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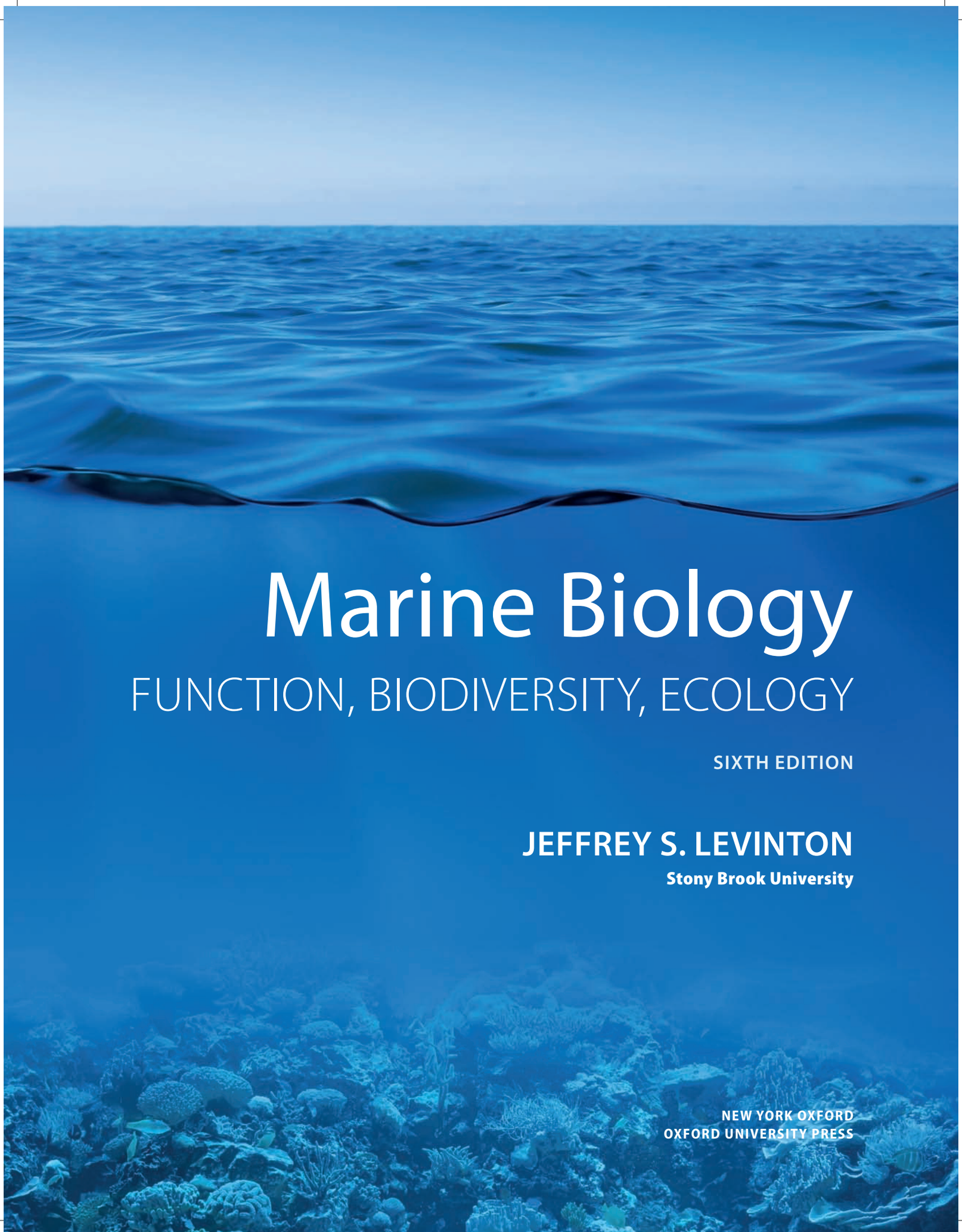
Spring ocean
Swaying gently
All day long.

