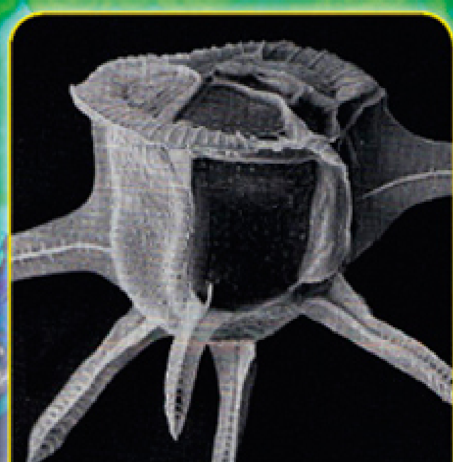
CHARLES B. MILLER
PATRICIA A. WHEELER

# BIOLOGICAL OCEANOGRAPHY



SECOND EDITION

WILEY-BLACKWELL

# Table of Contents

## Color plates

## COMPANION WEBSITE

This book is accompanied by a companion website:

www.wiley.com/go/miller/oceanography

With figures and tables from the book for downloading

# BIOLOGICAL OCEANOGRAPHY

SECOND EDITION

**Charles B. Miller**

and

**Patricia A. Wheeler**

*College of Earth, Ocean and Atmospheric Sciences*
*Oregon State University*
*Oregon, USA*

WILEY-BLACKWELL
A John Wiley & Sons, Ltd., Publication

This edition first published 2012 © 2012 by John Wiley & Sons, Ltd.

Blackwell Publishing was acquired by John Wiley & Sons in February 2007. Blackwell's publishing program has been merged with Wiley's global Scientific, Technical and Medical business to form Wiley-Blackwell.

*Registered office:* John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

*Editorial offices:* 9600 Garsington Road, Oxford, OX4 2DQ, UK

The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

111 River Street, Hoboken, NJ 07030-5774, USA

For details of our global editorial offices, for customer services and for information about how to apply for permission to reuse the copyright material in this book, please see our website at www.wiley.com/wiley-blackwell.

designed to provide accurate and authoritative information in regard to the subject matter covered. It is sold on the understanding that the publisher is not engaged in rendering professional services. If professional advice or other expert assistance is required, the services of a competent professional should be sought.

*Library of Congress Cataloging-in-Publication Data*

Miller, Charles B., 1940–

Biological oceanography / Charles B. Miller and Patricia A. Wheeler. – 2nd ed.

p. cm.

Includes bibliographical references and index.

ISBN 978-1-4443-3301-5 (cloth) – ISBN 978-1-4443-3302-2 (pbk.)

ISBN 978-1-1182-2316-1 (mobi) – ISBN 978-1-1182-2317-8 (epdf) – ISBN 978-1-1182-2318-5 (epub)

1. Marine ecology. I. Wheeler, Patricia A., 1949– II. Title.

QH541.5.S3M55 2012

577.7–dc23

2011046023

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

# *PREFACE TO THE SECOND EDITION*

Scientific scholarship has changed markedly in the nine years since writing was finished on the first edition. Our journals are no longer printed on paper and studied in a library. Rather journals come to us as computer files. Only ten years back, papers printed adjacent to those suggested to us by colleagues or indexing services were often interesting and took us afield to exciting and divergent facts and ideas. Now the indices can find almost everything written about almost anything (metagenomics of arctic archaea, growth rings in whale teeth, swimming mechanics of amphipods, …); but the leaps into unrelated subjects are rarer. Moreover, the shear quantity of oceanographic (and biological!) literature is intimidating. There are more scientists everywhere and virtually all of them are publishing in English. Many long-standing journals now run to thousands and tens-of-thousands of “pages” yearly, and to that has been added a layer of new open access, on-line only journals. Thus, it is difficult to keep up with even sub-subspecialties (say, replacement of phosphorus in *Prochlorococcus* metabolism). We suspect that you prospective oceanographers, for whom this book is intended, will need to become extremely specialized, descending into the narrow wells you will drill into the expanding array of biological and oceanographic problems. Nevertheless, starting with a fairly wide perspective in your field will serve you well, and maintaining a usable introduction across the diverse aspects of biological oceanography has been our goal in revising *Biological Oceanography*.

