spatial distribution pattern and biomass estimate of the major demersal fishes in Lake Victoria. Afr. J. Trop. Hydrobiol. Fish. 3: 15–31.
MELACK, J. M., AND P. KILHAM. 1974. Photosynthetic rates of phytoplankton in East African alkaline, saline lakes. Limnol. Oceanogr. 19: 743–755.
MUGIDDE, R. 1993. Changes in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). Int. Ver. Theor. Angew. Limnol. Verh. 25: 846–849.
NEWELL, B. S. 1960. The hydrology of Lake Victoria. Hydrobiologia 15: 363–382.
OCHUMBA, P. B. O., AND D. I. KIBAARA. 1989. Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. Afr. J. Ecol. 27: 23–34.
OGUTU-OHWAYO, R. 1990. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of the introduced species, especially the Nile perch, *Lates niloticus,* and the Nile tilapia, *Oreochromis niloticus.* Environ. Biol. Fish. 27: 81–96.
OIJEN VAN, M. J. P., F. WITTE, AND E. L. M. WITTE-MAAS. 1981. An introduction to ecological and taxonomic investigations on the hapochromine cichlids from the Mwanza Gulf of Lake Victoria. Neth. J. Zool. 31: 149–174.
TALLING, J. F. 1957. Some observations on the stratification of Lake Victoria. Limnol. Oceanogr. 2: 213–221.
———. 1966. The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). Int. Rev. Gesamten Hydrobiol. 51: 545–621.
VOLLENWEIDER, R. A. 1976. Advances in defining critical loading levels of phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33: 53–83.
WITTE, F., AND OTHERS. 1992. The destruction of an endemic species flock: Qualitative data on the decline of the haplochromine cichlids of Lake Victoria. Environ. Biol. Fish. 34: 1–28.
WORTHINGTON, E. B. 1930. Observations on the temperature, hydrogen ion concentrations and other physical conditions of the Victoria and Albert Hyanzas. Int. Rev. Gesamten Hydrobiol. 25: 328–357.

Submitted: 2 September 1993
Accepted: 17 February 1994
Amended: 19 April 1994

Limnol. Oceanogr., 39(6), 1994, 1481–1486
© 1994, by the American Society of Limnology and Oceanography, Inc.

Iron limitation and the cyanobacterium *Synechococcus* in equatorial Pacific waters

Abstract—Iron enrichments in bottle experiments in high nutrient, low chlorophyll (HNLC) surface waters typically stimulate the net growth of nanophytoplankton (2.0–20 μm) but not picophytoplankton (<2.0 μm), suggesting either that picophytoplankton are not Fe limited or that any increased picophytoplankton growth is balanced by increased microzooplankton grazing rates. Using a novel approach in which we diminish iron availability in seawater with the fungal siderophore deferriferrioxamine B, we demonstrate that growth of the abundant picoplanktonic cyanobacterium *Synechococcus* is not strongly rate limited by Fe in the HNLC equatorial Pacific Ocean. However, experiments at the equator and 5°S show an unsuspected non-uniformity in iron nutrition within this HNLC region. Furthermore, our results indicate that a major portion of "dissolved" (<0.4 μm) iron in these waters is unavailable to *Synechococcus,* providing the first evidence that a significant fraction of dissolved iron occurs in forms other than the simple hydroxy species predicted by thermodynamic models. Deferriferrioxamine B affords a powerful new tool for probing the iron nutrition of marine phytoplankton and can provide unique insight into the role of iron in marine biogeochemical cycles.

Acknowledgments
We are grateful to J. Dusenberry, M. Duran, and S. Chisholm for providing cell counts by flow cytometry. We thank G. Smith and E. Rue for assisting in the collection of water samples and G. Smith for the iron determinations. We also express our appreciation to S. DiMaulo of CIBY-GEIGY for providing a sample of deferriferrioxamine B.

