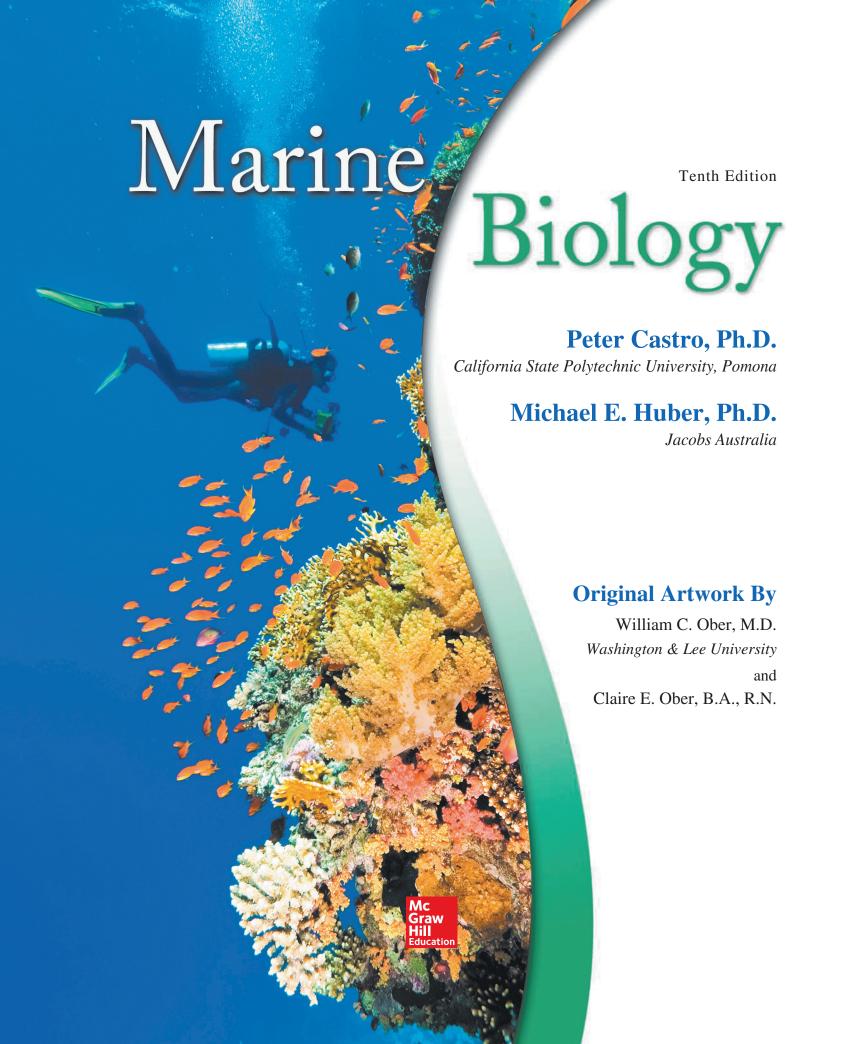
Tenth Edition









MARINE BIOLOGY, TENTH EDITION

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To all future marine biologists

—Peter Castro—

To Erin and Mason

—Michael Huber—

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About the Authors



Peter Castro, Ph.D.

Peter Castro realized that he had to become a marine biologist during a high school field trip to the coral reefs

in his native Puerto Rico. He obtained a B.S. in biology from the University of Puerto Rico, Mayagüez, but left the warm Caribbean for warm Hawaii to obtain a Ph.D. in marine zoology from the University of Hawai'i, Manoa. His first experience with cold water was a year of post-doctoral research at Hopkins Marine Station of Stanford University in Monterey Bay, California. He is currently Professor Emeritus at California State Polytechnic University, Pomona. He also holds a B.A. in history and art history from his home institution, something that took him 18 years to accomplish as a part-time student. He is fluent in five languages and taught marine biology (in English and Spanish) as a Fulbright Scholar at Odessa State University in the former Soviet Union. His research specialty is the biology of crustaceans symbiotic with reef corals and other invertebrates, research that has taken him anywhere where the water is warm enough to dive. He has also been doing research for almost the last two decades on the systematics of deep-water crabs, mostly, of all places, in Paris, France. His research also has taken him in the last couple of years to Singapore, Germany, and Brazil. Dr. Castro has so far published 58 peer-reviewed papers on his research. He is currently editor-in-chief of the Journal of Crustacean Biology, associate editor for Zootaxa, and editor for the volume on brachyuran crabs for the Treatise on Zoology.

Michael Huber, Ph.D.

Michael became fascinated by aquatic organisms when he caught his first trout on an Alaskan lake at age two. His

interest in marine biology grew, and he went on to obtain B.S. degrees in zoology and oceanography from the University of Washington in Seattle. He received his doctorate from Scripps Institution of Oceanography for research on a group of symbiotic coral crabs. He remained at Scripps as a research biologist, working on such diverse research topics as the genetics and cell biology of unicellular algae and bioluminescence in midwater organisms. In 1988 he moved to the Biology Department at the University of Papua New Guinea, where he had the opportunity to work on some of the world's most spectacular coral reefs and was Head of the University's Motupore Island Research Station. He also became increasingly involved in marine environmental science. This interest continued to grow when he left Papua New Guinea in 1994 to become the Scientific Director of James Cook University's Orpheus Island Research Station on Australia's Great Barrier Reef. In 1998 he became a full-time environmental advisor, providing scientific information and advice on marine environmental issues and the development of conservation programs to international agencies, governments, and private industry. Dr. Huber is a Member Emeritus of GESAMP, an international scientific body that advises the United Nations system on marine environmental issues.

