

BOOK REVIEWS

Limnol. Oceanogr., 46(2), 2001, 471–472
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KIRCHMAN, D. [ED.]. 2000. **Microbial ecology of the oceans**. Wiley-Liss. 542 p. US\$139. ISBN 0-471-29993-6.

Some of us may twitch when we think about the 10^5 bacteria living in happy symbiosis on every square centimeter of our skin. Some biological oceanographers also become twitchy when told that the 5×10^5 bacteria in every milliliter of seawater are responsible for most of the ocean's total respiratory oxygen consumption and for utilizing much of the net primary production. To make the concept even more difficult to swallow, we are now told that much of the photosynthesis in the blue water of central ocean gyres is accomplished by bacteria. Old paradigms die slowly, Thomas Kuhn told us—mainly through the death of their adherents. Many fisheries scientists do not yet believe it, but the marine food web consisting principally of diatoms, copepods, and fishes is now generally seen as an occasional excrescence from what is normally a microbial food web. David Kirchman has gathered an expert group of pallbearers to perform the last rites for the old paradigm.

The alternate paradigm, one of abundant and biogeochemically important microorganisms in the ocean, is not new, as it goes back at least 75 years to V. I. Vernadsky. Vernadsky lacked the technology to test what his intuition told him, and for most of the 20th century, microorganisms were dismissed as decomposers of little quantitative importance. An early chapter tells us that an important corner was finally turned in the 1970s, with two breakthroughs in technology. The first was the development of epifluorescence microscopy to count bacterioplankton, most of which are similar in size to the wavelength of visible light and are therefore impossible to resolve with ordinary light microscopy. This development was followed by the development, in rapid succession, of a series of methods for estimating the rate of growth of those bacteria. In the approximately 25 years since those developments, we seem to have traveled light years in marine microbial ecology. Kirchman's assembled experts now tell us which bacteria are in the ocean not by microscopy or by culturing them but by reference to rRNA libraries. The organisms are not just "bacteria" anymore but rather are specific phylotypes of Bacteria and Archaea, with all of their versatile metabolic attributes. They are, of course, running the nitrogen and sulfur cycles as well as the carbon cycle. And bacteria are a quantitatively major part of the microbial food web, which includes the myriad protozoans of the sea.

For their part, the protozoans also do their best to make life complicated for microbial ecologists. The routine method for quantifying autotrophs in the sea is to extract and measure their chlorophylls. However, some 20% of autotrophic dinoflagellates, as one example, also ingest solid food. A number of heterotrophic dinoflagellates regularly eat organisms that are much larger than themselves. Some ciliates eat autotrophs but then save and utilize their functioning chloroplasts for impromptu photosynthesis. Of course, in addition to eating organisms of all sizes from the smallest bacteria—and maybe even viruses—up to fish larvae, protozoans eat each other. The theoretician and the empiricist have something to agree upon: this is the "food web from Hell." Even describing it, to say nothing of quantifying its processes, is a daunting task. In spite of all this, several chapters of Kirchman's text report impressive progress in describing and quantifying transfers of energy and

the cycles of carbon and nitrogen through the maze of microorganisms.

Although each chapter has a different author or authors, each of whom has a unique viewpoint, there is a uniformity of rigor and clarity that is not always seen in such compendia. Many cross-references make it appear that the authors have read one another's chapters, but not everyone agrees on everything. For example, what is limiting the growth of bacteria in the ocean? Are bacterioplankton limited by top-down processes? More than one chapter says that bacterial populations are limited by protozoan grazing, but we are also variously told that bacterial mortality can be fully accounted for by either protozoan grazing or viral lysis. Is production of heterotrophic bacteria limited by bottom-up resource supply? More than one chapter says the limiting factor is mostly the supply of usable organic carbon, whereas another chapter indicates that this resource is unlimited, at least in theory. The authors of two of the three chapters on the nitrogen cycle tell us emphatically that nitrogen is always limiting, but a third chapter on nitrogen starts with the same standard story and then waffles. Then there is the chapter on modeling microbial food webs that cites papers published in the 1990s that report phosphorus limitation of bacterial growth or respiration in many places, from Norwegian fjords to the Sargasso Sea and the Gulf of Mexico. The provisional answer is probably all of the above (i.e., different factors are limiting at various seasons and locations in the ocean).

Because the roles of microorganisms in the ocean remain controversial, at least to some investigators in related disciplines, it is unfortunate that there is not a chapter devoted to the interactions of microorganisms and metazoans in the ocean—the whole food web. This is admittedly not yet a well-developed subject, but it is apparent that microorganisms are a part of one continuous food web that includes fishes, cetaceans, and polar bears and that microorganisms are a quantitatively significant part of that web. How do they relate to fisheries? How do they relate to climate and global warming by, for instance, modulation of the release of dimethyl sulfide and dimethylsulfoniopropionate from the ocean? Further, although there is an excellent chapter on ultraviolet light and its effects on microorganisms, photosynthetically active light and photosynthesis are not treated. There are, of course, many other books devoted to this topic. But the recent discovery of the major roles played in photosynthesis by the bacteria *Synechococcus* and *Prochlorococcus* would seem to be reason enough to devote a chapter to their distribution and to their role in primary production. I would also have liked to see a chapter on what has been learned using the flow cytometer, a powerful tool and a particularly nice example of the adaptation to oceanography of a clinical research tool; the challenges of assembling and using such a finicky instrument on a rolling, pitching, salty ship for analysis of something much more dilute than blood would have enlivened the book.

Despite these quibbles, *Microbial Ecology of the Oceans* provides a quite thorough treatment of the state of our knowledge of this newly transformed field, and the book's topics are presented by well-chosen authorities. The book comprises an excellent statement of where we stand, or rather where we stood in a very fast-moving field 2 or 3 years ago. It will be a useful sourcebook for microbial ecologists and for all marine scientists who want a detailed overview of the state of marine microbial ecology. Of course, much of

the text's material has application in freshwaters as well. Specialists in other marine and aquatic fields may find it rather detailed and specialized, but the selective reader can get the sense of our emerging understanding of the overarching importance of microbial processes in the sea. Although the information will soon be dated and a new edition required, this is a most timely publication. The revolution is over and it is time to move on, assimilating into marine

ecology the many roles of microorganisms and the quantitative magnitude of microbial processes.

Lawrence R. Pomeroy

Institute of Ecology
University of Georgia
Athens, Georgia 30602-2202