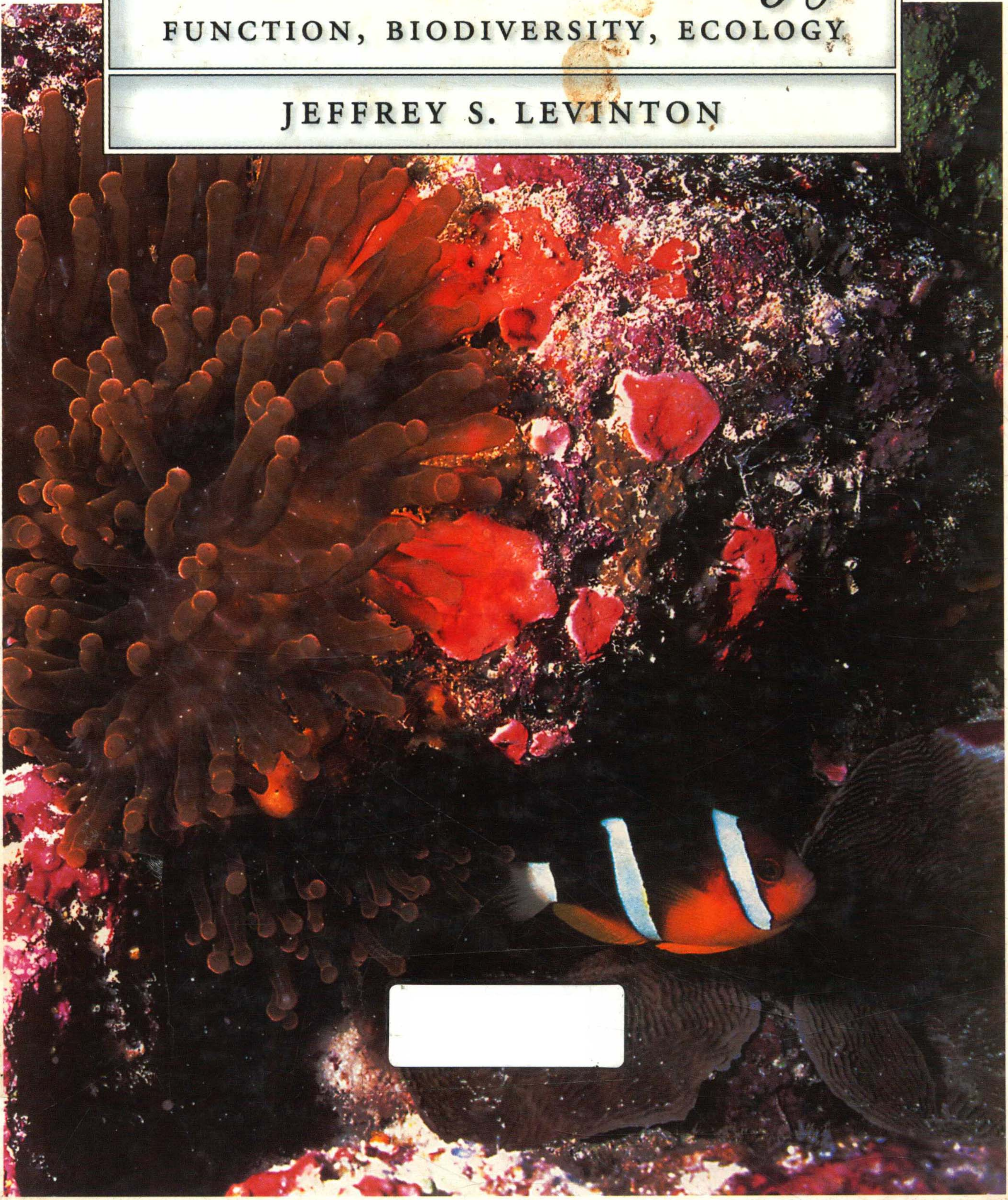
# Marine Biology

## FUNCTION, BIODIVERSITY, ECOLOGY

JEFFREY S. LEVINTON



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Marine Biology

*For Joan, Nathan and Andy—*
*all that matters*

# Preface

Marine biology is a hybrid subject that combines aspects of organismal function, ecological interactions, and the study of marine biodiversity. The ocean has always fascinated us, and students—actually, all of us—love the sea and marine creatures. There is an opportunity to use this excitement to attract the student to the important principles that govern marine biological systems. Why do animals burrow? What's the point of migrating hundreds of miles? Why dive? These unrelated questions can be woven together into a science. There is also a more global perspective. The ocean is a mobile and intertwining system of flowing rivers, waves, and slow-moving blobs of water. Heat, elements, organisms, and water move and create an ever-changing dynamic system.

This text is designed for one-semester courses at the sophomore to senior level in four-year colleges. It would help greatly if the students have already taken a college-level biology course, but I have successfully taught the sort of course for which this text is designed, and many of the students taking it had no other background in biology. This book could also be used in a more advanced undergraduate course in marine ecology, if it were supplemented with journal articles.

Marine biology is an applied subject, in which the principles of cell biology, biomechanics, ecology, and so on are applied to marine biological problems. This book addresses three major themes: function, biodiversity, and ecology. **Function** refers to the way organisms solve problems and how physical and chemical factors constrain the solutions. What shape should a maneuvering fish have? How does an animal reproduce by fragmentation? How does a cuttlefish stay at a specific depth? Of course there are also ecological dimensions to these questions. **Biodiversity** is an essential part of marine biology, and I introduce the topic in this book both through chapters on marine organisms and through materials on creatures in various habitats. A separate chapter discusses diversity and the processes that regulate it, both ecological and evolutionary. **Ecology** is the interaction of organisms with their environment, studied usually by trying to understand the distribution and abundance of organisms. This involves a series of processes, which I introduce as a hierarchy, from individuals to ecosystems. It also involves a discussion of the processes along with accounts of major marine living communities.

