

Displays of male warblers. Top, "wings out" display of chestnut-sided warbler (*Dendroica pennsylvanica*). Bottom, courtship display of American redstart (*Setophaga ruticilla*). [From *American Warblers*; redrawn by Brian Regal from painting by Dilger in M. S. Ficken and R. W. Ficken, *Living Bird* 1, 103–122 (1962)]

tion and ecology of these animals.

Themes that recur through the book include species diversity, resource exploitation patterns, habitat selection, and population limitation. The last is discussed in terms of whether such limitation occurs on the summer breeding grounds, or in winter, or both. Although the available information on winter season ecology of these warblers is limited, Morse presents a good overview of what is known. I find his discussion of warbler population dynamics in winter rather superficial and, in contrast to other parts of the book, lacking in insight or suggestions for further research. As Morse points out, understanding the habitat relations, patterns of resource use, and especially the factors affecting the population sizes of such species, which must include studies of populations in both summer and winter, is both timely and crucial to conservation efforts. The accelerating effects of human modification of habitats in both temperate and tropical zones will inevitably have an impact on populations of many migratory birds, including Paruline species.

One of the central issues that appears in nearly all chapters is the potential importance of food resources. Morse, as do many other ecologists, consistently invokes resource limitation as the underlying cause for many phenomena, including niche and habitat partitioning, species packing, territoriality, and population regulation. Yet, as Morse acknowledges (but doesn't emphasize sufficiently, in my opinion), there are few, if any, quantitative or experimental studies of warbler or other migratory songbird populations that provide adequate measures of resource availability, not to mention resource limitation. If indeed food resources are as important as Morse and many others suggest, it is essential that avian ecologists tackle this problem and develop methodologies for measuring food availability and for testing food limitation.

Morse's call for more experimental manipulations in the studies of warbler and other bird populations is laudable. Despite their inherent difficulties, field manipulations, with appropriate replications, of habitat structure, food supplies, predators, and the warbler populations themselves may be the only way to tease apart the ecological and evolutionary processes that affect bird populations and communities.

I think some of Morse's most useful contributions in *American Warblers* are the many

ideas and suggestions he makes for further research. Besides having a final chapter that explicitly describes ten areas in which research is clearly needed, he suggests numerous other hypotheses throughout the book. On a quick tally, I noted at least 40 such ideas that could lead to productive research projects, some of which would be short-term, perhaps done in a few weeks or a single season, and others of which would require many seasons and a large research budget. These should be of interest to both undergraduates and Ph.D. candidates looking for thesis projects, not to mention seasoned researchers.

This book clearly demonstrates that Paruline warblers are a fascinating group of organisms—they are diverse, colorful, and widely distributed and exploit their environments for breeding, wintering, and migrating in a variety of ways. Morse makes a convincing case for using them as a model avian system for further studies of ecological, behavioral, and evolutionary processes. Overall, this is an important book that will be of interest to field biologists and the general reader, as well as to avian ecologists and behaviorists.

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Foundations of Planktology

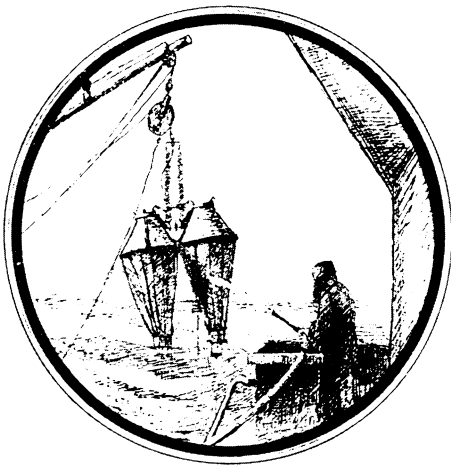
Biological Oceanography. An Early History, 1870–1960. ERIC L. MILLS. Cornell University Press, Ithaca, NY, 1989. xx, 378 pp., illus. \$47.95.

Given a sufficient supply of nutrients and light, photosynthesizing plankton will grow at their intrinsic rates until nutrients become limiting, light is reduced by shading, and grazing organisms become abundant enough to check the increase and reduce the standing stocks. What kinds of organisms are involved in this process presumably depends on the seed populations and their adaptations to the particular physical conditions prevalent at the sites and periods studied (temperature and salinity distribution and the mix of nutrients and trace substances).