—MATSUO BASHŌ



Marine Biology

FUNCTION, BIODIVERSITY, ECOLOGY

SIXTH EDITION

JEFFREY S. LEVINTON
Stony Brook University

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For Joan, Nathan, Andy, Molly, and all others in the choir

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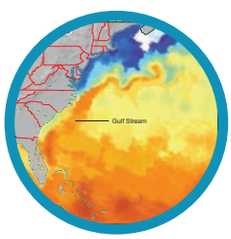

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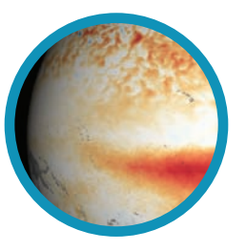

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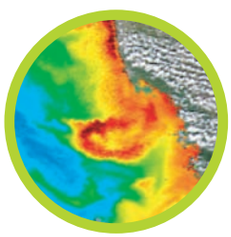

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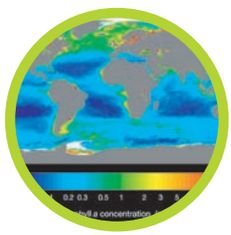

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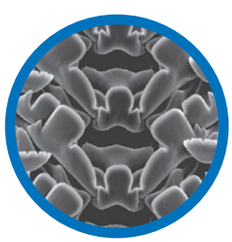

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PREFACE

I am happy to present this sixth edition of *Marine Biology: Function, Biodiversity, Ecology.* The goal of this text is to appeal to a wide range of students while also preparing future scientists with the knowledge and tools needed to conduct their thinking and research in marine biology. I continue to be convinced that, from the outset, students *must learn concepts* along with the facts and begin to *think and reason like scientists.* Just as important, they must feel the pulse of current happenings. Discovery is often excitement enough, but new ways of thinking and new methods appear frequently. Sadly, we must also deal with threats to the marine realm. We love marine creatures, but they are under challenge like at no time in the past. Humans are affecting the most basic organization of the ocean's environment, and students are anxious both to understand how to gauge this threat and to solve the wide range of threats to ocean life. I hope this text will continue to deal with these diverse challenges to educate and inspire students.

The continuing challenge of a marine biology text is to engage students in feeling the excitement of oceanic creatures while breathing life into the science that sharpens our thinking and develops the tools to deal with the many challenges of further understanding and protection of life and habitat in the sea. We marine biology instructors are lucky to have exciting creatures, great adventures, and continuing discoveries that manage to enchant and stimulate students. My greatest challenge is to find an organization that combines student inspiration with the principles and current practices they need to understand at a high level. Many students find marine biology a little daunting. There are so many different creatures and so many processes swirling about, all in an immense space that ranges from ocean scale to the minute realms of the cell and even the molecular scale. We must introduce this wondrous range of concepts, organisms, and scales effectively, without swamping the students with so many new concepts and facts.

That is why the text addresses three major principles and process-driven themes: *functional biology*, *ecological processes*, and *biodiversity.* It is why the text uses full color throughout in drawings that depict marine biological processes and a large number of photographs to connect students with marine environments and organisms. I have added yet more photographs to this edition, thanks to my own journeys and to my wonderful friends. I continue to include a series of essays called Hot Topics in Marine Biology. These features bring current, exciting research to the students, with a diverse range of marine systems. In both the text and the Hot Topics, I try to connect the students to some of the most important recent research with an extensive literature section that is now online so that students can get to the best work for term papers and projects without too much distraction in the text. Older Hot Topics are also available to instructors for use. In my own classes, I am convinced that a good teacher must show students the way to good science because reference databases are not user-friendly or self-explanatory where finding excellent science research is concerned.

The Philosophy of This Text

This text is designed for a one-semester course at the sophomore to senior level. Some students will have already taken a college-level biology course with coverage of organismal diversity, and they will benefit greatly. A small number may even have taken a course in marine invertebrates or vertebrates and an introductory course in oceanography.

That said, I have successfully taught from this text for many years, and many students had no background in organismal biology or ecology. If the book is supplemented with journal articles—many of which are cited and recommended in the text or can be gleaned from the extensive online reference list—it can also be used in a more advanced undergraduate course in marine ecology. The sixth edition contains many new references to the primary literature, which are now accessible online in a bibliography accessed by a simple link mentioned at the end of each text chapter. This is a valuable resource to get students started on term papers and essays. The Marine Biology Web Page (you.stonybrook.edu/marinebio), which I founded a number of years ago, links students to many more views of marine biology and to a greater diversity of organisms, referrals to exciting books, and links to summer field courses and graduate programs. My career advice page had over 1 million visits as of 2020. A wealth of photos are available in the Marine Biology Explorations section. Thanks to Mark Lang for reformatting an enormous amount of material to a new server.

