Iron limitation?

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The case for iron

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Abstract

Excess major nutrients occur in offshore areas ranging from the tropical equatorial Pacific to the polar Antarctic. In spite of the great ecological differences in these environments, we believe they share a common trait: iron deficiency. Here we present the case for iron; we point out that all of these areas are far from Fe-rich terrestrial sources and that atmospheric dust loads in these regions are amongst the lowest in the world. We summarize experiments performed in three nutrient-rich areas: The Gulf of Alaska, the Ross Sea, and the equatorial Pacific. In general, populations without added Fe doubled at rates 11–40% of the expected maxima at various temperatures. The addition of nanomole quantities of Fe increased these doubling rates by factors of 2–3.

In spite of the lack of Fe, tightly coupled phytoplankton/zooplankton communities seem to inhabit these major nutrient-rich areas. Since Fe is required for the synthesis of chlorophyll and nitrate reductase, little chlorophyll is found and NH_3 is the favored N source. Normal rate values of specific productivity indicate that these populations are healthy, but limited by the insufficient Fe supply. When Fe becomes available either artificially in bottle experiments or in the environment as Fe-rich land masses are approached, diatoms quickly bloom, chlorophyll levels increase, and nutrient stocks are rapidly depleted. These combined results indicate that Fe availability is the primary factor controlling phytoplankton production in nutrient-rich areas of the open sea.

We believe that phytoplankton growth in major nutrient-rich waters is limited by iron deficiency. This belief is based on the following facts.

Iron is essential for all life (Weinberg 1989). Because of its insolubility in oxygenated seawater (Moffett and Zika 1987; Millero and Sotolongo 1989), concentrations are very low in regions far removed from Fe-rich continental margins (i.e. <1 nmol kg^{-1}; Martin et al. 1989). In spite of these low concentrations, the Fe needs of open-ocean phytoplankton can usually be met via the fallout of Fe-rich atmospheric dust (Duce 1986; Martin and Gordon 1988). Fe demand is elevated in open-ocean upwelling areas that are rich in major nutrients; hence, it is logical to suspect deficiency because these regions are far removed from terrestrial Fe sources (Uematsu et al. 1983).

We have performed research in three upwelling areas of the open ocean where atmospheric dust-Fe input rates are known to be low (i.e. the northeast Pacific subarctic, the equatorial Pacific, and the Southern Ocean; *see* Duce and Tindale 1991). In these regions we seek proof of limited Fe availability by measuring dissolved and particulate Fe concentrations in the water column and by performing bioassay experiments in which we take water with resident phytoplankton populations and observe rates with and without added Fe. If rates of major nutrient uptake and chlorophyll, POC, and PON synthesis are similar with and without added Fe, we assume that environmental Fe amounts are sufficient. If little growth occurs in the controls and if addition of minute quantities of Fe results in enhanced growth we assume that ambient concentrations are not large enough to meet phytoplankton Fe requirements for chlorophyll

Acknowledgments

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and nitrate reductase synthesis. Relatively large amounts of these compounds must be available for the phytoplankton to bloom and use up the supplies of available major nutrients. Here we present the case for Fe using results we obtained in recent studies in the Ross Sea and the equatorial Pacific.

Methods

Avoiding spurious Fe contamination is very difficult and extreme precautions must be taken to prevent accidental addition of the ~0.5 nmol of Fe that will enable Fe-limited phytoplankton to grow. Our basic methods were published elsewhere (e.g. Martin et al. 1989) and will not be repeated here. Nevertheless, to give the reader a feel for some of the procedures necessary for Fe work we describe our polycarbonate culture bottle cleaning processes in detail.

