

COMMENT

Limnol. Oceanogr. 40(7), 1995, 1336–1343
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Status of the iron hypothesis after the Open-Ocean Enrichment Experiment¹

John Martin's vision, intellect, and drive resulted in a remarkable achievement—an unprecedented experiment to test his idea that iron limitation can control the biomass and productivity of phytoplankton in the open ocean (Martin et al. 1994). The result would surely have gratified him immensely, and rightly so: after a patch of surface water in the equatorial Pacific Ocean was enriched with iron, chlorophyll concentration doubled and primary productivity increased by a factor of four. Clearly, iron had affected the net growth of phytoplankton.

The experiment (IronEx), described as a test of the iron hypothesis, represents a milestone in a line of research (see de Baar 1994) that traces to the founders of biological oceanography and owes its prominence to the efforts of Martin and his colleagues (Martin and Fitzwater 1988; Martin 1992). Enrichment of the open ocean, a contentious proposition, was undertaken only after vigorous debate before and during a special symposium organized by the American Society of Limnology and Oceanography (ASLO). The debate was fruitful indeed; a broad cross-section of the oceanographic community reported their results and discussed their ideas (Chisholm and Morel 1991), and consensus was reached on a variety of issues, including the need for a modestly scaled ocean enrichment experiment. It seems clear that open discussion of the controversial topic, even by those who presented ideas and alternate interpretations rather than original results, was healthy. In that spirit, I offer some comments on the iron hypothesis as research on the topic enters a new stage.

Defining the iron hypotheses

It can be argued that effective research requires formal and systematic construction of multiple, falsifiable hypotheses (Platt 1964) and that precision is essential when formulating or discussing hypotheses about the control of primary production (Cullen 1991). Likewise, hypotheses can be clarified by careful review of their historical context (de Baar 1994), and they can be refined or questioned by exploring the processes responsible for experimental results (Banse 1991). Another approach is to pursue a powerful idea with unwavering purpose, developing new techniques, collecting novel data, and compiling a broad range of supporting evidence from other sources. Martin and his colleagues used the latter approach effectively, making a strong case for iron limitation in the major nutrient-rich waters of the sea (Martin et al. 1991).

The iron hypothesis is not explicitly defined by Martin et al. (1994), but the experiment clearly was testing the proposition “that phytoplankton growth in major nutrient-rich waters is limited by iron deficiency” (Martin et al. 1991, p. 1793). Let us define this as Martin's iron hypothesis and broaden the discussion to include other, more specific hypotheses, as well as alternate hypotheses. Recent reviews (de Baar 1994; Geider and La Roche 1994) can be consulted for background, insight, and more comprehensive descriptions of relevant research.

Martin's iron hypothesis

Experiments in bottles failed to resolve questions about Martin's iron hypothesis, principally because natural rate processes, especially grazing, could not be characterized. In principle, open-ocean iron enrichment would permit a robust test of the hypothesis: if iron were delivered to the photic zone in an available form and nothing happened, the hypothesis would be soundly rejected. The observed response—rapid physiological changes in phytoplankton followed by an increase in their biomass and productivity—supports Martin's iron hypothesis, but, as is discussed below, it leaves many questions unanswered. The results of IronEx did falsify an alternate, less comprehensive and evocative hypothesis: biomass and productivity of phytoplankton in the equatorial Pacific are controlled entirely by factors other than the availability of iron.

The HNLC-iron hypothesis

In most discussions of the iron hypothesis, the principal unexplained phenomenon is the existence of high-nutrient, low-chlorophyll (HNLC) waters in the open ocean (Chisholm and Morel 1991). Accordingly, at an early stage in the discussion of Martin's ideas (October 1990), participants at a workshop convened by the Board on Biology of the U.S. National Research Council formulated what I will call the HNLC-iron hypothesis: “An increase in the rate of supply of iron to the surface layer of the ocean will reduce to depletion the unused macronutrients, nitrate and phosphate” (see Cullen 1991, p. 1585). It was intended to be a testable explanation of the HNLC condition. During IronEx, the supply of iron to the surface layer was increased, but the concentrations of nitrate remained high and changes of CO₂ were minimal (Watson et al. 1994). At face value, the HNLC-iron hypothesis was rejected; however, neither the hypothesis nor the test were perfect. The hypothetical increase in the rate of sup-

¹ Accepted 13 April 1995.

ply of iron is not defined, and regardless, the open-ocean addition of iron was too ephemeral to constitute an unequivocal test of the HNLC-iron hypothesis.