I have taught Marine Biology for over 40 years and have always been amazed at the diversity of students who take the course. Biology majors, marine science majors, geology majors, psychology majors, and even some humanities majors sit side by side. At my university, marine science constitutes a separate undergraduate discipline, and these students have truly learned the interdisciplinary nature of marine biology. Sustainability has become an integrated part of our educational program, bringing poets, biologists, and social scientists together to educate and inspire. All learn a great deal, and all seem to come away with a love

for the ocean. You don't have to convince them to be there: They *want* to learn about marine biology.

I do my best to keep that excitement alive, and I find that field trips and the use of color photographs and other illustrations throughout the text help a great deal. So do the online resources accompanying this text. As mentioned, Marine Biology Explorations (available at the companion website) includes hundreds of photographs from habitats discussed in the text and a large number of links to exciting videos. As mentioned, an expanded and updated reference list is also available online. In class, I keep a large map of the oceans on the wall for the geographic context of our discussions. I have taken many of my students with me to marine labs, and they have launched careers in science or used their backgrounds to enter other areas. I hope the text will help a wider audience to get excited about marine life. I hope, too, that they will understand how the ocean works and why our marine realm is so threatened.

A Principles-Driven Approach

Marine biology uses the principles of ecology and evolution, applying crucial biological and ocean science tools to a wide range of marine biological studies. We have three overarching themes: functional biology, biodiversity, and ecology.

Functional biology refers to the way organisms solve problems and how physical and chemical factors constrain and select the solutions. What shape should a maneuvering fish have relative to a continuously swimming fish? How does a small peptide manage to be such an effective poison when injected by a snail into a prey? How does this specific biochemical adaptation feed into an understanding of biodiversity? I believe this textbook is unique in combining effectively functional biology with ecological thinking.

Biodiversity is an essential part of marine biology, and I introduce the topic both through discussing the principles used to study and explain biodiversity and the factors that strongly affect marine biodiversity. A separate chapter discusses biodiversity and the processes that regulate it, both ecological and evolutionary. It is crucial that the student see the historical roots of many current distributions, which are affected by processes ranging from plate tectonics to climate change. This edition adds a great deal of coverage of recent advances, including molecular tools used to study marine biodiversity (especially in difficult situations like the microbes in the plankton), dispersal, speciation, and the rise of marine adaptations. This edition also includes a revised *bonus chapter on molecular tools in marine biology*, available online. Your students can see how molecular tools, old and new, are used in a wide range of marine biological applications, done at a depth that is not overwhelming to beginning students.

Ecology examines the interactions of organisms with their environment and tries to understand the distribution and abundance of organisms. It involves a series of processes, which I introduce in the context of a hierarchy—from *individuals to populations* to *ecosystems.* It also involves a discussion of important ecological processes along with accounts of major marine habitats and communities. This edition pays special attention to modern concepts of populations and species interactions, including connectivity, metapopulations, regional genetic differentiation, large-scale control of dispersal, biological invasions, and alternative stable states of communities. My background in geology, ecology, and evolutionary biology allows me to frequently combine ecological, evolutionary, and geological thinking in discussing marine biology problems.

This edition greatly expands coverage of climate change, which continues to be the greatest challenge to the future survival of many major marine habitats and is causing a major reorganization of marine life, from the geographic and depth ranges of many species to the very integrity of major marine ecosystems to effects on human use of the seas. The last edition added a separate introductory chapter so that instructors and students alike can be introduced to major principles behind climate change, but there are also many expanded discussions of threatened ecosystems, effects on fisheries, and the dual roles of thermal change and ocean acidification on marine life. Students need to understand the magnitude, urgency, and trajectory of the climate change crisis.

Organization

We begin with a brief historical background. Marine biology has a history that is worth understanding, but it is also crucial to introduce the student to how science works. Chapter 1 therefore discusses framing and testing hypotheses, as well as making tests practical enough that they can be put to direct use. From the very beginning, I introduce the student not only to the scientific method, but also to how it translates into an intellectual tool with real-world applications. Chapters 1 through 7 introduce basic principles of how the ocean works in a physical, chemical, and ecological context and how marine organisms function with these constraints. Chapter 2 gives the student a comprehensive introduction to oceanography and the important properties of seawater that might affect marine organisms. Chapter 3 covers climate change and the interaction of climate oscillations, such as El Niño, with longer-term trends driven by human-caused inputs of greenhouse gases, including an introductory coverage of ocean acidification. In Chapter 4, I introduce ecological and evolutionary principles so that students can work their way through concepts using marine examples. This allows all students to be brought up to a level of ecological thinking and an understanding of oceanographic processes. They will see this "big picture" as they read the rest of the text. Chapter 5, on the physical-chemical environment, discusses how temperature, salinity, and other important physical variables affect marine organismal function and survival. The book extensively discusses both macro- and microscale effects of climate change, including ocean acidification, range changes, and ecosystem effects. Chapter 6 then introduces students to how the physics of fluids shapes the constraints and adaptations of marine