The difficulty in demonstrating iron limitation by measuring changes in phytoplankton abundance in iron-*enrichment* experiments stems from the complicating effects of grazing. Specific rates of picoplankton growth may increase, but net rates may remain unaltered because of compensatory increases in grazing rates by microzooplankton which cannot be excluded from samples. Recognizing this problem, we instead investigated picoplankton iron nutrition by *diminishing* iron availability in seawater samples containing natural populations. The fungal siderophore deferriferrioxamine B (DFB), a strong Fe-complexing agent (Hudson et al. 1992), was added to cultures to "titrate" ambient reactive Fe, making it less available to the biota for uptake. In this way, we turned the complicating effects of grazing pressure to our advantage by sensitizing the bioassay to

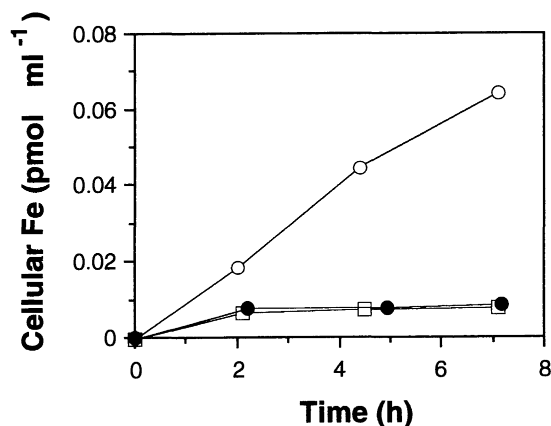

Fig. 1. Accumulation of cellular ^{59}Fe ml^{-1} of seawater over 7 h at the equator station. Unfiltered surface (15 m) seawater was added to 250-ml polycarbonate bottles and spiked with 2 nM ^{59}Fe (○), 2 nM ^{59}Fe premixed with 10 nM DFB (□), and 2 nM ^{59}Fe and 10 nM DFB separately (●). Duplicate samples were used for each time point. The apparent ^{59}Fe uptake in the DFB treatments during the first hour is likely due to the incomplete reduction (i.e. removal) of iron associated with detrital particles and plankton surfaces (R. J. M. Hudson pers. comm.). This interference is constant over the short incubation and does not affect calculations of uptake rates.

changes in iron stress; small increases in Fe limitation would lower picoplankton growth rates which, in turn, would be expressed quickly as a decrease in their abundance due to grazing.

Water was collected from 15-m depth at two stations in the Pacific equatorial upwelling zone (0°N, 140°W; 5°S, 138°W) with ultra-trace metal clean sampling methods (Teflon-lined 30-liter Go-Flo bottles on a Kevlar line) (Bruland et al. 1979; Martin and Gordon 1988). High nitrate (>4.5 μM) and nitrite (>0.1 μM) concentrations and low chlorophyll levels (0.2–0.3 μg liter^{-1}) confirmed that these stations were within the HNLC region. Fe concentrations in filtered samples (<0.4 μm) were ~25 pM Fe (2.5×10^{-11} M) at the equatorial station and 35 pM Fe at 5°S.

Subsamples were transferred immediately to 2-liter acid-washed polycarbonate bottles in a positive-pressure portable laboratory, and DFB was added to the treatments to final concentrations of 10 or 600 pM DFB. The bottles were triple-bagged in plastic and placed into an on-deck, flowing seawater incubator covered with a neutral density screen to attenuate light intensity to 50% that of ambient sunlight (Price et al. 1991). Cell numbers were measured each day by flow cytometry on subsamples drawn from one of the duplicate treatments; the other remained sealed until near the end of the bioassay. Random subsamples were also analyzed for Zn by anodic stripping voltametry (Bruland 1989) to monitor for Fe contamination (elevated Zn levels typically are indicative of Fe contamination—Martin et al. 1993); Zn concentrations remained at ambient seawater levels in all the bottles tested.

