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Twelfth Edition

Marine Biology

Peter Castro
Michael Huber

The cover features a photograph of two orcas swimming in the ocean. In the background, a large, white iceberg is visible. The sky is a clear, light blue. The orcas are dark with white patches on their heads. The water is a deep blue with some ripples.

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Marine

Twelfth Edition

Biology

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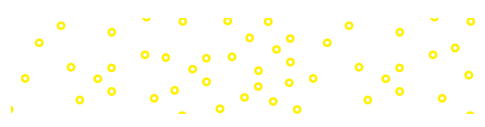
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MARINE BIOLOGY

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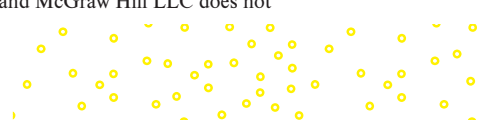
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Dedication

To all future marine biologists

—Peter Castro—

To Mason and Erin

—Michael Huber—

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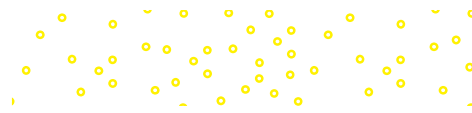
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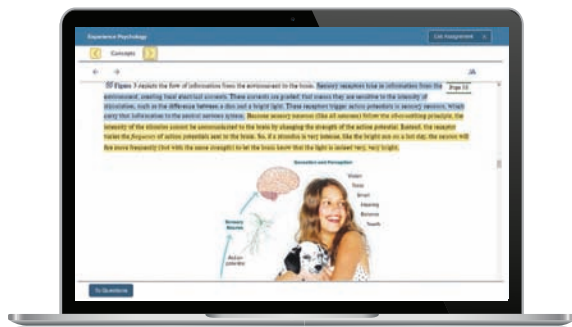
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- Jordan Cunningham,
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About the Authors



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 Hawai'i 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. Dr. Castro has so far published 70 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 2. 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. After his Ph.D., he worked at Scripps on 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 much of his work has been in the Asia-Pacific region. He has worked on a wide range of environmental issues including pollution control and waste management, underwater noise, habitat conservation and restoration, marine invasive species, endangered species management, long-term environmental monitoring, effects of mariculture, and deep-sea mining. Dr. Huber is a past Chairman of GESAMP, a United Nations scientific body that advises international agencies on marine environmental issues. Currently, he is helping coordinate GESAMP's role in the United Nations of Ocean Science for Sustainable Development. Mike has worked in more than 40 countries.

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

Preface

We are absolutely delighted to introduce *Marine Biology, twelfth edition*. When we first start working on the very first edition back in 1988, our focus was on getting through that task—and the book on shelves somewhere—and never dreamed we would find ourselves introducing a twelfth edition. We are profoundly grateful to the many instructors, reviewers, and most of all students who have carried us to this point.

Whether their interest originated from visiting the shore, scuba diving, recreational fishing, sailing, aquarium keeping, viewing television documentaries and movies, or just dreaming about the ocean, we hope this book reinforces, enhances, and informs the fascination of readers all over the world with the ocean. And, of course, we have tried in *Marine Biology* to provide 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 translated into six other languages. While keeping this range of users in mind, we have written the text primarily for 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 a focus on the organisms themselves, and

their vast diversity not only in taxonomic terms but also in structure, function, and ecology. The 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, twelfth 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 TWELFTH EDITION

Like all new editions of *Marine Biology*, we have made extensive revisions to the twelfth edition to correct errors, incorporate new information, and improve readability. In many cases, our revisions reflect comments by reviewers, whose suggestions we greatly appreciate. Unfortunately, perhaps the dominant theme of this revision reflects the inescapable reality of the existential threat of climate change to both the health of the ocean and human society. Even in the last edition, our coverage of global climate change reflected some scientific uncertainty, and tended to point to impacts in the future. Since then, the uncertainty has vanished and it is clear that climate change is happening *now*, at a faster rate and with more dire consequences than we thought. Other aspects of global change have also become more urgent. We have reflected this throughout our revision, in every chapter, to reflect that negative global change is not something that *might* happen, *in future decades*, but is happening now and urgently needs to be addressed to avert catastrophe. This theme carries into the other aspects of global change described in *Special Report: Our Changing Planet*.