organisms. As far as I know, this crucial subject is missing in all other marine biology texts and allows a connection to a complete understanding of how the marine organisms function in the rather complex fluid environment. This subject is absolutely essential to see how the ocean works and how the same seawater environment has drastically different impacts on organisms' different sizes and shapes. Chapter 7 concludes these discussions with a comprehensive introduction to reproductive strategies, larval dispersal, and migration, which sets up the big picture of the geographic distribution of marine species, down to the microscale of how mobile marine larvae succeed in finding a place to live in a turbulent and stressful world.

Chapters 8 through 12 cover the *organisms* and *processes* that are important in the water column of the open sea, including coverage of the major organisms from plankton to whales and the latest ideas on the rise and demise of phytoplankton blooms. This organism-process approach is essential so that students will understand the overall economy of the marine realm, while not forgetting the major players on the ecological stage. Chapter 10 emphasizes adaptations and processes in the water column, ranging from bioluminescence to diel vertical migrations. This leads to a detailed discussion of the processes that cause the genesis of phytoplankton blooms, the major drivers of global productivity, and often local, ecologically harmful blooms. Chapter 12 uses a global-scale approach to show how biological studies of the ocean lead to an understanding of the world's potential for fisheries and the global biological impact on the ocean of climate change.

Bottom organisms and habitats are covered in Chapters 13 through 18, which depend both directly and indirectly on the water world above. In Chapters 13 and 14, I cover benthic creatures, and then I go on to discuss the principles necessary to understand the ecology of marine bottom organisms (Chapter 15) and the major near-shore marine bottom habitats (Chapters 16–19). By necessity, I have been selective. I emphasize those habitats that are not only important and interesting, but also those in which important principles can be illustrated to their best advantage. This is a major reason why so much attention is paid to the tidelands, our ecologically best-known marine habitats, where many principles have been established for research. Community-level interactions are emphasized, as is global climate change as it relates to major changes in habitats such as coral reefs. I discuss a range of geographic locations so that the instructor will find local examples in many instances. Crucial habitats, such as the intertidal, seagrasses, coral reefs, mangroves, estuaries, salt marshes, kelp forests, and others, are discussed both from the points of habitat distinctions and ecological processes and the impacts of biological invasions and climate change. Oyster reefs are highlighted because of their great worldwide importance as foci for biodiversity and their role in ecosystem services. I discuss the drivers of coral reef ecology, but also the great problems they face from disease, ocean warming, and acidification. Restoration is also an important topic. So many marine habitats are in dire need of such attention.

Chapter 18 then looks at the important gradient from the continental shelf to the deep sea, paying special attention to some of the fascinating discoveries about biological function and fascinating habitats, from hot vents to deep-water coral mounds to the recently discovered subsurface bacterial realm over 500 m beneath the seafloor. I cover Arctic and Antarctic environments, which are on the front lines of climate change effects, in Chapter 19. I incorporate a wide range of discussions from the organismal to the ecosystem level, including the decline of sea ice, ice algae, and the crucial resource of krill in Antarctic food webs. Chapter 20 focuses on and summarizes what we know about marine biodiversity geographic patterns, including sections on invasive species, conservation of biodiversity, and conservation genetics. More and more, students and researchers have focused their attention to the deteriorating conditions of the ocean, and conservation is a major field of emphasis.

Finally, Chapters 21 and 22 tackle other human interactions with the sea, as both a source of food and, unfortunately, a waste receptacle. I cover human effects on the ocean. Throughout the text, the effects of climate change are brought up in many contexts, as are how those effects are related to chemical issues such as acidification and facilitation of biological invasions. I also place strong emphasis on the reorganization of communities that has been initiated by the interaction of human activities and strong ecological interactions found in natural communities and in food webs. The impact of overfishing on populations and trophic cascades is a crucial part of a complete chapter on fisheries and mariculture. I include in Chapter 21 a section on drug discovery in the ocean, because of the great student interest in this subject and the connections between biodiversity and the new sources of compounds to combat pain and disease such as cancer. It is a revelation, to me at least, how a dangerous animal like cone snails can synthesize toxins that hold great hope for reduction of pain without the side effect of drug addiction. The roles of toxic substances, eutrophication, and hypoxia are discussed clearly and in depth. I discuss the fascinating topic of evolutionary responses to stress and novel toxic substances introduced into the ocean. I also cover developing problems such as introduction of microplastic particles into the ocean. Lurking behind many of the chapters is the bonus chapter on molecular tools. This is a major component of the future of marine biological understanding.