Now that the first results of IronEx have been reported, the HNLC-iron hypothesis is in a state of tantalizing uncertainty. The fact is that the concentrations of nitrate and phosphate changed little in response to the iron addition. Explanations for the phenomenon differ (Kolber et al. 1994; Martin et al. 1994; Van Scoy and Coale 1994; Watson et al. 1994; Banse 1995). These are discussed below in the context of alternate working hypotheses.

The ecumenical iron hypothesis

By 1991, when the issue was finally discussed in a broad public forum (Chisholm and Morel 1991), those who were inclined to explore the ecological bases of Martin's iron hypothesis had developed remarkably consistent explanations for the HNLC condition. Morel et al. (1991b) called it the ecumenical iron hypothesis. Different proponents (e.g. Banse 1990, 1991; Chavez et al. 1991; Cullen 1991; Frost 1991; Miller et al. 1991; Price et al. 1991; Cullen et al. 1992a; DiTullio et al. 1993) emphasized particular aspects of the hypothesis, but in general they suggested that when iron is scarce, the dominant smaller cells with greater surface:volume ratios can grow more rapidly than larger cells (Morel et al. 1991a; Chisholm 1992). The specific growth rates of small cells are not strongly limited by iron (Price et al. 1991, 1994; Cullen et al. 1992a); rather, their numbers are controlled by microzooplankton grazers whose potentially high growth rates (Banse 1982) enable them to keep small phytoplankton populations in check (Frost 1991; Miller et al. 1991). Larger cells cannot attain high growth rates at ambient nutrient concentrations, but enrichment with iron would allow them to grow and assimilate nitrate, unfettered by microzooplankton grazing because of their large size, and unchecked by mesozooplankton grazing because those herbivore populations could not respond in time. Clearly, this latter supposition cannot be tested with incubation experiments.

The ecumenical iron hypothesis views the HNLC condition as "grazer controlled phytoplankton populations in an iron-limited ecosystem" (Price et al. 1994, p. 520). Although this hypothesis provides an excellent context for experimentation and discussion (Barber and Chavez 1991; Chavez et al. 1991; Price et al. 1991, 1994; Cullen et al. 1992a), it is not amenable to simple comprehensive tests and does not explain all results from enrichment experiments (see Coale 1991). The ecumenical iron hypothesis suggests that no single factor regulates primary productivity; rather, the interplay of factors is key (see de Baar et al. 1990). A goal, then, is to see whether iron plays a disproportionate role in determining the use of macronutrients (Geider and La Roche 1994).

The ecumenical iron hypothesis does not require that small cells grow at nutrient-saturated specific growth rates (μ_{\max} ; d^{-1}). Rather, it states that the specific growth rates (μ) of small cells are not strongly limited by iron, hence

grazing loss (g ; d^{-1}) is the predominant control on their net rate of increase (k ; d^{-1}). This criterion is not very precise, so the distinction between physiological limitation by iron and grazing control of small cells is fuzzy at best. Consider HNLC waters where k is normally near zero, and grazing is the dominant loss term for small cells (see Frost 1991; Cullen 1991): $k \approx \mu - g$, thus $\mu \approx g$. We can define the relative influence of physiological limitation on k as $(1 - \mu/\mu_{\max})$, and the relative influence of grazing as (g/μ_{\max}) . One would thus have to demonstrate strong iron limitation of μ (i.e. $\mu < 0.5 \mu_{\max}$) to infer that iron is the principal mechanism controlling net rates of growth. In HNLC waters of the equatorial Pacific, photochemical energy conversion efficiency is about half maximal and it increases during incubations with added iron (Greene et al. 1994). These observations are interpreted by the investigators as evidence of physiological control of photosynthesis and growth of phytoplankton. However, μ/μ_{\max} in situ is uncertain, and it is known that phytoplankton under "metal stress" can have strongly altered physiological characteristics even though growth rates exceed 90% of maximum (Morel et al. 1991a). The study of Greene et al. (1994) leaves us with a strong indication that specific growth rates of equatorial phytoplankton are less than maximal, but no accurate knowledge of μ/μ_{\max} and no direct information on how much k and g would change if iron-limited specific growth rates of small cells increased in response to iron enrichment. Their study is an excellent segue to the open-ocean enrichment experiment.

