sticks, and as fish meal. Fishing operations have been known to diversify into businesses

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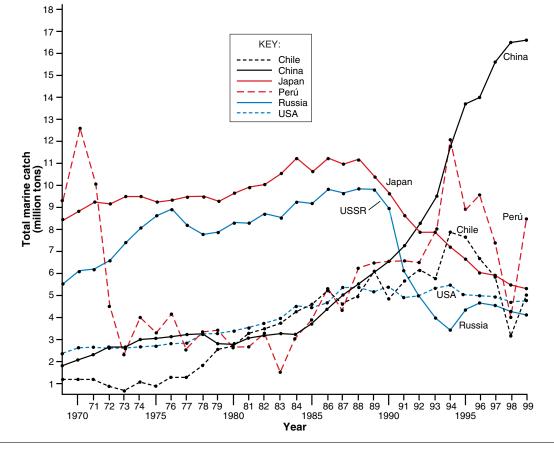


FIGURE 17.3 Total catches by the world's six major fishing nations. Marine fishes constitute the bulk of the catches, but shellfish and freshwater species are also included. Notice that annual catches by two of the leading nations, Japan and Russia, have decreased since the late 1980s. China has by far overtaken the rest of the world as a result of the rapid development of freshwater aquaculture. Economic and political instability have affected Russian catches, which until 1990 included those from the former Soviet Union. The figures for Perú show the dramatic ups and downs of its huge anchovy fishery (see "Of Fish and Seabirds, Fishers and Chickens," p. 393).

that develop new products such as boats and fishing gear. Some even get involved in the management of fishing resources to prevent them from disappearing. Modern fishing ventures thus provide jobs not only to fishers, but also to technicians, marine biologists, marketing specialists, economists, and other experts. Women and the elderly often undertake processing and marketing in developing countries, thus contributing to social equity. Commercial fisheries provide a considerable portion of the export earnings of countries like Canada and Iceland and help sustain these nations' economies.

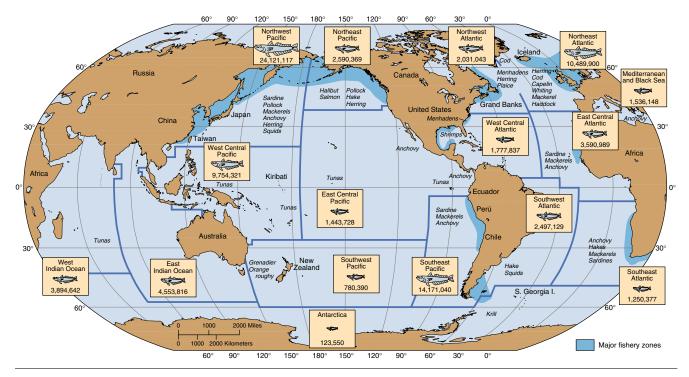
The amount of seafood consumed in various cultures varies widely because of both consumer tastes and the price and availability of seafood. The average Japanese eats 72.1 kg (159 lb) of fish a year, whereas Americans consume an average of 21.3 kg (46 lb) per person a year. Seafood consumption has been steadily increasing in the United States, Canada, and other developed countries as consumers look for healthy, low-fat sources of protein.

#### Major Fishing Areas

Most of the world's major fisheries are located near the coast (Fig. 17.4). These coastal fisheries exploit the rich waters of the **continental shelf**. Because shelf waters are shallow compared with the open ocean, it is relatively easy to harvest bottomdwelling, or **demersal**, species. Coastal fisheries also include **pelagic** catches: fishes, squids, and other animals that live in open water. **Primary production** is higher over the shelf than farther offshore, supporting much more abundant life (see Table 10.1, p. 228, and Fig. 15.25). Some of the richest fishing areas of the world are located in the highly productive waters where **upwelling** takes place, such as the coasts of Perú and southwest and northwest Africa (Fig. 17.4). Other significant coastal fisheries are found where the continental shelf is very wide, such as the Grand Banks of Newfoundland, the North Sea, and the Bering Sea.

Most of the world's fisheries are coastal. Coastal fisheries take both bottom, or demersal, and open-water, or pelagic, catches. They are mostly concentrated in waters where primary production is increased by upwelling.

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**FIGURE 17.4** The major marine fishing areas of the world, based on boundaries established by the Food and Agriculture Organization of the United Nations (FAO). Figures refer to the 1999 catches (in millions of tons) of each region. The figure for Antarctica incorporates catches for three separate FAO regions. Only five of the 18 FAO regions showed higher catches in 1999 than in 1989.

Notice from the map in Figure 17.4 that some of the largest catches are taken from the northwest Pacific and the northeast Atlantic. Being close to the major industrial nations, these areas have been intensively exploited for the longest time. A few other areas are less heavily exploited and still have some underexploited resources. This is the case in the Indian Ocean and around Antarctica. These areas are more remote and therefore more expensive to exploit. Fisheries in such remote areas, however, are rapidly increasing. Most fishing grounds in the Atlantic, Pacific, and Mediterranean are in decline or exhausted, while in the Indian Ocean catches have steadily increased.

Most marine food resources are taken from the continental shelf, which constitutes only about 8% of the total area of the ocean. Though the open ocean, the remaining 92%, supports fewer fisheries they are still very valuable. Many of these pelagic fisheries are located in upwelling areas beyond the continental shelf. Other fisheries, for example those for migratory species like tunas, extend far into the open ocean.

#### Major Food Species

There are thousands of species of fishes, crustaceans, and molluscs, but relatively few support major fisheries. A summary of the major commercial catches for the world is given in Table 17.1.

**Continental Shelf** The shallow, gently sloping edge of the continents, extending from the shore to the point where the slope gets steeper.

Chapter 2, p. 35; Figure 2.17

**Primary Production** The conversion by autotrophs of carbon dioxide into organic carbon, that is, the production of food.

Chapter 4, p. 73

The largest catches in the world are those for **clupeoid fishes**, small planktonfeeding fishes that form huge schools. They include herrings (often sold as "sardines"), anchovies (see the photo on page 383), sardines (or pilchards, as they are known in many parts of the world), menhadens, and shads (see Table 17.2).

They are usually concentrated over the continental shelf, but some species can also be found offshore in upwelling areas. They are caught with large **purse** 

**Upwelling** The upward flow of nutrient-rich deep water to the surface, resulting in greatly increased primary production.

Chapter 15, p. 349

*Plankton feeding fishes* use *gill rakers*, slender projections of the gills, to strain plankton from the water.

Chapter 8, p. 163

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| Table 17.2 Exam  | mples of Commercially Impo   | rtant Fishes Around the Wor   | ld  |
|--|--|---|---|
| Species  | Distribution and Habits  | Species   | Distribution and Habits   |
| Herrings ( <i>Clupea</i> )                                 | North Atlantic and Pacific;<br>schooling, plankton feeders;<br>38 cm (15 in)   |   | Temperate worldwide; demersal,<br>feed on bottom invertebrates<br>and fishes; 1 m (3 ft)                              |
| Sardines, or pilchards (Sardinops,<br>Sardinella, Sardina) | Mostly temperate worldwide;<br>schooling, plankton feeders;<br>30 cm (12 in)   | Hakes and whiting ( <i>Merluccius</i> )   | Mostly temperate worldwide;<br>demersal, feed on bottom<br>invertebrates and fishes;<br>2 m (6.5 ft) in some halibuts |
| Anchovies (Engraulis)                                      | Worldwide; schooling, plankton<br>feeders; 20 cm (8 in)  | Flatfishes: flounders, halibuts,<br>soles, and others ( <i>Platichthys</i> ,<br><i>Hippoglossus</i> , etc.) |   |
| Menhadens ( <i>Brevoortia</i> )                            | Temperate and subtropical<br>Atlantic; schooling, plankton<br>feeders; 38 cm (15 in)                                     | Tunas (Thunnus, Katsuwonus, etc.)   | Tropical and temperate; schooling,<br>carnivores; 4.3 m<br>(14 ft) in the bluefin tuna                                |
| Cods (Gadus)   | North Atlantic and Pacific;<br>demersal; feed on bottom<br>invertebrates and fishes; 1.5 m<br>(5 ft) in the Atlantic cod | Mackerels (Scomber,<br>Scomberomorus)   | Tropical and temperate worldwide;<br>schooling, carnivores;<br>2.4 m (8 ft)   |
| Haddock (Melanogrammus<br>aeglefinus)                      | North Atlantic; demersal, feed<br>mostly on bottom invertebrates;<br>90 cm (35 in)                                       | Salmon (Oncorhynchus, Salmo)  | North Pacific and Atlantic;<br>open ocean and rivers, carnivores;<br>1 m (3 ft)                                       |
| <i>Note:</i> Fishes are not drawn to scale.                | . The measurements given are the appro   | oximate maximum length of each speci  | es.   |

**seines** that surround and trap the schools (Figs. 17.5*b* and 17.6*b*).

Herrings, anchovies, and sardines are eaten fresh, canned, or pickled. Fish protein concentrate (FPC), or fish flour, an odorless powder used as a protein supplement for human consumption, is also made from these and other fishes. Most of the clupeoid catch, however—particularly that of menhadens and herrings—is ground into fish meal, an inexpensive protein supplement used in feed for poultry, livestock, and even other species of fish that are farmed. The fish are also pressed to obtain **fish oil**, used in the manufacture of products like margarine, cosmetics, and paints. Some of the catch finds its way into fertilizers and pet food as well. Fisheries such as these, where the catch is used for purposes other than direct human consumption, are known as **industrial fisheries**. Industrial fisheries are now estimated to account for over a third of the world's total.

Clupeoid fishes, herrings and their kin, provide the largest catches of fish. Most are used not directly as food but in industrial fisheries for fish meal and other products.

Cods and related fishes—the pollock, haddock, hakes, and whiting (Table 17.2)—make up another important group worldwide. These fishes are all demersal, cold-water species. They are caught with **trawls** that are dragged

TOLONOPE

INE

ERMEN

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(a)





**FIGURE 17.5** The European anchovy (*Engraulis encrasicholus*) is an important food fish. It is canned, salted, or cooked fresh. Basque fishers from the port of Bermeo (a) in the Bay of Biscay, northern Spain, make bountiful catches using purse seines (b). Fish is unloaded (c) and sold in the fish market (d). Women workers, or *neskatillas*, play an important role in the fishing routine. They are in charge of carrying and selling the fish.

(d)

(c)

along the bottom (Fig. 17.6c). The Atlantic cod (*Gadus morhua*) supported a very important fishery for centuries. European fishers were already fishing for it in the Grand Banks of Newfoundland a century before the arrival of the first colonists (and probably before Columbus). It was a vital source of inexpensive protein in many parts of the world. In an age before refrigeration, the cod was salted and dried for preservation before sailing back to Europe. The dried fish was soaked in water before cooking, just as it is done today in the Mediterranean and Caribbean. Now, however, most cods and related fishes are sold fresh or frozen.

The cod fishery on the Grand Banks lasted until 1992 when a moratorium was declared in an attempt to save the fishery from extinction. The Georges Bank fishery off New England was similarly closed

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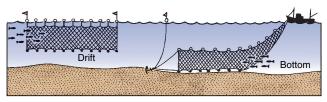
in 1994. The closure caused high unemployment among Canadian and American fishers and related workers, and higher prices for consumers. It also threatens to destroy traditional fishing cultures. But even worse, some experts predict that the cod populations will never recover.

Cod fisheries are also exhausted elsewhere in the North Atlantic. North Sea catches dropped from 277,000 metric tons in 1971 to 59,000 metric tons in 2000. As a result, vast areas were closed to cod fishing in 2001.

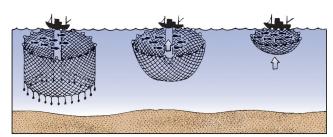
Jacks, mullets, rockfishes (including the ocean perches, also known as redfishes), and mackerels (Table 17.2) are also important in terms of worldwide tonnage. Canned mackerel from Japan and South America has become a cheap source of protein in some parts of the world. Flounders, halibuts, and other flatfishes are important catches in the United States, Canada, and other countries. Salmon, though now caught in much smaller numbers than formerly, are a very valuable catch. The salmon fishery is still important in the North Pacific in terms of the dollar value of the catch. Salmon are caught both along the coast and in the open ocean. The fishery is threatened, however, by environmental degradation, especially the destruction of salmon breeding sites (see "Migrations," p. 171).

The most important open-ocean fisheries are those for several species of tunas (Table 17.2). The migration routes of tunas crisscross the oceans, mostly in tropical waters (see Fig. 8.22). The skipjack, yellowfin, albacore, bigeye, and bluefin tunas command high prices in world markets. Most are eaten in affluent countries, either canned or raw as sashimi. They are caught by modern fleets that use sophisticated techniques to spot the schools in mid-ocean. The fishes are caught with large seines, surface longlines, and gill nets (Fig. 17.6). The fishing boats are equipped with freezers so that the fishes can be brought to port long after they are caught. Besides these high-tech fleets, some local, small-scale fisheries continue to exploit bonito, skipiack, and other tunas.

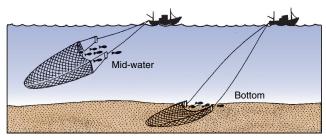
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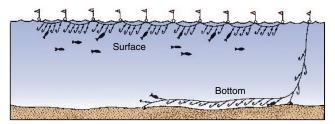
(a) Gill nets



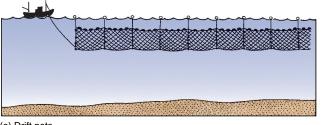
(b) Purse seine



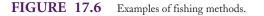
(c) Trawls



(d) Longline



(e) Drift nets



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Molluscs are the second most valuable group of marine food species after fishes. Several types of cephalopods provide the largest catches of molluscs (Table 17.1). Squids, cuttlefishes, and octopuses are especially popular in Far Eastern and Mediterranean countries (Fig. 17.7). Fishers use lighted boats to catch squid at night. Other important food molluscs are clams (Macoma and many others), oysters (Ostrea), mussels (Mytilus), scallops (Pecten), and abalones (Haliotis).

Crustaceans are prized as food the world over. Major fisheries exploit many types of shrimps and lobsters, all of which bring a high price. Blue crabs (Callinectes sapidus), king crabs (Paralithodes camtschaticus), Dungeness crabs (Cancer magister), and others are also harvested.

Many other groups of marine organisms are also eaten (Fig. 17.8), though they do not provide a great deal of food. Seaweeds, for instance, are eaten in many cultures, especially in the Far East (see "Seaweeds for Gourmets," p. 113). Sea urchins are esteemed for their gonads, or roe, which command an astronomical price, particularly in Japan. In California there is an expanding fishery for the red sea urchin (Strongylocentrotus franciscanus). Most of the roe is exported to Japan or sold to Japanese restaurants where, known as uni, it is eaten raw. Some species of sea cucumber are another common seafood. Called trepang or bêche-de-mer, they are dried, boiled, smoked, or eaten raw in the Orient. Examples of other invertebrates used as food are jellyfishes in the Orient, gooseneck barnacles in Spain, and polychaete worms in the South Pacific.

Sea turtles are still hunted and their eggs still gathered nearly everywhere they occur, even where they are officially protected. Seals and whales are also eaten in some places, and there are traditional fisheries for marine mammals in the Arctic (see Fig. 4.2), West Indies, and the South Pacific. These traditional fisheries are a source of considerable controversy because the species involved are endangered and modern technologies like powerboats are used. Should the fisheries be banned or left entirely unregulated? A compromise between these two extremes



FIGURE 17.7 Octopuses have long been valued as a culinary delicacy. These freshly caught individuals were photographed on the Greek island of Paros in the Aegean Sea.



FIGURE 17.8 Raw fish, shrimp, seaweed, and sea urchin roe are used in *sushi* and *sashimi*, Japanese delicacies that have become popular around the world.

involves questions of the rights of indigenous cultures, the ethics of conservation, and international politics.

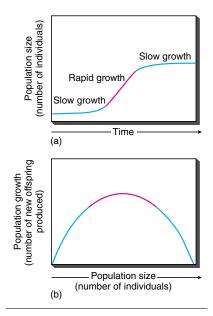
#### Optimal Yields and Overfishing

Like all living things, species we harvest for food can reproduce to replace the individuals that are lost to disease and predators, including humans. Because these living resources can replace themselves, they are known as **renewable resources.** Resources that are not naturally replaced, like oil and minerals, are called **nonrenewable resources** (see "Non-Living Resources from the Sea Floor," p. 401). Experience has shown, however, that though the food resources of the ocean are renewable, they are not inexhaustible. Renewable, yes; unlimited, no. Let's see why.

Imagine that fishers discover a new, untapped population of sardines. The new fishery is very successful, and the fishers make handsome profits. The news spreads, and soon other fishers join in. After several years, **overfishing** results: Catches dwindle, and the fish caught are smaller. The fishery becomes unprofitable, and many, if not most, of the fishers go out of business.

What happened? The reproductive rate of sardines—or salmon, scallops, or sharpnose surfperches—depends, at least in part, on the size of the population, or **stock**, as it is known to fisheries biologists. Like dinoflagellates growing in a jar (see Fig. 10.4), fish stocks grow fastest when there are neither too few nor too many individuals in the population. If the population size is very small, the number of young being born is also small because there are not many potential parents. If the population is too large, competition, overcrowding, and so forth slow down





**FIGURE 17.9** (*a*) The theoretical growth of a population that begins with just a few individuals. At first, with only a few adults to produce offspring, the population increases very slowly (*blue line*). As the population size gradually increases, so does the number of offspring, and the rate of growth begins to increase (*red line*). Eventually the population reaches the point where limiting factors such as food shortage and crowding prevent further growth (*blue line*). (*b*) Thus, the rate of growth is directly related to population size and is maximal at intermediate abundances.

the growth rate. The number of new young, that is, the population growth rate, is highest at some intermediate population density (Fig. 17.9).

To harvest the stock in the optimal way, one must consider this feature of population growth. Obviously, it would be foolish to harvest the entire stock at once, because no individuals would be left to reproduce, and the fishery would be destroyed forever. If the fishery is to last indefinitely, the number of fish caught can be no more than the number of new

**Cephalopods** Squids, octopuses, and related molluscs that use sucker-bearing arms to capture prey and, with a few exceptions, lack a shell.

Chapter 7, p. 131

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fish added through reproduction; if more are caught, the population will decline. The **sustainable yield** of a population is the amount that can be caught and just maintain a constant population size. In other words, the catch is just large enough to prevent the population from growing but not so large as to reduce it.

Because the growth rate depends on the population size, so does the sustainable yield. When the stock is large, it is held in check by natural mortality; even a small harvest causes a reduction in the population. Very small populations also have a low growth rate. In this case, fishing is more dangerous because it can threaten the seed stock and drive the species to the brink of extinction.

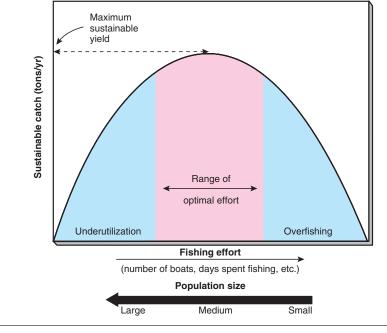
The highest catch that can be continued year after year without threatening the stock is called the **maximum sustainable yield.** It occurs at medium population size, when the natural growth rate is highest. From the point of view of profit and food production, this can be thought of as the optimal catch.

The size of the catch, and therefore of the stock, is directly related to **fishing effort:** how many boats and fishers there are, how long they stay at sea, and so forth. When little effort is put into the fishery, of course, the catch is small. Only a small fraction of the stock is removed by fishing, and the population grows until limited by natural factors. The population remains secure, but the fishery yields less food and less profit than it could safely sustain.

With intense effort the catch exceeds the maximum sustainable yield. Before long the stock declines and catches fall no matter how much fishing effort is expended: Overfishing has occurred.

A plot of the sustainable yield versus fishing effort, then, is very similar to a plot of the population growth rate versus the size of the stock (Fig. 17.10). The maximum sustainable yield occurs at moderate levels of effort, which result in intermediate stock sizes.

Unfortunately, the biological properties of most fisheries stocks do not mix well with the principles of economics. Most fisheries are profitable when harvested at the level of the optimum catch. As long as there is money to be made,



**FIGURE 17.10** A generalized, theoretical curve showing that as fishing effort increases, so does the catch, but only up to a point, which is the biologically optimal catch. After this point the overexploited fishery will yield smaller and smaller catches as the effort increases. The curve is called a catch-effort curve.

more fishers and more boats will be attracted to the fishery, and the catch will exceed the optimal level. In an open fishery, one that is completely unregulated, market forces inevitably lead to overfishing. Economic forces can even cause a species to be fished to extinction.

Overfishing results when catches are higher than the maximum sustainable yield, or optimal catch, of a fishery. Free-market forces almost always result in overfishing if a profitable fishery is left unregulated.

Overfishing is not just a theoretical problem. FAO has estimated that by 2000, 47% to 50% of all marine commercial fisheries were fully exploited, 15% to 18% were overexploited and had no potential for future exploitation, and 9% to 10% were depleted. Good examples are the stocks of cod, haddock, herring, halibut, salmon, and other fishes in the North Sea and the North Atlantic and North Pacific oceans. As with the great whales (see "Whales, Dolphins, and Porpoises," p. 190), fishing effort in these fisheries has long surpassed the optimal catch. The traditional major fishing areas of the world are not the only ones becoming exhausted. Small-scale local fisheries in the tropics, where most people live and where food is needed the most, are being rapidly decimated.

Most of the world's fisheries are already fully exploited, and a quarter or more are overexploited or even exhausted.

The danger of overfishing is particularly serious in herrings, anchovies, and other clupeoid fishes. These species often undergo dramatic population cycles and may therefore be especially vulnerable to fishing pressure. The Pacific sardine (*Sardinops caerulea*), for example, supported a booming fishery in California that collapsed in the 1940s. The collapse is thought to have occurred when heavy fishing amplified a natural low point in the cycle. Though there are signs of recovery and a limited catch is now allowed, the fishery may never fully recover. Another infamous collapse of a

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IV. Humans and the Seas 17. Resource

17. Resources from the Sea

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# OF FISH AND SEABIRDS, FISHERS AND CHICKENS

The ocean has been good to Perú. As the cold Perú Current flows northward, coastal upwelling (see Fig. 15.30) pumps nutrients from the depths in huge amounts. The resulting productivity supports a rich harvest of plankton that in turn feeds immense schools of the Peruvian anchovy,



Islas Ballestas, guano islands off Pisco, Perú.

or *anchoveta* (*Engraulis ringens*). This high productivity is a critical part of a complex cycle that has had tremendous consequences for the economy of Perú.

From time immemorial, clouds of cormorants, boobies, and other seabirds have gorged themselves on the anchovy schools. The birds roost and nest on small islands along the coast. With hardly any rain to wash them away, the birds' droppings slowly build up in the dry climate. Over thousands of years the droppings have accumulated into layers as thick as 45 m (150 ft). This thick crust, called **guano**, is rich in nitrogen and phosphorus and is an excellent fertilizer.

The fertilizer starts out thousands of miles away, when organic matter sinks from the surface to the dark depths of the Pacific. When the organic material decomposes, nitrate and phosphate, the main nutrients for phytoplankton, are released into the water. The nutrients remain in the deep, unavailable to phytoplankton, until upwelling eventually brings them into shallow water along Perú's coast (see Fig. 15.30). Here they are taken up in primary production by diatoms and other phytoplankton, which form the base of the food web. The plankton are eaten by the anchovies that feed the guano birds. Nutrients thus travel from the bottom of the Pacific to the coastal islands of Perú with the help of upwelling, plankton, anchovies, and seabird droppings!

And then people came along. Guano, a valuable agricultural fertilizer, was mined and exported. The guano industry brought considerable wealth to Perú, and by the end of the nineteenth century millions of tons had been mined. What took thousands of years to deposit was used up in a matter of decades.

The anchovies were next. A commercial anchovy fishery was established in the early 1950s and grew to unprecedented dimensions. It became the world's largest single fishery and made Perú



Immature boobies (*Sula*) on a Peruvian guano island.

the largest fishing nation (Fig. 17.3) in history. Catches continued to increase, except in years when El Niño, the warm currents that occasionally arrive at Christmastime, interfered with upwelling (see "The El Niño—Southern Oscillation Phenomenon," p. 351).

Ironically, anchovies are so small that they are not often used for human consumption. Most of the catch was exported as fish meal for chicken feed. Fish meal from Perú became the world's single largest source of protein meal. Most of this protein was consumed by farm animals in other parts of the world, while many Peruvians continued to have protein-deficient diets.

By the late 1960s, the annual catch surpassed the estimated optimal, or maximum sustainable, yield of around 10 million tons a year. After the 12.3-million-ton catch of 1970, the fishery collapsed. The guano birds also suffered a dramatic decline. The El Niño of 1972 added to these woes.

The collapse had widespread effects. The price of other protein meals, particularly soybean meal, increased. In Brazil alone, several million acres of tropical rain forest were cleared to grow soybeans.

The reasons for the collapse of the anchovy fishery are not entirely clear. Overfishing may not have been the only cause. Clupeoid fishes like the Peruvian anchovy naturally undergo population cycles. It may well have been that the *combination* of heavy fishing pressure, a dip in the natural cycle, and, a little later, an El Niño pushed the anchovy over the brink. Maybe the management of fisheries for species like the Peruvian anchovy needs to be tuned to the fishes' biology, with heavy fishing in some years and sharply curtailed harvests in others.

Since its collapse, annual catches of the Peruvian anchovy have varied from a low of 93,654 tons in 1984 to 9.8 million tons in 1994, becoming again the world's largest marine fish catch and making Perú the second-largest fishing nation. The 1997–98 El Niño, however, proved to be disastrous. It caused a 78% drop in the catch. The 1999 catch, however, jumped back to 8.7 million tons. Will the number of anchovy, and guano birds, eventually return to their former levels? Perhaps more important is whether any lessons have been learned. Will the same mistakes be repeated elsewhere?

large clupeoid fishery is the case of the Peruvian anchovy, or *anchoveta* (*Engraulis ringens*; see "Of Fish and Seabirds, Fishers and Chickens," above).

Tunas are heading the same way. The northern bluefin tuna (*Thunnus thynnus*; see Fig. 1.19) is among the largest of bony fishes and the most valuable; *sashimi* and *sushi* lovers have been known to pay as much as \$770 per kilogram (\$350 per pound) in Tokyo. Not surprisingly, bluefin are down to less than 10% of their former numbers in the western Atlantic. Fishing nations have been slow to act to save the bluefin, resisting efforts to declare it an endangered species. It was not until 1995 that nations agreed to cut their catches in half, which many fisheries scientists regard as too little, too late.

Another prized food fish, the swordfish (*Xiphias*), is close to commercial extinction in the North Atlantic. Populations here fell approximately 70%

between 1960 and the late 1990s, and most of the fish caught by U.S. fishing boats are caught before they are old enough to reproduce. Fisheries that target swordfish have closed in large areas of U.S. waters in the Atlantic and Gulf of Mexico.

There are other threats to fishery resources. Damage to critical habitats is another serious cause for concern. Estuaries, mangrove forests, seagrass beds, and other threatened environments are critical breeding grounds and nurseries for fishes, lobsters, shrimps, scallops, and other valuable species. Three-quarters of the commercial catch of the United States consists of species that inhabit estuaries during part of their life. Bottom trawls disrupt the sea floor, another form of habitat damage.

**By-catch**, organisms that are caught unintentionally while fishing for other species, is another problem. Even where deliberate fishing for swordfish is closed, for example, many swordfish are caught and killed on longlines set for tuna, impeding swordfish recovery. For this reason some areas have also been closed to longline fishing. Trawling also produces a lot of by-catch. This is particularly true of shrimp fisheries, where as much as 95% of the total catch is by-catch. Some of the by-catch is kept but much of it is discarded. Even if it is released alive, most of the discarded by-catch dies. A large part of the by-catch in trawl fisheries is juveniles of valuable species sought in other fisheries. Yet another threat to fisheries is pollution from oil spills, sewage, and toxic chemicals. The effects of habitat destruction and pollution are examined further in Chapter 18.

#### Managing the Resources

Given the danger of overfishing, most people agree that fisheries resources should be harvested in a way that does not deplete them beyond recovery. In other words, fisheries must be managed to ensure their long-term value. The wise management of fisheries stocks is much harder than it sounds. For one thing, the maximum sustainable yield can be very difficult to estimate. To do so, fisheries biologists need detailed information about the size of fisheries stocks, how fast the organisms grow and reproduce, how long they live, and what they eat (which often changes at different stages of the life cycle; see Fig. 15.23). Such information is rarely easy to obtain and often unavailable. Biologists may have to rely on rough "guesstimates" or questionable assumptions, which makes their estimates of the optimal catch less reliable.

Furthermore, real fisheries are much more complex than we have indicated. The smooth catch effort curve shown in Figure 17.10 represents a greatly simplified model and does not take many natural features into account. For example, the harvested species may be competing with other species, and fishing pressure might alter the competitive balance. Schools may get smaller as a result of fishing. This might not only make the fish harder to catch, it might adversely affect their behavior and reproduction. Simple models do not consider the size of the fish caught, but it makes a difference whether large, older individuals or small, younger ones are caught, for example, because large individuals typically produce many more eggs than small ones. Similarly, the time of year when fishing is done may be important, such as whether the catch is taken before or after the breeding season. These natural complexities can have dramatic consequences, and could cause a fishery to fail unexpectedly if not taken into account.

Given the uncertainties of determining optimal catches and the potentially disastrous effects of overfishing, it can be argued that the catch should be set somewhat lower than the estimated optimum just to be on the safe side. A fisher, however, with a family to feed and boat payments to make, might have different ideas. The same can be said of cannery and dockyard workers, gear merchants, bankers, and all the other people who depend directly or indirectly on the fishery. Thus, fisheries management is a complex, often controversial, matter that is affected by economic and political factors as well as biological ones. If the catch is harvested by more than one nation, international relations also come into play.

Once a desired catch level is agreed on, there are a number of ways to manage the fishery. Limits may be placed on the catch of each boat or, in an international fishery, each nation. Alternatively, the total catch may be limited, with the season being closed as soon as the target catch is reached. Restrictions can be placed on the number of boats or fishers, on the length of the season, or on the areas open to fishing. Fishers may be prohibited from taking individuals of certain sizes or, if the sexes can be told apart, from taking females. Governments may also reduce their subsidies or even pay fishers to give up fishing.

Many forms of fisheries management involve controls on the type of gear used. The size and power of boats, for example, can be limited. Certain methods of fishing can be banned altogether. Longlining, for example, might be permitted but not bottom trawls. The mesh size of nets, which partially determines their efficiency and the size and species of the individuals caught, can also be regulated (Fig. 17.11).