A Refined Learning Package

This text has a series of pedagogical features designed to help students absorb a wide range of information and concepts by engaging their imaginations, helping them organize and prioritize important principles, and keeping them focused on the big picture, without getting lost in the details. Hot Topics in Marine Biology essays throughout the text introduce students to recent advances in the understanding of marine biology and discuss current issues, especially marine biological debates and discoveries. Instructors can use these essays to kick off discussion, to expand a student's horizons,

for course assignments, or as topics for term papers. A section on the amazing discoveries of homing of sharks to highly localized reproductive sites is found in Chapter 7. The great strides made in reducing the scourge of shark finning is covered in an essay in Chapter 21. A Hot Topics essay in Chapter 16 addresses exciting new molecular techniques used to identify a virus associated with the recent catastrophic sea star wasting disease on the US west coast. I discuss in Chapter 15 the amazing story of how snapping shrimp seize their prey with astounding noise, vaporizing water, and blistering speed. I also focus in Chapter 21 the astounding story of how seafood is moving to higher latitudes. Some Hot Topics have been retained from the fifth edition because they are still "hot," such as the use of dogs to locate whale scat for molecular and hormonal data and the possible adaptation of microbes to breaking down oil in the Gulf of Mexico. Every day in the news, we see exciting new developments, so instructors need to embellish these hot topics with their own hot interests.

Key Concept full-sentence summary statements begin nearly every section of the text to help students identify central points of discussion and to foreshadow what's to come. These headings allow students to discern the forest from the trees and to quickly scan the basic progression of material by looking ahead through the chapter. Each chapter ends with a bulleted *Chapter Summary* and a variety of *Review Questions*. Instructors and students can use these to follow up on important issues in marine biology. The combination of these features and the Key Concept heading sentences successfully guides the student through a complex subject. Going Deeper boxes explain equations and related concepts in marine biology. Especially in early chapters, they will help students learn often-difficult material or refresh their memory of elementary courses (e.g., photosynthesis). They also allow instructors who choose to omit them to press on with no interruptions. An example is the discussion of Leslie matrices in Chapter 21, which give the student an idea of how age-structured population models help to understand impacts of various factors on fisheries and management decisions. Extensive *References* lists of classic and contemporary scholarship that instructors may assign as reading and that can lead students to further assignments are linked online from the text. These help students see that marine biology is a living field of research, not just a static textbook of "known" facts, without interrupting the flow of the text. A comprehensive *Glossary* of marine biology at the end of the text provides students access to get a quick definition of important concepts, processes, and terms. A *list of journals* is also included as a resource for students in writing term papers and for further research.

What Is New and Noteworthy in the Sixth Edition?

Expanded illustration program. We continue the sixth edition with using a rich color presentation to better demonstrate marine biological principles and introduce organismal diversity in a vivid and captivating visual presentation. The new edition includes many new photos and line drawings (many of the photos generously contributed by colleagues), and I believe students will benefit greatly from having the color photos integrated directly into the relevant textual discussion at hand. Lovely underwater photographs of a voracious subtidal sea star and a really cool sea squirt are among the newest, including the amazing deep-sea creatures endangered by submarine mining, and a very exciting new research vessel in Alaska, leading the way in high latitude Arctic research.

More applications. To engage students with the diversity of marine biology today and to highlight the real-world applications of what they are learning, I've written many new in-text examples, including seven new Hot Topics in Marine Biology. Students will see how molecular tools can be used to study the origin of a major disease, how conservation efforts have succeeded and will continue to succeed in reducing shark finning, and how ocean acidification is now a major danger to shellfisheries.