According to Mills, the investigation of this system constitutes the core of biological oceanography. He traces the history of the fieldwork, the experiments, and the concepts invented to elucidate the workings of the productivity machine of the ocean, beginning in the late 19th century and ending

in the middle of the 20th, prior to the advent of "big science and the one-track strategy of the research grant." He does this with an eye to the sociopolitical setting within which the research takes place. His focus is on the stages of emergence of a quantitative theory of plankton dynamics in the 70 years between Victor Hensen's plankton surveys and Gordon Riley's equations describing growth rates of phytoplankton as a function of environmental variables and of intrinsic population properties.

The first part of the book, a little more than half of it, is devoted to the origin of biological oceanography in Germany and Scandinavia, in the late 19th and early 20th centuries. The heroes are Victor Hensen (1835–1924) and Karl Brandt (1854–1931), who founded the "Kiel school" of planktology, and H. H. Gran (1870–1955) of Oslo, who made a major effort to integrate plankton biology and physical oceanography. Other major players are Hans Lohmann ("nannoplankton"), Emil Raben (nutrient distributions), Alexander Nathanson (importance of upward mixing of nutri-



"A pair of Hensen's vertically hauled nets being washed down just after return to the surface. Most hauls were made with single nets; double hauls like this one were used by Hensen and Lohmann to assess the uniformity of plankton distribution." [Reproduced in *Biological Oceanography* from Krümmel, 1892]

ents), and Trygve Braarud (complex origin of plankton blooms). The second part of the book, entitled *Biological Oceanography* in Britain and the United States, 1921–1960, describes the work at the Plymouth Laboratory and ends with a review of the contributions of Gordon Riley (1911–1985). The Plymouth heroes are E. J. Allen (1866–1942), H. W. Harvey (1887–1970), W. R. G. Atkins (1884–1959), Leslie Cooper (1905–1985), and F. S. Russell (1897–1984).

The story begins with Victor Hensen of Kiel, Mills's candidate for founder of biological oceanography. Hensen's pioneering plankton research was guided by his theory of uniform distribution, which holds that plankton disperse readily and can therefore be sampled with some confidence. Hensen thought that differences in adjacent samples arose either from sampling below the scale of uniformity or because different physical environments were being encountered. Ernst Haeckel, the German prophet of Darwinism, denied the concept: he doubted the value of spotty measurements of standing crops in a patchy environment and thought what Hensen did was a waste of time and money.

Hensen measured standing stocks of different kinds of plankton because he needed basic data to begin constructing the food chain, which he envisioned as a "cone of metabolism" rather like the trophic pyramid invented later. One cannot help feeling sympathetic. Assessing the productivity of the ocean—how much is being produced of what, and why—has remained one of the most challenging and least tractable problems in oceanographic research: there still is

no reliable world map of primary production, for example. We have maps of indices of productivity. We are not even clear about the meaning of "carbon fixation"—How long does the carbon have to remain "fixed" to be counted? Should recycled production and export production be shown separately? In mapping export, should not the quality of the export, rather than just "carbon," be recorded?

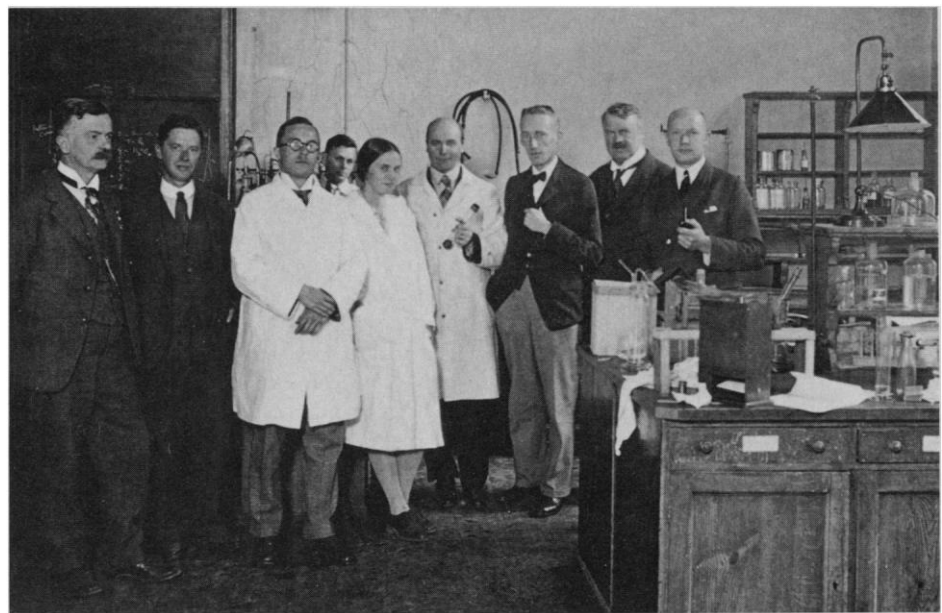
The common theme running through Mills's account is the effort to properly describe and explain the "spring bloom," a phenomenon typical of much of the northern North Atlantic—the North Sea, the Baltic, the waters off Norway, and Georges Bank. The research rationale (which allowed funding) was the improvement of fisheries and their management. There was the fond hope that fishery success would become predictable if the laws governing ocean currents and plankton dynamics were known. The International Council for the Exploration of the Sea was conceived (in 1899 in Stockholm) with this aim. The "spring bloom" provided the focus for discussion, from Karl Brandt of Kiel (who introduced Liebig's law and other agricultural concepts to the study of plankton) to Gordon Riley of Yale and Woods Hole (who introduced mathematical modeling).