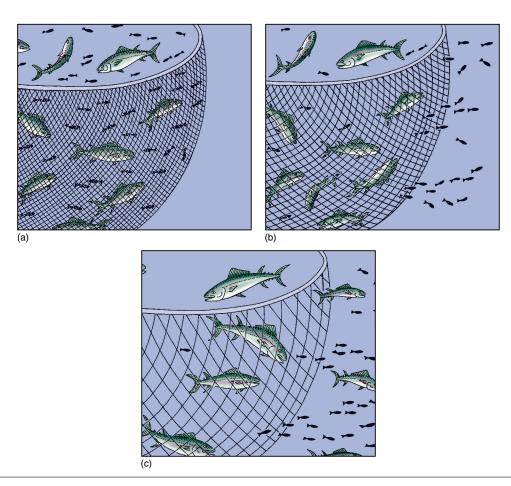
The total collapse of once thriving fisheries has forced the use of drastic measures. Complete bans, however, are in effect in less than 1% of the world's fishing grounds. The establishment of reserves or sanctuaries to preserve important habitats is another way to safeguard the survival of important species. The species can then repopulate outside areas that are open to fishing.

The management of fisheries to prevent overfishing includes the establishment of quotas, restrictions on the type of fishing gear, the establishment of reserves where fishing is banned, and other measures.

Besides preventing overfishing, management measures may be undertaken to help restore stocks that have become depleted. These measures may involve the improvement and protection of essential habitats or the transplantation of artificially raised young.

Fishing regulations can be implemented and enforced fairly easily in a small bay or estuary, but waters offshore are a different story. It has long been agreed that the resources of the open ocean outside the territorial waters of any nation are the common property of all nations. This has

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**FIGURE 17.11** Both the size and species of fishes caught by nets can be controlled by the net's mesh size. (*a*) A fine net might catch both sardines and tuna. (*b*) With a larger mesh size the sardines escape and only tuna are caught. (*c*) With an even larger mesh size only large tuna are taken.

led to contention over the boundaries of some nations' territorial waters, especially where the continental shelf is wide and rich in resources. Traditionally, a country's territorial waters extended 3 nautical miles (5.5 km) offshore, though this varied from country to country. Some nations then began to exclude fishing fleets from other nations by extending their borders farther offshore. Foreign vessels that failed to respect the new boundaries were confiscated, and fishing disputes led to war in some cases. In certain fisheries, nations have been able to agree on joint management schemes. The International Whaling Commission is one example; the shrimp fishery in the Gulf of Mexico is another. Unfortunately, such international regulatory efforts have been limited in scope and jurisdiction.

A more general compromise was finally reached in 1982 with the United Nations Convention on the Law of the Sea (see "Prospects for the Future," p. 435). The United States became the 105th nation to sign the treaty in 1989. It allows nations to establish an exclusive economic zone (EEZ) 200 nautical miles (370 km) offshore. Within this zone, nations can completely control their fisheries, oil, and mineral resources. They can keep foreign fishers out if they wish or sell fishing licenses to foreign fleets. In 1985, for instance, the former Soviet Union paid \$1.5 million for a one-year fishing agreement with the Republic of Kiribati. This Pacific nation consists of tiny islands with a total area of just 725 km<sup>2</sup> (280 mi<sup>2</sup>), but it has a 3.4 million-km<sup>2</sup> (1.3 million-mi<sup>2</sup>) EEZ!

EEZs cannot always be policed, of course, and foreign fishers may sneak in and fish without permission or with illegal gear. When caught, these pirate vessels are usually impounded.

The establishment of an exclusive economic zone (EEZ) allows nations to protect fishing and other resources 200 nautical miles around their shores.

**Competition** When one organism uses a scarce resource to the detriment of another.

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In the United States the Magnuson-Stevens Fisheries Conservation and Management Act, as amended in 1996, provides for the conservation and management of the fisheries resources within the EEZ. Vessels of foreign nations that have signed fishing agreements with the United States are allowed to fish in the EEZ only after receiving a fishing permit. They are given an allocation for particular species and are not permitted to catch more than the allotted amount.

More than 90% of the ocean's present fisheries lie within the EEZ of one nation or another, but the high seas are still considered common property. A number of potential new fisheries lie outside territorial boundaries and thus are open to all nations.

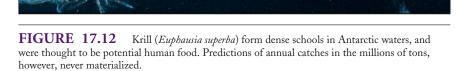
#### New Fisheries

The specter of overfishing casts doubt on the ocean's future ability to provide food. More effective management, the control of pollution, and the conservation of threatened environments may help, but a growing world population will place increasing demands on the sea's resources. Fisheries biologists have for decades been absorbed with the possibility of tapping new or underexploited fisheries.

One possibility is to increase the use of the by-catch. FAO has estimated that the marine by-catch is 29 million tons a year, about a third of the catch that is kept! The main problem with much of the by-catch is not so much that there is anything wrong with it but that people simply will not buy it. Consumer tastes are fickle and vary tremendously from place to place. What is considered a delicacy in one place is junk in another. Hake (Table 17.2), for instance, is prized in Europe but not in the United States. Croakers and sea robins are common throwaway fishes in the United States that are eaten elsewhere.

Squids are caught in large numbers in California, but most of the catch is exported, primarily to Japan and Europe. Squids are a delicious source of lean protein, but American consumers were suspicious of the sucker-armed molluscs, though marketing squid by its Italian





name of *calamari* has increased its appeal. A name change also helped overcome consumer resistance to eating dolphinfish (*Coryphaena hippurus*), certainly a fish and not a dolphin. The more seductive Hawaiian name of *mahimahi* helped enhance its marketability.

A potential use of the by-catch is to process it into products that have more market appeal. In the surimi process, for example, low-value fish is washed to remove fat, minced, and mixed with flavorings and preservatives. Appropriately shaped, it is sold as imitation crab, lobster, shrimp, or scallops. Alaskan pollock is now the main component, but less desirable fish species could also be used. Processed fish products such as fish sticks could also open the market to less popular catches. Unwanted catches could also be converted into fish flour and used to protein-enrich all sorts of processed foods.

The highly productive waters around Antarctica and its associated island groups are often mentioned as potential sources of increased commercial catches. Even here, however, overfishing is taking its toll. The waters around South Georgia Island, for instance, are already overfished. Illegal fishing has seriously depleted the Antarctic toothfish (*Dissostichus mawsoni*) in some areas of the Southern Ocean. Antarctic catches include various fishes, squids, the southern king crab, and krill (Fig. 17.12).

There are other potential sources of food from the sea. Some of these are underutilized or unconventional species like squid and other cephalopods, flying fishes, and pelagic crabs (Pleuroncodes; Fig. 17.13). Lanternfishes (Myctophum; see Fig. 16.8b) represent another potential fishery. They are found in deep water but migrate to the surface at night in the deep scattering layer. They form dense schools in most oceans. These and other species remain underexploited or completely unexploited mainly because of lack of consumer acceptance or the absence of efficient fishing methods. Some may eventually support successful fisheries, though probably for fish meal rather than food for human consumption.

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**FIGURE 17.13** *Pleuroncodes,* also called the lobster krill or tuna crab, is a pelagic crab that has been suggested as a potential source of human food. Large swarms of *P. planipes,* with a maximum length of 13 cm (5 in), are often washed ashore on the Pacific coast of California and Mexico, turning beaches bright red. A possible problem with this plan is that *Pleuroncodes* is an important food for tunas.

Fishing lower in the trophic pyramid as a result of the disappearance of the most valuable fishes, which happen to be higher in the pyramid, may have dangerous consequences. Such a shift may cause unexpected changes in the whole ecosystem, such as an increase in the number of non-utilized plankton or in undesirable predators like jellyfishes and comb jellies. Overfishing appears to be responsible for the destruction of kelp forests by sea urchins in the Aleutian Islands in Alaska. Because fish-eating seals and sea lions have become less common, killer whales that normally hunt them have turned instead to sea otters, which keep sea urchins under control (see "Kelp Communities," p. 290).

Measures to increase the supply of food from the sea include an increase in the exploitation of underutilized species and the development of new fisheries.

#### Mariculture

Instead of continuing to overfish the dwindling natural food resources of the oceans, why not raise marine organisms as we do farm animals? This is not a new idea: The Chinese have been doing it with freshwater fishes for thousands of years. The Romans farmed oysters, and the early Hawaiians built walled fish ponds along the coast to raise mullet and milkfish. The application of farming techniques to the growth and harvesting of marine organisms is known as mariculture, the agriculture of the sea. A more general term is aquaculture, which is applied to the farming of both freshwater and marine organisms. The worldwide culture of marine organisms reached 22.7 million metric tons in 1999, with an estimated value of \$29.0 million. These figures, almost three times the volume and more than twice the value of those in 1989, show the rapid growth of mariculture. The 1999 figures are higher if the culture of freshwater or-

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ganisms (20.3 million metric tons with a value of \$25.1 million) are included. Aquaculture has also grown more than three times faster than livestock production on land. Approximately 30% of the seafood consumed around the world is farmed, although this is mostly freshwater fish. The growth of fish farming averaged 11% a year during the 1990s, and the output for 2010 is predicted to be higher than cattle ranching around the world. Shrimp mariculture has shown tremendous growth, with an increase in volume of more than 300% since the mid-1980s. Farmed shrimp now account for around 25% of the estimated 3 million tons of shrimp consumed every year around the world. Though mariculture is used primarily to grow food species, it is also being used to grow commodities such as cultured pearls (see "Bivalves," p. 131) and fishes for the aquarium trade (see p. 400).

Mariculture is the farming of the sea for food and other resources. The term aquaculture includes the culture of freshwater species as well.

Traditional mariculture is still practiced in several parts of the world, particularly in the Orient. The milkfish (*Chanos chanos*) is farmed in ponds filled with brackish water, that is, partially diluted seawater (Fig. 17.14). The immature fish, or fry, are captured at sea, transferred to the ponds, and fed with agricultural byproducts. In this way, wastes are converted to fish flesh that is cheaper to produce than pork or beef. These fish farms provide not only high-protein food but jobs as well.

With various modifications, similar operations are used to farm other fishes, molluscs, shrimps, and seaweeds in many parts of the world. The fry or spat (immature bivalve molluscs) are transplanted to favorable sites in coves (Fig. 17.15), natural ponds, and estuaries, including

Deep Scattering Layer A group of organisms, mostly fishes and shrimps, that migrate vertically between the mesopelagic and epipelagic zones.

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**FIGURE 17.14** Milkfish (*Chanos chanos*) being harvested from a brackish-water pond in central Philippines. Some will be eaten, others allowed to mature and spawn to replenish ponds.

**FIGURE 17.15** The farming of oysters (*Crassostrea glomerata*) in Whangaroa, New Zealand.

fjords and mangrove forests. These may be enclosed with wooden fences, nylon netting, concrete, or other materials. Salmon and other fishes are raised in large floating pens or cages. Pacific thread fin, or *moi (Polydactylus sexfilis)* is raised in giant cages submerged off Hawai'i. Oysters, mussels, and other molluscs are grown on racks, in baskets, hanging from rafts, and in other ingenious ways. This type of mariculture, in which farming takes place under more or less natural conditions with relatively little manipulation by humans, is known as **open mariculture,** or **semi-culture.** 

In some countries, however, the farming of high-value food species is often a different story. In what can best be described as the domestication of marine organisms, growth is maximized by almost totally controlling the organisms and their environment. This type of mariculture is called **closed**, or **intensive**, **mariculture**.

Mariculture poses many problems, and only a small percentage of marine food species can be farmed under such artificial conditions (Table 17.3). Obviously, species like clupeoid fishes and tunas that require large, open spaces are not good candidates for intensive mariculture. To be farmed successfully, most species need specialized sites and equipment. Water pumped into tanks, pools, or other holding facilities must be free of pollutants and carefully checked for temperature, salinity, and other chemical factors. Toxic wastes from the organisms themselves must also be removed. Food can be a problem because the various stages of a species usually have different food requirements. This is a particular problem when trying to culture planktonic larval stages because they require specially cultured food. Predators and disease-causing organisms must be periodically removed or killed. Parasites and disease can be devastating under the crowded conditions typical of culture operations. Viral infections pose a serious threat to shrimp farming. Even sneaky seabirds and sea lions have learned to help themselves to the precious fish that are raised so painstakingly. Crowded conditions tend to cause cannibalism among fishes and crustaceans. Juvenile American lobsters, for instance, must be kept apart or they eat each other. Because of all these problems, the culture of some species, like lobsters, is still in the experimental stage. Commercial mariculture, however, is a challenge that many enterprising, business-oriented fisheries scientists are willing to accept. It is now possible, for example, to freeze shrimp sperm, ensuring year-round reproduction. We have learned to induce the settlement of the planktonic larvae of abalone, a valuable mollusc. Scientists can even create oysters with three sets of chromosomes, instead of the normal two. This makes them sterile. Normal oysters develop a strong taste when their eggs mature, but sterile ones, which do not produce eggs, are always tasty.

Rather than raising them all the way to harvest, some species are grown for only a short time, then released as fry or juveniles to enrich natural populations in a process known as seeding. Salmon are an interesting example of seeding. In some places, especially Europe, salmon are held in captivity their entire lives, from hatching to harvest. In other places the salmon are released as juveniles to feed and grow at sea. Several years later they return as full-grown adults to the stream where they were released. Not only can they be caught by commercial and sport fishers in the usual way, but they swim right back to the hatchery, where the ones not used for breeding can be caught and harvested. This practice, known as salmon ranching, originated in the Pacific Northwest of North America but has been transplanted to locations as far away as Chile and New Zealand.

Most mariculture operations require expensive equipment and specialized personnel. These demands further restrict the number of different species that are cultured: Some species that can be farmed are not because it is not profitable. Species that are cultured are usually those that command high prices. Table

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that someday intensive mariculture will provide a significant amount of relatively cheap food. They pin these hopes on the development of technological improvements and fast-growing varieties of food species. Already, shrimp mariculture is a significant source of foreign exchange earnings for several developing countries. The application of genetic engineering and other forms of **biotechnology** to mariculture is an exciting possibility. Genetic engineering may soon allow scientists to alter the genetic information contained in a species' DNA to produce faster-growing, more disease-resistant, or better-tasting strains. Another possibility is to pump nutrient-rich water from the deep sea or from sewage discharges and use it to grow the planktonic algae that are fed to the larvae of fish and other species. The use of warm-water discharges from power plants, producing faster growth rates, is another prospect (Fig. 17.16).

# Marine Life as Items of Commerce and Recreation

The living resources of the sea are used in many ways other than food. Timber and charcoal are obtained from mangroves. Jewelry is made from pearls, shells, and black and precious corals, and leather from the saltwater crocodile (Fig. 17.17), sea snakes, sharks, and other fishes. Seaweeds provide chemicals that are widely used in food processing, cosmetics, plastics, and other products (see "Economic Importance," p. 112). Many of these resources, however, are being over-exploited. Rich mangrove forests are used for rubbish disposal and cleared for shrimp farms. Black and precious coral have disappeared in many areas. Many endangered species are still taken. Fur seals, for example, are killed for their pelts, and hawksbill turtles are taken for tortoiseshell.

**DNA** Nucleic acid that contains the cell's genetic code. *Chapter 4, p. 70* 

| Species Cultured   | Major Areas Where Cultured   |  |  |
|--|--|--|--|
| Fishes   |  |  |  |
| Milkfish (Chanos chanos)   | Southeast Asia   |  |  |
| Pacific salmon (Oncorhynchus)  | U.S., Canada, Chile, Japan   |  |  |
| Atlantic salmon (Salmo)  | U.S., Canada, Chile, Europe  |  |  |
| Mullets (Mugil)  | Southeast Asia, Mediterranean                                      |  |  |
| Flatfishes (Solea and others)  | Europe   |  |  |
| Yellowtail (Seriola)   | Japan  |  |  |
| Red seabream (Pagrus major)  | Japan  |  |  |
| Horse mackerel (Trachurus)   | Japan  |  |  |
| Puffer (Fugu)  | Japan  |  |  |
| Molluscs   |  |  |  |
| Oysters (Crassostrea, Ostrea)  | U.S., Europe, Japan, Taiwan, Australia,<br>New Zealand             |  |  |
| Abalone (Haliotis)   | U.S., Japan  |  |  |
| Mussels (Mytilus, Perna)   | U.S., Europe, New Zealand  |  |  |
| Scallops (Pecten, Patinopecten)  | Europe, Japan  |  |  |
| Clams, cockles (Anadara and others)                                    | Southeast Asia   |  |  |
| Crustaceans  |  |  |  |
| Shrimps (Penaeus and others)   | Southeast Asia, Ecuador, China, India,<br>Bangladesh, Mexico, U.S. |  |  |
| Seaweeds   |  |  |  |
| Red ( <i>Porphyra, Eucheuma</i> ) and brown ( <i>Laminaria</i> ) algae | Japan, China, Southeast Asia, South Pacific                        |  |  |

Thus, instead of mass-producing cheap protein for a hungry world, mariculture tends to provide variety in the diet of the affluent.

Another drawback of mariculture is pollution. Fish farming in which thousands of fish are concentrated in ponds along the coast or in extensive floating pens releases huge amounts of feces, urine, and uneaten food that ultimately degrade water quality. The decomposition of these wastes depletes oxygen in the water and releases nutrients that can trigger harmful algal blooms.

Some fish farms also use chemicals like antibiotics, which may be potentially harmful. Another risk is the introduction of diseases to local marine species in the wild. Even more devastating can be the destruction of the natural environment. Clearing for shrimp farms, for example, has been responsible for the massive deforestation of mangroves in countries like Thailand and Ecuador (see "Modification and Destruction of Habitats," p. 407). This destruction has reduced the natural stocks of local species that use mangrove forests as nurseries. Though shrimp is a more profitable product, less food is actually produced. Catching fish from the wild to feed farmed fish, a common practice, may also deplete wild fisheries.

Still, some fisheries scientists and economists are optimistic. They predict



**FIGURE 17.16** A Japanese flounder, or bastard halibut (*Paralichthys olivaceus*), grown at a mariculture facility in Hawai'i. This operation uses cold, nutrient-rich water that is pumped from a depth of 600 m (2,000 ft) not just to raise fish but mainly to generate power. The flounder, or *hirame*, commands high prices because it is highly sought for raw fish dishes such as *sashimi*.



**FIGURE 17.17** Saltwater crocodiles (*Crocodylus porosus*), here grown together with freshwater crocodiles (*C. novaeguineae*), are farmed in Papua New Guinea for their valuable skin. This farm was set up as a way to dispose of chicken offal from a chicken farm and earn some money in the process. Saltwater crocodiles are worth more than their freshwater cousins because they have smaller scales and therefore more of the skin can be used. They are harvested when they reach approximately 1 m (3 ft) in length.

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#### Drugs from the Sea

Chemical compounds that are obtained from marine organisms, or marine natural products, have potential for use in medicine. The medicinal use of marine natural products by the Chinese probably goes back a few thousand years, but such use in the West has been limited. Recent years, however, have seen a dramatic upsurge in the systematic collection, analysis, and testing of new material. The search for drugs from the sea has become one of the most exciting branches of marine science, combining the fields of biology, chemistry, and pharmacology (see "Take Two Sponges and Call Me in the Morning," p. 401).

#### Fisheries for Fun

For millions, the living resources of the sea provide not a livelihood but relaxation, an ideal way to spend leisure time (see "Oceans and Recreation," p. 434). Recreational anglers catch everything from lobsters to big-game fishes like swordfish (Xiphias gladius) and marlins (Makaira, Tetrapturus). In the United States the marine recreational catch is estimated to be around 30% of the commercial catch of food fishes. Marine recreational fisheries are the basis of a multibillion-dollar business worldwide. Recreational fishers buy boating and fishing equipment, go on fishing charters, and travel long distances to pursue their hobby, supporting the tourist trade. There is a growing conservation ethic among the recreational fishing community. Many fishers do not keep their catch, but instead choose to release it alive. Although some released fish die, studies indicate that many survive. Many recreational fishers assist fisheries research by marking the fish with special tags before releasing them. Sport fishers in many places are also a powerful political voice for conservation. Still, recreational fisheries can exert tremendous pressure on fish stocks and therefore need to be carefully managed.

Business and fun are also combined in the thriving **aquarium trade**. Though the aquarium hobby is dominated by freshwater fishes, marine aquaria are growing quickly in popularity. Studies

### TAKE TWO SPONGES AND CALL ME In the morning

Obtaining drugs from the sea is not an easy task. It involves a sharp eye, intuition, good luck, and lots of frustration. It means diving in awesomely beautiful coral reefs as well as working countless hours in the chemistry lab.

Colorful attached invertebrates that live in coral reefs sponges, soft corals, nudibranchs, sea squirts—are good candidates for biomedical research. Though seemingly defenseless, these very visible, soft, attached animals are rarely eaten by hungry fishes or crabs. This fact suggests that they have some type of defensive mechanism. Many of these colorful invertebrates are known to produce unique chemical substances that make them taste bad or allow them to get rid of hostile neighbors, and these chemical substances may have properties that can be beneficial to humans too.

Marine organisms of potential value as drugs are collected, frozen, and sent to the lab for analysis. Crude extracts using alcohol and other solvents undergo trials to test their ability to kill or inhibit the growth of bacteria (that is, to act as antibiotics), fungi, and viruses. Extracts are also tested for their effect on cancer cells and for their potential use as anti-inflammatory agents. Laboratory animals and cultures of cells or tissues are used in these trials. Any promising extracts are further separated and chemically identified. Chemicals with particularly promising properties are then used by pharmaceutical companies to develop new drugs. This process entails another long series of tests that ultimately includes rigorous clinical testing on humans.

Many biomedical products have already been obtained from marine organisms. Some red seaweeds provide laxatives or chemicals that kill viruses. Sponges and soft corals are a rich source of natural products; some act as antibiotics, whereas others have anti-inflammatory or painkilling properties. A bryozoan (*Bugula neritina*) is the source of bryostatin, a promising drug in the fight against cancer. So is didemnin B from a Caribbean sea squirt (*Trididemnum*). Squalamine, which circulates in the blood of sharks, has antibiotic and antifungal properties. It is being tested for its ability to starve tumors by cutting off blood supply. Shark cartilage, however, has shown not to be effec-

tive against cancer as some had claimed. A glue that is naturally produced by bacteria that live on rocks may be used in the future to seal wounds in the skin and delicate tissues of humans. A good sunscreen has been obtained from corals. The toxins, or poisonous substances, found in many marine organisms are also of potential value in medicine. The powerful toxin from certain puffers and por-



This sponge from coral reefs in Fiji (*Acanthella cavernosa*) contains a potent chemical that kills worms, including some human parasites. The chemical is being tested for its potential as a drug. The sponges are cultured on ceramic plates tied to plastic netting.

cupine fishes (see "Symbiotic Bacteria—The Essential Guests," p. 94), for example, is used in Japan as a local anesthetic and as a painkiller in terminal cancer patients.

Many other marine organisms are being investigated as potential sources of drugs. Deep-sea bacteria, dinoflagellates, and seaweeds are cultured to study their antitumor capabilities. Even bacteria that are normally found on the eggs of shrimps and other crustaceans are being targeted as sources of antibiotics and antifungal drugs. Some of the toxins of cone shells are promising in the treatment of epilepsy and depression. A gel from seaweeds is being investigated to prevent HIV viruses from infecting women during sex.

Marine natural products may eventually provide us with the long-awaited miracle drugs that will conquer cancer or AIDS. They are probably waiting to be discovered in the tissues of a sponge, sea cucumber, or sea anemone on a distant coral reef. Unfortunately, such promises simply promote the further destruction of coral reefs.

have shown that watching aquarium fish reduces stress and may even help lower blood pressure.

The export of colorful marine tropical fishes such as lionfishes, butterflyfishes, and damselfishes is a significant component of trade in countries like the Philippines. The aquarium trade has now extended to other tropical marine organisms: sea anemones, corals, sea urchins, and just about anything that is colorful and might carry a price tag. Even "live rocks," rocks with their associated marine life, are sold. Marine life is being taken in large numbers from the natural environment, especially coral reefs (see "Modification and Destruction of Habitats," p. 407). The unrestricted and indiscriminate collection of marine life for the aquarium trade has been very destructive to the natural environment. In the Philippines and other places aquarium fish are often collected by using poisons or explosives that kill hundreds or thousands of fish for every one that makes it to the neighborhood pet shop. The farming of aquarium fishes, as is done in the Bahamas and a few other places, is a recent development that perhaps will reduce the impact of fish collecting on the environment.

The fisheries resources of the ocean are used for recreation by millions around the world.

## NON-LIVING RESOURCES FROM THE SEA FLOOR

In addition to its living resources, the sea contains many nonrenewable resources, resources that are not naturally replaced, such as oil, natural gas, and minerals. These resources are much harder and more expensive to locate and exploit under the sea than they are on land. Not surprisingly, the sea's nonrenewable resources went largely unused, while supplies on land were plentiful and were exploited. More and more,

however, land reserves are running out, and we are turning to the sea floor for new resources.

### Oil and Gas

Oil and natural gas were among the first of the sea's nonrenewable resources to be used commercially. In the late 1800s it was discovered that some California oil fields extended well offshore beneath the seabed. The oil was extracted using oil rigs mounted on wooden piers that extended out from shore.

The offshore oil industry underwent tremendous expansion during the 1970s, when the high price of oil and gas made offshore drilling immensely profitable. Oil and gas production on the continental shelf now occurs in the Persian Gulf, the Gulf of Mexico, the North Sea, and in other areas on all continents except Antarctica. A large percentage of the continental shelves around the world is considered a potential source of oil and gas. The enormous economic potential of these reserves was one of the factors that prompted the establishment of EEZs to protect national interests.

The continental shelves are a major source of oil and natural gas.

Exploiting offshore oil and gas can be a very complex, difficult, and costly operation, especially when the deposits lie many miles offshore as they do in the North Sea. Powerful currents, huge waves, and miserable weather compound the problems.

Overcoming these difficulties has been a major accomplishment of ocean engineering. Exploratory drilling is done from drill ships or partly submerged or elevated platforms that can be towed from place to place and anchored in position on the sea floor. Once oil or gas is found, huge steel or concrete platforms are erected and secured to the bottom to extract it (Fig. 17.18). Remotely controlled submarines are being used to build facilities on the bottom. Floating platforms now allow oil and natural gas to be extracted from depths below 1,000 m (3,200 ft).



**FIGURE 17.18** Oil-drilling rigs, like this one in the Gulf of Mexico off the Louisiana coast, are artificial islands built to cope with inhospitable conditions. They are serviced from land and incorporate the latest developments in undersea technology.

Another potential source of energy from the sea floor is **methane**. Vast stores of methane, both as bubbles and in the form of a solid compound, methane hydrate, have been found deep in the western Atlantic and other places. It will be some time, however, before the technology needed to exploit this resource is developed. Undersea pipelines transport the oil or gas to terminals on land.

The potential threat of oil pollution, however, is a factor of great concern (see "Oil," p. 413). Pollution from drilling operations can affect coastal fisheries, tourism, and recreation. As a consequence, oil and gas drilling have been banned or strictly regulated along some coastal regions.

### **Ocean Mining**

The seabed is a rich potential source of many types of minerals. Some people believe the bottom of the sea to be the planet's richest source of minerals. Though most marine deposits are not presently exploited, ocean mining will be-

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come more viable as we develop new technologies and high-grade ores on land become exhausted.

Sand and gravel for the construction industry are mined offshore in several parts of the world. The galleries of some coal mines on land extend offshore underground. Large deposits of coal have been discovered in deep water but remain unexploited. Some tin, iron, and even diamonds are mined from offshore deposits brought to the seabed by rivers. Other metals, including gold, are found in offshore sand and gravel; in some places, beach sands are mined.

Among the most promising sources of minerals from the sea are **manganese nodules**, lumps of minerals that are scattered on the sea floor beyond the shelf. Manganese nodules contain not only manganese but nickel, copper, and cobalt, all of which are important to industry. The nodules are most common in the deep-ocean basins, but only a few areas have nodules with a mineral content high enough to make mining economically feasible. Some of the richest deposits are found at a depth of about 5,000 m (16,000 ft) in the equatorial Pacific south of the Hawaiian Islands.

Other mineral-rich sediments are found along the mid-ocean ridges and **hydrothermal vents.** The minerals are extracted from deep in the earth's crust as hot water percolates through volcanic fissures and vents. They are deposited when the hot water emerges and hits the cold ocean water. These deposits are rich in iron, copper, and zinc.

Manganese nodules and other mineral-rich deep-sea deposits are potential sources of valuable minerals.

There are many technical problems associated with mining the deep-sea floor. For now it is too expensive, mainly because of the tremendous depths. The question of possible detrimental effects of mining on the surrounding marine environment has also been raised. The ownership of mineral resources that lie outside the EEZ is another unresolved issue. As metal prices rise, however, deep-sea mining may become more attractive. Several agencies and private companies continue to investi-



**FIGURE 17.19** Jago is a submersible being used to search for minerals off the coast of Namibia, southwestern Africa. It explores the seabed at depths of 80 to 130 m (260 to 430 ft). The submersible takes two people, a pilot and an observer. It is also used to document the marine life of the area and assess the potential environmental impact of mining.

gate the prospects of deep-water mining (Fig. 17.19). Future prospects include the use of specially designed dredges or suction pipes suspended from ships.

### NON-LIVING RESOURCES FROM SEAWATER

Ordinary seawater, which of course contains a combination of many different **ions**, is a potential source of almost incalculable resources. It is certainly plentiful and, to most coastal nations, easily accessible.

### **Fresh Water**

**Desalination** plants that convert seawater into fresh water have been built in coastal regions that lack a sufficient supply of fresh water, mainly in desert and semidesert regions such as the Arabian Peninsula. Desalination is also used to supplement the water supply in populous areas like Hong Kong.

Several desalination systems are currently employed. A widely used technique is based on the principle of distillation. Seawater is boiled; the resulting water vapor, when cooled, condenses into fresh water. The process of reverse osmosis uses a membrane that allows water to pass through but blocks the passage of ions, thus desalinating the water. Reverse osmosis plants are becoming very common in small-scale projects like resorts as well as in large desalination plants. Desalination, however, requires a great deal of energy and is therefore expensive. It also produces a highly saline residue that can cause environmental problems. Several promising new methods may one day make desalination more practical and economical.

### Minerals

Every element on earth is present in seawater, but most are found in extremely small quantities. The chief product

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presently obtained from seawater is **table salt**, or sodium chloride (NaCl), which is composed of the two main ions in seawater, sodium and chloride. Salt, a precious commodity to ancient civilizations, has been produced for centuries by evaporating seawater (Fig. 17.20). Most of the other constituents of seawater are difficult to extract because they are present in such small amounts (see Table 3.1, p. 48). Magnesium and bromine are the only other materials obtained from seawater in significant amounts, but valuable trace metals like uranium and gold may one day be commercially extracted.