Aspects of this overarching theme included in the revision include:

- A new Box 1.1 on the 2019–2020 *Polarstern* expedition to study changes in Arctic Sea ice
- A new section in Chapter 6 on the economic importance of seagrass, saltmarsh, and mangrove communities

- A new Box 10.3 on carbon sinks and blue carbon, introducing both terms and including two new figures, and further discussion of blue carbon sinks in other relevant sections throughout the book
- The addition in Chapter 14 of a new section on Human Impact on Coral Reefs, consolidating and updating coverage that was previously spread across multiple chapters
- New coverage of illegal, unreported, unregulated fishing in Chapter 17

There are many other changes, throughout the book, that update information on the health of the oceans.

Of course, as in every edition, we have updated the information in the book to reflect new research and recent data, to incorporate suggestions from reviewers, and especially to make the book more user-friendly. There are too many changes to fully list here, but examples include:

- Significant revision of the line art in every chapter to improve accessibility for readers with visual challenges
- Line art in many chapters was updated to include the latest available data
- Significant revision of the explanation of the Coriolis Effect—something we have always struggled to explain on the written page. We hope this time we made it better.
- A new Figure 3.36 showing part of an actual tide table
- New coverage of the importance non-coding (“junk”) DNA and epigenetic markers, including their heritability
- Added information on the importance of glycoproteins
- Updated coverage of the shortcomings of the traditional “biological species concept,” especially in light of prokaryote reproduction, horizontal gene transfer, and hybridization
- New Box 5.1 on the origins of eukaryotes
- New Figure 6.13 comparing marine seaweeds and flowering plants
- New Box 7.3 on mantis shrimp eyes
- Information on “predator fear” effects—ecological effects of predator avoidance by prey species
- Updated examples of transplantation, caging, and removal experiments in marine ecology
- New Figure 17.13 comparing marine and freshwater capture fisheries with aquaculture production

As in every revision, there are many smaller changes throughout the book to include corrections, updates, and clarifications. We have also included a number of new photographs, in our continuing effort to make the book more visually appealing.

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 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.

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The following people reviewed the eleventh edition and have provided valuable comments and suggestions for preparing the twelfth edition:

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Part One Principles of Marine Science



CHAPTER

The Science of Marine Biology



Kilili Yuyan

Researchers from the tribally managed Alutiiq Pride Marine Institute in Alaska collect clams, an important food for local indigenous people, to test for harmful toxins.

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 sea life often attract students to marine biology courses. This same sense of adventure and wonder is what leads marine biologists to their profession.

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 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 is vital to 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, and some marine organisms even help create new land. In economic terms, the ocean's living systems are worth *trillions* of dollars every 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. 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.

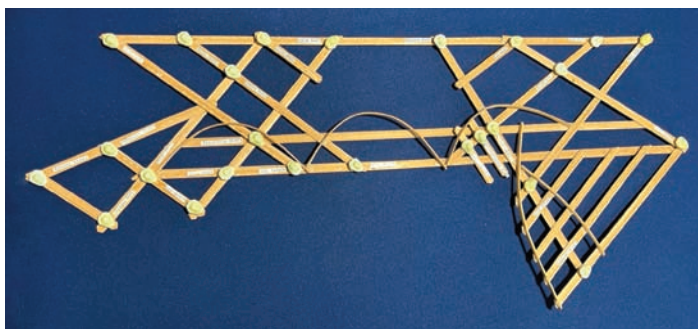
Marine biology is closely related to oceanography, the scientific study of the oceans. Like marine biology, oceanography has many branches. Geological oceanographers, or marine geologists, study the sea floor. Chemical oceanographers study ocean chemistry, and physical oceanographers study waves, tides, 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 most marine scientists don't worry about the difference.

