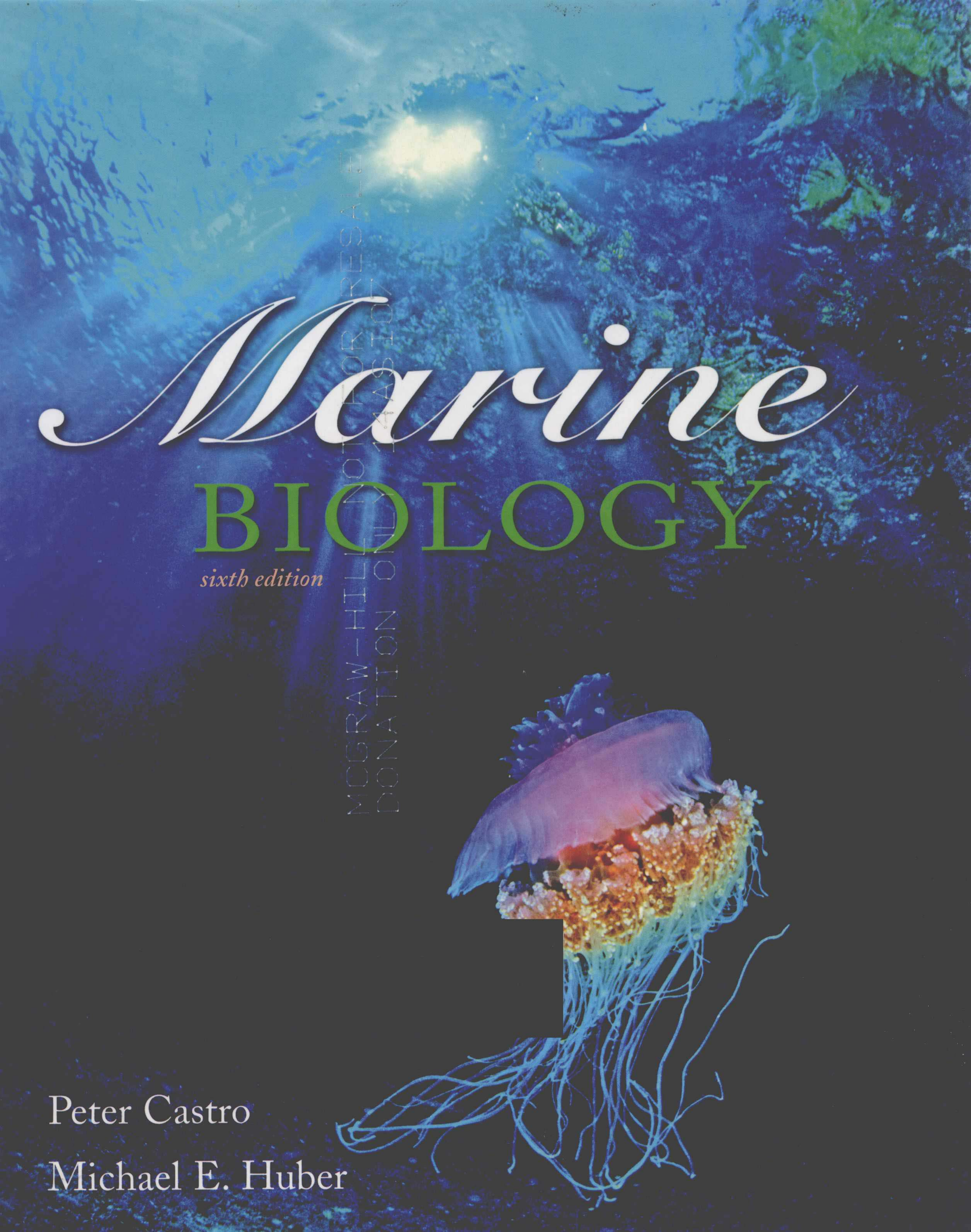

Marine BIOLOGY

sixth edition

Peter Castro

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Marine BIOLOGY

Sixth Edition

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Higher Education

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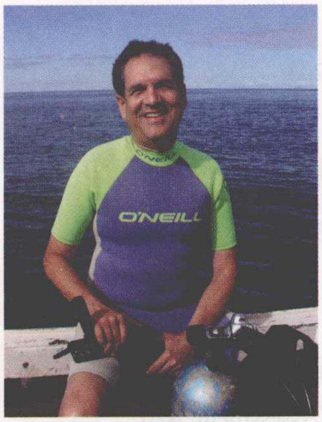
To all future marine biologists

—Peter Castro—

To Mason, Erin, and Kerry, for every little thing and to my parents for unfailing support.

—Michael Huber—

About the Authors



Peter Castro, Ph. D.

Peter Castro realized that he had to become a marine biologist during a high school field trip to the coral reefs in his native Puerto Rico. He obtained a B.S. in biology from the University of Puerto Rico, Mayagüez, but left the warm Caribbean for warm Hawaii to obtain a Ph.D. in marine zoology from the University of Hawaii, Manoa. His first experience with cold water was a year of post-doctoral research at Hopkins Marine Station of Stanford University in California. He is currently professor 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 eighteen years to accomplish as a part-time student. He is fluent in five languages and taught marine biology (in English and Spanish) as a Fulbright Scholar in the former Soviet Union. His research specialty is the biology of crustaceans symbiotic with reef corals and other invertebrates, a research that has taken him anywhere where the water is warm enough to dive. For the last decade he has also been doing research on the systematics of deep-water crabs, mostly, of all places, in Paris, France.

Michael Huber, Ph. D.