One prominent feature of IronEx—an apparently strong physiological response to iron by small phytoplankton with significant and similar net increases of chlorophyll in small as well as larger size classes (Kolber et al. 1994)—is consistent with the suggestion that the photosynthesis and biomass of small cells is controlled by physiological limitation (Greene et al. 1994). This view is contrary to the central tenet of the ecumenical iron hypothesis, that larger cells will dominate the response to iron enrichment. Cell counts and biomass estimates for all size classes (including prochlorophytes) should help resolve the degree to which iron enrichment influenced the biomass, as compared to the chlorophyll content of each size class.

As results are presented and discussed in future reports, it will be natural to compare results from IronEx to those from elsewhere in the equatorial Pacific. In doing so, it should be remembered that micronutrient inputs to the equatorial Pacific might be episodic and patchy (Donaghay et al. 1991) and, consequently, the nutritional status of natural phytoplankton assemblages may vary in space and time. We should thus recognize that the results of bottle experiments, IronEx, or subsequent enrichment experiments might not apply generally to the HNLC equatorial Pacific.

The grazing hypothesis

Although one could construct a grazing hypothesis that is exclusive of Martin's iron hypothesis, it is well recognized that grazing is but one factor controlling the bio-

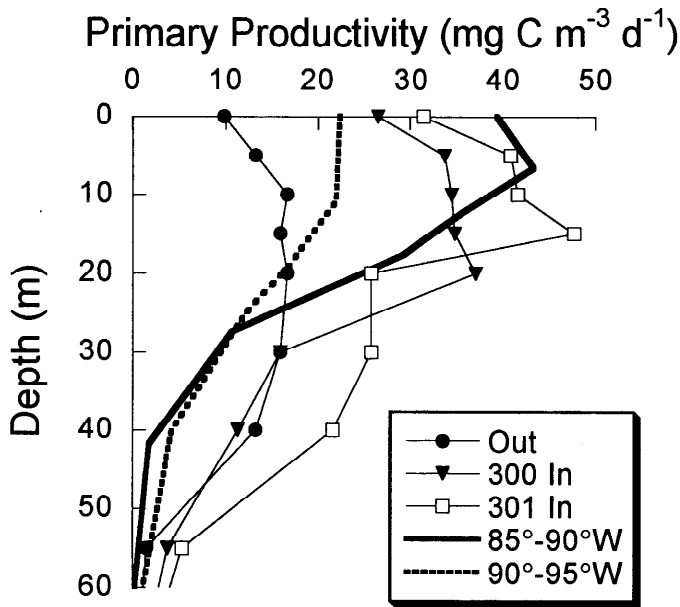


Fig. 1. Primary productivity at and near the site of the open-ocean enrichment experiment (near 5°S, 90°W). Profiles from out of the patch and in the patch 2 d (calendar day 300) and 3d (calendar day 301) after enrichment are from Martin et al. (1994). Profiles of historical averages east (4–6°S, 85–90°W; $n = 10$) and west of the site (4–6°S, 90–95°W; $n = 11$) are from R. Barber and F. Chavez as presented by Martin and Chisholm (1992). Error bars for the measurements during IronEx were presented by Martin et al. (1994) but not defined. For the average profiles, errors (presumed to be SE) were 16–22% ($\bar{x} = 18\%$) of the mean for 85–90°W and 7–22% ($\bar{x} = 13\%$) for 90–95°W.