Mike lives in Brisbane, Australia, with his wife and two children. His hobbies are fishing, diving, swimming, jazz and rock music, reading, and gardening.

Preface

The ocean fascinates people all over the world, including, of course, students enrolled in undergraduate marine biology courses. For many students, taking marine biology is the natural expression of an interest in marine life that began by visiting the shore, scuba diving, recreational fishing, aquarium keeping, or viewing one of the many television documentaries about the ocean. Many students are also concerned about the increasing impacts of humans on the marine environment. *Marine Biology*, tenth edition, was written to reinforce and enhance our readers' enchantment with marine life while providing a rigorous introduction to marine biology as a science.

Marine Biology is used by undergraduate, graduate, high school, and adult-education students, as well as by interested laypersons not enrolled in formal courses. We are gratified that many professional marine biologists use the book. The book is used in many countries outside the United States, and has been or is being translated into six other languages. While keeping this range of users in mind, the text is primarily written to meet the needs of lower-division, non-science majors at colleges and universities. For many of these students, marine biology will be their only tertiary science course, often taken to satisfy a general education requirement. We have therefore been careful to provide solid basic science coverage, including principles of the scientific method, the physical sciences, and basic biology. Our aim has been 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 all sciences less intimidating. To this end, we use an informal writing style that emphasizes an understanding of concepts over rigorous detail and

Not all marine biology courses, of course, are intended to fulfill a basic science requirement, and in many the students already have a science background. To balance the needs of instructors teaching courses with and without prerequisites in biology or other sciences, we have designed the book to provide as much flexibility as possible in the use of the basic science material, the order in which topics are presented, and overall emphasis and approach. We have tried to meet the needs and expectations of a wide variety of students, from the scuba-diving philosophy major to the biology major considering a marine science career. We hope a variety of readers other than university students also find the book useful and enjoyable.

Four major themes run through *Marine Biology*. One is the above mentioned coverage of basic science applied to the marine environment. Another is an emphasis on the organisms themselves, and their vast diversity not only in taxonomic terms but also in structure, function, and ecology. A third theme is an ecosystem approach that integrates this organismal diversity with the challenges imposed by the surrounding environment, both physical

and biological. A final theme that, unfortunately, becomes more relevant with each passing year is the impact of humans on the marine environment.

Marine Biology, tenth edition, adopts a global perspective to emphasize that the world's oceans and seas are an integrated system that cannot be understood by looking in any one person's own backyard. 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, not just in North America but around the world, 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 all our lives.

CHANGES IN THE TENTH EDITION

As in every edition, we have made extensive revisions to incorporate new information and improve readability, and in response to comments by reviewers, whose suggestions we greatly appreciate. We have added a large number of new photographs to all chapters and the Special Report: Our Changing Planet. We have also revised or added new illustrations to practically all chapters and the Special Report, all expertly prepared by Bill Ober and Claire Garrison. We have also updated the end-of-chapter references for all chapters and the Special Report. Much of the data presented in the tenth edition—among others, for the frequency of shark attacks, the conservation status of threatened species, global temperatures, the extension of the Gulf of Mexico's hypoxic zone, the status of some invasive species, whaling, sea otter transplantations, fisheries catches, aquaculture production, and seafood demand and consumption around the world—has been updated to the latest information available at the time of writing. The researches highlighted in the "Eye on Science" boxes, which have proven to be very popular among students and instructors alike, have been updated. Two "Eye on Science" boxes have been added, one on a cat parasite that has become more prevalent in marine mammals (Chapter 13) and another on the effects of climate change on Arctic peoples (Chapter 18). There are too many other topics for which we have updated or added new information to list in full here, but examples include the following:

- Modified Table 5.1 on the metabolism of marine prokaryotes to make it more reader-friendly
- · Updated the classification of protozoans
- Expanded information on marine fungi
- Added a new section on chlorophyll and accessory pigments in marine primary producers

