



Sounding the Deep

Marine Biology as a Discipline

On every coast of the world, scientists work in field locations and in marine stations ranging from multimillion-dollar structures to small shacks with fanciful paintings of lobsters and crabs above the door. Some put out to sea in large ships, whereas others scarcely wet their knees (Figure 1.1).

The purpose of this textbook is to give you an organized way of turning a fascination for the sea into an appreciation of the principles of marine biology that reflect the function and ecology of marine life. Snorkel on a coral reef and you will see coexisting schools of large numbers of species of fishes. But why do so many species coexist in a very limited space? How do all these creatures interact to form the seascape? Such questions require an organized approach to a complex and somewhat foreign world. By the time you have finished your course and this textbook, you will be more familiar with that world. You will also be familiar with many human activities that put this world in peril, which makes an understanding of marine biology extremely important.

■ Marine biology is a subject mixing functional biology and ecology.

Marine biology is a diverse subject, but its main elements are functional biology and ecology. **Functional biology** is the study of how an organism carries out basic functions such as reproduction, locomotion, feeding, and the cellular and biochemical processes related to digestion, respiration, and other aspects of metabolism. Problems relating to function are quite varied. They might deal with questions such as: When a whale dives for food to very great

depths, how does it conserve oxygen? **Ecology**, on the other hand, is the study of the interaction of organisms with their physical and biological environments and how these interactions determine the distribution and abundance of the organisms. For example, why do so many species requiring limited space coexist on a coral reef? Why doesn't one superior species win out and displace the others?

Because ecology is an environmental subject, the field of marine biology must cover the **basic aspects of marine**



FIG. 1.1 A fascination with marine creatures led the late Howard Sanders first to make major contributions to our understanding of the ecology of intertidal and shallow marine bottom communities. Later, he pioneered American research in the deep sea, discovered marine animals previously unknown to science, and unlocked the secret of the deep-sea bottom's great biodiversity. (Photograph courtesy of the Woods Hole Oceanographic Institution)

habitats. We shall therefore spend considerable space explaining the various seascapes that are important to marine life.

■ **Biodiversity is the third major factor in marine biological studies.**

Marine environments can be very rich in species but vary tremendously in the number of species, or **biodiversity**. Coral reefs may contain thousands of species, but a rocky shore in high latitudes may contain fewer than 50. How do species arise? Why is there variation in species numbers from habitat to habitat and from time to time within a given locality? What is the consequence of living in a very diverse community? How can so many different species make a living in a coral reef? Functional biology, ecology, and biodiversity, as you will see, are very interactive components.

Historical Background of Marine Biology

■ **Marine biology began with simple observations of the distribution and variety of marine life.**

A native lore of the biology of the sea has accumulated over thousands of years by those living near the shore and by fishing peoples. The earliest formal studies in marine biology date back to a time when there was little distinction among scientific specialties. Early biologists were “natural philosophers” who made general observations about anatomy and life habits. We owe the beginning of this tradition of natural philosophy to Aristotle (384–327 B.C.) and his Greek contemporaries, who recorded their observations on the distribution and habits of shore life. Aristotle described the anatomy of the octopus and other marine creatures, noticed that some sharks give birth to live young, and observed that some whales have structures that resemble hog bristles instead of teeth.

The next major steps forward took place in the eighteenth century, when a number of Europeans began to observe and classify living creatures. Most prominent among these was Linnaeus (1707–1778), who developed the modern means of naming species. He described hundreds of marine animal and plant species and developed larger-scale classifications. The great French biologist Georges Cuvier (1769–1832) classified all animals into four major classes of body plans: Articulata, Radiata, Vertebrata, and Mollusca.

The eighteenth century was an important era of oceanic exploration. A number of expeditions circumnavigated the globe, bringing glory to explorers and new Pacific territory to European nations. Many of these expeditions had scientific components as well, and scientific staff was charged with collecting terrestrial and marine plants and animals. The voyage of French captain Nicolas Thomas Baudin explored the tropical Pacific, and numerous marine mollusks were returned to France. Captain James Cook supervised the mapping of eastern Australia in 1770, and his scientific staff collected biological specimens all over the Pacific Ocean, which became the foundation of large collections in Great Britain.

Until the nineteenth century, most marine biology consisted of the description of anatomy and the naming and

classification of species. Little was known about function and ecology. The only knowledge of open-ocean life was confined to experience with animals that were fished or observed (or in the case of mermaids and sea monsters, imagined) in the open sea. By the early 1800s, however, the study of **natural philosophy** had become popular, and a number of brilliant individuals devoted their lives to studying the ocean and its denizens.

■ **In the nineteenth century, marine biology developed into a science involving ecology and hypothesis testing.**

Edward Forbes (1815–1854) of the Isle of Man was the first of the great English-speaking marine biologists. After failing at art and abandoning his medical school studies, he set out to sea and participated in a number of expeditions in which a bottom dredge was used to dig into the seabed and collect organisms. He was the naturalist on the *Beacon*, a ship that sailed on the Mediterranean Sea. Forbes found that the number of creatures decreased with increasing depth and then proposed what was probably the first marine biological **hypothesis**, or testable statement about the world of the sea: the **azoic theory**, which stated that no life existed on seafloors deeper than 300 fathoms (1,800 ft).

