CONTRIBUTIONS to SCIENCE
OPEN ACCESS

DISTINGUISHED LECTURES
Institut d'Estudis Catalans, Barcelona, Catalonia
www.cat-science.cat

MARGALEF PRIZE LECTURE OF 2013

Margalef's mandala, *Prochlorococcus*, and geoengineering*

Sallie W. Chisholm
Departments of Civil and Environmental Engineering and Biology, Massachusetts Institute of Technology, Cambridge, MA, USA

Correspondence:
Sallie W. Chisholm
Dept. of Civil and Environ. Engineering
Massachusetts Institute of Technology
77 Massachusetts Ave.
Cambridge, MA 02139, USA

E-mail: chisholm@mit.edu

Summary. Ocean phytoplankton played a central role in oxygenating our planet's atmosphere billions of years ago. Hence these early "geoengineers" were crucial for the evolution of life on Earth. Their modern-day ancestor, the marine cyanobacterium Prochlorococcus, is the most abundant photosynthetic cell on the planet. Its discovery 30 years ago served as a reminder of how little we understand about the complexities of marine food webs. Yet proposals to fertilize the oceans, either to mitigate climate or enhance fisheries, continue to gain momentum both within the scientific community and in the commercial sector. If implemented, the unintended consequences of these and other geoengineering proposals are likely to be enormous, and impossible to anticipate.

The most ubiquitous, important, and profound dimension of life on Earth is the process of photosynthesis. Had some ancient marine microorganism not acquired a key mutation some 3.5 billion years ago, allowing it to split water instead of hydrogen sulfide, the evolution of life on Earth would have taken an entirely different trajectory. Photosynthesis was the ultimate "disruptive technology" of its day—converting carbon dioxide gas into organic carbon molecules using solar energy and splitting water—releasing oxygen gas. Over billions of years oxygen transformed the very nature of our planet, making it possible for more complex forms of life to evolve and spread across the Earth. As that oxygen accumulated in the atmosphere, organic carbon was buried and compressed—becoming fossil fuel and accumulating over billions of years. This is the "buried sunlight" humans began to exploit a few hundred years ago, changing profoundly our civilization and its relationship to the natural world.

Picocyanobacteria—micron-sized unicells that thrive throughout the oceans—are the modern-day descendants of the ancient metabolic engineers that oxidized our planet. The sister clades *Prochlorococcus* and *Synechococcus* co-exist over vast regions of the tropical and subtropical oligotrophic oceans. Their global populations are roughly 10^{27} cells [41] and in some places they account for over 50% of the total photosynthetic biomass [16]. Since the oceans contribute just less than half of the global photosynthesis (35–50 Gtones of carbon per year, Gt C y^{-1}) these

*Based on the lecture given by the author at the Palau de la Generalitat of Catalonia, Barcelona, on 21 October 2013, on the occasion of receiving the Ramon Margalef Prize for 2013.

Keywords: *Prochlorococcus* · geoengineering · climate change · iron fertilization

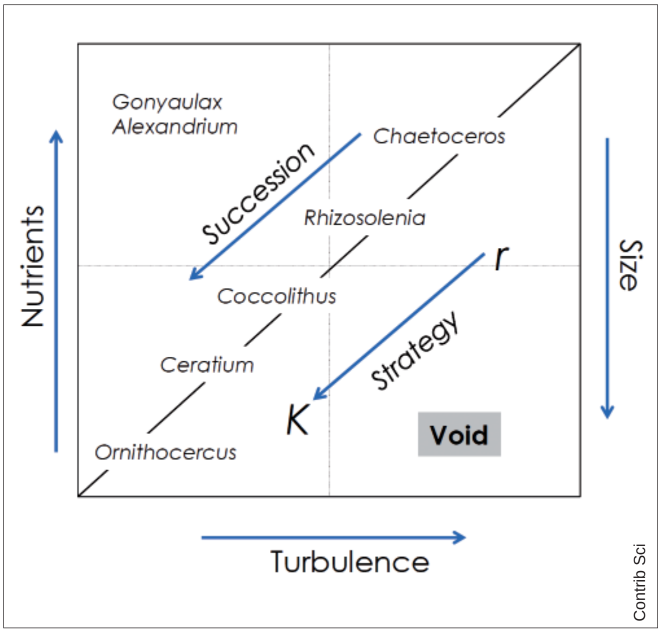

Fig. 1. Margalef's marine mandala showing the relationship between nutrient availability, turbulence, size and the niche space of characteristic genera. The diagonal line is the main sequence of succession and the arrow marks the progression from R-selected to K-selected groups as well as general size progression. Margalef predicted that there would be some group of phytoplankton yet-to-be discovered that would fill the void in the SE quadrant. Picocyanobacteria fill that void. Adapted from [30].

tiny cells single-handedly play a central role in global metabolism. Given their global significance, it is somewhat astonishing (and humbling) that *Synechococcus* was not discovered until 1979 [20,54] and *Prochlorococcus* in 1988 [9]. We can derive some comfort, however, from the fact that Ramon Margalef imagined the existence of these types of cells as he developed his theory of phytoplankton succession. He represented the phase space occupied by different eukaryotic phytoplankton groups as bounded by gradients of nutrients and turbulence, and identified a "void" in the southeast quadrant of his now-famous Mandala (Fig. 1). I am told that he predicted that there had to be some group of small phytoplankton that would fill this "void" in the diagram (Celia Marassé, pers. comm.), and indeed that is precisely where picocyanobacteria would fit.

