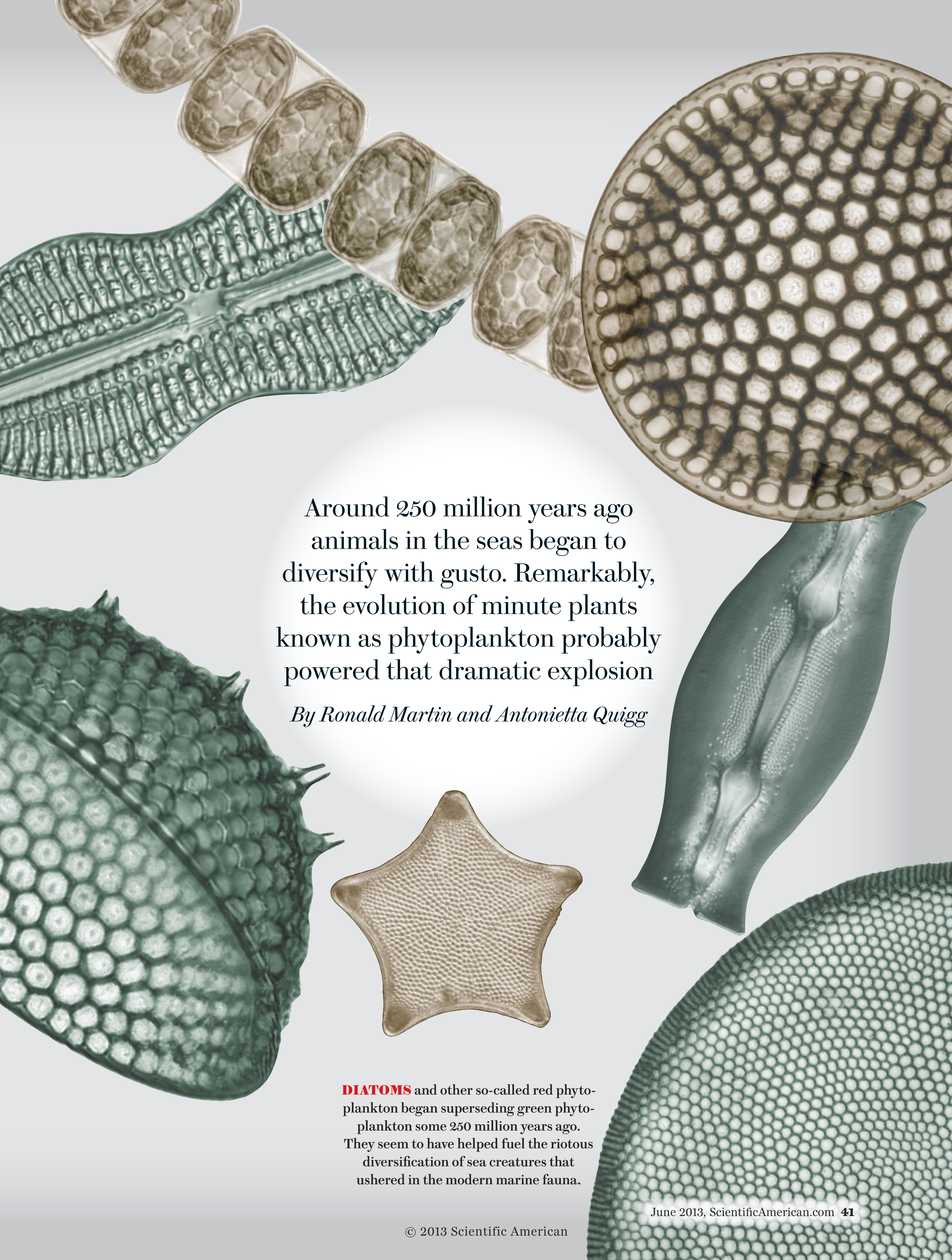
LIFE SCIENCE

Tiny Plants That Once Ruled the Seas



Around 250 million years ago animals in the seas began to diversify with gusto. Remarkably, the evolution of minute plants known as phytoplankton probably powered that dramatic explosion

By Ronald Martin and Antonietta Quigg

DIATOMS and other so-called red phytoplankton began superseding green phytoplankton some 250 million years ago. They seem to have helped fuel the riotous diversification of sea creatures that ushered in the modern marine fauna.