Michael was immediately fascinated by aquatic organisms when he caught his first trout on an Alaskan lake at age two. His interest in marine biology continued to grow over his ensuing school years, and he went on to obtain B.S. degrees in zoology and oceanography from the University of Washington in Seattle. After spending an Alaskan winter managing a laboratory for the trans-Alaskan oil pipeline project, he entered graduate school at Scripps Institution of Oceanography, at the University of California, San Diego. In 1983 he received his doctorate for research on a group of crabs that live symbiotically with corals. He remained at Scripps as a research biologist, working on such diverse research topics as the genetics and cell biology of unicellular algae and bioluminescence in midwater organisms. In 1988 he moved to the Biology Department at the University of Papua New Guinea, where he had the opportunity to work on some of the world's most spectacular coral reefs and was Head of the University's Motupore Island Research Station. He also became increasingly involved in marine environmental science, especially with regard to reefs, mangroves, seagrass beds, and other tropical systems. This interest continued to grow when he left Papua New Guinea in 1994 to become the Scientific Director of James Cook University's Orpheus Island Research Station on Australia's Great Barrier Reef. In 1998 he became a full-time environmental advisor, providing scientific information and advice on marine environmental issues and the development of conservation programs to international agencies, governments, and private industry. Dr. Huber is the Chair of GESAMP, an international scientific body that advises the United Nations system on marine environmental issues, and is currently assisting with the establishment of a permanent UN system to assess and report to governments on the state of the global marine environment.

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

Preface

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

Marine Biology is used by high school, undergraduate, graduate, and adult education students, and by interested laypersons not enrolled in formal courses. We are gratified that even some professional marine biologists find the book useful. While keeping this range of users in mind, we have written the text primarily to meet the needs of lower-division, non-science majors at colleges and universities. For many of these students, marine biology will be their only tertiary science course, often taken to satisfy a general education requirement. We have therefore been careful to provide solid basic science coverage including some 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.

We recognize that general science content is not a requirement for all marine biology courses, either because the course is not intended to satisfy general education requirements or because students already have a background in science. 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 career in marine science. 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 abovementioned coverage of basic science applied to the marine environment. Another is an emphasis on the organisms themselves, and their vast diversity not only in taxonomic terms but also in structure, function, and ecology. A third theme is an ecosystem approach that integrates this organismal diversity with the challenges imposed by the surrounding environment, both physical and biological. A final theme that, for better or worse, becomes increasingly relevant with each passing year is the interaction of humans with the marine environment.

***Marine Biology*, Sixth 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 our lives.

Changes in the Sixth Edition

We have introduced a new feature to the sixth edition of *Marine Biology*: each chapter includes an **Eye on Science** box; a vignette of a particular piece of ongoing or planned research. Rather than simply presenting factual information and summarizing results, the emphasis is on giving students a glimpse of what scientists actually do—the questions being asked, their significance, and how a scientist or research team has set about answering them. We hope this helps science seem less remote and gives students better insight into the daily process of scientific enquiry.

As in previous editions we have updated the text throughout to reflect recent events, new research, and changes in perspective, and to include information requested by reviewers. A few examples of such revisions or additions are:

- Larger, more attractive, and more detailed maps of the sea floor and the major coastal habitats of North America, now as an end-piece foldout
- A description of the importance of the United States Exploring Expedition (the Wilkes Expedition), which predated the *Challenger* expedition, to the history of marine biology
- A rewritten "Waves That Kill" boxed reading with in-depth coverage of the December 2004 tsunami in the Indian Ocean
- Updated coverage of the origin of chloroplasts by endosymbiosis
- Thorough revision of Table 5.1 on prokaryote metabolism to make it simpler, less imposing, and easier to understand

- New cladograms depicting phylogenetic relationships within both the invertebrates and the vertebrates
- An expanded Figure 9.18 showing various whale species
- A new boxed reading on deep-water coral communities and human impacts on them
- New findings about the benefits to hosts in the anemone-anemonefish symbiosis
- Additional information about trophic cascades
- Coverage on the effects of Hurricane Katrina

In addition to these and many other changes we have as usual updated facts and figures, corrected errors, and reorganized some sections to improve balance and logic flow. In every edition we seek to improve the illustrations and photographs, and in the sixth edition we have adopted a more colorful and open interior design that we think will better engage students and reinforce their fascination with marine life.

Organization

Marine Biology is organized into four parts. **Part 1** (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 critical that students understand how and why science works, and also 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 cover many abiotic aspects of the marine environment in the chapters where they are most relevant to the biology. Wave refraction, for example, is described in conjunction with intertidal communities (Chapter 11) and estuarine circulation is discussed as part of the ecology of estuaries (Chapter 12). This approach emphasizes the importance of the physical and chemical environment to the organisms of the sea throughout the book. At the same time, it provides flexibility for instructors to make best use of the material in light of general education requirements, course prerequisites, and students' backgrounds. Chapter 4, "Fundamentals of Biology," briefly reviews some essential biological concepts. In covering basic biology we have tried to balance the needs of a spectrum of students ranging from those with no prior university-level instruction to those who have taken a number of biology courses. Depending on the level of their students, instructors may choose to cover Chapter 4 in class, assign it as review reading, or omit it and rely on the In-Text Glossary entries in later chapters to remind students of the definitions of key terms.

Part 2 (Chapters 5 through 9) surveys the diversity of marine life from the perspective of organismal biology. As in Part 1, 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 illustration in 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. Nomenclature follows for the most part the FAO Species Catalog and Species Identification Guides for groups covered by these references.

Part 3 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 for Chapter 4, important concepts presented here are reviewed elsewhere in the In-text Glossary boxes. The remaining six chapters of Part 3 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.

Finally, **Part 4** 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 and mariculture, but also at more modern aspects such as the pharmacological use of marine natural products and the application of genetic engineering to mariculture. Chapter 18 discusses human-induced degradation of the marine environment, balanced by an examination of marine conservation and habitat restoration. The book closes with an essay on the interactions between the ocean and the human culture (Chapter 19) that we hope will stimulate students to reflect on the past and future significance of the world ocean to all our lives.

