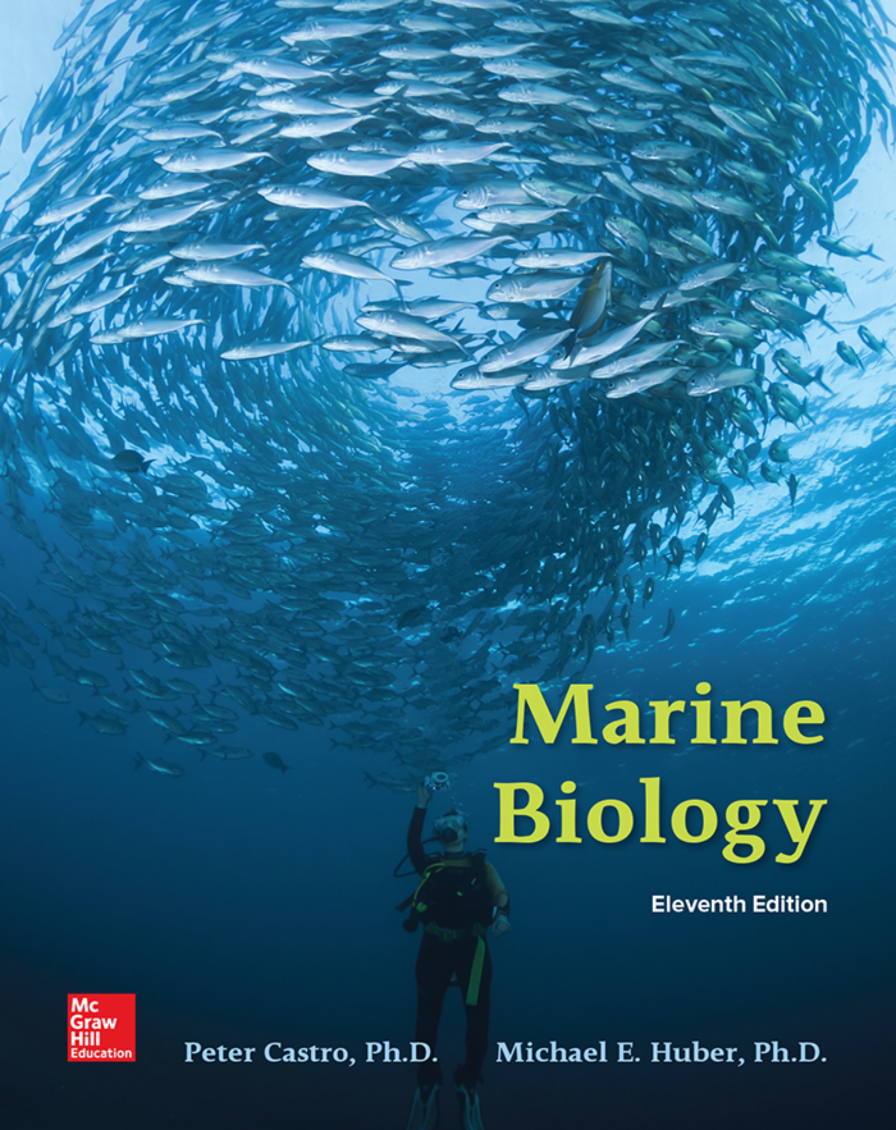
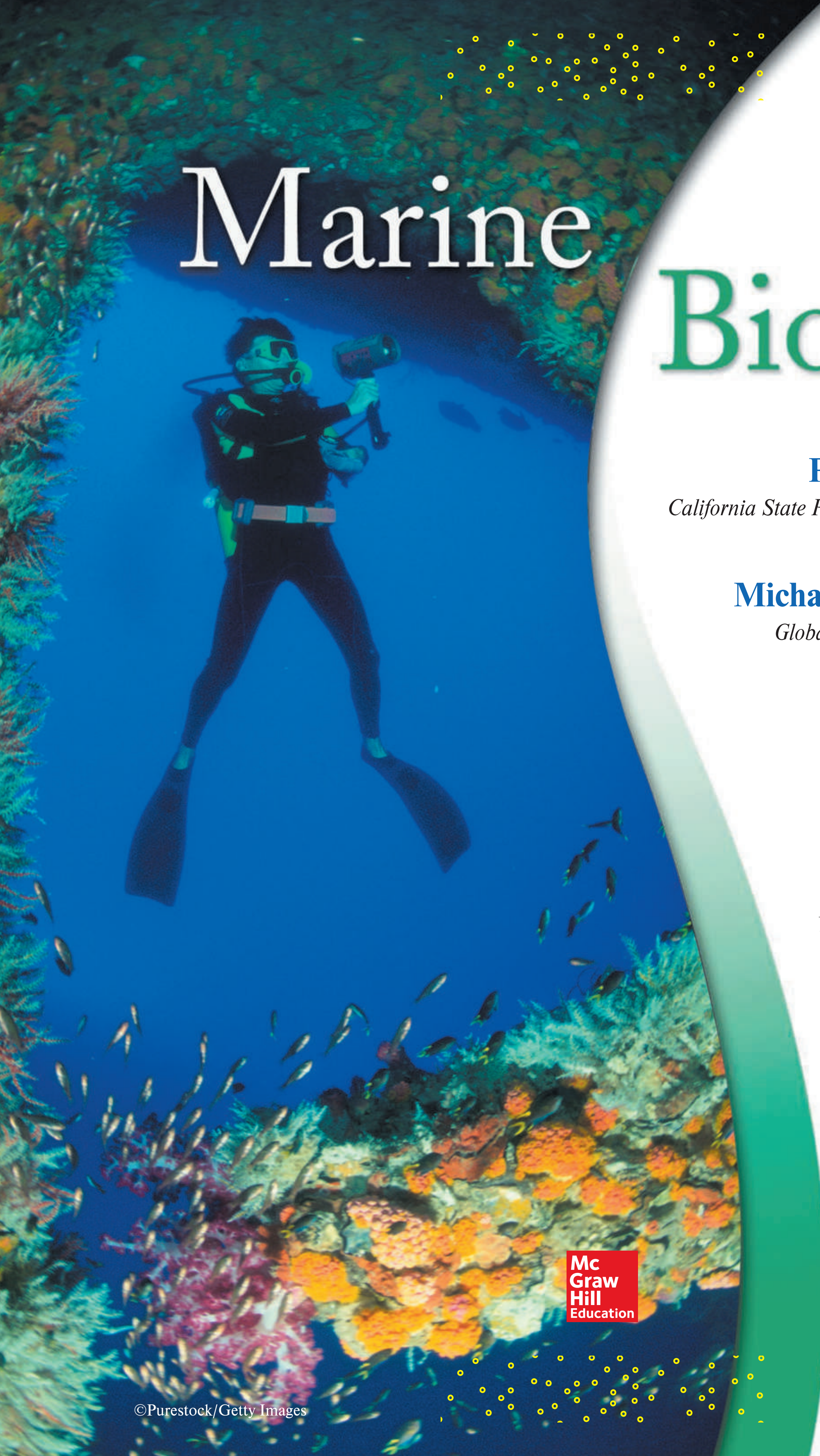