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IF YOU COULD HOP ONBOARD A TIME MACHINE AND VISIT THE EARTH as it was 500 million years ago, during the Paleozoic era, you'd be forgiven for thinking you had traveled not to another time period but to another planet altogether. In essence, you would have. The continents mostly sat in the Southern Hemisphere, the oceans had vastly different configurations and currents, the Alps and the Sahara had yet to form. Land plants had not even evolved. Perhaps the most dramatic difference, however, would lie in the animals that inhabited this primeval earth. Back then, most of the world's multicellular creatures lived in the sea. Clamlike creatures called brachiopods and trilobites—those extinct cousins of today's lobsters and insects, with their hard exoskeletons, long antennae and compound eyes—reigned supreme.

The diversity of marine animals grew substantially over the next 250 million years, until the so-called Permian extinction event snuffed out more than 90 percent of ocean species and brought the Paleozoic to a close. The loss of life was staggering. But change was on the horizon, and while life on land underwent a radical transformation with the rise of dinosaurs and mammals, life in the sea entered a dramatic phase of reorganization that would establish the dominance of many of the animal groups that prevail in the marine realm today, including modern groups of predatory fish, mollusks, crustaceans, sea urchins and sand dollars, among others.

The fossil record shows that over the ensuing Mesozoic and Cenozoic eras, marine life diversified at an unprecedented rate—so much so that scientists once questioned whether the pattern merely reflected the preferential preservation of geologically younger fossils, which have had less time to undergo erosion. Subsequent analyses indicated that this apparent florescence of species in the sea was indeed real, however. To explain the phenomenon, researchers have turned to a range of factors, including changes in climate and sea level, as well as mass extinctions, all of which could have fostered new opportunities. Yet although all these events may have contributed to the diversification that began around 250 million years ago, they cannot alone account for the pattern of the observed explosion.

There is another, underappreciated factor to consider: food availability. It turns out that increases in the quantity and nutrient content of microscopic plants known as phytoplankton, which form the base of marine food pyramids, accompanied the stunning emergence of new sea creatures in the Mesozoic and Cenozoic. We submit that the evolution of these modest plants fueled the rise of the modern marine fauna. This novel understanding of how phytoplankton transformed life in the ancient seas has something to say about the future of our planet as well. Phytoplankton continue to support food pyramids today; however, if future climate change and deforestation disrupt controls on their proliferation, as they have already begun to do, these plants could become a force of destruction.

FUEL CELLS

TO UNDERSTAND THE VITAL ROLE phytoplankton have played in the evolution of marine animals, it helps to know a bit about their biology and their relation to the microscopic animals that feed on them. Like all plants, phytoplankton convert the sun's energy into food through photosynthesis. Tiny, drifting herbivores collectively known as zooplankton then eat the phytoplankton and are themselves eaten by consumers higher up in the food pyramid. Nitrogen, iron, phosphorus and other nutrients in the water act like fertilizer to stimulate phytoplankton growth. The greater the availability of these nutrients, the more phytoplankton can

IN BRIEF

After a mass extinction 250 million years ago decimated marine life, sea creatures began diversifying like crazy.

Scientists traditionally chalked this evolutionary explosion up to physical factors, such as changing sea levels.

But mounting evidence suggests that the role of tiny aquatic plants known as phytoplankton has been overlooked.

Increases in the quantity and quality of phytoplankton seem to have fueled the rise of the modern marine animal groups.

