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The Once and Future Ocean

BY PAUL G. FALKOWSKI

Remarks from the Tenth Annual Roger Revelle Commemorative Lecture. This lecture was created by the Ocean Studies Board of the National Academies in honor of Dr. Roger Revelle to highlight the important links between ocean sciences and public policy. This year, the speaker was Paul G. Falkowski, and the lecture was held on March 17, 2009 at the Baird Auditorium at the Smithsonian's National Museum of Natural History.

THE OCEAN HAS BEEN a feature of Earth's surface for at least four of the past 4.5 billion years and has provided the primary environment for the evolution of microbes that drive Earth's biogeochemical cycles (Falkowski et al., 2008). Over this incomprehensively long time period, the ocean and the organisms in it have witnessed extreme changes, ranging from complete coverage with ice to extensive periods when there was no ice at all. There have been periods of extraordinary extinction of animal life due to meteorite impacts and volcanic outgassing, when the ocean became acidic and anoxic for extensive periods of time, and long intervals of relative stability that fostered the evolution of animals, from which we ultimately descend. Yet most of us never think about how the organisms that drive the biogeochemical cycles in the ocean evolved and have survived these extreme environmental changes to provide the backbone of life on Earth. Indeed, microbes in general, and marine microbes in particular, are the real stewards of life on Earth. We have a lot to learn about how they work and function to make this planet habitable. In this article, I examine how life evolved in the ocean, how it impacted the evolution of mammals, including humans, and how we are impacting the ocean.

Six major elements—H, C, N, O, S, and P—comprise the major building blocks of all biological macromolecules (Schlesinger, 1997). The biological fluxes of the first five are largely driven by microbially catalyzed, thermodynamically constrained reactions that involve the transfer of electrons from one molecule to another; in a real as well as figurative sense, life is electric. The movement of electrons leads to the evolution of coupled half cells, which in turn evolves into a global system of linked elemental cycles (Falkowski et al., 2008). For example, all animals transfer electrons from organic carbon to oxygen, thereby leading to the production of water vapor (which we exhale with each breath). This is one half cell. Photosynthetic organisms, like algae and plants, use the energy of the sun to oxidize water using the electrons and protons to make organic matter. That is the complementary half cell. These two half cells are extremely well coupled, so that on long time scales, there is very little change in oxygen on Earth; in other words, biological processes tend to reach a global steady state that is far from thermodynamic equilibrium, yet is robust over hundreds of millions of years (Falkowski and Godfrey, 2008).

Biological processes do not operate in a vacuum. On geological time scales, resupply of C, S, and P is critically dependent upon tectonics, especially volcanism and rock weathering (Figure 1). The role of geological processes in the evolution of life is seldom appreciated by biologists; yet without these processes, biogeochemical cycles would inevitably come to an end. Feedbacks between the evolution of microbial metabolic and geochemical processes create the average oxidation state of the ocean and atmosphere. The evolution of oxygen in Earth's atmosphere occurred about 2.3 billion years ago and is an emergent property of microbial life on a planetary scale. Earth's biological oxidation is driven by photosynthesis (Falkowski, 2002).

Over the past few years, biologists and geologists have worked to develop a metabolic map of Earth. The fluxes of the major elements correspond to

Paul G. Falkowski *(falko@imcs.rutgers.edu) is Professor, Department of Earth and Planetary Sciences and Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ, USA.*