Marine Biology

Eleventh Edition

Peter Castro, Ph.D.   Michael E. Huber, Ph.D.



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Marine Biology

Eleventh Edition

Peter Castro, Ph.D.
California State Polytechnic University, Pomona

Michael E. Huber, Ph.D.
Global Coastal Strategies, Australia

Original Artwork by

William C. Ober, M.D.
Washington and Lee University

and

Claire E. Ober, B.A., R.N.

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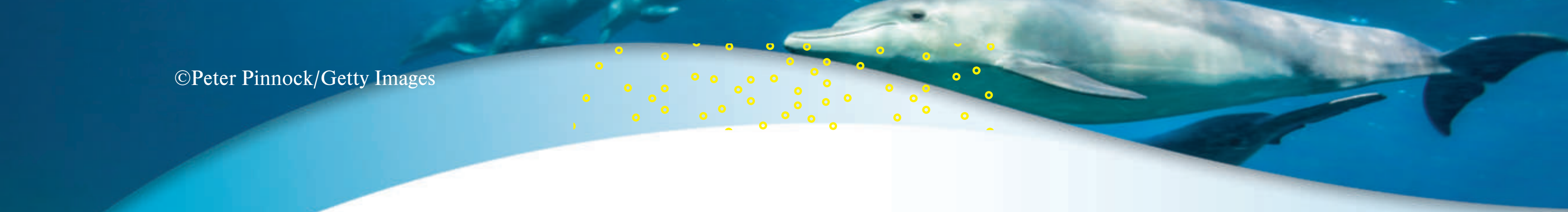

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Dedication

To all future marine biologists

–Peter Castro–

To my father, Francis Joseph Huber, may he rest in peace.

–Michael Huber–

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Part Three *Structure and Function of Marine Ecosystems*

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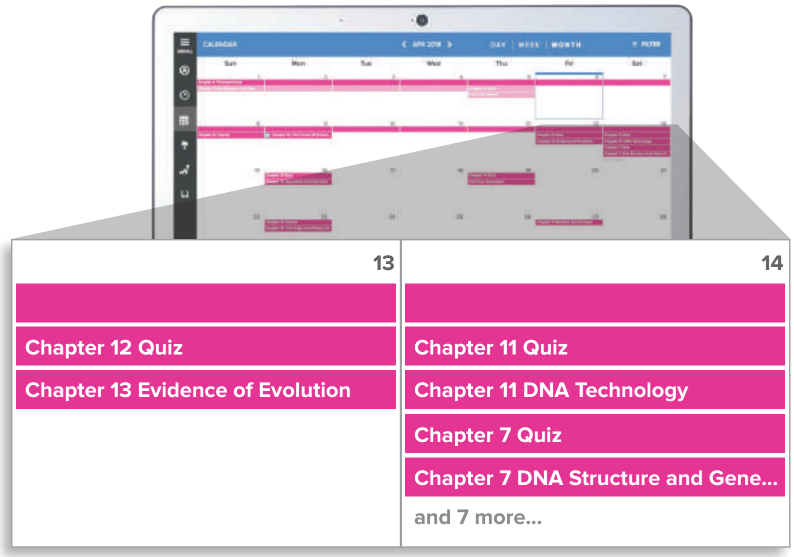

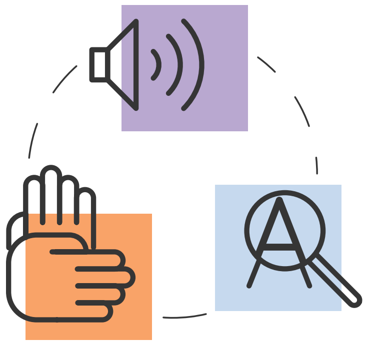

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Eye on Science Boxes

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, Mānoa. 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 four languages and has 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 Brazil, France, Germany, and Singapore. Dr. Castro has so far published 64 peer-reviewed papers on his research. He is currently editor-in-chief of the *Journal of Crustacean Biology*.

