SECOND EDITION

JAMES W. NYBAKKEN

MARINE BIOLOGY

AN ECOLOGICAL APPROACH

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and the Moss Landing Marine Laboratories

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Cover photo: An underwater scene on the Pacific Coast of North America. The large red anemone is *Talia lofotensis.* The dark blue irregular spot is a sponge, *Hymenamphiastra cyanocrypta,* which has in it a blue-green alga symbiont. The small yellow spots with tentacles are individuals of the solitary coral *Balanophyllia elegans.* © Lovell Langstroth, Carmel, California.

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PREFACE

In recent years, there has been an increasing interest in the field of marine biology at the undergraduate level in our two-year community colleges as well as in four-year colleges and universities. That interest apparently derives from the growing awareness and concern at all levels of society of the importance of the world's oceans as sources of food, as reservoirs of minerals, as major suppliers of oxygen and regulators of climates, and as the ultimate dumping ground for the mounting burden of human waste materials. This concern has been popularized and brought into focus by the various international disputes on fishing rights, the whale problem, international law of the seas conferences, and numerous television programs and books addressed to the general public about marine life.

As a result of this heightened public awareness, marine biology courses have attracted a wide spectrum of students with varying backgrounds who desire a basic understanding of the biological processes that operate in the oceans.

It is important to understand that in the oceans, just as on land, there are scientific principles that govern the organization and perpetuation of organisms and associations. Although those principles operate somewhat differently in the ocean than on land because of the physical properties of water, they can be readily set forth and may be understood by those with a minimum background in other sciences and in mathematics.

The texts in marine biology available to serve these courses appeared to me to lack an ecological approach to the entire marine environment; they tended to emphasize specific areas, habitats, and organisms to the exclusion of broader concepts and processes. I was thus stimulated to write this book as a basic introduction to marine biology, emphasizing ecological principles governing marine life throughout the world, not as a purely taxonomic or regional approach, so that it would be useful in all parts of the world. I have, furthermore, purposely downgraded any discussion of pure oceanography, except as it bears upon organization of the associations or communities, in order to increase coverage of the biology. The sequence of topics in this book closely follows the sequence in my undergraduate course in marine ecology, which I have taught for several years at the Moss Landing Marine Laboratories.

This text is designed for the undergraduate student in marine biology. It presumes a certain minimum of background in very basic concepts of chemistry, physics, and biology, but no more than would be obtained from a high school or introductory college course in each of these fields. Familiarity with the major invertebrate phyla is helpful, but not necessary. Some acquaintance with the basic ecological concepts is also helpful, but if lacking, may be obtained from Chapter 1. Although the text is generally aimed at the lower-division undergraduate student, I have tried to imbue this book with sufficient rigor and detail that it will also be useful in upper-division undergraduate courses in marine ecology and biological oceanography. To this latter end, I have included text citations to the primary literature.

This text stresses ecological processes and adaptations that act to structure marine associations and permit their persistence through time. It is thus not a guide to the local fauna and flora. It is presumed that familiarity with this, if necessary, will be obtained in laboratory and field trips in which the instructor will provide the taxonomic expertise.

Depending on the time available in the course, this book includes perhaps more material than can be adequately covered in a single quarter or semester. In that case, the instructor may choose to concentrate on those chapters or areas of most concern in his or her geographical region. Thus, for example, instructors in temperate zones may wish to de-emphasize coral reefs and many may wish to spend less time on deep-sea biology and more on the intertidal, to which they have direct access. Suggestions for use of the book under varying course conditions are given in the instructor's manual. However, I hope that the comprehensive nature of this book means that whatever instructional choices are made, information will be available from the book.

CHANGES IN THE SECOND EDITION

This edition is considerably changed and expanded from the first edition. The revisions reflect (1) additional coverage of subjects not treated or treated inadequately in the first edition, (2) the expanded knowledge about existing subjects that has been brought to light since the publication of the first edition, and (3) my own interest in strengthening the treatment. I trust that the inclusion of additional material and more rigorous treatment of all subjects will meet the criticisms of those teaching more advanced courses who found the first edition somewhat shallow with respect to content, while retaining the readability and explanatory information necessary to permit the nonbiologist to continue to use it.

