Biogeochemical Controls and Feedbacks on Ocean Primary Production

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REVIEW

Changes in oceanic primary production, linked to changes in the network of global biogeochemical cycles, have profoundly influenced the geochemistry of Earth for over 3 billion years. In the contemporary ocean, photosynthetic carbon fixation by marine phytoplankton leads to formation of ~45 gigatons of organic carbon per annum, of which 16 gigatons are exported to the ocean interior. Changes in the magnitude of total and export production can strongly influence atmospheric CO_2 levels (and hence climate) on geological time scales, as well as set upper bounds for sustainable fisheries harvest. The two fluxes are critically dependent on geophysical processes that determine mixed-layer depth, nutrient fluxes to and within the ocean, and food-web structure. Because the average turnover time of phytoplankton carbon in the ocean is on the order of a week or less, total and export production are extremely sensitive to external forcing and consequently are seldom in steady state. Elucidating the biogeochemical controls and feedbacks on primary production is essential to understanding how oceanic biota responded to and affected natural climatic variability in the geological past, and will respond to anthropogenically influenced changes in coming decades. One of the most crucial feedbacks results from changes in radiative forcing on the hydrological cycle, which influences the aeolian iron flux and, in turn, affects nitrogen fixation and primary production in the oceans.

The combination of vast areas of liquid water on its surface together with a high concentration of free molecular oxygen in its atmosphere is unique to Earth in this solar system. Calculations based on ultraviolet absorption cross sections indicate that whereas direct photolysis of water could have produced small amounts of O_2 (*1*), almost all of the gas was produced through the photobiologically catalyzed oxidation of the liquid (*2*). Geochemical evidence suggests that ~2.2 billion years ago, Earth's oxygen reached levels comparable to that found in the contemporary atmosphere (*3*, *4*) as a consequence of oxygenic photosynthesis by marine unicellular algae, the phytoplankton (*5*). These microscopic flora simultaneously (and not coincidentally) produced massive quantities of organic C that are preserved in the lithosphere (*6*), a small fraction of which literally fuels the industrial world in the present geological epoch (*7*). These biologically driven changes reflect a key transition in the geochemical evolution of Earth that profoundly influenced the subsequent course of evolution of life. Anthropogenic emissions of CO_2, resulting to a large extent from the combustion of fossil marine phytoplankton biomass, almost certainly will affect the spatial and taxonomic distribution of these oceanic biota as well as their photosynthetic activity in the coming decades. Effects will be both direct, through changes in

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ocean chemistry, and indirect, through climatically induced alterations in the ocean's physical circulation (*8*). Here we briefly examine the controls and feedbacks between oceanic phytoplankton and geochemical processes with an emphasis on factors that cause deviations from the steady state.

Phytoplankton Diversity and Biogeochemical Stability

Despite their geochemical importance, phytoplankton are often overlooked in vernacular concepts of the biosphere (*9*). These single-celled photoautotrophic organisms comprise 12 taxonomic divisions spanning three Kingdoms (*10*). Fossil records reveal that cells with structural similarities to extant cyanobacteria extend at least to 3.45 Ga (1 Ga = 10^9 years) before present (*11*). This group numerically dominates most phytoplankton assemblages in the contemporary ocean. Molecular phylogenetic trees suggest that these prokaryotes gave rise, through endosymbiotic associations, to all eukaryotic algae and, ultimately, to higher plants (*12*, *13*). Although phylogenetic diversity within the phytoplankton is deeply branching, many fundamental metabolic pathways are remarkably conserved and can be grouped into a handful of biogeochemical functions. The combination of deep genetic diversity and high functional redundancy has helped to ensure the continuity of oxygenic photosynthesis despite considerable changes in Earth's climate. Indeed, molecular biological data suggests that environmental stresses, some of which have been self-imposed by phytoplankton through chemical alterations within the ocean, are evolutionary selection mechanisms that helped foster phylogenetic diversity and ensured biogeochemical stability (*14*, *15*).