Short-term ^{59}Fe uptake experiments were conducted to confirm that the DFB-Fe complex was indeed unavailable to phytoplankton. Unfiltered surface (15 m) seawater was added to 250-ml polycarbonate bottles and spiked in duplicate with radiotracer to give a final concentration of 2 nM ^{59}Fe stock, 2 nM ^{59}Fe premixed with 10 nM DFB, or 2 nM ^{59}Fe and 10 nM DFB added separately. Samples were filtered gently (<7 mm of Hg) through 0.2-μm polycarbonate filters (Poretics) at different time intervals and the filters rinsed before drying with Ti(III) citrate EDTA reagent to reductively remove extracellular Fe (Hudson and Morel 1989). ^{59}Fe retained on the filters was detected by liquid scintillation counting. Radioactivity (cpm) was corrected for quenching and for radioactive decay. The net (maximum) uptake rate of ^{59}Fe was 9.2 pM Fe h^{-1} without DFB added, while little or no uptake occurred when DFB was present (Fig. 1). The latter was true whether DFB and ^{59}Fe were premixed or added separately. These results demonstrate that the DFB-Fe complex was unavailable to both phytoplankton and bacteria and that the complexation kinetics of Fe and DFB are rapid in seawater, going to completion within 3 min.

Deferriferrioxamine B is a hexadentate ligand with three hydroxamates and a terminal amine which is protonated. The thermodynamic stability constant between Y^{2-} and Fe^{3+} to form FeY^{+} is $10^{31.9}$ M^{-1}. Taking the ionic strength of seawater and the side reactions of both DFB and Fe(III) into account substantially lowers this thermodynamic constant to $\sim 10^{15}$ M^{-1}. Even so, this conditional constant is still high enough for added DFB to effectively complex any inorganic Fe species in these surface waters up to the concentration of added DFB.

Synechococcus sp. was abundant at both stations, with cell numbers of $\sim 1 \times 10^4$ cells ml^{-1}

(Fig. 2), and increased in the controls (no additions) at both stations despite observations of zero net growth of the picoplankton (cell division minus grazing) in this region (Cullen et al. 1992). Net *Synechococcus* growth was fastest in the equatorial control, where doubling rates were ~0.5 d^{-1} over the first 4 d of incubation. This net growth is very similar to that reported by Price et al. (1991) (0.64 doublings d^{-1}) and likely reflects major disruption of grazing in the bottles. The relatively rapid net growth of *Synechococcus* at this station demonstrates that *Synechococcus* growth was not strongly limited by Fe (or presumably by other metals). This finding is supported by separate, simultaneous experiments in which iron additions did not stimulate *Synechococcus* or any other picoplanktors (Price et al. 1994). Furthermore, in the DFB-amended samples, *Synechococcus* at least doubled in biomass and thus must have contained more than its minimum cellular Fe quota in situ (DFB prevented further iron uptake), suggesting that the seawater dissolved Fe was adequate for luxury consumption (sensu Droop 1974) by *Synechococcus* and was not strongly limiting its growth rate.

At the equator, addition of 10 or 600 pM DFB had no discernible effect on *Synechococcus* abundance during the first day of incubation. Subsequent cell densities in these treatments were significantly less than in the control and remained nearly constant, although the 10 pM DFB treatment had slightly higher cell densities than the 600 pM DFB treatment after 8 d (Fig. 2A). Thus, while initial growth *rates* of *Synechococcus* appeared to be relatively unaffected by the siderophore, cell *yields* were reduced significantly. Final cell yields in the 10 and 600 pM DFB treatments were 33 and 22% of the control. These reduced cell yields are unlikely to be due to greater grazing pressure in the treatments compared to controls. Because the fragile grazers tend to be disrupted during sample collection and dispersement, presumably because shear forces are higher than in situ conditions, a roughly uniform reduction of grazing pressure would be expected in the control and treatment bottles. The lower cell yields in DFB treatments at the equator were thus due mainly to a reduction in the specific growth rate of *Synechococcus*.