Among the subjects that have been substantially changed or upgraded from the first edition are niche theory, larval biology, succession, plankton size classes, nanoplankton and the significance of nanoplankton productivity, plankton patchiness, plankton food webs, whale feeding, deep-sea thermal-vent communities, deep-sea diversity patterns, physiological adaptations of deep-sea organisms, subtidal sedimentary communities, seagrass beds, the role of grazing in rocky intertidal communities, grazing in coral reefs, transfer of organic production from marshes to offshore, and the role of birds and fishes in sedimentary environments. New subjects in this edition include a discussion of the major planktonic communities worldwide and their ecological characteristics, subtidal rocky community organization, community structure of subtidal sedimentary environments, protected sand beaches and their ecology, the role of larval settlement on community structure, symbioses of sulfur bacteria and thermal vent organisms, coral reef cryptofauna, the role of El Niño as a catastrophic event for coral reefs, biological interactions in mangrove forests, and radioactive wastes in the oceans.

One common criticism of the first edition was the low number of examples and the lack of referencing of the scientists who actually did the work. Science, as one reviewer put it, is done by scientists, so why not give some name recognition? I have tried to do this throughout this edition and have included many more citations to the literature and to substantial review papers. As I see it, the main danger in this approach, particularly for an undergraduate text, is the chance that such references will become so abundant that the readability and flow of the text will be lost. I hope that I have avoided this trap by restraint in the use of literature references. I have also discarded the dual listing of references, which was disliked in the first edition, for a single system of listing all references for a given chapter at the end of the chapter.

In this edition I have purposefully included more information and examples that point out the controversies in marine ecology because I believe that it is important for the student to learn that not only are there many unsolved problems in the field of marine ecology, but that there are disagreements among scientists about how these various communities and systems are organized. In this latter connnection, I think it is particularly important for the student to recognize that studies elucidating the mechanisms of working of a given community in a given geographical area likely cannot be extrapolated as a "universal" explanation for the organization of communities in similar environmental settings throughout the world.

The first edition was perceived by many as distinctly biased toward the Pacific coast, even though I felt that I had made an effort to avoid that bias. I have tried to remedy that in this edition with more coverage of Atlantic and Gulf coast examples, particularly with respect to intertidal and subtidal sedimentary environments. I think that it is important to point out in this context that most of the East Coast of the United States south of New England as well as the Gulf Coast consists of sedimentary environments such as open sand beaches, protected sand beaches, muddy shores, and large estuaries and marshes. Rocky shores are rare. The Pacific coast, by contrast, consists mainly of rocky shores, with few estuaries and other sedimentary environments. I hope, therefore, that I will be forgiven for continuing to use Pacific coast examples in discussions of rocky shores and commended for expanding a discussion of the dominant Atlantic and Gulf coast sedimentary environments.

Some who have used this book in more advanced classes have suggested that I remove the very basic introductory ecology material from Chapter 1 because their students have had it already. I have chosen not to do so in deference to those who teach more basic courses without major prerequisites and who feel that their students need it. I can suggest only that those whose classes are more advanced simply ignore it.

As the author of this textbook, I am indebted to a large number of marine scientists whose research work is the foundation on which this book is based and who are too numerous to mention in entirety here. A few of this vast number are

mentioned in the text and listed in the literature cited. I am, however, particularly appreciative of the help given me by my colleagues and students at Moss Landing Marine Laboratories, many of whom offered suggestions, pointed out errors or additional literature to be studied, and read and criticized various chapters of the first edition. In this regard, I should like to thank Dr. Gregor Cailliet, Dr. George Knauer, Dr. Victor Morejohn, Dr. Michael Foster, and Dr. Michael Moser. I wish to thank also those colleagues who contributed photographs and drawings to the original edition, including Dr. Paul Dayton, Dr. Joseph Connell, Dr. Fred Grassle, Dr. Charles Birkeland, Dr. Richard Young, Dr. Richard Schwartzlose, Dr. Robert Hessler, Dr. Glen VanBlaricom, Dr. John Oliver, Dr. Lovell Langstroth, Mr. Michael Kelly, Dr. Richard Mariscal, and Dr. Clyde Roper. I am particularly indebted to Ms. Lynn McMasters, who was primarily responsible for transforming my scribbles into acceptable artwork; Ms. Rosemary Stelow, who did an outstanding job in typing, proofreading the original manuscript, and picking up my errors; and Ms. Sheila Baldridge, the Moss Landing librarian, who could always find the missing reference and who put up with long absences of a significant number of books and periodicals.