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 was 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 clam-bakes 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. There is evidence that even more ancient peoples voyaged across the sea.

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



Michael E. Huber

FIGURE 1.1 A stick chart of the Marshall Islands, in the Western Pacific Ocean. The shells represent island groups, and the sticks represent prevailing wind and wave patterns. Pacific Islanders navigated over vast distances between tiny islands using such charts.

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.

The Phoenicians were the first accomplished Western navigators. By 2000 BCE (Before Common Era, that is, before 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. The Greek philosopher Aristotle is often considered 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 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 (Fig. 1.2). 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

FIGURE 1.2 Viking explorers reached North America in ships like this reconstruction, *Sea Stallion*, centuries before Columbus.



PA Images/Alamy Stock Photo

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 and his crew were the first Europeans 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 new lands previously unimagined by Europeans. Cook was generally respectful and appreciative of indigenous cultures by the standards of the day, but not always. He was killed in 1779 in a fight after a dispute with native Hawaiians at Kealahou 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, also from England. 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). 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). 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, crustaceans that attach to surfaces (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 1838–42, often

called the "Wilkes Expedition" after its leader, Lt. Charles Wilkes of the U.S. Navy. The expedition included 11 naturalists and scientific illustrators. Wilkes was by all accounts a vain and cruel man who promoted himself to Captain as soon as he left port and was later 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 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.

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 E. Huber



robertharding/Alamy Stock Photo

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.

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.

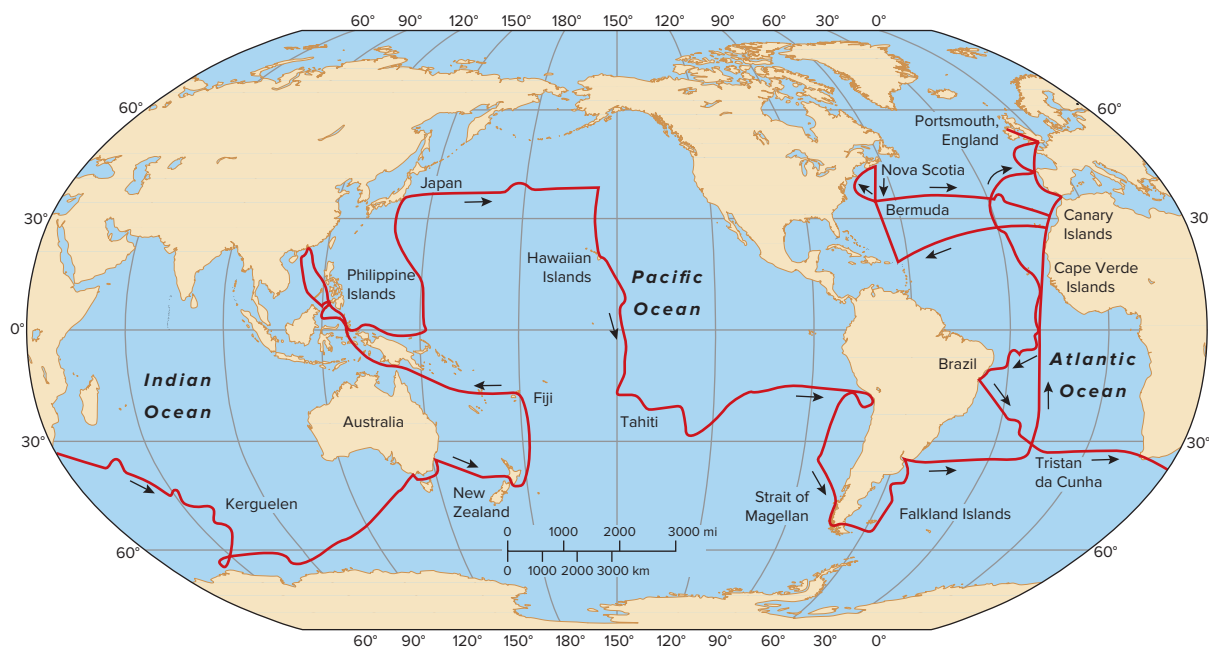
It was not just the duration of the voyage or the amount of information collected that set the *Challenger* expedition apart

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 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 French biologists, Henri Milne



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.