Forbes also discovered that different species live at different depths, and he proposed that the broader the depth zone of a species, the wider its geographic extent. Forbes opened up the ocean to scientific research and was appointed to the most prestigious post in natural philosophy of those times at the University of Edinburgh, Scotland. He published maps of geographic distributions of organisms along with a natural history of European seas. He inspired countless followers to an interest in natural science.

During this time, many great pioneers from a number of European countries joined Forbes. In 1850, Norwegian marine biologist Michael Sars disproved the azoic theory by collecting and describing 19 species that live deeper than 300 fathoms in Norwegian fjords. His work inspired a new interest in deep-sea biology. The first plankton net was used during this period, and crude submersibles were developed. Marine biology was on its way.

Although he is usually remembered for his theory of evolution by means of natural selection, Charles Darwin (1809–1881) is the other great English father of marine biology (**Figure 1.2**). As a young man, he worked as naturalist on the H.M.S. *Beagle*, which sailed around the world in the years 1831–1836. He later wrote *The Voyage of the Beagle*, one of the best-selling travel books of the nineteenth century. Darwin made extensive collections of marine animals and concentrated his own later efforts on the classification of barnacles.

While on the *Beagle*, Darwin (1842) formed a theory of the development of coral reefs. He pictured the growth of coral reefs as a balance between the growth of corals upward and the sinking of the seafloor. If Forbes’s azoic theory was the first important marine biology hypothesis, then Darwin’s coral reef theory was the second. This subsidence theory was published in Darwin’s first scientific book, and its brilliance was immediately recognized. Previously, most

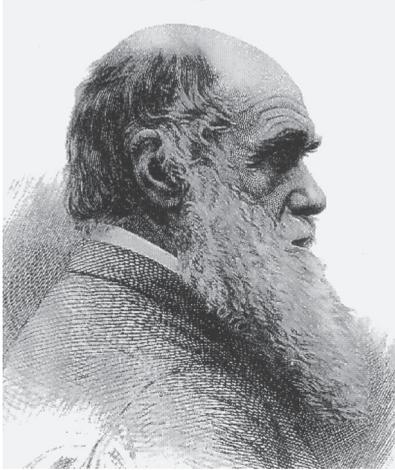


FIG. 1.2 Charles Darwin is best remembered for his theory of natural selection, but he made many important contributions to marine biology, including a book on coral reefs and a classification of barnacles that remains essentially unchanged to the present.

had believed that coral reefs in the open Pacific developed from the colonization and growth of corals on submerged extinct oceanic volcanoes. In contrast, Darwin argued that coral reefs developed around emergent rock that was slowly sinking, and this downward motion was balanced by upward growth of the corals. In this subsidence theory as applied to the development of atolls (horseshoe-shaped rings of coral islands), Darwin was proven correct. About 100 years after the theory was developed, scientists drilled a hole in Eniwetok Atoll in the Marshall Islands of the Pacific and bored through hundreds of meters of coral rock before hitting the volcanic rock basement below. Since reef corals can grow only in very shallow water, this finding proved that the reef had been growing upward for millions of years as the island was sinking. Darwin was not completely right about coral reefs, however, insofar as he theorized that all reefs in the world are stages of subsidence leading to atolls. This has proven to be wrong; many reefs are not subsiding, and atolls are special cases of reefs on volcanoes rising from oceanic crust (see Chapter 18).

Fisheries research began in earnest in the nineteenth century and became central in marine biological research. Such research was also the beginning of **applied marine biology** and was necessitated by a need to understand how to find and manage populations of fish. England was first at this activity in 1863. Many nations began research efforts later in the century (see Chapter 22). In the United States, the Fish Commission sought to relate characteristics of the oceanic environment to the life history of fishes. Marine ecology became synonymous with fisheries research, and Canada used a fisheries emphasis to develop distinguished laboratories on both the Atlantic and Pacific coasts.

W. B. Carpenter and C. Wyville Thomson led a major expedition in 1868–1869 that foreshadowed the later great *Challenger* expedition. Both had a passion for marine biology, and they convinced the British government to outfit the *Lightning*, a steam- and sail-powered ship that dredged the seabed of the northern waters of the British Isles. Like Norwegian biologist Michael Sars, they found marine life deeper than 300 fathoms and thus also helped disprove Edward Forbes's azoic theory. The deep maintained its allure to marine biologists, as it was thought to be a museum of living fossils because many animals such as stalked crinoids were found in ancient fossil deposits and in deep water in the living ocean as well. They also found distinct bodies of water with different temperatures, which was an early discovery of the distinctness of some oceanic water masses.

■ **The voyage around the world of the H.M.S. *Challenger* gave us the first global-scale view of marine biology.**

These expeditions set the stage for the great *Challenger* expedition (1872–1876) that circumnavigated the globe and provided the first global perspective on the ocean's biotic diversity (**Figure 1.3**). The voyage was led by C. Wyville Thomson and by the great naturalist John Murray. The *Challenger* sampled the waters and bottoms of all seas except the Arctic. After the expedition, 50 volumes were needed to describe the tremendous number of organisms that were recovered.