Prochlorococcus, mandalas within mandalas

As the smallest of the picocyanobacteria, *Prochlorococcus* embodies the minimal amount of information—2000 genes—that can generate life from solar energy and inorganic compounds. After its discovery we wondered how something so simple could be so ubiquitous, as general ecological theory would suggest such a system to be very unstable. The answer is, of course, that *Prochlorococcus* is not a single entity. It consists of unknown numbers of ecotypes, each with slightly different fitnesses along environmental gradients—in a sense creating a mandala of their own within the "void" space in Margalef's mandala. The relative abundance of these ecotypes shifts slightly as ocean conditions shift, insuring the stability of "the collective"—or "*Prochlorococcus* federation" as we sometimes call it (Fig. 2). The diversity within the collective is astounding. Each cell has about 1200 core genes that it has in common with all 10^{27} *Prochlorococcus* in the oceans [24]. The remaining 800 or so genes making up the complete genome are only shared with some other cells and to varying degrees. So although each cell has roughly 2000 genes, the "collective genome" or "distributed genome" of the 10^{27} members of the global *Prochlorococcus* federation is estimated to be 83,000 genes [2]. It is this collective gene pool that enables it to consistently occupy such a broad range of oceanic conditions.

What are the functions of the genes that give *Prochlorococcus* its collective diversity? This puzzle continues to unravel, but to date there are a number of niche axes upon which selection has operated to drive *Prochlorococcus* differentiation. These include adaptations to different light intensities, temperature sources and concentrations of essential nutrients such as phosphorus, nitrogen and iron, and defense mechanisms for different types of viruses (phage) that infect them [12]. More recently we have learned that some 'ecotypes' of *Prochlorococcus* can utilize organic carbon compounds including glucose [17] and amino acids [57], introducing further complexity and drawing attention to mixotrophy as an important dimension of the existence of some *Prochlorococcus* lineages.

What has also come to light as we begin to appreciate the diversity within *Prochlorococcus* is the degree to which the phages that infect them play a role in generating this diversity. Phages acquire genes from host cells during infection and use them to guide host metabolism [25,47]. These genes are subjected to different selective pressures while in the phage and thus evolve in ways that would not happen in the host cell. As such, phages are diversity generators for key genes involved in the cellular machinery of the host, providing great grist for the natural selection mill. These evolving genes can, in principle, reintegrate into the host's chromosome at any time, introducing variety for selection to operate upon. We find that many of the "niche-defining" genes in a particular