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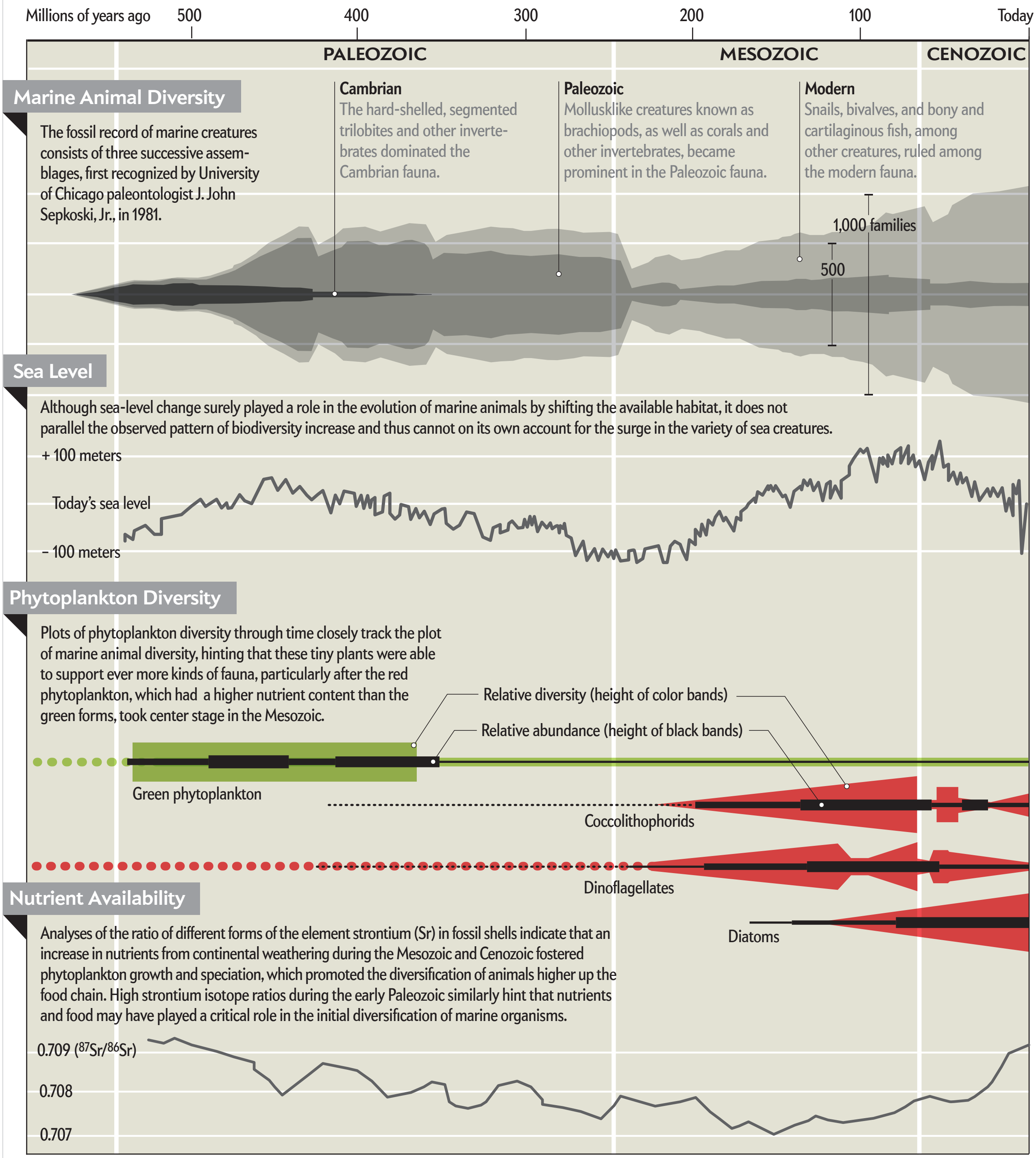
The Phytoplankton Effect

A mass extinction at the end of the Paleozoic era, around 250 million years ago, claimed more than 90 percent of marine species. But in the Mesozoic and Cenozoic eras that followed, ocean-dwelling animals staged a major comeback, reaching far higher levels of diversity than ever before. Scientists have traditionally attributed this explosion to physical factors such as sea-level change. Mounting evidence suggests, however, that the evolution of phytoplankton—the tiny plants that form the base of marine food chains—played a previously underappreciated role in fueling the florescence of animal life in the seas.