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 both zoology and oceanography from the University of Washington. 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 protection to international agencies, governments, and private industry. Much of his work has been in marine environmental protection at the global level, while regionally his focus is the Asia-Pacific region. He has worked on a wide range of environmental issues such as pollution control and waste management, habitat conservation and restoration, marine invasive species, endangered species management, long-term environmental monitoring, effects of mariculture, and deep-sea mining. Dr. Huber is Member Emeritus of GESAMP, a United Nations scientific body that advises international agencies on marine environmental issues. This work has taken him to more than 60 countries, most recently Chile, China, Indonesia, New Zealand, Perú, the Philippines, Singapore, Thailand, the Republic of Korea, and Vietnam.

Mike lives in Brisbane, Australia. His hobbies are fishing, diving, swimming, listening to and attempting to play music, reading, and gardening.

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Preface

The ocean fascinates people all over the world, including, of course, undergraduate marine biology students. 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,* eleventh 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 terminology.

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 urgent with each passing year is the impact of humans on the marine environment.

***Marine Biology,* eleventh 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 ELEVENTH EDITION

Like all new editions of *Marine Biology,* we have made extensive revisions to the eleventh edition to correct errors, incorporate new information, and improve readability. In many cases our revisions reflect comments by reviewers, whose suggestions we greatly appreciate. Much of the data presented in the eleventh edition has been updated to the latest information available at the time of writing. Updates include, among others, numbers of known species in various taxonomic groups, conservation status and population sizes of many threatened species, shark-attack frequency, data on global and regional climate, sea level, CO_2, hypoxic zones, paralytic shellfish poisoning, and the Antarctic ozone hole. The latest available data are also used for fisheries catches, aquaculture production, and seafood demand and consumption, and the extent of Arctic sea ice.

Many chapters in the eleventh edition include more information on the effects of global change on species and ecosystems in addition to the *Special Report: Our Changing Planet*. The coverage also in many cases reflects increasing scientific certainty regarding global change and its effects on the ocean.

We have updated or added information on many other topics. There are too many such changes to fully list here, but examples include the following:

- Discussion of the importance of natural experiments and the use of models in the scientific method
- Additional information on the role of the sea in ancient human migration
- Updated information on ocean observing systems
- Replaced Figure 2.6 with the most recent representation of the global sea floor

- Updated information on the formation of the Hawaiian Islands and mantle plumes
- New information on the role of viruses in the ocean
- Extensively revised coverage of sexual reproduction in seaweeds and marine plants, with a revised Figure 6.11
- New or updated information on the biology and ecology of many groups of organisms, from mangroves to marine mammals
- Additional information on the ecology of chemosynthetic bacteria
- Updated phylogenetic relationships and classification in invertebrates, with Figure 7.1 and Table 7.1 revised
- More information on the restoration of seagrass, saltmarsh, mangrove, and coral reef communities
- New information on hunting behavior and the role of older females in orcas, captive cetaceans, interactions among dolphins, and the reproductive tract of dolphins
- Extensive new information on small cetaceans including the vaquita and Maui's dolphin, with a new figure for the vaquita
- New information on infections of the cat parasite *Toxoplasma* in marine mammals
- Information on the effects of melting polar ice on cetaceans, polar bears, and polar subtidal communities
- How recent natural experiments are changing our view of the role of *Pisaster* as a keystone predator and potential roles of other sea stars
- Coverage of mass coral bleaching globally during 2014–2017
- New findings on the existing effects of climate change on human health
- Reproductive and physiological adaptation in the vampire squid
- Updated information on the ocean as a source of energy for humans
- Updated information on Alaska's *Exxon Valdez* oil spill, invasive marine species, and marine protected areas

The "Eye on Science" boxes, which have proven to be very popular among students and instructors alike, have been extensively updated. We have also added new Eye on Science boxes on a symbiosis between a barnacle and cyanobacteria in the intertidal, sea star wasting disease, coral reef resilience, and microplastic pollution.

Many of the eleventh edition's figures have been extensively revised and redesigned by Bill Ober and Claire Garrison to their usual standard of excellence. A number of figures have been modified to include the new data described above. In some cases, for example, Figures 6.11 on reproduction in marine macrophytes and 7.1 showing invertebrate phylogenetic relationships, the changes reflect important new information. Many other figure revisions include updated or added content, or make the figures more understandable, accurate, and eye-catching. We have also added a number of new photographs throughout the book.

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.