Edwards and Victor Andouin, who around 1826 began making regular visits to the shore to study marine life. Others 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.

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 didn't flourish. Several other short-lived laboratories later 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 lab 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. 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 *sound navigation and ranging*, was developed for 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 self-contained *underwater breathing apparatus*. 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.



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.

Using scuba, marine biologists could, for the first time, go under water for more than a few minutes at a time to observe marine 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).

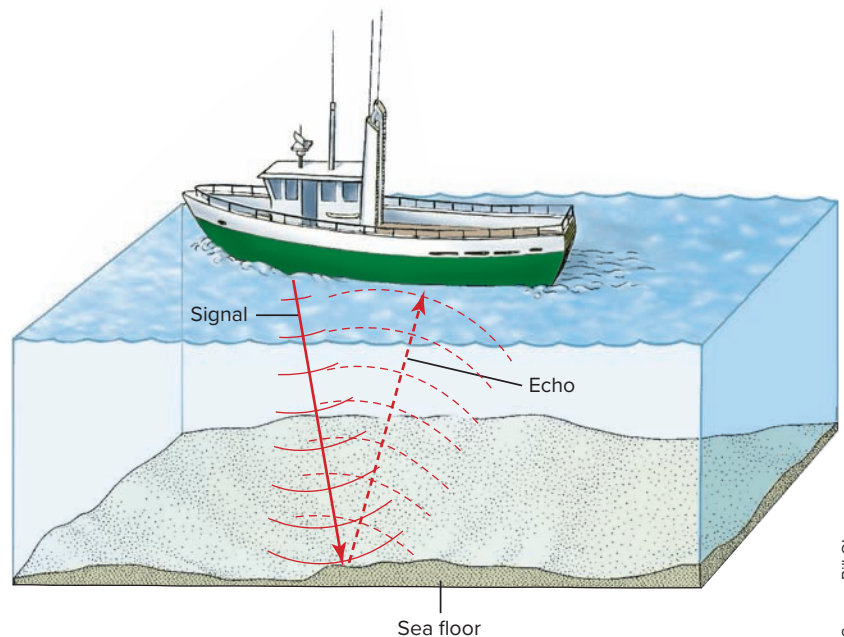
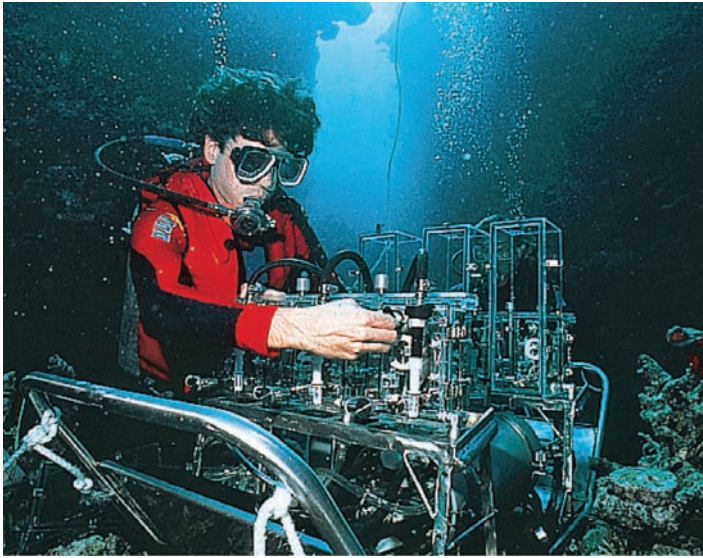


FIGURE 1.7 A ship uses sonar by “pinging,” or emitting a loud pulse of sound, and timing how long it takes the echo to return from the sea floor. The water depth can be determined from the return time. This, the most common form of sonar, is called “active sonar” because the sounds used are actively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



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.