Acknowledgments

Bill Ober and Claire Garrison have again done a wonderful job of bringing new life to the illustrations. We are delighted by the new design by Jamie O'Neal. We also thank the many contributors of photographs that add so much to the book, especially A. Charles Arneson, who has provided many excellent photos, and appreciate the diligent efforts of LouAnn Wilson in locating new photos. We are grateful to the editorial staff at McGraw-Hill Publishers, particularly Margaret Kemp, Publisher, Debra Henricks, Developmental Editor, Joyce Watters, Project Manager, and Karen Dorman, copy editor, for their patience, support, and efficiency in managing an enormous amount of detail.

Most of all we thank the students, friends, colleagues, former teachers, and reviewers who answered questions, pointed out errors, and made suggestions that have greatly improved the book. We take full credit, however, for any errors or shortcomings that remain.

We also give special thanks to the following researchers who provided information, photographs, and other assistance in the preparation of the new "Eye on Science" boxes:

Dr. David Crewz
Fish and Wildlife Research Institute, St. Petersburg, FL

Dr. Kerstin Fritsches
University of Queensland, Australia

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Marine Biological Laboratory at Wood's Hole, MA

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Pfleger Institute of Environmental Research, CA

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Reviewers

The following people have reviewed the fifth edition, and have provided useful commentary for preparation of the sixth edition:

Claude D. Baker
Indiana University Southeast

Nancy Eufemia Dalman
Cuesta College

Jeremiah N. Jarrett
Central Connecticut State University

Robert D. Johnson, Jr.
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Marjorie Reaka-Kudla
University of Maryland

Nan Schmidt
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Susan Schreier
Villa Julie College

Erik P. Scully
Towson University

Robert Whitlatch
University of Connecticut

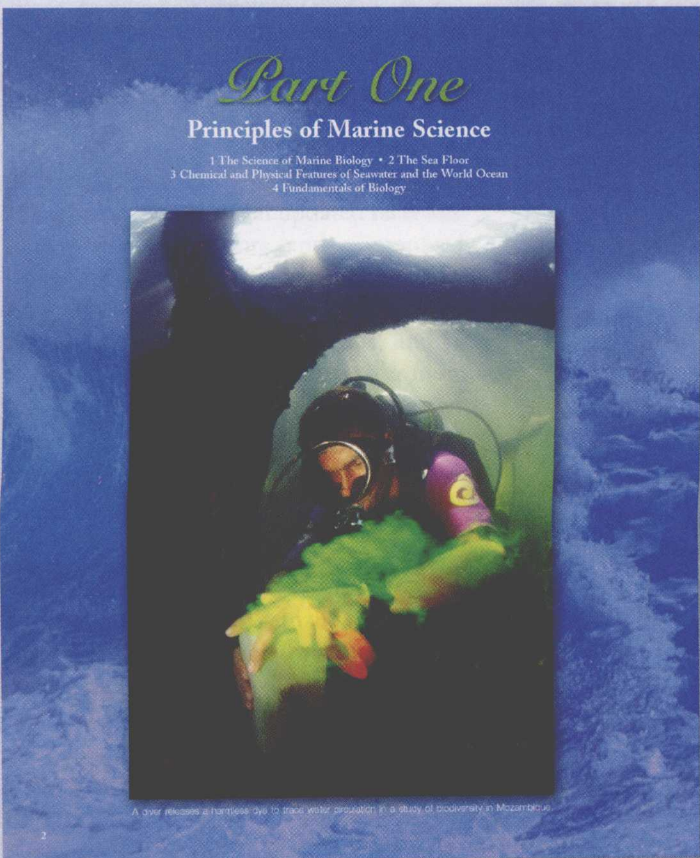
Mary K. Wicksten
Texas A&M University

Jennifer Wortham
University of Tampa

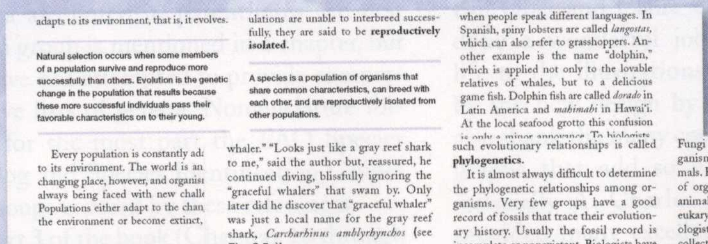
Jay Z. Zimmer
South Florida Community College

The Marine Biology Learning System

Chapters are organized into four parts and written as short, readily absorbed units to increase instructor flexibility in selecting topics.



Key concept summaries highlight the most important terms and ideas presented in preceding paragraphs.



adapts to its environment, that is, it evolves.

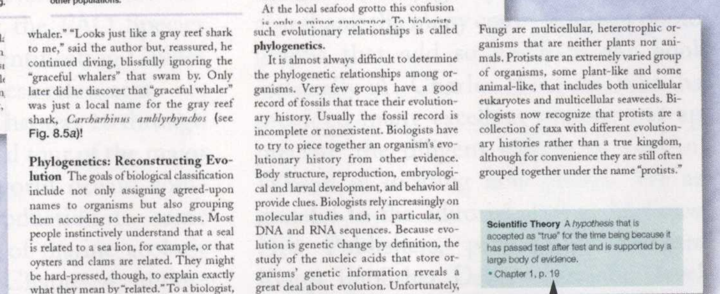
Natural selection occurs when some members of a population survive and reproduce more successfully than others. Evolution is the genetic change in the population that results because these more successful individuals pass their favorable characteristics on to their young.

Every population is constantly ad to its environment. The world is an changing place, however, and organis always being faced with new challe Populations either adapt to the chan the environment or become extinct,

ulations are unable to interbreed successfully, they are said to be **reproductively isolated**.