mass and productivity of phytoplankton (Walsh 1976; de Baar et al. 1990; Frost 1991). Nonetheless, there is good reason to conclude that in HNLC waters grazing keeps phytoplankton standing crops at a lower level than would be attained had available iron been completely consumed. Specific growth rates of phytoplankton are relatively high (Banse 1991; Miller et al. 1991; Cullen et al. 1992a), standing crops are fairly constant (Frost 1991), and during incubation experiments (in which natural grazing is disrupted), unenriched phytoplankton in the controls grow to higher concentrations than are observed in the natural systems (Buma et al. 1991; Price et al. 1991; de Baar 1994). Why are biomass levels poised at those concentrations? With respect to iron hypotheses, we can ask, “If iron supplies are enhanced, and the specific growth rates of phytoplankton increase, will standing stocks increase to the extent that macronutrients are consumed, or will grazers keep phytoplankton biomass low?” For an open-ocean enrichment experiment, an appropriate grazing hypothesis would be that after enrichment with iron, the response of grazers would prevent the biomass of phytoplankton from increasing enough to deplete macronutrients. Given the evidence of significant increases in grazing pressure (discussed below), along with the minimal depletion of nutrients despite stimulated growth of phytoplankton, it would seem at face value that a principal

result of IronEx was validation of the grazing hypothesis! Of course, it's more complicated than that.

Results of IronEx compared to natural variability

The response of equatorial Pacific surface waters to added iron was evaluated principally by comparison to waters outside an enriched patch (Kolber et al. 1994; Martin et al. 1994; Watson et al. 1994). Measurements upstream and downstream of the Galapagos Islands provided an important adjunct: they described changes associated with a natural perturbation that included enrichment of surface waters with iron.

One could also evaluate the results of IronEx by relating the changes associated with iron enrichment to natural variability in the study region. For a first look, we can examine background data used in the planning of the enrichment experiment (Martin and Chisholm 1992). These data suggest that primary productivity east of the IronEx site is generally higher than to the west (Fig. 1) and that there can be substantial spatial variability in primary productivity. Temporal variability associated with El Niño Southern Oscillation is also expected (Barber et al. 1994).

It seems that the open-ocean enrichment was performed on a particularly impoverished parcel of water: near-surface productivity outside the iron-enriched patch was much lower than the historical averages (Fig. 1). Anomalous low productivity may be a clue as to why small phytoplankton seemed to be iron limited at the IronEx site (Kolber et al. 1994) but not during other studies in the equatorial Pacific (Price et al. 1991, 1994; Cullen et al. 1992a). When iron limitation was relieved by enrichment, productivity was elevated close to historical averages for the region (Fig. 1). Failure to achieve rates substantially higher than what occurs naturally makes it difficult to reject the hypothesis that something other than iron has a strong influence on rates of productivity in the region.

Patterns of P^B [productivity normalized to chlorophyll; $g\ C\ (g\ Chl)^{-1}\ d^{-1}$] prior to and during IronEx (Fig. 2) merit examination. Interpreting vertical patterns is complicated because near-surface rates can be severely underestimated when samples from mixed layers are incubated all day at surface irradiance (Marra 1978; Cullen and Lewis 1995), as was done during IronEx. The maximum P^B in the water column thus may be more appropriate than surface-layer averages for comparison between sites and times (cf. Smith et al. 1980; Murray et al. 1994). Maximum values suggest that during IronEx, P^B started out unusually low and was elevated by iron enrichment to the historical average for the region. The pattern is consistent with that for productivity but is not easily interpreted in terms of phytoplankton growth. Remember that specific growth rate ($\mu; d^{-1}$) = $P^B / C : Chl$, where $C : Chl$ is the ratio of cellular carbon to chlorophyll [$g\ C\ (g\ Chl)^{-1}$]. As pointed out by Martin et al. (1994), specific growth rates of phytoplankton accelerated in response to iron, but P^B did not change as much, because the ratio of $C : Chl$ decreased. Such

nutrition-related changes in C:Chl can completely eliminate any relationship between P^B and μ for phytoplankton in balanced growth (Sakshaug et al. 1989). Productivity normalized to chlorophyll is thus inappropriate as a general diagnostic of nutrient limitation (Cullen et al. 1992b; Falkowski et al. 1992).