Our perspective in this book is resolutely organismal: what are the prokaryotes, algae, protists and animals living in the seas and how do they make their way in the water, survive through generations, feed themselves and each other? How are these organisms distributed and why? What specific adaptations are required to live in blazing surface sunshine, dark deep waters, in bottom mud and near hydrothermal vents? How will those adaptations serve and change as the oceans warm and grow more acidic from dissolving carbon dioxide? We take this approach for the lighted upper layers, dim mesopelagic zone and the seafloor, emphasizing for each some aspects of ecological studies conducted in them. There are other perspectives, particularly an emphasis on biological-physical interactions. Those are mentioned many times here, but a more directed treatment in that vein is provided in a third (2006) edition of *Dynamics of Marine Ecosystems* by K. H. Mann and J. R. N. Lazier, also published by Wiley-Blackwell. We recommend it when that emphasis is sought.

We have tried to select exemplary studies for many types of organism-organism and organism-habitat interaction. Some are recent. Many were left in from the first edition; not all topics have been studied recently and there is value in avoiding the impression that ocean ecology began in 2003. On the other hand, many topics have been "hot" in this decade, and for those we have chosen new examples. There is more molecular genetics, which has swept across all aspects of biology, including biological oceanography. A new first chapter considers some basic aspects of living in water, especially salt water. An updated discussion of spring blooms has been moved to Chapter 11 on pelagic biomes, and that discussion is greatly expanded. There is a new chapter on pelagic food chains, including identification of trophic levels from gut contents and from stable isotope ratios.

If you have been active in biological oceanographic research, your study may be shown or at least cited, but only a very small fraction of useful studies could be cited.

Yours could be “on the cutting room floor”, or likely we never found it at all. Not being included is not to be taken as judgment about your work. Some specialists found their fields under-represented in the first edition. That will happen again with the second edition, and we recommend to those who are teaching to fill gaps for their students with their own knowledge and distribution materials.

Like other scientists we are at least moderately opinionated about our subject matter and that of others. Much of that opinion has been allowed out on parade here. As you students and teachers find things to disagree with us about, perhaps something that can be explained better, let us know about it. For the moment we are still working and would like the communication to go both ways. Let us hear from you. Thanks.

Charles B. Miller and Patricia A. Wheeler

Corvallis, Oregon, USA

November 2011

# ACKNOWLEDGEMENTS

Most warmly, we thank Martha Clemons and John Westall, our spouses, for helping us through the long sieges of study that revising this book has required. Thanks to Dean Mark Abbott for making the College of Earth, Ocean and Atmospheric Sciences (CEOAS, Oregon State University) facilities available to us deep into “retirement”, and thanks to all our colleagues at CEOAS for sharing their expertise. Dave Reinert of CEOAS made improvements in many figures, and Guin Library staff Janet Webster, Susan Gilmont and Judy Mullen helped us with the mysteries of computerized literature. Thanks to the Oxford staff of Blackwell, particularly Ward Cooper for recruiting a second edition and Kelvin Matthews for seeing the manuscript through the press. Caroline Needham provided thoughtful copy editing, and Anne Bassett and Kevin Fung managed typesetting. Thanks to the one to three scientists who reviewed each chapter at the request of the publisher; Wiley-Blackwell resolutely kept your identities secret. All were helpful critics, offering useful suggestions. Even those disappointed in our chapters offered ways to improve them. We particularly thank Harold Batchelder, Michael Behrenfeld, Peter Franks, Bruce Frost, Erica Goetze, David Kirchman, Michael Landry, Tammi Richardson, Antoni Rosell Melé, Phillip Mundy, Evelyn Sherr, Barry Sherr, Suzanne Strom, Erik Thuesen, George Waldbusser and Jonathan Zehr, all of whom told us they provided reviews or looked at chapters at our request. Errors inevitably remain, all assignable to us not to the reviewers. Thanks also to the unhappy reviewer of Chapter 1, who felt it was too much an exercise in “cultural erudition”. How else could we know we even approached that goal?