A species is a population of organisms that share common characteristics, can breed with each other, and are reproductively isolated from other populations.

when people speak different languages. In Spanish, spiny lobsters are called *langostas*, which can also refer to grasshoppers. Another example is the name "dolphin," which is applied not only to the lovable relatives of whales, but to a delicious game fish. Dolphin fish are called *dorado* in Latin America and *mahimahi* in Hawai'i. At the local seafood grotto this confusion is only a minor annoyance. To biologists



whaler." "Looks just like a gray reef shark to me," said the author but, reassured, he continued diving, blissfully ignoring the "graceful whalers" that swam by. Only later did he discover that "graceful whaler" was just a local name for the gray reef shark, *Carcharhinus amblyrhynchos* (see Fig. 8.5a)!

Phylogenetics: Reconstructing Evolution The goals of biological classification include not only assigning agreed-upon names to organisms but also grouping them according to their relatedness. Most people instinctively understand that a seal is related to a sea lion, for example, or that oysters and clams are related. They might be hard-pressed, though, to explain exactly what they mean by "related." To a biologist,

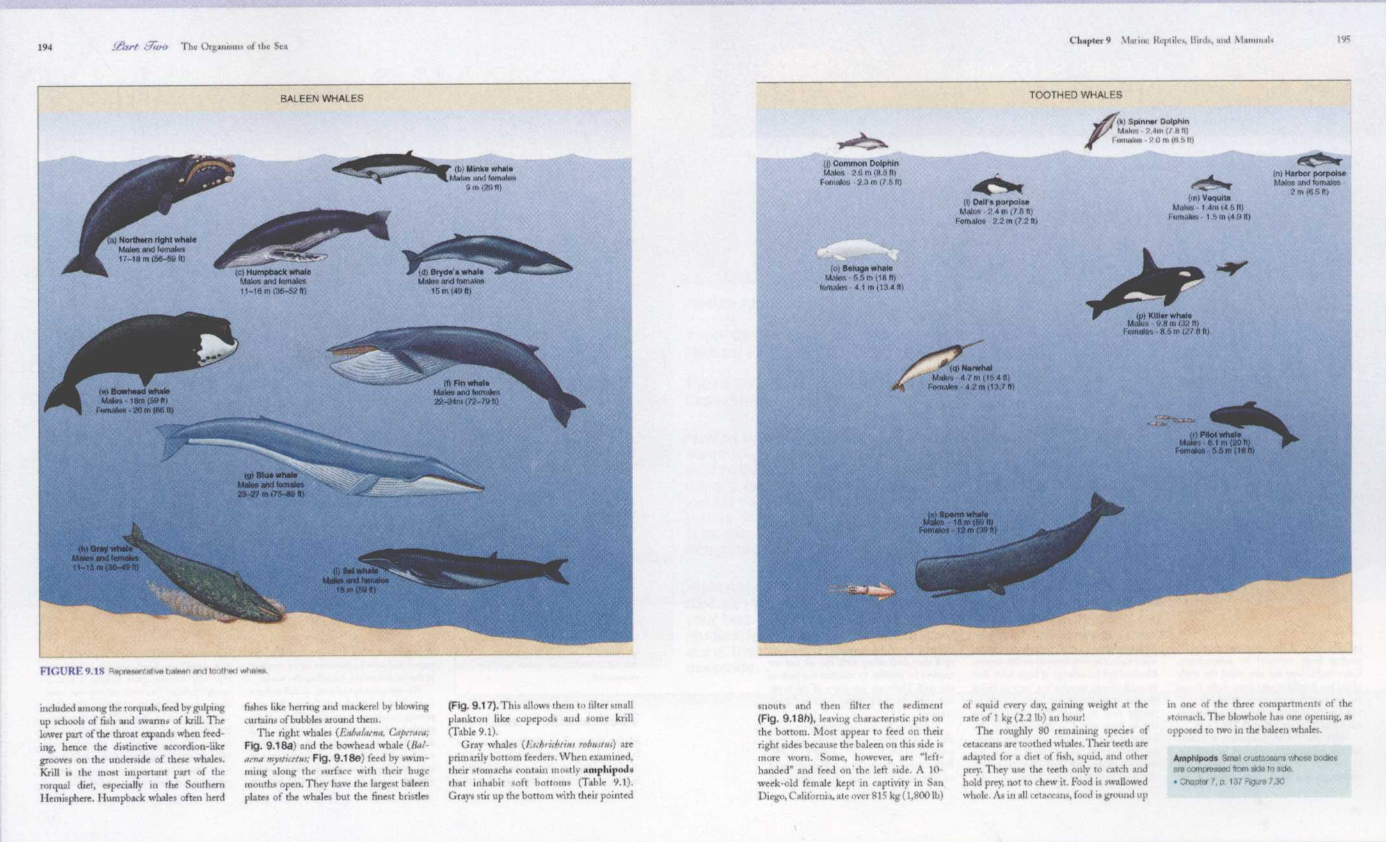
such evolutionary relationships is called **phylogenetics**.

It is almost always difficult to determine the phylogenetic relationships among organisms. Very few groups have a good record of fossils that trace their evolutionary history. Usually the fossil record is incomplete or nonexistent. Biologists have to try to piece together an organism's evolutionary history from other evidence. Body structure, reproduction, embryological and larval development, and behavior all provide clues. Biologists rely increasingly on molecular studies and, in particular, on DNA and RNA sequences. Because evolution is genetic change by definition, the study of the nucleic acids that store organisms' genetic information reveals a great deal about evolution. Unfortunately,

Fungi are multicellular, heterotrophic organisms that are neither plants nor animals. Protists are an extremely varied group of organisms, some plant-like and some animal-like, that includes both unicellular eukaryotes and multicellular seaweeds. Biologists now recognize that protists are a collection of taxa with different evolutionary histories rather than a true kingdom, although for convenience they are still often grouped together under the name "protists."

Scientific Theory *A hypothesis that is accepted as "true" for the time being because it has passed test after test and is supported by a large body of evidence.*
• Chapter 1, p. 19

An **in-text glossary** briefly explains key terms and concepts from other chapters. Chapter and page references point students to more detailed information. The extensive **glossary** in the back of the book provides complete definitions and often refers to illustrations or other key terms that help explain a concept.