Marine Biology Today

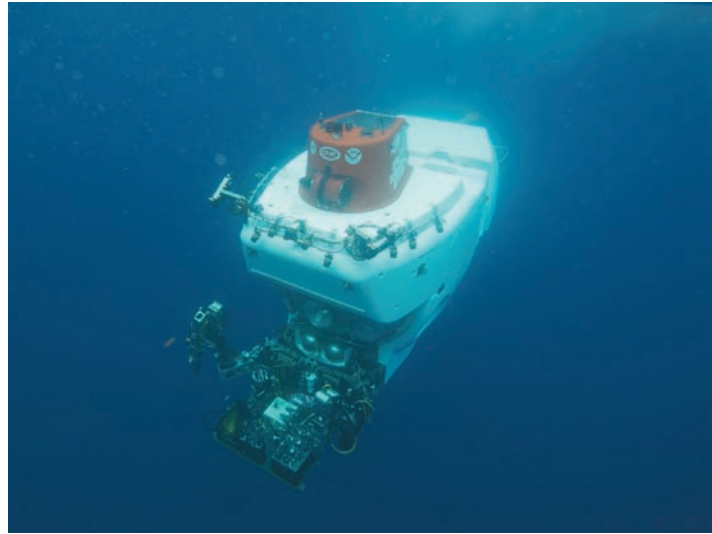
Oceanographic ships and shore-based laboratories are as important to marine biology now as ever. Today many universities and other institutions operate research vessels (Fig. 1.9). Modern ships are equipped with the latest technology for navigation, sampling, and studying marine life. Many, like *Challenger*, 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

FIGURE 1.9 The R/V *Thomas G. Thompson*, operated by the University of Washington, was the first of a new generation of dedicated 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



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.

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 undergraduate courses for students to study marine biology firsthand, 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



EYE ON SCIENCE

Box 1.1 The Best Laid Plans

The plan was audacious. For millennia, mariners venturing into polar waters feared being trapped in the ice, starving while their vessels were crushed by massive icebergs. But one group of researchers decided to deliberately wedge their research vessel, *RV Polarstern* in the Arctic ice and spend a year drifting with the floating icepack. The Arctic is warming much faster than the rest of our planet (see Special Report, Climate Change), and scientists are desperate to better understand the implications. An entire year of measurements and experiments would vastly improve our knowledge.

Over 10 years of careful planning and preparation—not to mention fundraising—went into the expedition, the Multidisciplinary Drifting Observatory for the Study of Arctic Climate (MOSAiC), the largest Arctic research expedition ever. But things don't always go according to plan. *Polarstern*, a converted icebreaker that can withstand the tremendous pressure of the ice, sailed from Norway in September 2019. A few weeks later, she was wedged in the ice and the scientists got to work.

To prevent their measurements from being effected by the operations of the ship itself, they set up much of the equipment on the surrounding ice up to 50 km (30 mi) away, getting around with snowmobiles and helicopters. As Arctic winter set in, the researchers had to learn to cope with constant darkness and temperatures down to -50°C (-60°F). They weren't expecting to encounter polar bears within days of their arrival, and scientists had to take turns away from their studies to stand watch. The bears also had an irritating habit of chewing the power and communication cables linking the various instruments. Despite their planning,

animals (see “Observing the Ocean,” below). 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), and information about the ocean pours in at an ever-increasing pace.