We thank all the scientists whose papers provided figures, over three hundred of you, some no longer alive. Dudley Chelton, Matthew Church, Erica Goetze, Nicolas Gruber, Christophe Menkes, Heidi Sosik, Taro Takahashi and Peter Thor provided modified figures or figure files with better resolution. Thanks to them.

Thanks to the following journals and organizations holding copyrights for permission to reprint figures: *Advances in Marine Biology* (Fig. 13.21); *American Naturalist* (7.19, 13.14, 13.16, 13.17); *Annual Review of Genetics* (Plate 2.1); *Applied Environmental Microbiology* (5.7, 15.6, Box Fig. 5.1.1); *Aquatic Microbial Ecology* (5.13, 7.10d&e, 9.6, 11.30); *Archiv für Hydrobiologie* (5.8); *Arctic* (Plate 11.3); *Biodiversity and Conservation* (13.20); *Biogeochemistry* (3.13); *Biological Bulletin* (12.18); *Biological Reviews* (12.10, 12.11); *British Journal of Experimental Biology* (Box Fig. 7.2); *Bulletin of the Ocean Research Institute, University of Tokyo* (10.10); (*Bulletin of Marine Science* (11.7, 17.12a&b); *Bulletin of the Scripps Institution of Oceanography* (10.5, 10.6, 10.7b, 10.8, 10.15); *CalCOFI Atlas* (6.7, 10.12, 10.24, 10.25); *CalCOFI Reports* (16.22a, 17.4, 17.21); *Canadian Journal of Zoology* (10.3, 15.4); *Current Opinion in Microbiology* (Plate 5.1); *Deep-Sea Research* (2.4, Box Fig. 2.3.2, 3.16); *Deep-Sea Research I* (13.9, 13.23a&b, 15.2, 15.8); *Deep-Sea Research II* (1.8b, 2.20, 3.9, 3.20, Plate 4.1, 4.10, 5.9, 8.5, 8.14, Plate 8.3, 10.14, 11.10, 11.11, 11.12, 11.15, 11.16, 11.18, 11.23, 11.25, 11.33, 11.34, 11.35, 13.26, 13.28, 13.29, Plate 13.1, 14.18, 14.29, Plate 16.4); *Discovery Reports* (6.5, 10.9); *Earth and Planetary Science Letters* (3.16); *Ecology* (Table 3.3, 11.14, 17.14); *Ecology Letters* (9.11); *Evolution* (10.22, 10.23); *Fisheries and Oceans Canada* (Plate 11.3); *Fisheries Investigations* (9.1); *Fishery Bulletin* (8.8, 10.16); *Geochimica et Cosmochimica Acta* (15.5); *GeoEye* (Plate 2.3); *Geophysical Research Letters* (11.17, 11.19, Plates 11.4, 11.6, 16.3); *Global*