Marine biology is such a diverse subject that some approach must be adopted to organize the subject. I firmly believe that principles must guide our understanding, rather than an accumulation of facts. The first part of the book introduces basic principles of how the ocean works and how marine organisms function, as individuals and at higher levels of the ecological hierarchy. Then I discuss the organisms and the processes important in the water column. This is essential in order to understand the overall economy of the marine part of the biosphere. Processes in the water column are also crucial for the benthos, which depends strongly upon the world above, both directly and indirectly. Next, I discuss benthic creatures and the principles necessary to understand the biology of marine bottom organisms, which is followed by coverage of major marine habitats. I have been selective, and have emphasized those habitats that are not only important and interesting, but those where important principles can be illustrated to their best advantage. I look at the important gradient from the continental shelf to the deep sea, paying special attention to some of the fascinating newer discoveries about functioning in the deep sea. A chapter on gradients in biodiversity sums up larger scale variation in the sea, including a section on conservation of biodiversity. Finally, I tackle human interactions with the sea, both as a source of food and, unfortunately, a waste receptacle. I cover human effects on the ocean, including the speculative but important new field of global change.

This text has a series of features designed to help the student absorb a great variety of material. I have tried to write with very few embedded references to the scientific literature. This allows reading without unnecessary clutter. At the end of each chapter, I have provided a number of references for further reading to allow the interested student to pursue a subject further, or even to get started on a term paper. Important terms are printed boldface when they are first introduced. Nearly every section has summary heading sentences that convey the essence of the material to follow. I find this of help to the student in anticipating what's ahead, and in studying for exams in a subject that deals with so much biological and terminological diversity. Text boxes are included to explain a few equations and concepts, in order to keep the main body of the text free of excessive details. There are also a number of essays scattered throughout the text, which are designed to point toward some recent advances in the understanding of marine biology or to discuss current issues, especially relating to pollution and fisheries. At the end is a glossary and each chapter is followed by a set of review questions.