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- Added information on the biology of marine angiosperms and particularly expanded coverage of their reproduction, including a new diagram contrasting the life histories of angiosperms with the four basic patterns of seaweeds
- Added many new photos of seaweeds, marine flowering plants, invertebrates, fishes, sea turtles, seabirds, and marine mammals
- Expanded Table 6.1 on the groups of marine autotrophs
- Updated, to follow more current views, the position of chaetognaths as protostomes and echiurans as annelids
- Added characters to cladograms in Figs. 7.1 (invertebrates) and 8.1 (vertebrates) and revised to follow latest interpretations on the phylogeny of invertebrate taxa
- · Updated species counts for all invertebrate and vertebrate groups
- Expanded Table 7.1 on the groups of invertebrates
- · Modified box on sharks to emphasize threats to their existence
- · Added information to the box on coelacanths
- Significantly expanded section on the biology of marine mammals, adding a great deal of information (swimming, diving, migrations, behavior, and reproduction) on non-cetaceans (pinnipeds, the walrus, sea otter, polar bear, and sirenians)
- · Expanded illustration of filter feeding in whales
- · Updated status of great whales and dolphins
- Updated some of the graphs in the Special Report
- Added information on the biology (physiology, ecology) of mangroves and seagrasses, including new photos
- Added information on bioturbation, fjord communities, and deep-water reefs
- Greatly expanded the box on Antarctic subtidal communities, now including the Arctic and the effects of human intrusion in both
- Added information on species composition, biodiversity, and biogeography of soft-bottom subtidal communities
- Added recent information, including a new figure, on a tropic cascade involving sea otters and the recovery of seagrass meadows
- · Expanded section on the human impact on seagrasses
- Redesigned figures on the rete mirabile of epipelagic fishes, adaptations for fast swimming in tunas, and the krill photophore
- Added new information on aquaculture and the use of methane hydrates as a source of energy
- Added new figure on ocean thermal energy conversion (OTEC)
- · Expanded and updated information on marine protected areas
- Added new figure on the Gulf of Mexico hypoxic, or "dead," zone

- Added new information on endangered marine species, including updating of our unique table on Red List and CITES lists for marine species
- · Expanded data on plastic pollutants and artificial reefs
- Added new section on prospects for the future of the marine environment and the role of marine biology

ORGANIZATION

Marine Biology is organized into four parts. Part one (Chapters 1 through 4) introduces students to marine biology and the basic sciences that underpin it. Chapter 1 describes the history of marine biology. It also explains the fundamentals of the scientific method. This feature emphasizes that science is a process, an ongoing human endeavor. We think it is critical that students understand how and why science works, that science has limitations, and that there is still much to be learned. Chapters 2 and 3 are a basic introduction to marine geology, physics, and chemistry. Marine Biology includes more information on these subjects, and places greater stress on their importance to understanding marine ecosystems, than other texts but we have kept Chapters 2 and 3 as short as possible and have covered many abiotic aspects of the marine environment in the chapters where they are most relevant to the biology. Wave refraction, for example, is described in conjunction with intertidal communities (Chapter 11) and estuarine circulation is discussed as part of the ecology of estuaries (Chapter 12). This approach emphasizes the importance of the physical and chemical environment to the organisms of the sea throughout the book. At the same time, it provides flexibility for instructors to make best use of the material in light of general education requirements, course prerequisites, and students' backgrounds. Chapter 4, "Fundamentals of Biology," briefly reviews some essential biological concepts. In covering basic biology we have tried to balance the needs of a spectrum of students ranging from those with no prior university-level instruction to those who have taken a number of biology courses. Depending on the level of their students, instructors may choose to cover Chapter 4 in class, assign it as review reading, or omit it and rely on the in-text glossary entries in later chapters to remind students of the definitions of key terms.

Part Two (*Chapters 5 through 9*) surveys the diversity of marine life from the perspective of organismal biology. As in Part One, we provide introductory information that is reviewed and expanded upon in later chapters. In discussing the various taxa we emphasize functional morphology, ecological and physiological adaptations, and economic importance or other significance to humanity. Classification and phylogeny are not stressed, though we do present cladograms illustrating widely accepted phylogenetic schemes for invertebrates and vertebrates. As in the rest of the book we have selected organisms from around the world for 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 provide comprehensive lists of genera.

Part Three of the book (Chapters 10 through 16) presents an ecological tour of the major environments of the world ocean, commencing with an introduction to some fundamental principles of marine ecology in Chapter 10. As in Chapter 4, important concepts presented here are reviewed elsewhere in the in-text glossary boxes. The remaining six chapters of Part Three proceed from nearshore to offshore and from shallow to deep water, describing the physical characteristics of each environment and the adaptations and interactions of the organisms that live there. This admittedly arbitrary sequence follows the teaching sequence of the greatest number of our reviewers, but the chapters are designed so that they can be covered in any sequence according to instructors' preferences and needs. Most chapters include generalized food webs with standardized color coding to indicate the nature of the trophic relationships. Part Three also contains the Special Report: Our Changing Planet, a feature on anthropogenic global change that was introduced in the seventh edition.

Finally, **Part Four** looks at the many ways in which humans interact with the world ocean: our use of and impact on the marine environment and the influence of the ocean on the human experience. The section presents 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, aquaculture, and oil and gas extraction, but also at more modern aspects, such as the emerging technologies to generate energy from the sea, the pharmacological use of marine natural products, and the application of genetic engineering and other technologies in aquaculture. *Chapter 18* discusses human-induced degradation of the marine environment, balanced by an examination of marine conservation and habitat restoration.