Seawater is a potentially rich but currently limited source of fresh water and minerals.

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### Energy

Most people don't realize that the ocean is a vast reservoir of energy that might be put to human use. The energy is contained not in oil or gas but in the seawater itself. Harnessing the sea's energy is the objective of several bold concepts that may help meet the energy needs of the twenty-first century.

Mill wheels have been used since ancient times to harness **tidal energy**, the tremendous energy contained in the normal ebb and flow of the tides. Modern schemes call for the construction of large barriers across narrow bays and river estuaries in areas where the **tidal range** is high, at least 3 m (10 ft). Water moving

Hydrothermal Vents Undersea hot springs associated with the mid-ocean ridges encircling the earth, where new material is added to the earth's crust. *Chapter 2, p. 38* 

Cisupier 2, p. 50

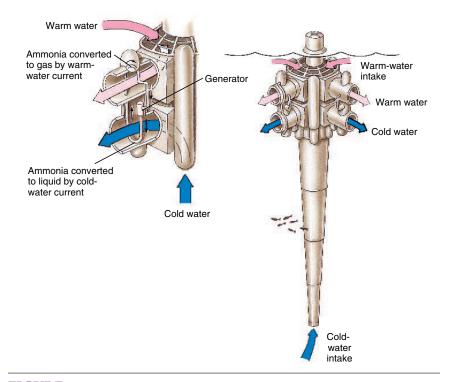
**Ions** Charged atoms or groups of atoms that are formed when salts are dissolved in water.

Chapter 3, p. 46

**Tidal Range** The difference in height between successive high and low tides. *Chapter 3, p. 59* 



**FIGURE 17.20** Aerial view of salt-evaporating ponds on the southwestern tip of Puerto Rico. The shallow ponds are flooded with seawater, and the sun and wind evaporate the water. Ponds like these have also become an important habitat for seabirds.



**FIGURE 17.21** This ocean thermal energy conversion (OTEC) plant is an experimental model consisting of a platform containing a control room, living quarters, and generators, plus a tube several hundred meters long for collecting cold water.

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in with the high tide is caught behind the barrier, and locks are opened to release the water at low tide. The flowing water drives turbines that generate electricity, just as in the hydroelectric plants in river dams. The mechanical energy contained in the tide is thus used to obtain electricity. One such electrical generation plant has been operational in Brittany, northwestern France, since 1966. A few other facilities have been built on an experimental basis. Large projects are envisioned on the River Severn in western England, the Bay of Fundy in eastern Canada, and other suitable areas.

The use of tidal energy is relatively efficient and pollution-free, but the resulting changes in the tidal patterns can be highly destructive to the nearby environment. The rich marshes and mudflats in estuaries may be damaged or destroyed. Pollutants from other sources tend to accumulate upstream because normal tidal flushing is restricted. River flows can also be altered, increasing the risk of floods inland.

Wind-generated waves and strong ocean currents are other potential sources of energy, particularly in areas subject to powerful, regular waves. As with tidal energy, water flow can be converted into electricity by turbine generators. One such system operates in Norway. Wave energy is used to provide power for the operation of distant navigation buoys. Several projects plan to use waves to produce energy for seawater desalination or to pump nutrient-rich deep water to the surface for use in mariculture.

Another possible source of energy from the ocean involves taking advantage of the temperature difference between surface and deep water. Proponents of ocean thermal energy conversion (OTEC) envision the development of electrical generating plants that float like giant buoys or are anchored to the bottom (Fig. 17.21). Temperature differences of at least 20°C (36°F) between the surface and below are essential. These conditions are met in the tropics. Ammonia, propane, or another liquid that boils at low temperature is circulated through pipes bathed in the warm surface water. The liquid evaporates and the gas is forced through turbine generators Castro–Huber: Marine Biology, Fourth Edition IV. Humans and the Seas

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to produce electricity. The pipes then flow through cold water pumped up from the deep, condensing the gas back into a liquid. The cycle is repeated over and over. This process, in which a difference in temperature is used to produce electricity, is sort of the reverse of a refrigerator, which uses electricity to produce a difference in temperature between the inside and outside. Electricity generated by OTEC could be sent ashore by power lines, or used at sea for various industrial operations. The cold, nutrient-rich water pumped from the deep can also be used in mariculture (see Fig. 17.16).

Potential sources of electricity from seawater include tides, waves, currents, and the temperature difference between surface and deep water.



## interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

### **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

### Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

### **Critical Thinking**

- 1. It is discovered that for the last three years the annual catches of a commercially important fish have been above the maximum sustainable yield. One option is to decrease the fishing effort by decreasing the number of fishers. This, however, would cause unemployment in a region where unemployment is already high. What other options might ensure a lower fishing effort? How could they be carried out?
- 2. The mariculture of many food species is expensive, and often only high-priced species are raised. This type of mariculture is of little help to the poor nations where food is needed the most. What measures and new developments might help increase the value of mariculture to these poor nations?
- 3. It has been suggested that cheap electricity generated from tides, waves, or currents could be used to pump nutrient-rich water from the deep. The water could then be used to grow algae to feed the larvae of farmed fishes and invertebrates. How else could this energy be used to decrease the costs of mariculture?

### For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol **Section**, and will contain live links when you visit this page in the Online Learning Center.

#### **General Interest**

- Binns, R. A. and D. L. Dekker, 1998. The mineral wealth of the Bismarck Sea. *Scientific American Presents*, vol. 9, no. 3, Fall, pp. 92–97. Deep-sea mining techniques are being proposed to harvest valuable minerals deposited by hydrothermal vents in the southwestern Pacific.
- Boyd, C. E. and J. W. Clay, 1998. Shrimp aquaculture and the environment. *Scientific American*, vol. 278, no. 6, June, pp. 58–65. Shrimp farming is a serious threat to mangrove forests, rich depositories of biodiversity in the tropics.
- MacKenzie, D., 2001. Cod's last gasp. *New Scientist*, vol. 169, no. 2275, 27 January, pp. 16–17. Drastic measures are being taken to help save the North Sea's cod fishery.
- Mestel, R., 1999. Drugs from the sea. *Discover*, vol. 20, no. 3, March, pp. 70–75. Some of the most recent developments in the use of marine natural products in medicine.
- Pauly, D., V. Christensen, R. Froese and M. L. Palomares, 2000. Fishing down aquatic food webs. *American Scientist*, vol. 88, no. 1, January–February, pp. 46–51. Many fisheries may ultimately collapse since fishing effort is being directed more and more to species that are lower on the food chain.
- The promise and perils of aquaculture. *Scientific American Presents*, vol. 9, no. 3, Fall 1998, pp. 64–69. A series of short articles deals with the effects of aquaculture on marine life.

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- Roman, J., 2000. Fishing for evidence. *Audubon*, vol. 102, no. 1, January–February, pp. 54–61. Scientists use analysis of DNA to trace illegal trade of whale meat and protected fishes.
- Whynott, D., 1999. The most expensive fish in the sea. *Discover*, vol. 20, no. 4, April, pp. 80–85. As bluefin tuna decrease in numbers, biologists make efforts to learn more about the biology of this remarkable fish.

#### In Depth

- Botsford, L. W., J. C. Castilla and C. H. Peterson, 1997. The management of fisheries and marine ecosystems. *Science*, vol. 277, pp. 509–515.
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- Kurlansky, M., 1997. Cod: A Biography of the Fish that Changed the World. Penguin, N.Y.
- Micheli, F., 1999. Eutrophication, fisheries, and consumerresource dynamics in marine pelagic ecosystems. *Science*, vol. 285, pp. 1396–1398.
- Murawski, S. A., R. Brown, H.-L. Lai, P. J. Rago and L. Hendrickson, 2000. Large-scale closed areas as a fisherymanagement tool in temperate marine systems: The Georges Bank experience. *Bulletin of Marine Science*, vol. 66, pp. 775–798.
- Pauly D., V. Christensen. J. Dalsgaard, R. Froese and F. Torres, 1998. Fishing down marine food webs. *Science*, vol. 279, pp. 860–863.

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Yodzis, P., 2001. Must top predators be culled for the sake of fisheries? *Trends in Ecology and Evolution*, vol. 16, pp. 78–84.

### See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center.

- Bycatch from shrimp fishing boat (Dry Tortugas)
- Salmon mariculture (Alaska)

### Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Resources from the sea
- · Economic and ecological importance of algae
- Fisheries
- · Impact of humans on the sea; harvesting
- · Fisheries and conservation issues concerning teleosts
- Food webs

### **Quiz Yourself**

Take the online quiz for this chapter to test your knowledge.

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18. The Impact of Humans on the Marine Environment

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# The Impact of Humans on the Marine Environment



he situation certainly doesn't look very good: The deep, blue sea is becoming messy, and the troubled waters are not that blue anymore. Rusting drums containing deadly chemicals rest on the bottom of the North Sea. A smelly brown substance that the Japanese call hedoro, a combination of the words for "vomit" and "muck," floats on once calm waters. Coral reefs are poisoned by fishers in Southeast Asia. Oil spills threaten coasts from the Persian Gulf to Alaska and oil globs are found even on the once pristine ice shelf of Antarctica. Sick, dying dolphins and seals are washed up on beaches. Salt marshes are being turned into garbage dumps and mangrove forests into ponds for shrimp mariculture.

The list is long and alarming. It is, however, only a small sample of anthropogenic impacts, or the effects of human activities, on the marine environment. More than 6 billion people now live on our planet (see Fig. 17.2), and more people now live within 100 km (62 miles) of the coast than lived on the whole planet in 1950! Everywhere, not just along industrial areas, the pressures of civilization are modifying the marine world. Water quality has decreased, fisheries and mariculture schemes are imperiled, recreational areas are at risk, and new health hazards are developing.



Trash washed up on a beach, Hawai'i.

### MODIFICATION AND DESTRUCTION OF HABITATS

Pollution is, unfortunately, not the only way we affect the marine environment. This section briefly summarizes problems caused by human activities like dredging, dumping silt or mud, landfilling, or even using explosives. Such activities modify or destroy **habitats**, the places where organisms live. The effects of such physical disturbances are direct and immediate, as opposed to indirect effects like those of pollutants released somewhere else. The indirect effects, however, can be over much larger areas, as when the nursery grounds of fish are destroyed.

Most destruction of habitats takes place along the coast close to where people live. It results mostly from coastal development, particularly unplanned or



FIGURE 18.1 Salt marshes in many locations around the globe have been obliterated by landfilling.

poorly-planned development. The problem is more acute in developing nations, where population growth, poverty, and the absence of effective management are harmfully combined. Destruction of marine habitats is nevertheless not exclusive to the poorer nations. Growing cities, increased tourism, and development for industrial and recreational uses are rapidly changing the coastlines of the richer nations.

### **Estuaries and Salt Marshes**

Estuaries and their fragile salt marshes are highly productive environments where many species of commercial importance reproduce and grow (see "Types of Estuarine Communities," p. 264). Estuaries also serve as feeding and resting grounds for many migratory birds; salt marshes offer protection against erosion and provide natural water purification systems (see Fig. 18.5). Salt marshes may one day provide food crops that will be irrigated with seawater, of special significance in arid regions.

The dredging of navigation channels increases the exposure of estuaries to wave action, which often results in the destruction of salt marshes. Marinas and artificial harbors have made unspoiled estuaries a rare sight. Another problem is the further reduction or elimination of the normal freshwater input as more rivers are dammed or diverted. Many estuaries have been reduced and even completely wiped out by landfill; they have been filled to create new land for everything from oil refineries to cities (Fig. 18.1). About onethird of all estuaries in the United States have disappeared altogether; some 67% of those in California have been lost.

### **Mangrove Forests**

The same factors that threaten salt marshes and other estuarine communities are menacing the mangrove forests that develop along estuaries and other protected coasts in the tropics. Mangrove forests also are very productive, providing food and shelter to many species. They help reduce coastal erosion and, by trapping excess nutrients, they reduce coastal pollution. Like salt marshes, however, they are often considered as "wastelands."

Shrimp mariculture, a booming operation in Southeast Asia, South America, and other tropical shores (see "Mariculture," p. 397), has been particularly destructive to mangroves. Forests are razed

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to build ponds to raise the shrimp. Water from the ponds, which contains large amounts of waste, excess nutrients, and uneaten food, is sometimes flushed out to sea, causing serious pollution.

Mangrove forests have also been cleared at an alarming rate to provide space for crops, urban development, roads, and garbage dumps. The growing use of mangrove wood as fuel and timber in some areas is another cause for concern. Mangrove forests once covered around 75% of all sheltered tropical coastlines, but about half have already been destroyed. The figure is much higher for the diverse mangrove forests of Southeast Asia.

### **Coral Reefs**

Coral reefs are threatened by human activities all over the tropics. More than a quarter of the world's coral reefs have already been lost or are at high risk. Though coral reefs support luxuriant life that provides much-needed protein and potentially life-saving drugs, they are subject to much stress. This includes pollution by excess nutrients (see "The Kane'ohe Bay Story," p. 305), overgrowth by seaweeds (see "Grazing," p. 318), and overfishing. Like their also-threatened terrestrial counterparts, the tropical rain forests, coral reefs are among the oldest and richest environments on earth. Ironically, the rapid disappearance of tropical rain forests threatens coral reefs too. The clearing, or deforestation, of the forests for agriculture, logging, and urban expansion increases the amount of soil washed out to sea by the plentiful tropical rain. In some places the resuspension of sediments by nearshore dredging also increases sediment loads (Fig. 18.2).

Corals can tolerate moderate levels of sediment, but the higher levels produced by human activities smother them. Furthermore, young corals do not settle on surfaces that are covered with sediment. Another harmful effect is that sediment in the water makes it more murky, reducing the amount of light that reaches the corals, which depend largely on food produced by **zooxanthellae**. Due to these various effects, sedimentation is a serious threat to many of the world's reefs.

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FIGURE 18.2 Dredging on or near coral reefs releases a large amount of sediment, which is harmful to reef-building corals in many ways. Dredging is common in the small island nations of the South Pacific, where the dredged material is used for landfill or as construction material.

Coral reefs are extensively damaged or destroyed by explosives used to kill fishes. Even though illegal, dynamite fishing is practiced in many places. It may take several decades for damaged coral reefs to recover their former splendor. Explosives also are used to open channels for navigation and in military testing.

Fishing with poisons such as bleach and cyanide kills coral reefs as well. Though this is generally banned, such poisons are widely used in Southeast Asia and parts of the western Pacific. Other related threats are the mining of coral for construction material and the indiscriminate collection of corals for the aquarium trade and for sale as souvenirs and decorations. Shell collectors can be very destructive to coral reefs by turning over or breaking corals to get their specimens. Damage by anchors, fish traps, reef walking, and scuba diving has also taken its toll.

Another indication of stress to coral reefs is a worldwide outbreak of mass coral **bleaching** that began during the late 1980s. Shallow parts of about twothirds of all coral reefs around the world showed bleaching in 1998. Bleaching occurs when corals expel their symbiotic zooxanthellae, causing white patches to form on the colonies (Fig. 18.3). Recovery may take place because corals have different species of zooxanthellae and a new type may replace one that has been



**FIGURE 18.3** These colonies of a brain coral (*Meandrina meandrites*) in the Caribbean have become almost white after losing their symbiotic algae, or zooxanthellae, a phenomenon known as bleaching.

expelled. Bleached corals never lose all their symbionts. Even dying colonies have large numbers of zooxanthellae in their tissues, not enough to give color but enough to reestablish normal numbers when conditions are better. Bleached corals, however, do not grow and are vulnerable to disintegration. Some biologists have suggested that bleaching may be the result of increased temperature caused by global warming (see "Living in a Greenhouse: Our Warming Earth," p. 410).

An increase in the appearance of killing diseases is additional evidence of coral stress. Infections typically show as a line of discolored dead tissue that exposes the underlying white skeleton as it advances over the colony. Various infections have been described, and their names ("black-band disease," "white-band disease") refer to the color of the advancing infection. These diseases seem to be caused by bacteria and fungi that take hold on damaged or stressed colonies (see Fig. 14.16).

Estuaries, mangrove forests, and coral reefs are being destroyed in many parts of the world as a result of direct human interference.

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### Trawling

Trawls that are dragged along the bottom for fish and shrimp are a potential threat to subtidal habitats. Trawling scours the seafloor and leaves scars on soft sediments, particularly muddy bottoms. Boulders are displaced or overturned, harming or killing organisms living on their surface, and the resuspension of sediment kills suspension feeders. This disturbance may also decrease hiding places for juveniles and food sources for others. Deep-water trawling also threatens many vulnerable species that inhabit seamounts in deep water (see "Biodiversity in the Deep Sea," p. 372).

### POLLUTION

Pollution-visible or invisible, on land, air, or water-is by now an unwanted but familiar part of our lives. Pollution can be described as the introduction by humans of substances or energy that decreases the quality of the environment. Many of these substances, or pollutants, are artificial substances that do not occur naturally. Some pollutants, however, have natural as well as anthropogenic sources, such as natural oil seeps and volcanic eruptions. Such natural sources are not considered to be sources of pollution. By contrast, the liberation by humans of naturally occurring substances, for example when mining releases metals that are naturally stored in rocks, is considered to be pollution.

The role of humans in decreasing the quality of the marine environment has been enormous. The potentially detrimental effects of pollution can directly or

Zooxanthellae Dinoflagellates (single-celled, photosynthetic algae) that live within animal tissues.

Chapter 6, p. 99; Figure 14.7

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As sunlight strikes the planet, most of the solar energy, about 70%, is absorbed by the earth. Of the absorbed energy, some is radiated back as infrared radiation. Carbon dioxide, a normal component of the atmosphere, traps part of this heat energy, like the glass of a greenhouse, and warms the earth. It has been estimated that without this **greenhouse effect** the earth would be about  $10^{\circ}C$  (18°F) colder.

Living organisms, both in the sea and on land, affect the amount of carbon dioxide in the atmosphere. Primary producers, in the ocean mostly phytoplankton, remove carbon dioxide from the atmosphere through photosynthesis; both producers and consumers (animals) return it through respiration. Life on the planet removes about as much carbon dioxide from the atmosphere as is added. Humans, however, have been increasing the amount of carbon dioxide in the atmosphere by burning enormous amounts of fossil fuels. These fuels, oil and coal, are nothing but the fossilized remains of ancient forests. We release their energy and turn them into carbon dioxide when we drive our cars and run our power plants. We also cut down the tropical rain forests that consume a great deal of carbon dioxide, burn them, and release even more carbon dioxide in the process!

Carbon dioxide has increased by 25% since 1850, and the planet is warming up—an effect known as **global warming.** How warm it will get and what the consequences will be is debatable. A rise of about  $0.5^{\circ}$ C ( $0.9^{\circ}$ F) occurred in the twentieth century. A panel of scientists appointed by the United Nations predicts a rise of 1.0° to  $5.8^{\circ}$ C ( $2.1^{\circ}$  to  $11.0^{\circ}$ F) by the end of this century. Warming will cause more water to evaporate from the oceans, increasing precipitation, hurricanes, and other storms. Some areas will be wetter, others drier. Scientists fear that the polar ice caps will begin to melt

and that sea level will rise and flood coastal lands. How far up and how fast sea level will rise is something scientists don't agree on. Projections from computer models vary from a rise of 0.3 to 1.5 m (1 to 5 ft) by 2030. This may seem like a small change, but some nations have started planning for the consequences of rising waters. Large portions of Florida and the Netherlands would be flooded, for example, and island nations like the Maldives and Kiribati may disappear altogether!

How will global warming affect the marine environment? No one knows, but several likely effects have been predicted. One is that the flow of some major ocean currents may change, affecting many marine ecosystems. Already stressed ecosystems such as mangrove forests and estuaries will be flooded; coral reefs may not grow fast enough to keep up with rising sea levels. Fisheries will also change, as would the regions influenced by the currents. A change in the Gulf Stream, for instance, will make northwestern Europe much colder. Two separate studies published in 2001 showed that the heat content of the ocean has increased since the 1950s and that the warming was probably due to an increased greenhouse effect.

Some areas of the world, those located in the most densely populated and polluted regions, appear to be cooling, not warming as predicted. It seems that the tiny particles of dust and pollutants that float over most of these areas help cool them. Some of the dust particles come from the relentless burning of tropical rain forests. Some are from natural sources like volcanic eruptions. These particles, called aerosols, scatter sunlight and encourage the formation of cooling clouds. One of the activities that creates cooling aerosols, the emission of sulfates from power plants, also emits gases that contribute to global warming!

indirectly affect all parts of the ocean, from beaches to the deepest depths. Pollution can also present a hazard to human health when marine organisms are eaten or when we go swimming, diving, or surfing.

Pollution of the ocean by humans involves adding or liberating substances that decrease the quality of the marine environment. Many of these pollutants are toxic or harmful to marine life.

The diversity in the types, distribution, and effects of marine pollutants is almost unlimited. The sources of these pollutants also are widespread and alarming, but most pollutants come from *us* on land. Pollutants can be traced to cities, oil drilling, agriculture, shipping, and mining, to name but a few sources. Here we will briefly discuss only the most important types of marine pollutants and some of their effects on marine life.

### **Eutrophication**

Fertilizers in agricultural runoff and sewage (see "Sewage," p. 412) are major anthropogenic sources of nitrate, phosphate, and other nutrients to the marine environment. Atmospheric input from fossil fuel combustion is a major source of nitrogen. In fact, it has become the largest source of nitrogen to the open ocean. Anthropogenic inputs of nitrogen to the oceans now exceed natural inputs. Thus, humans have come to dominate the global nitrogen cycle, and the situation will worsen because fertilizer use, fossil fuel combustion, and other human activities that increase nutrient inputs to the sea are increasing.

Though nutrients are needed by marine primary producers, excessive amounts encourage excessive algal growth, a phenomenon known as **eutrophication**. At present, eutrophication is primarily a problem of coastal waters, particularly in shallow, partially enclosed areas. Eutrophication can damage important habitats such as seagrass beds and coral reefs by causing a chronic increase in phytoplankton abundance, reducing the penetration of sunlight to the bottom, and accelerating the growth of seaweeds that overgrow the bottom (see "The Kane'ohe Bay

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Other gases contribute to the greenhouse effect. One is **methane**, which is released from rice paddies and swamps. A major culprit is the **chloro-fluorocarbons (CFCs)** used in sprays and air conditioners. CFCs are being gradually phased out by international agreement.

CFCs also are involved in another potential disaster: the gradual destruction of the **ozone layer** in the atmosphere. This natural layer of ozone gas  $(O_3)$  protects life from the sun's ultraviolet radiation, harmful because it causes genetic mutations and cancer. There is concern that surface plankton in the waters

around Antarctica will be harmed by the increased radiation. This may drastically alter life in Antarctica, most of which directly or indirectly depends on plankton for its survival. The destruction of the ozone layer will not, by the way, allow more heat to leave the atmosphere and cancel out global warming. Already an ozone hole appears every year over Antarctica, and it gets larger every year. In 2000 it reached 28.3 km<sup>2</sup> (11 million mi<sup>2</sup>), three times the size of the United States.

atmosphere.

What can be done about global warming? It was not until 1997 that a meeting of the industrialized nations was convened to tackle the problem. The Kyoto Climate Change Conference agreed to a 6% to 8% reduction below 1990 levels in the emission of  $CO_2$  and greenhouse gases by 2012. To accomplish this, a cut in the use of fossil fuels by industries and consumers alike must take place. A

major setback took place in 2001 when the United States withdrew from the Kyoto agreement.

Other than reducing greenhouse gas emissions, another possibility is the deliberate fertilization of wide areas of the ocean in order to increase the amount of phytoplankton. Photosynthesis by the phytoplankton would increase the intake of  $CO_2$  from the water, most of which comes from the atmosphere. Fertilization with iron (see "Nutrients," p. 344) is seen by some as a potentially successful option. Such massive human intervention, however, poses some problems. We simply don't know what may happen. Some species will be favored, while others, perhaps the majority, will not.

To quote a recent statement by an American scientist, the question is not whether global warming is actually taking place but rather how it will affect us. Time will tell.

Story," p. 305). It may also trigger phytoplankton blooms, short-term, explosive increases in the abundance of phytoplankton, sometimes of toxic ones.

Organic matter in the form of the remains of the phytoplankton blooms and the feces of the zooplankton and fishes that feed on the plankton fall to the bottom. Decay bacteria then break down the organic matter and use up the oxygen on the bottom. Seasonal anoxic zones, areas where the water lacks oxygen, that result from the effects of agricultural runoff have become common in a number of areas, including the Gulf of Mexico, Chesapeake Bay, and the Black Sea. The Gulf of Mexico anoxic zone, sometimes called a "dead zone," has doubled in size since 1985, growing to a record 20,000 km<sup>2</sup> (7,700 mi<sup>2</sup>) in 1999.

Coastal pollution may also be causing frequent red tides and other phytoplankton blooms (see "Red Tides and Harmful Algal Blooms," p. 326). These events seem to be occurring more frequently in many coastal waters. In Japan and Hong Kong, for example, they endanger valuable mariculture operations. Blooms of phytoplankton and other algae have also become a recurrent problem in the Baltic and Adriatic seas. They cause millions of dollars worth of damage to fisheries, mariculture, and tourism.

Agricultural runoff, fossil fuel combustion, and other sources of increased nutrient inputs to the ocean are responsible for eutrophication, the excessive growth of phytoplankton and seaweeds. **Phytoplankton** The minute, drifting organisms that are a critical part of openwater communities because they perform practically all the photosynthesis in the open ocean.

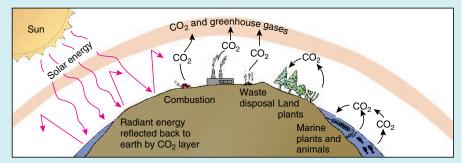
Chapter 15, p. 324

**Decay Bacteria** Types of bacteria that break down, or decompose, non-living organic matter into nutrients and other simple chemicals.

Chapter 10, p. 224

Anoxic Conditions Absence of oxygen that results in the accumulation of *hydrogen sulfide* ( $H_2S$ ) in the sediment, which turns the sediment black.

Chapter 11, p. 254



The role of carbon dioxide (CO<sub>2</sub>) and greenhouse gases in the retention of heat by the earth's

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Ironically, cutting down the amounts of nutrients that naturally enter the ocean can also be harmful. Dams and reservoirs that divert water for agricultural and other uses reduce the amount of nutrients that otherwise would have enriched the productivity of coastal regions, thus affecting fisheries. The building of dams and the diversion or canalization of rivers also reduce the amounts of sediments entering the ocean, severely increasing the erosion of the immediate coast.

#### Sewage

Disposing of ever-increasing amounts of **sewage** is a major problem in cities around the world. **Domestic sewage** carries all kinds of **wastewater** from homes and city buildings. It may also carry storm runoff water. **Industrial sewage** contains a variety of wastes from factories and the like. Most of society's sewage is discharged into the sea, or into rivers that flow to it. The vast amounts of sewage that enter the ocean threaten both the marine environment and human health.

#### Impacts of Sewage

Sewage discharges into coastal waters are a serious health hazard. Sewage contains many viruses and bacteria that cause disease. The threat of marine sewage pollution as a health hazard is known to be more serious than once thought. Infectious hepatitis, for example, is carried by viruses found in human feces. Some 2.5 million cases of infectious hepatitis annually result from people eating oysters, clams, and other shellfish that concentrate the viruses as they filter the water for food. Swimming in sewage-polluted water can also be hazardous; people can get sick from swallowing contaminated water or develop ear, throat, and eye infections just from contact with the water. The closing of beaches because of spills of raw sewage, common when sewers overflow after a rainstorm, has now become routine in many areas, especially where sewage and stormwater are discharged near shore. The economic impact due to lost tourism and the closure of shellfish farms can also be considerable.

Sewage is discharged into the sea by many communities around the world. Sewage is a major health hazard to humans because it spreads disease.

#### Sewage Treatment and Sludge

The harmful effects of sewage can be reduced by sewage treatment, and many countries require by law some form of treatment before sewage is discharged. The sewage may simply be allowed to sit in a basin for a time, so that much of the solid matter settles out. A more advanced, but also more expensive, option is to allow decay bacteria and other organisms to break down the organic matter in the sewage. The addition of chemicals or other steps may be included to further purify the sewage. After treatment, the sewage is often disinfected by using chlorine to kill bacteria and some of the viruses. Ozone treatment and UV irradiation are other methods of disinfection. Advanced forms of treatment can produce water that is pure enough to be used for irrigation or even for drinking water.

Sewage treatment greatly reduces the impacts of sewage on the marine environment and human health, but is not without drawbacks. The cost of sewage treatment increases sharply as more advanced treatment methods are used, and many communities cannot afford advanced treatment, or are unwilling to pay for it. Chlorine used for disinfection may remain in the discharged wastewater and is toxic to marine life. Sewage treatment also creates a new waste disposal problem: what to do with sludge, the wastes that are taken out of the sewage. This semiliquid material is much more concentrated than the original sewage, and often contains higher levels of heavy metals and other toxic substances. If the sludge is disposed of in the ocean, it smothers the natural communities on the bottom, creating black deserts around outfalls (Fig. 18.4).

It is impossible for most detritus feeders to handle the massive amounts of organic matter contained in sludge. The organic matter is instead decomposed by bacteria that thrive under these conditions. The decay bacteria use oxygen to

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**FIGURE 18.4** Treated sewage effluents from the Hyperion treatment plant being released at a depth of 60 m (180 ft) at the end of an 8-km (5-mi) outfall in Santa Monica Bay, Southern California. Large sea anemones (*Metridium*) surround the site. Santa Monica Bay is actually getting cleaner. The dumping of sludge from another outfall ended in 1987, and part of the wastewater at this outfall is now undergoing additional treatment. Treatment at the plant has been improved in order to meet standards set by the Environmental Protection Agency.

such an extent that anoxic conditions develop. The total number of species decreases as many of the natural inhabitants disappear. They are replaced by hardier forms of life, such as certain species of polychaete worms. Bottom fishes collected around sludge disposal sites tend to show skin tumors, erosion of fins, and other abnormalities, apparently a result of the high concentration of toxic substances and bacteria.

High volumes of sludge discharged into the sea greatly modify or destroy bottom communities.