IronEx showed that P^B was relatively insensitive to changes in iron nutrition because there were complementary changes of specific growth rate and C:Chl (see also Coale 1991). Changes of P^B independent of μ indicate that previous analyses of equatorial Pacific growth processes, in which P^B was considered proportional to growth rate (Barber and Chavez 1991; Murray et al. 1994), should be reconsidered. Short-term changes in P^B are reflected to some extent in growth rates, but relatively constant P^B in a region does not mean that growth rates are likewise constant (Cullen et al. 1992b). Thus, the relative uniformity of water-column P^B in the eastern equatorial Pacific Ocean (Barber and Chavez 1991) may mask considerable variability in the nutrient-limited growth rates of phytoplankton. It follows that future enrichment experiments may encounter fundamentally different populations than were enriched during IronEx; if responses of assemblages differ between experiments, it will be a challenge to determine the extent to which initial conditions vs. experimental differences influenced the results.

Interpreting IronEx in the context of iron hypotheses

The principal result of IronEx was exciting and unequivocal: a patch of water was enriched with iron and the phytoplankton responded with an increase in biomass and productivity. However, the bloom terminated quickly, macronutrients were hardly depleted, and CO_2 was only minimally drawn down (Watson et al. 1994). Why? Martin et al. (1994) presented a thoughtful discussion with reference to parallel studies in the Galapagos plume. Additional information and interpretations have been published by IronEx participants (Kolber et al. 1994; Van Scoy and Coale 1994; Watson et al. 1994), and Banse (1995) has elaborated the importance of zooplankton. Here, I offer another perspective, based only on information published to date.

As discussed by Martin et al. (1994), at least three hypotheses could explain why the response of phytoplankton to iron enrichment did not culminate in a larger bloom and depletion of macronutrients: another micronutrient ran short; iron was lost to the system; and grazing increased rapidly. Let us consider these explanations.

Depletion of a second micronutrient—Martin et al. (1994) discounted, but did not entirely exclude the possibility that a second micronutrient was depleted in the enriched patch. They argued that there were no significant depletions in dissolved Zn, Cu, Ni, Co, or Cd within the patch and that macronutrients are depleted (i.e. other trace elements do not become limiting) in trace-metal clean bottle incubations with additions of iron alone (e.g. Martin et al. 1991; Price et al. 1994). These are good arguments for an early stage of analysis. If possible, it

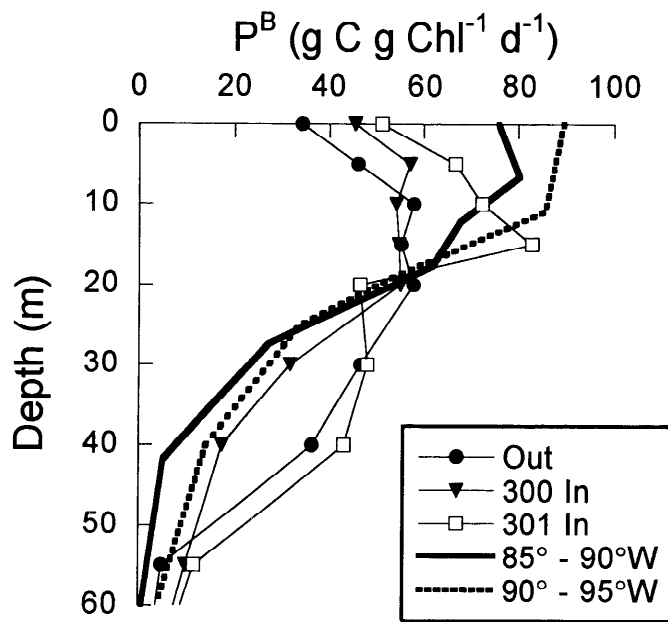


Fig. 2. Primary productivity normalized to chlorophyll *a* at and near the site of the open-ocean enrichment experiment. Locations, symbols, and sources as in Fig. 1. In the tables presented by Martin and Chisholm (1992), the depths and stations for average chlorophyll concentrations were not the same as for productivity, so estimates of P^B for 85–90°W and 90–95°W were obtained using depth-interpolated values of chlorophyll.

would be useful to determine the complexation of trace elements (Bruland et al. 1991) in and out of the patch. Also, as discussed above, it would be prudent to consider that results from experiments elsewhere in the equatorial Pacific might not apply to IronEx, and vice versa. For example, Wells et al. (1994) found contrasting responses to iron in two different assemblages from the equatorial Pacific. They interpreted one response as being consistent with depletion of a micronutrient other than iron. It seems reasonable that iron nutrition, and perhaps ratios of trace-element bioavailability, are variable in HNLC waters affected by aeolian input and variable influence of the equatorial undercurrent (see Martin 1992; Murray et al. 1994). At this time, we know very little about the patchiness of bioavailable micronutrients in HNLC waters (Donaghay et al. 1991). It is clear, however, that trace-element interactions can be quite complicated in the open ocean (Bruland et al. 1991).