194 *Part Two* The Organisms of the Sea

Chapter 9 Marine Reptiles, Birds, and Mammals 195

FIGURE 9.18 Representative baleen and toothed whales.

included among the rorquals, feed by gulping up schools of fish and swarms of krill. The lower part of the throat expands when feeding, hence the distinctive accordion-like grooves on the underside of these whales. Krill is the most important part of the rorqual diet, especially in the Southern Hemisphere. Humpback whales often herd fishes like herring and mackerel by blowing curtains of bubbles around them.

The right whales (*Eubalaena, Caperaea;* **Fig. 9.18a**) and the bowhead whale (*Balaena mysticetus;* **Fig. 9.18e**) feed by swimming along the surface with their huge mouths open. They have the largest baleen plates of the whales but the finest bristles **(Fig. 9.17).** This allows them to filter small plankton like copepods and some krill (Table 9.1).

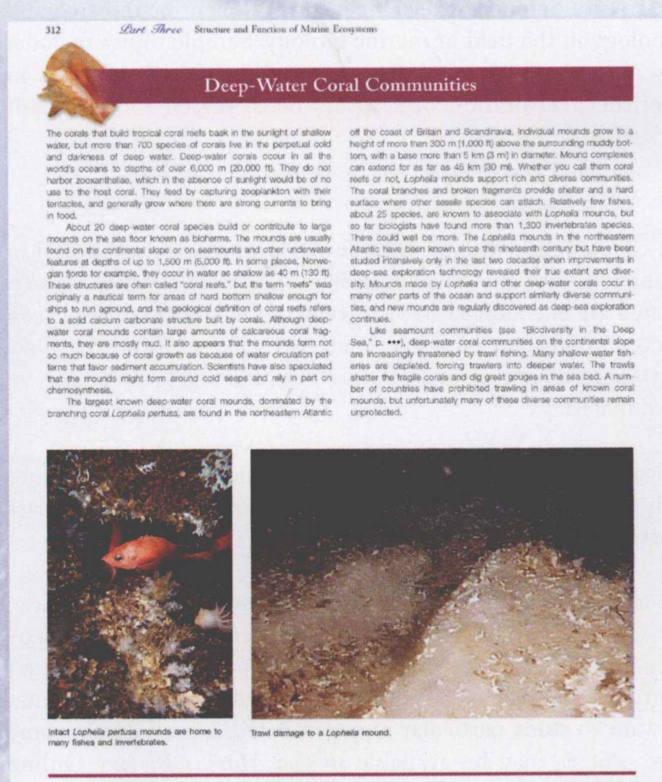
Gray whales (*Eschrichtius robustus*) are primarily bottom feeders. When examined, their stomachs contain mostly **amphipods** that inhabit soft bottoms (Table 9.1). Grays stir up the bottom with their pointed snouts and then filter the sediment **(Fig. 9.18*h*)**, leaving characteristic pits on the bottom. Most appear to feed on their right sides because the baleen on this side is more worn. Some, however, are "left-handed" and feed on the left side. A 10-week-old female kept in captivity in San Diego, California, ate over 815 kg (1,800 lb) of squid every day, gaining weight at the rate of 1 kg (2.2 lb) an hour!

The roughly 80 remaining species of cetaceans are toothed whales. Their teeth are adapted for a diet of fish, squid, and other prey. They use the teeth only to catch and hold prey, not to chew it. Food is swallowed whole. As in all cetaceans, food is ground up in one of the three compartments of the stomach. The blowhole has one opening, as opposed to two in the baleen whales.

Amphipods Small crustaceans whose bodies are compressed from side to side.
• Chapter 7, p. 137 Figure 7.30

Effects of Hurricane Katrina, August 2005 (bottom) on barrier island off the Louisiana coast.

Illustrations and photographs have been carefully designed and selected to complement and reinforce the text. The sixth edition contains many new illustrations and photographs.


312 *Part Three* Structure and Function of Marine Ecosystems

Deep-Water Coral Communities

The corals that build tropical coral reefs bask in the sunlight of shallow water, but more than 700 species of corals live in the perpetual cold and darkness of deep water. Deep-water corals occur in all the world's oceans to depths of over 6,000 m (20,000 ft). They do not harbor zooxanthellae, which in the absence of sunlight would be of no use to the host coral. They feed by capturing zooplankton with their tentacles, and generally grow where there are strong currents to bring in food.

About 20 deep-water coral species build or contribute to large mounds on the sea floor known as bioherms. The mounds are usually found on the continental slope or on seamounts and other underwater features at depths of up to 1,500 m (5,000 ft). In some places, Norwegian fjords for example, they occur in water as shallow as 40 m (130 ft). These structures are often called "coral reefs," but the term "reefs" was originally a nautical term for areas of hard bottom shallow enough for ships to run aground, and the geological definition of coral reefs refers to a solid calcium carbonate structure built by corals. Although deep-water coral mounds contain large amounts of calcareous coral fragments, they are mostly mud. It also appears that the mounds form not so much because of coral growth as because of water circulation patterns that favor sediment accumulation. Scientists have also speculated that the mounds might form around cold seeps and rely in part on chemosynthesis.