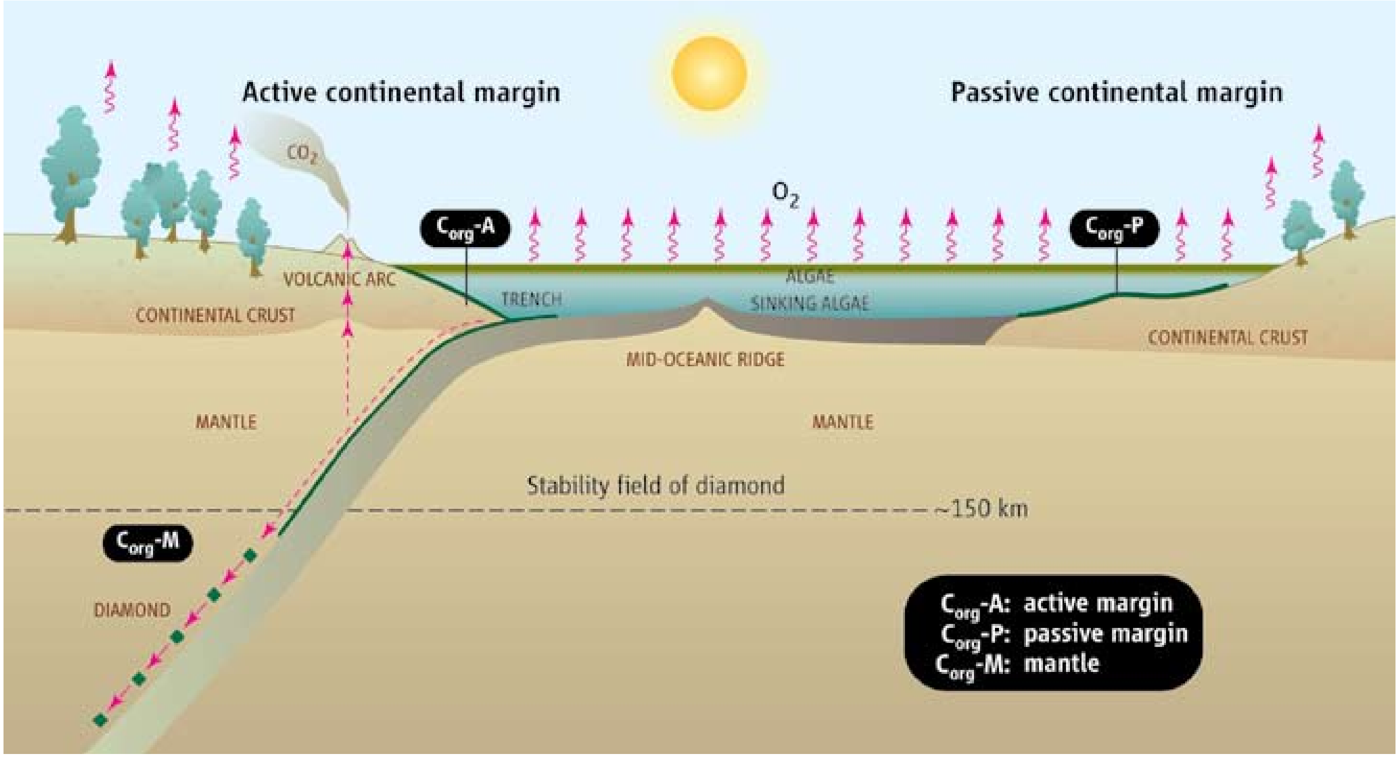

Figure 1. Processes controlling the flux and accumulation of O_2 on Earth. *Falkowski and Isozaki, 2008, reprinted with permission from AAAS*

specific microbial pathways, all of which originated in the ocean and all of which can still be found there. The genes encoding the machinery responsible for these fluxes are the "core" genes of life on Earth. These microbial "machines" catalyze the electron transfer reactions that drive the half cells described earlier. Although the genes are often highly conserved, complexes did not evolve instantaneously. Indeed, the order of their appearance in metabolism and analysis of their evolutionary origins are obscured by lateral gene transfer and extensive selection. These processes make it extremely challenging to reconstruct how electron transfer reactions came to be catalyzed (Falkowski and Godfrey, 2008). Regardless, the pathways that evolved to sustain this electron market contain relatively few genes. Indeed, this appears to be one of the most amazing things about life—a very small number of "core" genes are responsible for the operation of this planet.

There is little understanding of how long it took for the various reactions to develop from local events to global alteration of the planet. However, the most transformative process, beyond doubt, was the evolution of oxygenic photosynthesis—the splitting of water. That process is the most complex energy transduction process in nature: over 100 genes are involved in making several macromolecular complexes (Shi et al., 2005), and it appears to have been one of the last pathways to have evolved. Perhaps most profoundly, we still do not really understand how it works! Regardless, the evolution of oxygenic photosynthesis per se did not lead to an atmosphere containing oxygen—for that to occur, organic matter formed by algae had to be buried in Earth's interior—a very small fraction of that organic matter would eventually become the fossil fuels that we extract to drive our industries. Indeed, without the contribution of geological processes, we never would have had oxygen on the planet (Falkowski and Isozaki, 2008). Once the processes got going, though, oxygen became the second most abundant gas on Earth and profoundly influenced the evolution of life forever after. All the oxygen on Earth is ultimately derived from the water in the ocean—the energy required to produce the 4 x 10^{18} moles of oxygen is equivalent to the explosion of over a trillion hydrogen bombs. No wonder there is a lot of thought being given to trying to understand the mechanism responsible for splitting water with energy from the sun.