On this expedition, chemist John Buchanan was able to disprove the existence of a so-called primordial slime on the



FIG. 1.3 The H.M.S. *Challenger* at St. Paul's Rocks, a remote equatorial mid-Atlantic Island.

seafloor, called *Bathybius*, which was supposed to be capable of giving rise to higher forms of life. The famous zoologist Thomas H. Huxley had published a well-known paper claiming that a whitish material found in samples from the seabed was evidence of the presence of a material that was continuously giving rise to life forms. This idea was very controversial. Buchanan discovered that the slime, which had been observed in collected samples of seawater, was merely an artifact of preserving seawater with alcohol. The chemical reaction of seawater with alcohol resulted in a white precipitate, which Buchanan claimed was previously mistaken by Huxley to be the mysterious *Bathybius*. He therefore falsified a major claim about the continuing origin of life on the seafloor. This discovery fit well with Louis Pasteur's earlier conclusion from lab experiments that life did not just spring from inanimate substances. The explanation for the white slime named *Bathybius* still remains an open question.

Toward the end of the nineteenth century, marine stations began to spring up over the world, starting in 1875 with the Stazione Zoologica in Naples, Italy. This station set a pattern of international participation by the scientific community. In the 1880s, marine stations were established in England and Scotland. During the same years, Prince Albert I of Monaco outfitted several yachts and larger ships that sampled the ocean, and in 1906, he eventually founded an oceanography institute and museum in Monaco. This facility came to be directed by famous inventor-oceanographer Jacques-Yves Cousteau, who died in 1998. In America, zoologist Alexander Agassiz led oceanographic expeditions, was the first to use piano wire instead of rope to lower samplers, and studied the embryology of starfish and their relatives. The now-famous Marine Biological Laboratory was founded on Cape Cod in 1886, and a number of marine stations were founded in Europe toward the end of the century. By the turn of the twentieth century, marine stations existed in many European countries. Marine laboratories such as the Friday Harbor Laboratories in Washington State made their appearance in the United States soon thereafter (Figure 1.4). Marine biology was now a full-fledged science with a proud history of exploration and theorization.

■ **Advances in modern marine biology included the development of major research institutions, faster ships, better navigation, and greatly improved diving technology.**

The early part of the twentieth century witnessed the founding of great oceangoing institutes and a new technological ability to explore the ocean to its greatest depths. In America, the founding of the Scripps Institution of Oceanography in southern California (1903) and the Woods Hole Oceanographic Institution on Cape Cod (1930) gave the United States a unique ability to study the open sea. A large number of open-sea expeditions expanded our knowledge of marine life. The voyage of the Danish *Galathea* (1950–1952) was the last great deep-sea expedition of this era. As had happened in Europe toward the end of the nineteenth century, marine stations were opened in every coastal state in America. Marine biology also flourished in many universities. Our knowledge of the ocean expanded during World



FIG. 1.4 Friday Harbor Laboratories, located in the San Juan Islands of Washington State, are a major site for marine biological research and education in rocky-shore ecology, biomechanics, larval biology, neurobiology, and many other areas of study. (Photograph by Jeffrey Levinton)

War II owing to the need for more navigational information. Advances in navigation, deep-sea bottom drilling, remote sensing, and other techniques led to a great expansion of our knowledge of the sea. A rich diversity of open-ocean and shore biological research has since flourished to the point that scores of journals now record the activities of a community of thousands of scientists. The number of such scientists in 1850 could have fit comfortably within a single room.

■ **Technology in both the laboratory and the open sea has played an important role in the development of marine biology.**

Before the nineteenth century, poor navigation, inadequate sailing vessels, and generally crude bottom dredges and plankton nets prevented researchers from sampling the ocean systematically or completely. By the late 1800s, however, steam vessels allowed for the rapid lowering and raising of samplers, and navigation was better. In the twentieth century, modern diesel-driven ships such as the R.V. *Knorr*, ported in Woods Hole, Massachusetts, could navigate accurately by means of satellite navigation (Figure 1.5).

Before the mid-twentieth century, the deep-sea bottom could not be seen unless a piece of it was dredged and



FIG. 1.5 The R.V. *Knorr*, one of the U.S. oceanographic research fleet, has its home base at the Woods Hole Oceanographic Institution on Cape Cod, Massachusetts. (Photograph courtesy of Woods Hole Oceanographic Institution)



FIG. 1.6 The *Alvin*, a submarine capable of diving to 4,500 m, is equipped with accurate navigation and photography equipment and underwater manipulators. The *Alvin* is the great workhorse of the world research submarine fleet and is scheduled to be replaced in the coming years. (Photograph courtesy of Richard Lutz)

brought to the surface. This has changed dramatically owing to the development of manned submarines, remotely operated vehicles, and scuba diving. William Beebe pioneered deep diving when he descended in a metal sphere, the bathysphere, to a record depth of 923 m in 1934 off the Bermuda coast. In 1960, the spherical steel bathyscaph *Trieste* made a spectacular descent into the deepest oceanic trench off the Marianas Islands in the western Pacific Ocean. By the 1970s, a number of submarines routinely dived to depths of 2,000 m and more, and scientists were able to film and collect marine life (Figure 1.6). Mechanical arms made it possible to perform experiments, and accurate navigation systems permitted returns to remote sites in the ocean.