Phytoplankton Productivity in the Contemporary Ocean

The carbon cycle is critically dependent on net primary production (NPP), which is defined as the photosynthetically fixed C available for other trophic levels (*16*, *17*). Oceanic NPP can be calculated from remotely sensed information. The selective absorption of blue and blue-green wavelengths by photosynthetic pigments, especially chlorophyll a (*18*), allows quantification of phytoplankton biomass in the contemporary oceans on the basis of satellite-derived measurements of ocean color (*19*, *20*) (Fig. 1). Chlorophyll concentrations and the taxonomic composition of phytoplankton communities are qualitatively correlated with oceanic circulation and mesoscale physical processes, especially as they influence the fluxes of essential nutrients from the subsurface nutrient reservoir into the euphotic zone. In the central ocean gyres, nutrient fluxes from deep waters are relatively small, and chlorophyll concentration in the upper portion of the euphotic zone averages ~0.2 mg/m^3 (*21*). In coastal upwelling regions, seasonally mixed regions of temperate and boreal seas, and divergent subpolar gyres or mesoscale features with eddy-induced pumping, vertical fluxes of nutrients can support transient chlorophyll concentrations in excess of 5 mg/m^3 (*22*, *23*). Together with knowledge of sea surface temperature, incident solar irradiance and mixed layer depths, chlorophyll data can be used to estimate NPP for any region of the ocean (*24*, *25*). Results of such calculations suggest that global oceanic NPP is ~45 to 50 Pg C per annum (*17*, *25*). This carbon flux is driven by a phytoplankton biomass of ~1 Pg C, which is only 0.2% of the photosynthetically active C biomass on Earth (*17*). Consequently, on average, phytoplankton biomass in the oceans turns over on the order of once per week.

Nutrient Sources for Primary Production

To sustain this C flux through marine ecosystems, essential nutrients must be supplied. The mean elemental ratio of marine organic particles is 106C/16N/1P by atoms and is highly conserved (26). Such a specific elemental ratio in organic matter is unique to ocean ecosys-

tems and reflects the average biochemical composition of marine phytoplankton and their early degradation products (27, 28).

In the steady state, phytoplankton production is balanced by mortality due to grazing, viral attack, autocatalyzed cell death, or sinking into the ocean interior, where virtually all of the reduced
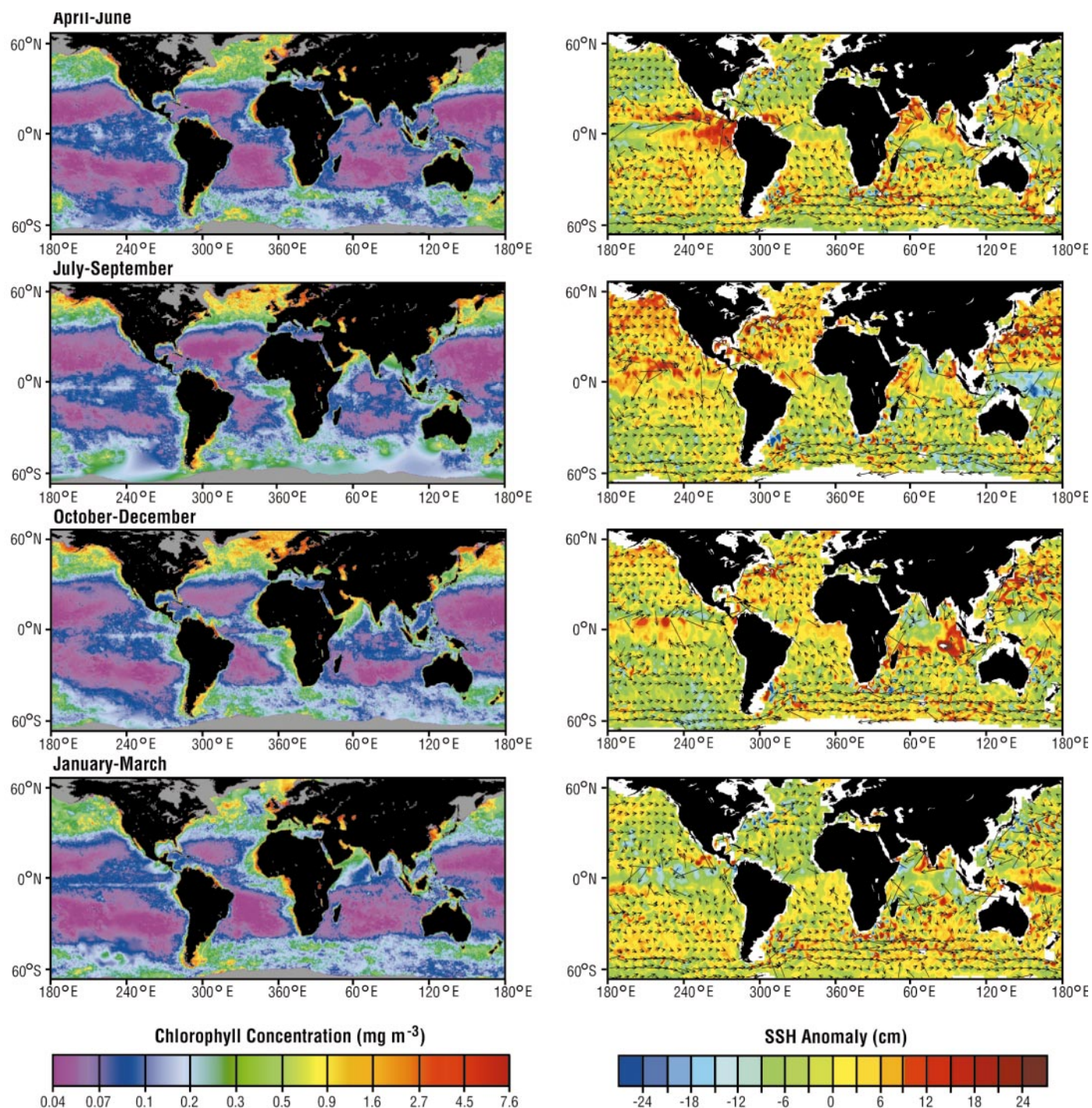