From a biogeochemical perspective,

Earth's history can be divided into two major periods. The first 2.5 billion years was the "Research and Development" eon, when all the major metabolic pathways evolved. The last two billion years has been the "Microsoft" eon, when life appropriated the metabolic processes derived during the first half of Earth's history and marketed them in new forms. From a metabolic perspective, evolution basically stopped around two billion years ago. Animals and plants are examples of new incarnations of ancient metabolic processes; the world can go along very well without these minor evolutionary distractions. However, the core set of genes that runs the planet is very precious. To make sure the core set is not lost, nature distributed the genes across the tree of life—but the entire repertoire is retained in marine microbes. Indeed, the ocean is the corporate memory of the planet. In essence, microbes can be viewed as vessels that ferry metabolic machines through strong environmental perturbations on into vast stretches of relatively mundane geological landscapes. The individual species come and go, yet the core machines survive surprisingly unperturbed.

It is likely that the individual reactions that make life possible on Earth will be reasonably well described within the next few decades. Delineating how these machines co-evolved and operate together to create the electron flows that predominate today on Earth's surface remains a grand challenge. However, understanding how biogeochemical cycles function is critical to the survival of human beings as we continue to influence the fluxes of matter and energy on a global scale. In that regard, understanding the maintenance of the reservoir of core genes in the ocean is not simply an academic exercise; it is critical to our survival as a species. Marine microbial life can easily live without us, but we cannot survive without the global catalysis and environmental transformations they provide.

In the twentieth century of the common era, the ensemble of the subpopulations comprising *Homo sapiens* rapidly expanded. Over a period of 100 years, the population grew from ca. 950 million to more than 6 billion. This unprecedented rate of population expansion was accompanied by an unprecedented strain on Earth's natural resources. Humans presently consume or exploit roughly 42% of the terrestrial net primary production (Vitousek et al., 1997). Our species has displaced, extinguished, or impacted virtually

Table 1. Examples of human intervention in the global biogeochemical cycles of carbon, nitrogen, phosphorus, sulfur, water, and sediments (data are for the mid 1900s). *Reprinted with permission from Falkowski et al., 2000*

Element	**Flux**	**Magnitude of flux (millions of metric tons per year)**		**% change due to human activities**
		Natural	**Anthropogenic**	
C	Terrestrial respiration and decay CO_2	61,000		
	Fossil fuel and land use CO_2		8,000	+13
N	Natural biological fixation	130		
	Fixation owing to rice cultivation, combustion of fossil fuels, and production of fertilizer		140	+108
P	Chemical weathering	3		
	Mining		12	+400
S	Natural emissions to atmosphere at Earth's surface	80		
	Fossil fuel and biomass burning emissions		90	+113
O and H (as H_2O)	Precipitation over land	111×10^{12}		
	Global water usage		18×10^{12}	+16
Sediments	Long-term preindustrial river suspended load	1×10^{10}		
	Modern river suspended load		2×10^{10}	+200

every extant vertebrate species (Jackson et al., 2001). With very few exceptions, humans have altered the flow and chemical form of all naturally occurring elements and all of the freshwater on the planet (Falkowski et al., 2000) (Table 1). Continued population growth through at least the first half of the twenty-first century will undoubtedly force an even greater exploitation of resources, with an inevitable increase in the human footprint on the ecological landscape. Clearly, such a condition is not sustainable. Perhaps most disturbingly, no off-ramp is visible in the trajectory of human domination of Earth's ecosystems. Economic policy simply is at odds with biogeochemical reality, and money cannot substitute for microbial metabolism. We have to pay attention to how the world functioned before human domination of the planet because, ultimately, we will have to repair what we have broken.