A number of smaller submarines allowed longer-term observation of depths of 300 m and less. One of the more

whimsical submersibles was used in a marine station near Nice, France. The steel hull was connected to the surface by an air hose, and the investigator sat inside on a bicycle seat in a very cramped space. The first recorded observations in the Bay of Villefranche included one of a soup can on the murky bottom. Recently, researchers have used more modern submarines in the same area to observe spectacular bioluminescent planktonic jellyfish. To expand greatly the efficiency of deep-sea observation, **remotely operated vehicles (ROVs)** have been developed. These vehicles are unmanned but can make precise surveys and even take samples (Figure 1.7). Remotely operating vehicles are tethered to a ship by a cable, but a great deal of data are now collected by **autonomous underwater vehicles (AUVs)**, which are robots not connected to the ship. An interesting variant



FIG. 1.7 The *Ventana*, an ROV operated by the Monterey Bay Aquarium Research Institute in central California. The vehicle is connected to the mother vessel by a cable and is equipped with high-definition video, two grabber arms, and a variety of samplers, including a sample box that can be seen in the front. Newer versions have been launched. (Photograph by Jeffrey Levinton)

of AUVs are **gliders**, which use simple balancing devices to allow the vehicle to rise and fall through the water column or be moved by vanes in a constant direction by wave action. Ensembles of gliders now are being used by various shore-based laboratories and are deployed from ships because they are much cheaper than ship-based sampling.

Nothing in shallow water, however, has matched the importance of scuba diving, developed in the 1940s. This form of underwater exploration was not used often or effectively until the late 1950s, when biologist Thomas Goreau pioneered the study of coral reefs. Today, direct observations and experiments can be done on rich shallow-water marine biota.

Although many advances have been made in diving and other technologies, the coming decades will see enormous strides toward **remote sensing** of the sea by satellite imaging. In the 1970s and 1980s, an American satellite known as the *Coastal Zone Color Scanner* provided images and conducted sophisticated light-based estimates of water temperature, chlorophyll, and other parameters. Now, new satellites are investigating with far more resolution. In conjunction with the new detectors, marine biologists are trying to use “ground-truthing” to produce equations that relate color information received by satellites to measurements taken at sea. In the long run, this will allow us to process worldwide data sets, a capability that is crucial in our current studies of global climate change.

The most recent advances in **ocean observatories** have taken advantage of Global Positioning System (GPS) located fiber-optic cable systems, with ports for remote video observation, sensing of physical variables such as temperature and current speed, and chemical measurements. This exciting new area is only now being developed and will

allow a series of permanent and continuous observation posts to be established within shore and estuary locales but also on the deep-sea floor and in midwater locations. Most exciting is the *Monterey Accelerated Research System* in Monterey Bay, California, where a submarine canyon (see Chapter 2) cuts the continental shelf and extends to the deep-sea floor (**Figure 1.8**). This cable has data-collection ports, including video, and allows scientists to continuously monitor and observe remote localities with Internet communication for research and education. The U.S. National Science Foundation has initiated a large-scale **Ocean Observatories Initiative**, which combines observations from moorings, autonomous vehicles, and underwater cabled observatories.

Observation and Hypothesis Testing

- **Marine biologists, like all scientists, use the scientific method, which is a systematic means of reasoning and observation.**

Marine biology, like all science, depends on a generalized system of observation and inference of the natural world known as the **scientific method**. This may sound unduly stiff and distant, but the scientific method is merely a systematic way to reason about and observe our world and universe. It depends on observations, deduction, and prediction. We are constantly making observations about the natural world, and many of these are repeatable. For example, we might find that all fish we observe live only in water (most do!). This would lead to a conclusion about the biology of fishes: Fishes live in water.

The accumulation of specific observations to make a generalization is called **induction**. By contrast, we might take