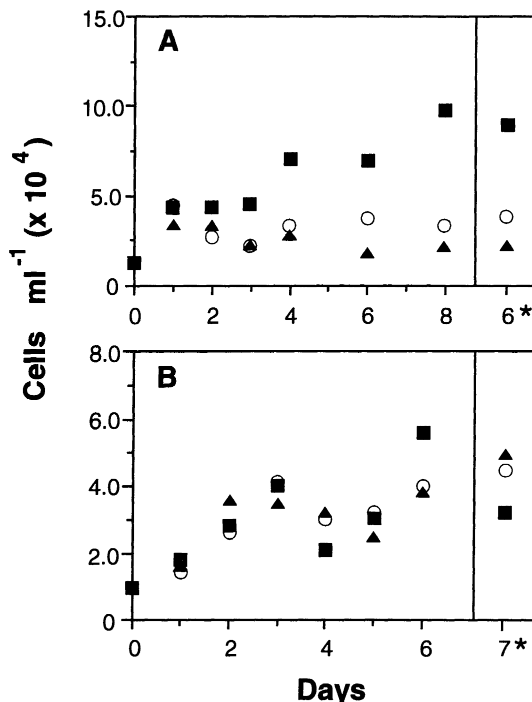

Fig. 2. Growth response of *Synechococcus* to additions of the iron chelator deferriferrioxamine B (DFB). A. 0°N, 140°W. B. 5°S, 138°W. DFB was added to give the following final concentrations: no DFB (control) (■), 10 pM DFB (○), and 600 pM DFB (▲). One of the duplicate treatments remained sealed until near the end of the bioassay (*).

By contrast, at 5°S where the dissolved Fe concentration was somewhat higher (~35 pM vs. ~25 pM Fe at the equator), DFB additions had no apparent effect on *Synechococcus* density or growth rates; cell numbers increased slowly in all treatments, even those with 600 pM DFB (Fig. 2B).

The abundance of other autotrophic picoplankton at the equator (*Prochlorococcus* and eucaryotic sp.) declined steadily in the controls and DFB treatments (data not shown), demonstrating that loss (grazing/death) exceeded production over the course of the bioassay. We calculate that the decrease of *Prochlorococcus* and eucaryotic populations over 6 d could have released up to ~16 pM Fe (cell decrease of 9×10^4 and 5×10^3 cells ml^{-1}; assumed Fe quota of 5.8×10^{-20} and 2.1×10^{-18} mol Fe $cell^{-1}$, Brand 1991), which may have helped fuel *Synechococcus* growth in the control. Certainly, the maximum ^{59}Fe uptake rate of 9.2 pM Fe h^{-1} (Fig. 1) supports arguments that

cellular iron can be recycled rapidly in low Fe regions (Hutchins et al. 1993; Price et al. 1991).

The siderophore-induced limitation of *Synechococcus* at the equatorial station illustrates three central points. First, while *Synechococcus* growth was not (strongly) limited by Fe in situ, conditions were very near Fe limitation; only 10 pM DFB in the presence of 25 pM dissolved Fe substantially curtailed cell yields. Second, the absence of net growth in DFB treatments after day 1 shows that the in situ cellular Fe reserves of *Synechococcus* were insufficient to sustain net growth. Third, the nearly identical (restricted) cell yields with 10 and 600 pM DFB additions (Fig. 2A) strongly suggest that less than half the dissolved Fe (i.e. 25 pM Fe in the <0.2-μm fraction) was biologically available; if >10 pM of Fe were available for uptake, then cell yields would have been substantially lower in the 600 pM DFB bottles.

Possible alternative explanations for the strong effect of 10 pM DFB on cell yields are that a significant proportion of dissolved Fe was adsorbed (removed) to bottle walls or that DFB addition decreased the soluble, reactive Fe concentrations to the point that the Fe uptake rate by *Synechococcus* became diffusion limited. Although we cannot entirely rule out wall adsorption effects, this explanation requires that the amount of iron adsorbed to the bottle walls coincidently matches the 10 pM DFB addition, because adding 600 pM DFB yielded the same result. Further, the increase in *Synechococcus* biomass in the equatorial control indicates that a large portion of the iron remained available in the bottle, ruling out a significant negative wall adsorption effect. Moreover, the wall surface area of the bottles was several orders of magnitude less than the surface area associated with small colloidal matter in these samples (*see below*), greatly reducing the likelihood that a significant fraction of the ambient seawater iron would become adsorbed to the bottle walls. Note that wall adsorption effects are of greater concern with iron addition experiments, in which the soluble Fe added may become associated with the bottle walls before it can equilibrate among natural iron species.