BOX 1. SELECTED TRAITS THAT DISTINGUISH HUMANS FROM OTHER APES

(adapted from Carroll, 2003)

Body shape and thorax
Cranial properties (brain case and face)
Relative brain size
Relative limb length
Long ontogeny and lifespan
Small canine teeth
Skull balanced upright on vertebral column
Reduced hair cover
Elongated thumb and shortened fingers
Dimensions of the pelvis
Presence of a chin
S-shaped spine
Language
Advanced tool making
Brain topology
Economic structure

THE RED QUEEN HYPOTHESIS

There is a notion, put forward in an elegant paper by van Valen (1973), that coevolution increases stability by maintaining a constant rate of extinction and radiation over millions of years. The basic idea is called the Red Queen hypothesis. The gist of this hypothesis is that in tightly co-evolved interactions, evolutionary change in one species (e.g., a prey or host) could lead to the extinction of the other species (e.g., a predator or parasite). This idea, named after Lewis Carroll's character in *Alice in Wonderland*, postulates that a species must evolve to keep pace with environmental selection or the species will go extinct. In other words, the species has to "run" to stay in place. It is a useful heuristic device—which may or may not be correct—that can serve as a starting point for examining how human evolution diverged from other species that inhabit Earth.

THE EVOLUTION OF HUMANS

Our species evolved approximately 200,000 years ago—a mere blink of an eye in Earth's history (Carroll, 2003). The evolution of *H. sapiens* rapidly changed Earth. Two major attributes of humans distinguish us from all other organisms (Box 1). These attributes have allowed humans to dominate the terrestrial landscape but not without ecological costs, many of which are not yet recorded in the ledger of natural history.

A distinguishing feature of human evolution is clearly the evolution of complex language (Lieberman, 2000). Human language permits communication of abstract thoughts through oral, visual, and written media. In the modern epoch, our communication skills are so honed that we can transfer, virtually instantaneously, vast bodies of knowledge across generational and geographic boundaries without changing a single gene within our gametes. Although other organisms, especially vertebrates, have limited communications skills, the quantum evolution that led to the extraordinary development of such attributes in *H. sapiens* appears unprecedented in the history of the planet. Language gave humans an incredible capacity to rapidly accommodate to, and indeed affect, the environment in ways no other organisms can.

The second attribute is the ability to create advanced tools. In this capacity, humans have excelled not only in fabricating instruments to acquire food and build shelters more efficiently—processes that clearly have parallels in other organisms—but also in altering natural materials to produce substances that otherwise never would have been found in nature. The examples of such massive alterations of materials are so enormous and so obvious to most of us that we tend to overlook their importance.

The result of the evolution of language and the ability to create advanced tools is, however, more subtle and more dangerous. These two traits have permitted and, ultimately perhaps even required, a new form of knowledge, which I call "distributed knowledge." If we consider what each of us individually knows or knows how to do, we are hard pressed to recreate the world most of us know. For example, someone somewhere knows how to make a light bulb, but very few of us individually have that knowledge. Moreover, we no longer go to a professional light-bulb maker and contract with him or her to make some specific light bulbs for us. Rather, a community of people has made machines that make and shape the glass for the bulbs; extract, purify, and fashion the tungsten elements or the fluorescent gas; make the metal base; pull the vacuum during the manufacturing; and so forth. Light bulbs are now made anonymously by groups of individuals, working with machines, made by other groups of people, each with specific individual knowledge. The knowledge is distributed.

The ensemble of human knowledge and skills is transmitted across geographical boundaries without need for genetic alteration. In so doing, skills are traded to create an economy. I assert that a fundamental emergent property of the evolution of speech and tool making is economic structure—a phenomenon unique to human society. Economic structure has led to global resource plunder—unlike anything seen at any time in our planet's history. In one year, we extract the equivalent of one million years worth of fossil fuel. We burn these stored reserves to produce energy—a primitive technology—but have developed the tools to plunder all fossil fuel reserves on the planet. The result is clearly damaging; the upper

ROGER REVELLE

For almost half a century, Roger Revelle was a leader in the field of oceanography. Revelle trained as a geologist at Pomona College and at the University of California, Berkeley. Then, in 1936, he received his PhD in oceanography from the Scripps Institution of Oceanography. As a young naval officer, he helped persuade the Navy to create the Office of Naval Research (ONR) to support basic research in oceanography and was the first head of ONR's geophysics branch. Revelle served for 12 years as the Director of Scripps (1950–1961, 1963–1964), where he built up a fleet of research ships and initiated a decade of expeditions to the deep Pacific that challenged existing geological theory.