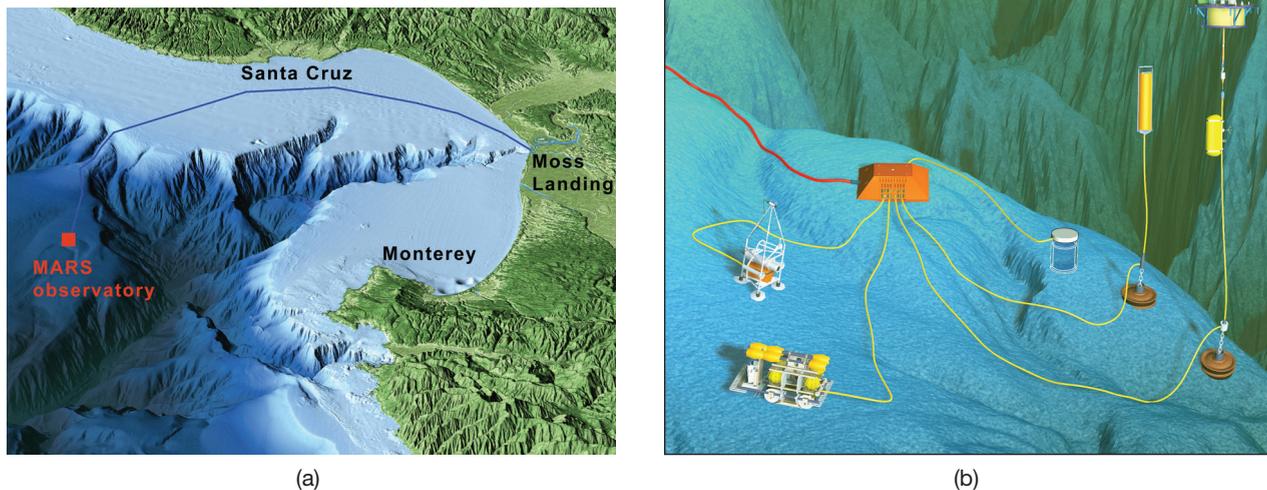


FIG. 1.8 Fiber-optic networks are being installed at many sites to create ocean observatories, which allow continuous monitoring of video, physical, and chemical variables. Here, we see the cable installation in Monterey Bay. (a) Map of cable installation in Monterey Bay, constructed by combining computer-generated topographic and bathymetric data to show the Monterey canyon; (b) deployment of instruments at the end of a 52-km-long fiber-optic cable. (Courtesy of David Fierstein and Monterey Aquarium Research Institute)

some premise and use logic to make a **prediction**. Such an inference, predicated on logical associations of conclusions with facts and premises, is a **deduction**. If you counted all the spectators in a football stadium drinking a beer, you might come to the conclusion that at 2 p.m. during the game, 10 percent of the spectators drink beer. That is an induction. Instead, you might reason that most spectators like beer, but all could not be drinking all the time because the lines at the beer concession are very long and only one beer is sold at a time. Therefore, you might deduce that only a fraction of the crowd will be drinking. If you knew the length of the game, how long it took to buy and drink a beer, how much blood alcohol it took to get drunk, and how fast alcohol is metabolized to non-inebriating products, you might be able to deduce how many spectators were holding a beer at any one time and how many are drunk. This line of reasoning is far more valuable because it has led you to develop a prediction that could be applied to other stadiums. Deduction has the beautiful property of prediction.

Here's a more biological example. We might find that there is genetic variation in a population and, knowing that the environment may change, we might predict that some variants will perform better and become more frequent in the population as the environment changes. If we know how genetic transmission works and the relative survival and reproduction rate of those variants, we can predict the rate at which they will increase in frequency in the population. This is Darwin's theory of natural selection, which uses the method of deduction. This form of inference always depends on general premises and a logical pattern of reasoning to draw some specific conclusion. Most scientists strive to develop generalizations and theories from which predictions follow by deduction. Perhaps it is worthwhile to count all the days of the year that are cloudy and then conclude that most of the year is cloudy, but it would be

much better to have a set of premises, a predictive relationship, and a theory to understand why it is cloudy most of the year. Induction, however, is a necessary part of science and can even be an inspiration for deduction.

■ **Most marine biological research requires extensive observations and correlations, but experimentation is usually the most efficient way to answer a question.**

Marine biological research involves a great deal of observation. In some cases, the observation is general and not directed toward any specific research problem. It is essential, for example, to know the distribution of temperature, salt content, water depth, and other properties of seawater because such information is required to solve a diverse array of specific problems. In other cases, observations are targeted toward more specific questions. To understand the migration route of a species of fish, it may be necessary to sample the ocean to detect tagged fish by remote signal or by catching fish directly at various times of the year and at various geographic locations and water depths.

In many instances, observations by themselves cannot solve a marine biological problem. One of the most common types of observation is a **correlation**, which is an observed relationship between one factor and another. You might discover an increase of fish abundance with increasing water depth. This would be a **positive correlation** between abundance and water depth because both variables change in the same direction. On the other hand, you might discover a **negative correlation**, which in this case would mean that fish abundance decreases with increasing depth: As one variable decreases, the other increases. In either case, however, finding such a correlation does *not* prove that depth specifically is the cause of changes in fish abundance. The negative correlation might be coincidental. A decrease of fish abundance with increasing depth might

be due to an increase of predator abundance with increasing depth. The next year, the number of predators might be in a different relationship (correlation) with depth. This underscores a familiar saying among scientists: “Correlation does not prove causality.”

■ **Experimentation is a much sharper and more powerful way of establishing cause.**

Suppose that, after finding a negative correlation between fish abundance and depth, you could perform an experiment and remove all the predators that are living in deeper water. If the prey fish then spread equally to all depths, you could reasonably conclude that the presence of predators, and not water depth itself, was the cause of the negative correlation. **Experimentation** is an important tool for both laboratory and field studies. Unfortunately, many marine problems cannot be approached by experimentation; often, organisms and environments cannot be studied except by observation. This is especially true when the spatial scale is so great that it is impractical to perform experiments. Try to imagine changing the circulation of an ocean experimentally to study nutrient transfer, and you’ll get the idea. It is possible, however, to formulate hypotheses that employ tests using distributional data.

■ **Marine biological research involves the testing of hypotheses and may involve experimentation or sampling.**

When solving problems in marine biology, additional observations beyond a certain point are not necessarily helpful. You could count all the fish in the ocean and still not know why they are abundant in some places but absent in others. To solve a scientific problem in a satisfying way, a **hypothesis** must first be stated. A hypothesis is a *statement that can be tested*.