The Census of Marine Life With all of these advances, marine biologists are equaling if not surpassing milestones from past centuries such as the *Challenger* expedition. Despite the achieve-



MOSAiC researchers drill through the ice.

dpa picture alliance archive/Alamy Stock Photo

severe storms sometimes disrupted their instruments. But overall the expedition was going more or less as planned, and data on the Arctic air, ice and water, and the things living in them, started flooding in.

Then the world changed. When the coronavirus hit, hundreds of scientists scheduled to rotate for a stint on *Polarstern* were faced with cancelled flights, travel restrictions, quarantine, expired visas, and closed borders. And the prospect of an outbreak onboard ship, in the remote Arctic, was unthinkable. It became essentially impossible to conduct resupply and crew swaps by air as planned. As the expedition's logistics coordinator said “there you have a plan B, C, D, and X, and then a virus like this comes along and just thwarts all the plans.”

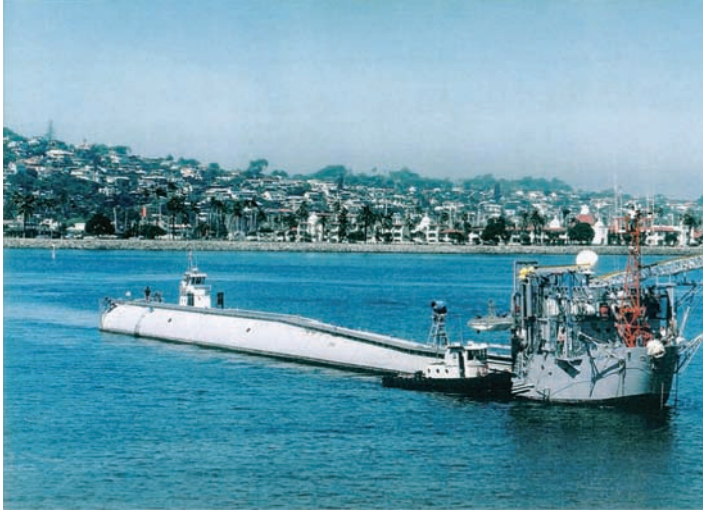
The project leaders were forced into the difficult decision to break free of the ice and head to the edge of the ice pack, where crew swap and resupply could be done by ships lacking *Polarstern's* icebreaking capability. They left much of the research facility on the ice, hoping to return as soon as possible

but not knowing for sure when. New logistics plans and coronavirus procedures were frantically developed. Other oceanographic expeditions were cancelled due to coronavirus, but almost miraculously *Polarstern* was able to return to its base camp after only two weeks! In the end, the expedition spent over a year in the ice pack, moving from the constant darkness of winter to the unending days of summer, before returning to port in October 2020. In all, nearly 500 scientists from 20 countries participated.

Unfortunately, MOSAiC brought bad news. Results show that Arctic ice is thinning faster, and more ice is lost in summer, than was expected. Researchers were surprised to see fishes from the North Atlantic, indicating that marine species are moving northward as their normal home waters warm. Such rapid changes in the Arctic are a worrying harbinger of what is in store for the rest of our planet.

For more information, explore the links provided in the *Marine Biology Online Learning Center*.

ments of the past, at the turn of the twenty-first century less than 1% of the oceans had been explored, and we had probably discovered an even smaller fraction of marine species. We knew hardly anything about most species that had been discovered. To make a dent in this ignorance, marine scientists launched the 10-year Census of Marine Life (COML) in the year 2000. COML was a massive undertaking, involving some 2,700 scientists, at nearly 700 institutions in 81 countries. It included some 24 projects focused on a particular region, a specific group of organisms, or individual ecosystem types. The individual scientists and research groups involved



(a)

Scripps Institution of Oceanography, UC San Diego



(b)

Scripps Institution of Oceanography, UC San Diego

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.

would have done their research anyway, but through networking, data sharing, and cooperation, their work was greatly magnified.