April-June

July-September

October-December

January-March

Chlorophyll Concentration (mg m^{-3})

0.04 0.07 0.1 0.2 0.3 0.5 0.9 1.6 2.7 4.5 7.6

SSH Anomaly (cm)

-24 -18 -12 -6 0 6 12 18 24

Fig. 1. (Left) Seasonally averaged upper ocean chlorophyll concentrations derived from spectral radiance reflectance algorithms with the use of Coastal Zone Color Scanner (CZCS) data for the world oceans. This satellite-based sensor was replaced by SeaWiFS in September 1997. The data reveal a lack of phytoplankton throughout most of the central ocean gyres, with relatively high concentrations of chlorophyll biomass in the North Atlantic, coastal upwelling regions, and in the Arabian Sea. Compare how the distributions of chlorophyll are related to physical circulation as inferred from sea surface height (SSH) anomalies (right). The SSH anomalies were derived from sea-surface topography maps with the use of TOPEX/POSEIDON altimetry data. Superimposed on the SSH anomaly fields are calculated current vectors for the upper ocean derived from a data assimilation model (86). Congruent vectors correspond to regions of convergence (downwelling), and divergent vectors indicate areas of upwelling. The strong correlation between depressed sea height in the Arabian Sea in summer and fall with elevated chlorophyll concentrations is apparent (original CZCS data courtesy of NASA Goddard Space Flight Center).

organic matter not consumed by macrofauna is oxidized by heterotrophic microbes (*29*). In nutrient-poor waters, characteristic of the central ocean gyres, excretory products of consumers in the euphotic zone are rapidly assimilated by extremely small photoautotrophic cells (picocyanobacteria and nanoflagellates ranging from 1 to 5 μm in diameter). These pico-phytoplankton have, by virtue of large surface area/volume ratios, a competitive advantage over large cells when external nutrient concentrations approach the limit for facilitated uptake (*30*). The recycling grazer and microbial network [that is, the "microbial loop" (*31*)] is extremely efficient; very little organic matter escapes remineralization (*32*). The major output of such ecosystems is mineral shells with negligible loss of organic C or inorganic nutrients from the euphotic zone (*33*). Such highly efficient, nutrient-regenerating communities are characteristic of nitrate-limited subtropical gyres and so-called "high-nutrient, low-chlorophyll" (HNLC) regions (*34*).

When incident solar radiation is sufficient and the depth of the upper mixed layer constrains cells within the euphotic zone, transient physical processes, such as eddies, coastal upwelling, and wind or convective mixing, can promote the growth of larger cells, such as diatoms, by increasing the flux of nutrients from deeper, nutrient-rich waters (*23*, *35*). A competitive advantage to larger cells is conferred by their ability to rapidly take up and temporarily store the "new" nutrients in vacuoles which can later be used for growth. Blooms occur when phytoplankton escape their grazer gauntlet. For larger cells, this occurs because their consumers are primarily larger zooplankton which, unlike protozoan micrograzers, regenerate via larval stages and have a reproductive delay of a few days (longer than the generation time of most phytoplankton) (*36*). Hence, the production of large phytoplankton and grazing losses become temporarily uncoupled (*37*), and the vertical flux of organic matter into the ocean interior is greatly enhanced by the higher sinking rates associated with larger, heavier cells, especially diatoms (*38*, *39*). From a perspective of oceanic ecology, the production, accumulation, and export of such "new" phytoplankton sustains the world's fisheries and sets the upper bound for sustainable yields (*40*).