I am also grateful to the following outside reviewers whose comments and suggestions were of great help to me in improving the original manuscript: Dr. Peter Frank, Dr. Robert Hessler, Dr. William Jorgensen, Dr. James Lanier III, Dr. Roger Lloyd, Dr. Don Mauer, Dr. John Morrill, Dr. J. A. Musick, Dr. C. H. Peterson, Dr. E. R. Pariser, Dr. Wendell Patton, Dr. Robert Simon, and Dr. Ivan Valiela.

In addition to those colleagues named above who helped me in the first edition of this book, I should like to thank the many who have helped with this edition by providing me with constructive criticisms of the first edition and pointing out errors. I am particularly indebted here to Dr. Joy Zedler, Dr. Don Redalje, Dr. Peter Fankboner, Dr. Michael Foster, Dr. Bernd Wursig, Dr. Greg Cailliet, and four anonymous reviewers. I am also grateful to Dr. Eugene Kozloff, Dr. Joseph Simon, and Dr. Thomas Niesen for their helpful critiques of the manuscript of this edition. Additional photographs for this edition were graciously provided by Dr. Fred Grassle and Drs. Lovell and Libby Langstroth.

Finally, I should like to thank the staff of Harper & Row, particularly Claudia Wilson, Biology Editor, for her great patience and encouragement in the process of this revision. This was especially needed, since I was engaged in another major writing project at the time and was especially stressed at what seemed at many times to be overpowering demands on my time.

Because of the broad scope of the book and necessary limitations in pages, I have often been forced to treat certain complex or poorly understood processes through generalizations that some many consider serious oversimplifications. Undoubtedly some errors and omissions remain. I therefore close with a request to all who may use this book that they feel free to pass on to me any errors, omissions, mistakes in interpretations, comments, or suggestions that they may have, so that I might correct my ignorance and improve any future revisions.

James W. Nybakken

CONTENTS

chapter **1**

Introduction to the Marine Environment

About 71 percent of the surface of this planet is covered by salt water. Beneath this surface, the water depth averages 3.8 km, giving a volume of 1370×10^6 km^3. Since life exists throughout this immense volume, the oceans constitute the single largest repository of organisms on the planet. These organisms include representatives of virtually all phyla and are tremendously varied. All, however, are subject to the properties of the seawater that surrounds them, and many features common to these plants and animals are the result of adaptations to the watery medium and its movements. Before we can begin a consideration of the major associations or assemblages of organisms, we need to examine briefly the physical and chemical conditions of seawater and aspects of its motion (oceanography), and some basic ecological principles and terms that will be central to an understanding of the processes discussed in the remainder of this text. Finally, we will make some comparisons between aquatic and terrestrial ecosystems to point out some fundamental differences in organization.

PROPERTIES OF WATER

Water is the substance that surrounds all marine organisms. It also composes the greater bulk of the bodies of marine plants and animals, and it is the medium in which various chemical reactions take place, both inside and outside living organisms.

Chemical Composition

Pure water is a very simple chemical compound composed of two atoms of hydrogen (H) joined to one oxygen (O) atom. Expressed symbolically, it is H_2O.

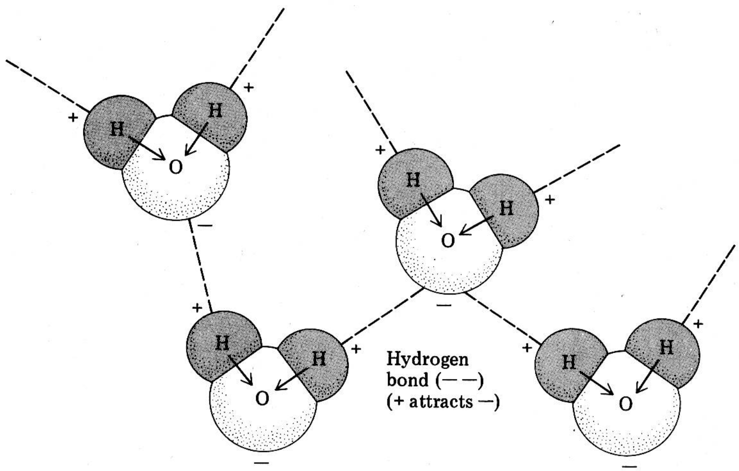

Figure 1.1 Diagrammatic representation of a series of water molecules, indicating the polar nature of the molecules and the hydrogen bonding.