The cessation of growth in the DFB treatments is also not a consequence of diminishing dissolved Fe concentrations below the diffusion-limited barrier for iron uptake by *Synechococcus*. The non-DFB complexed Fe concentration of ~ 15 pM in the 10 pM DFB treatment is substantially above the diffusion-limited uptake concentration for this size cell, which we calculate conservatively as ≤ 1 pM (0.8-μm-diam cell; cell quota of 1.6×10^{-19} mol Fe $cell^{-1}$; max growth rate of 2 d^{-1}) (Hudson and Morel 1993). Differences between the control and DFB treatments in the equatorial bioassay thus reflect an inability of *Synechococcus* to access the ~ 15 pM of Fe not complexed by DFB.

Initial net growth of *Synechococcus* was nearly identical in control and treatment bottles at the equatorial station and was in reasonable agreement with estimated in situ absolute growth rates of phytoplankton in the equatorial Pacific (Cullen et al. 1992). However, while *Synechococcus* had enough iron before the incubation to support a short (1 d) burst of growth, further iron uptake was needed to fuel substantial increases in cell abundance. We suggest that the reduced cell yields in DFB treatments were not caused by iron limiting cell *rate* processes. Based on the minimum Fe quota of a Pacific Ocean isolate of *Synechococcus* (clone A2169: 1.6×10^{-19} mol Fe $cell^{-1}$) (Brand 1991), we calculate that the amount of iron contained in *Synechococcus* biomass ranged from ~ 3 to 15 pM during the incubations. This quantity is significant compared to dissolved Fe (~ 25 pM) in this region and represents $\sim 30\%$ to $>100\%$ of the apparent 10 pM of biologically available iron indicated by DFB addition. Thus, modest net growth of *Synechococcus* alone would consume the major proportion of the available iron, which underscores the high biological demand for iron in this region. Picophytoplankton biomass simply cannot increase significantly in this region without increased iron input.

In contrast, the initial net growth rate of *Synechococcus* in the control at 5°S was half that at the equatorial station, and DFB did not measurably affect growth *rates* or cell *yields* (Fig. 2B). The most straightforward interpretation of this result is that iron was not limiting in situ; i.e. the preincubation cellular Fe content had built up to a sufficient level to entirely support the growth measured during the bioassay. This "luxury" Fe uptake scenario is

plausible given the slightly higher dissolved Fe concentration at 5°S (35 vs. 25 pM Fe). Our data provide no evidence for the underlying cause of slower net growth rates of *Synechococcus* at 5°S, but we speculate that limitation by one or more other trace elements may be partially responsible. Although it is possible that grazing was disrupted to a smaller degree at 5°S than at the equator, this explanation seems unlikely, given that sample-handling procedures were identical at both stations. In any event, differences in the response of *Synechococcus* to DFB additions at the equator and 5°S provide the first evidence of a nonuniform degree of Fe stress within the equatorial Pacific HNLC region. Identifying the magnitude and spatial scales of this variability remains an important issue.

Our findings have significance in the broader context of biogeochemical cycling. *Synechococcus* is first among the picoplankton to respond to NO_3^- inputs (Glover et al. 1988), which is an index of new (and export) production (most picoplankton use recycled NH_4^+). Fe is essential for NO_3^- assimilation, and generous Fe enrichment of HNLC seawater stimulates new production by causing a transformation to a nanoplankton-dominated (mainly NO_3^- utilizing) algal assemblage (Price et al. 1991). The findings here suggest that smaller aeolian iron inputs, too scant to induce such a major shift in phytoplankton assemblage, may nonetheless stimulate new production by enhancing *Synechococcus* growth.