*Biogeochemistry* (Plate 16.2); *Global Change Biology* (16.21, 16.23); *Memoires of the Faculty of Fisheries, Hokkaido University* (7.16); *Hydrobiologia* (6.6); *IATTC Bulletin* (17.5a); *IATTC Annual Report* (17.15); *ICES Journal of Marine Science* (8.3, Plate 8.2, 9.9, 11.31, 11.32); *International North Pacific Fisheries Commission Bulletin* (17.6a) International Pacific Halibut Commission Technical Reports (17.8); *International Review of Cytology* (2.7a&b); *International Review of Hydrobiology* (7.11, 7.12); Isaacs Papers-Scripps Institution of Oceanography Library (13.1); *Izdatel'stvo Nauka, Moskow* (12.1); *Journal du Conseil* (11.9); *Journal of Crustacean Biology* (7.2, 15.7); *Journal of Experimental Biolog*y (7.9, Plate 7.1, 12.8); *Journal of Experimental Marine Biology and Ecology* (8.6, 8.7); *Journal of Fisheries Biology* (17.2); *Journal of Fluid Mechanics* (1.4); *Journal of Geophysical Research-Oceans* (Box Fig. 2.5.2, Table 3.2, 11.36, 11.39, 11.42, Plate 11.2); *Journal of Marine Research* (10.13, 14.19); *Journal of Marine Science* (3.5, 8.15); *Journal of Marine Systems* (4.11, 4.12, 16.22b&c, 17.20); *Journal of Phycology* (1.7, 2.6, 2.7c&d, 2.8, 2.9, 2.13, 2.14, 2.15, 3.2, 3.3, 3.7, 3.11, 3.12); *Journal of Plankton Research* (1.8a); *Journal of the Marine Biological Association, United Kingdom* (12.7, 12.9, 13.3a); *Limnology and Oceanography* (Table 2.3, 3.10, 3.14b, 3.17, 3.19, Box Fig. 3.1.1, Table 3.1, 7.1, 7.3, 7.4, 7.7, 7.8, 7.10a,b&c, 7.18, 7.20, 8.2, 8.4, 8.11, 8.12, 8.16, 8.19, 9.4, 9.5, 10.4a, 11.3, 11.26, 11.28, Plate 11.1, 14.21, 14.22, 14.26, 14.27, 14.28); *Limnology and Oceanography-Methods* (11.13); *Marine Biological Research* (11.20, 14.25a&b); *Marine Biology* (3.6c, 4.3, Plate 6.7, 7.5, 7.6, 7.13, 7.14, 7.15, Box Fig. 7.4, Box Fig. 7.5, 12.13, 12.14, 12.15, 12.16, 12.17, 14.1, 14.3, 14.4, 14.5, 14.5, 14.7, 14.8); *Marine Ecology Progress Series* 5.6, 5.10, 7.17, 9.2, 12.19, 14.20, 14.24, 16.19); Marine Geology (14.17c); *Memoires of the Geological Society of America* (1.6, 10.17, 10.19, 10.20, 10.21); *Microbiology and Molecular Biology Reviews* (5.3); Monterey Bay Aquarium (Plates 6.2, 6.3);

Monterey Bay Aquarium Research Institute (13.6); *National Geographic* (Plates 6.6, 6.12); *Nature* (1.1, 3.15, 5.4, 8.17, 11.2, Plate 11.5, 14.16, 16.2, 16.15, 17.23); *Nature Geoscience* (16.13); *Nature Reviews* (5.1); *New Zealand Journal of Marine and Freshwater Research* (14.9, 14.10); *North Pacific Anadromous Fish Commission Bulletin* (17.6b); *OCB News* (11.24); *Oceanography* (13.24, 13.25); *Oceanography and Marine Biology Annual Review* (13.7c&d, 14.12, 14.23); *Oceanologica Acrta* (16.17); *Philosophical Transactions, Royal Society of London* (8.1, 12.2, 12.4); *Physiologia Plantarum* (3.6a&b); *Proceedings of the National Academy of Sciences* (17.22); *Proceedings, Royal Society of London* (8.18); *Progress in Phycological Research* (2.5a); *Progress in Oceanography* (3.4, 3.8, 4.9, 4.8, 9.3, 9.7, 9.13, Plate 10.2, 11.37, 11.38, 11.40, 11.41, 16.24, 17.10); *Quaternary Science Review* (16.12); *Rapports et proces-verbaux, Conseil permanent, Exploration Mer* (17.9a,b&c); *Remote Sensing of Environment* (2.16); *Review of Fish Biology and Fisheries* (17.19); *San Francisco Estuary and Watershed Science* (14.11, Plates 14.1, 14.2, 14.3); *Science* (2.10, 3.1, 9.10, 10.18, 11.27, 12.3, 12.5, Plate 14.4); *South African Journal of Marine* Science (17.18); *The Veliger* (6.3); *Treatise on Geochemistry* (Elsevier) (15.1); *Trends in Biochemical Science* (15.3).