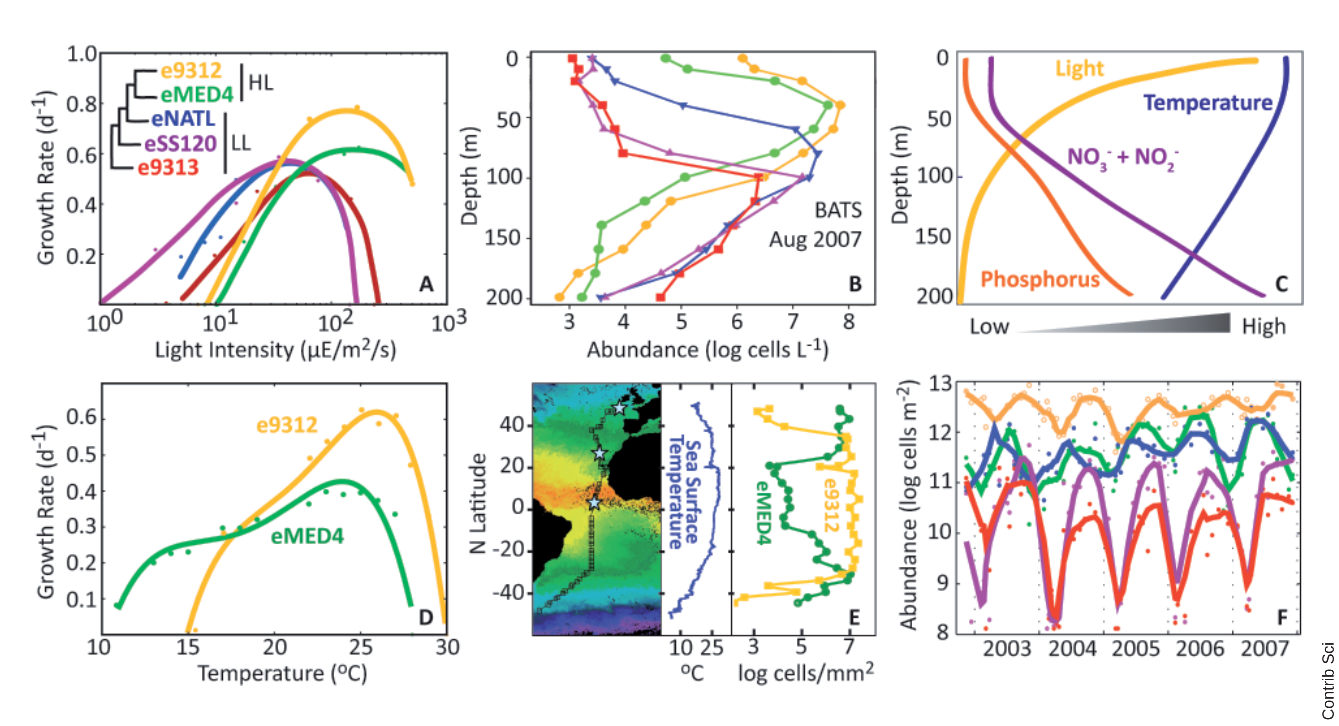

Fig. 2. *Prochlorococcus*, the collective, consists of high- and low-light adapted ecotypes with sub-clades within each group (represented here in a 'cartoon tree') (**A**). The ocean habitat has strong vertical gradients of light, temperature, and nutrients (**C**), and the ecotypes distribute themselves along these gradients in ways that are consistent with their growth optima as a function of light intensity (**B**). Strains from the two clades within the HL adapted group (green and yellow) have different temperature tolerance ranges (**D**), and the relative abundances of cells belonging to these clades along longitudinal temperature gradients are consistent with these physiological optima (**E**). Strong seasonal forcing drives seasonal succession in ecotype abundances that are repeated with great regularity from year to year (**F**). The "eNATL" ecotype in particular is able to withstand the fluctuating light due to deep winter mixing much better than the other low-light adapted strains [1,21,28,36,55,56].

Prochlorococcus lineage are located in hyper-variable island regions of the genome, and these regions have signs that phage are involved in shuttling their genes around [13].

The iron hypothesis

Prochlorococcus thrives in the most nutrient impoverished regions of the oceans. Their chemical composition is finely tuned to the austerity of the oligotrophic ocean habitat, and has features that reflect this. Their lipids, for example, consist primarily of sulfo- rather than phospho-lipids, reflecting the extremely low concentrations of phosphorus in their habitat [50], and over 90% of the phosphorus in a *Prochlorococcus* cell is in its nucleotides [53]. There is also evidence of N-sparing in the amino acids that it uses in its proteins [18]. But *Prochlorococcus* also thrives in equatorial pacific waters which are among the so called "high nutrient-low chlorophyll" (HNLC) regions of the oceans where iron limitation prevents phytoplankton from assimilating available nitrogen and phosphorus. And it is these *Prochlorococcus* that ultimately drew me into a debate about ocean stewardship and geoengineering (Fig. 3).

In the early 1980s one of the questions troubling oceanographers was: "Why aren't equatorial Pacific waters greener?" There are abundant N and P supplies in these regions as a result of equatorial upwelling, but phytoplankton are not able to assimilate them and grow to densities one would expect [8]. John Martin had already shown that if you put equatorial Pacific water in bottles and add iron—in effect pushing the system into the northeast quadrant of Margalef's mandala—phytoplankton did indeed bloom [33]. Even with this evidence, some oceanographers were slow to accept the "iron hypothesis" so Martin designed the definitive experiment—one that would circumvent all criticism about the potential "bottle effects" in his experiments. He designed, and his team implemented, the first unenclosed open-ocean fertilization experiment, IRONEX-I, in which iron was added to a 100-km^2 patch of

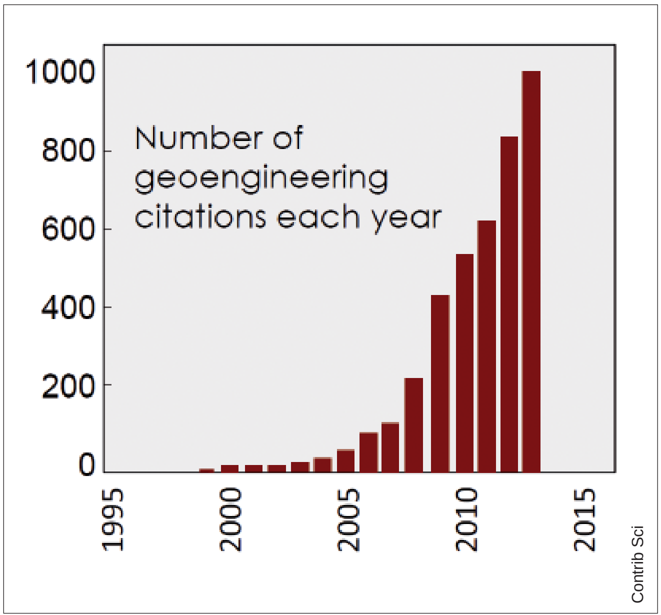

Fig. 3. Geoengineering comes of age. The number of citations of papers on geoengineering has increased dramatically in the past decade (Source: ISI Web of Knowledge, Web of Science).

ocean, and the response of the phytoplankton community was followed for several weeks. The results were unambiguous [32]. Iron addition created a large phytoplankton bloom, dominated by diatoms, and the drawdown of excess nitrogen.

IRONEX-I was followed by IRONEX-II, and my laboratory was fortunate enough to participate in those historic experiments to study how *Prochlorococcus*—not known to be a bloom former—responded to release from iron limitation. True to form, their population sizes held steady throughout the iron-induced diatom bloom, but their cell division rates doubled, proving that even the smallest cells in the community were severely iron limited [29]. Population sizes held constant because the microzooplankton that eats *Prochlorococcus* responded to the increased supply of cells and kept their numbers in check. What is unclear from these experiments, and all that followed [4], is how these communities would respond to sustained iron enrichment.

