BIOLOGICAL OCEANOGRAPHY

Drifters Through Time

Robert Riding

In hindsight, it is not surprising that floating cells evolved to take advantage of sunlight, water, and carbon dioxide at the surface of a habitable planet such as Earth. Phytoplankton—myriad small, mostly unicellular algae and bacteria that occupy the surface waters of seas and lakes—dominate aquatic primary production, and over time they have radically altered Earth's atmosphere. But reconstructing their multimillion-year history is a daunting task. Those with tough shells or cysts have a good fossil record, whereas others have left scarcely a trace. In *Evolution of Primary Producers in the Sea*, editors Paul Falkowski and Andrew Knoll take a forthright approach to this challenge. They rely on resourceful detective work, integrate all available strands of biological and geological information, and wherever possible emphasize large-scale interconnections between life and environment.

The star of the show is oxygenic photosynthesis—the physiological process employed by most present-day phytoplankton—which uses sunlight as energy to create organic matter from carbon dioxide and water, releasing oxygen as a by-product. As a result, atmospheric carbon dioxide is buried as organic carbon, while oxygen is liberated to permeate the oceans and atmosphere. Phytoplankton have been no more immune to the dramatic consequences of these effects than other organisms, and how they responded to the changes they helped create is one of the volume's fascinating central themes.

The authors work hard to place phytoplankton evolution in its geological perspective, but the fossil record can be inscrutable. Some key questions, such as when cyanobacteria (the organisms believed to have originated oxygenic photosynthesis) first appeared, are surprisingly hard to resolve. We thought we had the answer until serious doubts were raised about the nature of 3500-million-year-old cyanobacteria-like microfossils in Australia (*1*). Currently it seems more likely that cyanobacteria and oxygenic photosynthesis arose later, perhaps ~2900 million years ago (Ma) (*2*).

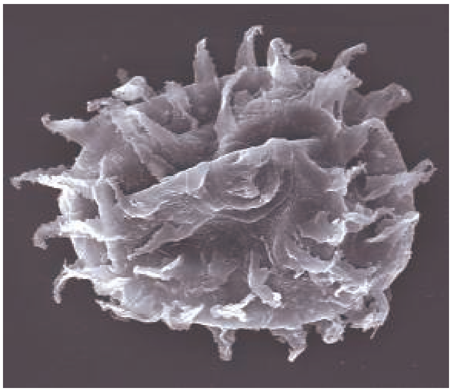
The inception of the phytoplankton record, ~1700 Ma, raises further questions by introducing enigmatic organic walled microfossils that look algal—some resemble present-day dinoflagellates and others prasinophyte green algae—but whose precise affinities are unknown. These fossils guard their secrets so well that they are called acritarchs: the only major group of organisms defined as being "of uncertain origin." Acritarchs dominated the phytoplankton record until 250 Ma, so the uncertainties that surround them hamper understanding of an immensely long period in the evolution of marine life.

Evolution of Primary Producers in the Sea

Paul G. Falkowski and Andrew H. Knoll, Eds.

Academic Press (Elsevier), Burlington, MA, 2007. 470 pp. $79.95. ISBN 9780123705181.

Even so, large-scale patterns are discernible in acritarch history: very slow diversification prior to 550 Ma, acme at 450 Ma, followed by a decline that was steepest 360 Ma. The protracted initial diversification from 1700 Ma to 550 Ma might reflect the gradual pace of Earth's oxygenation. Persistent deep ocean anoxia may have retarded nutrient release until oxygen levels finally rose ~550 Ma, stimulating algal phytoplankton and animal diversification as suspension feeders and zooplankton grazers evolved.



Origin uncertain. The acritarch *Peteinosphaeridium septuosum* from the Sylvan Shale (Late Ordovician, Oklahoma).

How eukaryotes acquired oxygenic photosynthesis after it was developed by cyanobacteria is almost the stuff of science fiction. Nonphotosynthetic organisms reinvented themselves as red and green algae by engulfing cyanobacterial cells and transforming them into photosynthetic organelles, plastids. The process was repeated when red and green algae were in turn engulfed as secondhand plastids. Red-algal plastids, for example, were incorporated into coccolithophores and diatoms. Dinoflagellates have the distinction of receiving plastids thirdhand, from diatoms and other algae. This remarkable "pass the plastid" history, and much else that is known about phytoplankton, is deduced from present-day organisms, but fossil evidence is required to confirm absolute ages and reconstruct past ecologic interactions. During the 300 million years of the Paleozoic era, ocean oxygenation continued to shift the availability of trace metals essential for cell biochemistry in a direction that favored the red-algal plastids acquired by dinoflagellates, coccolithophorids, and diatoms in the Mesozoic era. This suggests an intimate link between seawater chemistry and the rise of these important groups, as well as the continuing overriding influence of oxygen on algal evolution.

After the difficulties posed by acritarchs, there is an almost-palpable sigh of relief when, at 250 Ma, the story finally reaches the familiar Mesozoic algae, whose resistant cysts and shells permit their record to be tracked in detail to the present day. But an important group is missing. Cyanobacteria outnumber if not outweigh present-day algal phytoplankton in abundance, but they are unknown as body fossils. Many of their cells are less than two micrometers in size. Even in present-day seas, the importance of such picophytoplankton went unrecognized until 30 years ago (*3*). Reconstructing the history of cyanobacterial phytoplankton is a major challenge.