# Chapter 1

# Ocean ecology: some fundamental aspects

Biological oceanography could also be termed ocean ecology. The term encompasses the ecology of oceans just a short distance from the shore – perhaps from the lowest low-tide level onward, right out to the centers of the great oceanic gyres. Often, estuarine habitats are included in the study of the oceans. Oceanographers deal with questions like: what sorts of organisms inhabit different sectors and depths, and why? How is organic matter produced, by what types of “plants” (although we rarely say that word, as we will explain), and what controls their growth? Which animals constitute the herbivores and which the carnivores; and how do the carnivores locate their prey? How do the changing seasons affect the biota? What relationships prevail between organisms – from microbes to whales – and the chemical and physical character of seawater? How can worms and isopods make a living in mud beneath 4000 m of water in near-total darkness? What can we expect to harvest from the sea, and how can exploitation of fisheries or seafloor mines be achieved without damaging the resource or the habitat? How will ocean biota be affected by global climate change? Sometimes the key issues and answers to our questions come from marine biology, sometimes mostly from chemistry or physics. Fundamentally, biological oceanography straddles many disciplines, a fact which makes it a joy for the oceanographer.

# Seawater

The root word in "ecology" is *oikos* (οικοσ), which is Greek for "house" or "habitat". It is the study of life in relation to its habitats, and obviously the key habitat in oceans is water – salt water. So, let us begin by considering water in some detail. The molecular structure of water, dihydrogen oxide, involves moderately strong covalent bonds between each of two hydrogen atoms sharing their single electrons with an oxygen atom. The water molecule is not linear; rather the hydrogen protons repel the overall electron shell to the far side of the oxygen atom and assume an angle of 105° from each other. Thus, the overall molecule is polar, being electropositive on the hydrogen side, and negative near the oxygen atom. This polarity creates a weaker bonding potential among the water molecules, especially in the liquid and solid phases. These *hydrogen bonds*, H-side to O-side, create a chaining effect, amounting in the liquid phase to arrays of "flickering clusters", and, in ice, to a weakly ordered crystal. As liquid water cools, the hydrogen bonds are less frequently disrupted by thermal motion, and the spatial array of more tightly bonded clusters progressively occupies less space. This means that water reaches its maximum density at 3.98°C (Caldwell 1978). However, the molecular ordering within ice is such that more space is filled by fewer molecules, so that the volume of ice is actually ~10% greater than the liquid phase at the density maximum, with the result that ice floats on water. Appropriately, much has been made of this unusual way in which water differs from comparable liquids. Lakes, for example, must cool entirely to ~4°C, becoming vertically homogeneous, before surface freezing can begin. Ocean salt water has a rather different equation of state (density being a function of temperature, salinity, and pressure), such that the temperature at which the maximum density occurs decreases with both salinity and pressure (see the data in

Caldwell 1978), and overturning is not a necessary preliminary to freezing.

In addition, because of the hydrogen bonding, water has a very large *specific heat capacity* (“specific” means relative to the mass). The amount of heat required to warm a gram of water by 1°C (the specific heat) is defined as 1 calorie. The calorie is now considered to be an “archaic” unit equal to ~4.180 joules $g^{-1}$ $°K^{-1}$, varying somewhat with temperature and pressure (Why should anything be left as easy to remember?) which is a very large amount of energy when compared with the requirement for, say, ethanol with weaker hydrogen bonding at 0.58 calories $g^{-1}$ $°C^{-1}$. This means that oceans are very slow to warm and very slow to cool, enabling currents headed poleward from the tropics to carry massive amounts of heat to high latitudes. In addition, very large amounts of heat must be added to water to force evaporation (2257 kJ $kg^{-1}$ = 540 calories $g^{-1}$), and removed to allow ice formation (334 kJ $kg^{-1}$ = 80 calories $g^{-1}$). For reasons that we will leave to the physical chemists, the temperature of liquid water remains fixed during freezing, at 0°C for pure water, and a few degrees lower for salt water (hence the salting of icy highways). Once frozen, ice can become even colder. Water also has a fixed boiling point at a given pressure, where the molecules escape explosively to the gaseous phase. This is 100°C at 1 atmosphere pressure. The effect of pressure on the phase transition is important in deep-sea hydrothermal vents, such that the boiling point of water at a depth of 2000 m is over 330°C. Thus, magma-heated water can emerge from the seafloor without exploding into steam. Water does evaporate into overlying air at sub-boiling temperatures, and this evaporation is more rapid when the temperature difference between the air and the water is greater. Thus, oceans, lakes, puddles, wet sand, and plant transpiration all pump water vapor into the atmosphere, leading to cloud formation, enhanced reflection of sunlight back to space, and rainfall that varies geographically, seasonally, and year to year. As is becoming obvious here, every aspect of the chemistry and physics of water is ecologically important.