It is possible to implement alternatives to the discharge of sewage into the sea. Additional and improved treatment, mandated in the United States by the Clean Water Act of 1972, has reduced



industrial waste, may also contain pesticides, heavy metals, and other toxic chemicals. In these cases special treatment may Oil

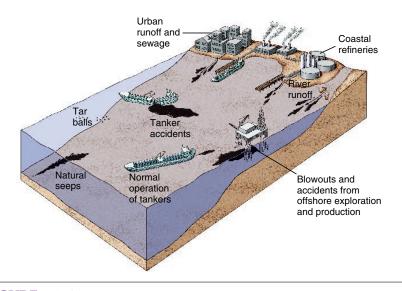
Crude oil, or petroleum, is a sticky, dark, greenish-brown mixture of many chemical compounds. Most of these chemicals are hydrocarbons, long chains of carbon and hydrogen. Crude oil is a valuable commodity that is refined to yield not only fuels but raw materials for making plastics, synthetic fibers, rubber, fertilizers, and countless other products.

Sources

Oil is also one of the most widespread pollutants in the ocean. Though in several coastal regions oil comes from natural seeps, most enters the marine environment as a pollutant released by humans (Fig. 18.6). It is extracted from the seabed (see "Non-living Resources from the Sea Floor," p. 401), transported across the oceans, and refined in plants along the coast. These processes are potential contributors to pollution. Large amounts of crude oil and derivatives like fuel, heating, and lubricating oil also are present in runoff from coastal cities and rivers. Marine pollution by ships is strictly controlled by the International Convention for the Prevention of Pollution from Ships (MARPOL). Yet oil tankers discharge oil while unloading, illegally cleaning their tanks at sea, and emptying the water they use as ballast on their return trips to load oil. Tanker operations and wastes from cities are considered the two most important sources of oil pollution. Infrequent but potentially disastrous are the blowouts of offshore rigs used in the

One metric ton of crude oil = 7.33 barrels (bbl), or 308 U.S. gal.

**FIGURE 18.5** This lush, sweet-smelling artificial marsh is part of a network of marshes where domestic sewage from the town of Arcata in northern California is naturally purified before it is piped into the ocean. Sewage, which is mostly water, is given preliminary treatment, and chlorine is added to kill harmful bacteria. It is then pumped into the marshes where mud bacteria break down the organic matter. The released nutrients fertilize the marsh plants. The marshes prevent the pollution of the ocean by sewage and attract many species of birds and other wildlife.



**FIGURE 18.6** Sources of oil in the marine environment.

the amount of suspended solids in the sewage being discharged in the country. But why not consider sewage a resource and turn sludge into something useful? Ideally we could recycle the large amounts

of precious water and nutrients that go to waste. Some small communities are taking advantage of the ability of marshes to recycle large amounts of nutrients by using the marshes for natural sewage

Chapter 18 The Impact of Humans on the Marine Environment 413 extraction of oil (see Fig. 17.18). The underwater blowout of an exploration well in the Gulf of Mexico in 1979 spilled at least half a million tons (about 3.6 million barrels) of oil over a period of 9 months.

The magnitude of this spill was not much higher than another blowout in the Persian Gulf in 1983. As much as 1 million tons (about 8 million barrels) of oil were spilled during the 1991 Gulf War.

Of all mishaps, however, the massive oil spills that result from the sinking or collision of supertankers are the most devastating to the marine environment. The 1978 grounding of a supertanker, the Amoco Cadiz, poured 230,000 tons of crude oil along the coasts of Brittany, in northwestern France. In 1989 more than 35,000 tons of crude oil were spilled by the Exxon Valdez along the unspoiled coast of southern Alaska, the home of whales, sea otters, salmon, fish-eating bald eagles, and other wildlife. Accidents have prompted tighter restrictions, such as having double hulls, on the construction and operation of tankers. Older tankers, however, do not necessarily have double hulls.

Most of the components of oil are insoluble in water and float on the surface. They appear as thin, iridescent slicks on the surface or as black deposits on sandy and rocky beaches. You would expect large areas of the ocean to be covered with the oil that has accumulated over the years. Fortunately, some of its lighter components evaporate, and bacteria ultimately break the oil down. Oil is said to be almost completely **biodegradable** because, though very slowly, it is broken down, or decomposed, by bacteria. The breakdown rate, however, is different among marine communities. For instance, it lasts much longer in salt marshes and mangrove forests.

Some of the components of crude oil sink and accumulate in sediments, especially after the lighter ones evaporate. Floating oil residues, or tar balls, have become common on the water surface along the shipping lanes that crisscross the oceans. They may persist for many years in the water and have been observed in remote areas far from shipping traffic. Some even have barnacles living on them! Extensive oil spills form huge layers that coat everything in their path as they are carried by wind and currents.



**FIGURE 18.7** An oil-coated loon (*Gavia*) during the *Exxon Valdez* spill in Alaska. Detergents, which can be used to disperse the oil and help prevent situations like this, were widely used during the *Torrey Canyon* spill on the English coast in 1967 but proved to be toxic and actually caused more damage than the oil itself.

Yet, the oil and shipping industries have made considerable progress in the protection of the marine environment. Illegal dumping is still a problem but it is becoming less severe. An indication of this is a decrease in the number of tar balls on many beaches.

Oil is a widespread pollutant that enters the sea as waste from land, from accidents during its extraction from the seabed, and as a result of its transportation across water.

#### Effects of Oil on Marine Life

Even in small amounts, oil has been shown to cause a variety of effects in marine organisms. Organisms accumulate oil components from the water, sediments, and their food. Some of the substances contained in crude oil are toxic. Toxicity is dependent on the type of crude oil or refined products, which tend to be more toxic than crude oil. There is evidence, for instance, that oil interferes with the reproduction, development, growth, and behavior of many organisms, particularly the eggs and larvae. Oil also increases susceptibility to diseases in fishes and inhibits growth of phytoplankton.

Major oil spills can have disastrous effects on marine life, especially in coastal environments. Seabirds and marine mammals like the sea otter are particularly susceptible. Many die of exposure when feathers or hair are coated with oil. When coated with oil, feathers and hair lose the ability to maintain the thin layer of warm air that is needed for insulation from cold water (Fig. 18.7). Birds that rely on flying to catch food are unable to do so and die of starvation. It is difficult to determine the number of birds killed by oil spills because many sink without reaching the coast, where the corpses can be counted. About 3,200 dead birds, some belonging to rare species, were counted immediately after the Amoco Cadiz spill. The Exxon Valdez spill is believed to have killed between 100,000 and 300,000 seabirds and 3,500 to 5,000 sea otters. Estimates are that it will take up to 70 years for the wildlife in the area of the spill to fully recover.

The effect of oil spills on exposed rocky shores is less devastating than it may appear at first sight. Initially there is mortality among many attached inhabitants,

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but wave action and tides help clean away the oil. Rocky shore communities do recover, though recovery is dependent on factors such as the amount of oil, wave action, and temperature. Degradation, or breakdown, by bacteria takes place, but it is very slow, especially in cold water. Spills are degraded more quickly by bacteria if an oil-soluble fertilizer is added to the water or sprayed on rocks and sediment. Experience has shown that recovery begins within months and that an apparent nearnormal condition may occur as early as one or two years after the spill. Higher oil concentrations in sediments and isolated pockets, however, have been found to remain for 15 years or longer.

Large spills, on the other hand, can have catastrophic effects when they drift to salt marshes and mangrove forests. These communities are characteristic of sheltered coasts and estuaries where oil cannot be dispersed by wave action. Massive mortality of the dominant plants takes place, and recovery is very slow. Oil is absorbed by the fine sediment characteristic of these communities and may persist here for decades. Shallow-water coral reefs and seagrass beds also are greatly affected by oil spills. Coral colonies show swollen tissues, excessive production of mucus, and areas without tissue. Reproduction and feeding in surviving coral polyps are known to be affected by oil. There is little evidence, however, of dramatic long-term effects.

Oil is harmful to most marine organisms. It is especially destructive to communities typical of shallow, sheltered waters.

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Containing an oil spill and cleaning up the mess is a major headache. Fencing off the spill with floating, fire-resistant booms prevents the spill from moving into shore. "Skimmers," boats equipped with U-shaped booms, are used to skim off and recover some of the oil. These methods, however, cannot be used in heavy seas. Chemical **dispersants** are added to the spill to break the surface oil into small droplets that can then disperse in the water. Unfortunately, dispersants also are harmful to marine life, and the dispersed oil still remains toxic underwater. The use of powerful streams of hot water to wash oil from beaches after the *Exxon Valdez* spill was also harmful to many forms of life, perhaps as harmful as the oil itself.

The cost of oil spills to the local economy can be enormous. Commercial fishing is one of the first sectors to be affected. Fish and filter-feeding shellfish like oysters and clams that are tainted with oil are simply unmarketable. The size of fish catches, particularly of bottom-dwelling species, may decrease because of the initial mortality of adults and juveniles or a drop in the abundance of their food. Furthermore, oil-soaked beaches are disastrous to resort areas dependent on tourism. Claims by those affected plus the cleanup bill can run well past the billion-dollar mark for major spills. Exxon Corporation was ordered to pay \$5 billion in fines for damage caused by the Exxon Valdez. The fines were greatly reduced in 2001. This is in addition to \$287 million it was ordered to pay Alaska fishers and about \$3.5 billion Exxon paid in cleanup costs.

#### **Toxic Chemicals**

Other pollutants also reach the sea from land. They are toxic chemicals that are synthetic, that is, manufactured by humans. Though organic—and thus made up of at least carbon—most are nevertheless foreign to all forms of life as a consequence of being artificial.

#### Pesticides

One major group of synthetic chemical pollutants are the chlorinated hydrocarbons. They include a large number of pesticides, chemicals used to kill insects and to control weeds, including DDT, aldrin, dieldrin, heptachlor, and chlordane. Millions of tons of these and many thousands of other chlorinated hydrocarbons have been used, mostly in agriculture, since the 1940s when DDT made its debut. These pesticides have been used to save plant crops from insect pests and to control insects that carry diseases. Pesticides have saved millions from disease and starvation, but unchecked use of chlorinated hydrocarbons has now brought to our attention their more sinister side, the fact that they are harmful to many non-targeted forms of life.

These pesticides have not been used directly in the ocean. Nevertheless, chlorinated hydrocarbons are highly mobile, and large amounts end up contaminating the marine environment. They are easily carried by wind from land (Fig. 18.8). They are brought in by rivers, runoff from land, and domestic and industrial sewage. The atmosphere carries them everywhere, even way out at sea far from where they were originally used. Pesticides are absorbed by phytoplankton and particles suspended in the water and can be concentrated in tissues of animals. In this way they find their way into other marine organisms.

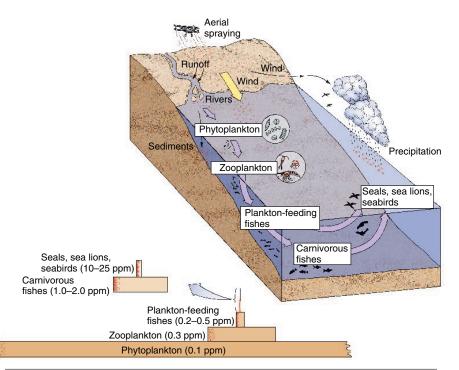
Chlorinated hydrocarbons are synthetic, and organisms have not evolved ways of breaking many of them down. They are therefore **nonbiodegradable**, and getting rid of them is not easy. They hardly dissolve in water, are not excreted, and accumulate in fats, remaining there almost indefinitely. Chlorinated hydrocarbons and many other nonbiodegradable chemicals are said to be persistent; they circulate in the environment for many years, even decades. The concentration of chlorinated hydrocarbons in a particular animal is higher than in its food supply, and it increases as one moves higher in the food chain. Among marine animals, chlorinated hydrocarbons are therefore more concentrated in carnivorous fishes and especially in the fish-eating birds and mammals that feed on them (Fig. 18.8). These carnivores are said to be at the top of the trophic pyramid and are known as top carnivores. Because organisms retain the chlorinated hydrocarbons, the carnivores end up concentrating the pesticides that accumulate along the food chain leading

**Food Chain** The steps of transfer of energy from *producers*, the algae and plants, through *consumers*, the animals. *Chapter 10, p. 222; Figure 10.11* 

**Trophic Pyramid** The pyramid-like relationship of energy, number of individuals, or biomass of the organisms found in a food chain.

Chapter 10, p. 223; Figure 10.13

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**FIGURE 18.8** The concentration of chlorinated hydrocarbons increases with the relative position organisms have in the food chain, thus showing biological magnification. In the trophic pyramid that summarizes this generalized food chain, the concentration of pesticides is expressed in ppm, or parts per million.

to them. This phenomenon is known as **biological magnification.** 

Chlorinated hydrocarbons, which include many widely used pesticides, are nonbiodegradable and persistent. Many accumulate in the food chain and thus show biological magnification.

The alarming effects of worldwide use of chlorinated hydrocarbons began to be noticed during the 1960s. Fishes caught for human consumption in the United States had to be destroyed because they contained too much pesticide. Pesticides began to accumulate in top carnivores in concentrations that were thousands and even millions of times above those found in seawater.

The effects on birds, on land and at sea, were particularly dramatic. Birds were not actually poisoned, but the high concentrations of chlorinated hydrocarbons in their body fat interfered with reproduction, specifically with the deposition of calcium in eggshells. Their eggshells became so thin that they broke during incubation before chicks became fully developed.

Such was the case of the brown pelican (Fig. 18.9). This once-abundant bird became a rare sight in most of the United States as the result of a near-disastrous failure in its reproduction during the late 1960s and early 1970s. Females sat on broken eggs, or adults simply did not attempt to nest. The Channel Islands off Southern California, the only nesting colony on the Pacific coast north of Mexico, recorded one chick in 1970 and seven in 1971. High amounts of DDT and some related chemicals were found in the tissues of birds taken from these and other nesting colonies and in other marine animals in the area, from filter feeders like sand, or mole, crabs to top carnivores like sea lions.

By 1972 most uses of DDT and several other chlorinated hydrocarbons were banned in the United States and many other industrialized nations. DDT www.mhhe.com/marinebiology



FIGURE 18.9 The brown pelican (*Pelecanus occidentalis*) is again a common sight along the southeast, Gulf, and west coasts of the United States.

residues in marine animals and sediments then began to decrease. The brown pelican, once nearly extinct in the United States, has recovered, and its reproduction appears to have returned to normal. DDT and related residues, however, can still be found in bottom-dwelling fishes. One of these residues, DDE, was found to be degraded by bacteria under laboratory conditions. A 2000 international agreement restricting the production and use of certain toxic substances allowed continued use of DDT because it provides inexpensive control of insects in developing nations. It is primarily used in the control of mosquitos, which transmit malaria, a prevalent disease in many tropical regions.

#### PCBs and Other Toxic Chemicals

Another group of toxic chemical pollutants are the **PCBs**, the polychlorinated biphenyls. Like chlorinated hydrocarbon pesticides, PCBs are nonbiodegradable and persistent, and show biological magnification. Their use proliferated, and after the

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**FIGURE 18.10** Hazardous chemicals such as PCBs and pesticides and cancer-causing agents like vinyl chloride and dioxine can be disposed of by incinerating them on the high seas rather than using dumps on land. Incinerator ships like this one burn hazardous organic chemicals at high temperatures, which results for the most part in safe chemicals like carbon dioxide and water. Transporting the toxic waste by sea, however, adds to the danger of spills. There are also concerns about the toxicity of hydrogen chloride and other chemicals that can be formed in the process. Very few nations dispose of all of the hazardous waste they produce on their own turf. Most simply export the waste and have other, usually poorer, nations get rid of it for a fee. A 1989 international treaty restricts, but does not ban, the international movement of toxic wastes.

1930s they were employed in electric transformers and capacitors, in the manufacturing of plastics and paints, and in many other products. They were eventually found to be highly toxic, causing cancer and birth defects. PCBs, together with other chlorinated hydrocarbons, have been detected in the blubber of whales and other marine mammals. The production and use of PCBs were gradually regulated or banned by many nations; PCBs were not banned until 1979 in the United States.

This ban, however, came after PCBs had spread throughout the oceans. PCBs continue to be used in some parts of the world, and electrical equipment containing them is still around us. Equipment is required to remain sealed, and the PCBs must be carefully disposed of when the equipment wears out. Invariably, PCBs are a main ingredient of the large amounts of hazardous wastes that accumulate and have to be disposed somehow, somewhere (Fig. 18.10). PCBs have become widespread in landfills and waste dumps. Like chlorinated hydrocarbons, decades of use and dumping have also left significant amounts of these persistent pollutants, especially around sewage outfalls and in the sediment of harbors of industrial cities. Some marine bacteria, however, are known to degrade PCBs that have accumulated in sediments. They have been found mostly in areas with high concentrations of PCBs such as the Hudson River estuary.

In addition, chlorinated **dioxins** and **furans**, two groups of chlorinated hydrocarbons, enter the marine environment from land. Pulp mills and waste incinerators are important sources of the chemicals, which also occur naturally as a result of forest fires. Some dioxins are among the most toxic of all chemical pollutants. They are carcinogenic and are known to cause birth defects and damage to the immune system of many vertebrates and humans. Furthermore, they show biological magnification.

PCBs and certain pesticides and other toxic chemicals evaporate into the atmosphere, where the wind can carry them considerable distances before they condense in the cool upper atmosphere. When they condense, they are carried in rain or snow back to the ground, where the process starts all over again. Because of wind patterns and the fact that more condensation of the chemicals takes place near the poles, where it is cold, the chemicals are concentrated in polar regions. This global system of evaporation and condensation of substances, many of which are toxic, is known as global distillation. Global distillation has been implicated in whale kills, and high levels of PCBs and other toxic chemicals have been found in seals, polar bears, whales, and even Eskimos, all inhabitants of the once pristine Arctic region and thousands of miles from where the pollutants were used.

PCBs, dioxins, and furans are pollutants notable for their toxicity. They are persistent and show biological magnification.

Even at low concentrations years after being banned, PCBs and chlorinated hydrocarbons have been implicated in abnormal sexual behavior and reproductive ability in seabirds, marine mammals, and fishes. These pollutants form chemicals that are similar to sex hormones and thus seem to disrupt reproduction.

#### Heavy Metals

An additional category of chemical contaminants of the world's oceans is metals, particularly those classified as **heavy metals.** Very minute amounts of some metals are needed by most if not all organisms, but an excess of some metals can be toxic.

One particularly troublesome heavy metal is **mercury**. Mercury reaches the ocean through several natural processes: the weathering of rocks, volcanic activity, rivers, and dust particles from the atmosphere. Even so, human activities appear to play an increasingly important role, especially along the coast. Mercury was once 50

40

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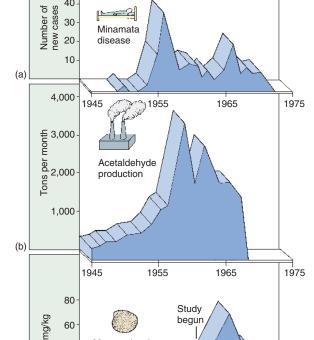
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an active ingredient in chemicals used to kill bacteria and molds and in antifouling paints. It also is used in the production of chlorine and plastics and other chemical processes and in batteries, fluorescent lamps, drugs, and even tooth fillings. Discharges from industries and cities and the burning of coal, which contains traces of mercury, have increased the concentration of mercury in the marine environment.

Pure, liquid mercury, like that in your thermometer, is harmless unless its vapors are inhaled. It is a different story when mercury combines with organic chemicals, as when transformed by some bacteria and other microorganisms in the water or sediment. These organic compounds, especially methyl mercury, are persistent and accumulate in the food chain. Levels of mercury too high for human consumption have been found in large fishes such as tuna and swordfish. The older the fish, the higher the mercury content. Methyl mercury also can be found in coastal sediments, particularly around areas where wastes are dumped. Mercury compounds also undergo global distillation. They are very difficult to eliminate and are highly toxic to practically all forms of life. In humans they cause brain, kidney, and liver damage and are responsible for birth defects.

The dangers of the presence of mercury in seafood were demonstrated by the appearance in the 1950s and 1960s of a crippling neurological disorder among the inhabitants of a town in southern Japan (Fig. 18.11). The victims were poisoned by eating fish and shellfish that had concentrated mercury discharged at sea by a chemical plant.

Other heavy metals are carried to the ocean as toxic pollutants. Lead is one of the most widely distributed. As with mercury, organic lead compounds are persistent and concentrate in the tissues of organisms. Lead is toxic to humans, causing nervous disorders and death. The principal source of lead pollution in the marine environment is the exhaust of vehicles run with leaded fuels. The lead reaches the water by way of rain and windblown dust. Lead has also found its way into all sorts of products, such as paints and ceramics, that eventually make their way to the ocean.



**FIGURE 18.11** In the 1950s and 1960s a serious neurological disorder that often ends in severe brain damage, paralysis, or death appeared among the inhabitants of Minamata, Japan. The number of new cases (a) was directly related to the production of acetaldehyde by a chemical plant in this traditional fishing town (b). A mercury compound was used in the production of acetaldehyde and vinyl chloride, which are used in making plastics. As a result, an estimated 200 to 600 tons of waste mercury was discharged into Minamata Bay between 1952 and 1968, when it was finally stopped. The disease, now called Minamata disease, was related to the ingestion of mercury in seafood, here indicated by its concentration in the edible clam Venus (c).

1955

1965

1975

Mercury levels

in clams

1945

40

20

(c)

The removal of lead from gasoline has been responsible for a decrease in lead levels in surface water, especially in the North Atlantic. This represents a success story that demonstrates that environmental problems can certainly be addressed.

Mercury and lead compounds are highly toxic. They are persistent and accumulate in the food chain.

Cadmium and copper are other toxic heavy metals that are slowly concentrated in marine life. Mining and refining operations are major sources of these metals. Cadmium is also present in the waste from battery manufacturing and in discarded batteries, and often seeps into rivers or the ocean from disposal sites. Sources of copper include wood treatment and other industrial processes. Unlike lead and mercury, which are transported in the atmosphere, unnaturally high levels of cadmium, copper, and most other heavy metals remain localized near the source.

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#### **Radioactive Wastes**

Radioactive substances have been contaminating the marine world since the first atomic bomb explosions in the early 1940s. Radioactivity is a property exhibited by certain unstable atoms that emit radiation in the form of energy or particular types of particles. Exposure to some types of radiation is harmful to all forms of life. In humans it causes cancer, leukemia, and other disorders. Radioactive waste does not need to be ingested because it can penetrate through living matter. Radioactive material also may continue to emit radiation for thousands of years. Some radioactive isotopes occur in nature but in minute amounts, and some harmful radiation reaches us from outer space. One important source of radioactivity is a byproduct, or waste, of the use of the atom as a source of energy, in medical applications, and nuclear weapons.

Radioactive waste is dangerous and must be disposed of somewhere. Some is stored in containers and dumped into designated areas of the ocean. Sunken nuclear-powered submarines and ships, fallen satellites, and crashed planes carrying nuclear weapons are additional sources of radioactive waste. Accidents in nuclear reactors along the coast and industrial effluents add to the risk.

### Solid Waste

A look at the upper reaches of most beaches will reveal an amazing assortment of trash brought in by high water. Most of it is plastic: bottles, bags, styrofoam cups and packaging, nets, and thousands of other items. Add rubber, glass, and metal and you have quite a heap of trash. Solid waste from land still flows to sea at an alarming rate. Landfill sites are filling fast, and burning trash pollutes the air, so ocean dumping is one possible way out.

Plastic is especially troublesome because it is strong and durable. It is nonbiodegradable. Styrofoam and other plastics eventually break down into tiny particles that are now found in every remote corner of the ocean. They have been found in the guts of many animals that ingest them by mistake. Larger plastic debris is a threat to some marine life.



FIGURE 18.12 Plastic debris can be more than an eyesore. It has been estimated that it kills as many as two million seabirds and 100,000 marine mammals every year. Plastic bags kill sea turtles that swallow them thinking they have caught a jellyfish. Six-pack rings present a particular risk to seabirds because they are easily ensnared by them. Unable to feed or fly, they face a certain, slow death. This California sea lion (*Zalophus californianus*) is being strangled by nylon fishing line.

Sea turtles, seabirds, seals, and others are maimed or killed after getting entangled in plastic fishing line (Fig. 18.12). Many die with their digestive tract clogged with plastic bags and other debris.

### **Thermal Pollution**

Seawater is often used as a coolant in power plants, oil refineries, and other industries; thus, many of these industries are

**Fouling Organisms** Organisms, such as barnacles and shipworms, that bore into or encrust on boats and underwater structures.

Chapter 7, p. 131

built along the coast. The heated water that results from the cooling process is pumped back to sea, causing alterations to the environment known as **thermal pollution.** Local warm pockets can be created in poorly mixed bays. Even

**pollution.** Local warm pockets can be created in poorly mixed bays. Even though some fishes may be attracted to the site, such temperature increases are known to adversely affect some organisms. Higher temperatures also decrease the ability of water to dissolve oxygen.

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Thermal pollution results when heated water is pumped into the sea.

The effects of thermal pollution on marine life are especially pronounced in the tropics. In contrast to organisms living in temperate and polar regions, corals and some other tropical species normally live just below the highest tolerable temperatures. Reef-building corals are particularly sensitive (Fig. 18.3).

### THREATENED AND ENDANGERED SPECIES

The alteration or destruction of habitats by humans may have another disastrous effect: driving species to their eventual disappearance, or **extinction**, from the face of the earth. Recall that individuals become adapted to changes in the environment as a result of **natural selection**. If they cannot adapt, extinction will be the eventual outcome. Extinction is therefore a natural consequence of the process of evolution. To make a distinction, some biologists refer to humaninduced extinction as **extermination**.

Species that face extinction are classified as **rare** when they are not in immediate danger but are at risk, **threatened** 

**Isotopes** Different atomic forms of an element.

Chapter 2, p. 35

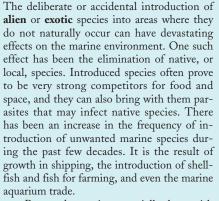
**Natural Selection** The production of more offspring by the best-adapted individuals in a population.

Chapter 4, p. 84

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## BIOLOGICAL INVASIONS: THE UNINVITED GUESTS



Bays and estuaries, especially those with busy ports, are particularly vulnerable. Seaweeds and invertebrates like sponges, barnacles, and sea squirts that grow as fouling organisms on ships have become established around the world. Many other species have been introduced as planktonic larvae in ballast water, which is used to fill ships' ballast tanks for stability. Others have been introduced with commercial fishery products, particularly shellfish. One good example is the Asian clam (Potamocorbula amurensis) that was accidentally introduced in San Francisco Bay, California, apparently as a direct result of the opening trade with China. These clams did not live in the bay in 1985, but by 1990 they literally covered whole sections of the bay's muddy bottom. As many as 10,000 clams per square meter carpet the bottom in some sections.

About 250 introduced species have so far been found in San Francisco Bay. It's actually tough to find a native species in the bay. San Francisco is not only a busy port, but the bay is much disturbed. It is probably easier for an introduced species to become established when the environment is off balance. Many invaders do well in such unstable environments because they are often more tolerant than native species to wide fluctuations in factors such as salinity.



#### Have You Seen This Crab?

Biologists are trying to map the distribution of the European Green Crab, a non-native species which was introduced into San Franciso Bay around 1989. It is extending its range northwards and mature, adult individuals were recently caught in Coos Bay, Oregon, in April, 1997. This is about half way to British Columbia, and because of oceanographic conditions, we expect this species will extend its range further northwards even faster. If you see what you believe is an adult Green Crab, please collect it carefully (it's big enough to pinch!), freeze it, record the precise date and location found, and contact either of us.

#### Contact either:

Glen S. Jamieson Pacific Biological Station Fisheries and Oceans Canada Nanalmo, B.C V9R 5K6

(250) 756-7000 (250) 756-7138 (fax)

Underside of male green crab with a smaller native shore crab for size comparison



Canadã

Jim Morrison South Coast Division Fisheries and Oceans Canada 3225 Stephenson Point Rd. Nanaimo, B.C. V9T 1K3 (250) 756-7233 (250) 756-7162 (fax)

Female green crab carrying eggs and a smaller native shore crab for size comparison



Fahahan and Gospee Petram at Gold Games Carves Galarten Gospee

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One of the more recent invaders to San Francisco Bay is the European green, or shore, crab (*Carcinus maenas*). It was first recorded in the bay in 1989, probably introduced as larvae in ballast water. It soon extended its range along stretches of the Pacific coast. The green crab has also been introduced, and has become a pest, in the northeastern coast of the United States, Australia, and South Africa. The green crab lives in a wide range of salinities. It is also a voracious predator, feeding on commercially valuable oysters and young Dungeness crabs.

Another notorious guest is a comb jelly (*Mnemiopsis leidyi*; see Fig. 7.10) that was accidentally introduced into the Black Sea. It normally occurs along the coasts of North and South America. First recorded in the Black Sea in 1982, it has become a monumental pest, practically taking over the sea. It not only competes with fish for zooplankton food but also feeds voraciously on fish eggs and larvae. Along with overfishing, its impact on the Black Sea fisheries has been devastating. Fish catches have sharply decreased, causing huge economic losses in the area. And yes, it has been found in San Francisco Bay, too!

More than 250 species of invertebrates and fishes have migrated from their original home in the Red Sea to the Mediterranean Sea. These introduced species migrated by way of the Suez Canal, which opened in 1869 to provide the shortest sea route between Europe and the Indian Ocean. The 160-km (100-mile) journey through the canal is increasing because the high salinity of the lakes through which the canal passes has decreased, thus becoming less of a barrier to planktonic larvae brought in by tides. Most migrants have moved from the Red Sea to the Mediterranean because the high tide carries larvae further up the canal from the Red Sea. The migration of these introduced species has been called Lessepsian migration after the builder of the canal, Ferdinand Lesseps. Migration between the Atlantic and Pacific oceans across the Panamá Canal has not taken place because only fresh water flows through the canal, killing any marine life that is brought in by the tide (also see Fig. 9.4).

Inland waters have not escaped uninvited guests. The small freshwater zebra mussel (*Dreissena polymorpha*) was introduced, probably in ballast water from Europe, into the Great Lakes. It was first found in 1988 but quickly spread. It is now found in all five Great Lakes, the Hudson River estuary, and the Ohio River drainage basin as well. The clam has taken over the shallow-water bottom in many areas. It has caused costly damages because it disrupts water supplies by invading water-intake pipes. The intentional introduction, or **transplantation**, of species for commercial purposes can also bring in introduced species. The Japanese oyster (*Crassostrea gigas*) was introduced as spat, or young individuals, on the Pacific coast of North America. It was a successful transplantation in the sense that the oyster is now of significant commercial value. Unfortunately, many species living on the spat shells were also introduced. One nasty introduced species is an oyster drill (*Ceratostoma inornatum*), a marine snail that preys on oysters and other native bivalves. Also introduced was *Sargassum muticum*, a Japanese brown seaweed that is now established from British Columbia to Southern California. The same species has also been introduced into England, probably with transplanted Japanese oysters.