SOURCE: "EVOLVING PHYTOPLANKTON STOICHIOMETRY FUELED DIVERSIFICATION OF THE MARINE BIOSPHERE," BY RONALD MARTIN AND ANTONIETTA QUIGG, IN *GEOSCIENCES*, VOL. 2, NO. 2; JUNE 2012

Graphic by Jen Christiansen

grow and the more zooplankton eat them and keep proliferating.

In addition to boosting phytoplankton numbers, an abundance of nutrients can make phytoplankton more nutritious for zooplankton—more stuffed with readily available fuel and thus better able to support the maintenance, growth and reproduction of the minuscule animals. As populations grow, they spread out, spawn new populations that become isolated from their forebears, adapt to new circumstances and form new species.

One of the first hints that a bump in phytoplankton abundance might have had a part in triggering life's explosion after the Paleozoic came in the 1990s. Researchers, including Richard Bambach, now at the Smithsonian Institution, and one of us (Martin), independently inferred from the fossil record of marine animals that food availability must have increased from the Paleozoic to the Cenozoic. They drew that conclusion because predators and other species that have higher energy requirements than zooplankton made up an increasing proportion of marine life over time. More recently, the two of us (Martin and Quigg), along with Victor Podkovyrov of the Russian Academy of Sciences, have found evidence in the fossil record of marine plankton to support that conclusion.

We have discovered that back in the Paleozoic, enigmatic phytoplankton grouped under the informal name of green algae, formed the base of marine food pyramids, and predators were relatively rare. But after the Permian mass extinction wiped out the vast majority of marine life, including most of the green algae, new kinds of phytoplankton appeared, starting with coccolithophores, so named for the calcium carbonate shells, or "coccoliths," they secrete, possibly for protection. These distinctive plants were soon joined by the dinoflagellates and diatoms, which would go on to become the most diverse and abundant phytoplankton in the oceans. These three groups—dubbed red algae because of the type of chlorophyll they use in photosynthesis—largely replaced the green algae of the Paleozoic, setting the stage for the emergence of animal species that could exploit this new bounty.

The realization that red algae were so key made us wonder what allowed them to prevail over the green forms that survived the mass extinction. Shifts in the availability of micronutrients (nutrients available in low concentrations) used in photosynthesis appear to have played an important role. Studies of the micronutrient content of modern green and red algae, conducted by Quigg and her colleagues at Rutgers University, suggest that, as is true today, green algae had higher concentrations of iron, zinc and copper than their red counterparts, whereas red forms had higher amounts of manganese, cobalt and cadmium. Those differences mean that the micronutrients needed by the red algae must have become more abundant than those needed by the green algae.

Geologic evidence supports this notion. The abundance of carbon-rich rock known as black shale dating to the Paleozoic indicates that oxygen levels in the oceans must have been low back then because exposure to higher levels of oxygen would have caused the carbon to decay. Under these low-oxygen conditions, iron and the other micronutrients green phytoplankton thrive on would have dissolved more easily in the ocean and thus been more readily available for use in photosynthesis. In contrast, black shales from the Mesozoic are much rarer, restricted to brief periods when the seas became depleted of oxygen. The relative rarity of Mesozoic black shales implies that, on the whole, oxygen levels were much higher in that era. These conditions would have helped the micronutrients used by the red phytoplankton to remain dissolved in the oceans and available for uptake.

GREEN VS. RED

BUT SHIFTS IN THE AVAILABILITY of micronutrients during the Mesozoic do not fully account for the red algae's rise to dominance. We propose that changes in the availability of macronutrients (nutrients available in higher concentrations), such as phosphorus, also contributed significantly to the success of these groups. And these macronutrients, which phytoplankton use in such fundamental biochemical processes as DNA synthesis, appear to have entered the seas as a result of events taking place on terra firma.