I have taught marine biology and ecology for nearly 20 years and have always been amazed at the diversity of students who take the course. Biology majors, geology majors, and humanities majors sit side by side. All learn a greal deal and all seem to have that love for the ocean. I do my best to try to keep that love alive, and I find that field trips and use of many color slides help a great deal. I hope that this text will do its share in this area.

Many people have helped me, too many to mention individually, with the preparation of this manuscript and I actually absorbed a few, but probably not enough, of their helpful suggestions. I am especially grateful to those many individuals who shared their photographs and research experiences with me. The manuscript was reviewed by Susan Bell, Paul Dayton, Alan Kohn, Larry McEdward, and Alan Stiven. I am very grateful for their constructive criticisms.

Most of this manuscript was prepared in my home university, but I am very grateful as well to the staff of the Friday Harbor Laboratories and the Zoology Department, University of Washington, where I was able to finally complete it. I am grateful to my wife Joan, who as usual tolerated more than she should, and to my son Nathan, who is now beginning to give me advice and even lectures on marine biology. My other son Andy has thrown himself, quite literally, into many new and wet areas of marine biology.

*Stony Brook, N.Y.* J. L.
*September 1994*

Harvest moon—
the tide rises
almost to my door.
—Matsuo Bashō, 1644–1694

It's nothing at all when the tide is high
It's just a bunch of waves
They whip all around the rocks
And chase all the fish into caves
But if you get there when the tide is low
And the pool is clear and clean
You can see to the bottom
The damnedest collection of creeps you ever seen

Hungry flowers that feed on fish
Scooping in whatever comes
Crabs that grab another crab
And chew his legs, the dirty bum!
Starfish having himself a lunch
Eats a mussel off a shell
Shrimps and limpets and snails and eels
What a smelly tale they tell
Biting each other and eating each other and lousing up the sea
Stupid sons of fishes, if you're asking me!
—Richard Rogers and Oscar Hammerstein III, *Pipe Dream*

# Contents

# I

# PRINCIPLES OF OCEANOGRAPHY AND MARINE BIOLOGY

# 1

# Sounding the Deep

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, collecting snails along the shore (Figure 1.1). Some are content only when they are out sighting whales, whereas others peer through a microscope, patiently counting thousands of protozoa. It is the purpose of this textbook 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.

Why study marine biology? I suppose mainly for the love of the sea and marine life. From a kayak, I once saw three killer whales jump up all at once and stand on their tails. I couldn't believe what I saw, but I later wondered why they would do such a thing. You would be amazed at how much there still is to learn about why these whales behave as they do. Snorkel on a coral reef and you will see a wondrous beauty filled with never-ending change and almost unbelievable variety. But why? How did such variety come to be, and what is its meaning? How do all these creatures interact to form the seascape? Why do turtles, salmon, and even tiny larvae of snails and corals move thousands of miles? 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.

* 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 the basic functions such as reproduction, feeding, and the cellular and biochemical processes relating to digestion, respiration, and other aspects of metabolism. Problems relating to function are quite varied. They might deal with questions such as: What skeletal and muscular arrangements do organisms as diverse as parrot fish and sea urchins use to eat seaweeds? When a whale dives for food to very great depths, how does it conserve oxygen? Why do some fish heat their heads only, whereas others heat their entire body? **Ecology**, on the other hand, is the study of the interaction of organisms with their physical and biological environments, and of how these interactions determine the distribution and abundance of the organisms. For example, how does a snail living on a smooth exposed rock avoid being eaten by predatory birds? How does a gray whale feed, when it dives to the bottom and plunges its mouth into the mud? A major objective of the science of ecology is to understand the entire set

**Fig. 1.1** A fascination with marine creatures led 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.

of processes that underlie the distribution and abundance of organisms.