Loss of iron from the system—A second explanation, much more consistent with the ideas of Martin and his colleagues, is that “iron was lost from the system due to colloidal aggregation and/or sinking of large particles containing iron” (Martin et al. 1994, p. 128). Martin et al. (1994) did not elaborate on how colloidal aggregation may have led to loss of iron from the system. The transformations and availability of iron are being actively studied (e.g. Hutchins et al. 1993; Johnson et al. 1994; Wells et al. 1994) though, and the complex interactions between competing processes will surely be addressed in the future.

Sinking of large particles was carefully considered by Martin et al. (1994). They pointed out that the sinking of large phytoplankton, specifically diatoms, can keep the population low, thereby limiting absolute rates of nutrient uptake by preventing the accumulation of photosynthetic biomass in the photic zone. This hypothesis, related to ideas presented by Chavez et al. (1991), bears careful examination because it may be key to the eventual explanation of ecosystem response to iron.

First, we should ask whether sinking of diatoms could be responsible for the rapid loss of iron from the system—a loss that may have prevented the complete utilization of macronutrients. Remember that the iron enrichment was more than adequate to support complete utilization of macronutrients if the system had responded like a bottle experiment (initial nitrate = $10.8 \mu\text{M}$, Fe on day 2 = 3.6 nM ; Martin et al. 1994; N : Fe of 5,000; Martin 1992). If diatoms took up most of the iron and sank from the system, they would have brought stoichiometric equivalents of macronutrients and carbon dioxide with them. However, only about $7 \mu\text{M CO}_2$ was utilized (Watson et al. 1994), hence $1 \mu\text{M}$ nitrate, so the N : Fe ratio of the sinking particles would have been 280, or a factor of 17 lower than expected. Perhaps large amounts of iron were adsorbed to sinking diatoms and other particles, such as fecal pellets. Regardless, it seems likely that other processes besides biological uptake and sinking were responsible for the rapid loss of iron from the IronEx system.

The sinking of diatoms may still be important in explaining the feeble utilization of macronutrients during IronEx. As pointed out by Martin et al. (1994), if sinking had kept the population of diatoms low, then absolute rates of macronutrient uptake would be less than if diatoms had accumulated. If the only losses of iron to the system had been associated with the sinking of biogenic particles (i.e. C, N, and P are exported with the sinking Fe), then at first order, sinking would influence the rate of macronutrient depletion, but not the amount of macronutrients consumed per unit of added iron. However, if iron were simultaneously being removed from the system in a competing process without concomitant removal of macronutrients, then sinking would definitely influence the stoichiometry between iron additions and the utilization of macronutrients and CO_2 . Much greater amounts of iron would be necessary to satisfy the HNLC-iron hypothesis, and processes that influence the net growth of phytoplankton assemblages (e.g. grazing, sinking, and light limitation associated with the observed subduction of the Fe-enriched patch) would have to be considered quantitatively in a robust analysis of results. It will be interesting to see how observations of large losses of iron from the IronEx system are reconciled with results indicating rapid and efficient recycling of iron in equatorial Pacific HNLC waters (Hutchins et al. 1993).

Grazing control—The HNLC-iron hypothesis and the ecumenical iron hypothesis would be falsified if grazers checked the net growth of phytoplankton, thereby preventing nutrient depletion in iron-enriched HNLC wa-

ters. Watson et al. (1994, p. 145), using the parlance of geochemists, suggested that this is exactly what happened during IronEx: “after a brief [period] of disequilibrium, the ecosystem responded by recycling carbon rapidly back to the inorganic form.” Calculations of grazing losses (Banse 1995) also support the hypothesis of grazing control. Although grazing was not quantified directly, there were indications that it increased in the patch. Not only did microheterotrophic biomass jump 50%, mesozooplankton biomass in the surface layer increased and vertically migrating zooplankton apparently remained in the patch during the day rather than descending as they normally do (Martin et al. 1994; Van Scoy and Coale 1994; see also Banse 1995).