A similar situation has taken place on the northeastern coast of the United States. A green seaweed (*Codium fragile*), apparently brought over on oysters transplanted from Europe or the Pacific coast, has become a pest by growing in masses on rocks and oysters.

Another notorious introduced species is *Caulerpa taxifolia*. This single-celled green seaweed grows into branches that may be as long as 3 m (9 ft). It was accidentally introduced into the Mediterranean from the Caribbean in 1984. The fast-growing seaweed has spread rapidly, particularly in the western Mediterranean, where it smothers seagrasses and other native species and depletes oxygen from the bottom. Unfortunately, the bright-green seaweed is widely used in marine aquaria. Its importation into the United States was banned in 1999, but in 2000 it was found in shallow water off Southern California, perhaps the result of someone emptying a fish tank into a storm drain. Its spread may pose a threat to marine life in the region. A red alga introduced in Hawai'i, *Kappaphycus striatum*, grows over corals (see Fig. 14.13).

Transplanted species of cordgrass (*Spartina*) cause problems in many regions of the world. They have spread over mudflats, oyster grounds, and eelgrass beds. These environments are important habitats for native benthic species or are nurseries and feeding grounds for native fishes, some of commercial importance.

It is difficult to prevent the introduction of uninvited guests. One possible option is to control or regulate the use of ballast water. The use of filtered or sterilized ballast water has been explored. The exchange of ballast water in mid-ocean far from land is another. The transplantation of species from different geographical regions must also be strictly regulated. Rigorous studies of the biology of the species involved and those in the proposed new locations should also be undertaken before such transplantations are carried out.

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| Table 18.1                 | Endangered and Threatened Marine Species   |  |  |  |  |  |  |
|----------------------------|--|--|--|--|--|--|--|
| Group of Marine<br>Animals | <b>Red List of Threatened Species</b><br>(Critically endangered, endangered,<br>and threatened species; compiled by<br>the International Union for<br>Conservation of Nature and<br>Natural Resources) | CITES List of Species<br>on the Risk of Extinction<br>(Appendix I, Convention<br>on International Trade in<br>Endangered Species of Wild<br>Flora and Fauna) | CITES List of Species<br>Vulnerable to Exploitation<br>(Appendix II, Convention<br>on International Trade in<br>Endangered Species of Wild<br>Flora and Fauna) |  |  |  |  |
| Corals                     | 2  | —  | All stony and black corals   |  |  |  |  |
| Marine molluscs            | 10   | —  | 10   |  |  |  |  |
| Marine fishes              | 111  | 2  | —  |  |  |  |  |
| Sea turtles                | 9 (all)  | 7  | 1  |  |  |  |  |
| Sea birds                  | 61   | 4  | 1  |  |  |  |  |
| Sirenians                  | 4 (all)  | 3  | 1  |  |  |  |  |
| Seals, sea lions           | 12   | 3  | 9  |  |  |  |  |
| Sea otter                  | 1  | 1  | —  |  |  |  |  |
| Whales, dolphins           | 14   | 22   | All  |  |  |  |  |
|                            |  |  |  |  |  |  |  |

Updated and modified from A Sea of Troubles, GESAMP Reports and Studies, no. 70, United Nations Environment Programme, 2001.

when their numbers have become low, and **endangered** when in immediate danger of disappearing forever.

Marine species may be threatened by overexploitation for food, hides, and other products. Many species of fishes, sea turtles, and other marine animals are killed and discarded as fisheries by-catch (see "Optimal Yields and Overfishing," p. 391). Habitat destruction, pollution, and the introduction of pests (see "Biological Invasions: The Uninvited Guests," p. 420) and diseases also place species at risk. The Steller's sea cow, a **sirenian**, is a shocking example of a marine animal that was rapidly exterminated because of unregulated hunting for food (Fig. 18.13).

Species are categorized as rare, threatened, or endangered when they face the possibility of extinction or extermination.

The future of many marine species is at stake (Table 18.1). Perhaps the most widely known case is that of the whales (see "Whales, Dolphins, and Porpoises," p. 190), but there are many other examples. Giant clams (*Tridacna*; see Fig. 14.34) are taken for food and for their shells in such



**FIGURE 18.13** The Steller's sea cow (*Hydrodamalis gigas*), weighing an estimated 10 tons or more, ate mostly kelp. It became known to science in 1741, when it inhabited the kelp beds of the Commander Islands in the western Bering Sea. Demand for its meat, which was considered "as good as the best cuts of beef," led to its extermination at the hands of whalers. The species was slaughtered to extinction soon after its discovery; the last known live individual was taken in 1768. numbers that they have become rare or even locally extinct in most parts of the tropical Pacific. Marine snails like cowries (Cypraea) and cones (Conus), whose shells are eagerly sought by collectors (Fig. 18.14), have similarly disappeared from many areas. Intense commercial fishing to satisfy the growing markets for shark meat and fins, recreational fishing, and by-catch on longlines threatens many species of sharks. Sharks, like whales, reproduce slowly. It is feared that many shark species may be pushed to the brink of extinction in a decade or two. Atlantic swordfish are already threatened by fishing and longline by-catch (see "Optimal Yields and Overfishing," p. 391). Sea snakes have been exterminated in some places because of hunting for their skins. All seven species of sea turtles are endangered. Adults as well as eggs have been exploited for food and tortoiseshell (Fig. 18.15; also see "The Endangered Sea Turtles," p. 182). Their nesting sites have been overrun by development, and they drown in fishing nets.

Seabirds have not fared too well either. Overfishing has been responsible for a decline in the number of seabirds in

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FIGURE 18.14 Shells and reef-building corals from the tropical Pacific for sale in Venice, Italy.



**FIGURE 18.15** One of the many types of tortoiseshell products that are regularly confiscated by the U.S. Fish and Wildlife Service. They are part of the illegal multimillion-dollar world trade in endangered species.

many parts of the world. The great auk (*Pinguinus impennis*), a penguin-like seabird that inhabited the North Atlantic, is gone forever because of our appetite for its eggs, feathers, and meat.

Many other marine organisms that face extermination are marine mammals that have low reproductive rates. Some species of seals, sea lions, and walrus have been decimated for their skins, meat, blubber, or the precious ivory of their tusks. Monk seals (Monachus) are endangered; one species, the Caribbean monk seal (M. tropicalis), is probably now extinct. The number of Steller sea lions (Eumetopias jubatus) has sharply declined in the northwestern Pacific. The sea otter (Enhydra lutris; see Fig. 9.12) has made a partial comeback but is still threatened (see "Kelp Communities," p. 294). Manatees (Trichechus; see Fig. 9.13) and the dugong (Dugong), the smaller cousins of the extinct Steller's sea cow, are both in danger of extinction.

Many marine species are at a risk of being exterminated because of unregulated exploitation and other anthropogenic impacts. Whales, sea turtles, manatees, and other marine mammals are especially imperiled.

Practically everywhere we look in the marine environment there are alarming indications of a loss of biodiversity through the disappearance of species as a result of the loss and degradation of habitats (see "Biodiversity: All Creatures Great and Small," p. 232). Conservation of biodiversity aims at the conservation of a vast number of species, their habitats, and entire communities, not merely the preservation of a limited number of endangered species.

### CONSERVING AND ENHANCING THE ENVIRONMENT

The threats of destruction of habitats, overexploitation, and pollution do not suggest a very optimistic future for the marine environment. A growing human population (see Fig. 17.2) guarantees further pressures. At stake is the survival of our very own species. Some forms of life will certainly survive at sea and on the rest of the planet, but will *we* survive? Is it too late? Can something be done?

### Conservation

The **conservation** of marine life and its protection from human abuse is one solution. Conservation efforts include many local, national, and international projects dedicated to the protection of species and environments (Fig. 18.16). Many countries strictly regulate the types



**FIGURE 18.16** Biologists tagging a hawksbill turtle (*Eretmochelys imbricata*) in Papua New Guinea in an effort to learn more about its migrations and habits. Papua New Guinea is the only place with breeding grounds for six species of sea turtles. This photograph was taken at Wuvulu Island, where sea turtles are common because the inhabitants do not eat turtle meat and eggs as a result of religious restrictions.

and amounts of pollutants that can be dumped at sea. Oil drilling has been banned along some coasts, such as that of central California. Commercial fisheries are regulated by national governments,

**Sirenians** A group of marine mammals collectively known as the sea cows and characterized by a pair of front flippers, no rear limbs, and a paddle-shaped tail.

Chapter 9, p. 190

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### SAND ON THE RUN, OR WHAT TO DO With our shrinking beaches

Sandy beaches constitute one of our most valuable coastal resources. Millions use them for recreation, and their importance as a tourist attraction is evident from Atlantic City to Waikiki. Unfortunately, beaches have been shrinking and disappearing everywhere.

Sandy shores happen to be among the most restless of all marine environments. Sand shifts, so disruptions like storms, hurricanes, winds, and currents periodically modify the shore. The Atlantic and Gulf coasts of the United States are protected by **barrier islands**—long, low, sandy islands that run parallel to the coast. This long stretch of islands comprises one of the world's most splendid sandy beaches. Barrier islands are characteristic of shores bordering wide continental shelves. They were formed as sea levels began to rise between 12,000 and 14,000 years ago (see "Climate and Changes in Sea Level," p. 35). Waves and wind began pushing bottom sediments and formed bars on the flat shelf. Sand bars eventually formed barrier islands, which migrated toward the shore as the sea level continued to rise.

The value of barrier islands goes beyond protecting coastline by absorbing the stress of storms and currents. Their **sand dunes** are inhabited by salt-resistant plants and land animals. Seabirds use them as nesting sites. Barrier islands may include salt marshes, seagrass meadows, freshwater sloughs, and even forests. Florida's barrier islands feature mangrove forests. Untouched barrier islands, however, are becoming rare. Bridges and roads have made some more accessible, and as a result they have been overrun by residential and commercial development.

Development is not the only concern. Their origin may give us a hint that barrier islands were not planned to be with us for a long time. Their size and shape are always changing. Wind and **longshore currents** erode their seaward side by continually shifting sand from one tip to the other, north to south in the eastern United States. Channels between islands may fill up, and islands may be sliced in half.



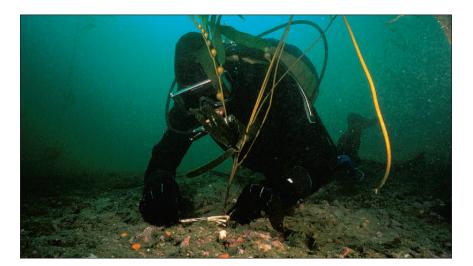
Barrier island along the southern coast of Long Island, New York.

Not everybody realizes that sandy beaches and barrier islands will not tolerate permanent structures for too long. Seawalls, breakwaters, jetties, and groins may be built as a safeguard but often make the problem worse. Erosion may be controlled by encouraging the natural development of dunes or by planting vegetation that helps stabilize the sand. Replenishing sand by bringing it periodically from offshore is one expensive, but temporary, way to save a beach. This is what is being done in highly urbanized Southern California, where rivers, which once brought in sand to the shore, now end behind dams or have been transformed into concrete-bottomed channels. Managing beaches and barrier islands, however, may simply be a waste of time and money. In many cases, efforts serve only to disrupt the natural coastal processes that sooner or later will triumph over our ingenuity.

partly as a result of the establishment of exclusive economic zones, or EEZs, and by international commissions (see "Managing the Resources," p. 394). Unfortunately, many of these quotas are being set above maximum sustainable yields (see Fig. 17.10). Governments have also established marine protected areas for the protection and management of areas of ecological significance. The National Estuarine Reserve Research System of the United States, for example, designated 17 reserves in 14 states and Puerto Rico protecting almost 1,200 km<sup>2</sup> (3,100 mi<sup>2</sup>) of estuaries, salt marshes, and mangrove forests. The Great Barrier Reef in Australia, the Florida Keys, Monterey Bay in California, and other areas around the world have been designated marine protected areas. Groups and organizations like the Cousteau Society, the Sierra Club, the World Wildlife Fund, and the United Nations Environment Programme play an active role in conservation through education, the sponsoring of projects, and even lobbying for legislation.

Protection of coastal regions against the advancing wave of development is of crucial importance. The conflict between economic development and the preservation of coastal resources, though especially intense in developing countries, occurs everywhere. Development should be sustainable, that is, it must meet the needs of today without affecting the ability of future generations to meet their needs. Laws have been passed by many governments, but there is still a lot of work to be done. Coastal management aims at promoting the wise use of our coasts while ensuring that the benefits of this use can be sustained for future generations. The multiple use of coastal resources and the need to manage them calls for judicious planning to accommodate the often-conflicting interests of developers, fishers, surfers, power-plant builders, beachgoers, and nesting seabirds. Coastal management

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**FIGURE 18.17** Restoration of marine habitats has included the transplantation of young giant kelp (*Macrocystis pyrifera*) plants into areas where kelp forests have diminished or vanished.

deals with issues as varied as historical preservation, beach access, military uses, tourism, and water quality.

Efforts to stop the deterioration of the marine environment include conservation and effective coastal management.

Antarctica is of special significance on the agenda of conservationists. Its coasts support unique forms of life found nowhere else, and its ice cap holds about 70% of the earth's freshwater. But nobody owns Antarctica. Potentially rich oil, coal, and mineral deposits there raised the specter of development, with disastrous consequences. A 50-year ban on mining and oil exploration, however, was signed by 31 nations in 1991.

#### **Restoration of Habitats**

Another strategy for improving the quality of the environment is to help habitats recover from modifications caused by pollution and habitat destruction. **Habitat**  restoration helps recovery from stress by transplanting, or restocking, key species from healthier areas. The loss of priceless salt marshes and mangrove forests through landfilling or the building of boat marinas can be at least partially compensated for by creating or improving a similar habitat elsewhere. These efforts of course assume that the new location meets the physical requirements (such as tides, salinity, and the type of substrate) needed for the development of a healthy biological community. Successful examples of habitat restoration include the transplantation of cordgrass (Spartina), one of the dominant plants of salt marshes, and mangrove seedlings. Introduced species of cordgrass, however, have taken over habitats normally inhabited by native species (see "Biological Invasions: The Uninvited Guests," p. 420). The restoration of salt marshes has been facilitated by reopening blocked connections to the open sea in order to restore tidal flow. Channels are constructed and accumulated sediment dredged. Tides slowly

bring in the larvae of other components of the community. Young giant kelp (*Macrocystis*), with their root-like holdfasts tied to concrete blocks or to submerged nylon lines, have been used to help restore kelp forests (Fig. 18.17). New techniques in the culture of coral promise the reseeding of damaged reefs. Seabirds are being attracted to old nesting grounds by using painted decoys and solar-powered tape recorders that play bird calls!

### Artificial Reefs

Fishing can be greatly enhanced by building artificial reefs. The irregular surfaces and the hiding places provided by the reefs attract fishes, lobsters, and other forms of life, as well as anglers and divers. Shellfish and seaweeds like kelp can thrive on their surfaces. Everything from concrete blocks, discarded tires, and toilets to scuttled ships, useless battle tanks, an old 727 jet, and custom-made frames and structures have been used to build artificial reefs around the world (Fig. 18.18). Hundreds have been built in Japan, where tsukiiso, or reef-construction, has been successful in increasing commercial yields of fish, abalone, sea urchins, and seaweeds. It has been argued, however, that artificial reefs may only concentrate fishes and wildlife in one spot, making them easier to catch and contributing to their depletion.

Conservation efforts such as the establishment of marine protected areas and the restoration of habitats may reduce anthropogenic threats to the marine environment.

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**Exclusive Economic Zone (EEZ)** A zone 200 mi (370 km) wide along the coast, in which nations have exclusive rights to fishing and other resources. *Chapter 17, p. 395*  IV. Humans and the Seas

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### FIVE SIMPLE THINGS YOU CAN Do to save the oceans

Our impact on the health of the oceans is much more serious than we often assume. We all impact the oceans, no matter how far we live from the seashore. You can do a lot to help save the oceans. Here are five simple things inspired by *50 Simple Things You Can Do to Save the Earth* by the Earthworks Group.

- 1. *Get involved. Keep informed.* Be aware of and keep up with environmental issues. Read, ask questions, listen carefully. Numerous organizations, societies, and agencies are committed to help save our planet. Hear what they have to say and sponsor them.
- 2. Take care of the environment. If you go to the seashore or go snorkeling or diving, do not disturb in any way the environment. Return any overturned rocks to their original positions. Leave all forms of life where they are. If you go fishing, know the regulations and take only what you really need for food. Return undersized fish. If you travel overseas, don't buy products made from endangered or threatened species like tortoiseshell or ivory, which may come from walruses. Corals and shells should be left alone, and alive, in their natural home. Be sure to tell merchants you object to their sale of shells, corals, sand dollars, and other marine life, which were most probably collected alive and killed for sale. Don't buy the yellowfin tuna that is caught in nets that trap dolphins. Look for the "dolphin-safe" seal on the label.
- 3. *Dispose of hazardous materials properly.* The list of toxic chemicals we use is endless. Paints, disposable batteries, permanent-ink markers, household cleaners, used crankcase oil, and many other products contain toxic chemicals, everything from heavy metals to PCBs to sprays that may contain chlorofluorocarbons (CFCs). Dumping them down the drain or storm drain simply adds them to sewage, which may ultimately drain right into the ocean . . . untreated!
- 4. *Recycle plastics, motor oil, bottles, and other forms of trash.* Reduce the risk of plastics being washed to sea by recycling them. Don't forget to pick up any plastic you may have left around the beach. Cut open those six-pack rings before disposal; you don't know where they may end up. Oil dumped onto the ground, into storm drains, sewer, or trash pollutes rivers, which ultimately empty into the ocean. Your local recycling center can tell you how to recycle.
- 5. *Save energy*. Saving on energy keeps carbon dioxide, a greenhouse gas that promotes global warming, out of the atmosphere. Saving gasoline, heating oil, coal, and electricity reduces the need for oil and thus the threat to the marine environment from more offshore oil drilling and oil spills. It also reduces the need for nuclear power plants, which increases the possibility of radioactive wastes and thermal pollution.

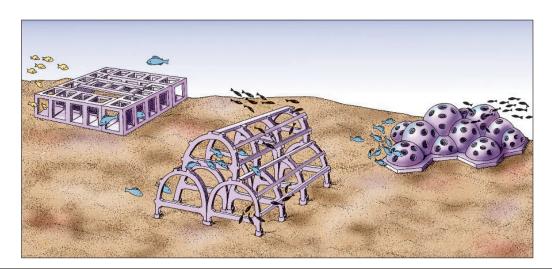


FIGURE 18.18 Artificial reefs built of various types of prefabricated concrete blocks.

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# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

### **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

### Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

### **Critical Thinking**

- Wastes from duck farms used to wash into two shallowwater bays on Long Island, New York. The wastes, rich in nutrients such as nitrate and phosphate, polluted the water. What do you suppose was the immediate effect of the pollutants? Can you speculate on the likely effects on the commercially valuable shellfish of the area?
- 2. It is found that a chemical present in effluents coming from a factory is being stored in the tissues of herring, a plankton-feeding fish. What type of observations and possible experiments would you suggest to find out if the chemical is biodegradable? What is the significance of finding out if the chemical is biodegradable or not?
- 3. Tourism and its effects (for example, pollution from hotels and the impact of boats and tourists on fragile habitats) often clash with conservation efforts. Sometimes, however, tourism can help. The economic impact of banning the hunting of harp seals in eastern Canada has been compensated for, in part, by the influx of tourists that now come to see the seals. Can you think of other examples? What recommendations can you make to minimize the impact of tourism on unspoiled marine environments?

### For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol **()**, and will contain live links when you visit this page in the Online Learning Center.

### **General Interest**

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### In Depth

- Barnett, T. P., D. W. Pierce and R. Schnur, 2001. Detection of anthropogenic climate change in the world's oceans. *Science*, vol. 292, pp. 270–274.
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- Cloern, J. E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series*, vol. 210, pp. 223–253.
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### See It in Motion

Video footage of the following can be found for this chapter on the Online Learning Center:

• Zooxanthellae partially absent in corals: bleaching or whiteband disease (Solomon Islands)

### Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- · Resources from the sea
- Impact of humans on the sea; pollution
- Water pollution
- Red tides
- Pfisteria
- · Global warming
- Fisheries
- · Conservation issues concerning reptiles
- Marine turtles
- Conservation issues concerning birds
- · Conservation issues concerning mammals

### **Quiz Yourself**

Take the online quiz for this chapter to test your knowledge.

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# The Oceans and Human Affairs



e would like to close the book by briefly outlining the many ways the ocean has molded, affected, or influenced human cultures. We have already seen in Chapter 17 how we use the resources of the ocean, and in Chapter 18 how we are affecting the health of the ocean. Now we look at the other side of the coin to see how the ocean has influenced us.

### OCEANS AS BARRIERS AND AVENUES

Once upon a time, people believed that our planet was flat and that sailing beyond the horizon meant falling into the gaping mouths of sea monsters (Fig. 19.1). The peoples of the world were separated from each other by unknown continental masses or by the great expanses of uncharted waters. The oceans served as barriers between cultures. Even the few kilometers of channel that separates England from mainland Europe had an isolating effect and helped define and distinguish English culture. The cultures of Ireland, Madagascar, Japan, and other island nations were similarly affected.

Few people risked venturing beyond the horizon. There were, however, exceptions. For centuries Arab sailors regularly sailed across the western Indian Ocean. The Vikings crossed the North Atlantic during the ninth and tenth centuries; as did Basque whalers not long after. Polynesian double canoes sailed the great expanses of the Pacific, and Chinese sailors may have reached the easternmost shores



Traditional fishing, Indonesia.

of the Pacific Ocean. It was not until the fifteenth century, however, that the European voyages of discovery began to change the ancient and medieval view that the world was flat.

The quest to discover new lands beyond the sea was pioneered by the Portuguese, who sailed around the southern tip of Africa and on to India by the late fifteenth century (see "Tall Ships and Surface Currents," p. 59). Their intention was to take a share of the profitable spice trade. Also looking for a shorter way to the Orient was Christopher Columbus, who first crossed the Atlantic in 1492. Unlike the Vikings, who landed in America centuries before, Columbus' "discovery" was soon known by everyone. Many other seaborne explorers followed, not all looking for spices (see "The History of Marine Biology," p. 4). Between 1480 and 1780, these explorers opened all oceans and, except for most polar regions, few coastlines remained unexplored. The oceans then became very powerful avenues of culture and commerce, war, and disease. Colonialism was carried across the oceans, and so were immigrants, slaves, religions, languages, traders, scientific discoveries, products, and ideas.

The oceans, which before the age of discovery and exploration helped effectively isolate the peoples of the earth, eventually became an avenue for change.

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Today the oceans have become vital freeways that link world economies by transporting raw materials and manufactured goods to the four corners of the globe. Shipping remains the cheapest way to move large quantities of goods over long distances, so most international trade moves by sea. Globalization of economies will further strengthen the growth of marine trade. The volume and type of goods moved by sea vary according to the geographical distribution of resources, location of industries and markets, population, and economic growth. Total seaborne trade grew dramatically after World War II. It decreased by around 10% during the 1980s but only because of a drop in crude oil shipments. Crude oil, nevertheless, still accounts for the largest volume of seaborne trade. Businesses that deal in commodities such as iron ore, coal, and grain rely heavily on shipping. The enormous variety of goods being shipped has led to the development of vessels specialized in the transport of such exotic cargoes as liquified gas, livestock, and wine. Today a large percentage of maritime cargo moves by large steel containers that are carried to the docks by trucks and lifted by cranes into giant containerships (Fig. 19.2). Cargo is then unloaded at the final destination without ever having been touched by human hands.

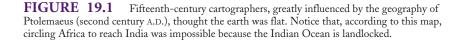
As far as carrying people is concerned, the oceans are no longer the avenue of choice, except for short distances along the coast. Jets now transport people between the continents. Large passenger ships, however, have found a new life carrying tourists to sunny islands.

Nowadays, the oceans are also connected by rubbish. The oil from the Middle East, lobster tags from Newfoundland, shampoo bottles from Greenland, and ice-cream containers from Brazil that were washed ashore on a beach in Ireland bear witness to the sad reality.

### OCEANS AND CULTURES

Our association with the ocean probably goes back to our early beginnings. It has even been suggested that some of the early







**FIGURE 19.2** This giant containership, seemingly making its way across land, is actually crossing from the Pacific to the Atlantic Ocean by way of the Panamá Canal.

stages of human evolution were spent on the seashore and that our ancestors were coastal inhabitants who frequently waded in the water searching for food. The evidence for this, so goes the argument, is our scanty hair, a relatively streamlined body, and the presence of a layer of fat for insulation adaptations also found in cetaceans! Most scientists dismiss this hypothesis. Nevertheless, there is no doubt that the ocean strongly influenced the human cultures that began developing along coastal regions from prehistoric times.

**Culture,** which includes the components of the environment created by humans, is reflected in a multitude of ways. It encompasses objects like tools, ornaments, and dwellings, and immaterial things like customs, institutions, and beliefs. An intimate relationship with the

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ocean has molded many cultures around the world. Some anthropologists refer to these cultures as **maritime cultures**.

Fishhooks were one of the first tools made by humans. Excavations of prehistoric waste dumps give evidence of the importance of marine life as food and of the advantages of living near the seashore. Prehistoric shell middens, the accumulation of leftover shells, have been found in coastal areas around the world. Remains of fishes, sea turtles, seabirds, sea urchins, and pinnipeds are often found in prehistoric deposits located near the coast. They have allowed archaeologists to describe the food habits, diet changes, and sometimes the overexploitation of food resources by ancient cultures.

Humans then began to learn to fish using nets, traps, and other more sophisticated techniques. The extraction and trading of salt were of tremendous importance, influencing the development of cities and states. Boats were subsequently improved, allowing fishing peoples and salt traders to roam farther from shore. The trading of food and manufactured goods was just a small step away.

Fishing was a very important activity for many coastal Native Americans. Nowhere is this more evident than among the northwest coastal Indians that inhabited the Pacific shores from southern Alaska to northern California. Their livelihood depended to a great extent on salmon, sea mammals, shellfish, and other marine life. These coastal peoples knew the seasonal changes in abundance and the migration patterns of the species that fed them. Some tribes were even aware that red tides made mussels poisonous. Marine life also provided a basis for religious beliefs. The salmon, for instance, was for some tribes a supernatural being who took the shape of a fish and sacrificed itself every year to help humans. The fish spirits returned to their homes at sea to be transformed back into fish if their bones were thrown back into the water. Rituals and observances were carried out to prevent salmon from being offended and thus refusing to return and swim up the rivers to be caught for food. Other rituals welcomed salmon back before their migrations to spawn upstream. Marine life also provided inspiration for

superb wood carvings, such as totem poles, carved by some tribes (Fig. 19.3). Shells from abalone and other marine gastropods were used in making masks and ornaments.

The Inuit and Inupiaq Eskimos and other peoples native to the Arctic carved a precarious existence from the icy waters. They fished and hunted whales and other marine mammals from kayaks, one- or two-person boats made of seal or walrus skins, or umiaks, larger boats also made from skins. Native folklore is rich in stories of hunting incidents in which the hero is helped by spirits and other supernatural forces arising from the sea. Though native cultures have changed, some continue to follow traditional ways of fishing and hunting. The closely related Aleuts inhabited the Aleutian Islands farther south. They hunted seals, sea otters, whales, and other marine mammals. The Aleuts are now greatly reduced in number, and their once splendid association with the ocean is little more than a memory.

The Seri Indians of northwestern Mexico regularly used the seeds of eelgrass (*Zostera*) from the Gulf of California as a traditional food source—the only known case of a grain being harvested right from the ocean. Eelgrass is now harvested only occasionally by the Seri. Its flour is used to make a gruel that is flavored with honey, cactus seeds, or sea turtle oil. In the old days, toasted grains were used to cure children's diarrhea. The dry eelgrass was used as roofing and to make dolls. A deer or bighorn sheep scrotum filled with dry eelgrass made a ball for children to play with.

The early Polynesians, Micronesians, and other peoples of Oceania had the whole Pacific Ocean as their backyard. As a result, they developed extraordinary skills as navigators. Unlike Europeans, they were not afraid of the ocean that stretched beyond the horizon. They settled the farthest reaches of the Pacific, from New Zealand and the Mariana Islands to Hawai'i and Easter Island. For this remarkable feat, they relied on doublehulled canoes that were carved from trees and secured with coconut fiber (Fig. 19.4).

The ocean and its creatures also provide images and symbols for the folklore and art of the peoples of Oceania (see

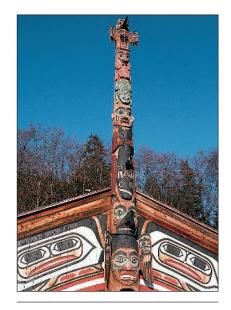


FIGURE 19.3 Totem poles carved by the native inhabitants of the Pacific Northwest often include marine motifs such as halibut (shown here), killer whales, and sea otters.

Fig. 1.1). According to legend, New Zealand was discovered when Polynesian fishers pursued an octopus that stole their bait. The ocean has a chief role in their creation myths and other aspects of their mythology. In some cultures a giant clam is said to have been used in the making of heaven and earth. In others a great spotted octopus holds heaven and earth together. There are also countless stories involving marine life: tales of porpoise girls, pet whales, and shark gods falling in love with locals.

The sea helped mold many of the maritime cultures that developed in coastal regions around the world.

**Red Tides** Blooms of some dinoflagellates, cyanobacteria, and other organisms that discolor the water and produce toxins that, if accumulated in shellfish, cause *paralytic shellfish poisoning* in humans.

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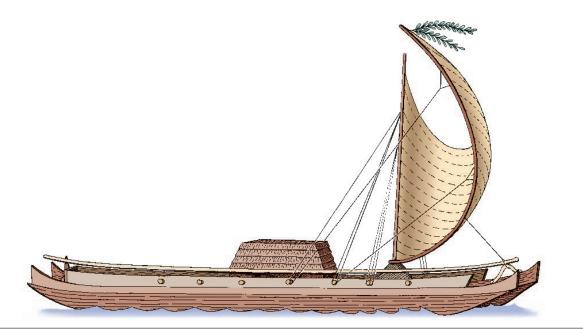


FIGURE 19.4 Wa'a kaulua, a Hawaiian double-hulled canoe.



FIGURE 19.5 The Romans often used marine motifs in mosaics to decorate floors and walls.