The expanded iron hypothesis

John Martin not only hypothesized that iron limits HNLC areas of the contemporary ocean but he also suggested that variations in the availability of iron to the oceans could have played a role in regulating Earth's past glacial/interglacial cycles. He saw evidence of coupling between iron dust flux to the oceans and atmospheric CO_2 concentrations suggesting that iron-stimulated blooms of plankton in the southern ocean played a role in the drawdown of atmospheric CO_2. The inference was that this played a role in cooling the Earth on geological time scales [31]. This idea spread like wildfire in the popular press as people began to postulate that perhaps one could reduce the growing fossil fuel-derived CO_2 load to the atmosphere by fertilizing the oceans with iron. Indeed, John Martin planted the seed for this idea when he made the now famous remark "Give me a half-tanker of iron and I will give you an ice age" while giving a lecture on his theory about the climate connection [8].

Over the years since Martin made that statement, the iron fertilization approach to mitigate climate change has received attention in many circles. Although never explicitly stated, this application was a subtext for the numerous ocean iron fertilization experiments designed to explore various dimensions of "the iron hypothesis" [4]. While none of those experiments were studying iron fertilization as a "geoengineering tool", the focus of the experiments coalesced on studying how much carbon could be captured in an iron-enriched bloom, and what fraction of this might be exported to deeper waters where it would be isolated from the atmosphere. Much less attention was given to studying the food web and down stream biogeochemical consequences of iron enrichment or the potential unintended consequences of scaled-up versions of these experiments. This single minded focus—CO_2 drawdown and carbon export below the surface mixed layer—and the language used in research papers, for example "… iron triggered a massive phytoplankton bloom which consumed large quantities of carbon dioxide…" [11] fueled coverage of the experiments in the popular press from the perspective of geoengineering potential. Entrepreneurs were in turn drawn by the allure of being able to control an ecosystem with such a small quantity of a relatively cheap and "natural" substance.

One can understand the appeal. Because phytoplankton requires very little iron relative to nitrogen and phosphorus to fix carbon and grow, if the latter is available in excess, a tiny amount of iron can make them available to the phytoplankton by freeing the iron bottleneck. Sunlight is free, acreage (the ocean commons beyond the 200 mile limit) is free, and so is the nitrogen and phosphorus "fertilizer" in ocean waters. Iron is relatively cheap, and now it has been demonstrated over and over that if you add iron to certain regions of the oceans they turn green with phytoplankton relatively quickly. But despite the allure, there are many good arguments, based on what we already know about how ocean ecosystems function, that iron fertilization is not a viable option for mitigating climate change [7,45,46]. First, ocean fertilization causes a shift in the phytoplankton community thus changing the structure of the entire food web that depends on it. This is not an unintended consequence but rather it is the intended consequence of the perturbation. Without this shift there would be no bloom because only certain species capable of rapid growth dominate an iron-induced bloom. Second, when phytoplankton bloom and synthesize massive amounts of organic carbon, bacteria consume the carbon, and in doing so they consume oxygen, changing the redox state of ocean ecosystems. Many of the bacteria that thrive in low oxygen regions of the oceans generate nitrous oxide and methane, both very powerful greenhouse gases. And finally, models suggest that at the unrealizable limit—if one fertilized all of the HNLC regions of the oceans for 100 years—at most 1 Gt C y^{-1} would be sequestered in the ocean. This — even if achievable, which it is not— would not change the trajectory of global warming significantly. The cost would be a massive restructuring of ocean biogeochemistry, the long-term consequences of which on the global biosphere are completely unknown.

Despite these limitations and concerns, calls for more research on ocean fertilization as a geoengineering option persist within the oceanographic community [5,61]. I suspect that implicit in these calls is the understanding that these experiments, regardless of purpose, are powerful tools for learning how ocean ecosystems function and hence of value in their own right. But one chooses to measure different things in mission-oriented research compared to basic research. If the talent and ingenuity among our scientific ranks is focused on seeing how much carbon one can generate and export to the deep ocean through fertilization, it will not be focused on understanding ocean ecosystems in all their complexity. This understanding is essential for the effective management of ocean resources and modeling the trajectory of ocean processes in the face of climate change.

It's not just about climate

In August 2008, the Kasatochi volcano in the Alaskan central Aleutian Islands erupted, delivering iron-rich volcanic ash to the ocean waters downwind. Satellite images of surface ocean waters in the Gulf of Alaska revealed phytoplankton blooms downwind of the iron dust plume. The spatial and temporal relationship between the dust plumes and ocean blooms looked compelling [19], and the quantities of iron that could be delivered to the oceans via the dust were sufficient to account for a bloom [38]. In 2010, two years after the eruption and phytoplankton bloom, the returns of sockeye salmon to the Frasier River were the largest on record—34 million fish. Some attributed this bumper crop of salmon to increased survival of juveniles caught in the phytoplankton bloom [40], but the causal link between the bloom and the salmon has been questioned [34] and continues to be debated [39]. While it is impossible for the non-expert to judge which side of the debate is more compelling, attributing cause and effect to events so far separated in time, occurring in a complex fluid environment, and involving complex food webs, takes an enormous leap of faith.