Although one can define a difference between functional biology and ecology, in specific cases it is usually difficult to make a clear distinction between the two. Almost all functional problems have ecological dimensions. The apparatus required to feed on a seaweed may depend on the mechanical toughness of the seaweed or on the presence of toxic poisons in the seaweed, among other factors. An organism's degree of protection usually corresponds to the number of effective predators that are present. Function thus has an ecological context. It is also pointless to study ecology without an understanding of an organism's function. How can we determine how much a diving sperm whale is going to eat until we can determine its attack speed, its diving ability, and its jaw construction?

Because ecology is an environmental subject, the field of marine biology must cover the basic aspects of marine habitats. Without an understanding of the ocean in general, and of its specific habitat types in particular, it is not possible for you to understand just how and why marine organisms live the way they do, and how they survive in the particular habitats they occupy. We shall therefore spend considerable space explaining the various seascapes that are important to marine life.

## Historical Background of Marine Biology

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

Of course there has always been a native lore of the biology of the sea, 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. 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 (see below). He described hundreds of marine animal and plant species, and developed larger-scale classifications. In the eighteenth century, the great French biologist Georges Cuvier (1769–1832) developed a major scheme under which all animals could be classified. He classified all the animals into four major classes of body plans (Articulata, Radiata, Vertebrata, and Mollusca).

Until the nineteenth century, most marine biology consisted of the description and the classification of anatomy. Little was known about function and ecology. The only knowledge of open ocean life was confined to experience with those animals that were fished, or observed (or, in the case of mermaids, imagined) in the open sea. By the early 1800s, however, it became popular to study natural philosophy, and a number of brilliant individuals devoted their lives to the study of the ocean and its denizens.

* In the 19th 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 his medical school studies, he set out to sea and participated in a number of expeditions in which a bottom sampler, known as a dredge, was used to dig into the sea bed and collect organisms. He was hired as the naturalist on the *Bea-*

*con*, a ship that sailed on the Mediterranean Sea. He found the number of creatures decreased with increasing depth, and he 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 sea beds deeper than 300 fathoms (1800 feet). Forbes also discovered that different species lived at different depths, and he proposed that the broader the depth zone of a species is, the wider is 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. During this time, Forbes was joined by many great pioneers from a number of European countries. In 1850, the Norwegian marine biologist **Michael Sars** disproved the azoic theory by describing 19 species that lived deeper than 300 fathoms. 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 (Fig. 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*, which was one of the best-selling travel books of the nineteenth century. Darwin made extensive collections of many types of marine animals, and concentrated his own later efforts on the classification of the barnacles.

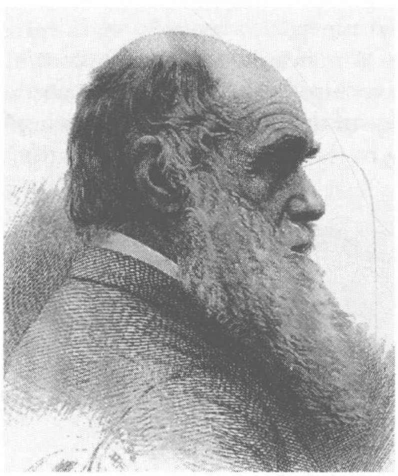

Fig. 1.2 Charles Darwin is best remembered for his theory of natural selection, but he made many important contributions to marine biology, including a book on coral reefs and a classification of barnacles that still remains essentially unchanged to the present day.

Darwin developed a theory of the development of coral reefs. In this theory, he described their overall growth as a balance between the growth of corals upward and the sinking of the sea floor. If Forbes' 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 serious scientific book, and its brilliance was immediately recognized. Previously, most 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 later sank. The sinking 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 to be correct. About 100 years after the theory was developed, scientists drilled a hole in Enewatak atoll in the Marshall Islands of the Pacific and bored through hundreds of meters of coral rock before hitting the volcanic rock basement below. This proved that the reef had been sinking for millions of years because the corals can grow only in very shallow water. Darwin was not completely right about coral reefs, however, theorizing 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 in oceanic crust (see Chapter 15).