The *Special Report: Our Changing Planet*, lying roughly in the middle of the book, presents some of the global-scale threats to the ocean resulting from human activities. Much of the material in the *Special Report* could appear in chapters where it is most relevant to specific ecosystems or species. In our opinion, bringing this material together in a single section emphasizes both the global nature of human-induced change in the ocean and the multiple stresses we are imposing. Placing the *Special Report* in the middle of the book results in important related material being covered in later chapters. We think the current placement gives prominence to this critically important issue even if the *Special Report* has to look forward to later chapters.

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. 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 tenth edition and have provided useful valuable comments and suggestions for preparing the eleventh edition:

Elena D. Cainas, *Broward College, Central Campus, Davie, Florida*

Hector Douglas, *University of Alaska Fairbanks, Kuskokwim Campus*

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Jennifer Harper, *Bainbridge State College, Bainbridge, Georgia*

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Amy Reber, *Georgia State University, Atlanta*

Anne Michelle Wood, *University of Oregon, Eugene*

Laurel Zahn, *Occidental College, Los Angeles, California*

Part One
Principles of Marine Science

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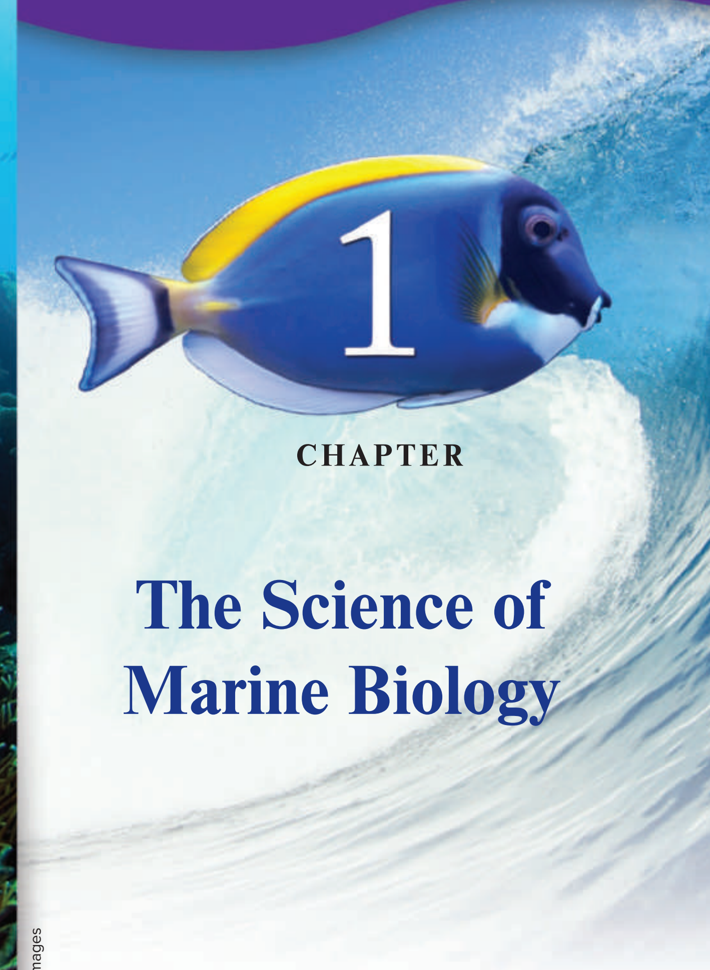
Marine biologists collecting coral larvae on a Caribbean coral reef.



1 CHAPTER
The Science of Marine Biology

Marine biology is the scientific study of life in the sea. The ocean is vast, home to countless strange and wonderful creatures. The beauty, mystery, and variety of life in the sea often attracts students to marine biology courses. 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, nerve conduction in squids, and barnacle muscles.

Marine life is also 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. Some marine 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 the oxygen we breathe and help regulate 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's 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 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 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 humans. 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.

One of the paths of early human migration from Africa into Europe probably followed the coast, with its abundant seafood. Humans also probably migrated down the west coast after arriving in the Americas. That migration seems to have been very rapid and may have been by boat.

The use of marine resources improved peoples' knowledge of marine organisms and drove improvements in seamanship and navigation. Ancient Pacific Islanders had detailed knowledge of marine life, which their descendants still retain. They were consummate mariners (Fig. 1.1), using clues such as wind, wave, and current patterns to navigate over vast distances, perhaps as far as South America.

FIGURE 1.1 *Haunui* is a faithful replica of the double-hulled voyaging canoes that brought Polynesian explorers—the ancestors of the Maori—to New Zealand. Polynesians sailed similar vessels throughout the vast Pacific. Replica vessels like *Haunui* have recreated these voyages, not only demonstrating that such canoes were capable but also keeping ancient cultural traditions alive.

The Phoenicians were the first accomplished Western navigators. By 2000 BCE (Before Common Era, that is, before the year 1 in the Gregorian calendar that we use today), 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 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

FIGURE 1.2 The tile mosaics wealthy Romans used to decorate their villas often depicted marine animals. This one shows several types of fishes, an octopus capturing a lobster, a squid, and other Mediterranean marine life. The mosaic was excavated from Pompeii, a city buried in 79 CE by an eruption of Mount Vesuvius.

the ninth and tenth centuries CE, or Common Era, the Vikings continued to explore the north Atlantic. In 995 CE a Viking party led by Leif Eriksson discovered Vinland, what we now call North America. Arab traders were also active in the Middle Ages, voyaging to eastern Africa, southeast 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 led the first expedition to sail around the globe. Other epic voyages increased our knowledge of the oceans. Fairly accurate maps began to appear for the first time, especially for places outside Europe.