As recognized by Donaghay et al. (1991), rapid responses of zooplankton to episodic nutrient enrichments may keep levels of phytoplankton biomass relatively low. Martin et al. (1994) accepted that increased grazing exerted some control on the IronEx bloom, but argued that grazing was not a likely mechanism for preventing depletion of major nutrients. Rather, retention of iron in the system was seen as the critical factor. Shallow waters near the Galapagos Islands were presented as an example of natural waters in which nitrate was depleted because iron was supplied continuously. The key assumption is that the potential for enhanced grazing is similar over the Galapagos platform as compared to the IronEx site. However, the relatively restricted, shallow and hydrographically complex region where nitrate depletion was observed (see Chavez and Brusca 1991) may not fully represent the open-ocean ecosystem that was experimentally enriched. For example, it is not clear that the increases of mesozooplankton biomass within the iron-enriched patch, apparently associated with altered vertical migration (anticipated by Donaghay et al. 1991 and reported by Van Scoy and Coale 1994), were or could be a feature of the nitrate-depleted, iron-rich waters of the Galapagos platform. No doubt, careful assessment of grazing will figure in future studies of iron enrichment. Grazing pressure can be measured by various means (see Murray et al. 1994), but it might be difficult to interpret the responses of zooplankton to a localized enrichment because the purported enhancement of grazing pressure by altered migration patterns should be a scale-dependent phenomenon.

Independent arguments have been presented to discount the role of grazing in limiting the IronEx bloom. Kolber et al. (1994) assessed the photosynthetic physiology of phytoplankton using sensitive fluorescence methods (Kolber and Falkowski 1993). The response within the patch was rapid, striking, and strongly consistent with expectations based on laboratory studies of phytoplankton relieved from iron starvation (Greene et al. 1992). The evidence for higher specific growth rates in the patch is convincing. The observed increase of biomass was not sustained for long, however, Kolber et al. (1994) noted that net growth may have halted not because of grazing, but because the specific growth rates of phytoplankton slowed, either due to limitation by another trace element

or because iron ran out. Measurements of photosynthetic energy conversion efficiency (F_V/F_M ; maximum value in the upper 30 m of the water column) increased sharply after iron enrichment, then declined after day 2, with a reported e -folding time of 6 d. However, during this same period, the iron-enriched patch was subducted to a depth of 30–35 m (Martin et al. 1994), so observations in the upper 30 m had shifting relevance. Also, two other measures related to iron limitation (τQ_A and σ_{PS2} ; see Kolber et al. 1994) showed little or no reversion to the pre-enriched state after day 2. More extensive analysis will be required to make a convincing refutation of grazing control.

The iron hypothesis reconsidered

The grazing issue may be clarified soon. For now, it seems that the insignificant consumption of macronutrients during IronEx, apparently associated with increased grazing and subduction of the Fe-enriched patch, is a strong indication that even though iron can stimulate growth of HNLC phytoplankton, grazing may prevent depletion of macronutrients or at least greatly retard the utilization of major nutrients during the long residence of HNLC waters near the surface (Minas et al. 1986; Fiedler et al. 1991). Such effective control of nutrient utilization by grazing, if demonstrated rigorously, would lead to rejection of the HNLC-iron hypothesis, but it would leave Martin's more general iron hypothesis intact.

