Phytoplankton bloom on iron rations

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An iron-enrichment experiment in the equatorial Pacific Ocean shows that increased availability of this trace nutrient induces dramatic biological and biogeochemical changes in the surface waters.

EXPERIMENTS in the open ocean are particularly challenging. Take the study of biological and biogeochemical processes occurring near the ocean surface. An unambiguous test of some hypotheses about these processes practically dictates an *in situ* experiment, but lateral and vertical exchanges due to advection and turbulent diffusion impose severe logistical difficulties on the approach. Fortunately, the technology for such experiments now exists. It has been successfully applied to a salient oceanographic question, as described in a remarkable study by Coale *et al.* (page 495 of this issue[1]) and companion papers by Behrenfeld *et al.*[2], Cooper *et al.*[3] and Turner *et al.*[4] which begin on page 508.

The question is, what regulates phytoplankton abundance and production in the equatorial upwelling zone of the eastern Pacific Ocean? The major nutrients required for phytoplankton growth, such as nitrate and phosphate, are available there in high concentrations, yet phytoplankton seem unable to use them efficiently, and phytoplankton abundance remains low. These features are common to the three so-called 'high-nitrate, low-chlorophyll' (HNLC) regions, which include, besides the eastern equatorial Pacific, the ice-free Southern Ocean and the open subarctic North Pacific Ocean. Clarifying the regulatory mechanisms concerned is necessary for understanding ocean ecology, the oceanic carbon cycle, and the involvement of the upper-ocean biota in transfer of carbon from the atmosphere to the ocean depths.

The papers report an experimental test of the late John H. Martin's hypothesis[5] that it is the availability of iron that limits phytoplankton in the HNLC regions. Iron is nearly insoluble in sea water, but is an essential trace nutrient required by phytoplankton for many biochemical processes (chlorophyll synthesis and nitrate reduction, for example). Measurements showing that surface-water concentrations of dissolved iron are extraordinarily low (sub-nanomolar) led Martin to first test the iron hypothesis using shipboard nutrient bioassays. Natural phytoplankton incubated in bottles usually increased in abundance when provided with extra iron. But bottles of sea water as microcosms of the ocean are always suspect. So an *in situ* iron-fertilization experiment was designed and has been carried out twice, first in 1993 and then again last year.

In the first experiment (IronEx I), reported without fanfare in this journal two years ago[6–8], a single dose of iron, raising the dissolved iron concentration to 4 nM in a 64-km^2 patch, resulted in significant increases in phytoplankton abundance and production rate, but had little effect on nitrate concentration or partial pressure of CO_2. Sadly, the experiment ended prematurely when the fertilized patch sank beneath a layer of less dense water; the ecosystem response to iron became attenuated for unknown reasons. Although the experiment verified the iron hypothesis, it left the issue of whether iron fertilization could relieve the HNLC condition unresolved[9,10].

In contrast, during the second experiment (IronEx II, described in this issue), the fertilized patch remained at the surface and retained its integrity while drifting 1,500 km. The same amount of iron was added as in IronEx I, but in three sequential infusions over a week to effect a more sustained increase of dissolved iron in the surface layer of a 72-km^2 patch. The fertilization had an immediate and dramatic effect. Within the enriched patch, phytoplankton photosynthetic capacity, growth rate and abundance increased, and nitrate decreased. As the phytoplankton bloomed, its species composition changed radically. Diatoms became dominant and accounted for most of the increased use of nitrate[1]. Significantly, these events parallel those observed in previous shipboard nutrient bioassays in the equatorial Pacific[11].

The fate of the added iron is not reported, but the stimulated biological production was short-lived. Within a week of the last iron infusion, indicators of phytoplankton physiological condition returned to the same levels as those in the iron-limited ambient waters[2] and the phytoplankton bloom waned, presumably due to grazing and sinking (although the tracer budget indicated mixing losses as well)[3]. Contrary to expectation[12], there was no sign that iron was retained and efficiently recycled within the biota of the surface layer. So episodic natural inputs of iron, either from the atmosphere[5] or from below[13], should induce episodic pulses of short duration in phytoplankton abundance and production. The consequences of larger-scale, longer-term inputs of iron are uncertain; from observations in the

IronEx II — the principal results

IN IronEx II, dissolved iron was infused from a ship into the surface layer of a square patch of ocean in the eastern equatorial Pacific. The measurable growth response of phytoplankton to nutrient enrichment occurs on a timescale of days, so the success of the experiment hinged on staying with the fertilized patch as it drifted 10–100 km per day in the current. This was accomplished by tagging the patch with a drogued buoy and a biologically inert tracer (SF_6) added with the iron. The response of the natural, unenclosed plankton assemblage to iron was monitored by repeated surveys of the patch over several days. Untreated water outside the tagged patch served as a control. The main results are these:

- Specific growth rate (cell division rate) of the phytoplankton doubled, phytoplankton abundance increased by more than 20 times (approaching levels observed in coastal phytoplankton blooms), and nitrate concentration declined by half. Larger sizes of phytoplankton, chiefly diatoms, dominated[1].
- Indicators of phytoplankton photosynthetic capacity (photochemical energy conversion efficiency, light absorption capability) showed immediate and sustained increases[2].
- As the bloom developed, the partial pressure of CO_2 in the centre of the patch decreased rapidly, reducing the ocean-to-atmosphere CO_2 flux by 60 per cent[3].
- The concentration of dimethyl sulphide (DMS), a potential biogenic precursor of atmospheric sulphate particles which may be implicated in modifying climate through their effects on global albedo, increased by more than three times in the bloom[4].