These myosin II molecules from smooth and non-muscle cells also exhibit an interesting property in the dephosphorylated state, in which the rod portion of the molecule folds up (the so-called 10S myosin) and makes contact with the neck region of the head, trapping the ATP in the active site[12]. The contact between the rod and the neck could be at this RLC–ELC interface, also disrupting their interaction. Even the scallop myosin in the absence of Ca^{2+} will fold in this way[13].

As Rayment *et al.*[4] have pointed out, the way in which the light chains clamp on to the heavy-chain helix closely resembles that in which calmodulin binds to its target peptides[14,15]. This is not surprising given the homology between the light chains and calmodulin, and the fact that more unconventional cellular myosins[11] contain calmodulin rather than light chains in their neck region (Fig. 1). A consensus sequence motif, the IQ motif, has been identified as the heavy-chain binding site for these subunits. The structural basis for the interaction between the light chains or calmodulin and this motif has been further clarified by Xie *et al.*, and the sequence motifs extended to include another bulky hydrophobic residue separated by 12 residues from the Ile (IQXXXRGXXXRXXY(W)). This now encompasses all known calmodulin-binding sites, but it remains a mystery as to why light chains bind to myosin II molecules and calmodulin to the rest.

There are now at least nine groups in the myosin molecular motor family[11] and the basic design of the molecular motor can be perceived (Fig. 1). The number of calmodulins binding to the regulatory domain can be anything from one to six, presumably each capable of binding four Ca^{2+}. If the scallop myosin poses problems in understanding the structural basis of the single Ca^{2+}-binding trigger event, it makes the mind boggle at the possibilities that exist with the more conventional members of this superfamily. ☐

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MARINE BIOLOGY

Pumping iron in the Pacific

Mark L. Wells

LAST November, in the largest scientific manipulative experiment in oceanographic history, 480 kilograms of iron was added to the surface waters of the Pacific Ocean 500 km south of the Galapagos Islands. The objective was to test the contentious suggestion that iron limits phytoplankton production and biomass in regions of the world's oceans otherwise rich in plant nutrients. Scientists eagerly gathered at a meeting last month* to hear the preliminary findings of this experiment, known as 'IronEx1'.

The surface waters of the northeast Pacific, the equatorial Pacific and the Southern Ocean — over 10 per cent of the world's ocean — are replete in major nutrients such as nitrate and phosphate but support comparatively low biomass. The keen interest in understanding this enigma stems in part from suggestions that sustained increases in photosynthesis in these regions might in the past have removed enough carbon dioxide from the atmosphere to induce periods of glaciation[1].

The suggestion that iron limits ocean productivity in these areas is not new[2]. But the concentrations of iron involved are tiny, and only recently have experimental methods improved enough to avoid metal contamination during sampling or analysis. John Martin of the Moss Landing Marine Laboratory helped to pioneer these 'clean' methods and convincingly demonstrated in bottle experiments that nanomolar iron enrichments of high-nitrate, low-chlorophyll waters did indeed increase phytoplankton growth and biomass[3,4]. A criticism often levelled at this 'iron hypothesis', though, is that bottle incubations may not adequately reflect the natural ecosystem response.

John Martin therefore orchestrated the scientific and logistical planning for a large-scale iron enrichment experiment in the open ocean. Tragically, his untimely death prevented him from seeing the outcome, but his plan proceeded under the joint leadership of Ken Johnson and Kenneth Coale.

In mid-November 1993, the RV *Columbus Iselin* arrived south of the Galapagos Islands, so laden with equipment and personnel that it could hold only half its freshwater reserve. Iron and a highly sensitive inert tracer (SF_6; see ref. 5) were pumped into the propeller wash as the vessel steamed to and fro across an 8×8 km field over 24 hours, raising iron concentrations from the ambient (about 0.05 nM) to about 4 nM. The 'patch' was subsequently traced chemically by flow injection analyses of iron and SF_6 in water from the ship's pumping system.