Based on the conservation of elemental ratios, it follows that in the steady state the sinking flux of particulate organic matter from the euphotic zone represents a stoichiometric loss of associated nutrients that must be balanced by "new" nutrient inputs (*41*, *42*). Because the physical processes that promote new production are transient, there is ample observational data demonstrating that steady-state export of organic matter is seldom achieved in any given location on time scales of days, weeks, or interannually (*37*, *43*). Storms, mesoscale eddies, and El Niño conditions are a few examples of nutrient delivery processes that are affected by transient physical processes.

Biologically Mediated Exchange of CO_2 Between the Ocean and Atmosphere

Biological processes in the ocean affect atmospheric gas composition through phase-state transitions of specific elements. For example, photosynthetic sequestration of inorganic C converts CO_2 into organic solutes and particles with a corresponding decrease in the partial pressure in the surface layer. The resulting change in the partial pressure gradient at the air-sea interface potentially provides a driving force for the invasion of CO_2 from the atmosphere into the ocean. Conversely, heterotrophic oxidation of organic solutes and particles leads to the formation of CO_2, and the potential efflux of CO_2 from the ocean to the atmosphere. The export of organic material from the euphotic zone to the ocean interior, followed by biological oxidation of the organic C, leads to an inverse concentration gradient in inorganic C (that is, the concentration of inorganic C below the upper 500 m of the ocean is greater than that at the air-sea interface). In the contemporary ocean, this flux is ~16 Pg C per annum, or approximately one-third of the total ocean production (Fig. 2). Once the organic C sinks beneath the main ocean thermocline, it is effectively sequestered from the atmosphere for centuries to millennia. It is frequently assumed in biogeochemical models that this "biological carbon pump" (*44*) is in a steady state on time scales of decades to centuries (*45*). Such an assumption leads to the unsubstantiated conclusion that the biologically mediated net exchange of CO_2 between the ocean and atmosphere is virtually nil (*45*, *46*).

Compared with terrestrial ecosystems, where dendrochronology, pollen records, and geochemical measurements can be used to reconstruct ecological patterns on time scales of decades to centuries, time series of biological measurements in the oceans are very short and often contain unreliable or unverifiable data (*47*). Except in a few,

Fig. 2. Global map of annual mean export production for the world oceans. The map was generated with the relation between total and export production proposed by Eppley and Petersen (*42*) and monthly mean total production maps produced from CZCS chlorophyll distributions according to the algorithm of Behrenfeld and Falkowski (*25*). The annual export production calculated from these algorithms is 16 Gt C. The influence of coastal upwelling in supporting high export production is especially apparent. The export production in the coastal regions supports most of the world's ocean fisheries (*40*, *87*).

Export photosynthetic carbon (g C/m²)
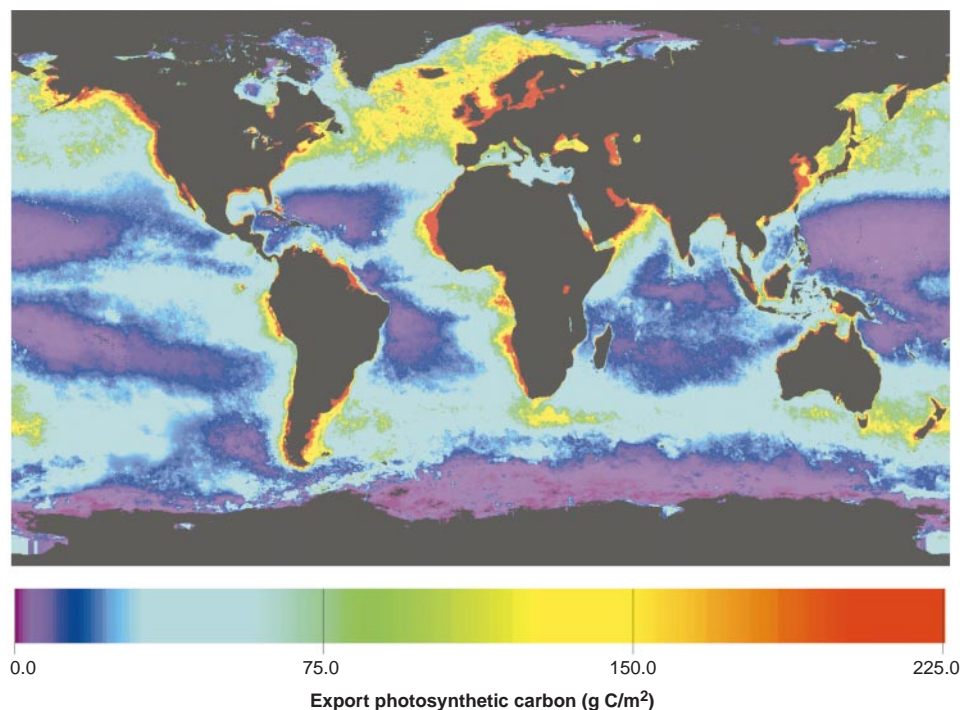
relatively anomalous areas, the sedimentary record is notably poor in preserving basin-scale information on time scales comparable to those inferred from proxy data in terrestrial ecosystems. Nonetheless, resolving whether phytoplankton productivity is in steady state on such time scales is so important to understanding how ocean ecology functions in the context of atmospheric forcing and climatological feedbacks, that this issue has been one of the major foci of oceanographic research over the past decade (48).