COML found an amazing amount of undiscovered marine biodiversity, discovering nearly two new species a day. Genetic studies, analysis of historical records and other investigations established that past populations of some species exploited by humans (for example, some whales and fishes) were much larger before exploitation than previously thought, and that they declined earlier. For example, fishing reduced the Nova Scotian cod population by 96% as early as 1850. This established new understanding of what constitutes “healthy” baseline populations. From a global decline in phytoplankton to evidence that most harvested fish species have become fewer and smaller, COML painted a picture of oceans even more profoundly affected by human activities than we thought. But COML also documented that populations can recover with sound conservation measures.

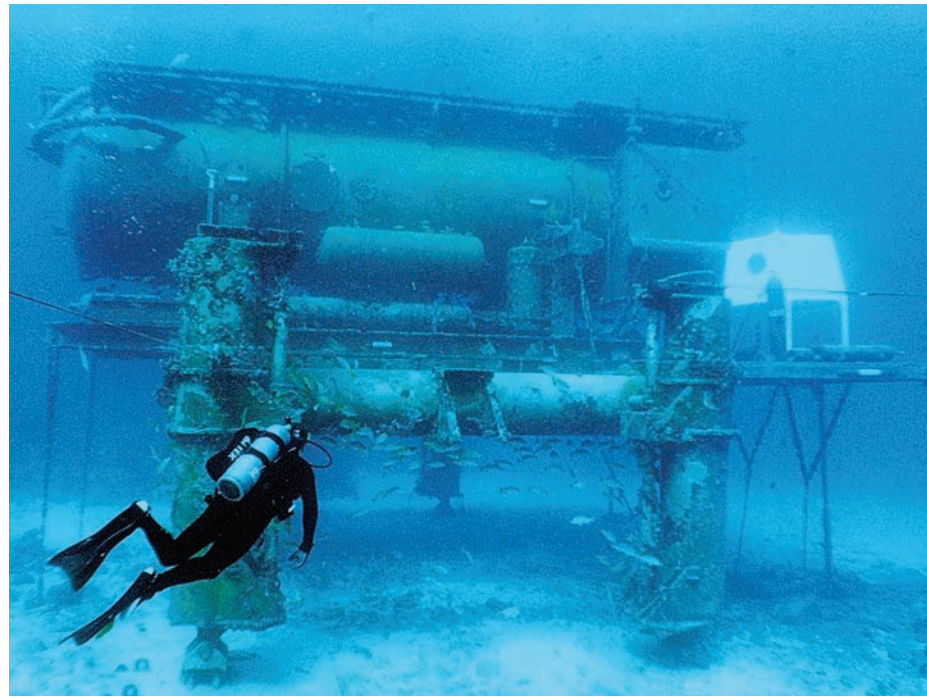
COML officially ended in 2010 but created a lasting legacy. New technologies were developed, the networks for international cooperation continue, and data platforms that were created provide free access to data by not only scientists but also the general public. The Ocean Biogeographic Information System (OBIS) makes the vast amount of information COML collected about what species live where not only continues to operate but is growing. You can still follow online the movements of tagged sharks, seals, and sea turtles on systems developed by COML. Some COML results are even on Google Earth.

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.

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.