The following are examples of hypotheses:

- Predatory snails reduce the population size of mussels on the intertidal rocks on the coast of Monterey, California.
- Increasing temperature increases the rate of oxygen consumption of crabs.

The following is not a hypothesis:

- Mermaids can never be observed, but they exist.

I hope you can see the difference easily. One can *test* a hypothesis. To test a hypothesis, it must be possible to produce an outcome that shows the hypothesis is false. One makes a prediction, which must follow from the hypothesis. We therefore formulate an **experiment**, whose outcome will be consistent or not consistent with the hypothesis. If one has hypothesized that predators control a population, it is appropriate to remove the predator population and observe whether the prey population increases, as would be expected from the hypothesis.

It is also possible that the *premises* of the hypothesis are inappropriate. Take the following hypothesis:

- Sea stars cannot attack mussels, and they therefore have no effect on mussel populations.

Because the premise of the first clause is incorrect, the hypothesis is inappropriate. All hypotheses should be internally consistent and testable, and they should be based on correct premises.

Although some hypotheses are best tested by experiments, many cannot be. Sometimes the predictions will then be stated in terms of relationships even if the relationships could, on occasion, conceivably have more than one explanation. For example, we might state the following hypothesis:

- When circulation of a very large water body deeper than 100 m has a current speed of less than 2 cm s^{-1} , the oxygen there will decrease faster than it is replenished by circulation from shallow water, and the deep-water body will lack oxygen.

We obviously cannot perform an experiment on such a deep-water body. We might then look at current speeds in all water bodies and classify on the basis of current speed those that lack oxygen. If the results of the classification are consistent with the hypothesis, we might look for any alternative hypotheses that could explain the same information. If none are obvious, then we might lean toward the correlation study as a correlation-based test of the hypothesis.

■ **Hypothesis testing is most powerful when specific predictions for an experimental treatment can be contrasted with difference from a control.**

The most difficult aspect of hypothesis testing is to formulate a hypothesis that lends itself to a specific program of experimentation or data collection. **Figure 1.9** shows a technique that captures the best-known way to think deductively and formulate hypotheses. All science usually derives from initial observations that arouse curiosity,

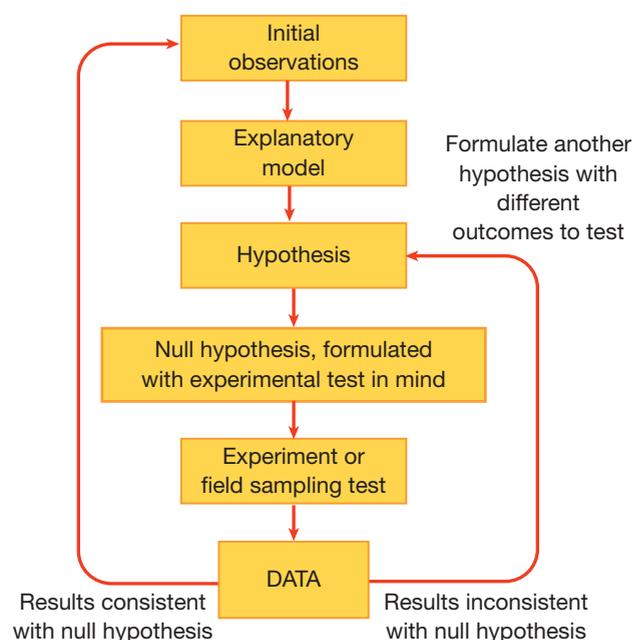


FIG. 1.9 A flowchart for the formulation and testing of hypotheses. (After Underwood and Chapman, 1995)



FIG. 1.10 A rocky shore near Bamfield, British Columbia, with abundant starfish at the base of a mussel bed. (Photograph by Jeffrey Levinton)

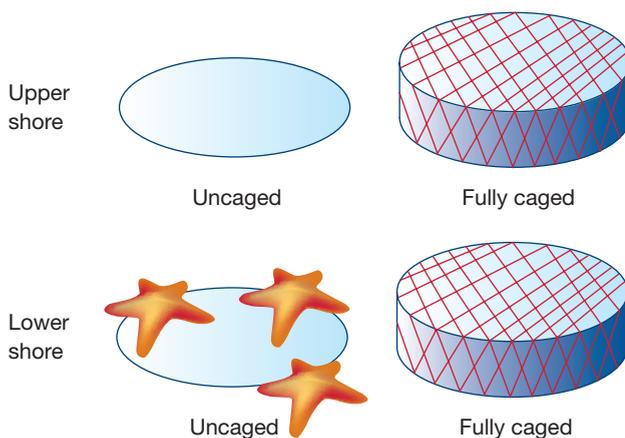


FIG. 1.11 A caging system to test whether predation affects the abundance of a rocky-shore community at different tidal levels. Results from fully caged areas, which exclude predators at high and low levels, are compared with results from uncaged areas.

such as finding that a barnacle species is abundant only on the high shore. Then an explanatory *model* is formulated, which uses general principles to attempt to explain why that barnacle would be associated with a high shore location. One might argue that predation, which occurs only on the lower parts of the shore, prevents barnacles from surviving there, but the absence of predation on the high shore allows barnacles to settle as planktonic larvae and accumulate in this upper microhabitat.