ACKNOWLEDGMENTS

Bill Ober and Claire Garrison have again done a superb job of bringing new life to the illustrations, including new ones. We also thank the many contributors of photographs that add so much to the book, and appreciate the expert and diligent efforts of LouAnn Wilson in locating new photos and information about them. We are grateful to the editorial and production staff, particularly Rebecca Olson, Fran Simon, Patrick Reidy, and Lisa Bruflodt, for their patience, support, and efficiency in managing an enormous amount of detail. Most of all 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.

REVIEWERS

The following people reviewed the ninth edition and have provided useful commentary for preparation of the tenth edition:

Dr. Chantale Bégin, University of South Florida

Paul Detwiler, San Diego Mesa College

Dr. Michelle L. Hardee, University of South Carolina

Dr. Rob McDowell, American Public University

Dr. Christopher Osovitz, University of South Florida

Dr. Christina L. Richards, University of South Florida

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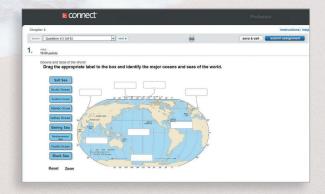




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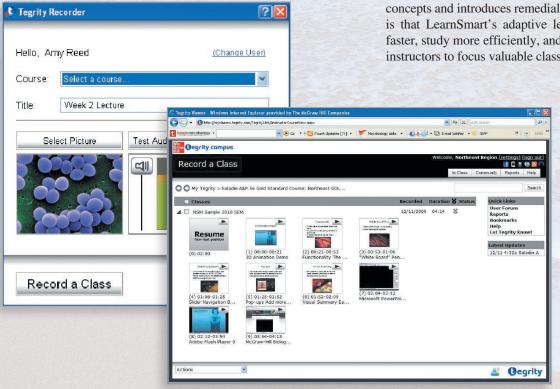
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Instructor's Manual

Prepared by Peter Castro, this helpful ancillary provides student learning outcomes for each chapter, chapter outlines and summaries, a listing of audiovisuals and software, and answers to the Critical Thinking questions within the text. Instructors will also find suggestions on presenting concepts to students and organizing materials for class presentation.

Test Bank

A computerized test bank utilizing testing software to quickly create customized exams is available with this text. The user-friendly software allows instructors to search for questions by topic or format, edit existing questions or add new ones, and scramble questions to create multiple versions of the same test. Word files of the test bank questions are provided for those instructors who prefer to work outside the test-generator software.

Laboratory Exercises

Ideal for a one-quarter or one-semester course, this collection of eight laboratories and field investigations in marine biology has been specially designed for use in conjunction with the tenth edition of *Marine Biology*. Each of the exercises includes review questions that integrate information learned in the laboratory or field with material covered in the text. The exercises can be accessed via McGraw-Hill Connect[®].

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Part One
Principles of Marine
Science

CHAPTER

The Science of Marine Biology

Marine biologists collecting coral larvae on a Caribbean coral reef.

arine biology is the scientific study of life in the sea. The ocean is vast, home to countless strange and wonderful creatures. It is often the beauty, mystery, and variety of life in the sea that attract 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. Life on Earth probably originated in the sea, so the study of marine organisms teaches us much about all life on Earth, not just marine life. Many medical advances, for example, have been underpinned by research on marine organisms, such as studies of the animal immune system in sea anemones and sea star larvae, the fertilization of sea urchin eggs, squid nerve cells, and barnacles.

Marine life also represents a vast source of human wealth. It provides food, medicines, and raw materials, offers recreation to millions, and supports tourism all over the world. Marine organisms can also cause problems. For example, some organisms harm humans directly by causing disease or attacking people. Others harm us indirectly by injuring or killing other marine organisms that we value for food or other purposes. Marine organisms can erode piers, sea walls, and other structures in the ocean, foul ship bottoms, and clog pipes.

At a much more fundamental level, marine life helps determine the very nature of our planet. Marine organisms produce around half 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.

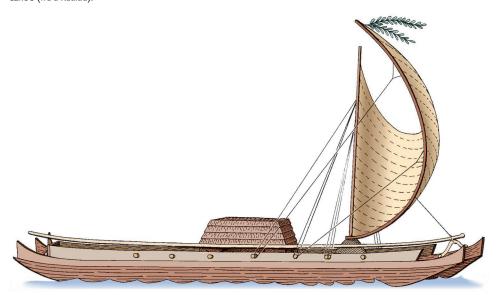
To make full and wise use of the sea, to solve the problems that marine organisms create, and to predict the effects of human activities on the ocean, we must learn all we can about marine life. In addition, marine organisms provide valuable clues to the Earth's past, the history of life, and even our own bodies. This is the challenge, the adventure, of marine biology.

1.1 THE SCIENCE OF MARINE BIOLOGY

Marine biology is really the more general science of biology applied to the sea rather than a separate science. 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 whole organisms: how 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, whereas biological oceanographers

FIGURE 1.1 Pacific islanders have navigated the Pacific for millennia in canoes like this Hawaiian double-hulled canoe (wa'a kaulua).



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 what an organism eats), while biological oceanographers tend to take the perspective of the ocean (for example, studying how food energy 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.