Despite limited—and contested—evidence linking iron dust supply and increased salmon returns, it was inevitable that someone would suggest that intentional iron fertilization might be a way to enhance fisheries. Claims that global stocks of phytoplankton may be decreasing [3] had already triggered arguments that the oceans are in need of "nourishment" [63]. The stage was set for the inhabitants of Old Massett Village, in British Columbia, whose livelihood has been greatly compromised by the decrease in salmon stocks in recent years, to take great interest in the iron-salmon connection. Their Haida Salmon Restoration Corporation (HSRC) [59] hired a California businessman, Russ George, to fertilize a 10,000 sq mile patch of ocean with 120 tons of iron sulfate/iron oxide in the summer of 2012 [48]. The area fertilized was orders of magnitude larger than any of the scientific ocean fertilization experiments conducted to date. The experiment, described as an "ocean restoration project" by its leader [27], was conducted 200 miles west of the coast of British Columbia where phytoplankton blooms are already a persistent feature in satellite images of ocean color. For their 2.5 million dollar investment in the project, the HSRC was allegedly promised not only return of the salmon runs by George, but also the sale of carbon credits for the atmospheric CO_2 that would purportedly be sequestered as a result of the fertilization. At present there is no market for the latter and no established mechanism for verifying the amount of carbon sequestered as a result of ocean fertilization.

The Haida Gwaii Fertilization project constitutes the first "rogue" geoengineering experiment in history and the largest iron fertilization experiment to date. It is considered "rogue" because these types of experiments are not allowed in international waters under the 2008 statutes of the UN London Convention, except for "legitimate scientific purposes". If not legitimate, they are considered disposal at sea which is prohibited under the Canadian Environmental Protection Act. Astonishingly, the Haida Gwaii experiment did not receive public attention until a year after it had been completed. The story was uncovered by the Canadian environmental wathdog group Action Group on Erosion, Technology and Concentration (ETC) and released in a series of articles by the *Vancouver Sun* [35]. A "legitimate scientific experiment" of this scale would not have gone undisclosed for this length of time.

There is nothing published in the scientific literature about the HSRC experiment and data have not been made public. But oceanographers familiar with the region say that it would be very difficult to differentiate between a natural bloom of phytoplankton and one resulting from the addition of iron [58]. At the moment the entire experiment is under investigation by Environment Canada. Meanwhile, the London Convention of the International Maritime Organization [62] was recently amended to tighten the restrictions surrounding ocean fertilization. A permit is now required for "any activity undertaken by humans with the principal intention of stimulating primary productivity in the oceans" and will be granted only for "legitimate scientific research taking into account any specific placement assessment framework."

While this new, stricter regulation will serve to discourage unauthorized ocean fertilization experiments, it also makes more difficult the small-scale experiments that are effective tools for oceanographers trying to understand the function of ocean ecosystems [6]. This is unfortunate as it is only by perturbing a complex dynamic system that one can get a glimpse of the connections that regulate and stabilize it. As John Martin argued, 'bottle experiments'—a standard oceanographic experimental tool—exclude higher trophic levels and eliminate physics, giving us a distorted picture of the full consequences of any experimental perturbation. There is no substitute for unenclosed nutrient enrichments on a relatively small scale, but large enough to preserve physics and be able to measure some food web consequences. A particularly promising technology for these types of experiments is simple pumping systems to move nutrient-rich deep water to the surface, simulating ocean upwelling. These would allow us to study, experimentally, the response of the microbial community to this natural, episodic, ocean process. Unfortunately, the technology is already on the radar screen for several geoengineering applications [26], and several patents have already been filed on "artificial ocean upwelling". Were this technology to be used for basic research purposes, one can be certain that the experiment would be interpreted as a test of geoengineering potential, and the results would be co-opted and interpreted selectively by those with a profit motive. We can only hope that the specter of "rogue" experiments, commercial interests, and geoengineering applications does not discourage legitimate small-scale ecosystem experiments in the future. They could play a unique role in helping us to understand the biogeochemistry of the oceans and we are in desperate need of advancing this understanding at this point in Earth's history.

Geoengineering goes mainstream

Ocean fertilization is but one of many proposed geoengineering approaches for mitigating the effects of human activities on the Earth System [51]. Most of the approaches fit under two broad categories. They are either designed to sequester atmospheric CO_2 or to manage the amounts of solar radiation reaching the Earth. The latter is an attempt to treat directly the symptoms of greenhouse gas emissions—i.e., warming Earth—whereas the former is directed at redistributing the global carbon inventory so less CO_2 accumulates in the atmosphere. While neither approach gets at the root cause of global warming, it strikes me that CO_2 removal is much closer to the cause than is solar radiation management and should be considered remediation—i.e., "removal of a contaminant"—rather than geoengineering. Lumping both of these approaches under the rubric of geoengineering is not logical.

Regardless of what is included under the definition of geoengineering, the concept is no longer a "fringe idea". It made the transition to "legitimate inquiry" with the publication of two influential papers in 2006 calling for research on it [10,14]. And extensive report on the topic by the UK Royal Society followed [44], which concluded that "geoengineering is likely to be technically feasible, and could substantially reduce the costs and risks of climate change." This firmly established it as something to be considered seriously by the scientific and engineering communities, and interest in the topic soared (Fig. 3). Just recently, the mention of geoengineering in the 2013 report of the International Governmental Panel on Climate Change (IPCC) [60] gave a significant boost to its global visibility. In their summary to policy makers they wrote: "Methods that aim to deliberately alter the climate system to counter climate change, termed geoengineering, have been proposed. Limited evidence precludes a comprehensive quantitative assessment of both Solar Radiation Management (SRM) and Carbon Dioxide Removal (CDR) and their impact on the climate system." The report does not shy away from highlighting the risks and enormous uncertainties inherent in geoengineering but the mere mention of it by this influential international body boosted its legitimacy enormously.