The electrostatic polarity of water molecules also means that they will take on a preferential orientation adjacent to ionically bound molecules, to salts. For sodium chloride, for example, the oxygen atoms will tug on the sodium ion, and the hydrogen atoms will pull on the chloride. This tugging will be sufficient to dissociate the ionic bonds of many salts, and the water molecules will then encase the freed ions. Thus, dissolved salts will accumulate as the water flows over the land and rises through magma-heated rocks. These salts will then be transported into the sea. The sea is at the bottom of the hill, so to speak – an enormous evaporation basin in which the salts accumulate. Over sufficient time, a balance will emerge between the delivery rate and the processes that convey the salts into sedimentary structures (coastal salt-beds, manganese nodules, hydrothermal vent towers, etc.), such that the proportions of the different ions are relatively constant. Thus, the overall "salinity" is established by the remarkably constant proportions of the major dissolved ions (see Table 1.1).

**Table 1.1** The proportions of the major dissolved ions in seawater. Total salts = 35.17 g $kg^{-1}$ seawater.

| CATIONS | IN SEAWATER ($g kg^{-1}$) | ANIONS | IN SEAWATER ($g kg^{-1}$) |
|---|---|---|---|
| $Na^{+}$ | 10.78 | $Cl^{-}$ | 19.35 |
| $Mg^{2+}$ | 1.28 | $SO_4^{2-}$ | 2.71 |
| $Ca^{2+}$ | 0.41 | $HCO_3^{-}$ | 0.126 |
| $K^{+}$ | 0.40 | $Br^{-}$ | 0.067 |
| $Sr^{2+}$ | 0.008 | $B(OH)_4^{3-}$ | 0.026 |
| | | $F^{-}$ | 0.001 |

All of those are termed *conservative* ions, and their proportions vary only slightly – a fact recognized by Forchhammer in 1864, but confirmed by the careful analytical work of William Dittmar (1884) with samples collected from the world's oceans on the Challenger Expedition (1873–1876). Calcium content does vary somewhat with depth, due to dissolution, under high pressure, of shells made from $CaCO_3$, and the bicarbonate content varies according to the amount of carbon dioxide in solution (the $CO_2$ content of the oceans is rising because seawater is absorbing the carbon dioxide generated by the burning of fossil fuels). Because of the near-constant proportions of major salts, the total salinity can be quite closely estimated by determining any one of the dissolved ions, e.g. chloride can be measured using a silver nitrate titration, or by measuring the overall electrical conductivity of the water. In modern practice, salinity of a sample is expressed as a ratio of its conductivity to that of a "standard" seawater, and is taken to have no units (the units in the ratio cancel), and is expressed on a "practical salinity scale". Salinity is often expressed simply as, say, $S = 35$, a number related to the grams of salt per kilogram of seawater, but no longer stated as such (parts per thousand). $S = 35$ is close to the overall average of ocean salinity. The upper range of $S$ is ~40 in parts of the Red Sea. Unlike those conservative ions, others, like nitrate ($NO_3^-$), that are taken up by photosynthesizing algae and by bacteria, can vary *non-conservatively*. Nitrate varies from almost immeasurable amounts in the surface layers of oligotrophic central gyres to 45 µM (micromolar) in the deep North Pacific. These µM quantities are not large enough to make the measurement of chloride or conductivity unreliable as an index of the overall mass of dissolved salts, $S$, although nitrate does make a measureable addition to seawater density in very deep waters in the Pacific.