Perhaps it is time to recast the iron hypothesis. The shift away from HNLC conditions toward the blooming of phytoplankton as the phenomenon to be explained by the iron hypothesis is reflected in a recent study by de Baar et al. (1995, p. 412), who framed the iron hypothesis as a "suggestion that iron is a limiting nutrient for plankton productivity and consequent CO_2 drawdown." They explored the role of iron in the Southern Ocean—another important HNLC region—where several factors, including light, are thought to influence primary production (Dugdale and Wilkerson 1990; Buma et al. 1991; Mitchell et al. 1991; Nelson and Smith 1991). By relating natural levels of chlorophyll, primary productivity, macronutrients, and CO_2 to distributions of iron in open-ocean Antarctic waters, de Baar et al. (1995) made a case for the regulation of diatom blooms by iron. They asserted that blooms can occur in the iron-rich jet of the polar front, but not in the iron-poor waters of the Antarctic circumpolar current. Their study of the polar jet and adjacent waters can be compared to the work in and near the Galapagos reported by the IronEx team. A difference is that the Antarctic waters are truly oceanic.

de Baar et al. (1995) made no claims that iron is solely responsible for high nutrient conditions in the Southern Ocean. Rather, they argued that iron is biogeochemically important because it permits significant drawdown of surface CO_2 in blooms. The blooms they discuss (Chl a concentrations of 2–3 mg m^{-3}) consumed only a small fraction of available nitrate, phosphate, and silicate. As

de Baar et al. (1995) acknowledged, other factors, such as vertical mixing and grazing, prevent complete utilization of nutrients (see also de Baar et al. 1990; Buma et al. 1991). A corollary is that iron is not predominately responsible for the HNLC condition in those waters (see Mitchell et al. 1991; Nelson and Smith 1991).

Regardless of unresolved issues, the results of IronEx and the study by de Baar et al. (1995) signal an important shift in the iron hypothesis. The HNLC-iron hypothesis has not been strongly supported nor has it been conclusively rejected. It seems that future studies will focus on the *degree* to which surface concentrations of macronutrients and CO_2 are depleted as a function of iron supply, without the need to demonstrate complete depletion of nutrients. Controls on the rate of macronutrient depletion (a community-level process; Banse 1995) and on the losses of iron from surface waters, as well as the residence time of surface waters (Minas et al. 1986), must be considered in order to explain the role of iron in HNLC waters. The work will be difficult and complicated but exciting, involving the collaboration of "clever biologists and skillful chemists" (Bruland et al. 1991, p. 1574). Open discussion and international, interdisciplinary collaboration will help in planning, implementation and interpretation of results.

Future directions

The role of iron in ocean biology has been studied for many years, but the most rapid progress, made possible by technological advance has occurred during the past decade, propelled by the efforts of Martin and his colleagues and strengthened by contributions from many other researchers. As judged by the course of events, the open discussion and vigorous debate at the ASLO special symposium facilitated this progress and paved the way toward IronEx, even though the experiment stayed true to the ideas of those who originally proposed the work (Watson et al. 1991; Martin 1992). There is clear justification for more open-ocean enrichment experiments. Likewise, there are good reasons to pursue thorough studies of natural enrichment, such as in the Galapagos plume and the Antarctic polar jet. Interpretations can be strengthened through the expression of numerous points of view.

It will be healthy for a broad spectrum of marine scientists to become involved in discussing published results and suggesting designs for future experiments. Here is a suggestion. Moor several barges in open, high-nutrient waters of the equatorial Pacific. Attach several thousand kilograms of metallic iron on each, engineered with plenty of surface area to encourage corrosion (rusting) at a predetermined, environmentally relevant rate. Incorporate an inert tracer, if possible (Watson et al. 1991). Treat the persistent enrichment site as an international scientific resource, and encourage as many groups as possible to study the chemical and ecological changes associated with the iron plume. Such an open research plan would encourage a broad diversity of approaches and interpreta-

tions, leading, one would hope, to rapid progress toward resolving a key issue in modern oceanography. The iron hypothesis might change in the process, but its central message, promoted so well by John Martin, is likely to survive.

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Acknowledgments

I thank the Office of Naval Research, NASA, and NSERC for support; K. Banse, R. F. Davis, H. de Baar, G. A. Jackson, M. E. Webb, and an anonymous reviewer for comments; S. W. Chisholm for a review; and D. Kirchman for editorial comments and the invitation to present these ideas. K. H. Coale's review contained many useful comments and suggestions, which are much appreciated. However, some differences of perspective or opinion remain. Certain ideas presented by reviewers and colleagues would have improved this commentary, but the ideas were based on data not yet published and are not presented here.

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