Explorers soon 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 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, taking a naturalist along on expeditions was commonplace. 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. *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 the formation of the distinctive rings of coral reef called atolls (see "Atolls," in 14.2, Kinds of Coral Reefs). He used nets to capture the tiny, drifting organisms known as plankton, which marine biologists still 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 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; upon his return he was court-martialed for flogging his crew to excess. Only two of the expedition's six ships made it home. Nevertheless, the Wilkes Expedition's achievements are 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 mid-nineteenth century, a few lucky scientists were able to make 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 age 39, but was the most influential marine biologist of his day. He discovered many previously unknown organisms and recognized that sea-floor 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 life on 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

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.

©Michael Nolan/Robert Harding Images

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.

short, but their studies produced many valuable 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.*

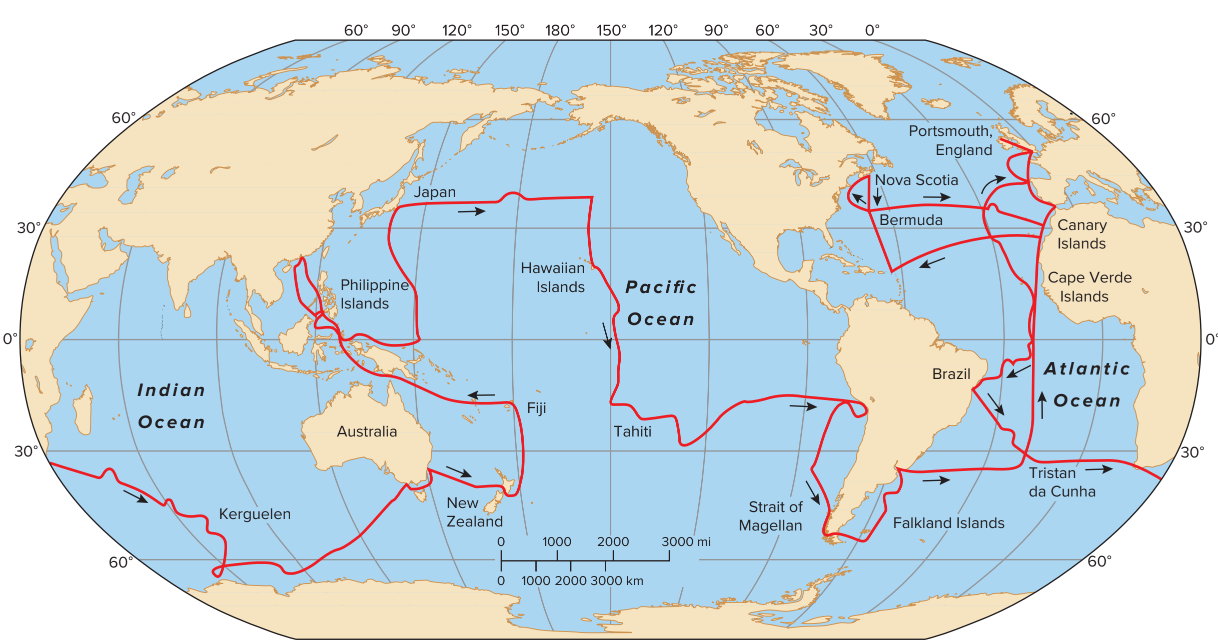
Challenger underwent extensive renovations in preparation for the voyage. Laboratories and quarters for the scientific crew were added, and gear for collecting samples in deep water was installed. Though primitive by modern standards, the scientific equipment on board was the best of its day. Finally, 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 marine science.

The Growth of Marine Labs Even before *Challenger* set off, biologists were excited about the organisms brought back by ocean expeditions. Unfortunately, the ships had quarters for only a few scientists. Most biologists only got to see the preserved specimens the ships brought back to port. Such specimens revealed much about



Source: Bill Ober

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

marine life around the world, but biologists wanted to know how the organisms actually lived: what they did and how they functioned. 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.

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 *Challenger* embarked. The laboratory of the Marine Biological Society of the United Kingdom was founded at Plymouth, England, in 1879.

Courtesy of the Stanford University Archives

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.