Fisheries research began in earnest in the nineteenth century, and became central in marine biological research. England was first at this activity, in 1863. Many nations began research efforts later in the century (see Chapter 18). 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 its fisheries effort to develop distinguished laboratories on both the Atlantic and Pacific coasts.

The last great advance in nineteenth-century oceanic exploration was initiated by the great biologists **W. B. Carpenter** and **C. Wyville Thomson**. Both had a passion for marine biology and convinced the British government to outfit the *Lightning*, a steam- and sail-powered ship that dredged the northern waters of the British Isles. Like the Norwegian biologist Michael Sars, they found marine life deeper than 300 fathoms and thus also helped to disprove Edward Forbes' azoic theory.

* 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 would circumnavigate the globe and provide the first global perspective on the ocean's biotic diversity (Figure 1.3). The voyage was led by Wyville Thomson and by the great naturalist **John Murray**. The *Challenger* sampled the waters and bottoms of all seas but the Arctic, and 50 volumes were needed to describe the tremendous numbers of organisms that were recovered. On this expedition, the chemist J. Buchanan was able to disprove the existence of a so-called primordial slime, called *Bathybius*, that was supposed to be ubiquitous on the sea floor and capable of giving rise to higher forms of life. Buchanan discovered that the slime, which had been observed in collected samples of sea water, was merely an artifact of preserving sea water with alcohol.

During those same years, **Prince Albert I of Monaco** outfitted several yachts that sampled the ocean, and he eventually founded an oceanography institute and museum in Monaco. This facility is now directed by the famous inventor–oceanographer Jacques Cousteau. In America, the zoologist Alexander Agasiz 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 towards the end of the century. By the turn of the twentieth century, marine stations existed in many European countries. Marine laboratories such as the Marine Biological Laboratory and Friday Harbor Laboratories 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 ocean-going institutes, and a new technological ability to explore the ocean to its greatest depths. In America, the founding of the Scripps Institute 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 towards the end of the nineteenth century, marine stations were opened in America, in nearly every coastal state. Marine biology also flourished in many universities. Our knowledge of the ocean expanded during World War II, owing to the need for more navigational informa-