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 have been living by the sea since the dawn of humanity, and seafood is thought to have been crucial to early human survival and migration. The earliest known stone blades, from 165,000 years ago, were discovered in a seaside cave in South Africa, along with piles of shells from Stone Age clambakes and the earliest traces of ochre pigment, thought to be used for symbolic body painting and decoration. Ancient bone or shell harpoons and fishhooks have also been found, as well as the earliest known jewelry in the form of shell beads from as long as 110,000 years ago. As they used its resources, people steadily gained a store of practical knowledge about the sea.

Knowledge of the ocean and its organisms expanded 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. The Phoenicians were the first accomplished Western navigators. By 2000 B.C. they were sailing around the Mediterranean Sea, Red Sea, eastern Atlantic Ocean, Black Sea, and Indian Ocean.

The ancient Greeks had considerable knowledge of nearshore organisms in the Mediterranean region (Fig. 1.2). The Greek philosopher Aristotle is considered by many to be the first marine biologist. He described many forms of marine life and recognized, among other things, that gills are the breathing apparatus of fish.

During the centuries known as the Dark Ages, scientific inquiry, including the study of marine life, came to a grinding halt in most of Europe. 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 active during the Middle Ages, voyaging to eastern Africa, southeast

FIGURE 1.2 Romans often used marine animals in the magnificent mosaics that decorated the floors and walls of their villas. This mosaic depicts in great detail several types of fishes, an octopus capturing a lobster, a squid, and other Mediterranean marine life. The mosaic was originally in Pompeii, a city destroyed and buried in 79 A.D. by an eruption of Mount Vesuvius.



Asia, and India. In the Far East and the Pacific, people also continued to explore and learn about the sea.

During the Renaissance, spurred in part by the rediscovery of ancient knowledge preserved by the Arabs, Europeans again began to investigate the world around them, and several undertook 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.

Before long, explorers became curious about what lived in the ocean they sailed. 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 use a chronometer, an accurate timepiece that enabled him to determine his longitude precisely, 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 had become common for vessels to take a naturalist along to study the organisms encountered. Perhaps the most famous of these shipboard naturalists was Charles Darwin, 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 made 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," in 4.5, The Diversity of Life in the Sea). Though best known for the theory of evolution, Darwin made many other contributions to marine biology. He explained, for example, the formation of the distinctive rings of coral reef called atolls (see "How Atolls Form," in 14.2, Kinds of Coral Reefs). He

used nets to capture the tiny, drifting organisms known as plankton, which marine biologists continue to do today (Fig. 1.3). Darwin's many interests also included barnacles, attached crustaceans (see Fig. 7.33). Specialists still refer to his treatise on them.

In the United States the most important early exploratory voyage was probably the United States Exploring Expedition of 1838-1842, often called the "Wilkes Expedition" after its leader, Lt. Charles Wilkes of the U.S. Navy. The expedition included only 11 naturalists and artists, derisively called "clam diggers" by the rest of the crew, and some historians conclude that it was more about projecting American influence than scientific discovery. Wilkes was by all accounts a vain and cruel man who promoted himself to Captain as soon as he left port, and upon his return was courtmartialed for flogging his crew to excess. Only two of the expedition's six ships made it home. Nevertheless, the Wilkes Expedition's achievements were impressive. The expedition charted 2,400 km (1,500 mi) of the coast of Antarctica, confirming it as a continent, as well as the coast of the Pacific Northwest of North America. It explored some 280 islands in the South Pacific, collecting information about peoples and cultures as well as flora and fauna. The 10,000 biological specimens included some 2,000 previously unknown species (Fig. 1.4). The expedition, the first international survey sponsored by the U.S. government, also laid a foundation for government funding of scientific research.

The Challenger Expedition By the middle of the nineteenth century, a few lucky scientists were able to undertake voyages specifically to study the oceans, instead of having to tag along on ships doing other jobs. One was Edward Forbes, who in the 1840s and 1850s carried out extensive trawling 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 seafloor life varies at different depths (see Box 16.2, "Biodiversity in the Deep Sea"). Perhaps his most important contribution, however, was to inspire new interest in the life of the sea floor.

Forbes's contemporaries and successors, especially from Britain, Germany, Scandinavia, and France, carried on his studies of sea-floor life. Their ships were poorly equipped and the voyages short, but their studies produced many interesting results. They were so successful, in fact, that 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*.

FIGURE 1.3 These marine scientists are hauling in a net known as a "bongo net" used to capture minute marine plankton. One is signaling instructions to the winch operator.





FIGURE 1.4 Peale's dolphin (*Lagenorhynchus australis*), named after the Wilkes Expedition naturalist who first described it, is one of 2,000 marine and terrestrial species discovered by the expedition.

Challenger underwent extensive renovations in preparation for the voyage. Laboratories and quarters for the scientific crew were added, and gear for collecting 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.