New 2-liter polycarbonate bottles are soaked in "micro" detergent bath for a week to remove any dirt, oil, or organic catalyst used in the manufacturing process. Next they are rinsed three times in deionized (DI) water, then filled completely with DI and soaked for 2–3 d, emptied and rinsed two more times with DI followed by one rinse with milli-Q water. Bottles are then soaked in 10% quadruple quartz-distilled (subboiling) HCl for 3 d (it takes four distillations to remove the Fe from HCl). After rinsing with milli-Q the bottles are filled and soaked in milli-Q for 1–3 d. The bottles are drained and dried in a laminar flow hood and triple plastic bagged for transport to the field. Before filling at sea, bottles are rinsed three times with 200 ml of seawater sample. This procedure is carried out in a clean-air van. Plastic gloves are worn for these operations. Bottles are capped and sealed in three plastic bags before placement in the on-deck incubator. The incubator water level is kept below the shoulder of the bottle. This, plus triple bags, ensures that no "high Fe" flow-through cooling water is allowed to contaminate samples. During subsampling procedures, performed in the filtered, clean-air van, 100–200-ml subsamples are poured into bottles without touching the lip of culture bottle to anything. The culture bottles are recapped, put back in three plastic bags, and returned to the incubator.

During the equatorial Pacific study, seawater was collected from depths of 20, 40, 60, and 80 m on the equator at 140°W in June–July 1990. Aliquots of the water with its resident phytoplankton were placed in 2-liter polycarbonate bottles to which either 1 nmol of unchelated Fe, or 1 nmol of a hexanuclear Fe(III)-sorbitol species $[Fe_6(OH)_{12}Sorb_6]^{6-}$ (provided by N. M. Price and F. M. M. Morel), or 1–2 nmol atmospheric-dust-leachate Fe liter^{-1} were added. The latter was obtained from the partial dissolution of an atmospheric dust sample that had been collected at the University of Rhode Island air-sampling tower at Oahu, Hawaii, during a period of high concentrations of atmospheric dust. The dust was collected by sucking air through a precleaned Whatman 41 cellulose filter. A portion of this filter was leached for an hour with seawater collected during the cruise at 60-m depth. The leachate was filtered through a 0.4-μm Nuclepore filter and diluted before adding it to the experimental bottles. Identical replicates with nothing added serves as controls.

Results

The equatorial Pacific—As in previous enrichment experiments (Martin et al. 1989, 1990*a*), we monitored chlorophyll increases and nutrient decreases every day or every other day. In comparison to the controls, greater Chl increases and NO_3 decreases were always found with the addition of various types of Fe. Nevertheless, there was variability in some POC and PON concentrations measured at the ends of the experiments in relation to various Fe sources. This variability was especially pronounced at 60 m where 2–3 times more POC was found with use of aerosol Fe as with other Fe sources (Fig. 1).

The apparent reason for these differences was determined when the experiment particulates were analyzed for Fe. While the controls had $\leq$0.25 nmol Fe liter^{-1}, and the bottles with chelated and unchelated Fe had between 0.30 and 0.92 nmol liter^{-1}, the bottles with aerosol leachate had 1.27–1.63 nmol Fe liter^{-1} in particulates at the end of the experiment (Fig. 1; Table 1). Obviously