While there seems to be more focus on the policy, ethical, and governance dimensions of geoengineering than there is on the science itself (see Climatic Change Vol. 121, 2013), solar radiation management via sulfur aerosols seems to be gaining momentum as the most 'feasible' technology for cooling the Earth. This is in part because research on it has a very strong and vocal advocate in David Keith [23], and in part because this technology has a natural analog in the cooling effect of volcanic eruptions [15] which renders it slightly less 'alien' than many other approaches. At the same time, it is also one for which the specter of "rogue" applications looms large. This concern has even lead to game theory analyses of the global politics of solar radiation management, which concludes that the technology should theoretically lead to small but powerful coalitions of nations who would ultimately "set the global thermostat" [42]. While it is important that these types of scenarios are getting scholarly attention, they should not draw our attention away from facing the ecological uncertainties inherent in any type of large-scale manipulation of the climate system. Biospheric feedbacks are represented in the most rudimentary of fashions in models of geoengineering approaches—precisely because of their inherent complexity. There is one point upon which all models agree however: Once you start, you cannot stop. Termination of solar radiation management after several decades would result in a rapid increase in global mean temperature, precipitation, and sea-ice melting [22].

Hindsight and humility

As we contemplate geoengineering we might draw some humility from our limited predictive capabilities, and the degree to which hindsight has played a role in our understanding the complexities of the Earth system. We have been surprised, for example, to see that the global temperature anomaly has shown very little warming in the last decade even though greenhouse gases are increasing steadily. Do we understand why? We have some good hypotheses [49] but the precise fate of the "missing heat" is still not entirely understood. Only in hindsight have potential causes emerged. The Biosphere 2 experiment in the 1990s [37] is a more "down-to-Earth" example of our limited predictive capabilities when it comes to complex living systems. Eight people were enclosed in a sealed 3-acre structure designed to have all the ecosystem components to sustain them for 2 years. The experiment ended prematurely because oxygen concentrations decreased to levels unsafe for the inhabitants. It was later learned that the decline was due to the bacteria in the organic-matter-rich soil whose respiration far surpassed the photosynthesis of the plants in the enclosure. What was puzzling, however, was that the CO_2 in the enclosure's "atmosphere" did not increase stoicheometrically with the decreased oxygen, as one would expect if the latter were due to respiration. Where was the missing CO_2? Ultimately it was shown that it had reacted with the cement structures in the enclosure [43]—a cause-and-effect chain that could only be established in hindsight. Yes, we do learn from our mistakes, and now that we understand this dimension of designing artificial biospheres we might get it right the next time. But it is one thing to make a mistake with a 3-acre experiment that people can walk away from when things do not go as planned. It is yet another to forge ahead in relative ignorance, hoping for the best, while geoengineering the Earth. As Margalef suggested: "if God has put us on this Earth, we have the right to make use of it, but we might as well do so with a modicum of intelligence" [52].

Acknowledgements. The *Prochlorococcus* story outlined here has unfolded in large part through the talent and hard work of generations of students and post-docs in my laboratory. It has been a privilege and a pleasure to work with them and I share the honor of the Margalef Prize with all of them. There are many others who have made significant contributions to our understanding of *Prochlorococcus* as well. Their significant work has been slighted here because this paper is drawn from lectures about my work. I would also like to thank John Cullen for partnering with me on the issue of ocean fertilization over the years, and to the US National Science Foundation, Department of Energy, Office of Naval Research, the Seaver Foundation, and most recently the Gordon and Betty Moore Foundation for their support. Finally, I must acknowledge the significant role Ramon Margalef's books and papers played in my choice to pursue phytoplankton ecology as a career.

References

1. Ahlgren NA, Rocap G, Chisholm SW (2006) Measurement of *Prochlorococcus* ecotypes using real-time polymerase chain reaction reveals different abundances of genotypes with similar light physiologies. Environ Microbiol 8:441-454
2. Baumdicker F, Hess WR, Pfaffelhuber P (2012) The infinitely many genes model for the distributed genome of bacteria. Genome Biol Evol 4:443-456
3. Boyce DG, Lewis MR, Worm B (2010) Global phytoplankton decline over the past century. Nature 466:591-596
4. Boyd PW, Jickells T, Law CS, et al. (2007) Mesoscale iron enrichment experiments 1993-2005: Synthesis and future directions. Science 315:612-617
5. Buesseler KO, Doney SC, Karl DM, et al. (2008) Ocean iron fertilization-moving forward in a sea of uncertainty. Science 319:162-162
6. Carpenter SR, Chisholm SW, Krebs CJ, Schindler DW, Wright RF (1995) Ecosystem experiments. Science 269:324-327
7. Chisholm SW, Falkowski PG, Cullen JJ (2001) Oceans. Dis-crediting ocean fertilization. Science 294:309-310