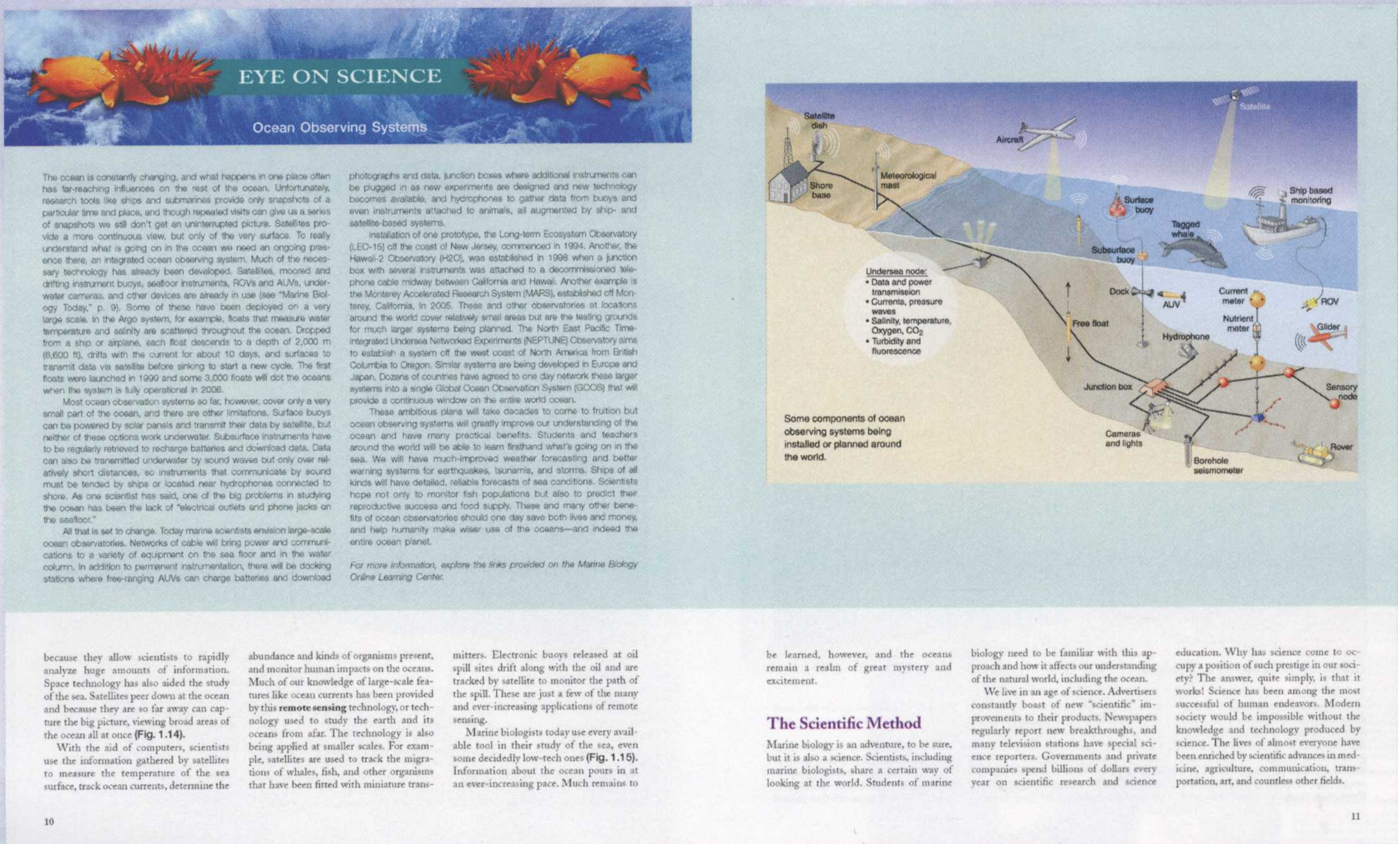
The largest known deep-water coral mounds, dominated by the branching coral *Lophelia pertusa*, are found in the northeastern Atlantic off the coast of Britain and Scandinavia. Individual mounds grow to a height of more than 300 m (1,000 ft) above the surrounding muddy bottom, with a base more than 5 km (3 mi) in diameter. Mound complexes can extend for as far as 45 km (30 mi). Whether you call them coral reefs or not, *Lophelia* mounds support rich and diverse communities. The coral branches and broken fragments provide shelter and a hard surface where other sessile species can attach. Relatively few fishes, about 25 species, are known to associate with *Lophelia* mounds, but so far biologists have found more than 1,300 invertebrates species. There could well be more. The *Lophelia* mounds in the northeastern Atlantic have been known since the nineteenth century but have been studied intensively only in the last two decades when improvements in deep-sea exploration technology revealed their true extent and diversity. Mounds made by *Lophelia* and other deep-water corals occur in many other parts of the ocean and support similarly diverse communities, and new mounds are regularly discovered as deep-sea exploration continues.

Like seamount communities (see "Biodiversity in the Deep Sea," p. •••), deep-water coral communities on the continental slope are increasingly threatened by trawl fishing. Many shallow-water fisheries are depleted, forcing trawlers into deeper water. The trawls shatter the fragile corals and dig great gouges in the sea bed. A number of countries have prohibited trawling in areas of known coral mounds, but unfortunately many of these diverse communities remain unprotected.

Intact *Lophelia pertusa* mounds are home to many fishes and invertebrates.

Trawl damage to a *Lophelia* mound.

Boxed Essays present interesting supplemental information on varied subjects such as deep-water coral communities, tsunamis, and red tides.

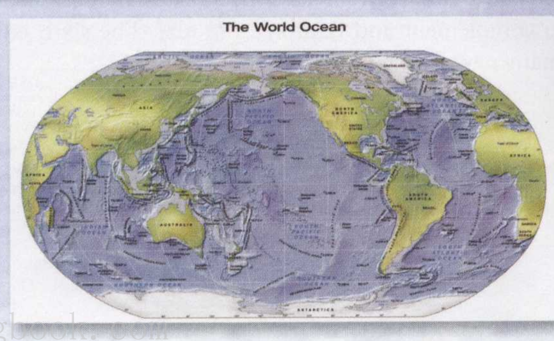


New! Eye on Science boxes reflect current scientific research and technology in the field of marine biology. Sample topics include: ocean observing systems, deep-ocean drilling, female mimicry in cuttlefishes, restoration of seagrass beds, search for the giant squid, etc.