By the later Paleozoic and Mesozoic, forests were spreading on land, and climate was becoming more humid, elevating weathering rates on the continents. Increased physical and chemical weathering resulting from tree roots breaking up the earth, leaves decaying and soil forming would have promoted the runoff of nutrients from the land and dead plants into the shallow inland seaways where plankton thrived. The emergence of flowering plants during the Mesozoic would have added to this runoff because their leaf litter decays much more rapidly than that of conifers, cycads and other trees that formed the earliest forests.

Evidence of continental weathering comes from analyses of the ratio of different forms of the element strontium found in fossil shells. Because continental rocks are enriched in strontium 87 as compared with oceanic rocks, the observed increase in the ratio of strontium 87 to strontium 86 in the shells over time indicates nutrients were flowing from land into the ocean in ever greater amounts, as would be expected if continental weathering were taking place. Similar isotope studies conducted using another element, lithium, confirm the trend.

Isotope studies not only confirm the existence of such fluxes from land, they also lend credence to the idea—first proposed by Martin in 1996—that nutrient runoff from continental weathering could increase marine biodiversity both in phytoplankton and in the animals that eat them. If nutrient input from land was in fact critical to the diversification of plankton, and thus other creatures, during the Mesozoic and Cenozoic, one would expect rises in the ratio of strontium 87 to strontium 86 in the shells to parallel increases in the diversity of marine creatures over time. Indeed, recent plots of strontium ratios do march in step with a diversity curve developed by John Alroy of Macquarie University in Australia in 2010. Another study published that same year, by Andrés Cárdenas and Peter Harries of the University of South Florida, found a similar correlation.

Higher oxygen levels in the oceans and the spread of forests and flowering plants on land would not have been the only factors acting to enhance the availability of nutrients to phytoplankton. Widespread mountain building that occurred as continental collisions formed the supercontinent Pangaea, along with the falling sea levels of the era, would have begun to increase the rates of weathering and nutrient runoff into the seas before the Mesozoic. And the continental glaciers that occupied the Southern Hemisphere during most of the later Paleozoic would have promoted relatively rapid circulation and oxygenation of the oceans, together with the upwelling of waters already enriched in phosphorus from the decay of organic matter and oxygen-sensitive trace metals. All told, these factors would have created favorable conditions for the red algae to flourish, providing them with plenty of the exact kinds of micronutrients and macronutrients they were best suited to exploit.

The reign of the nutrient-poor green algal lineages during the first half of the Paleozoic seems to have kept the evolution of marine animals in check, delaying the appearance of new forms with higher metabolic rates. But as the nutrient-rich red algae took center stage, the marine animals that ate these phytoplankton underwent dramatic diversification, as the fossil record shows. Novel groups of predatory fish burst onto the evolutionary scene, along with new varieties of mollusks, crustaceans, corals and bivalves, among other animals.

Two recent field experiments offer a proof of principle that the kind of nutrient runoff we have described could have sparked diversification of multicellular animals. In the first, Tron Frede Thingstad of the University of Bergen in Norway and his colleagues added phosphorus to surface waters of the eastern Mediterranean Sea, which are naturally extremely poor in nutrients generally and starved of phosphorus specifically. These waters resemble the conditions that Martin postulated to exist early in the Paleozoic. The experimental nutrient input stimulated rapid uptake of the phosphorus by local phytoplankton—much more than required for normal growth—thus enriching the nutrient content of the tiny plants within little more than a week.

In the second experiment, James Elser of Arizona State University added phosphorus to communities of so-called cyanobacteria in a stream in Coahuila, Mexico. These cyanobacteria obtained their food through photosynthesis the way plants do and were similar to cyanobacteria that lived during the early Paleozoic. The extra phosphorus lowered the ratios of carbon (a nonnutrient) to phosphorus in these communities from as much as 1,100:1 down to 150:1, at which point the growth rate, the total amount of living tissue and the survivorship of the snails grazing on the cyanobacteria all markedly increased.