Ancient seafaring cultures also emerged in the Mediterranean and the Middle East. Egyptians, Phoenicians, Greeks, Persians, Romans, Arabs, and other ancient mariners fished, traded, and made war with each other at sea. They were often inspired by the sea (Fig. 19.5). Many of their shipwrecks have yet to be discovered (see "Marine Archaeology," p. 433).

Fishing and commerce remained the basis of coastal economies in Eu-



**FIGURE 19.6** Shanghai became China's leading port and the base for commercial penetration by the Western powers after the city was opened to unrestricted foreign trade in 1842. This 1860 drawing shows the great variety of ships and vessels used in the transoceanic and local trade.

rope during the Middle Ages. The Baltic Sea herring fishery, for example, was the livelihood of the Hanseatic League, a thriving federation of Baltic and North seaports. When the fishery collapsed in the fifteenth century, so did the League. England, the Netherlands, and Portugal owed much to seaborne trade and sea power for their emergence as leading nations during the late Middle Ages and early modern times (Fig. 19.6). In many ways they simply followed the example of Venice and Genoa, the great rival seaports

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### MARINE ARCHAEOLOGY

The discovery, salvage, and interpretation of the part of humankind's cultural heritage that remains undersea is the aim of a relatively new and exciting field, **marine archaeology**. New tools, like scuba diving and remotely operated undersea vehicles, have allowed marine archaeologists to reveal secrets that had remained concealed by sediment at depths beyond our reach.

Marine, or underwater, archaeology as a modern science was born in 1960 when archaeologists excavated a 3,000-year-old ship off the Mediterranean coast of Turkey. Before that time, the chance recovery of sunken artifacts was occasionally carried out by sponge fishers, not by trained archaeologist-divers. Underwater digs have since been investigated around the world. The oldest so far seems to be that of a Bronze Age ship loaded with fascinating artifacts that sank off the southwestern coast of Turkey 3,500 years ago.

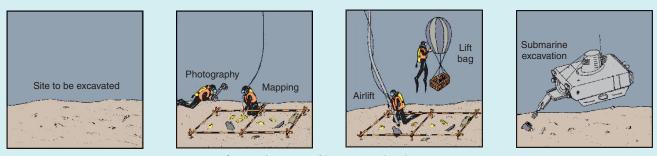
These underwater digs have provided invaluable information about different aspects of ancient cultures: ship construction, life aboard ship, trade and discovery routes, and naval warfare. Tools, utensils, footwear, weapons, coins, and jewelry found on sunken ships have given us details of the products that were traded, food habits, and other aspects of everyday life.

Underwater sites may also yield art treasures, gold, and other valuables. Already a few priceless bronze Greek sculptures have been recovered from the Mediterranean. Some wrecks of Spanish galleons, as well as more modern ships, hide a fortune in gold, coins, and jewelry. The plundering of wrecks for valuables is a major problem because archaeologically significant sites may be damaged or dispersed.

Shipwrecks may be located by analyzing old documents and charts. Shallow-water wrecks have been discovered by alert divers attracted by half-buried hull fragments, an anchor, or a pottery amphora that stored olive oil or wine in better days. Underwater surveying of wrecks involves dives, underwater photography and television, air photography, and charting the site using a grid system. More sophisticated techniques are also being used. Side-scan sonars use reflected sound waves to survey large sections of the ocean floor, whereas sub-bottom sonars can profile sites covered with sediment. A computer-controlled system called sonic highaccuracy ranging and positioning system, or SHARPS, provides archaeologists with three-dimensional maps of sites. A remotely controlled underwater vehicle sends live pictures to a surface vessel that beams them to a satellite in charge of relaying them to museums and institutions to be studied by experts. The image thus moves from the bottom to the water surface to space to the land surface thousands of kilometers away in a matter of seconds!

Marine archaeologists are also involved in excavating towns and harbors that became submerged. They can provide an awesome variety of data on the economy and the use of technology of past cultures. Port Royal in Jamaica, which sank as a result of an earthquake in 1692, is an example of such a submerged dig. So is the nowsubmerged port of Cesarea Maritima, a Roman city on the coast of Palestine.

Sometimes sunken ships remain intact, as in the case of the *Vasa*, a Swedish warship that sank during its maiden voyage in 1628. It rested quietly in Stockholm harbor until 1961, when it was lifted whole from a depth of 33 m (108 ft). The wreck had been preserved by cold water and thick mud. Luckily, wood-eating ship-worms were absent because of the low salinities of the Baltic. Another case is that of the *Mary Rose*, an English warship that sank in 1536. Its starboard half, the only surviving part, was raised in 1982 after yielding valuable artifacts. The *Monitor*, a Civil War ironclad, lies 67 m (220 ft) below the surface off Cape Hatteras. It may be next, or perhaps the *Titanic*, which lies some 4,000 m (13,000 ft) under the sea!



Some techniques used by marine archaeologists.

in Mediterranean trade. Fishing, trade, and naval power in particular began to play other important roles. By stimulating shipbuilding, they strongly encouraged exploration, science, and technology.

"Those who rule the sea, rule the land" soon emerged as a motto of the emerging nation-states of the world. Echoes of Lepanto, the defeat of the Spanish Armada, Trafalgar, Navarino, and other legendary sea battles still ring in our ears as heroic sagas. *The Influence of Sea Power upon History*, a book written in 1890 by the American naval officer and historian Alfred T. Mahan, emphasized the importance of sea power. This book was extremely influential in persuading major powers to build modern fleets in the years before World War I. Mahan's predictions were quickly confirmed: In 1905 the Russian Empire was lethally crippled when the Japanese sank their Pacific fleet. The Jutland, Midway, Coral Sea, and other World War I and II naval battles further proved the strategic importance of the oceans in modern warfare.

Since the birth of "gunboat diplomacy," nations have continued to employ sea power to exert their influence by defending their local or global interests. Missile-carrying nuclear submarines, long-range bomber planes, and nuclear missiles have replaced battleships as a first-strike force for the superpowers. Nevertheless, incidents and even actual combat at sea over maritime boundaries and fishing rights have been making news headlines year after year. The control of sea lanes, critical to world economies, and the defense of oil, fishing, and other coastal resources will ensure the continuous importance of naval power for many nations.

In the meantime, many of the maritime cultures that managed to survive through historic times have been greatly modified and transformed. Only traces may remain of times when life depended on the cycles of the ocean and on the food caught from it.

Some unique maritime cultures still survive. Fishing villages populated by maritime peoples who are still faithful to a unique livelihood and who depend on the ocean for their survival survive in isolated spots such as the coast of Labrador, the Faeroe Islands, and the island of Tristan da Cunha in the South Atlantic (see map in Appendix B). Some have managed to survive along coasts no longer classified as isolated (Fig. 19.7). The Bajaus, or "sea gypsies," of the southern Philippines and North Borneo are boat dwellers who, like their ancestors, have followed a nomadic life at sea, fishing and diving for pearls. Korea's women divers, the henyo, continue a grueling livelihood of diving for sea urchins, octopus, and abalone (see the photo on p. 381). The Kuna Indians of the Caribbean coast of Panamá literally cling to several hundred tiny offshore islands, some built out of coral and filled in by the Kuna themselves. And then there are the Dutch, a maritime people by tradition who still manage to inhabit land they have reclaimed from the bottom of



**FIGURE 19.7** Fishers and traders have used the traditional Arab *dhow* for centuries. These fishers in Tanzania, East Africa, are using a small one-masted version. *Dhows* still sail between India and ports in the Arabian Peninsula, Red Sea, and East Africa along what is considered the world's oldest commercial sailing route.

the North Sea by using dikes and canals. A large portion of their densely populated country actually lies below sea level. Many modern societies still include fishers, fish and shellfish farmers, sailors, commercial divers, and other occupational groups that depend on the ocean (Fig. 19.8). As such, they are regarded as maritime subcultures.

The imprint of the oceans on humankind still survives in our daily lives in cultural elements that transcend food, commerce, politics, and war. The sea and its lore endures in the work of writers, painters (Fig. 19.9), and musicians such as Conrad, Melville, Hemingway, Neruda, Turner, Monet, Debussy, and Mendelssohn. The sea has even inspired architects (Fig. 19.10).

## OCEANS AND RECREATION

Another legacy of pure enjoyment from the ocean is **recreation**. Rising standards of living and increased leisure



**FIGURE 19.8** Sailors like this man mending fishing nets in Malaysia belong to a maritime subculture that remains tightly linked to the rhythms of the ocean.

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FIGURE 19.9 The *Gulf Stream* (1899), an oil painting by Winslow Homer, an American painter much influenced by marine subjects.



**FIGURE 19.10** Architecture inspired and influenced by the sea: the *Itsukushima-jinja* shrine in Japan. Both the shrine and its famous gate, or *torii*, were designed to appear to float on water at high tide.

time, particularly in the developed countries, have opened up the opportunities people have for the recreational enjoyment of the ocean.

Practically anybody who can afford it, even those living far from the coast, can now fly to a faraway beach or take a cruise among once remote paradise islands. Ecotourism in spots like the South Pacific, Galápagos, and Antarctica offers tours for divers and nature lovers. Catering to those seeking the sun and fun of the sea has developed into a giant tourist industry, one that keeps afloat many national and local economies. Seaside resorts sprang up along European coasts in Roman times; now they are built practically anywhere there is sand, sun, and reasonably warm water. In many areas, however, tourism has displaced fishing and other traditional activities. Water pollution is often a result of the extra millions of gallons of sewage generated by development. The destruction of habitats from the building of hotels and other facilities and the increase in the number of divers and boat traffic are other harmful side effects.

Recreation for many revolves around a multitude of water sports, like snorkeling, scuba diving, sailing, water skiing, and surfing. Surfing alone is for many a way of life, a subculture of its own. Together with marine sports fishing (see "Fisheries for Fun," p. 400), ocean sports provide relaxation and support a thriving recreation industry.

Recreational opportunities offered by the ocean influence the way people spend their leisure time. They have also affected those who depend on the tourist industry for a living.

### PROSPECTS FOR THE FUTURE

It is impossible to predict accurately what lies ahead for our world ocean. Optimists have visions of cities built underwater or on floating islands, food provided by mariculture, unlimited energy from the water and seabed, and no pollution to speak of. Others are less confident. They point out that our impact on the marine

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environment will further escalate as the world's population continues to expand. There is little doubt that our use of ocean resources will continue to increase. Modern technology will lead to new means of exploitation, and for resources never imagined before. The prospects are therefore not very promising. Pollution, the destruction of habitats, and the disappearance of unique species will certainly escalate if no drastic measures are taken. Perhaps even more alarming is the possibility of a rise in sea levels as a result of **global warming**.

The oceans, the common heritage of all humankind, must be safeguarded by all to save them from overexploitation and pollution. This has been one of the aims of the **Third United Nations Conference on the Law of the Sea (UNCLOS-3),** the 1982 treaty that culminated many years of complicated deliberations by the many nations that were represented. Only a few nations have ratified the treaty, however. Nevertheless, many nations have already implemented some of the provisions of the treaty.

The treaty, for example, led to the establishment of the **exclusive economic zones (EEZs)** that extend a nation's economic interests 200 nautical miles (370 km) from the coast. This agreement has already had significant consequences for the present and future management of marine resources, particularly fisheries (see "Managing the Resources," p. 394). Nations owning tiny islands and reefs barely above high water can now claim large portions of the surrounding seabed, which may hold untold riches in fish, oil, or minerals. Such is the case of the Paracel and Spratly islands in the middle of the South China Sea, now claimed by several nations in the region. The treaty also allows free passage beyond a 12-nautical mile (22-km) territorial sea around a nation's shores. Unimpeded surface and underwater transit is guaranteed through straits that fall within the territorial sea of one or more nations. This includes the straits of Hormuz (in the Persian Gulf), Bering, and Gibraltar, all of which have great strategic and economic importance. More significantly, perhaps, the treaty calls for individual nations to enact laws and regulations to prevent and control pollution. It also guarantees the freedom to undertake scientific research in the high seas.

The Third United Nations Conference on the Law of the Sea initiated a series of international agreements in an effort to define the use of the oceans by all nations. They included the establishment of exclusive economic zones.

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Other international agreements have attempted to solve other problems. The **U.N. Conference on Environment and Development** at Rio de Janeiro, known as the Rio Earth Summit of 1992, is one example. It resulted in an international agreement to preserve biodiversity on the planet (see "Biodiversity: All Creatures Great and Small," p. 232). One particular commitment was to protect the interests of the traditional fisheries of indigenous people.

From the early beginnings the oceans have influenced humankind by providing food and avenues of commerce and culture. It is clear, however, that the relationship has been reversed. The oceans are now being influenced by humankind—the destruction of habitats, pollution, overfishing, and the potential effects of global warming. Limited progress has been made, but the future of the oceans doesn't seem to be very bright after all. Is it too late to say "Let's wait and see?"

**Global Warming** Rise in the temperature of the earth as a result of an increase in the intensity of the *greenhouse effect* as the levels of carbon dioxide  $(CO_2)$  and other gases in the atmosphere increase.

Chapter 18, p. 410

19. The Oceans and Human Affairs © The McGraw–Hill Companies, 2003



# interactive exploration

Check out the Online Learning Center at <u>www.mhhe.com/marinebiology</u> and click on the cover of *Marine Biology* for interactive versions of the following activities.

## **Do-It-Yourself Summary**

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.

# Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

# **Critical Thinking**

- 1. Most maritime cultures are either long gone or have been radically modified by others. Which elements of a rapidly changing maritime culture do you predict would be the first to disappear? Which would tend to remain unchanged the longest?
- 2. The Third United Nations Conference on the Law of the Sea made no provisions for Antarctica. Some of the land is probably rich in resources like oil, so the eventual exploitation of the land is probably inevitable. Several nations have already established claims, sometimes overlapping each other, to sections of the continent. How would you deal with these claims? Would you give first preference to nations, like Argentina or New Zealand, that claim geographical proximity to the continent or to those, like Norway or Britain, that arrived at the claimed land first? How can resources be exploited if it is decided that the land does not belong to any particular nations?

# For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol  $(\begin{screen} \begin{screen} \line \end{screen}, \end{screen} \end{screen}, \end{screen} \end{screen}$ , and will contain live links when you visit this page in the Online Learning Center.

#### **General Interest**

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# Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

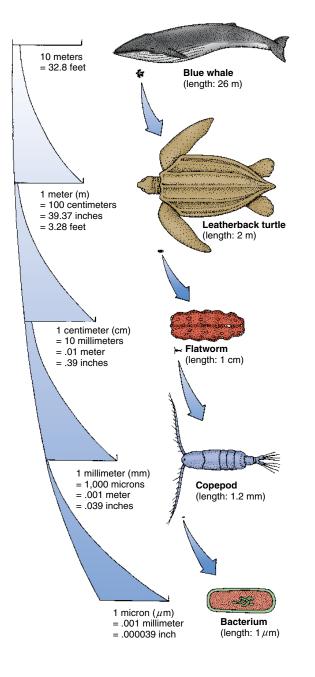
- · Marine archaeology and maritime history
- Fisheries
- Red tides

# Quiz Yourself

Take the online quiz for this chapter to test your knowledge.

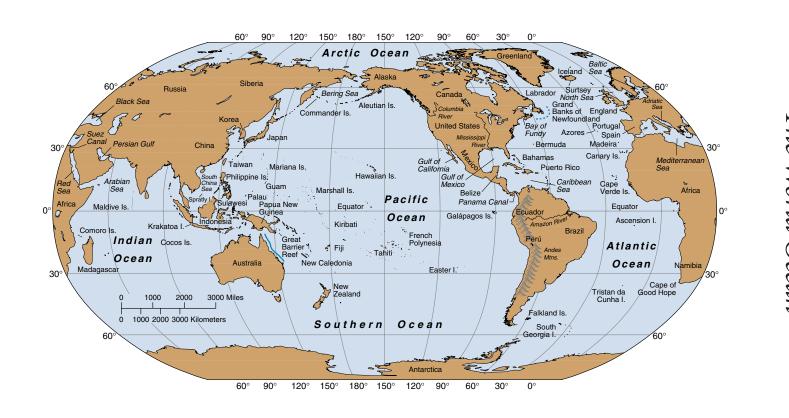
Appendix A: Units of Measurement © The McGraw–Hill Companies, 2003

# appendix A Units of Measurement





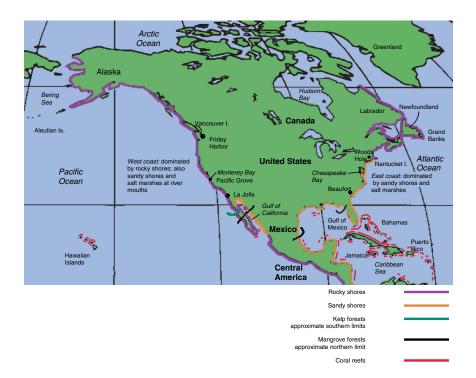
# appendix B



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# appendix C Major Coastal Communities of North America



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Glossary

# glossary

Words in **boldface** are defined separately in the glossary. Other key terms are given in italics.

#### a

**abiotic** A non-living (physical or chemical) component of the environment. *Compare* **biotic.** 

**aboral surface** The surface opposite the mouth (or *oral surface*) in **echinoderms**.

**abyssal plain** The nearly flat region of the deep-sea floor.

**abyssal zone** The bottom from a depth of approximately 4,000 m (13,000 ft) to 6,000 m (20,000 ft) (Fig. 10.20).

abyssopelagic zone The pelagic environment from a depth of 4,000 m (13,000 ft) to 6,000 m (20,000 ft) (Fig. 10.20).

# acorn worms (enteropneusts) See hemichordates.

active continental margin A continental margin that is colliding with another plate and as a result is geologically active (Fig. 2.20). *Compare* passive continental margin.

**active transport** The transfer of substances across membranes by a cell against a *concentration gradient*.

#### adenosine triphosphate See ATP.

**agar** A commercially important **phycocolloid** extracted from **red algae**.

**alga** (pl. **algae**) Any of several groups of **eukaryotic, autotrophic protists** that lack the structural features (true leaves, roots, and stems) of plants.

**algal ridge** A ridge of **coralline algae** that is found on the outer edge of some **coral reefs**.

**algal turf** A dense growth of often filamentous **algae**.

**algin** A **phycocolloid** extracted from **brown algae** that is widely used in food processing.

**alternation of generations** A reproductive cycle in which a **sexual stage** alternates with an **asexual** one, as in the case of a **gametophyte** alternating with a **sporophyte**.

**ambergris** Undigested material that accumulates in the intestine of the sperm whale.

**ambulacral groove** Each of the radiating channels of **echinoderms** through which **tube feet** protrude.

**amino acid** One of the 20 nitrogencontaining molecules that make up **proteins**.

**amphibians** (class *Amphibia*) **Vertebrates** that lay their eggs in fresh water: frogs, salamanders, and allies.

**amphipods** A group of small, laterally compressed **crustaceans** that includes *beach hoppers* (Fig. 7.30) and others.

**ampulla** (pl. **ampullae**) Each of the muscular sacs that extend inside the body opposite the **tube feet** of **echinoderms**.

**ampulla** (pl. **ampullae**) **of Lorenzini** One of several sensory structures in the head of sharks that detect weak electric fields (Fig. 8.3).

**anadromous** Marine fishes that migrate to fresh water to breed. *Compare* **catadromous**.

anaerobic bacteria Bacteria that do not need oxygen.

**anaerobic respiration** The breaking down of organic matter by organisms in the absence of oxygen. *Also see* **respiration.** 

**anal fin** The last **ventral** fin of fishes (Fig. 8.8).

angiosperms See flowering plants.

animals Members of the kingdom *Animalia*, which consists of heterotrophic, eukaryotic, multicellular organisms.

annelids See segmented worms.

anoxic Lacking oxygen.

**antenna** A sensory appendage on the head of **arthropods.** 

**anthozoans** (class *Anthozoa*) **Cnidarians** whose life cycle consists of a complex **polyp** and no **medusa**.

**anthropogenic impact** Disturbance to the natural environment caused by humans.

appendicularians See larvaceans.

**aquaculture** The farming of marine and freshwater organisms. *Also see* **mariculture**.

archaea (sing. archaeum) Prokaryotic, unicellular microorganisms in the domain *Archaea*.



#### 444 Glossary

Aristotle's lantern The set of jaws and associated muscles used by **sea urchins** to bite off food.

**arrow worms (chaetognaths;** phylum *Chaetognatha*) Planktonic **invertebrates** characterized by a streamlined, transparent body (Fig. 7.41).

arthropods (phylum *Arthropoda*) Invertebrates that have jointed appendages and a chitinous, segmented exoskeleton.

ascidians See sea squirts.

**asexual (vegetative) reproduction** The type of reproduction that takes place without the formation of **gametes**. *Compare* **sexual reproduction**.

**asthenosphere** The layer of upper **mantle** that lies below the **lithosphere** (Fig. 2.3).

**atoll** A **coral reef** that develops as a ring around a central **lagoon** (Fig. 14.22).

**atom** The smallest unit into which an **element** can be divided and still retain its properties.

ATP (adenosine triphosphate)

A molecule that stores **energy** and releases it to power chemical reactions in organisms.

**autotroph** An organism that manufactures its own organic matter by using **energy** from the sun or other sources. *Compare* **heterotroph.** 

**auxospore** The resistant stage of **diatoms** that restores the maximum size characteristic to the species.

# b

**back reef** The inner part of a **barrier reef** (Fig. 14.17) or **atoll** (Fig. 14.22).

**bacteria** (sing. **bacterium**) **Prokaryotic,** unicellular microorganisms in the domain *Bacteria*.

**baleen** The filtering plates that hang from the upper jaws of **baleen whales.** 

baleen whales The filter-feeding whales.

**bar-built estuary** An **estuary** that is formed when a **barrier island** or *sand bar* separates a section of the coast where fresh water enters (Fig. 12.1).

**barnacles** Crustaceans that live attached to surfaces and are typically enclosed by heavy calcareous plates (Fig. 7.29).

**barophilic Pressure**-loving. Applied to organisms or enzymes that grow or function best, or only, at high pressure.

**barrier island** A long and narrow island that is built by waves along the coast.

**barrier reef** A type of **coral reef** that develops at some distance from the coast (Fig. 14.17).

**basalt** The dark-colored rock that forms the sea floor, or oceanic **crust**.

**bathyal zone** The bottom between the **shelf break** and a depth of approximately 4,000 m (13,000 ft) (Fig. 10.20).

**bathypelagic zone** The **pelagic** environment from a depth of 1,000 m (3,000 ft) to 4,000 m (13,000 ft) (Fig. 10.20).

**beard worms (pogonophorans;** phylum *Pogonophora)* Tube-dwelling **invertebrates** that lack a digestive system (Fig. 7.18).

**benthos** Organisms that live on the bottom (Fig. 10.19).

**big bang theory** The theory that a cosmic explosion produced clouds of dust and gas from which the earth and solar system originated.

**bilateral symmetry** The arrangement of body parts in such a way that there are only two identical halves, with different *anterior* and *posterior* ends and **dorsal** and **ventral** surfaces (Fig. 7.11). *Compare* radial symmetry.

**binomial nomenclature** A system of naming species using two names, the first of which refers to the **genus**.

**biodegradable** Able to be broken down by bacteria or other organisms.

**biogenous sediment** Sediment that is made up of the skeletons and shells of marine organisms. *Also see* **calcareous** and **siliceous ooze**.

**biological clock** A repeated rhythm that is synchronized with time.

**biological magnification** The increased concentration of **nonbiodegradable** chemicals in the higher levels of the **food chain**.

**bioluminescence** The production of light by living organisms.

**biomass** The total mass of living organisms.

**biotic** A living component of the environment. *Compare* **abiotic**.

**bioturbator** A member of the **infauna** that moves sediment while burrowing or feeding.

**birds** (class *Aves*) **Vertebrates** that have feathers and lay eggs with calcified shells on land.

**bivalves** (class *Bivalvia*) *Clams*, *mussels*, and other **molluscs** that possess a two-valved shell, filtering gills, and a shovel-like **foot**.

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**black corals** (order *Antipatharia*) Colonial **anthozoans** that secrete a black protein skeleton.

**black smoker** A chimney-like accumulation of mineral deposits that is found at **hydrothermal vents** (Figs. 2.24 and 2.25).

**blade** The leaf-like portion of the **thallus** of a **seaweed**.

**bleaching** The expulsion of **zooxanthellae** by reef corals in response to stress.

**bloom** A sudden increase in the abundance of an **alga** or **phytoplankton**.

**blowhole** The nostrils, or nasal openings, of **cetaceans**.

**blubber** A thick layer of fat under the skin of many marine **mammals**.

**bony fishes** (class *Osteichthyes*) Fishes with a skeleton made mostly of bone; they also have **gill covers** and **fin rays**.

**boring sponges Sponges** that bore through **calcareous** skeletons and shells.

bottom layer See deep layer.

brachiopods See lamp shells.

**breaching** Leaping into the air by whales (Fig. 9.28).

**brittle stars** (class *Ophiuroidea*) **Echinoderms** with five flexible arms that radiate from a conspicuous central disk and **tube feet** that are used in feeding.

**brown algae** (phylum *Phaeophyta*) **Seaweeds** with a predominance of yellow and brown pigments.

**bryozoans** (phylum *Ectoprocta* or *Bryozoa*) Small, colonial, **encrusting invertebrates** with delicate, often lace-like, skeletons (Fig. 13.17*e*).

**budding** A type of **asexual reproduction** by which a separate new individual is produced from a small outgrowth, or *bud.* 

**by-catch** Non-target catch that is taken while fishing for other species.

**byssal threads** Strong fibers secreted by mussels for attachment.

#### С

calcareous Made of calcium carbonate.

calcareous algae Green algae that deposit calcium carbonate in their thallus.

**calcareous ooze** A type of **biogenous sediment** that is made of the **calcium carbonate** shells and skeletons of marine organisms.

Glossary

#### Glossary 445

**calcium carbonate (CaCO<sub>3</sub>)** A mineral that is the major component of the shell, skeleton, and other parts of many organisms.

**carapace** (1) The shield-like structure that covers the anterior portion of some **crustaceans.** (2) The shell of *sea turtles*.

**carbohydrate** An **organic compound** that consists of chains or rings of **carbon** with **hydrogen** and **oxygen** attached to them.

**carbon (C)** An **element** that is an essential constituent of all **organic compounds.** 

**carbon cycle** The cyclic reconversion of **carbon dioxide** into **organic carbon** (Fig. 10.17).

**carbon dating** A procedure used to determine the age of recent fossils.

**carbon dioxide (CO<sub>2</sub>)** A colorless gas that is required in the process of **photosynthesis.** 

**carbon fixation** The conversion of inorganic **carbon** into energy-rich **organic carbon**, usually by **photosynthesis**.

**carnivore** An animal that eats other animals. A *top carnivore* is one that feeds at the top of the **food chain**. *Also see* **predation**.

**carnivores** (order *Carnivora*) **Mammals** with teeth that are adapted to eat other animals. The marine members of this group are the *sea otter* and the *polar bear*.

**carotenoid** One of a group of yellow, orange, and red plant pigments.

**carposporophyte** A **diploid** generation found in the **red algae.** It produces non-motile *carpospores*.

**carrageenan** A **phycocolloid** extracted from **red algae** that is widely used in food processing.

**carrying capacity** The maximum population size that can be sustained by the available resources in a given environment.

**cartilaginous fishes** (class *Chondrichthyes*) Fishes with a skeleton made of *cartilage: sharks, rays, skates,* and *ratfishes* (or *chimaeras*).

**catadromous** Freshwater fishes that migrate to sea to breed. *Compare* **anadromous**.

**caudal fin** The posterior, or tail, fin of fishes.

**cellulose** A complex **carbohydrate** that is the main component of fibers and other support structures in plants.

**central nervous system** The *brain* (or a similar aggregation of **nerve cells**) and one or more **nerve cords**.

**central rift valley** A depression in the **mid-ocean ridge** (Fig. 2.23).

**cephalopods** (class *Cephalopoda*) *Octopuses, squids,* and other **molluscs** that possess a **foot** modified into arms that surround the head.

**cephalothorax** The anterior portion of the body of many **arthropods**, which consists of the head fused with other body segments.

**cetaceans** (order *Cetacea*) Marine **mammals** with anterior flippers, no posterior limbs, and a **dorsal** fin: *whales, dolphins,* and *porpoises.* 

CFCs See chlorofluorocarbons.

chaetognaths See arrow worms.

**chemosynthetic (chemoautotrophic) bacteria** Autotrophic bacteria (such as the *sulfur bacteria*) that use **energy** by releasing it from particular chemical compounds.

**chitin** A complex derivative of **carbohydrates** that is the main component of the skeleton of many animals.

**chitons** (class *Polyplacophora*) **Molluscs** that have a shell divided into eight overlapping plates (Fig. 7.26).

**chloride cells** Cells in the **gills** of fishes that are involved in the excretion of excess salts.

**chlorinated hydrocarbons** A group of **nonbiodegradable**, synthetic chemicals. Some are toxic and become pollutants.

**chlorofluorocarbons (CFCs)** Chemicals, used in sprays, air conditioners, and other products, that affect the **ozone layer**.

chlorophyll A green photosynthetic pigment.

**chloroplast** The **organelle** where **photosynthesis** takes place (Fig. 4.8*b*).

choanocyte See collar cell.

**chordates** (phylum *Chordata*) Animals that display a hollow **dorsal nerve cord, gill slits**, and a **notochord**. Includes the **protochordates** and the **vertebrates**.

**chromatophore** A skin cell that contains pigment.

**chromosome** The cell structure where **DNA** is located.

**ciguatera** A type of food poisoning contracted from eating certain tropical fishes. It results from a toxin produced by a **dinoflagellate.** 

**ciliary comb** One of eight bands of **cilia** fused at the base that is found in **comb jellies**.

**ciliates** (phylum *Ciliophora*) A group of **protozoans** that have **cilia**.

**cilium** (pl. **cilia**) A short, hair-like **flagellum** that is found in large numbers and used in movement, for pushing food particles, and in other functions.

**clasper** A copulatory organ along the inner edge of each **pelvic fin** in male sharks and other **cartilaginous fishes** (Fig. 8.26).

**cleaning associations** A **symbiotic** association in which a smaller partner regularly removes parasites from fishes.

**climax community** The final stage in an **ecological succession**.

**cloaca** The common opening for the intestine and the excretory and reproductive systems of **cartilaginous fishes** and other animals.

**clone** A series of genetically identical cells or individuals that have developed from a single cell or individual.

cnidarians (phylum *Cnidaria* or *Coelenterata*) Invertebrates with nematocysts and radial symmetry.

**coastal management** The use of coastal resources with the intention of preserving them.

coastal plain estuary See drowned river valley estuary.