Revelle's early work on the carbon cycle suggested that the sea could not absorb all the carbon dioxide released from burning fossil fuels. He calculated the first continual measurement of atmospheric carbon dioxide, leading to a long-term record that makes present-day discussions on research on global warming possible and very valuable. Revelle kept the issue of increasing carbon dioxide levels before the public and spearheaded efforts to investigate the mechanisms and consequences of climate change.

Revelle was a proponent of daring programs, like Mohole and the International Indian Ocean Expedition, which addressed fundamental scientific questions and pioneered international cooperation. In 1960, Revelle left Scripps for critical posts as Science Advisor to the Department of the Interior (1961–1963) and as the first Director of the Center for Population Studies at Harvard (1964–1976). Revelle applied his knowledge of geophysics, ocean resources, and population dynamics to the world's most vexing problems: poverty, malnutrition, security, and education.

In 1957, Revelle became a member of the National Academy of Sciences to which he devoted many hours of volunteer service. He served as a member of the Ocean Studies Board, the Board on Atmospheric Sciences and Climate, and many committees. He also chaired a number of influential Academy studies on subjects ranging from the environmental effects of radiation to understanding sea-level change. *Photo Credit: SIO Archives, UCSD* ocean is about 0.5°C warmer today than 50 years ago and is getting warmer each decade. That process itself is changing ocean circulation and productivity. Simultaneously, the ocean is getting more acidic, and organisms that build carbonate structures, like corals, are greatly endangered. Yet, in the halls of industry, global climate change may be viewed with skepticism, or worse. Clearly, this course is not sustainable—yet we have not invested in the technological solutions. It is still much cheaper to buy oil that was produced by algae 50 million years ago than to make oil from algae today, although, in the long run, the latter is sustainable. How can we escape from this dead end?

THE ROLE OF SCIENCE

Over the past 30 years or so, scientists have increasingly documented the effects of humans plundering Earth's resources. The documentation has had a relatively modest effect on societal responses. Sustainable development requires the mass expansion of individual altruistic behavior, a process that itself requires education and a re-evaluation of how human economic structures can be used to preserve and conserve natural resources for future generations of humans. Education in developed countries can markedly alter patterns of resource use, but this change must be coupled with intelligent investment of wealth in technologies that are inherently sustaining. For example, the photocatalyzed extraction of hydrogen from water would provide a potentially limitless, clean energy source (Lewis and Nocera, 2007); however, in the United States, the investment in this process is less than $10 million per annum. A single breakthrough in catalysis could change the world forever. Similarly, the development of N_2-fixing crops or the replacement of relatively rare metals (such as titanium) in machines with alternatives derived from renewable resources can alter the course of human impact on Earth.

But science and technology are not the only solutions—human ingenuity must be coupled to human behavior. The concept that humans are partners in ecosystems is not new but does not pervade the human psyche, except in isolated, nomadic tribes, where there is a clearer, intuitive appreciation for habitat and a respect for it. We must leave the "documentation" stage of scientific enquiry and enter a social/technological stage, where realistic outcomes (both positive and negative) can be envisioned and integrated solutions explored. Nonlinearities in policy that can lead to dramatic changes in human behavior should be identified. Science does not simply serve as a knowledge base—it must also serve as a conscience of society—reminding wealth "creators" that sustainable resource management is the only viable option for future generations.

FINAL REMARKS

The ocean and atmosphere are huge, and we are small. We tend to think we cannot really make an impact on the ecology or biogeochemical cycles of Earth. Yet, over the past 100 years, in particular, we have increasingly altered the trophic structure of the ocean, as well as its physical circulation and chemical properties. Although human impacts will surely alter ecosystem functions, the core metabolism of the ocean will go on. The microbes will long outlive us. Rather, ironically, humans are the fragile species that will lose capabilities for using the ocean as a source of food and novel molecules. Our future is intimately tied to that of the ocean. We have to begin viewing the ocean as the key component of the Earth system—one that we cannot live without. We still have a long way to go.

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