Brandt regarded nitrogen as the limiting nutrient and postulated that denitrifying bacteria are the key to ocean productivity, since they "restore the prevailing equilibrium," destroying nitrate introduced by runoff. Brandt's brilliant research paradigm—

based purely on a leap of faith—has re-emerged more recently in connection with long-term controls on ocean fertility and hence controls on atmospheric $p\text{CO}_2$. Regarding patterns of productivity, however, Brandt's time scale was off by several orders of magnitude. Brandt's conversion from his denitrification hypothesis to a complex theory of blooms (put forward by Gran and colleagues) makes for fascinating reading. Once converted, Brandt discovered the seeds of the new ideas in his earlier writings. However, to his everlasting credit he did finally abandon his pet theory, which he had vigorously defended for decades.

The Plymouth story is just as interesting but treats of more familiar paradigms—the interplay of mixing by winds, seasonal irradiation, water stability, and cropping by grazers. There is much to explore and enjoy here. I was glad to learn about Harvey's personality, his emphasis on thinking before doing. Harvey was (I think) the first to have a clear conception of the ocean's production system, that is, the great loop of production and decay. He realized that the rate-limiting factors are remineralization and overall upwelling. Hence the present ocean, in its biologically driven deviation from equilibrium, is a "Harvey ocean."

Mills writes well, in an eclectic, unhurried, and entertaining fashion. He goes to great lengths to dig up the facts that let the story emerge, but also editorializes freely about the flow of ideas and the political background. The book is a must-read for everyone interested in biological oceanogra-



International Council for the Exploration of the Sea "meeting of experts" in Oslo, October 1928, "during which standard methods were tested and recommended for the analysis of the major plant nutrients." At extreme left, H. H. Gran and H. W. Harvey. [From *Biological Oceanography*; courtesy of Trygve Braarud; published with permission of the Department of Biology, Section for Marine Botany, University of Oslo]

phy and meets a high standard of scholarship. Not everyone will agree with Mills, however, regarding the congruency of plankton dynamics with biological oceanography or the composition of his list of heroes. The predominance of chemists on this list is striking. Some might wish for a more economic treatment of the plankton story and more room for other aspects of biological oceanography, including benthic processes and fisheries research. Also, one might question whether Riley deserves such exclusive prominence as he is given among U.S. researchers in this field (perhaps he does). The non-specialist reader should start with the conclusion of the book for introduction: the single paragraph on controls on plankton productivity at the beginning is insufficient background for understanding the arguments that follow. Perhaps that is Mills's intention: to let the reader run the same maze as the pioneers.

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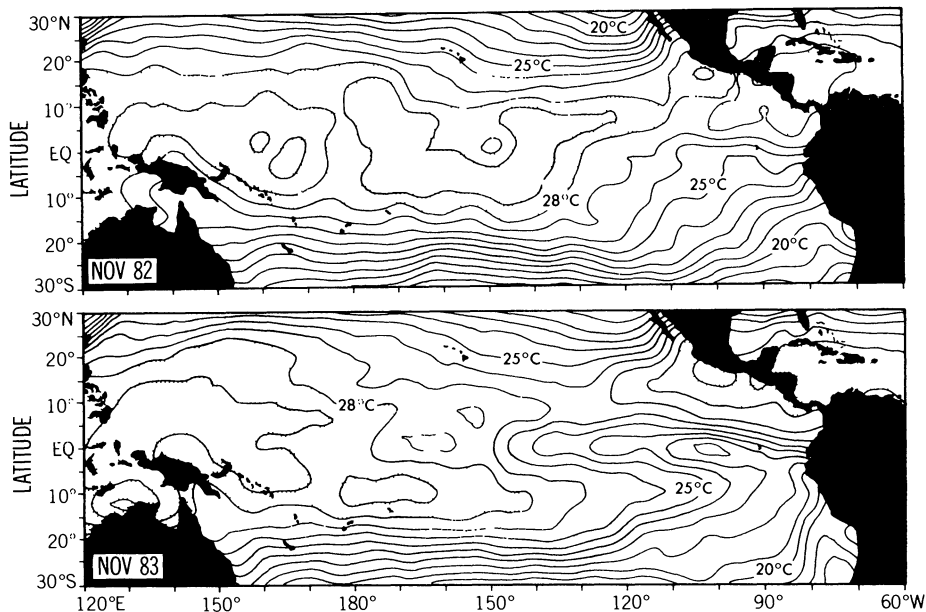
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Geophysical Interplays