Now the crucial point arrives. One must formulate a hypothesis that is **testable**. The specific explanatory hypothesis here is that predation is more intense on the lower shore. **Figure 1.10** shows a rocky shore on the outer coast of British Columbia, and you should note the great

abundance of starfish below the mussel bed. Starfish can kill and digest mussels and barnacles, but they need to move about on very delicate tube feet, which work only in a moist environment. They are therefore able to rise onto the mussel bed only as the tide rises. Hence, we might expect that predatory starfish will have only the time to seize and eat prey on the lower shore because of the sluggish movement of the starfish.

But how does one test that there is an effect of shore height on predation? We could place a wire-mesh cage over the rocks that keeps predators out but allows the rocky-shore animals kept within the cage to function normally. A cage is placed on both the lower and upper shore and compared with open-uncaged areas at the two levels. So the caged areas exclude predation, and the open areas are **controls** (**Figure 1.11**). The working hypothesis states that starfish would be able to kill mussels only on the lower shore, so we expect prey abundances to be much lower in the uncaged area on the lower shore but higher in the open area of the upper shore and also higher within cages at both lower and upper shore levels.

The **null hypothesis** in this case would state: After the cages have been in place for a set period of time, there would be no differences in mussel population density between the open and caged rocky shore regardless of shore level.

One must always remember that even an experimental result is a correlation of outcome with experimental treatment. The treatment effect, however, may have nothing to do with the hypothetical effect being studied. For example, the open low-shore area might show a decline because of full exposure to the sun, while higher-shore mussels have adjusted to this exposure. This may seem contrived, but it is consistent with the caging comparisons.

In any test of a hypothesis, one must be aware of *variation*. *Statistics* is the field that deals with the calculation of trends and differences from repeated collections of information (e.g., measuring the height of all barnacles individually in the caging experiment and calculating the mean height per treatment) and assessments of variation. The difference in barnacle abundance between treatment and control may differ, but is the difference important? Two issues must be settled. First, a test of statistical significance must be established to determine whether the average barnacle density is greater within cages than outside cages. We need an estimate of variation and therefore need replicates of each treatment. If the variation among replicates is relatively low and the magnitude of mean difference high, then the difference may be statistically significant (Sokal and Rohlf, 2011). Usually, a test is devised that can estimate the probability that the data are distributed non-randomly and to estimate the **effect size** of the factor you are studying (i.e., the presence or absence of predation). It is crucial to realize that the probability levels used in a statistical test (e.g., 0.05) are a reflection of nothing more than the probability of the data you collected and analyzed for this particular experiment, not a general truth of a scientific relationship.

Habitats and Life Habits: Some Definitions

■ Some terms are necessary to describe life habits of marine organisms: neuston, plankton, nekton, benthos.

It is useful to classify marine organisms by their general habitat (Figure 1.12). **Plankton** are organisms that live suspended in the water. They may have some locomotory power but not enough to counteract major ocean currents or turbulence. They include protists, animals, plants, and bacteria that are at most a few centimeters long. **Neuston**

are organisms associated with the sea surface and include microorganisms that are bound to the surface slick of the sea. **Nekton** are usually larger animals that swim in the water column, but they can move against a current or through turbulent water. They range from small shrimp, crabs, and fish to the largest of whales. **Benthos** include animals and plants associated with the seafloor. Some animals are **infaunal**, which means they can burrow within the soft seabed, whereas others live on the seabed surface, or are **epifaunal**. Most clams are infaunal, whereas oysters and barnacles are epifaunal. Mobile organisms associated with the seabed that can swim (e.g., bottom fish) are said to be **demersal**.

Figure 1.13 gives a general classification for marine habitats based on water depth. The **intertidal zone** is the range of depths between the highest and lowest extent of the tides. In some parts of the world, there is little or no tide, and wind mainly determines the vertical range of this fringing environment (see Chapters 2 and 17). The **subtidal zone** is the entire remainder of the seabed from the low-water tidemark to the greatest depth of the ocean. **Continental shelf** (or neritic) habitats include all seafloor and open-water habitats between the high-water mark and the edge of the continental shelf. Seaward of the shelf is a series of oceanic or pelagic habitats: the **epipelagic zone** includes the upper 200 m of water, the **mesopelagic zone** ranges from 200 to 1,000 m depth, the **bathypelagic zone** ranges from 1,000 to 4,000 m depth, and the **abyssopelagic zone** ranges from 4,000 to 6,000 m depth; **bathyal** benthic bottoms range from 1,000 to 4,000 m depth, and **abyssobenthic** bottoms range from 4,000 to 6,000 m depth. **Hadal** environments include those of the seabed and the waters at the bottoms of the trenches, often far deeper than 6,000 m depth. For example, the Marianas Trench reaches about 11,000 m depth.