Over the next three and a half years, *Challenger* and her crew sailed around the world, gathering information and collecting water, sediment, and biological samples (Fig. 1.5). The sheer volume of data gathered was enormous—it took 19 years to publish the results, which fill 50 thick volumes. *Challenger* brought back more

information about the ocean than had been recorded 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. The expedition set new standards for ocean research. *Challenger*'s scientists collected data in a more systematic way than previous expeditions and kept meticulous records. For the first time, scientists began to get a coherent picture of what the ocean was like. They also learned about the enormous variety of marine life, for *Challenger* brought back thousands of previously unknown species. Thus, the *Challenger* expedition laid the foundations of modern marine science.

Other expeditions continued the work begun by *Challenger*, and 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, the vessels had quarters for only a few scientists. Most biologists only got to see the dead, preserved specimens that the ships brought back to port. Such specimens revealed much about marine life around the world, but biologists wanted to know how the organisms actually lived: how they functioned and what they did. Living specimens were essential for this, but ships usually stayed in one place for only a short time, making long-term observations and experiments impossible.

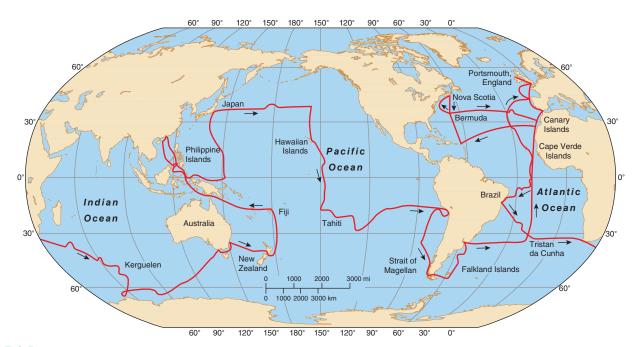


FIGURE 1.5 The route of the Challenger expedition, which from 1872 to 1876 conducted the first systematic survey of the world ocean.

As an alternative to ships, biologists began to work at the seashore. Among the first were two Frenchmen, Henri Milne Edwards and Victor Andouin, who around 1826 began making regular visits to the shore to study marine life. 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. Eventually, biologists set up permanent laboratories where they could keep organisms alive and work over long periods. The first such laboratory was the Stazione Zoologica, founded in Naples, Italy, 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. It is hard to pinpoint the exact date when this laboratory was established. The first marine laboratory at Woods Hole was started by the United States Fish Com-

mission in 1871, but it did not flourish. Several other short-lived laboratories subsequently appeared in the area. Harvard biologist Louis Agassiz, who also studied many of the specimens collected by the Wilkes Expedition, established a laboratory on nearby Cape Ann in 1873. In 1888 this laboratory 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 labs.

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 (Fig. 1.6), Scripps 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, and new ones are being established even today.

The onset of World War II had a major effect on the development of marine biology. A new technology, **sonar**, or *so*und *na*vigation and *r*anging, was developed in response to the growing importance of submarine warfare. Sonar is based on the detection of underwater echoes—a way of detecting sound in the sea (Fig. 1.7). 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),



FIGURE 1.6 An early marine biology class at Stanford University's Hopkins Marine Station. The station, established in 1892, is the third oldest in the United States.

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 practical **scuba**, or *s*elf-*c*ontained *u*nderwater *b*reathing *a*pparatus. The basic technology was developed in occupied

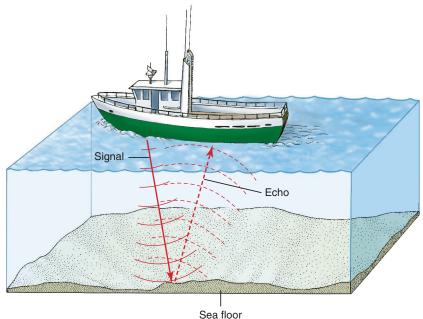


FIGURE 1.7 A ship uses sonar by "pinging," or emitting a loud pulse of sound, and timing how long it takes the echo to return from the sea floor. The water depth can be determined from the return time. This, the most common form of sonar, is called "active sonar" because the sounds used are actively generated by the equipment.

Box 1.1 Observing the Ocean

ost of the ocean is incredibly remote, and difficult and expensive to get to. The ocean is also a vast, interconnected network, and conditions at one place are affected by events far away. To cap things off, events such as storms and earthquakes-not to mention the interactions and movements of marine organisms—occur suddenly, making them hard to capture unless you happen to be in just the right place at the right time. Ships, submarines, and scuba diving, and studies in the laboratory and on the shore, will always have an important place in marine science, but they can't provide the continuous coverage of broad areas of the ocean, throughout its depths, that is needed to really understand the ocean. Satellites can observe vast areas of the ocean (see "Marine Biology Today," below), but only at the surface.