Results from the equatorial bioassay also provide important insight into iron speciation in seawater. Fe concentrations in these waters are substantially below the solubility of amorphous ferric oxyhydroxides, and current thermodynamic models predict that under these conditions, iron exists as inorganically complexed hydroxy species (Byrne and Kester 1976; Kuma et al. 1992; Morel 1983; Motekaitis and Martell 1987)—forms which are readily available for uptake by phytoplankton (Hudson and Morel 1990) or complexation by DFB. However, the inability of *Synechococcus* to access the ~15 pM "free" Fe in the 10 pM DFB equatorial treatment is evidence that a major proportion of the dissolved Fe exists in other chemical forms. These forms may include soluble complexes with organic ligands, such as siderophores, which are known to be produced by some oceanic bacteria (Reid and Butler 1991; Trick 1989).

The equatorial DFB treatments provide indirect evidence that organic-iron complexes indeed exist in these waters. Cell yields in these treatments remained constant (Fig. 2A) despite the expectation that some grazing occurred, particularly near the end of the bioassay, when protozoan populations likely had recovered. Fe released to solution through grazing in the form of simple hydroxyspecies would be bound rapidly by DFB (Fig. 1), leading to a continual decrease in biologically utilizable iron and thus a reduction in cell yield. But cell yields remained constant, indicating that most of the released Fe did not bind rapidly with DFB but instead was recycled back to *Synechococcus* to fuel the continued growth needed to maintain the cell population constant. Such iron recycling might be facilitated by the release of Fe-containing enzymes and storage products occurring in the cytosol of phytoplankton by the sloppy feeding of grazers.

Colloidal complexes of Fe are also likely to be an important Fe phase within the <0.4-μm fraction. Small colloids (<0.2 μm), largely organic in nature, are extremely abundant in these waters (~2×10^9 ml^{-1}) and represent an immense surface area (~12 m^2 m^{-3} of seawater) for interaction with soluble Fe (data not shown). Iron complexed to these colloids could be thermodynamically or kinetically hindered from exchanging with or buffering the soluble Fe forms sequestered by algae. The direct source of these colloids is unknown, although they may arise from phytoplankton or bacteria or possibly result from protozoan feeding (Koike et al. 1989; Wells and Goldberg 1994).

The novel approach used here offers a valuable new addition to the methodological quiver from which marine scientists draw to study the role of iron in marine systems. We have demonstrated that the fungal siderophore deferriferrioxamine B has extremely rapid complexation kinetics with iron in seawater (a medium foreign to the terrestrial fungi which produce DFB) and that the resultant DFB-Fe complex is unavailable for uptake by either marine phytoplankton or bacteria. Thus, it is now feasible to experimentally determine how planktonic communities respond to both increased and decreased iron inputs. DFB is a

unique tool for probing the nature of dissolved Fe speciation and the potential role of organic chelators and colloids—factors which remain the principle challenges to understanding the biogeochemical cycle of iron in the sea.

Mark L. Wells

Institute of Marine Sciences
University of California, Santa Cruz
Santa Cruz 95064

Neil M. Price

Department of Biology
McGill University
Montreal, Quebec H3A 1B1

Kenneth W. Bruland

Institute of Marine Sciences
University of California, Santa Cruz

References

BRAND, L. E. 1991. Minimum iron requirements of marine phytoplankton and the implications for the biogeochemical control of new production. Limnol. Oceanogr. **36:** 1756–1771.

BRULAND, K. W. 1989. Complexation of zinc by natural organic ligands in the central North Pacific. Limnol. Oceanogr. **34:** 267–283.

———, R. P. FRANKS, G. KNAUER, AND J. H. MARTIN. 1979. Sampling and analytical methods for the determination of copper, cadmium, zinc, and nickel in seawater. Anal. Chim. Acta **105:** 233–245.

BYRNE, R. H. AND D. R. KESTER. 1976. Solubility of hydrous ferric oxide and iron speciation in seawater. Mar. Chem. **4:** 255–274.