Limitations on CO₂ Fluxes

Changes in the net biologically mediated flux of CO_2 between the atmosphere and ocean require changing one or more of (i) ocean nutrient inventories, (ii) the utilization of unused nutrients in enriched areas (that is HNLC regions), or (iii) the average elemental composition of the organic material (49). Based on the analysis of the proximate elemental composition of marine organisms, the late Alfred Redfield concluded that P limits primary production in the oceans (50). In this context, "limiting" denotes a factor that constrains the formation of total phytoplankton biomass in the euphotic zone, not necessarily the rate of formation of the biomass. The distinction between these two processes is critical (51). Light, for example, always limits the instantaneous rate of primary production in the euphotic zone, but as long as nutrients brought into the euphotic zone are eventually consumed in the production of biomass, the

Fig. 3. Cross sections showing the nutrient conveyor in the Southern Ocean. Nitrate and silicate-rich deep water is advected into the upper ocean, where it flows north in Antarctic surface waters entrained in the Antarctic Circumpolar Current. Most of the N (and P) is returned to depth north of the Antarctic Polar Front. The Si is utilized by diatoms, many of which sink out of the upper ocean. The arrow on the bottom axis indicates where the core (Fig. 4) was taken in relation to the present frontal system. This schematic is based on data collected during the R.V. *Polarstern* austral winter cruise of 1992 along the Greenwich Meridian. The location of the fronts (STF, Subtropical Front; SAF, Sub-Antarctic Front; and PF, Polar Front) and the sediment core presented in Fig. 4 (arrow on the bottom axis) are also shown. Upwelling of ocean interior water (thick upward-pointing arrows), northward transport of the surface layer, and subduction of Antarctic Intermediate Water (AIW, downward pointing arrows) at the SAF are also shown. AIW is identified by its temperature and salinity properties.

vertical fluxes of the nutrients (including inorganic C) will be sustained.

Redfield's tenet of P limitation was based on three fundamental concepts. First, because N_2 is the most abundant gas in the atmosphere and can, in principle, be biologically reduced to the level of NH_3, Redfield assumed that N_2 fixation should keep pace with demands of the photoautotrophs. Second, P has no biological or atmospheric source, but rather is supplied to the ocean largely from fluvial sources. As the rate of supply of P is lower than that for N, the residence time of the former in the oceans is significantly longer than that of the latter element. The longer residence time implies that the source of the element limits its availability to consumers (that is, phytoplankton). Finally, the ratio between biological fixation of N_2 and losses of fixed N resulting from denitrification determines the concentration of fixed N in the ocean interior (52, 53). Redfield proposed that the maximum concentration of fixed N in the oceans is ultimately determined by the availability of P, such that the fixed N/P ratio will adjust to the ratio of the two elements in the sinking flux of particulate organic matter (that is about 16/1 by atoms).

Biological oceanographers have repeatedly demonstrated through nutrient enrichment experiments and observations of nutrient distribution that throughout most of the coastal and open oceans, phytoplankton productivity is most often limited by the availability of fixed inorganic N (41, 54). Indeed, in the contemporary ocean, vertical profiles of the two elements invariably reveal a deficiency of fixed N relative to P in the ocean interior. Below the upper 500 m, the average N/P ratio for the world oceans is ~14.7, corresponding to a deficit of ~2.9 mmol N per kilogram of seawater (55). The deficiency in fixed inorganic N reflects losses mediated by anaerobic denitrifying bacteria, which are primarily found on continental margins and in hypoxic regions of the open ocean (53, 56). N fixation and denitrification are not coupled; that is, imbalances between these processes occur on geological time scales, thereby leading to a change in the inventory of fixed N in the oceans (52, 53, 57).