8. Chisholm SW, Morel FMM (eds) (1991) What controls phytoplankton production in nutrient-rich areas of the open sea? Limnol Oceanogr 36
9. Chisholm SW, Olson RJ, Zettler ER, Goericke R, Waterbury JB, Welschmeyer NA (1988) A novel free-living prochlorophyte abundant in the oceanic euphotic zone. Nature 334:340-343
10. Cicerone RJ (2006) Geoengineering: Encouraging research and overseeing implementation. Climatic Change 77:221-226
11. Coale KHK, Johnson KSK, Fitzwater SES, et al. (1996) A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. Nature 383:495-501
12. Coleman ML, Chisholm SW (2007) Code and context: *Prochlorococcus* as a model for cross-scale biology. Trends Microbiol 15:398-407
13. Coleman ML, Sullivan MB, Martiny AC, Steglich C, Barry K, DeLong EF, Chisholm SW (2006) Genomic islands and the ecology and evolution of *Prochlorococcus*. Science 311:1768-1770
14. Crutzen PJ (2006) Albedo enhancement by stratospheric sulfur injections: a contribution to resolve a policy dilemma? Climatic Change 77:211-220
15. Dutton EG, Christy JR (1992) Solar radiative forcing at selected locations and evidence for global lower tropospheric cooling following the eruptions of El-Chichon and Pinatubo. Geophys Res Lett 19:2313-2316
16. Flombaum P, Gallegos JL, Gordillo RA, et al. (2013) Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and *Synechococcus*. Proc Natl Acad Sci USA 110:9824-9829
17. Gómez-Baena G, López-Lozano A, Gil-Martínez J, Lucena JM, Diez J, Candau P, García-Fernández JM (2008) Glucose uptake and its effect on gene expression in *Prochlorococcus*. PLoS ONE 3:e3416
18. Grzymski JJ, Dussaq AM (2011) The significance of nitrogen cost minimization in proteomes of marine microorganisms. ISME J 6:71-80
19. Hamme RC, Webley PW, Crawford WR, et al (2010) Volcanic ash fuels anomalous plankton bloom in subarctic northeast Pacific. Geophys Res Lett 37:n/a-n/a
20. Johnson PW, JM S (1979) Chroococcoid cyanobacteria in the sea: A ubiquitous and diverse phototrophic biomass. Limnol Oceanogr 24:928-935
21. Johnson ZI, Zinser ER, Coe A, McNulty NP, Woodward EMS, Chisholm SW (2006) Niche partitioning among *Prochlorococcus* ecotypes along ocean-scale environmental gradients. Science 311:1737-1740
22. Jones A, Haywood JM, Alterskjaer K, et al (2013) The impact of abrupt suspension of solar radiation management (termination effect) in experiment G2 of the Geoengineering Model Intercomparison Project (GeoMIP). J Geophys Res Atmos 118:9743-9752
23. Keith D (2013) The case for climate engineering. MIT Press, Cambridge, MA
24. Kettler GC, Martiny AC, Huang K, et al. (2007) Patterns and implications of gene gain and loss in the evolution of *Prochlorococcus*. PLoS Genet 3:e231
25. Lindell D, Jaffe JD, Coleman ML, et al. (2007) Genome-wide expression dynamics of a marine virus and host reveal features of co-evolution. Nature 449:83-86
26. Lovelock JE, Rapley CG (2007) Ocean pipes could help the Earth to cure itself. Nature 449:403
27. Lukacs M (2012) World's biggest geoengineering experiment 'violates' UN rules. The Guardian. 18 January 2014 [Online] Available at: http://www.theguardian.com/environment/2012/oct/15/pacific-iron-fertilisation-geoengineering
28. Malmstrom RR, Coe A, Kettler GC, Martiny AC, Frias-Lopez J, Zinser ER, Chisholm SW (2010) Temporal dynamics of *Prochlorococcus* ecotypes in the Atlantic and Pacific oceans. ISME J 4:1252-1264
29. Mann EL, Chisholm SW (2002) Iron limits the cell division rate of *Prochlorococcus* in the eastern equatorial Pacific. Limnol Oceanogr 45:1067-1076
30. Margalef R (1997) Our biosphere. Ecology Institute, Oldendorf/Luhe, Germany
31. Martin JH (1990) Glacial-interglacial CO_2 Change: The Iron Hypothesis. Paleooceanography 5:1-13
32. Martin JH, Coale KH, Johnson KS, et al. (1994) Testing the iron hypothesis in ecosystems of the equatorial Pacific Ocean. Nature 371:123-129
33. Martin JH, Gordon RM, Fitzwater SE (1991) The case for iron. Limnol Oceanogr 36:1793-1802
34. McKinnell S (2013) Challenges for the Kasatoshi volcano hypothesis as the cause of a large return of sockeye salmon (*Oncorhynchusnerka*) to the Fraser River in 2010. Fish Oceanogr 22:337-344
35. McKnight Z (2013) B.C. company at centre of iron dumping scandal stands by its convictions. Vancouver Sun, 4 September 2013
36. Moore LR, Chisholm SW (1999) Photophysiology of the marine cyanobacterium *Prochlorococcus*: Ecotypic differences among cultured isolates. Limnol Oceanogr 44:628-638
37. Nelson M, Burgess TL, Ailing A, Alvarez-Romo N, Demster WF, Walford RL, Allen JP (1993) Using a closed ecological system to study Earth's biosphere: Initial results from Biosphere 2. BioScience 43:225-236
38. Olgun N, Duggen S, Langmann B, Hort M, Waythomas CF, Hoffmann L, Croot P (2013) Geochemical evidence of oceanic iron fertilization by the Kasatochi volcanic eruption in 2008 and the potential impacts on Pacific sockeye salmon. Mar Ecol Prog Ser 488:81-88
39. Parsons T, Whitney F (2014) On the effect of the Kasatoshi volcano on the large return of sockeye salmon (*Oncorhynchusnerka*) to the Fraser River in 2010. Fish Oceanogr 23:101-102
40. Parsons TR, Whitney FA (2012) Did volcanic ash from Mt. Kasatoshi in 2008 contribute to a phenomenal increase in Fraser River sockeye salmon (*Oncorhynchusnerka*) in 2010? Fish Oceanogr 21:374-377
41. Partensky F, Garczarek L (2010) *Prochlorococcus*: Advantages and limits of minimalism. Annu Rev Marine Sci 2:305-331
42. Ricke KL, Moreno-Cruz JB, Caldeira K (2013) Strategic incentives for climate geoengineering coalitions to exclude broad participation. Environ Res Lett 8:014021
43. Severinghaus JP, Broecker WS, Dempster WF, MacCallum T, Wahlen M (1994) Oxygen loss in Biosphere 2. Eos, Trans Amer Geophys Union 75:33-37
44. Royal Society of London (2009) Geoengineering the climate: Science governance and uncertainty. RS Policy document 10/09. RS1636. ISBN: 978-0-85403-773-5
45. Strong A, Chisholm S, Miller C, Cullen J (2009) Ocean fertilization: time to move on. Nature 461:347-348
46. Strong AL, Cullen JJ, Chisholm SW (2009) Ocean fertilization science, policy, and commerce. Oceanography 22:236-261
47. Thompson LR, Zeng Q, Kelly L, Huang KH, Singer AU, Stubbe J, Chisholm SW (2011) Phage auxiliary metabolic genes and the redirection of cyanobacterial host carbon metabolism. Proc Natl Acad Sci USA 108:E757-E764
48. Tollefson J (2012) Ocean-fertilization project off Canada sparks furore. Nature 490:458-459
49. Trenberth KE, Fasullo JT (2010) Tracking Earth's energy. Science 328:316-317
50. Van Mooy BAS, Fredricks HF, Pedler BE, et al. (2009) Phytoplankton in the ocean use non-phosphorus lipids in response to phosphorus scarcity. Nature 457:69-72
51. Vaughan NE, Lenton TM (2011) A review of climate geoengineering proposals. Climatic Change 109:745-790
52. Vilalta JM (2004) Biography of Ramon Margalef. Generalitat de Catalunya [Online] Available at: http://www.gencat.cat/premiramonmargalef/cat/biografia.htm
53. Waldbauer J (2010) Molecular biogeochemistry of modern and ancient marine microbes. PhD Thesis, MIT and WHOI, pp 1-344

