gral part of the model used to explain the layer of iron atoms (*11*). A difficulty that has only been resolved recently was pointed out by Bates: Sodium atoms are readily ionized by solar ultraviolet and by charge transfer from other ions such as O_2^+; the same is true of any other metallic atom, including iron. Recombination of any atom with an electron is extremely slow, and it is necessary to find a molecular ion that participates in the much faster process of dissociative recombination. But any simple ion like NaO^+ or FeO^+ will rapidly be converted back to the atomic ion by reaction with an O atom. More complex ions such as $Fe{\cdot}N_2^+$, $Fe{\cdot}O_2^+$, and $Fe{\cdot}H_2O^+$ seem to be responsible (*11*).

Above the tropopause (a boundary region at roughly 8- to 17-km altitude depending on latitude) lies the middle atmosphere: the stratosphere and mesosphere, divided by the stratopause at the 50-km temperature maximum and ending at the mesopause, a deep temperature minimum at about 82 km. It is this low temperature that is the site of PMCs, and the abundant atomic oxygen at nearly the same level makes the existence of the metallic layers possible. Now we learn that these two remarkable phenomena are linked: The tiny ice particles that can form during polar summer can "eat" the iron layer and nearly cause it to disappear. Similar effects are likely for sodium and the other metals, and it will be interesting to see if they are real.

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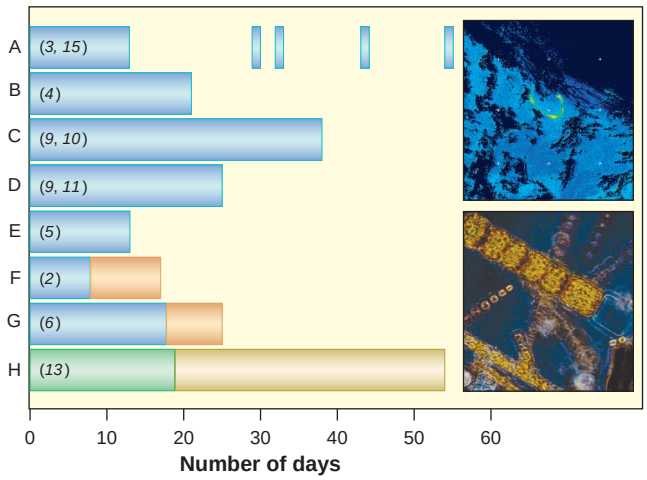
Ironing Out Algal Issues in the Southern Ocean

Philip Boyd

In a third of oceanic waters, termed high-nitrate low-chlorophyll (HNLC) regions, plant nutrients are abundant, yet puzzlingly phytoplankton stocks remain constantly low. It was hypothesized that this HNLC condition resulted from iron limitation of phytoplankton growth, and thus that observed reductions in atmospheric CO_2 concentrations over geological time scales were mediated by periods of elevated iron supply to the ocean (*1*). In the last decade, purposeful iron enrichment of >100-km^2 patches of HNLC waters have resulted in massive phytoplankton blooms with concurrent uptake of nutrients and CO_2 drawdown (*2*–*6*). These spectacular results led geoengineers to consider iron enrichment of HNLC waters as a potential fix to rising atmospheric CO_2 concentrations (*7*).

There has been heated debate over the merits, and potential side effects, of oceanic iron enrichment as a CO_2-mitigation strategy (*7, 8*). However, informed discussion of such topics requires data on a fundamental issue—the efficacy of iron enrichment for the sequestration of algal carbon to deep waters (*8*). Such data provide a test for the hypothesis (*1*) that iron supply ultimately leads to enhanced export of particulate organic carbon (POC) following the decline of phytoplankton blooms. In addition, iron-mediated blooms in mesoscale studies have all been caused by diatoms (*2*–*6*), cells with opal cell walls that require silicon for biomineralization. Thus, in waters low in silicic acid, adding iron alone might not stimulate blooms. The fate of carbon fixed during iron-stimulated diatom blooms, and the role of silicic acid supply in setting the bloom biogeochemical signatures, were targeted by SOFeX (Southern Ocean Iron Experiment) in austral summer 2002. On page 408 in this issue, Coale *et al.* (*9*) report on how purposeful iron enrichment of both low–silicic acid subantarctic waters and high–silicic acid polar waters led to blooms dominated by different phytoplankton groups. Bishop *et al.* (*10*) on page 417 and Buesseler *et al.* (*11*) on page 414 present evidence of iron-elevated export of POC from these subantarctic and polar blooms, respectively.

The Southern Ocean is characterized by a north-south gradient in silicic acid. Coale *et al.* (*9*) enriched mesoscale patches of surface waters with iron at two HNLC sites: low–silicic acid subantarctic waters in the north (SOFeX-N) and high–silicic acid polar waters in the south (SOFeX-S). As previously observed in polar waters (*3*, *4*), SOFeX iron enrichment resulted in massive blooms and concurrent nutrient uptake and CO_2 drawdown. However, Coale *et al.* (*9*) report—although based on limited data sets—important differences in the algal taxa that composed these blooms: SOFeX-S was dominated by diatoms, whereas at SOFeX-N, flagellated algae (that is, non-



Phytoplankton blooms. Summary of the phases of mesoscale blooms induced by purposeful iron enrichment. Blue denotes bloom evolution (defined here as a period of increasing or sustained biomass and elevated photosynthetic competence F_v/F_m), and orange denotes bloom decline (defined here as a period of decreasing biomass and decreasing F_v/F_m, both returning to ambient HNLC levels). The green and yellow bars [in (H)] denote these phases for a naturally occurring polar bloom. The discrete blue bars [in (A)] denote SeaWiFS Ocean Color satellite "snapshots" of the bloom on days 30, 33, 44, and 55. The right, upper panel is a SeaWiFS Ocean Color image of the SOIREE polar bloom (*15*). The lower panel is a photomicrograph of diatoms, the algal functional group that has bloomed in each of these iron-enrichment studies.