A range of new technologies is allowing scientists—and the general public—to observe the oceans in ways that would have seemed like science fiction not long ago. In the Argo system,

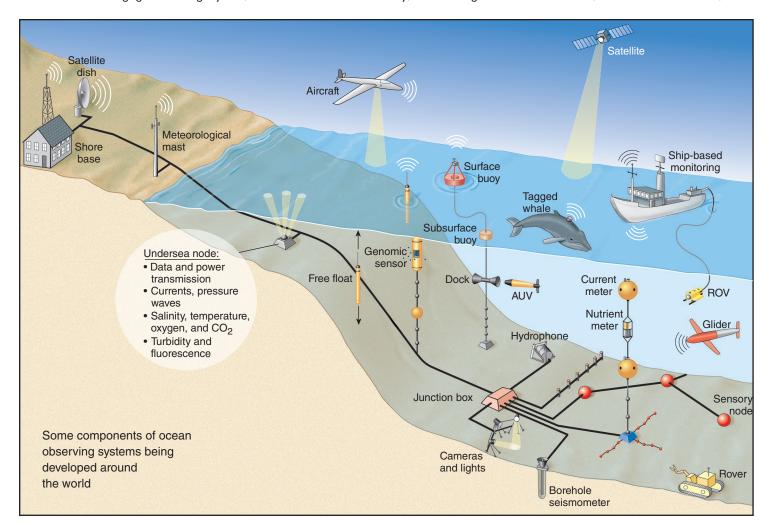
for example, 3,000 or more automated floats, looking a bit like torpedoes turned on end, are scattered throughout the ocean. Each float continuously bobs between the surface and a depth of 2,000 m (6,600 ft), over about 10 days, continuously measuring water temperature and salinity and transmitting the data via satellite when at the surface. Argo floats are providing huge amounts of new information, especially from areas, such as the winter seas around Antarctica, that are difficult to study from ships. A few Argo floats have now been equipped with sensors to measure oxygen, and additional sensors are being developed, as well as floats that can go even deeper. Oceanographers have also launched robotic gliders that cruise across entire oceans for years at a time, like Argo floats, collecting data and surfacing to relay the data by satellite.

Oceanographers are also wiring the sea floor, providing power and communications for an amazing array of instruments that measure currents and water chemistry, detect the slightest



Marine biologists fit a southern elephant seal (Mirounga leonina) with electronic instruments.

sea-floor tremors, and track biological activity. The first such system in the United States was the Long-term Ecosystem Observatory (LEO), installed off the New Jersey coast in 1996. LEO, now known as the Coastal Ocean Observation Laboratory (COOL), has grown to include underwater gliders, shore-based radar, ship measurements, and moored instruments, and is



being integrated with similar systems into a single network covering the United States from Maine to Florida. In the Pacific, the first cables for the Victoria Experimental Network Under the Sea (VENUS) were laid in 2006 off the coast of British Columbia, Canada, and for the Monterey Accelerated Research System (MARS) off the coast of California in 2007. VENUS and MARS are both now fully operational. VENUS and MARS form part of a larger network, the North East Pacific Time-integrated Undersea Networked Experiments (NEPTUNE) Observatory, which extends from British Columbia to Oregon. NEPTUNE is itself part of an even larger program, the Ocean Observatories Initiative (OOI). Similar networks are being developed in Europe, Japan, the Gulf of Mexico, and the Arctic Ocean. Exciting new devices are on the way, such as genomic sensors that will not only measure the abundance of plankton but also identify their DNA, and docking stations where free-ranging autonomous underwater vehicles (AUVs) can charge batteries and download information. There are even proposals for self-powered AUVs that use plankton for fuel.

Like all cutting-edge endeavors, developing these observing networks has its challenges. High-tech electronics can be fickle even in the laboratory, much less the depths of the sea. A NEPTUNE scientist says, "We're learning a lot, which is another way of saying that things are breaking." But most of NEPTUNE's instruments are transmitting photos, audio, and

video—in vast amounts—that are freely available online, and the system will only get more reliable.

The networks have also brought unexpected benefits, in part because they are used by scientists from widely varying disciplines. For example, marine geologists use the NEPTUNE network to monitor for earthquakes, but the endangered fin whale (*Balaenoptera physalus*) sings at a sound frequency that interferes with the earthquake measurements. The geologists developed software tools to identify and filter out fin whale songs that marine biologists are now using to track the whales. In another example, forensic scientists have used VENUS's underwater video to monitor the decomposition of pig carcasses in the ocean to help them determine the time of death of human bodies recovered from the sea.

Not all ocean observing systems are inanimate—marine animals are being recruited to help. Seals, sea lions, sharks, and other large marine animals move underwater faster than humans can ever hope to follow and are unlikely to behave naturally when humans are present. To get a firsthand look at what these animals do beneath the surface, scientists developed "crittercam," a compact underwater video camera that is attached to the animals themselves. Crittercam has been deployed on sea turtles, sharks, whales, seals, sea lions, and penguins. It provided the first underwater views of feeding humpback whales using curtains of bubbles

to herd herring, social diving behavior in Adélie (*Pygoscelis adeliae*) and chinstrap (*P. antarctica*) penguins, and the movements of endangered sea turtles in Mexico. A crittercam attached to a sperm whale (*Physeter catodon*) provided new views of life in the deep sea.

Scientists use animals to study the ocean as well as the animals themselves. An "Autonomous Underwater Sampler" is another name for an animal, such as an elephant seal, with a transmitter glued to its back. Originally the transmitters, which measure temperature, depth, and salinity, were used to record the diving behavior of the animals, but oceanographers realized that the sensors also provide valuable data on ocean circulation, as the animals can go to places that scientists can't access any other way.