The initial response of the ecosystem response was mapped from the pumped water while the ship was under way and from hydrographic stations occupied each day both inside and outside the patch. Overhead, optical measurements from NASA's aeroplane-borne P-3 Orion laboratory looked for changes in phytoplankton pigments.

On the fifth day of the 9-day experiment, a low-salinity front moved into the region, subducting the patch to a depth of 30–35 m, where it remained confined to a 5–10-m-thick interval above the thermocline but still within the photic zone. By this time, iron concentrations within the patch had decreased from their initial values of about 4 nM to less than 0.2 nM (K. Johnson and K. Coale, Moss Landing Marine Laboratory).

And the response? From the preliminary findings, it seems that phytoplankton growth was indeed stimulated. Photosynthetic efficiency increased within 12 to 24 hours after the iron had been added, and reached maximal rates after 2 to 3 days (Z. Kobler and P. Falkowski, Brookhaven National Laboratory). By this point, primary production rates and chlorophyll concentrations had more than doubled (R. Barber, Duke University) and the patch was readily discernible by airborne laser-induced fluorescence measurements (F. Hoge, NASA Goddard Space Flight Center). Clearly, one of the central tenets of the iron hypothesis had been confirmed.

But the magnitude of the ecosystem response fell a long way short of that predicted from the experiments carried out in bottles. Chlorophyll concentrations increased to only 0.7 μg per litre (Barber) in contrast to the peak concentrations of about 6 μg per litre typically found in bottle incubations. Furthermore, the main growth appeared to be that of phycoerythrin-containing picophytoplankton less than 2.0 μm in size (Barber), whereas in bottle experiments the overwhelming response is from larger, chlorophyll-containing diatoms. These shipboard results have yet to be reconciled with contrasting airborne fluorescence measurements which showed that chlorophyll — rather than phycoerythrin, a different photosynthetic pigment — dominated within the patch (Hoge).

The increase in phytoplankton biomass caused ammonia concentrations to decrease by a factor of 3, but ambient nitrate concentrations fell only imperceptibly. In addition, total carbon dioxide decreased by only ~6 μM and CO_2 fugacity by only

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*Ocean Sciences Meeting, San Diego, California, 21–25 February 1994.

~10 μatm from their original values after 4 days (K. Van Scoy, University of East Anglia; F. Millero, University of Miami). The decreases are about a tenth of those expected if photosynthesis had used up all the available nitrate.

Not surprisingly, the debate continues on the causes for the difference between bottle-scale and mesoscale iron enrichments. Although we shall learn more when the final results become available, it probably will not be possible to solve this puzzle without repeating the experiment. Two loss terms were not well characterized: the loss of phytoplankton through zooplankton feeding within the patch, and the time-dependent loss of available iron in surface waters. In defence of the planners, however, no more equipment could have been brought on board without risk of capsizing the vessel.

The grazing question is a tricky one. Based on bottle experiments, the prevailing wisdom has been that stocks of the smaller picophytoplankton are limited by the tiny marine animals that 'graze' on them, and the larger phytoplankton are iron-limited. So the apparent increase in picophytoplankton within the patch came as a surprise.

Part of the explanation for the low response from larger phytoplankton may be increased grazing by zooplankton normally excluded or damaged in most bottle experiments. Microscopic examination of seawater samples during IronEx showed about a 50 per cent increase in microzooplankton (Barber), and net tows indicated that mesozooplankton which normally migrate daily to the ocean surface from deeper waters were remaining there to profit from the extra food supply (Coale) — at the meeting, Bill Sunda (National Marine Fisheries Service, NOAA) likened this behaviour to that of seagulls flocking in to feed.

So consumption by mesozooplankton could be reducing the concentration of phytoplankton below what is expected from bottle experiments. It may be that these larger zooplankton also feed on the smaller grazers and that the lifting of grazing pressure allows the picophytoplankton to capitalize on the higher iron availability.