The volume rightly emphasizes the effects of Earth's oxygenation on phytoplankton evolution. After all, these organisms were presumably largely responsible for the significant oxygen increase that occurred before terrestrial plants greened the continents. At the same time, decrease in carbon dioxide has also strongly influenced phytoplankton, because inorganic carbon is fundamental for photosynthesis. The effects of low carbon dioxide levels is one of the few topics that I would have given more prominence in the volume. After all, many phytoplankton have mechanisms to deal with present-day low levels of carbon dioxide, and this ability is likely to have played an important role in phytoplankton history. Cyanobacteria, for example, overcome carbon limitation by pumping bicarbonate into their cells, and they may have been doing this since carbon dioxide declined substantially ~360 Ma (*4*).

Any attempt to tell the phytoplankton story

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CREDIT: COURTESY OF REED WICANDER/CENTRAL MICHIGAN UNIVERSITY AND GEOFFREY PLAYFORD/THE UNIVERSITY OF QUEENSLAND is welcome. The authors of *Evolution of Primary Producers in the Sea* go further and succeed in making a complex and at times perplexing subject accessible and exciting. Comprehensive and authoritative, their explorations of fundamental questions and global geobiological trends are engaging and thought provoking. The volume will be influential, and it should signal a turning point in phytoplankton research.

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10.1126/science.1151316

ECOLOGY

Give Way to the Migrants

Thomas Alerstam

Migration represents a spectacularly successful strategy among animals, providing access to a richness of ephemeral and seasonal resources that can sustain large populations. Its importance for promoting abundance was stressed by Alfred Russel Wallace in his 1858 paper that set forth the fundamentals of natural selection in biological evolution and stirred Darwin to finally publish his long-considered ideas (*1*). Wallace pointed to the example of the passenger pigeon, which—in spite of its limited fecundity and flagrant exposure to predation—reached its immense abundance through rapid long-distance movements from depleted to fresh feeding grounds. The example illustrates, he argued, that animal populations "can never increase beyond the supply of food in the least favourable season." What he did not realize at that time was the passenger pigeon's great vulnerability to human exploitation. Within Wallace's lifetime (1823–1913), the species plummeted from tens of millions of birds. The last-known individual died in captivity in 1914.

The view of animal migration as a phenomenon of abundance and vulnerability forms the central theme of David Wilcove's *No Way Home*. His alarming message is that around the world great animal migrations are disappearing. Thus, international conservation efforts are urgently needed to save the migrants from the devastating effects of overexploitation, habitat destruction, human-created obstacles, and climate change.

Animals traveling thousands or tens of thousands of kilometers in the air, on land, or in water inspire much awe. To complete its annual return journey between northerly breeding latitudes and tropical winter regions, a tiny songbird must keep to seasonal and daily timetables, change its physiological machinery between phases of fuel consumption and fuel deposition, vary flight steps and fuel loads in relation to the crossing of benign or hostile regions, find its way by compass and navigation systems, negotiate weather and winds, and correctly adjust flight speed and altitude. The bird's endowment with all necessary instructions represents a striking manifestation of the accomplishments achieved by biological evolution.

No Way Home
The Decline of the World's Great Animal Migrations

by David S. Wilcove

Island Press, Washington, DC, 2008. 253 pp. $24.95. ISBN 9781559639859.

Wilcove, an ecologist at Princeton University, presents elegant and informed accounts of migrations in various taxa: birds (the New and Old World systems of billions of songbirds traveling to and from tropical winter quarters, red knots flying between the latitudinal extremes of the American continents, and bellbirds moving down and up the slopes in Central American cloud forests), insects (dragonflies that behave like migrating birds; monarch butterflies that depart each spring from high-altitude fir forests in Michoacán, Mexico, to start a multigenerational annual cycle of movement across North America; and now-extinct Rocky Mountain locusts that once moved in swarms of millions), terrestrial mammals (wildebeest of the Serengeti, springbok of South Africa, white-eared kob of Sudan, and bison and pronghorn of North America), sea mammals (right whale in the Atlantic and gray whale in the Pacific), sea turtles, and fish (Atlantic and Pacific salmon).

For each case, Wilcove takes us into the field to meet the animals (or to the scene of now-extinct migrations), often in company with researchers conducting exciting projects. Migration studies are currently in a phase of dynamic development, with novel tracking, physiological, and molecular techniques (*2*). In addition, the author provides fascinating stories of the animals' natural history, glimpses of recent scientific discoveries about migration performance and navigation mechanisms, and historical sketches. He also describes population trends and describes the threats and conservation efforts. These strands are skillfully woven together, making his comprehensive perspective on animal travelers a delight to read.

Some of the migrants' predicaments stem from the complexity in seasonally and spatially shifting uses of resources. Increased specialization often goes hand in hand with increased vulnerability. However, the picture is not altogether dark. Some migratory populations, such as the gray whale, have shown encouraging recoveries. In recent decades, reduced persecution and the banning of toxins have led to the comeback of many birds of prey, including both short- and long-distance migrants. Changing their migration routes to exploit new resources provided by farming, some populations of geese and cranes have dramatically expanded. Their opportunistic flexibility is facilitated by learning; knowledge of migration routes is transferred between generations that travel together in families or mixed flocks (*3*). For still other species, migration may promote range expansion, leading to the establishment of new travel routes and the colonization of new breeding destinations. I would have appreciated more discussion of factors that differ between declining and expanding migratory populations. How important in this respect are cultural versus genetic evolution of migratory routes, short versus long migration distances, and levels of complexity in the annual cycle and habitat requirements?

Absorbing and thought provoking, *No Way Home* deserves to be widely read and used to promote conservation action. It illustrates the importance of science for deepening our appreciation of animal migrations and for guiding our efforts to preserve them. There is no conflict between scientific exploration of migratory mechanisms and connectivity and aesthetic marveling at the superb arrangements of nature. The investigation of animal migration is a major challenge in biology, more fascinating and urgent than ever. Wilcove urges us to proactively protect threatened migration systems while the migrants are still abundant.

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