The Role of Iron and Its Supply

Over the past several years, it has become increasingly apparent that, for the ocean as a whole, N_2 fixation is itself limited by some factor, probably Fe (52). The vast majority of N fixation in the open ocean appears to be accomplished by a handful of species of cyanobacteria, notably *Trichodesmium* spp. (58). The paucity of marine N_2-fixing species (that is, functional singularity) suggests that the net flux of fixed N to the ocean by way of this critical biogeochemical pathway is especially sensitive to environmental perturbations. In *Trichodesmium* spp., the ratio of photosystem (PS) I to PSII is extremely high, on the order of ~25 (59). PSI contains 12 Fe atoms, and is responsible for both protecting the oxygen-sensitive nitrogenase from molecular oxygen generated by PSII (60), as well as generating adenosine 5′-triphosphate for the energy-intensive N_2-fixation pathway (61). Moreover, nitrogenase itself has a strict Fe requirement, and the Fe use efficiency (that is, enzymatic catalysis rate per unit of Fe) is among the lowest of any Fe-containing enzyme known (62). The limitation of N_2 fixation by Fe is especially apparent in the South Pacific, where the aeolian flux of Fe-rich dust is exceptionally low (63, 64).

As the fourth most abundant element in Earth's crust, Fe would appear to be unlikely to limit biochemical processes; however, the bioavailability of Fe is critically dependent on its redox state (65). Reduced (ferrous) Fe is highly soluble in seawater, whereas the oxidized (ferric) form is virtually insoluble. Hence, the oxidation state of the ocean, which on geological time scales is determined by the ratio of photosynthetic oxygen evolution to the sum of biological respiration and chemical reducing equivalents, is a critical determinant of trace element selection and supply.

Before the evolution of oxygenic photosynthesis, the ocean was anoxic and mildly reducing; Fe was present in very high concentra-
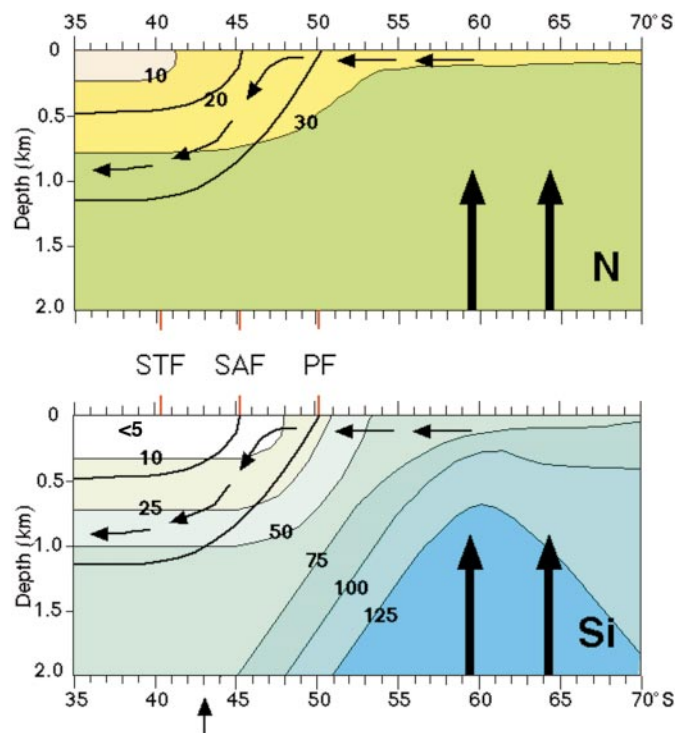
tions (estimated at about 25 mM) (*3*). Oxygenic photosynthesis ultimately led to the oxidation and subsequent precipitation of Fe. In the contemporary ocean, soluble Fe concentrations rarely exceed a few nanomolar. The massive precipitation of Fe by oxygenic photo-autotrophs is a clear example of a negative feedback in the evolution of biogeochemical cycles on Earth. Evidence of this biologically induced change in Earth's chemistry is etched in Fe-stress induced gene sequences of extant cyanobacteria (*66*) that have been preserved from the Proterozoic epoch (*67*). Similarly, the selective use of Fe rather than Cu to ferry electrons to PSI in diatoms suggests that the evolution of Heteronkonts in the early Triassic (*15*) corresponded with reducing conditions in the oceans that mark the end-Permian extinction (*68*).