Each chapter ends with an **Interactive Exploration** to be used in conjunction with the Marine Biology Online Learning Center. Students are encouraged to visit **www.mhhe.com/castrohuber6e** for access to chapter quizzing, interactive chapter summaries, key terms flashcards, marine biology video clips and web links to chapter-related material.

Critical thinking questions challenge students to think more deeply about the chapter material and also help stimulate class discussion.

For Further Reading lists "General Interest" articles in publications such as Scientific American, Discover and National Geographic, which are appropriate for students with limited backgrounds in science; and "In Depth" readings for students who want to study particular topics in detail. Live links for some of the articles may be available in the *Marine Biology* Online Learning Center.



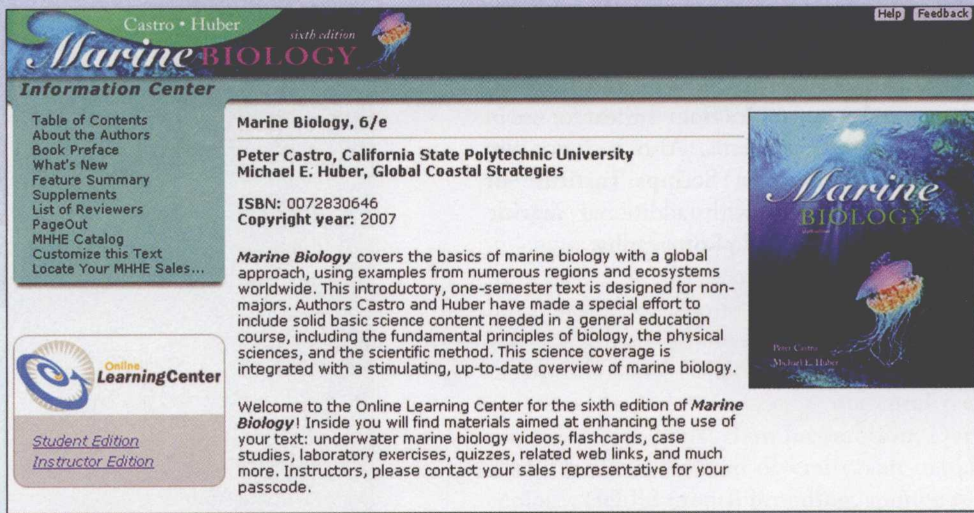
New! A foldout map at the end of text provides quick reference to the World Ocean.

Stay Afloat with the Marine Biology Online Learning Center!

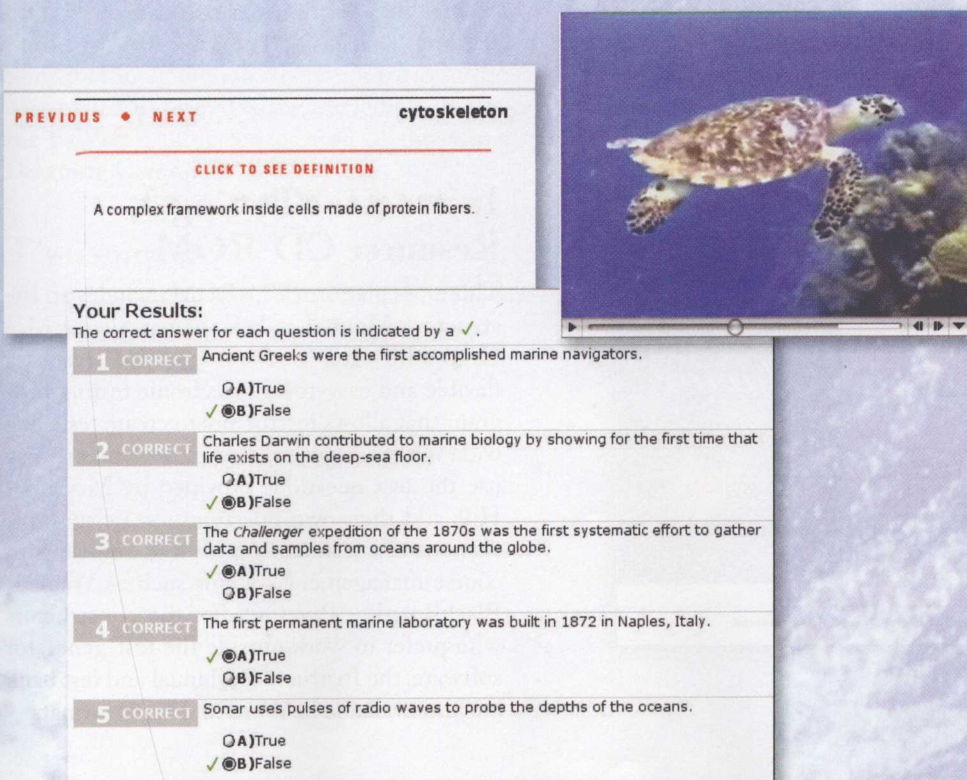
www.mhhe.com/castrohuber6e

The ***Marine Biology*** **Online Learning Center** offers a wealth of learning and teaching aids for instructors and students

Instructors will appreciate a password-protected **Instructor's Manual,** a **PowerPoint image library** containing all the art and photos for the text, **laboratory exercises,** and more.