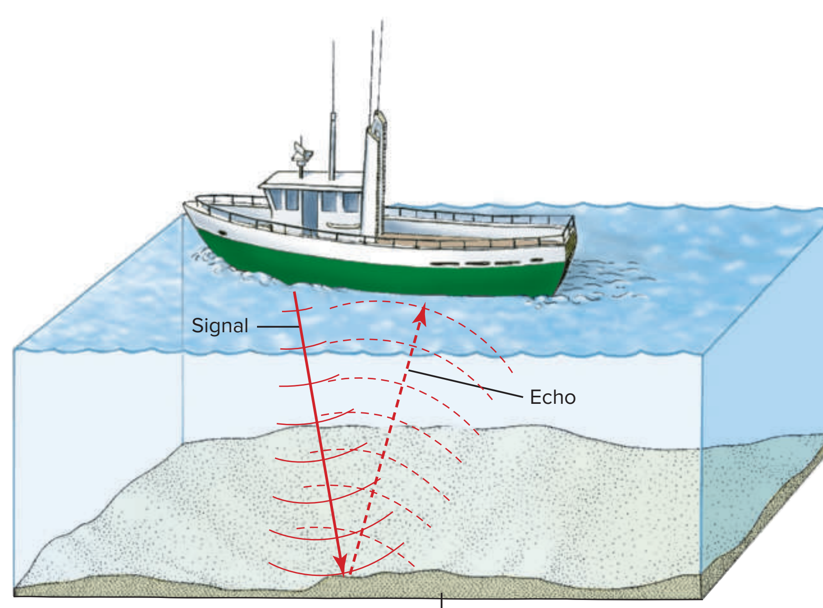
The first major American marine laboratory was the Marine Biological Laboratory at Woods Hole, Massachusetts. It is hard to pinpoint the exact date when this laboratory was established. The first marine laboratory at Woods Hole was started by the United States Fish Commission in 1871, but it did not 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 Hopkins Marine Station in Pacific Grove, California (Fig. 1.6), Scripps Institution of Oceanography in La Jolla, California, and 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.

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 because of the importance of submarine warfare. Sonar is based on detecting underwater echoes (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), grew rapidly. 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 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, go under water for more than a few minutes at a time to observe marine



Source: Bill Ober

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

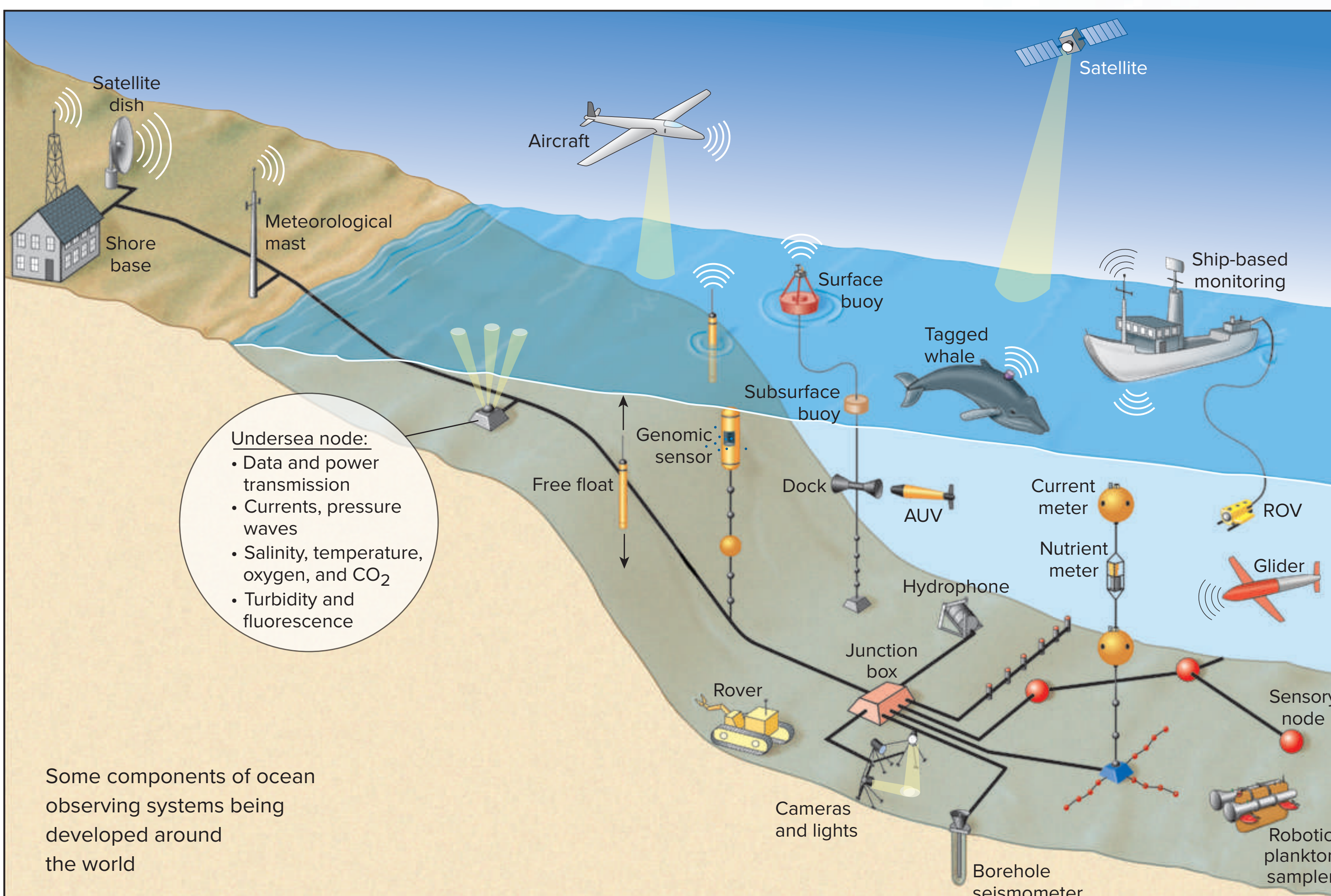
Most of the ocean is incredibly remote, and difficult and expensive to get to. The ocean is also a vast, interconnected network, and conditions at one place are affected by events far away. To cap things off, events such as storms and earthquakes—not to mention the interactions and movements of marine 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, some 3,800 automated floats, looking a bit like torpedoes turned on end, drift throughout the ocean. Each float continuously bobs between the surface and a depth of 2,000 m (6,600 ft), over about 10 days, measuring water temperature, salinity, and in some cases other ocean properties. When they surface, the floats transmit via satellite their location as well as the data, so currents can also be measured from the floats' movements. Argo floats provide huge amounts of information at the scale of the entire global ocean. Robotic gliders cruise across the oceans for years at a time, like Argo floats, collecting data and surfacing to relay the data by satellite.