A major source of Fe for the oceans is wind-blown, terrestrially derived dust (*64*). This aeolian flux limits phytoplankton photosynthesis throughout much of the contemporary Pacific Ocean (*69*), but not the Atlantic (*70*). Examination of aeolian dust particles obtained from ice-cores suggests that during glacial periods, the supply of Fe to the world oceans was at least approximately an order of magnitude higher than during interglacial periods (*71*). As glaciation led to a reduction in sea level of ~120 m, denitrification on continental shelves essentially ceased while the supply of Fe would have stimulated biological N_2 fixation (*52*), thereby leading to an increase in the global pool of fixed N in the oceans. The Fe-based N enrichment would enhance phytoplankton C fixation until ultimately primary production became limited by phosphate. Assuming that the average proximate elemental composition of phytoplankton during glacial epochs conformed to that of the contemporary ocean (that is, the ratio of inorganic N/P in the ocean interior increased from 14.7 to 16), simple box model calculations suggest that the enhanced production would have lowered atmospheric CO_2 from ~275 to 245 parts per million, accounting for 30% of the interglacial-glacial difference in CO_2 (*72*). If strong deviations in the average elemental composition of phytoplankton occurred, this effect could be much greater (*73*).

The Role of the Southern Ocean

Of the three major HNLC regions in the contemporary ocean (*74*), the Southern Ocean has the greatest potential to affect atmospheric CO_2 levels (*75*). Despite physical processes that supply extremely high concentrations of macronutrients (N, P, and Si) to the euphotic zone from the deep ocean, total and export production are far below their potential. Approximately half of the N and P in the euphotic zone return unused as the surface layer of the Antarctic Circumpolar Current (ACC) subducts beneath nutrient-poor waters along its northern rim (Fig. 3). Along the way, this nutrient conveyor becomes relatively depleted in dissolved silica, which is used to support the growth of diatoms (*76*). Over two-thirds of the total ocean silica burial presently occurs under the ACC, south of the Polar Front that demarks the Southern Ocean (*77*). Indeed, the position of the Polar Front is reflected in the silica content of the underlying sediment. Cores taken from South Atlantic sites far north of the present Polar Front exhibit a negative correlation between carbonate and silica composition that roughly corresponds to interglacial and glacial periods, respectively (Fig. 4). During glacial periods, cold, silica-rich surface water apparently extended much further north than today.

Assuming that the HNLC conditions for the Southern Ocean are a consequence of Fe limitation at present, the enhanced aeolian flux of Fe during glacial periods would have directly stimulated phytoplankton production (*71*). Removal of only 50% of the macronutrients from the surface waters in the Southern Ocean by Fe stimulation would have led to a further drawdown of atmospheric CO_2 to ~190 ppm, corresponding to the glacial minimum (*78, 79*). Shifting the productive zone further to the north would have greatly enhanced the surface area of the Southern Ocean and improved the light climate for the region; both effects would have enhanced biological sequestration of atmospheric CO_2 by stimulating export of organic C. Such a stimulation is consistent with the sedimentary record north of the contemporary Polar Front (*80*).