54. Waterbury JB, Watson SW, Guillard R, Brand LE (1979) Widespread occurrence of a unicellular, marine, planktonic, cyanobacterium. Nature 277:293-294
55. Zinser ER, Coe A, Johnson ZI, Martiny AC, Fuller NJ, Scanlan DJ, Chisholm SW (2006) *Prochlorococcus* ecotype abundances in the North Atlantic ocean as revealed by an improved quantitative PCR method. Appl Environ Microbiol 72:723-732
56. Zinser ER, Johnson ZI, Coe A, Karaca E, Veneziano D, Chisholm SW (2007) Influence of light and temperature on *Prochlorococcus* ecotype distributions in the Atlantic Ocean. Limnol Oceanogr 52:2205-2220
57. Zubkov MV, Tarran GA, Fuchs BM Depth related amino acid uptake by *Prochlorococcus* cyanobacteria in the Southern Atlantic tropical gyre. FEMS Microbiol Ecol 50:153-161
58. McKnight Z (2012) Iron-fertilizing experiment took place in worst possible spot: scientists. Vancouver Sun. 24 October 2012 [Online] Available at: http://www.vancouversun.com/technology/n+fertilizing+experiment+took+place+worst+possible+spot+scientists/7436066/story.html
59. Haida Salmon Restoration Corp (2014) [Online] Available at: http://haidasalmonrestoration.com
60. IPCC Summary for Policy Makers (2013) 24 December 2013 [Online] Available at: http://www.climatechange2013.org/images/uploads/WGI_AR5_SPM_brochure.pdf
61. ISIS Consortium (2014) To promote in-situ iron studies of the ocean [Online] Available at: http://isis-consortium.org
62. International Maritime Organization (2014) New regulations for ocean fertilization [Online] Available at: http://www.imo.org/OurWork/Environment/LCLP/Pages/default.aspx
63. Ocean Nourishment Corporation (2014) [Online] Available at: http://www.oceannourishment.com

***

Resum. El fitoplàncton oceànic juga un paper central en la oxigenació de l'atmosfera del nostre planeta fa milers de milions d'anys. Per tant, aquests primers "geoenginyers" van ser crucials per l'evolució de la vida a la Terra. Els seus descendents actuals, el cianobacteri marí *Prochlorococcus* és la cèl·lula fotosintètica més abundant del planeta. El seu descobriment, fa 30 anys, va servir com a recordatori del poc que coneixem sobre la complexitat de les xarxes tròfiques marines. La proposta de fertilització dels oceans, ja sigui per mitigar el clima o per millorar la pesca, continua guanyant adeptes dins la comunitat científica i el sector comercial. Si s'arribés a implementar, les conseqüències no desitjades d'aquesta i altres propostes de geoenginyeria poden ser enormes i impossibles de preveure.

Paraules clau: *Prochlorococcus* · geoenginyeria · canvi climàtic · fertilització amb ferro