©Dan Costa, University of California, Santa Cruz

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

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 sea-floor tremors, and track biological activity. The first such system in the United States was the Long-term



Some components of ocean observing systems being developed around the world

Source: Bill Ober

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 Victoria Experimental Network Under the Sea (VENUS) has been operational since 2006. The North East Pacific Time-integrated Undersea Networked Experiments (NEPTUNE) Observatory, which extends off the coast from British Columbia to Oregon, has operated since 2008. The Monterey Accelerated Research System (MARS) has also operated since 2008, off the coast of northern California. Science and Technology University Research Network (SATURN) Collaboratory (for some reason marine scientists on the west coast of North America like to name their networks after planets) was established to measure interactions between the Columbia River in the Pacific northwest and the coastal ocean. The Ocean Observatories Initiative (OOI) has instrument arrays at locations around the Americas, from Antarctica to the North Pacific and Atlantic oceans. Similar networks have been developed in Europe, Japan, the Gulf of Mexico, and the Arctic Ocean. These observation networks are being integrated into a single Global Ocean Observing System (GOOS).

Many exciting devices have been developed for these networks, such as genomic sensors that identify plankton DNA and measure toxins, and free-ranging autonomous underwater vehicles (AUVs) that move across the seabed or in the water making measurements and collecting samples. The observation networks include docking stations for AUVs to recharge batteries and upload data.

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 once said, "We're learning a lot, which is another way of saying that things are breaking." But more and more the networks are reliably collecting data and transmitting photos, audio, and video that are freely available online, often in real time. An Internet search can take you to some amazing places in the ocean depths.

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 can use 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 determine the time of death of human bodies recovered from the sea.

Not all ocean observing systems are inanimate—marine animals are being recruited. Seals, sea lions, sharks, and other large marine animals move underwater faster than we can ever hope 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, penguins, and other marine animals. 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 currents, as the animals can go places scientists can't access otherwise.

Ocean observing systems aren't just for science. They bring concrete benefits to society. They help track storms, warn of tsunamis, (see Box 3.3, "Waves That Kill") 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.

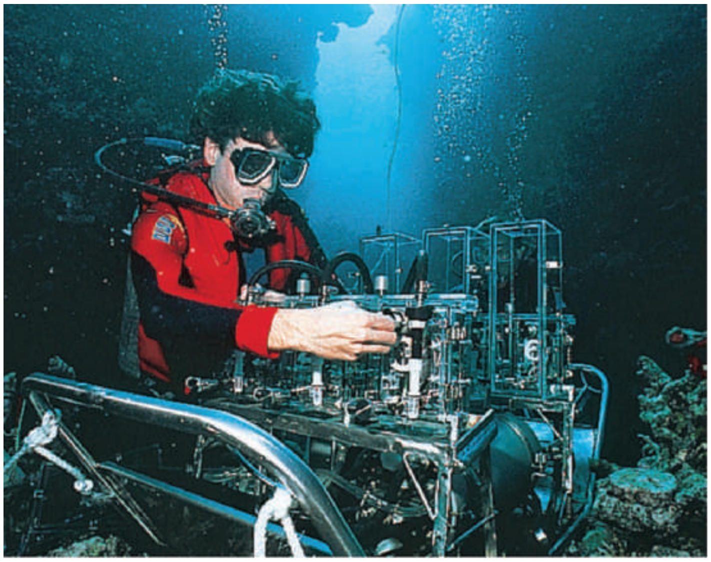
organisms in their natural environment (Fig. 1.8). They could work comfortably in the ocean, collecting specimens and performing experiments, though still limited to relatively shallow water, generally less than 50 m (165 ft).

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 technology for navigation, sampling, and studying marine life. Many, like *Challenger*, were originally built for other uses, but more and more research vessels are purpose-built for marine science.