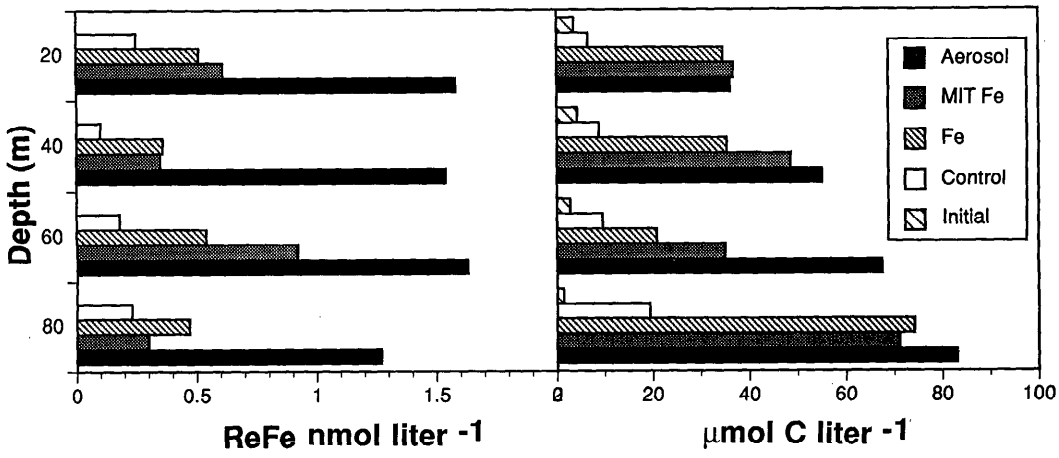

Fig. 1. Particulate refractory Fe and POC concentrations measured at the end of the equatorial Pacific enrichment experiments. Aerosol: >1 nmol Fe liter^{-1} added in form of aerosol leachate (*see text*); MIT Fe: 1 nmol chelated Fe liter^{-1} (N. M. Price and F. M. M. Morel); Fe: 1 nmol of $FeNO_3$ liter^{-1}. Water was collected from depths indicated; all incubations were at the same light intensity and temperature in on-deck incubators.

our estimates of the amounts of aerosol Fe we were using were in error; we were adding more than the 1 nmol of leachate Fe we thought we were.

It may have been fortuitous because apparently the addition of only 1 nmol Fe was insufficient, at least in the 40- and 60-m experiments. Only about a quarter of the added Fe ended up with the phytoplankton. The proportions of the 75% remaining in solution vs. that adsorbed on the walls will be estimated in future analyses. Since it appeared that adding 1 nmol of Fe was not enough to completely reverse deficiency in the 40- and, especially, 60-m experiments, we decided to rely primarily on the aerosol results. Obviously, the amounts of added Fe were sufficient and this source is the closest to that occurring in the environment.

Comparisons of Chl and NO_3 concentrations vs. time for the four experiments with and without added aerosol Fe showed marked differences; Chl levels were generally an order of magnitude higher with Fe than without, and with Fe, NO_3 stocks were rapidly depleted in comparisons to the controls where relatively small amounts of NO_3 were removed (Table 1).

The effects of added Fe were also evident in the PON and especially POC data (Table 1). Not only was more PON produced with Fe but the amounts of C per unit N were also larger. This effect is shown in the regressions for POC found vs. NO_3 removed for controls and added aerosol Fe (Fig. 2); C : N ratios were almost twice as high with Fe, and C : P ratios (Table 1) were three times higher. These findings thus suggest that more C fixation per unit of major nutrients may occur when Fe is abundant. Of the species we examined via SEM, the one that benefited most from additional Fe was a small penate diatom, *Nitzschia* sp. (Fig. 3). It is probably the same species mentioned by Chavez et al. (1990).

Although we feel that these results demonstrate the powerful effects of minute Fe additions, others contend (Banse 1990) that the only way to demonstrate real differences is to compare specific growth rates and resulting doubling rates. These results are presented below, together with those from the Antarctic.

The Antarctic—Initial results obtained at four stations in the Ross Sea have been described elsewhere (Martin et al. 1990*a*); here we concentrate only on the two extremes: the nearshore Sta. 1 with local Fe sources and the offshore, deep-water (3,200 m) Sta. 4. Station 1 was in pack ice near McMurdo Sound. Because of meltwater low salinities, the water was fairly stable and large standing crops of POC were found (Fig. 4). Because of the high particle load, light intensity di-

Table 1. Amounts of particulate Fe (nmol liter^{-1}) and POC and PON (μmol liter^{-1}) found at the end of equatorial Pacific (0°, 140°W) Fe enrichment experiments. NO_3 and PO_4 taken up (used) and various ratios are also shown.