Cell membranes mostly only pass salt ions through specific, energy-using, protein channels, but water passes through more freely, passing from the side with the lower solute (salt and everything else) concentration to the side with the higher solute concentration. This *osmotic* flow is actually down the gradient of water concentration. Cells and tissue fluids of much marine life, including algae and most invertebrates, are *isosmotic* with seawater. That is, solute and water concentrations are the same inside and outside their cells. Cells of freshwater plants and animals, on the other hand, must contain some salts and dissolved organic matter, so they have water pushing in through any porous cell surface. To avoid over-inflation, rupture, and death, they must steadily pump water back out. Protists have specialized organelles which do that, and metazoans have kidneys at several levels of complexity to perform this function for the body as a whole.

Fish evolved in fresh water. The impermeability of their skin and scales limits water influx to the gill membranes, which must be exposed to the water for oxygen exchange, and that lessened influx is pumped out by their efficient kidneys. When some fish colonized the estuaries and oceans (probably stepwise in that order), the problem was reversed, with water moving out through the gills. Several solutions evolved. Sharks and rays came to tolerate large tissue concentrations of urea, giving their tissues osmotic equivalence with the sea. Bony fishes developed a system of swallowing water and then excreting the salts both via the kidneys and from desalination glands on the gills. Fish that come and go between fresh water and salt water, including salmon, shad, eels, and others, must shift between these modes, in some cases (e.g. steelhead trout) back and forth many times. Many seabirds, although not impacted by the osmotic differential with seawater, must drink to replace water lost at their lungs; they eliminate the salt with glands in their nostrils. Marine mammals do not have much cell membrane exposed to water, and by and large they avoid drinking. They are very efficient at retaining water from their prey and water produced by their metabolic reactions. Their specialized kidneys manage the balance of tissue electrolytes (salts). Estuarine animals and plants living in brackish water have a variety of means for tolerating both the intermediate and highly variable osmolarity. Studies of osmoregulation support a minor research industry favored by university faculty members spending the summer at marine stations.

The covalent bonds of hydrogen to oxygen in water are labile enough that the oxygen side of one molecule occasionally pulls one of the hydrogen atoms off another, producing hydronium ($H_3O^+$) and hydroxyl ions ($OH^-$). In suitably pure water (actually rather difficult to obtain), the abundance of each is $10^{-7}$ molar. In solutions of acid, the acid protons form more $H_3O^+$, increasing its molarity to $10^{-6}$ or much less, and neutralizing an equivalent amount of the $OH^-$, reducing its molarity to $10^{-8}$. In solutions of bases, the opposite happens. The balance in any given acid or base solution is given by the negative logarithm of the hydronium molarity, or pH value, which then is 7 at neutrality, 1.0 for 1 M acid and 14.0 for 1 M hydroxide. Seawater is buffered at pH values ranging in surface waters from 7.9 to 8.4 (the near-surface ocean average is ~8.1) by a combination of its carbonate and borate components, with the carbonate contributing about 95% of the buffering effect. The chemistry of the system is complex, primarily because it involves the multiple dissociations of the carbonic acid ($H_2CO_3$) that forms when carbon dioxide ($CO_2$) dissolves in water. A very large part of the total carbonate load is as bicarbonate ($HCO_3^-$), which can both dissociate further – acting as an acid, or take up a proton – i.e acting as a base, hence the strong buffering action. The entire system is under stress from increasing dissolution of carbon dioxide from fossil-fuel burning and other human activities, a topic to be considered later. However, the most important concern arises from the fact that the dissociation of more carbonic acid both reduces the stability of shells and coral skeletons and increases their formation costs. Organisms have some capability for internal pH management, but, as acidity increases, the energetic costs of regulation increase. The acid–base relations of seawater have been extensively and carefully studied, and therefore we will leave their description to the ocean chemists. A point to keep in mind is that the pH scale, so commonly used, is logarithmic to base 10. Thus, a change from pH 8.1 down to7.8, which may come about, would represent a factor of two increase in hydronium-ion molarity – a very large shift indeed.