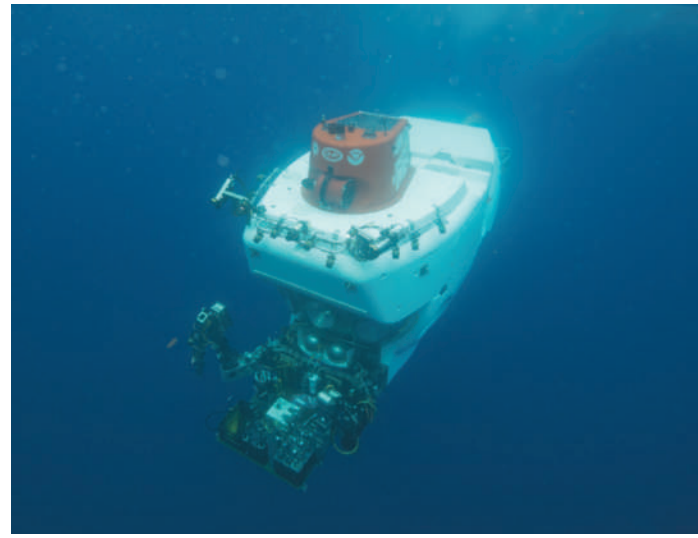
In addition to ships as we normally think of them, some remarkable craft are used to study the marine world. High-tech submarines descend to the deepest parts of the ocean, revealing a once-inaccessible world (Fig. 1.10). Various odd-looking vessels ply the oceans, providing specialized research platforms (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 "bed, breakfast, and boats" in remote locations. Often the scientists even have to bring their own breakfasts! There are undersea habitats where scientists can live for weeks at a time, literally immersed in their work (Fig. 1.12). Marine labs are important not only for research but also for education. Many offer hands-on



Courtesy of Australian Institute of Marine Science; http://www.aims.gov.au/docs/cc-attribution.html

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



©Woods Hole Oceanographic Institution

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.

undergraduate courses for students to study marine biology first-hand, and most provide facilities where graduate students begin their careers in marine science.

We all know technology is exploding. Even today's elementary school students have lived through major changes that have affected all of society—our personal lives, business, even politics. Needless to say, technology has and continues to transform marine science. Satellites peer down at the ocean and this **remote sensing** technology has revealed much of what we know about large-scale features like ocean currents and the geographic distribution of marine life (Fig. 1.13). Satellites only see the surface of the ocean, however, and a lot of the action is a long way down. Submarines are one way to penetrate the depths, but scientists increasingly use underwater robots, including remotely operated vehicles (ROVs), which are controlled from the surface, and autonomous underwater vehicles (AUVs; see Fig. 16.23), which operate independently of direct human control. Marine scientists continue to develop 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 use every available tool to study 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, though, and the oceans remain a realm of mystery and excitement.

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 that offer more work space and can travel to research sites faster and stay there longer than earlier research ships.

©Robert Hinton, University of Washington

1.2 THE SCIENTIFIC METHOD

Marine biology is an adventure, for sure, but it is still 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.

We live in an age of science. Advertisers boast of "scientific" improvements to their products. News sites regularly report new breakthroughs, and many media outlets have dedicated science reporters. Governments and private companies spend billions of dollars a year on scientific research and education. Why does science have 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, industry, 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 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 explaining 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. Science is based on observations, and not on preexisting ideas of how the world is or should be.

Relying on observations means that others can verify the observations. A person's thoughts, feelings, and beliefs are internal. No one has access to the minds of others. On the other hand, the world studied by scientists is external to any one person. Different people can look at the same object. Sensory perception may be

©Scripps Institution of Oceanography, UC San Diego

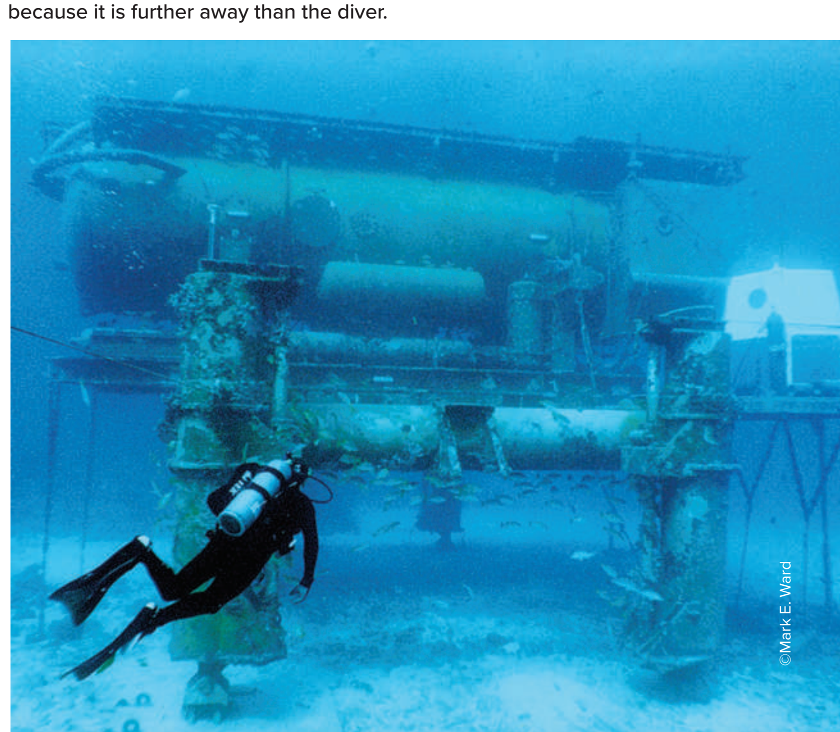
(a)

©Scripps Institution of Oceanography, UC San Diego

(b)

FIGURE 1.11 R/V *FLIP*, short for *f*loating *i*nstrument *p*latform, 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.

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.



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