Although these experiments did not demonstrate evolutionary diversification (because of their short duration), they show that increased availability of key nutrients in the seas could have quickly raised the nutrient content of phytoplankton and that enriched phytoplankton could have in short order passed these benefits up the food chain to the animals that ate them, freeing those animals up to devote more energy to reproduction, which is a prerequisite to diversification.

RETURN TO THE PALEOZOIC

UNDERSTANDING HOW PHYTOPLANKTON responded to shifting environmental conditions in the past could help scientists predict what the future holds for marine life in our changing world. Carbon dioxide emitted as a result of human activities is both heating the earth and acidifying the sea. In coming centuries, the oceans will, to a certain extent, come to resemble those of the Mesozoic or Paleozoic. In the deep ocean, thick calcium carbonate–rich deposits formed from the accumulation of sunken coccolithophore shells will tend to neutralize the dissolved carbon dioxide. But in the surface waters, the coccolithophores and other calcifying phytoplankton that live there may be devastated by the acidification, which reduces the availability of minerals needed to make and maintain their shells. Although such organisms have endured environmental change for hundreds of millions of years, the current influx of carbon dioxide is happening so quickly that they may not be able to adapt to it fast enough.

The loss of these organisms could exacerbate warming. Today blooms of the coccolithophore *Emiliania huxleyi* can cover areas greater than 100,000 square kilometers, and they produce significant amounts of the compound dimethyl sulfide, which, in turn, seeds cloud formation. And clouds reflect sunlight back into space, cooling the planet. Without coccolithophores, then, the earth would absorb more solar energy than it already does.

Calcifying phytoplankton that live in reef communities will suffer a double whammy from anthropogenic CO_2. Not only will acidification dissolve their skeletons, but warming will quickly surpass the limits of their temperature tolerance (reef species tend to live near the upper limits of their temperature tolerance).

Carbon dioxide emissions are not the only threat humans pose to phytoplankton. Soil erosion from deforestation and other human activities are flooding coastal systems—where reef species thrive—with nutrients, leading to excessive growth, and subsequent decay, of aquatic plants. Reefs will be devastated by the invasion of new species that will outcompete the slower-growing reef forms. Although nutrient inputs to the ocean fueled the diversification of life over hundreds of millions of years, the current pace of "enrichment" is clearly too much of a good thing.

As the oceans warm, they may also become increasingly stratified: warm water acts as a lid on the cold water, thus impeding upwelling and circulation. Dinoflagellates dominate under such conditions, which could increase the frequency and surface area covered by toxic blooms in coastal habitats. Because these habitats also serve as refueling stops for migratory birds and nurseries for commercially important fish and crustaceans, we humans will feel the effects of their degradation acutely.

Future studies will flesh out scientists' understanding of how environmental change affected the evolution of phytoplankton in the past and how the rise of the red forms spurred the diversification of marine animals. We are eager to determine, for example, how the low oxygen conditions of areas such as the Mississippi Delta affect nutrient uptake by phytoplankton and how this shift in nutrient uptake affects the community of animals that feed on them. Similar studies have been conducted in lake settings, in which the community structure is rapidly altered via domino effects.

Such findings may help researchers better predict how modern phytoplankton—and the species that depend on them—will fare in the future. But one thing is clear. Although deniers of climate change often argue that life on earth routinely adapted to environmental shifts in the past and can thus handle future fluctuations, this is the wrong way to think about our current situation. Human activities are altering ocean conditions at a speed unsurpassed in our earth's history. We are thus unwittingly conducting an experiment that has never been run on this planet, the exact outcome of which will not be known until it has occurred. SA

MORE TO EXPLORE

Evolving Phytoplankton Stoichiometry Fueled Diversification of the Marine Biosphere. Ronald Martin and Antonietta Quigg in *Geosciences*, Vol. 2, No. 2, pages 130–146; June 2012.

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View a slide show of phytoplankton at **ScientificAmerican.com/jun2013/phytoplankton**