**coccolithophorids** (phylum *Haptophyta*) Unicellular, **eukaryotic** members of the **phytoplankton** that have calcareous, buttonlike structures, or *coccoliths* (Fig. 5.9).

**coelacanths** A group of lobed-fin fossil fishes. *Latimeria* was first discovered alive in 1952 (see figures on p. 170).

**coelom** The body cavity found in structurally complex animals.

**coelomic fluid** The fluid that fills the **coelom** of **echinoderms** and other **invertebrates**.

**coevolution** The process in which one **species** evolves in response to another.

**collar cell (choanocyte)** A flagellated, food-trapping cell of **sponges.** 

**colloblast** Sticky cell used for the capture of small prey in **comb jellies**.

**comb jellies** (phylum *Ctenophora*) The **invertebrates** with a gelatinous body, **radial symmetry**, and eight rows of **ciliary combs** (Fig. 7.10).

**commensalism** The type of **symbiosis** in which one species obtains shelter, food, or other benefits without affecting the other, or *host*.

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**community** The **populations** that live and interact in an area.

**competition** The interaction that results when a resource is in short supply and one organism uses the resource at the expense of another.

**competitive exclusion** The elimination of one species by another as a result of **competition**.

**compound eye** An eye typical of **arthropods** that consists of numerous light-sensitive units.

**conditioning** A form of learning in which a behavior is associated with a reward such as food.

**constant proportions, rule of** A principle that states that the relative amounts of ions in seawater are always the same.

**consumer** A heterotroph. A *primary consumer* feeds directly on a **primary producer,** whereas a *secondary consumer* feeds on a primary consumer.

**continental drift** The movement of continental masses on the surface of the earth.

**continental margin** The edge of a continent; the zone between a continent and the deep-sea floor (Fig. 2.17). *Also see* **active** and **passive continental margins.** 

**continental rise** The gently sloping area at the base of the **continental slope** (Fig. 2.17).

**continental shelf** The shallow, gently sloping section of the **continental margin** that extends from the shore to the point where the slope gets steeper (Fig. 2.17).

**continental slope** The steeper, seaward section of the **continental margin** (Fig. 2.17).

**convection** The movement that results when heat is transferred in a fluid, such as the heat-driven motion observed in the earth's mantle.

**convergent evolution** Evolution in which two different species evolve similar structures because of similar lifestyles.

# conveyor circulation *See* great ocean conveyor.

**copepods** Small, mostly planktonic **crustaceans** (Fig. 7.28).

**copulation** The sexual union undertaken to transfer **gametes**.

**coral knoll (pinnacle)** A column of coral within the **lagoon** of an **atoll** (Fig. 14.22).

coralline algae Red algae that deposit calcium carbonate in their thallus.

coralline sponges See sclerosponges.

**coral reef** A massive deposit of **calcium carbonate** by colonial **stony corals** and other organisms.

coral rubble Coral fragments.

**cordgrasses** Salt-tolerant grasses, species of *Spartina*, that inhabit **salt marshes** (Fig. 12.7).

**core** The innermost layer of the earth (Fig. 2.3).

**Coriolis effect** The tendency of objects moving large distances on the earth's surface to bend to the right in the Northern Hemisphere and to the left in the Southern Hemisphere (Fig. 3.15).

**counterillumination** The emission of light by **midwater** animals to match the background light (Fig. 16.17).

**countershading** A color pattern that results in a dark back and a light belly; most common in **epipelagic fishes** (Fig. 15.17).

**courtship behavior** Behavior related to attracting the opposite sex and mating.

**crinoids** (class *Crinoidea*) The **echinoderms** with a small, cup-shaped body and feathery arms: the *sea lilies* and *feather stars* (Fig. 7.47).

**crown-of-thorns sea star** (*Acanthaster planci*) A *predator* of reef corals (Fig. 14.31).

**crust** The outermost layer of the earth (Fig. 2.3).

crustaceans (subphylum *Crustacea*) Arthropods that have two pairs of antennae and an exoskeleton hardened by calcium carbonate.

**cryptic coloration** A color pattern that allows an organism to blend with the surroundings.

**cryptomonads** (phylum *Cryptophyta*) Unicellular, **eukaryotic** members of the **phytoplankton** that have two flagella and no skeleton.

**crystal** A solid that consists of a regular pattern of molecules.

**crystalline style** An **enzyme**-releasing rod in the stomach of **bivalves** (Fig. 7.22*b*).

ctenophores See comb jellies.

current A horizontal movement of water.

cyanobacteria A group of generally photosynthetic bacteria. Formerly known as *blue-green algae*.

**cytoskeleton** A complex framework inside cells made of protein fibers.

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# d

**decapods Crustaceans** with five pairs of walking legs and a well-developed **carapace**. The group includes the *shrimps*, *lobsters*, *hermit crabs*, and *crabs*.

**decomposers** Organisms such as decay **bacteria** and **archaea** that break down dead organic matter into smaller molecules.

**deduction** Reasoning from general principles to specific conclusions.

**deep (bottom) layer** The deepest and coldest of the three layers of the ocean (Fig. 3.33).

**deep scattering layer (DSL)** A soundreflecting layer of many types of organisms that migrates daily from the **mesopelagic zone** to the **epipelagic zone**.

**deep sea** The dark waters below the **mesopelagic zone** (Fig. 10.20).

**deep-sea fan** A fan-like accumulation of sediment at the base of a **submarine canyon**.

deep-sea hot spring See hydrothermal vent.

**delayed implantation** The delay in the attachment of the early **embryo** to the womb in **pinnipeds** and some other **mammals** in order to time birth with favorable conditions.

demersal fish A bottom-dwelling fish.

**density** The weight (or more correctly the *mass*) of a given volume of a substance.

**deoxyribonucleic acid (DNA)** Nucleic **acids** that contain the inherited genetic code that specifies how each organism is made up and how it functions.

**deposit feeder** An animal that feeds on organic matter that settles on the bottom (Fig. 7.16). *Compare* **suspension feeder**.

**desalination** The conversion of seawater into fresh water.

detritus Particles of dead organic matter.

**diatomaceous ooze** A **biogenous sediment** that consists mostly of the **siliceous frustules** of **diatoms.** It is known as *diatomaceous earth* when found inland.

**diatoms** (phylum *Bacillariophyta*) Unicellular and **eukaryotic autotrophs** with a **siliceous frustule;** mostly **planktonic** (Fig. 15.3).

**diffusion** The movement of molecules from an area of high concentration to an area of low concentration.

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**digestive gland** An **enzyme**-producing gland in several groups of **invertebrates** where digestion and absorption take place.

**dinoflagellates** (phylum *Dinoflagellata* or *Pyrrophyta*) Unicellular, **eukaryotic**, mostly **autotrophic protists** with two unequal **flagella** (Fig. 5.7).

**dioxins** A group of toxic **chlorinated hydrocarbon** pollutants.

**diploid (2***n***) cell** A cell, such as a body cell, that contains two similar sets of **chromosomes**, one from each parent. *Compare* **haploid**.

**dispersal** The manner in which organisms get from place to place.

**disruptive coloration** A color pattern that helps break the outline of an organism.

**dissociation** The breaking up of a salt molecule into **ions** when placed in water or other solvents (Fig. 3.5).

**dissolved organic matter (DOM)** Organic matter that is dissolved in water rather than being in particles.

**diurnal tide** A tidal pattern with a high and a low **tide** each day (Fig. 3.29*c*).

**diversity** The total number of species inhabiting a particular environment.

DNA See deoxyribonucleic acid.

**domestic sewage** Wastewater from homes and non-industrial buildings. *Compare* **industrial sewage**.

**dorsal** The upper or back surface of an animal with **bilateral symmetry** (Fig. 7.11).

**drag** Resistance to movement through water or any other medium.

**drift net** A fishing net that is allowed to drift for a long time before it is pulled on board (Fig. 17.6*e*).

**drowned river valley (coastal plain) estuary** An **estuary** that is formed when sea level rose at the end of the last glacial age (see photo on p. 259).

#### e

**ear stone (otolith)** A calcareous body in the **inner ear** of fishes and other **vertebrates** that is used in the maintenance of equilibrium. *Also see* **statocyst**.

echinoderms (phylum *Echinodermata*) Invertebrates with five-way radial symmetry and a water vascular system.

echiurans (phylum *Echiura*) Burrowing invertebrates that have an unsegmented body and a non-retractable **proboscis** (Fig. 13.9). echolocation The ability of some animals to sense their surroundings by analyzing the reflection of sound waves, or *clicks*, they emit.

**ecological niche** The full range of ecological characteristics of a species, such as its feeding habits, specific **habitat**, and reproductive strategy.

ecological succession The regular replacement of species by others in a given area.

**ecology** The study of the interactions among organisms and their environment.

**ecosystem** A **community** or communities plus the physical environment, interacting in a large, more or less self-contained, area.

ectoprocts See bryozoans.

**ectotherm** An organism that loses metabolic heat to the environment without it affecting their body temperature. *Compare* **endotherm.** 

**Ekman spiral** The spiral change in the movement of water in the **water column** when the water is pushed by wind (Fig. 15.29). The *Ekman layer* is that part of the water column affected by wind; *Ekman transport* is the net water movement 90° from the wind direction.

**element** A substance consisting of **atoms** of the same kind and one which cannot be decomposed by ordinary chemical means.

El Niño–Southern Oscillation (ENSO) Large-scale changes in atmospheric and ocean current patterns in which, among other things, warm surface water in the Pacific Ocean moves further to the east than normal. *El Niño* refers specifically to the warming of the surface water in the Eastern Pacific. *Compare* La Niña.

**embryo** The early developmental stage that, through *embryological development*, ultimately becomes an adult individual.

**encrusting** Describing an organism that grows as a crust over rocks and other hard surfaces.

**endangered species** A species that is in immediate danger of **extermination**.

**endolithic alga** An alga that burrows into **calcareous** rocks or corals.

**endophyte** A photosynthetic organism that lives within the cells or tissues of algae or plants. *Compare* **epiphyte**.

**endoplasmic reticulum** An extensive system of folded membranes present in most **eukaryotic cells** (Fig. 4.8).

endoskeleton A skeleton under the external surface of an animal. *Compare* exoskeleton.

**endotherm** An organism that retains some metabolic heat, which raises its body temperature. *Compare* **ectotherm.** 

**energy** The ability to do work.

**enzyme** A **protein** that speeds up a specific chemical reaction.

**epifauna** Animals that live on the surface of the **substrate**. *Compare* **infauna**.

**epipelagic zone** The **pelagic** environment from the surface to a depth of 100 to 200 m (350 to 650 ft) (Fig. 10.20).

**epiphyte** A photosynthetic organism that lives on algae or plants. *Compare* **endophyte.** 

**equatorial currents** Major ocean currents that move parallel to the Equator (Fig. 3.19).

**erythrocyte (red blood cell)** A specialized type of blood cell that carries **hemoglobin** in **vertebrates.** 

**estuary** A semi-enclosed area where fresh water and seawater meet and mix.

**eukaryote** An organism that consists of one or more **eukaryotic cells**.

eukaryotic cell A cell that contains organelles (Fig. 4.8). *Compare* prokaryotic cell.

**euryhaline** An organism that can tolerate a wide range of salinities. *Compare* **stenohaline**.

**eutrophication** Accelerated growth of algae in response to increased nutrient input.

**evaporation** The escape of molecules from the liquid phase into the gaseous phase, or vapor.

**evaporative cooling** The lower speed and hence lower temperature of molecules remaining in the liquid phase after **evaporation** of the fastest molecules.

**evisceration** The expulsion of internal organs in **sea cucumbers**.

**evolution** A change in the genetic makeup of a species, usually as a result of **natural selection** favoring some individual characteristics over others.

**evolutionary adaptation** The genetic adaptation of a population to its environment through **evolution**.

**exclusive economic zone (EEZ)** A zone 200 nautical miles (370 km) wide along the coast where nations have exclusive rights to any resource. It was initiated by the *United Nations Convention on the Law of the Sea (UNCLOS).* 

**exoskeleton** A skeleton that forms the external surface of an animal, as in **arthropods**. *Compare* **endoskeleton**.

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**experiment** An artificially created situation that is used to test a **hypothesis.** In a *controlled experiment*, additional variables that might affect the experiment are prevented from doing so.

**extermination (extirpation)** The **extinction** of a species that is caused by humans.

**extinction** The disappearance of a species.

**extracellular digestion** Digestion that takes place outside cells, usually in a gut, or digestive cavity. *Compare* **intracellular digestion**.

# f

**fault** A crack in the earth's crust usually formed when two pieces of crust are moving past each other.

#### feather stars See crinoids.

**fertilization** The union of **gametes**. It can be *external* and take place in the water, or *internal* and take place within the body.

**fetch** The span of the sea surface over which the wind blows to form wind-driven **waves** (Fig. 3.23).

**filter feeder** A suspension feeder that actively filters food particles (Fig. 7.16).

**fin ray** Each of the bony spines in the fins of **bony fishes.** 

**fish meal** A fish-protein supplement used in animal feeds.

**fish protein concentrate (FPC or fish flour)** A fish protein supplement for human consumption.

**fission** A type of **asexual reproduction** that results when one individual splits into two individuals.

**fjord** An **estuary** that is formed in a deep valley created by a retreating glacier (Fig. 12.2).

**flagellum** A long, whip-like **organelle** that is usually involved in locomotion.

flatworms (phylum *Platyhelminthes*) Invertebrates that are dorsoventrally flattened and have an incomplete digestive tract, true organs, and organ systems.

**flowering plants (angiosperms;** division *Anthophyta*) Plants that have flowers, seeds, and true leaves, stems, and roots.

fluke The fin-like tail of cetaceans.

flukes A group of parasitic flatworms.

food chain The steps of transfer of energy from primary producers through consumers.

**food web** All of the interconnecting feeding relationships in a **community**.

**foot** The muscular locomotory structure of **molluscs**.

for a biogenous sediment that consists mostly of the calcareous shells of for a miniferans.

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foraminiferans (forams) (phylum Foraminifera) Protozoans with a calcareous shell, or *test*, and pseudopodia (Fig. 5.10).

**fore reef** The outer part of a **barrier reef** (Fig. 14.17) or **atoll** (Fig. 14.22).

**fouling organisms** Organisms that live attached to submerged surfaces such as boats and pilings.

**fringing reef** A **coral reef** that develops as a narrow band close to a shore (Fig. 14.14).

**frustule** The **siliceous**, box-like cell wall of **diatoms**.

fucoxanthin The yellow to golden brown photosynthetic pigment of brown algae.

**fungi** (sing. **fungus**) Plant-like but nonphotosynthetic organisms; members of the kingdom *Fungi*.

g

**gamete** A **haploid** reproductive cell that develops into a new individual after its union with another gamete.

gametophyte The haploid, gameteproducing generation in many seaweeds. *Compare* sporophyte.

**gas exchange** The movement of **oxygen** and other gases between the atmosphere and the ocean, or between the water or atmosphere and living organisms, in which case it is often called **respiratory exchange**.

**gastropods** (class *Gastropoda*) Snails and other **molluscs** that typically possess a coiled **dorsal** shell and a **ventral** creeping **foot**.

**genetic engineering** The artificial alteration of the genetic information of an individual.

genital slit The genital opening of cetaceans.

genus A group of similar species.

**gestation** The length of time between **fertilization** and birth in **mammals**.

**gill** Thin-walled extensions of the body that are used in **gas exchange**.

gill arch A supporting structure of fish gills.

gill cover See operculum.

**gill filament** The thin projection of a fish **gill** where **gas exchange** takes place (Fig. 8.17*b*).

**gill raker** Each of the projections along the inner surface of fish **gills** (Fig. 8.17*b*).

**gill slit (pharyngeal slit)** One of several pairs of openings along the **pharynx** in **chordates** (Figs. 7.48*b* and 7.49).

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glass sponges Deep-water sponges with a skeleton of fused silica spicules.

**global distillation** Evaporation and condensation of substances on a global scale, leading to the net transport of certain pollutants to the poles.

**global warming** An increase in the **greenhouse effect** brought about by the increase of **carbon dioxide** and other gases in the atmosphere.

**glucose** A **simple sugar** that plays an important role in the **metabolism** of most organisms.

**Golgi complex** An arrangement of sacs and membranes in many **eukaryotic cells** that is involved in collecting and transporting molecules (Fig. 4.8).

**gonad** An organ that contains the *germ tissue* that produces the **gametes:** *ovary* and *testis*.

**Gondwana** One of two large continents, the southern one, that formed when the supercontinent **Pangaea** broke up about 180 million years ago (Fig. 2.15*b*). *Also see* **Laurasia**.

**gorgonians** (order *Gorgonacea*) Colonial **anthozoans** that secrete a skeleton made of protein (Fig. 7.9).

**granite** The light-colored rock that forms most of the continental **crust**.

**grazer** An organism that feeds primarily on plants.

**great ocean conveyor** A global circulation pattern in which water cycles throughout the ocean basins (Fig. 16.3).

great whales Large whales: the sperm and the baleen whales.

green algae (phylum *Chlorophyta*) Seaweeds in which chlorophyll is not masked by other pigments.

**greenhouse effect** The increase in the earth's temperature that results from the presence of **carbon dioxide** and other gases in the atmosphere.

**guano** The accumulation of the excrement of seabirds.

guyot A flat-topped seamount.

**gyre** A large, nearly circular system of winddriven surface currents that center around latitude 30° in both hemispheres (Fig. 3.19).

#### h

**habitat** The natural environment where an organism lives.

**habitat restoration** The recovery of stressed or destroyed habitats.

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hadal zone The bottom below 6,000 m (20,000 ft) (Fig. 10.20).

hadopelagic (hadal pelagic) zone The pelagic environment below 6,000 m (20,000 ft) (Fig. 10.20).

halophyte A salt-tolerant terrestrial plant.

**haploid** (*n*, or 1*n*) **cell** A cell, such as a **gamete**, that contains only half the normal number of chromosomes found in **diploid**, or body, **cells**.

**harem** A large group of females herded by a large male **pinniped** for the purpose of mating; harems also occur in some fishes.

**harmful algal blooms** Unusual population explosions, or **blooms**, of **phytoplankton** that are detrimental to humans.

**heart urchins** Burrowing **sea urchins** with a flattened test and short spines (Fig. 13.7).

**heat capacity** The amount of heat that must be added to a substance to raise its temperature by a given amount, which reflects the substance's ability to store heat.

**heavy metals** A group of toxic metals: *mercury, lead,* and others.

hemichordates (phylum Hemichordata) Invertebrates with a dorsal nerve cord and gill slits. Includes the *acorn worms*, or *enteropneusts*.

**hemoglobin** A blood **protein** that transports **oxygen** in many animals.

**herbivore** An animal that eats plants.

**heredity** The transmission of genetic characteristics from one generation to the next.

**hermaphrodite** An organism that has both male and female **gonads.** In *sex reversal*, or *sequential hermaphroditism*, an individual begins life as one sex but changes into the opposite sex.

hermatypic coral Corals that build coral reefs.

**heterotroph** An organism that obtains **energy** from organic matter.

**holdfast** The root-like portion of the **thallus** of a **seaweed**.

**holoplankton** Organisms that spend their entire lives in the **plankton**. *Compare* **meroplankton**.

**homeotherm** An organism that is able to keep its body temperature more or less constant regardless of the temperature of the environment. *Compare* **poikilotherm.** 

**homing** The ability of an animal to find its home area.

**hormone** A substance that acts as a chemical messenger in an organism.

horseshoe crabs (class *Merostomata*) Arthropods with a large horseshoe-shaped carapace (Fig. 7.38).

**hydrogen** An element that is one of the constituents of water, organic matter, and many other chemicals. Hydrogen gas  $(H_2)$  is composed of two hydrogen **atoms**.

**hydrogen bond** A weak bond between the **hydrogen** atoms of adjacent **molecules**, as in the case of water (Fig. 3.1).

 $\label{eq:hydrogen} \begin{array}{l} \text{hydrogen sulfide} \left(H_2S\right) \quad \text{The gas that is} \\ \text{produced in anoxic sediments.} \end{array}$ 

**hydrostatic skeleton** A system that uses water pressure against the body wall to maintain body shape and aid in locomotion.

**hydrothermal vent (deep-sea hot spring)** A place where heated seawater forces its way up through the **crust** (Figs. 2.24 and 2.25).

**hydrozoans** (class *Hydrozoa*) **Cnidarians** whose life cycle typically includes a **polyp**, which is often colonial, and a **medusa**.

hypothesis A statement that might be true.

**ice age** A period of time when significant amounts of ice form on the continents, inducing a fall in sea level.

**Indo-West Pacific region** The tropical Indian and western and central Pacific oceans.

**inducible defenses** Defense mechanisms that an organism uses only in response to predators.

**induction** Reasoning from specific observations to a general conclusion.

**industrial fishery** A fishery in which the catch is used for purposes other than direct human consumption.

**industrial sewage** Wastewater from industries. *Compare* **domestic sewage**.

**infauna** Animals that burrow in the **substrate**. *Compare* **epifauna**.

**ink sac** A gland found in some **cephalopods** that secretes a dark fluid used to discourage predators.

**inner ear** A paired, sound-sensitive organ in **vertebrates.** 

**insects** (class *Insecta*) **Arthropods** with three pairs of legs and one pair of **antennae**. Few are marine, an exception being the *water strider* (Fig. 15.16).

**interglacial period** A geological period between **ice ages** when, as at present, the earth's climate is relatively warm.

**intermediate layer** Of the three main layers of the ocean, the one below the **surface**, or **mixed**, layer. It includes the main **thermocline** (Fig. 3.33).

**International Whaling Commission** (IWC) An agency that regulates *whaling* around the world.

interspecific competition Competition among members of different species. *Compare* intraspecific competition.

interstitial fauna Animals living between sediment particles. *Also see* meiofauna.

**interstitial water** The water contained between sediment particles.

**intertidal (littoral) zone** The area between the highest and lowest tide (Fig. 10.20).

**intracellular digestion** Digestion that takes place within cells, usually those lining the gut or digestive tract. *Compare* **extracellular digestion**.

intraspecific competition Competition among members of the same species. *Compare* interspecific competition.

**introduced species (alien** or **exotic species)** A species introduced into a new environment by humans. *Compare* **native species.** 

**invertebrates** Animals that lack a backbone.

**ion** An atom or group of atoms that is electrically charged.

**iridophore** A **chromatophore** with light-reflecting **crystals**.

**island arc** A curved chain of volcanic islands that form along a **trench**.

**isopods** Small, dorsoventrally flattened **crustaceans** such as the *sea louse* (Fig. 7.31).

**isotopes** Different atomic forms of an **element.** 

#### 1

**jawless fishes** (class *Agnatha*) Fishes that lack jaws and paired fins: *hagfishes* (or *slime eels*) and *lampreys* (Fig. 8.2).

#### k

**kelp** Brown algae characterized by their large size and complexity. Some, like the giant kelp, form dense *kelp beds* or *kelp forests*.

**keystone predator** A predatory species whose effects on its community are proportionately much greater than its abundance.

**krill (euphausiids)** Planktonic **crustaceans** that are an important food of whales and other animals (Fig. 17.12).

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# 1

**lagoon** A shallow, sheltered body of water separated from the open sea by **coral reefs**, *sand bars*, and/or **barrier islands** (Figs. 14.17 and 14.22).

**lamella** (pl. **lamellae**) Each of the many thin plates that make up the **gill filaments** of fish **gills** (Fig. 8.17*c*).

**lamp shells (brachiopods;** phylum *Brachiopoda)* **Invertebrates** that have a lophophore and a shell that consists of **two valves.** 

**lancelets** (subphylum *Cephalochordata*) **Chordates** with the three basic chordate characteristics but lacking a backbone (Fig. 7.49).

La Niña Large-scale changes in atmospheric and ocean current patterns in which, among other things, warm surface water in the Pacific Ocean moves further to the west than normal. *Compare* El Niño–Southern Oscillation.

**larva** Immature stage of an animal that looks different from the adult.

**larvaceans (appendicularians;** class *Larvacea*) **Tunicates** that retain the body of a **tadpole larva** throughout life (Fig. 15.9).

**latent heat of evaporation** The amount of heat **energy** that is needed to evaporate a substance, that is, to change it from a liquid to a gas.

**latent heat of melting** The amount of heat **energy** needed to melt a substance, that is, to change it from a solid to a liquid.

**lateral line** A system of canals and sensory cells on the sides of fishes that helps them detect vibrations in the water (Fig. 8.19).

Laurasia One of the two large continents, the northern one, that formed when the supercontinent **Pangaea** broke up about 180 million years ago (Fig. 2.15*b*). *Also see* **Gondwana.** 

**leeches** (class *Hirudinea*) **Segmented worms** that are specialized predators and parasites.

**leptocephalous larva** The leaf-shaped larva of freshwater eels and other fishes.

**lichen** The organism that results from the **symbiosis** of a **fungus** and an **autotroph** such as a **green alga**.

**limiting resource** An essential factor whose short supply limits the growth of a **population**.

**lipid** A group of **organic molecules** that are often used by organisms in the long-term storage of **energy**, waterproofing, buoyancy, and insulation. **lithogenous sediment** Sediment that is derived from the breakdown, or **weathering**, of rocks. *Also see* **red clay**.

**lithosphere** The **crust** and the top part of the mantle that covers the earth's surface. It is broken into separate *lithospheric plates* (Fig. 2.10).

littoral zone See intertidal zone.

**lophophore** A feeding structure that consists of ciliated tentacles.

**loriciferans** (phylum *Loricifera*) Tiny invertebrates that live among sediment particles and have a body enclosed by six plates.

#### m

macrophytes See seaweeds.

**macroplankton** The component of the plankton that consists of large organisms 2 to 20 cm in size (Fig. 15.2).

**madreporite** A porous plate that connects the **water vascular system** of **echinoderms** to the exterior.

**magnetic anomalies** Magnetic bands in the sea floor that run parallel to the **midocean ridge** (Fig. 2.8).

**magnetite** A magnetic, iron-containing material.

main thermocline See thermocline.

**male parasitism** The permanent attachment of a male to a female in some deep-sea fishes (Fig. 16.23*b*).

mammals (class *Mammalia*) Vertebrates that have hair and mammary glands.

**mammary glands** The milk-secreting glands of **mammals**.

**manganese nodules** Lumps of minerals (including manganese and other valuable minerals) that are found on the sea floor beyond the **continental shelf**.

**mangroves** Shrubs and trees that live along the seashore in tropical and subtropical regions and tolerate inundation by seawater (Fig. 6.14).

mantle (1) The semi-liquid region between the crust and core of the earth (Fig. 2.3).
(2) The outer layer of tissue that secretes the shell of molluscs (Fig. 7.19).

**mantle cavity** The space lined by the **mantle** of **molluscs** (Fig. 7.19).

**mariculture** The culture of marine organisms. In *open mariculture* (or *semiculture*), organisms are cultured in natural environments; in *closed mariculture* (or *intensive mariculture*), organisms are cultured in a controlled environment.

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**marine archaeology** The discovery, salvage, and interpretation of material remains of humankind's past that have been preserved in the sea.

**marine natural products** Chemical compounds that are obtained from marine organisms.

**marine snow** Detritus and other particulate organic matter that is found in the water column.

**maritime culture** A human culture with a very close relationship with the sea.

**maxillipeds** The food-sorting appendages of some **crustaceans**.

**maximum sustainable yield** The maximum catch of a **stock** that can be harvested year after year without diminishing the stock.

**medusa** The bell-shaped, free-swimming stage of **cnidarians**.

**megaplankton** The component of the plankton that consists of very large organisms over 20 cm in size (Fig. 15.2).

**meiofauna** Microscopic animals that live on the bottom, often used as a synonym of **interstitial fauna**.

**meiosis** Cell division that results in the formation of **gametes**.

**melon** A fatty structure on the forehead of some **cetaceans** that is used to direct sound waves emitted during **echolocation** (Fig. 9.26).

**meroplankton** Planktonic organisms that spend only part of their life in the **plankton**. *Compare* **holoplankton**.

**mesenterial filament** Any of the long, thin tubes attached to the gut of corals and other **cnidarians** that are involved in digestion and absorption.

**mesoglea** The layer between the *epidermis* and *gastrodermis* in **cnidarians** (Fig. 7.7).

**mesopelagic zone** The **pelagic** environment from a depth of approximately 100 to 200 m (350 to 650 ft) to 1,000 m (3,000 ft) (Fig. 10.20).

**mesoplankton** The component of the **plankton** that consists of organisms 0.2 to 2 mm in size (Fig. 15.2).

**metabolism** All the chemical reactions that take place in an organism.

**metamorphosis** A marked change in form during embryological development.

**microbial loop** A component of **pelagic food webs** in which **dissolved organic matter** is cycled through the **picoplankton** and **nanoplankton** back into the main part of the food web (Fig. 15.24).

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microfossils The microscopic shells and other remains of marine organisms that make up biogenous sediments.

microplankton The component of the plankton that consists of organisms 20 to 200 microns ( $\mu$ m) (0.02 to 0.2 mm) in size (Fig. 15.2).

mid-ocean ridge The continuous chain of volcanic submarine mountains that extends around the earth. It includes the Mid-Atlantic Ridge and East Pacific Rise (Figs. 2.5 and 2.6).

midwater Pertaining to the mesopelagic zone.

migration The regular movement of one organism from one place to another.

mitochondrion The organelle in which respiration takes place in eukaryotes (Fig. 4.8).

mitosis The cell division in which a cell divides into two daughter cells that are identical to the original cell.

mixed layer See surface layer.

mixed semidiurnal tide A tidal pattern with two successive high tides of different heights each day (Fig. 3.29b).

molecule A combination of two or more atoms.

molluscs (phylum Mollusca) Invertebrates with a soft, unsegmented body, a muscular foot, and, with some exceptions, a calcareous shell.

molt The exoskeleton that is shed during the molting process.

monoplacophorans (class Monoplacophora) A small group of **molluscs** that are thought by some to represent a link with invertebrates that show segmentation.

**monsoon** Winds in the northern Indian Ocean that blow from the southwest in summer and from the northeast in winter.

**mudflat** A muddy bottom that is exposed at low tide.

mutualism The type of symbiosis in which both partners benefit from the relationship.

myoglobin A type of muscle protein that stores oxygen in vertebrates.

myomere Each of the bands of muscles along the sides of fishes.