Global Feedbacks

Whereas it is clear that phytoplankton specifically play a profound role in regulating atmospheric CO_2, the regulation of oceanic primary production is the consequence of interconnected biogeochemical networks with poorly understood climatic feedbacks. To a first order, the aeolian flux of Fe to the ocean is regulated by the hydrological cycle, which is, in turn, strongly influenced by atmospheric radiative forcing.
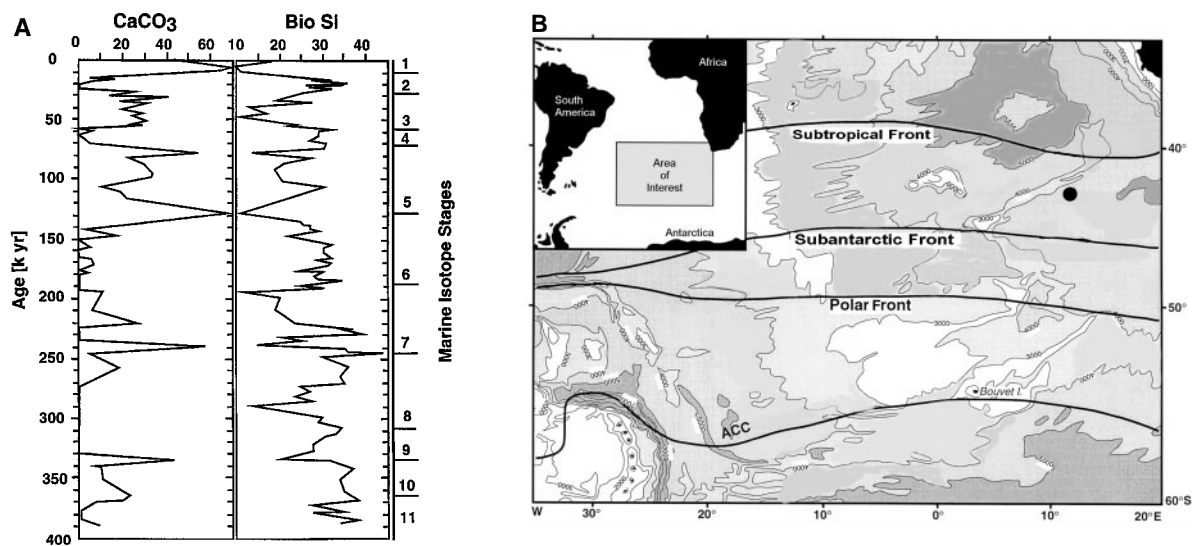
Fig. 4. (A) A core analysis shows the percentage of carbonate (CaCO₃) and biogenic silica (Bio Si) of sediment accumulation rates from a sediment core (PS2082-1) taken from the South Atlantic at 43°13′S and 11°44′E ~6° N of the present-day Polar Front (**B**, **inset**). The reciprocal oscillations in the proportions of calcium carbonate and opaline silica correspond to warm and cold periods, respectively, as defined by the marine stratigraphy record (as inferred from isotope fractionation analyses, shown as the marine isotope stages on the right axis). The deposition of silica during cold periods suggests that cold, silicate-rich water extended further north by at least 6° during those periods. [Data provided by G. Kuhn (AWI) and G. Bohrmann (GEOMAR, Kiel); stratigraphy (aging) done by A. Mackensen *et al*. (*88*).]

Soil moisture variability determines episodic aridity, which is the primary regulation on dust supply (*81*). The transport of aeolian Fe is related to wind speed and direction, which are related to the temperature contrast between the continents and ocean (*82*). Silica supply, essential for diatom blooms, is primarily dependent on riverine fluxes and upwelling from the ocean interior. The distribution of N_2-fixing cyanobacteria is not only dependent on Fe fluxes but also a warm, relatively quiescent euphotic zone. Food-web structure, which is a strong determinant of export flux (*32*), is critically dependent on mesoscale physical processes that promote nutrient pulses. The rapid increase in CO_2 at the end-terminal glacial periods is consistent with ocean biological control of the termination process, yet the data do not conclusively indicate which process (or processes) specifically dominated. Given the lack of mechanistic understanding of many of the feedbacks, and the paucity of observational data on decadal to century time scales, it is presently beyond credible capability to quantitatively represent these processes within coupled, time-dependent, three-dimensional ocean-atmosphere models (*8*, *83*). Hence, our ability to quantitatively predict ecosystem structure and biogeochemical feedbacks on the basis of forecasted climate change scenarios is limited.

Although differing in details, all coupled ocean-atmosphere climate models predict that the mean temperature of Earth will increase given the projected Intergovernmental Panel on Climate Change "business as usual" CO_2 emissions scenarios (*84*). The warming will be accompanied by increased heat storage in the surface ocean that will generally enhance stratification in both high-latitude areas (as a consequence of decreased salinity from melting ice) and in low-latitude regions (as a consequence of direct heating of the upper mixed layer) (*8*). Moreover, the general warming trend is associated with increased precipitation (*85*), although there is no consensus on the regional precipitation patterns (*84*). If this scenario holds, the implications for marine ecosystems are profound. Increased stratification will lead to an increased area of oligotrophic low-latitude gyres. The affected regions will have reduced nutrient fluxes to the upper ocean, thereby leading to a loss of export production. The enhanced precipitation could lead to a reduction in the aeolian flux of Fe, thereby retarding N_2 fixation and potentially expanding HNLC regions. The combination of these effects will be a lessening of both internally derived export production and externally supplied nutrients. Such a scenario predicts a decrease in the effectiveness of the biological pump and potentially contributes to a net efflux of CO_2 from the oceans to the atmosphere; that is, a positive feedback. Clearly such an analysis is greatly oversimplified, perhaps even naïve. Our intention is not to make quantitative predictions of the feedbacks, but to call attention to the sensitivity of marine ecosystems, on all time scales, to climatic and geophysical processes external to the ocean, and the role marine ecosystems have played in regulating Earth's chemistry. Our predictive capabilities will improve only when the need for an international network of coordinated long-term (multidecadal) observations of oceanic biology is addressed, and our ability to incorporate the biological processes and feedbacks in coupled ocean-atmosphere models is dramatically improved.

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