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siliceous phytoplankton) and diatoms were equally abundant. Biogeochemical signatures of the two blooms such as CO_2 drawdown were comparable, but significantly at SOFeX-N, this drawdown was fueled mainly (60 to 70%) by regenerated nitrogen (ammonium and urea), whereas at SOFeX-S the bloom was driven mostly by nitrate (60%) (*9*). Also, silicic acid depletion was considerably higher at SOFeX-S, because at SOFeX-N (and despite entrainment of silicic acid from surrounding waters) the diatoms were silicic acid–limited (*9*). These differences have important implications for the uptake stoichiometry of carbon, nitrate, and silicon during each bloom.

POC export from the blooms into the deep ocean was measured throughout the experiments. At SOFeX-N, an optical particle interceptor on an autonomous profiler "parked" at 100-m depth recorded the daily export flux for more than 50 days (*10*), whereas at SOFeX-S daily export fluxes were obtained for 28 days using the thorium-234 deficit approach (*11*). Both methods reported severalfold higher export from iron-enriched waters relative to adjacent HNLC waters (*10*, *11*). These export fluxes (*10*, *11*) are the best estimates to date for the Southern Ocean of the ratio of iron added:POC exported. This term is essential to model the impact of elevated iron supply on carbon biogeochemistry during the geological past (*8*), and to estimate the efficacy of oceanic iron enrichment as a geoengineering fix (*7*, *8*). The molar ratio of iron added:carbon exported at 100-m depth was 1.5×10^{-4} at SOFeX-S (*11*), compared to 1×10^{-4} to 1×10^{-5} for SOFeX-N (*10*); both ratios are higher (a less efficient fix) than those previously used by geoengineers in theoretical calculations of carbon sequestration (*8*).

How did the different bloom populations (*9*) impact POC export at each site? At SOFeX-N, export increased between days 30 and 55, resulting in enhanced export of 120 to 1170 mmol C m^{-2} [upper and lower limits assume that the optical "sediment trap" intercepted the particle rain intermittently or continuously, respectively (*10*)], whereas at SOFeX-S enhanced fluxes of 225 mmol C m^{-2} were recorded over 28 days (*11*). However, several issues prevent a direct comparison. The SOFeX-N export event was probably triggered by the subduction of phytoplankton to depth when the bloom filament encountered a front (*10*), whereas no such vertical-transport mechanism was evident at SOFeX-S (*11*). Also, throughout both experiments, phytoplankton exhibited elevated photosynthetic competence F_v/F_m (*9*), suggesting that both blooms were characterized by "healthy" cells, and that they had yet to reach termination by resource limitation (see the figure). Thus, at SOFeX-S, the export flux from the bloom is probably an underestimate (*11*), whereas at SOFeX-N, subduction of "healthy" cells may have prematurely terminated the bloom, and provided an overestimate of export (*10*).

SOFeX has yielded exciting and important findings—in particular, that iron enrichment of low–silicic acid HNLC waters results in a bloom that is dominated by nonsiliceous cells (*9*), which are probably fueled by regenerated nitrogen. Previously it was thought that such taxa exhibited only transient increases in stocks before being grazed by microzooplankton (*12*). Evidence of the fate of the SOFeX blooms was equivocal, with neither bloom exhibiting signs of termination (see the figure). To date, iron-stimulated polar blooms have been observed for periods ranging from 20 to 50 days without evidence of decline, whereas natural polar blooms persist for less than 25 days (*13*) before terminating (see the figure). Such longevity of iron-stimulated blooms may be due to multiple iron enrichments [four over 30 days for SOFeX-N (*9*)], resulting in iron-supply rates considerably higher than occur in nature. Alternatively, artifactual entrainment of surrounding HNLC waters into the iron-enriched bloom may retard algal aggregation and subsequent POC export (*14*). The design of future polar mesoscale iron enrichments must reconsider the magnitude of iron supply, and the spatial and temporal scale of these experiments.

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GENOMICS

Beyond Nature and Nurture

Gene E. Robinson

The horns of a dilemma
are usually on the same bull (*1*).

When it comes to behavior, the nature-nurture controversy has not disappeared. The public is leery of attributing behavioral influence to DNA rather than to the environment and free will; worries abound over the ethical implications of biological determinism. Many social and behavioral scientists are skeptical as well, either because the concept of "DNA as destiny" does not jibe with their understanding of the dynamic nature of behavior or because they consider human behavior to be much more complex than that of animals studied from a genetic perspective. By contrast, biologists have long accepted that genes, the environment, and interactions between them affect behavioral variation. Traditionally, behavioral variation has been partitioned using statistical analysis into genetic (G), environmental (E), and G × E components, an approach that began long before the advent of molecular biology. This retains the flavor of the nature-nurture dichotomy, which influences how research in this field is interpreted. Fortunately, we can now study genes in enough detail to move beyond the nature-nurture debate. It is now clear that DNA is both inherited and environmentally responsive.

Behavior is orchestrated by an interplay between inherited and environmental influences acting on the same substrate, the genome (see the figure). For behavior, gene expression in the brain is the initial readout of the interaction between hereditary and environmental information. Inherited influences ("nature") include variations (polymorphisms) in DNA sequence transmitted from generation to generation over an evolutionary time scale. DNA polymorphisms can affect protein activity (sometimes via posttranslational mechanisms) and gene expression in the brain: when, where, and how much of each protein is produced. The environment ("nurture") also influences gene expression in the brain during the lifetime of an individual (*2*, *3*). Environmental effects occur over developmental and physiological

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