El Niño, La Niña, and the Southern Oscillation. S. GEORGE PHILANDER. Academic Press, San Diego, CA, 1989. x, 293 pp., illus. \$59.50. International Geophysics Series, vol. 46.

El Niño is a phenomenon of the coasts of Peru and Ecuador that in recent years has come to be understood as one element of a grand and dramatic shift of the climatic state of the ocean circulation and the atmosphere. It is a prototype of the sort of coupling between the ocean and atmosphere that oceanographers, meteorologists, and climatologists have been pointing to as probably crucial to understanding both weather and climate change.

Parts of El Niño and its associated atmospheric partners are very conspicuous elements of the weather and climate of the tropical Pacific Ocean. Indeed, the phenomena were well known to Spanish explorers of Latin America as early as the days of Pizarro. One of the more sobering aspects of the struggle to understand climate is that it took over 400 years (until the middle of the 20th century) before these elements were recognized as part of a global system, leading to droughts in some regions, torrential rains in others, disturbed biological cycles throughout the tropical Pacific Ocean, and many more manifestations. With hindsight, El Niño is not very subtle; the signals are large and conspicuous when one knows to



"Sea surface temperatures in November 1982 during El Niño and one year later during La Niña."
[From *El Niño, La Niña, and the Southern Oscillation*]

look for them. Which slightly smaller signals in the ocean-atmosphere system now go unremarked because we do not know what to look for?

Following the work of the meteorologist J. Bjerknes in the 1960s, the existence of El Niño as a component of an oscillation known in its atmospheric manifestation as the Southern Oscillation (the two together are often known as ENSO) has come to involve a large and growing number of meteorologists and oceanographers in attempts to understand this system. Ever more obvious climatological, economic, and even political implications have emerged. Such has been the intensity of interest that the subject has become nearly a specialty in its own right, with a growing and very technical literature.

George Philander, one of the pioneers of the study of ENSO, has written a monograph that will be of great importance to anyone attempting to enter this field, to understand its theoretical underpinnings and the degree to which mysteries remain. The focus of the book is on the ocean—on how the ocean responds to various forcing functions imposed by a changing atmosphere—and only secondarily on the atmospheric response to oceanic changes. This emphasis is appropriate, given the much greater maturity of meteorological science. As a story of the need to understand ocean-atmosphere coupling, the book is compelling.

Philander first guides the reader through a primarily verbal portrayal of the seesawing of atmospheric pressure and winds, coupled to a rapid and highly interesting oceanic

motion that in turn reacts back onto the atmosphere. He depicts the ocean as existing in one of two extreme states, one being called El Niño, with the eastern Pacific Ocean warmer than normal and with certain specific accompanying atmospheric values. The opposite state produces an eastern Pacific colder than normal with a very different meteorology. "El Niño," meaning "The Child," and specifically "The Christ Child," was the name given by natives of the west coast of South America to the warm state because of its tendency to set in shortly before Christmas. Philander christens the cold state "La Niña" for "The Girl"; whether the opposite of "The Christ Child" is "The Girl" is presumably more a question for theologians or feminists than for scientists. I suspect the name will stick.

With this qualitative background, the book begins the construction of a more quantitative picture, beginning with description of mean and time-variable states and going on to write equations for important dynamical elements that are then invoked to explain many of these observations.

The book will be indispensable to anyone attempting to penetrate the large and confusing literature; Philander has made a good story of it. In many ways, he has produced the theoretician's view in that, presumably in the interest of brevity, much of the complexity of the observational problems has been slighted. For example, the windfield over the Pacific Ocean is presented as "the" windfield in the form of a two-dimensional vector plot without any comment about possible uncertainties. A novice would not