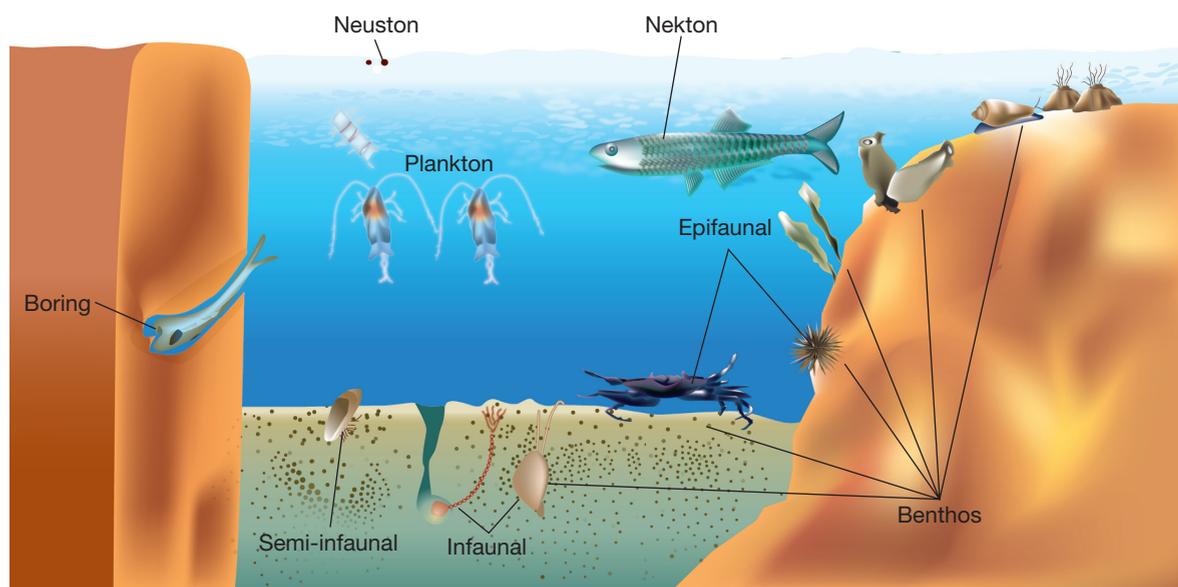


FIG. 1.12 General habitats of marine organisms.

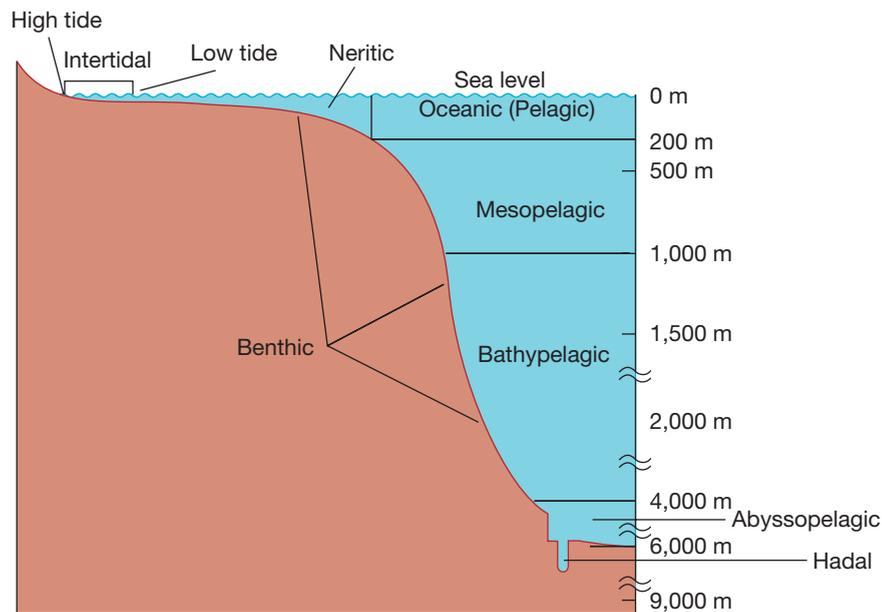


FIG. 1.13 A cross section of the ocean from the shoreline to the deep sea, showing the location of major marine habitats.

CHAPTER SUMMARY

- Marine biology combines functional biology, ecology, and the study of biodiversity.
- Marine biology began with simple observations of the distribution and variety of marine life. In the nineteenth century, marine biology developed into a science involving

hypothesis testing. The voyage of the H.M.S. *Challenger* gave us the first global view of marine biology. The twentieth century brought major research institutions, faster ships, better navigation, and greatly improved diving technology. Technology in both the laboratory and the open sea has

played an increasingly important role thanks to precise navigation, mapping of the seabed, and the development of submarine vehicles.

- Marine biologists use the scientific method—or systematic reasoning, observation, and experiment—to frame and test hypotheses.

REVIEW QUESTIONS

1. What was the azoic theory, and why could it be considered a testable hypothesis?
2. What might be the difference in potential contributions to marine biology by research done on the great oceanographic expeditions as opposed to research done at zoological stations on the coastline?
3. What was *Bathybius*, and why was its supposed existence of importance to the basic understanding of biology?
4. Why was the use of submarines so important in the development of marine science? Why was the use of scuba important in this development?
5. Distinguish between correlation and experimentation in the understanding of scientific relationships.
6. Devise a testable hypothesis about something in the room in which you are located now. How would you test this hypothesis?
7. Explain why the following is a poor hypothesis: Because whales are very small, they must be vulnerable to predation by snails.

Visit the companion website for *Marine Biology* at www.oup.com/us/levinton where you can find Cited References (under Student Resources/Cited References), Key Concepts, Marine Biology Explorations, and the Marine Biology Web Page with many additional resources.