## Pelagic Autotrophs are Small

In sharp contrast to the land, large complex plants are usually absent. Sargassum weed (*Sargassum* spp.) suspended from gas bladders in the subtropical gyre of the North Atlantic is a special and localized exception. However, it provides a model that it is a little surprising not to find everywhere; examples exist of large, floating plants, but they just are not typical. Instead, almost all of the photosynthetic organisms in the water itself, that is in *pelagic* habitats, as opposed to attached to the bottom, are small, unicellular algae known as *phytoplankton*. The word "plankton" comes from Greek (πλαγκτος) and implies a necessity to drift with the currents. Clytemnestra, in Aeschylus's *Agamemnon*, used it in denying that her thoughts were wandering (*planktos*). A classical scholar suggested the word to Victor Hensen, a founder of planktology, to describe relatively passive swimmers. Phytoplankton range in cell diameter from about 1 μm to about 70 μm, with a few representatives up to 1 mm. It is important to form a mental sense of this size range. Typical bacteria are 1 μm diameter; red blood-cells are 7 μm; an object of 50 μm is just visible to the naked eye if contrast is high. Most algal cells in the sea are at the lower end of this range. Definitions for the "size jargon" of biological oceanography are in found in Box 1.1.

## Box 1.1 Plankton sizes

Several sets of prefixes have been proposed to distinguish size classes of plankton. We seem to have settled on those proposed by Sieburth *et al*. (1978).

| CHARACTERISTIC LENGTH | TERM (EXAMPLES) |
|---|---|
| <0.2 μm | Femtoplankton (viruses) |
| 0.2–2 μm | Picoplankton (bacteria, very small eukaryotes) |
| 2–20 μm | Nanoplankton (diatoms, dinoflagellates, protozoa) |
| 20–200 μm | Microplankton (diatoms, dinoflagellates, protozoa, copepod nauplii, etc.) |
| 0.2–20 mm | Mesoplankton (mostly zooplankton) |
| 2–20 cm | Macroplankton |

Why are pelagic autotrophs so small? Biological oceanographic dogma, which will not be contradicted here, says they are small in order to provide a large surface area relative to their biomass in order to absorb nutrients like nitrate, phosphate, and iron from extremely dilute solution. Soil water in land habitats provides somewhat higher levels of nutrients (Table 1.2). The modest difference is augmented in the soil-water case, however, by rapid resupply from the closely adjacent mineral phase; nutrients do not become so thoroughly depleted in soil water. Thus, rootlets and root hairs over a small fraction of a plant's surface can supply nutrients for growth and maintenance of very large structures. In the sea, the rate of supply is limited by diffusion from dilute solution to the absorbing cell surface, so surface area must be maximized relative to cell volume. This is achieved by being small. For example, diatoms are an abundant group among the phytoplankton. Many of them are cylindrical, and if we fix the length/diameter ratio at 1, then the surface-area to volume ratio varies as 6/length, increasing strongly as size gets smaller. The surface area of a 30 µm diatom of this shape is 4241 $µm^2$, while that of a 15 µm one is a quarter of that, 1060 $µm^2$. However, the smaller one has twice the *surface area per unit volume*. Surface-to-volume (*S/V*) ratios of spheres vary similarly as 6/diameter. The effect of size on *S/V* is stronger for more elongate shapes (you can prove that to yourself by doing the calculations).

**Table 1.2** Relatively low values of major nutrient concentration in surface waters compared to natural (as opposed to fertilized) soil-water values. Units are micromoles $liter^{-1}$ (µM).

| **UPPER-OCEAN CONCENTRATIONS IN WINTER** | **$NO_3^-$** | **$PO_4^{3-}$** |
|---|---|---|
| North Atlantic subarctic | 6 | 0.3 |
| North Pacific subarctic | 16–20 | 1.1 |
| Natural soil water | 5–100* | 5–30** |

*Soil and agricultural chemists use strange units like kg $NO_3^-$ $hectare^{-1}$ to 20 cm soil depth. They rarely attempt to extract soil water *per se*, which is difficult because soil is relatively dry and much of the water is associated with organic matter.

**Also hard to characterize. This range came from a soil-science text, but do not put much faith in it (units were 0.05 to 3.0 ppm, a usual unit in that field). Most published data are measured in µg $PO_4^{3-}$ $(g\ soil)^{-1}$.

It is not surface *per se* that matters, since phytoplankton cells only cover a small fraction of their surface with transport enzymes to move nutrients from outside to inside.