Understanding the rate at which available iron is lost from the patch is crucial for explaining the extent of the ecosystem response. In contrast to what occurs in 'contained' experiments, total iron concentrations within the patch decreased by about 90 per cent by the fifth day of the open-ocean experiment (Johnson). Even then, we cannot quantify iron availability rigorously because current iron analysis techniques probably overestimate the biologically available fraction[6]. Repetitive fertilization will probably be necessary before direct comparisons to bottle incubations become meaningful. The pulse of iron input appears to have been sufficient to 'kick-start' the ecosystem, only for it to stall as the iron ran out.

Although grazing effects and diminishing iron availability probably contributed to differences between the bottle-scale and mesoscale iron enrichments, several alternative hypotheses were raised at the meeting (F. Morel, Massachusetts Institute of Technology). These included indirect effects arising from reactive photochemical products created by iron photolysis, and adsorption of other metals onto the colloidal iron oxides formed upon iron enrichment, which then aggregated and sank from surface waters. Finally, bottle incubation results can differ from site to site (M. Wells, University of California, Santa Cruz), and the Galapagos region is several thousand kilometres from where most of the bottle experiments were conducted.

Has the 'iron hypothesis' been verified? So far, the answer is a qualified yes. Phytoplankton production and biomass did increase upon iron enrichment, although the results differed from those of bottle experiments. Nonetheless, oceanographers should not neglect bottle experiments in future work, as they provide perhaps the best way to probe the specific response of individual members of the plankton community[7]. On the other hand, mesoscale enrichments offer the chance to test the whole ecosystem response, but they are difficult to interpret because of unexpected or unquantifiable factors. Spin-offs of the 'iron hypothesis' — namely the depletion of important nutrients and carbon dioxide in surface waters — cannot be properly evaluated from the current results. The effects may be understood better after the follow-up iron fertilization experiments scheduled for next year.

The most resounding success of this complex experiment was to prove that it is possible to modify and then track a patch of open ocean surface water while measuring the ecosystem response. The experiment could hardly have been undertaken without the tireless effort and tenacity of John Martin. Regardless of the final judgement on the 'iron hypothesis', establishing the feasibility of such experiments may well turn out to be John's most enduring legacy. □

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DAEDALUS

Superficial gain

In the noble army of solids, metals form a regiment of their own. They owe their unique ductility, shine and conductivity to their special lattice of positive metal ions in a sea of negative electrons. Daedalus points out that many non-metallic molecules, such as ammonium and the related alkylammoniums, also exist as stable positive ions. They might fit rather well into a metallic lattice. Indeed, ammonium forms an alloy with mercury. So Daedalus now plans to infiltrate various alien ions into the metallic lattice. By inserting ionic relatives of ammonium, ideally polymeric ones, he hopes to create a whole new class of organometallic 'hybrid alloys'.

His scheme is to electroplate the ions onto the metal from a suitable molten salt. Very high pressure may be needed to collapse the deposited ions into the dense metallic state so that they can alloy with the metal cathode and diffuse into it. The cathode will acquire a subtly graded composition: pure metal in the interior, but with a steadily increasing proportion of alloyed non-metallic ions towards the surface. Metal plated in this way should transform engineering.

Thanks to its loading of organic ions, a hybrid-alloy surface will be rust-proof, and will bind to paint and glue tenaciously. Its organic content will give it a degree of flexibility, making the surface layer slightly softer than the underlying metal. The resulting 'case softening', claims Daedalus, should make the metal extremely tough. For a loaded component usually fails from the surface inwards: the stress is greatest there, and small surface irregularities invite cracks to start. A case-softened surface would yield more easily, reducing the surface stresses. The stresses inside would be higher, of course; but the smooth inward gradation from surface alloy to pure bulk metal would give no sharp discontinuity from which a crack could begin. So, paradoxically, by softening its surface you would strengthen the whole component. It could be stressed right up to the elastic limit of the underlying metal without fear of brittle failure.

Daedalus also hopes to make homogeneous metal–organic hybrid alloys in bulk form, thus bridging the gap between metals and non-metals. Far lighter than most alloys, they should still retain that special metallic ability to be bashed and deformed enormously without breaking or losing strength. They might not be magnetic, but they should conduct electricity in intriguing ways. Indeed, they could even form a whole new range of cunning semiconductors.

David Jones