The H atoms are bounded to the oxygen asymmetrically such that the two hydrogens are at one end of the molecule and the oxygen at the other. The bonding between the H atoms and the oxygen is via shared electrons, each H sharing its single electron with the oxygen. In this manner, oxygen receives the two electrons needed to complete its outer electron shell, and each hydrogen the one needed for its outer shell. However, the oxygen atom tends to draw the electrons furnished by the hydrogen atom closer to its nucleus. This creates a slight negative charge at the oxygen end of the molecule, while the removal of the electrons away from the hydrogens results in a slight positive charge at that end. This electrical separation creates a polar molecule.

The polar nature of the water molecule means that the hydrogen end, which is positive, will attract the negative, or oxygen, end of other water molecules. This gives rise to weak bonds, called *hydrogen bonds,* between adjacent water molecules. These bonds are only about 6 percent as strong as the bonds between the hydrogen and oxygen in the water molecule itself, and they are easily broken and re-formed (Fig. 1.1). It is this hydrogen bonding between adjacent water molecules and the polarity of the water molecule that is responsible for many of the unique chemical and physical properties of water. Indeed, if water were not polar and did not form such bonds with adjacent molecules, it would be a gas, not a liquid, at room temperature, and its freezing point would be lower than temperatures found over most of the earth's surface. Under such conditions, life would be impossible.

Physical and Chemical Properties

Because of the hydrogen bonding, water tends to stick firmly to itself, resisting external forces that would break these bonds. This is called *cohesion.* At air-water interfaces, the strength of cohesion forms a "skin" over the water surface, strong enough to support small objects. This phenomenon is called *surface tension.* The surface tension of water is the highest of all common liquids and permits the existence of associations of organisms either suspended below it or moving over the top. Cohesion is also responsible for the *viscosity* of water. Viscosity is a property measuring the force necessary to separate the molecules and allow passage through the liquid. This resistance to flow or movement is important in the sinking rate of objects (pp. 58–63) and in problems of movement in the water by animals (see pp. 112–114). Cohesion properties are temperature dependent, increasing with decreasing temperature.

Another set of properties concerns the effects of heat. Water, when heated, evaporates slowly in comparison with other liquids of simple molecules. This means that the *heat of vaporization* of water is high—the highest of most common substances. This is a direct result of the strength of the hydrogen bonding between molecules, which must be broken in order to allow the escape of a molecule. Because of the high heat of vaporization, water evaporates slowly and, by so doing, absorbs considerable heat, leading to cooling. Similarly, this high heat of vaporization means a high boiling point (100° C), with the result that water is a liquid on earth rather than a gas. Related to this is the *latent heat of fusion,* which is the amount of heat gained or lost per unit mass when a substance changes from a solid to a liquid or vice versa. Water, again, has the highest value of most common liquids. Ice, when melting, therefore takes up large quantities of heat. When ice is formed, large quantities of heat are given off.

The high values for both the heat of vaporization and latent heat of fusion mean that it takes more heat to effect a change in temperature in a given quantity of water than in virtually any other common substance. This high *heat capacity* means that water is a strong cushion against both rising and falling temperatures and therefore ameliorates the climate; also, it means that the range of temperatures experienced within any body of water is less than that in air.

Water has a peculiar *density-temperature* relationship. Most liquids become more dense as they are cooled. If cooled until they become solid, the solid phase of such liquids is more dense than the liquid phase. This is not true for water. Water becomes more dense as it is cooled until it reaches 4° C. Cooling below this temperature decreases the density, and when freezing occurs, there is a marked decrease in density. Therefore, ice is lighter than water and floats upon it. This property is of utmost importance to life in the oceans; otherwise, major volumes of the oceans would be uninhabitable as large blocks of ice.

The chemical properties of water that are of importance are those concerned with the solvent capacities (Fig. 1.2). Water is almost a universal solvent, with the ability to dissolve more substances than any other liquid. This is because the solvent action is of two types: one depends on the polar character of the molecule and the other on the hydrogen bonding. Various nonpolar organic and inorganic compounds containing oxygen atoms or hydrogen atoms bonded to either oxygen or nitrogen atoms are held in solution by hydrogen bonding. The polar dissolving action of water for various salts depends on the interaction of the salt ions with the charges on the water molecule. When a salt is dissolved in water, it breaks into its component ions. Thus, common table salt, NaCl, when put into water, breaks into Na^+ and Cl^- ions. It is through interaction of the charges on the salt ions and the water molecules that salts are held in solution.