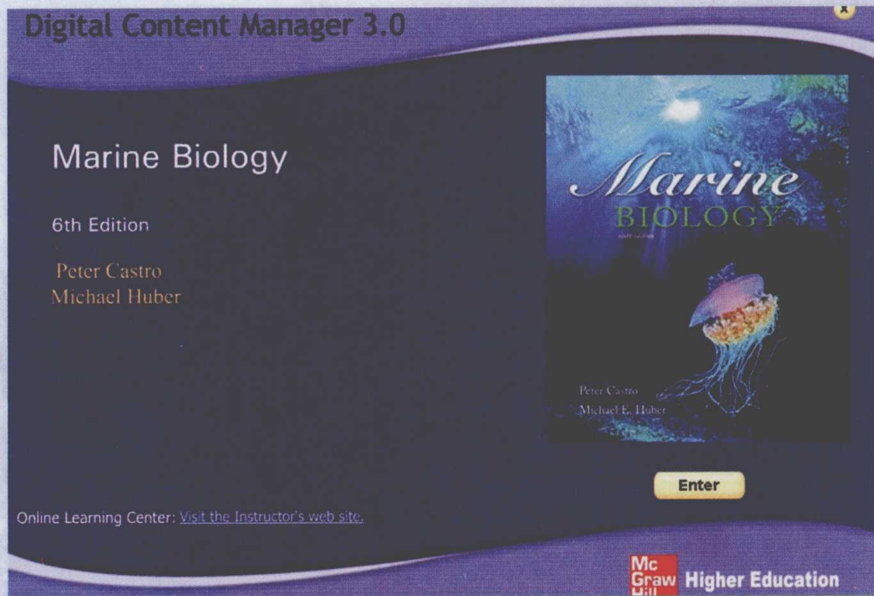
Students will benefit from **interactive quizzing, key terms flashcards,** and **web links.** Also included are **underwater video clips,** featuring footage of marine animals, their behaviors, and ecosystems.



Ancillaries

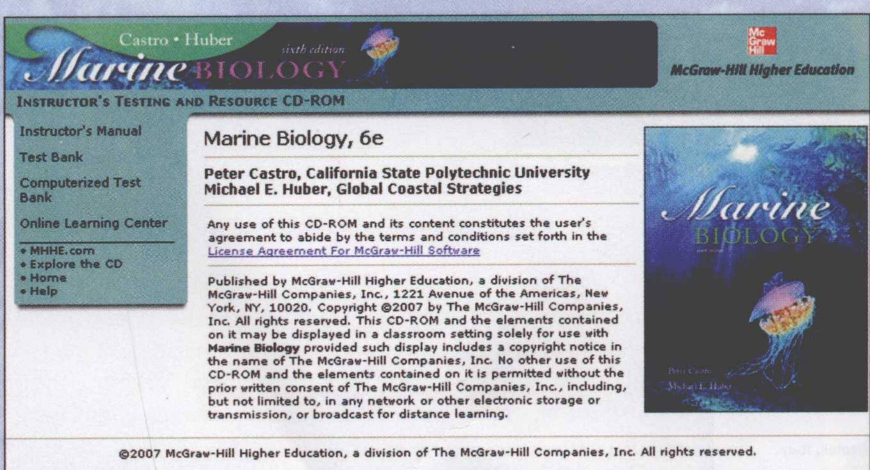
Digital Content Manager CD-ROM/DVD

This useful tool contains all of the **illustrations, photographs,** and **tables** from the text for use in multimedia presentations. Also included are **video segments from Scripps Institute of Technology,** along with additional **marine biology videoclips** and **photographs.**



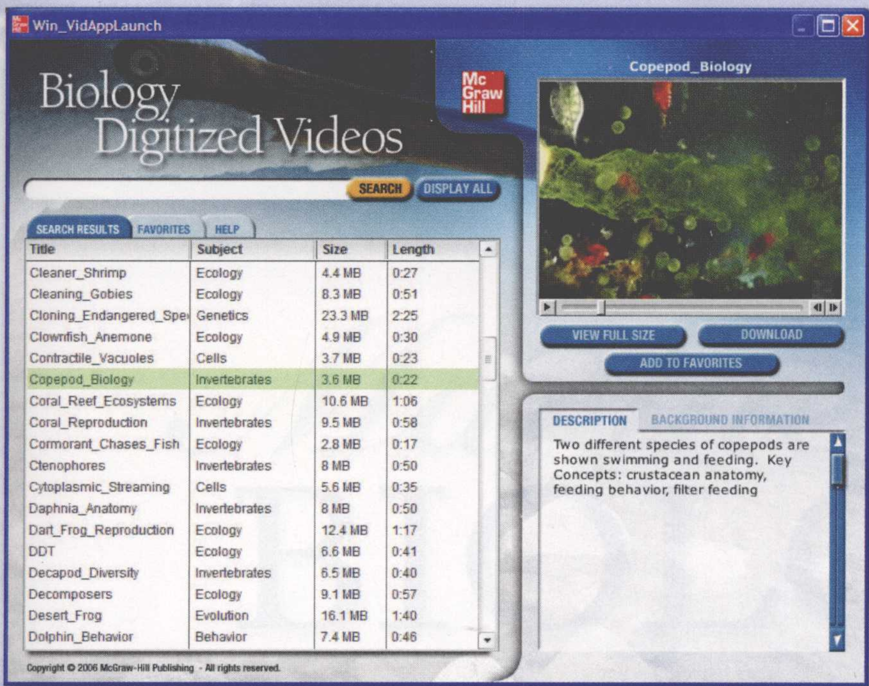
Instructor's Manual

Prepared by Peter Castro, this helpful ancillary provides chapter outlines and summaries, a listing of audiovisuals and software, and answers to the Critical Thinking questions within the text. Instructors will also find suggestions on presenting concepts to students and organizing materials for class presentation. The Instructor's Manual can be accessed via the password-protected portion of the ***Marine Biology*** **Online Learning Center** as well as the Instructor's Testing & Resource CD-ROM.



Instructor's Testing & Resource CD-ROM

This cross platform CD-ROM includes an **Instructor's Manual** and **test bank** utilizing McGraw-Hill's EZ Test software. EZ Test is a flexible and easy-to-use electronic testing program that allows instructors to create tests in a wide variety of question types. Instructors may use the test questions provided by McGraw-Hill, add their own questions, create multiple versions of a test, and export tests for use with course management systems such as WebCT, BlackBoard or PageOut. For those instructors who prefer to work outside the test-generator software, the Instructor's Manual and test bank are also available in Word and PDF formats.



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