CULLEN, J. J., M. R. LEWIS, C. O. DAVIS, AND R. T. BARBER. 1992. Photosynthetic characteristics and estimated growth rates indicate grazing is the proximate control of primary production in the equatorial Pacific. J. Geophys. Res. **97:** 639–655.

DROOP, M. R. 1974. The nutrient status of algal cells in continuous culture. J. Mar. Biol. Assoc. U.K. **54:** 825–855.

GLOVER, H. E., B. B. PRÉZELIN, L. CAMPBELL, M. WYMAN AND C. GARSIDE. 1988. A nitrate-dependent *Synechococcus* bloom in surface Sargasso Sea water. Nature **331:** 161–163.

HUDSON, R. J. M., D. T. COVAULT, AND F. M. M. MOREL. 1992. Investigations of iron coordination and redox reactions in seawater using ^{59}Fe radiometry and ion-pair solvent extraction of amphiphilic iron complexes. Mar. Chem. **38:** 209–235.

———, AND F. M. M. MOREL. 1989. Distinguishing between extra- and intracellular iron uptake in marine phytoplankton. Limnol. Oceanogr. **34:** 1113–1120.

———, AND ———. 1990. Iron transport in marine phytoplankton: Kinetics of cellular and medium coordination reactions. Limnol. Oceanogr. **35:** 1002–1020.

———, AND ———. 1993. Trace metal transport by marine microorganisms: implications of metal coordination kinetics. Deep-Sea Res. 40: 129–150.

HUTCHINS, D. A., G. R. DITULLIO, AND K. W. BRULAND. 1993. Iron and regenerated production—Evidence for biological iron recycling in two marine environments. Limnol. Oceanogr. **38:** 1242–1255.

KOIKE, I. S., S. HARA, K. TERAUCHI, AND K. KOGUE. 1989. Role of sub-micron particles in the ocean. Nature **345:** 242–244.

KUMA, K., S. NAKABAYASHI, Y. SUZUKI, AND K. MATSUNAGA. 1992. Dissolution rate and solubility of colloidal hydrous ferric oxide in seawater. Mar. Chem. **38:** 113–143.

MARTIN, J. H., S. E. FITZWATER, R. M. GORDON, C. N. HUNTER, AND S. J. TANNER. 1993. Iron, primary production and carbon-nitrogen flux studies during the JGOFS North Atlantic Bloom Experiment. Deep-Sea Res. **40:** 115–134.

———, AND R. M. GORDON. 1988. Northeast Pacific iron distributions in relation to phytoplankton productivity. Deep-Sea Res. **35:** 177–196.

MOREL, F. M. M. 1983. Principles of aquatic chemistry, 1st ed. Wiley-Interscience.

MOTEKAITIS, R. J., AND A. E. MARTELL. 1987. Speciation of metals in the ocean. 1. Inorganic complexes in seawater, and influence of added chelating agents. Mar. Chem. **21:** 101–116.

PRICE, J. M., L. F. ANDERSON, AND F. M. M. MOREL. 1991. Iron and nitrogen nutrition of equatorial Pacific plankton. Deep-Sea Res. **38:** 1361–1378.

PRICE, N. M., B. A. AHNER, AND F. M. M. MOREL. 1994. The equatorial Pacific Ocean: Grazer-controlled phytoplankton populations in an iron-limited ecosystem. Limnol. Oceanogr. **39:** 520–534.

REID, R. T., AND A. BUTLER. 1991. Investigation of the mechanism of iron acquisition by the marine bacterium *Alteromonas luteoviolaceus*: Characterization of siderophore production. Limnol. Oceanogr. **36:** 1783–1792.

TRICK, C. G. 1989. Hydroxamate-siderophore production and utilization by marine eubacteria. Curr. Microbiol. **18:** 375–378.

WELLS, M. L., AND E. D. GOLDBERG. 1994. The distribution of colloids in the North Atlantic and Southern Oceans. Limnol. Oceanogr. **39:** 286–302.

Submitted: 23 September 1993
Accepted: 23 March 1994
Amended: 19 April 1994