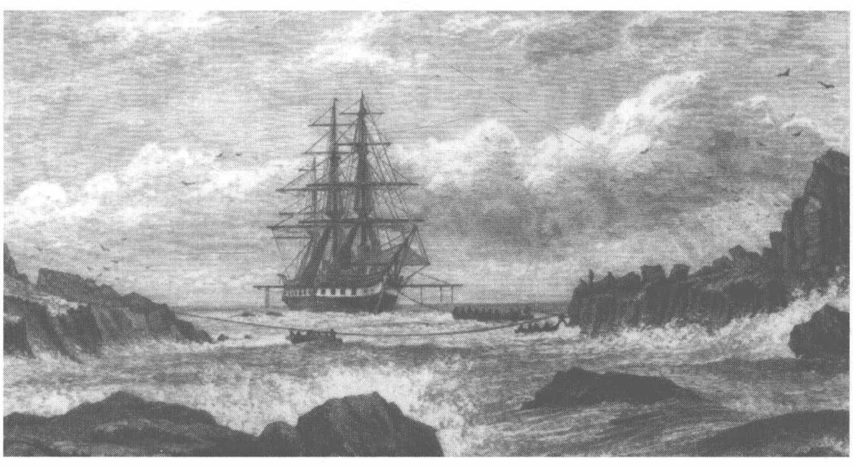

**Fig. 1.3** The H.M.S. *Challenger* at St. Paul's Rocks, a remote equatorial mid-Atlantic Island.

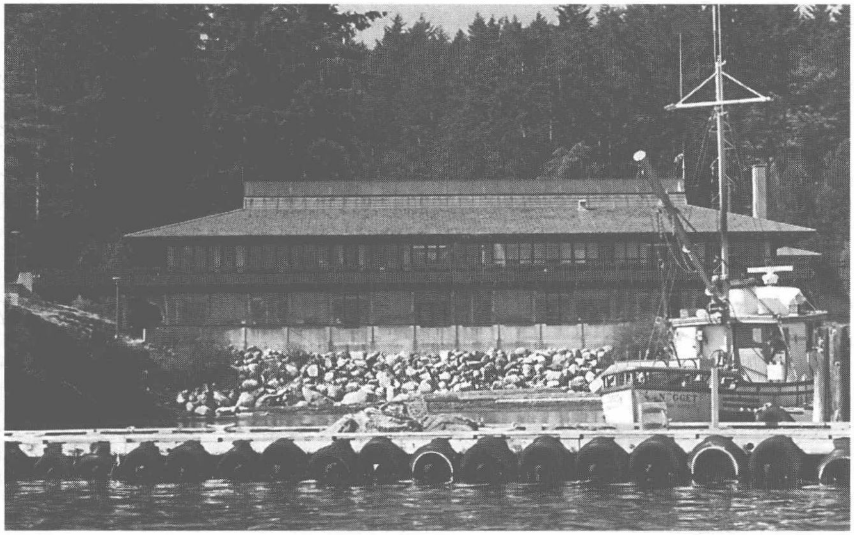

**Fig. 1.4** Friday Harbor Laboratories are located in the San Juan Islands of Washington State and are a major site for marine biological research in rocky-shore ecology, biomechanics, larval biology, neurobiology, and many other areas of study.

tion. 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 biology has since flourished, to the point that scores of journals now record the activities of a community of thousands of scientists. The numbers of such scientists in 1850 could have fit comfortably within a rather small 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 anyone from sampling the ocean systematically or completely. By the late 1800s, however, steam vessels allowed for the rapid lowering and raising of samplers, navigation was better, and vessels depended less upon the vagaries of the wind. In the twentieth century, modern diesel-driven ships such as the R. V. *Knorr* could navigate accurately by means of radio triangulation, and eventually by very accurate satellite navigation (Figure 1.5).

Before the mid-twentieth century, the deep-sea bottom could not be seen unless one dredged a piece of it and brought it to the surface. This has changed dramatically, owing to the development of manned submarines, remotely operated vehicles, and the development of SCUBA diving. In 1960 the spherical steel bathyscaphe *Trieste* made a spectacular descent into

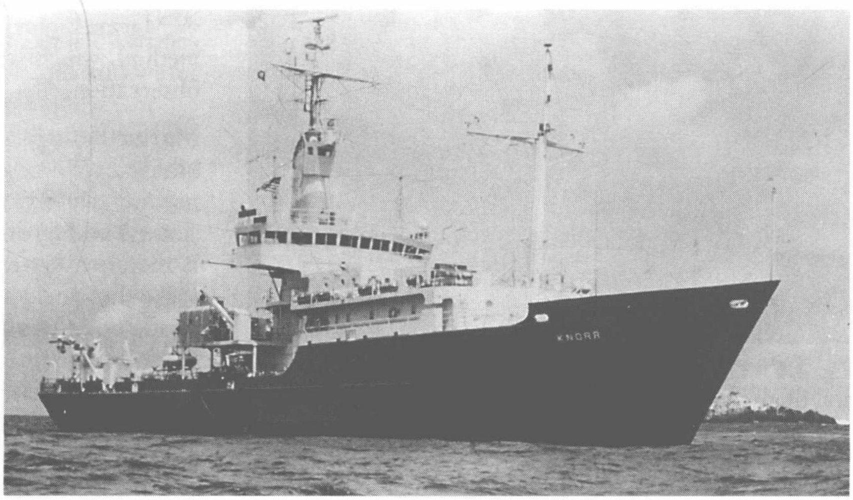



**Fig. 1.5** The R.V. *Knorr,* one of the United States oceanographic research fleet, has its home base at the Woods Hole Oceanographic Institution on Cape Cod, Massachusetts. (Photograph by Richard J. Bowen, 1984.)