Mark E. Ward



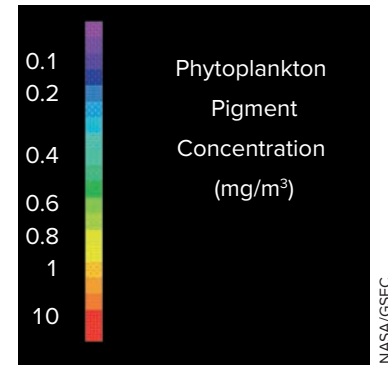
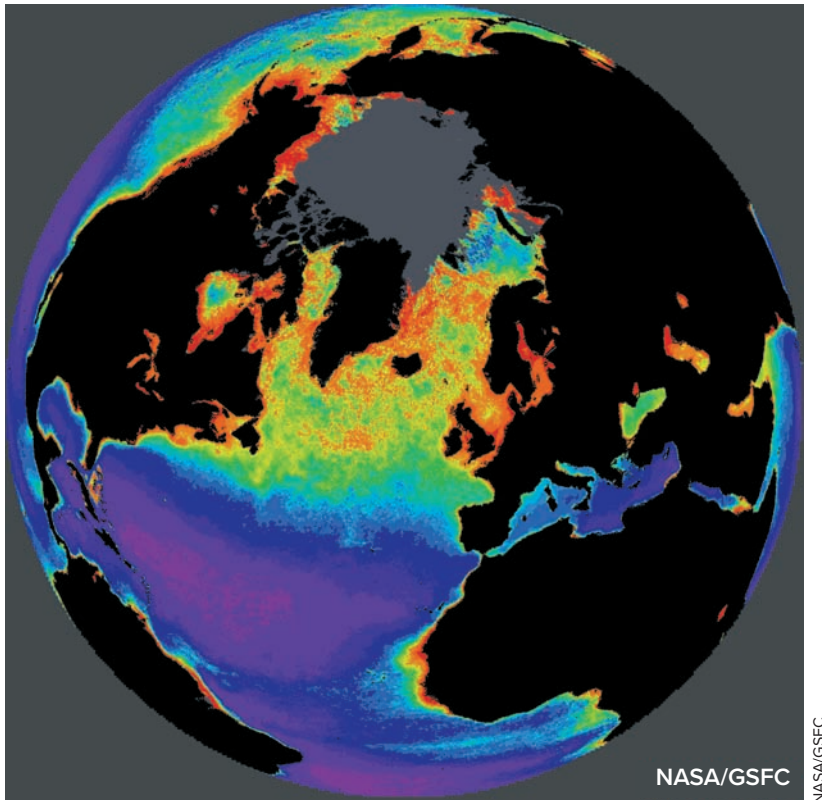


FIGURE 1.13 A satellite image showing the abundance of photosynthetic organisms in the ocean, as indicated by the amount of pigment in the water. This photo was taken by the Coastal Zone Color Scanner (CZCS), which was mounted on the *Nimbus-7* satellite. It is actually a composite of information gathered over nearly an eight-year period. Advances in computer and space technology made this image possible.

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

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 may disagree over the fine points of the scientific method and may apply the method in slightly different ways. In

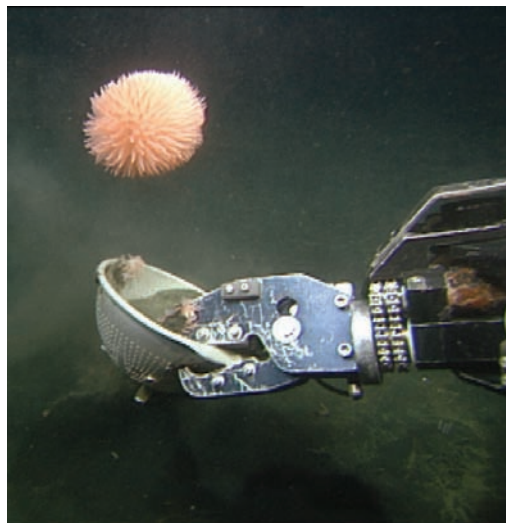


FIGURE 1.14 High-tech meets low-tech: The robotic arm of the ROV *Ventana* captures a pom-pom anemone (*Liponema brevicornis*) in an ordinary kitchen colander.

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 imperfect, and scientists, like anyone else, are not always impartial, but the object is there for all to see and measure. Thus, there is a way to check and validate any one person’s observations.

Observation is critical to all phases of the scientific method. To begin with, it allows us to describe the natural world. The only way to learn what organisms live in a particular part of the ocean, how many of them there are, how fast and how large they grow, when