Current and expanded topics. These maintain the excitement that underlies my philosophy of teaching and have been carefully selected to bring the text up-to-date while still remaining focused on the most important *principles* students need to learn:

- *Evidence and effects of climate change.* I have greatly expanded coverage of climate change and revised Chapter 3, which introduces the important issues, especially the difference between climate oscillations and protracted climate trends. I pay special attention to temperature change in the global ocean and in coastal areas (Chapter 3), ocean acidification (Chapters 2, 3, 8, 12, 17, and 21), and the role of climate change in changing species distributions, facilitating biological invasions, and causing thermal stress (Chapters 2, 3, 5, and several others).
- *New ideas that challenge us all.* It is hard to accept sometimes that textbook accounts are incomplete or even wrong. But our field is rapidly changing, with new discoveries and outlooks. I pay special attention to an incipient revolution in our thinking about the advent of the spring phytoplankton bloom, which for many years has been explained using the classic Sverdrup model of spring phytoplankton blooms. This is about to change, and I attempt to show the problems with the classic model and how we might build a new approach, based on recent research. I look forward to hearing how students react to this.
- *Ecological interactions.* Strong attention is paid to major ecological interactions that are relevant to ecosystem structure, such as trophic cascades (Chapters 16 and 17), ecological reorganizations in New England and elsewhere (Chapter 16), molecular approaches to ecology and evolution (Chapters 4, 5, 6, 7, and others, including a bonus chapter online), natural and human-induced phase shifts (Chapters 3 and 17), biological invasions (Chapters 3, 7, 8, 16, 17, 18, 19, and 20), and climate

change (Chapters 2, 3, 4, 5, 7, 8, 10, 11, 12, 16, 17, 19, and 20).

- *Methods of environmental assessment, from remote sensing to the molecular level.* I have also expanded coverage of the latest methods for remote sensing, estimating world productivity, and assessing the stress on and change of ecosystems, including satellite methods and ocean observatories (Chapters 1 and 12), acoustic detection of fish and marine mammals (Chapter 7 and 10), genetic and molecular studies of population differentiation (Chapters 5, 7, 9, and 20), the shifting baseline concept (Chapter 20), diversity gradients and the tropical origins of biodiversity (Chapter 20), and molecular methods to assay the cause of disease and the diversity of microorganisms in the water column (Chapters 11 and 16).
- *Human impact on biodiversity.* This edition expands coverage of the decline of coral reefs and adds insights on other biological impacts, such as the increase of sponges at the expense of corals (Chapter 17), overfishing and the issue of relating management decisions to management of the basis of ecosystem function (Chapter 21), the declines of sharks and other apex predators (Chapter 21), and the effects of pollution, especially oil pollution and the expansion of inputs of plastics into the ocean (Chapter 22).
- *Emphasis on polar biology*. We notice right away from the new accomplishments of polar ecologists how much there is to learn about polar food webs and how climate change is rapidly changing the nexus of sea ice, productivity in the nearby ocean, and especially the changing nutrient supplies and productivity of crucial food species such as krill. Chapter 19 discusses these issues and the dangers that lie ahead for polar communities in the face of climate change.
- *Molecular approaches.* I continue to emphasize molecular studies because they are becoming so important in the study of environmental stress, identification of genetic differentiation of species, and identification of difficult groups of microorganisms. As mentioned, there is a free online bonus chapter on molecular methods that your students can use as a resource.

Supplements

Marine Biology, Sixth Edition, is accompanied by a wealth of electronic resources for both students and instructors, including a FREE companion website (www.oup.com/us/levinton) and FREE access to the Instructor's Resource Ancillary Resource Center (www.oup.com/us/levinton/resources).

Companion website. Maintained by the author, this companion website (www.oup.com/us/levinton) provides a multitude of resources for both students and instructors:

- **Student Resources**
  - *Marine Biology Explorations*. Explore the ocean's biodiversity through nine different marine habits, with over 450 photos with annotations!
  - *Marine Biology in the News.* Frequently updated current breakthroughs in marine biology research.
  - *Extensive web links.* Numerous links to marine biology topics and research literature. You will also find information on careers in marine biology and worldwide marine laboratories.
  - *Bonus molecular tools chapter.* An overview of how molecular tools, old and new, are used in a wide range of marine biological applications.
  - *Hot Topics Archive.* Hot topics may cool off, but their relevance to marine biology is lasting. The student website will now feature a full archive of past hot topics.
- **Instructor Resources** (available to adopters of the text and password-protected)
  - *Electronic images.* All illustrations from the text available in electronic format for download for lecture presentations.
  - *PowerPoint lecture notes.* Over 400 lecture-notes slides, organized by chapter.
  - *Video guide.* A guide to video and multimedia most relevant to marine biology topics.
  - *Test bank.* Includes approximately 400 questions written by the author himself in editable Word files for easy customization (available on the Ancillary Resource Center; contact your Oxford University Press sales representative for details).

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Marine Biology