Ocean observing systems aren't just for science. They bring concrete benefits to society. In 2006, for example, COOL helped forecast the track of Tropical Storm Ernesto for emergency response authorities and the public. Observing networks are providing early warning of tsunamis, potentially saving hundreds of thousands of lives (see Box 3.3, "Waves That Kill"). The systems will help forecast earthquakes and storms, track the effects of climate change, monitor fish populations, and make shipping more efficient. Ocean observatories will save lives and money and help humanity make wiser use of the oceans—and indeed the entire ocean planet.

France by the engineer Émile 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 to scuba diving and the oceans.

Using scuba, marine biologists could, for the first time, descend below the surface to observe marine organisms in their natural environment (Fig. 1.8). They could now work comfortably 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 ever. Today many universities and 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, like *Challenger*, were originally built for other uses, but growing numbers of vessels are purpose-built for scientific research at sea.

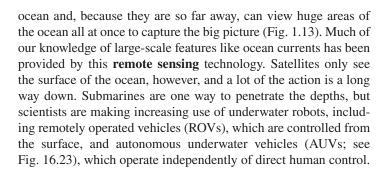
In addition to ships as we normally think of them, some remarkable craft are used to study the marine world. High-tech submarines can descend to the deepest parts of the ocean, revealing a world that was once inaccessible (Fig. 1.10). Various odd-looking vessels ply the oceans, providing specialized facilities for marine scientists (Fig. 1.11).

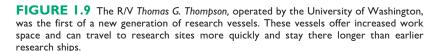
Marine laboratories, too, have come a long way since the early days. Today labs dot coastlines around the world and are used by an international community of scientists. Some are equipped with the most up-to-date facilities available. Others are simple field stations, providing a base for scientists 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 centers not only of research but also of education. Many offer hands-on undergraduate courses in which students can study marine biology firsthand, and most provide facilities where graduate students begin their careers in marine science.

New technology offers exciting opportunities for studying the oceans. It goes almost without saying that computers and electronics have had profound impact. Satellites peer down at the



FIGURE 1.8 Scuba is an important tool in the work of many marine biologists. This scientist is using an apparatus called a respirometer to measure the production and consumption of oxygen by organisms on a coral reef.







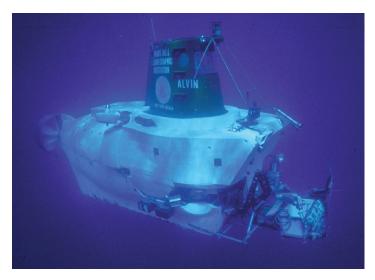


FIGURE 1.10 Alvin, a deep-sea submarine operated by the Woods Hole Oceanographic Institution, is one of the most famous vessels in the history of marine science.

Marine scientists are also developing an array of instruments that sit on the bottom, float in place, drift with the currents, or are even attached to animals (see "Observing the Ocean," above). Space technology has a role to play here as well; many oceanographic instruments relay their data through satellites.

Marine biologists today use every available tool in their study of the sea, even some decidedly low-tech ones (Fig. 1.14). Information about the ocean pours in at an ever-increasing pace. Much is yet to be learned, however, and the oceans remain a realm of great mystery and excitement.

1.2 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 "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 education. Why has science come to occupy a position of such prestige in our society? The answer, quite simply, is that it works! Science is among the most successful of human endeavors. Modern society could not exist without the knowledge and technology produced by science. Everyone's lives 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



(a)



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. (a) Most of the hull consists of a hollow tube that floats while the vessel is towed into position. When the hull is flooded and sinks, *FLIP* swings into a vertical position (b) in which it is largely unaffected by the rise and fall of waves.

as a place where things just happen, for no reason. They assert instead that the universe can be explained by physical laws. Scientists don't go about discovering these laws haphazardly; they proceed according to time-tested procedures. The set of procedures that scientists use to learn about the world is called the **scientific method.**

Scientists sometimes disagree over the fine points of the scientific method. As a result, they may 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, which should be seen as a flexible framework guiding the study of nature and not a rigid set of rules.

Observation: The Currency of Science

The goal of science is to discover facts about the natural world and principles that explain these facts. At the heart of the scientific method is the conviction that we can learn about the world only through our senses or with tools that extend our senses. Microscopes, for example, extend our vision to help us see what is otherwise too small to see. Thus, scientific knowledge is fundamentally derived from the observation of nature. Scientific conclusions are based on observations, and not on preexisting ideas of how the world is or should be.

One of the advantages of relying on observations is that they can be verified by 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. Different people can look at the same object. Sensory perception may be imperfect, and scientists, like anyone else, are not always impartial, but the object is there for all

FIGURE 1.12 A diver swims outside Aquarius, the world's only underwater marine science laboratory. Aquarius is located in the Florida Keys Marine Sanctuary at a depth of about 20 m (60 ft). The living quarters are in the large cylinder at the upper left, which, fortunately for the crew, is larger than it appears here because it is further away than the diver.