#### n

nanoplankton The component of the plankton that consists of very small organisms 2 to 20 microns (µm) (0.002 to 0.2 mm) in size (Fig. 15.2); they are too small to catch in a standard plankton net.

native species A species that naturally occurs in a given area. Compare introduced species.

natural selection A mechanism of evolutionary change that results when individuals that are better *adapted* than others in meeting the challenges of the environment produce more offspring.

nauplius The planktonic larva of many crustaceans (Fig. 7.37).

neap tides The tides with a small tidal range. They occur around the times when the moon is in quarter. Compare spring tides.

negative estuaries Estuaries where loss of fresh water through evaporation is higher than freshwater input from rivers.

nekton Organisms that swim strongly enough to move against the current (Fig. 10.19).

nematocyst The stinging structure of cnidarians.

nematodes (roundworms; phylum *Nematoda*) **Invertebrates** with a cylindrical body, a conspicuous body cavity, and a complete digestive tract.

nemerteans See ribbon worms.

neritic zone The pelagic environment above the continental shelf (Fig. 10.20).

nerve cell A cell specialized to originate or transmit nerve impulses.

nerve cord A long, compact bundle of nerve cells that is part of the central nervous system.

**nerve net** The network of interconnecting nerve cells in cnidarians and other invertebrates.

net plankton Plankton that can be caught in a standard plankton net.

neuston Organisms that live on the surface of the sea.

niche See ecological niche.

nictitating membrane A thin layer of tissue that can be drawn across the eye in sharks and some other vertebrates.

nitrate (NO<sub>3</sub><sup>-1</sup>) An important nutrient in the ocean.

**nitrogen** (N<sub>2</sub>) A colorless and tasteless gas that is an essential constituent of proteins.

nitrogen cycle The cyclical reconversion of nitrogen into various nitrogen compounds (Fig. 10.18).

nitrogen fixation The conversion of gaseous nitrogen (N<sub>2</sub>) into nitrogen compounds that can be utilized by autotrophs. It is performed by nitrogen fixers.

nonbiodegradable Unable to be broken down by bacteria or other organisms.

nonrenewable resource A resource that is not naturally replaced.

**notochord** A flexible rod that lies below the nerve cord of chordates.

nucleic acid Organic molecules that store and transmit genetic information. Also see deoxyribonucleic acid, ribonucleic acid.

nucleus The organelle of eukaryotic cells that contains the chromosomes (Fig. 4.8).

nudibranchs (sea slugs) Gastropods that lack a shell and have exposed gills.

**nutrient** A raw material other than carbon dioxide and water that is needed by an **autotroph** to produce **organic** matter. Examples are nitrate and phosphate.

nutrient regeneration The release of nutrients from organic matter by decomposers.

#### Ο

#### ocean thermal energy conversion

(OTEC) A process for obtaining energy by exploiting depth differences in temperature (Fig. 17.21).

oceanic zone The pelagic environment beyond the shelf break (Fig. 10.20).

olfactory sacs Structures on both sides of the head of fishes that are sensitive to chemical stimuli.

**omnivore** An animal that feeds on a variety of foods, typically from different trophic levels.

**operculum** (1) The tough lid that closes the shell opening of many gastropods when the body is withdrawn. (2) The flap of bony plates that covers the gills of bony fishes.

organ A group of tissues specialized for one function.

organelle A membrane-bound, specialized structure within a cell (Fig. 4.8).

organic compound A molecule that contains carbon, hydrogen, and usually oxygen.

organization, level of The extent of specialization and organization of the cells of an organism. Organization may be at the cellular, tissue, or organ level.

osculum A large opening in many sponges.

osmoconformer An organism that allows its internal salt concentration to change with the salinity of the surrounding water.

osmoregulator An organism that controls its internal salt concentration.

osmosis The movement of water across a selectively permeable membrane, such as the cell membrane, which allows only certain molecules to pass through.

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**outwelling** The export of **detritus** and other organic matter from estuaries to other ecosystems.

**overturn** The sinking of surface water that has become more dense than the water below (Fig. 3.32).

**oviparous** An animal that releases eggs.

**ovoviviparous** An animal that produces eggs that hatch inside the female immediately before birth.

**ovulation** The release of an egg from the ovary.

**oxygen** An **element** that is one of the constituents of water, organic matter, and many other chemicals. Oxygen gas  $(O_2)$ , composed of two oxygen **atoms**, is needed for **respiration** and is produced by **photosynthesis**.

**oxygen minimum layer** A layer of water at a depth of approximately 500 m (1,600 ft) where **oxygen** is depleted (Fig. 16.20).

**oyster reef** A dense oyster bed present in some **estuaries** and other marine environments.

**ozone layer** Ozone  $(O_3)$  in the atmosphere that deflects ultraviolet radiation, which is harmful to life.

# p

**Pangaea** The single large landmass, or supercontinent, that broke up to form today's continents (Fig. 2.15*a*).

**Panthalassa** The large ocean that surrounded the supercontinent **Pangaea** and which was the ancestor of the modern Pacific Ocean (Figs. 2.15*a* and 2.15*b*).

#### paralytic shellfish poisoning

A condition caused when humans eat shellfish that have become contaminated with the toxin present in certain **dinoflagellates** that cause **red tides**.

**parapodium** A usually flat lateral extension present on each of the body segments of **polychaetes** (Fig. 7.14).

**parasitism** The type of **symbiosis** in which one partner, the *parasite*, derives benefit from the other, the *bost*.

#### passive continental margin

A **continental margin** that is located at the "trailing edge" of a continent and as a result shows little geological activity (Fig. 2.20). *Compare* **active continental margin**.

**patchiness** The grouping of organisms in clumps or **patches**.

PCBs See polychlorinated biphenyls.

**peanut worms** (**sipunculans**; phylum *Sipuncula*) Burrowing **invertebrates** with an unsegmented body and an anterior end that can be pulled into the body (Fig. 7.17).

**pectoral fin** Each of the pair of fins just behind the head of fishes (Fig. 8.8).

**pedicellaria** One of the minute pincer-like organs of some **echinoderms** that help keep the body surface clean.

**pelagic organisms** Organisms that live in the **water column**, away from the bottom, including the **plankton** and **nekton** (Fig. 10.19).

**pelvic fin** Each of the second pair of **ventral** fins of fishes (Fig. 8.8).

pen The reduced, thin shell of squids.

**perennial** A plant that lives more than two successive years.

**pharynx** The anterior portion of the digestive tract of many animals. It is located directly behind the mouth cavity.

**pheromone** A chemical that organisms use to communicate with other members of their species.

**phoronids** (phylum *Phoronida*) Tubedwelling, unsegmented **invertebrates** that possess a horseshoe-shaped or circular **lophophore.** 

**phosphate** ( $PO_4^{-3}$ ) An important **nutrient** in the ocean.

**photic zone** The surface layer where there is enough light for **photosynthesis** to occur. *Also see* **epipelagic zone**.

**photophore (light organ)** An organ that produces **bioluminescence**.

**photosynthesis** The chemical process involved in the transformation of solar energy into **glucose** (Fig. 4.4):

$$CO_2 + H_2O \longrightarrow glucose + O_2$$

**photosynthetic pigment** A molecule such as **chlorophyll** that is responsible for capturing solar **energy** in **photosynthesis**.

**phycobilins** A group of **photosynthetic pigments** that includes *phycocyanin*, a bluish pigment in **cyanobacteria**, and *phycoerythrin*, a red pigment in **red algae**.

**phycocolloid** One of several **starch**-like chemicals found in some **seaweeds**. They are of significant commercial importance. *Also see* **agar, algin,** and **carrageenan**.

phycocyanin See phycobilins.

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#### phycoerythrin See phycobilins.

**phylogeny** The evolutionary history of a **species** or other **taxon**.

**phylum** The **taxon** that represents a main division of a kingdom. The equivalent term *division* is used in the kingdom Plantae.

**phytoplankton** The photosynthetic component of **plankton** consisting primarily of single-celled algae and bacteria. *Compare* **zooplankton**.

**picoplankton** The component of the **plankton** that consists of extremely small organisms, 0.2 to 2 microns ( $\mu$ m) (0.0002 to 0.002 mm) in size (Fig. 15.2); they are too small to catch in a standard plankton net.

**pinacocyte** The flat cells on the outer surface of sponges.

**pinnipeds** (order *Pinnipedia*) Mammals with paddle-shaped flippers: *seals*, *eared seals* (*sea lions* and *fur seals*), and the *walrus*.

**placenta** A membrane that connects the mammalian **embryo** with the mother's womb to provide nourishment.

**planktivore** An animal that feeds on **plankton**.

**plankton** Organisms that drift in the water (Fig. 10.19).

**plants** Members of the kingdom *Plantae*, which consists of photosynthetic, **eukaryotic**, and multicellular organisms.

planula The ciliated larva of cnidarians.

**plate tectonics** The process involved in the movement of large plates on the earth's crust.

**Pleistocene** A geological period, which began about two million years ago, characterized by a series of **ice ages**.

**pneumatocyst** A gas-filled bladder in **seaweeds** (Fig. 6.1).

**pneumatophore** Upward extension of roots of some **mangroves** (Fig. 12.1).

pod A school of cetaceans.

pogonophorans See beard worms.

**poikilotherm** An organism whose body temperature varies with that of its surroundings. *Compare* **homeotherm**.

**polar easterlies** Variable winds that blow at high latitudes (Fig. 3.17).

**pollen** The structure that produces the male **gamete** in **flowering plants.** 

**pollution** The introduction of harmful substances or heat energy into the environment by humans.

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**polychaetes** (class *Polychaeta*) Segmented worms that have parapodia (Fig. 7.14).

polychlorinated biphenyls (PCBs) A group of chlorinated hydrocarbon pollutants.

**polyp** The cylindrical, typically attached, stage of **cnidarians** (Fig. 7.5).

**population** A group of organisms belonging to the same **species** and living in the same place.

**pore cell** (**porocyte**) The tube-like cell of **sponges** that forms a pore, or *ostium* (pl. *ostia*).

precious corals Gorgonians that secrete a red or pink skeleton consisting of fused calcareous spicules.

**predation** The act of an animal, or *predator*, eating another organism, or *prey*. A *top predator* is one that feeds at the top of the **food chain**.

**pressure** The weight exerted over a unit area of surface. This is equal to 1 *atmosphere* (14.7 lb per square inch) at the sea surface and 1 atmosphere plus the pressure exerted by the **water column**, which is 1 atmosphere per 10 m (33 ft) of depth.

primary producer (producer) An autotroph. An organism that carries out primary production.

**primary production** The conversion of the inorganic carbon in **carbon dioxide** into organic carbon by **autotrophs**.

**primary productivity** The rate of **primary production,** that is, the amount of carbon fixed under a square meter of sea surface in a day or in a year (Fig. 10.14).

**proboscis** An extension near the mouth that in some **invertebrates** helps in the capture or collection of food.

**profile** A graph that shows changes in temperature, salinity, or any other parameter with depth (Fig. 3.8).

**prokaryote** An organism, such as bacteria, that consists of one or more **prokaryotic cells**.

**prokaryotic cell** The simplest type of cell, one that lacks **organelles** (Fig. 4.7). *Compare* **eukaryotic cell**.

**protective coloration** Coloration that benefits the individual by providing concealment from predators.

**protein** A large group of complex **nitrogen**-containing **organic molecules** that play many crucial roles in organisms.

**protists** Members of the kingdom *Protista*, which consists of unicellular, **eukaryotic organisms**. Some combine characteristics of both **animals** and **plants**.

**protochordates** Chordates that lack a backbone.

**protozoans** Animal-like **protists;** the various groups of unicellular, **eukaryotic protists** that are mostly heterotrophic.

**pseudopodium** A thin or blunt extension of the cytoplasm.

**pteropods** Pelagic gastropods in which the **foot** is modified for swimming and the shell is reduced or absent (Fig. 15.10).

**pyloric caecum** (pl. **caeca**) Each of the slender blind tubes found in the intestines of many bony fishes.

**pyramid of biomass** The decrease in biomass that is observed in each higher level of a **food chain**.

**pyramid of energy** The decrease in energy that is observed in each higher level of a food chain.

**pyramid of numbers** The decrease in the number of individuals that is observed in each higher level of a **food chain**.

#### r

radial symmetry The regular arrangement of similar body parts around a central axis (Figs. 7.5 and 7.11). *Compare* bilateral symmetry.

**radioactivity** The emission of *radiation* by unstable **atoms** in the form of particles and rays.

radiolarian ooze A type of biogenous sediment that consists mostly of the silica shells of radiolarians.

radiolarians (phylum *Polycystina*) Protozoans with a silica shell and pseudopodia (Fig. 5.11).

**radula** The ribbon-like band of teeth of **molluscs** (Figs. 7.19 and 7.20).

**recombination** The formation of new genetic combinations, such as the one that takes place during **fertilization**.

**recruitment** The entry of young individuals into a **population** or, in fisheries biology, into a fished stock.

rectal gland A gland in the cloaca of cartilaginous fishes that excretes excess salts.

**red algae** (phylum *Rhodophyta*) **Seaweeds** that have a predominance of red pigments.

**red clay** A fine sediment that is the most common type of **lithogenous sediment** in the open ocean floor.

**red tide** An extensive **bloom** of **phytoplankton** that discolors the water.

**reef crest** The shallow outer edge of the **reef slope** of a **coral reef** (Fig. 14.14).

**reef flat** The wide and shallow upper surface of a **coral reef** (Fig. 14.14).

**reef slope** The outer, steep margin of a coral reef (Fig. 14.14). *Also see* **fore reef.** 

**refraction** The change in the direction of a wave as it moves into shallow water (Figs. 11.6 and 11.7).

**regeneration** The ability of an organism to grow a body part that has been lost.

**renewable resource** A resource that is naturally replaced.

**replication** The copying of a cell's **deoxyribonucleic acid (DNA)** before the cell divides.

**reproductive isolation** The inability of separate **populations** to interbreed.

**reproductive strategy** The reproductive patterns that are followed by a particular species.

**reptiles** (class *Reptilia*) **Vertebrates** with scales on their skin and leathery eggs that are laid on land. Marine reptiles include *sea turtles, sea snakes,* the *marine iguana,* and the *saltwater crocodile.* 

**resource partitioning** The sharing of resources by specialization.

**respiration** The chemical process involved in the release of **energy** from organic matter (Fig. 4.5):

Organic matter +  $O_2 \longrightarrow CO_2 + H_2O$ energy

respiratory exchange See gas exchange.

**respiratory tree** The branched extensions of the posterior end of the digestive tract of **sea cucumbers** that are involved in **gas exchange**.

**rete mirabile** A network of blood vessels that in some fishes functions as a heat-exchange system to help keep internal body temperature higher than that of the water (Fig. 15.21).

**ribbon (nemertean) worms (**phylum *Nemertea*) **Invertebrates** with a complete digestive tract, a true circulatory system, and a long **proboscis** to capture prey (Fig. 7.13).

ribonucleic acid (RNA) Nucleic acids that translate the genetic information contained in deoxyribonucleic acid (DNA) into proteins.

**ribosomes** Organelles where a cell's **proteins** are made.

**rift** A crack in the earth's crust formed as pieces of the crust separate.

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**rockweeds (wracks)** Brown algae such as *Fucus* that inhabit rocky shores in temperate areas.

**rorquals** Blue, fin, and the other **baleen** whales that display long grooves on the underside (Fig. 9.18).

roundworms See nematodes.

#### S

**salinity** The total amount of **salts** dissolved in seawater. It is generally expressed in parts per thousand (‰).

**salivary gland** Any of the glands in **molluscs, vertebrates,** and other animals that release digestive **enzymes** into the mouth.

salmon ranching Practice in which cultured juvenile salmon are released into fresh water and allowed to migrate to sea so they can be harvested later when they return as adults.

**salps** (class *Thaliacea*) Pelagic **tunicates** with a transparent, cylindrical body, sometimes forming long colonies (Fig. 15.8).

**salt** A substance that consists of **ions** that have opposite electrical charges.

**salt gland** A gland that secretes excess salts in seabirds and sea turtles.

**salt marsh** A grassy area that extends along the shores of **estuaries** and sheltered coasts in temperate and subpolar regions.

**salt wedge** A layer of denser, saltier seawater that flows along the bottom in **estuaries** (Fig. 12.3).

**sand dollars** Sea urchins with a flat, round test and short spines that live partly buried in soft sediments (Fig. 7.45*b*).

Sargasso Sea The region of the Atlantic Ocean north of the West Indies that is characterized by floating masses of *Sargasso weed*, a brown alga.

scaphopods See tusk shells.

**scavenger** An animal that feeds on dead organic matter.

**school** A well-defined group of fishes or **cetaceans** of the same species. *Also see* **pod**.

scientific method The set of procedures by which scientists learn about the world (Fig. 1.21).

sclerosponges (coralline sponges) Sponges with a massive calcareous skeleton (Fig. 7.4c).

**scuba** (self-contained underwater breathing apparatus) Equipment that allows breathing underwater from tanks of compressed air.

**scyphozoans** (class *Scyphozoa*) Cnidarians whose life cycle includes a conspicuous **medusa** and a much reduced or absent **polyp**.

**sea** A **wave** that has a sharp peak and a relatively flat **wave trough.** Seas are found in areas where waves are generated by the wind (Fig. 3.24).

**sea anemones** Anthozoans that consist of one large **polyp.** 

sea cows See sirenians.

**sea cucumbers** (class *Holothuroidea*) **Echinoderms** with a soft, elongate body that lacks spines.

**sea-floor spreading** The process by which new sea floor is formed as it moves away from *spreading centers* in **mid-ocean ridges**.

**seagrasses** Grass-like **flowering plants** such as *eelgrass* that are adapted to live at sea (Fig. 6.13).

sea lilies See crinoids.

**seamount** A submarine volcano in the **abyssal plain.** 

sea slugs See nudibranchs.

**sea spiders** (class *Pycnogonida*) **Arthropods** that have a reduced body and four pairs of legs (Fig. 7.39).

**sea squirts (ascidians;** class *Ascidiacea*) **Tunicates** with a sac-like, attached body as adults (Fig. 7.48*a*).

**sea stars** (**starfishes**; class *Asteroidea*) **Echinoderms** with five or more radiating arms and **tube feet** that are used in locomotion.

**sea urchins** (class *Echinoidea*) **Echinoderms** with a round or flattened test and movable spines.

seaweeds (macrophytes) Large, multicellular algae.

**sediment** Loose material such as sand and mud that settles on the bottom. *Also see* **biogenous** and **lithogenous sediments.** 

**seeding** In **mariculture**, the release of cultured juvenile individuals to enrich a natural **stock**.

**segmentation** The division of the body into similar compartments, or *segments*.

**segmented worms (annelids;** phylum *Annelida)* **Invertebrates** that display an elongate body with distinct **segmentation** and a digestive tract that lies in a **coelom**.

seismic sea waves See tsunami.

**self-regulating population** A **population** with a growth rate that is dependent on its own numbers.

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**self-shading** Reduction in the amount of light available to **phytoplankton** that live below other phytoplankton.

**semidiurnal tide** A tidal pattern with two high and two low **tides** each day (Fig. 3.29*a*).

**septa** The thin tissue partitions in the **polyp** of **anthozoans**.

**sequence (of nucleic acids)** The order in which *nucleotides* occur on a **nucleic acid** molecule, which specifies the information contained in the molecule.

**sessile** An organism that lives attached to the bottom or to a surface.

seta (pl. setae) The bristles of polychaetes.

**sex hormone** A **hormone** that controls the timing of reproduction and sexual characteristics in **vertebrates**.

**sexual reproduction** Reproduction that involves the union of **gametes**. *Compare* **asexual reproduction**.

**shear boundary** The boundary between two plates that move past each other on the earth's surface. *Also see* **fault**.

**shelf break** The section of the **continental shelf** where the slope abruptly becomes steeper, usually at a depth of 120 to 200 m (400 to 600 ft) (Fig. 2.17).

**silica (SiO<sub>2</sub>)** A mineral similar to glass that is the major component of the cell wall, shell, or skeleton of many marine organisms.

siliceous Made of silica.

siliceous ooze A type of biogenous sediment that consists mostly of the silica shell and skeletons of marine organisms. *Also see* diatomaceous ooze and radiolarian ooze.

**silicoflagellates** (phylum *Chrysophyta*) Unicellular and **eukaryotic** members of the **phytoplankton** that have a star-shaped **silica** skeleton (Fig. 5.8).

**simple sugar** A sugar, such as **glucose**, that cannot be broken down into simpler sugar molecules.

**siphon** The tube-like extension through which water flows in and out of the **mantle cavity** in **bivalves** and **cephalopods**, and in **tunicates**.

**siphonophores** Hydrozoans that exist as drifting colonies.

sipunculans See peanut worms.

sirenians (sea cows; order *Sirenia*) Marine mammals with anterior flippers, no rear limbs, and a paddle-shaped tail (Fig. 9.13). Glossary

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**sludge** Concentrated wastes extracted from sewage during sewage treatment.

**soft corals** (order *Alcyonacea*) Colonial **anthozoans** with no hard skeleton.

solute Any material dissolved in a solvent.

**sonar** (*so*und *na*vigation *r*anging) A technique or equipment used to locate objects underwater by the detection of echoes (Fig. 1.6).

Southern Oscillation See El Niño— Southern Oscillation.

**spawning** The release of **gametes** or eggs into the water.

**species** Individuals of the same kind that cannot breed with those belonging to other kinds.

**spermaceti organ** The **melon** of sperm whales. It contains *spermaceti*, an oil once widely used in candle making.

**spermatophore** A packet of sperm in **cephalopods.** 

**spicule** Any of the small **calcareous** or **siliceous** bodies embedded among the cells of **sponges** or in the tissues of other **invertebrates**.

**spiracle** One of two openings behind the eyes of **cartilaginous fishes**.

**spiral valve** A spiral portion in the intestine of **cartilaginous fishes**.

**sponges** (phylum *Porifera*) **Invertebrates** that consist of a complex aggregation of cells, including **collar cells**, and have a skeleton of fibers and/or **spicules**.

spongin The resistant fibers of sponges.

**spore** The **asexual**, sometimes resistant structure produced by some **algae**. *Also see* **zoospore**.

**sporophyte** The **diploid**, **spore**-producing generation in many **seaweeds**. *Compare* **gametophyte**.

**spout (blow)** The water vapor and seawater that is observed when whales surface and exhale.

**spring tides** The **tides** with a large **tidal range**; they occur around the times of full or new moon. *Compare* **neap tides**.

**standing stock (standing crop)** The total amount, or **biomass**, of an organism at a given time.

starch A carbohydrate that consists of chains of simple sugars.

**statocyst** A fluid-filled cavity provided with sensitive hairs and a small free body that is used to orient animals with respect to gravity.

**stenohaline** Organism that can tolerate a narrow range of salinities. *Compare* **euryhaline**.

**stipe** The stem-like portion of the **thallus** of **seaweeds** (Fig. 6.1).

stock The size of a population.

**stony corals** Anthozoans, often colonial, that secrete a **calcareous** skeleton.

**stratification** The separation of the **water column** into layers, with the densest water at the bottom and the least dense at the surface (Fig. 3.31). A stratified water column is said to be *stable*. An *unstable* column results when the surface water becomes more dense than the water below.

**stromatolites** Massive calcareous skeletons formed by cyanobacteria (Fig. 5.3).

**structural color** A color that results when light is reflected by a particular surface.

**structural molecule** A molecule, such as **cellulose**, that provides support and protection.

**subduction** The downward movement of a plate into the mantle that occurs in **trenches**, which are also known as *subduction zones*.

sublittoral zone See subtidal zone.

**submarine canyon** A narrow, deep depression in the **continental shelf** formed by the erosion of rivers or glaciers before the shelf was submerged (Fig. 2.18).

**subsidence** The sinking of a landmass.

**substrate** The type of bottom or material on or in which an organism lives.

**subtidal zone** The bottom above the **continental shelf** (Fig. 10.20).

succession See ecological succession.

**succulent** A fleshy plant that accumulates water.

**sulfide** One of the minerals that is abundant in the hot water that seeps through **hydrothermal vents.** 

**surf** A wave that becomes so high and steep as it approaches the shoreline that it breaks.

**surface (mixed) layer** The upper layer of water that is mixed by wind, waves, and currents (Fig. 3.33).

**surface-to-volume ratio (S/V ratio)** The amount of surface area relative to the total volume of an organism (Fig. 4.17).

**suspension feeder** An animal that feeds on particles suspended in the water (Fig. 7.16). *Compare* **deposit feeder, filter feeder.**  **swarming** The aggregation of individuals for **spawning** or other purposes.

**sweeper tentacle** A type of **tentacle** in corals that is used to sting neighboring colonies.

**swell** A wave with a flatter, rounded wave crest and trough. Swells are found away from the area where waves are generated by the wind (Fig. 3.24).

**swim bladder** The gas-filled sac in the body cavity of **bony fishes** that is involved in the adjustment of buoyancy (Fig. 8.12).

**symbiosis** A close relationship between two species, including *commensalism*, *mutualism*, and *parasitism*.

**system (organ system)** A group of **organs** specialized for one function.

#### t

tadpole larva The larva of tunicates.

**tapeworms** Parasitic **flatworms**, typically consisting of a chain of repeated units.

**taste buds** Structures in the mouth and other locations of fishes that are sensitive to chemical stimuli.

**taxon** (pl. **taxa**) A group of organisms that share a common ancestry.

**tectonic estuary** An **estuary** that results from the sinking of land due to movements of the **crust**.

tentacle A flexible, elongate appendage.

**territory** A home area that is defended by an animal.

**Tethys Sea** A shallow sea that once separated the Eurasian and African sections of the supercontinent **Pangaea**. It eventually gave rise to the modern Mediterranean Sea (Figs. 2.15*a* and 2.15*b*).

tetrapods Vertebrates that have two pairs of legs, a group that includes the cetaceans.

thallus The complete body of a seaweed.

**theory** A **hypothesis** that is accepted as "true" for the time being because it has passed test after test and is supported by a large body of evidence.

**thermal pollution** Pollution by heated water.

**thermocline** A zone in the **water column** that shows a sudden change in temperature with depth. The *main thermocline* is the zone where the temperature change marks the transition between the warm surface water and the cold deep water (Figs. 3.8 and 3.31).

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thermohaline circulation Ocean circulation that is driven by differences in water density, due to variations in water temperature and salinity, rather than by the wind or tides.

threatened species A species that occurs in unnaturally low numbers.

**tidal bore** A steep wave generated as high tides move up some estuaries and rivers.

**tidal current** A **current** that is generated by **tides**.

**tidal energy Energy** that can be harnessed as a result of the movement of **tides**.

tidal marsh See salt marsh.

**tidal range** The difference in water level between successive high and low **tides**.

**tide** The periodic, rhythmic rise and fall of the sea surface.

**tide pool** A depression that holds seawater at low tide.

**tide table** A table that gives the predicted time and height of **tides** for particular points along a coast.

tintinnids Ciliates that secrete vase-like cases, or *loricas* (Fig. 5.12).

**tissue** A group of cells specialized for one function.

**tortoiseshell** The polished shell of hawksbill turtles.

**trade winds** Steady winds that blow from east to west toward the Equator, replacing the hot air that rises at the Equator (Fig. 3.17).

**transform fault** A large horizontal displacement in the mid-ocean ridge.

**transplantation** The intentional introduction of a species.

trematodes See flukes.

**trench** A narrow, deep depression in the sea floor (Figs. 2.11 and 2.12).

trochophore A planktonic larva found in polychaetes, some molluscs, and other invertebrates (Fig. 15.11*d*).

**trophic level** Each of the steps in a **food chain.** 

**tsunami (seismic sea waves)** Long, fast waves produced by earthquakes and other seismic disturbances of the sea floor.

**tube foot** Any of the external muscular extensions of the **water vascular system** of **echinoderms.** 

**tubular eyes** Specialized eyes of many **midwater** animals that allow acute upward or downward vision.

tunic The outer covering of sea squirts.

**tunicates** (subphylum *Urochordata*) **Chordates** that show the three basic chordate characteristics only in the larva.

**turbellarians** Mostly free-living **flatworms** (Fig. 7.12).

**tusk shells (scaphopods;** class *Scaphopoda*) **Molluscs** that have an elongate, tapered shell that is open at both ends.

#### u

**upwelling** The process by which colder water rich in **nutrients** rises from a lower to a higher depth. It includes *coastal* and *equatorial upwelling* (Figs. 15.30 to 15.33).

**urea** A toxic waste product of some vertebrates.

**urogenital opening** The common opening for urine and **gametes** in **bony fishes** and other animals.

**uterus (womb)** The portion of female mammals' reproductive tract in which the **embryo** develops.

#### V

valve Any of the two shells of bivalves and lamp shells.

vegetative reproduction See asexual reproduction.

**veliger** A planktonic **larva** in **gastropods** and **bivalves** (Fig. 15.11*a*).

**ventral** The underside or belly surface of an animal with **bilateral symmetry** (Fig. 7.11).

**vertebra** (pl. **vertebrae**) Each of the bones that make up the backbone.

**vertebrates** (subphylum *Vertebrata*) **Chordates** with a backbone.

**vestimentiferans** Pogonophorans that are common at hydrothermal vents (Fig. 16.31).

**viviparous** An animal whose eggs develop inside the female while the **embryo** derives nutrition from the mother.

#### W

warning coloration Coloration that allows organisms to escape from predators by advertising something harmful or distasteful.

water column The vertical column of seawater that extends from the surface to the bottom.

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water mass A body of water that can be identified by its temperature and salinity.

water vascular system A network of water-filled canals in echinoderms used in locomotion and food-gathering.

wave The undulation that forms as a disturbance moves along the surface of the water. Waves can be described by their *height* (the vertical distance between wave crest and trough), *wavelength* (the horizontal distance between adjacent crests), and *period* (the time the wave takes to move past a given point) (Fig. 3.21).

wave crest The highest part of a wave (Fig. 3.21).

wave shock The intensity of the impact of a wave.

**wave trough** The lowest part of a **wave** (Fig. 3.21).

**weathering** The physical and chemical breakdown of rocks.

**westerlies** The winds that blow from west to east at middle latitudes (Fig. 3.17).

wetlands Areas flooded by tides or with visible standing water such as saltmarshes, mangrove forests, and freshwater marshes.

**world ocean** A concept that is used to indicate that all oceans on earth are interconnected.

#### У

**yolk sac** A yolk-containing sac that is attached to the **embryo** of *fishes* and other **vertebrates**.

#### Ζ

**zonation** The presence of organisms within a particular range, as in the *vertical zonation* observed in the **intertidal**.

**zooid** Each individual member of a colony of **bryozoans** and other colonial **invertebrates**.

**zooplankton** The **heterotrophic**, animal and protozoan component of **plankton**. *Compare* **phytoplankton**.

**zoospore** A **spore** provided with one or more **flagella**.

**zooxanthellae Dinoflagellates** that live within the tissues of reef corals and other marine animals (Fig. 14.7).

**zygote** The **diploid** cell that results from **fertilization**; that is, a fertilized egg.