Treatment*	Fe	POC	PON	NO_3 used	POC:PON	PO_4 used	NO_3:PO_4	POC:PO_4
20 m								
I	—	3.62	0.70	—	5.17	—	—	—
0Fe	0.25	6.52	1.40	1.2	4.66	0.13	9.2	50.2
1Fe	0.51	34.59	4.04	4.6	8.56	0.29	15.9	119.3
MFe	0.61	36.78	4.25	4.6	8.65	0.29	15.9	126.8
AFe	1.58	36.07	4.72	4.6	7.64	0.29	15.9	124.4
40 m								
I	—	4.29	0.74	—	5.80	—	—	—
0Fe	<0.1	8.77	2.04	2.2	4.30	0.23	9.6	38.1
1Fe	0.36	35.37	5.36	6.4	6.60	0.42	15.2	84.2
MFe	0.35	48.56	5.44	6.4	8.93	0.42	15.2	115.6
AFe	1.54	55.08	7.12	6.4	7.74	0.42	15.2	131.1
60 m								
I	—	2.76	0.50	—	5.52	—	—	—
0Fe	0.18	9.54	2.12	2.1	4.50	0.20	10.5	47.7
1Fe	0.54	20.83	4.05	5.3	5.14	0.40	13.2	52.1
MFe	0.92	35.02	6.14	8.4	5.70	0.52	16.2	67.3
AFe	1.63	67.52	8.56	8.4	7.89	0.52	16.2	129.8
80 m								
I	—	1.34	0.26	—	5.15	—	—	—
0Fe	0.23	19.36	3.64	5.3	5.32	0.57	9.3	34.0
1Fe	0.47	74.18	8.34	10.1	8.89	0.62	16.3	119.6
MFe	0.30	71.08	7.92	10.1	8.98	0.62	16.3	114.6
AFe	1.27	83.08	8.38	10.1	9.91	0.62	16.3	134.0

* I—initial value (20-, 40-, 60-, 80-m initial concentrations were 4.6, 6.4, 8.4, and 10.4 μmol liter^{-1} for NO_3 and 0.29, 0.42, 0.52, and 0.62 μmol liter^{-1} for PO_4); 0Fe—control with nothing added; 1Fe—1 nmol Fe liter^{-1} added (MLML); MFe—MIT Fe compound, ~1 nmol Fe liter^{-1}; AFe—aerosol leachate Fe (URI), ~1.5 nmol Fe liter^{-1}.

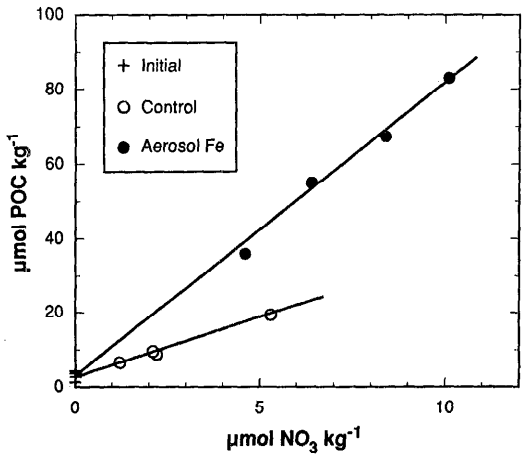

Fig. 2. POC found vs. NO_3 removed in controls and aerosol-Fe-added equatorial Pacific experiments (data from Table 1). Regression for controls and initials: POC = 2.90 + 3.05 (NO_3 removed); n = 8, r = 0.988. Regression for aerosols and initials: POC = 2.76 + 7.86 (NO_3 removed); n = 8, r = 0.999.

minished rapidly with depth (1% light level—15 m). In addition to high POC concentrations, depletion of major nutrients also pointed to good growth conditions (e.g. surface NO_3 = 1–5 μmol liter^{-1} at or near Sta. 1).

As observed in previous Antarctic studies (Martin et al. 1990*b*), shallow, nearshore waters and ice (depending on history of formation) can be rich sources of Fe. Thus it was not surprising that particulate Fe levels at Sta. 1 were high (Fig. 4). And in accordance with our hypothesis, the addition of 5 nmol Fe kg^{-1} had little effect on NO_3 uptake (3.11 vs. 2.54 μmol NO_3 kg^{-1} d^{-1}, with and without Fe) and Chl synthesis (*see* figure 2 of Martin et al. 1990*a*). Clearly, Fe amounts seem to be adequate in this nearshore environment. Growth is probably limited by low light intensities resulting from self-shading of the phytoplankton-rich surface waters.

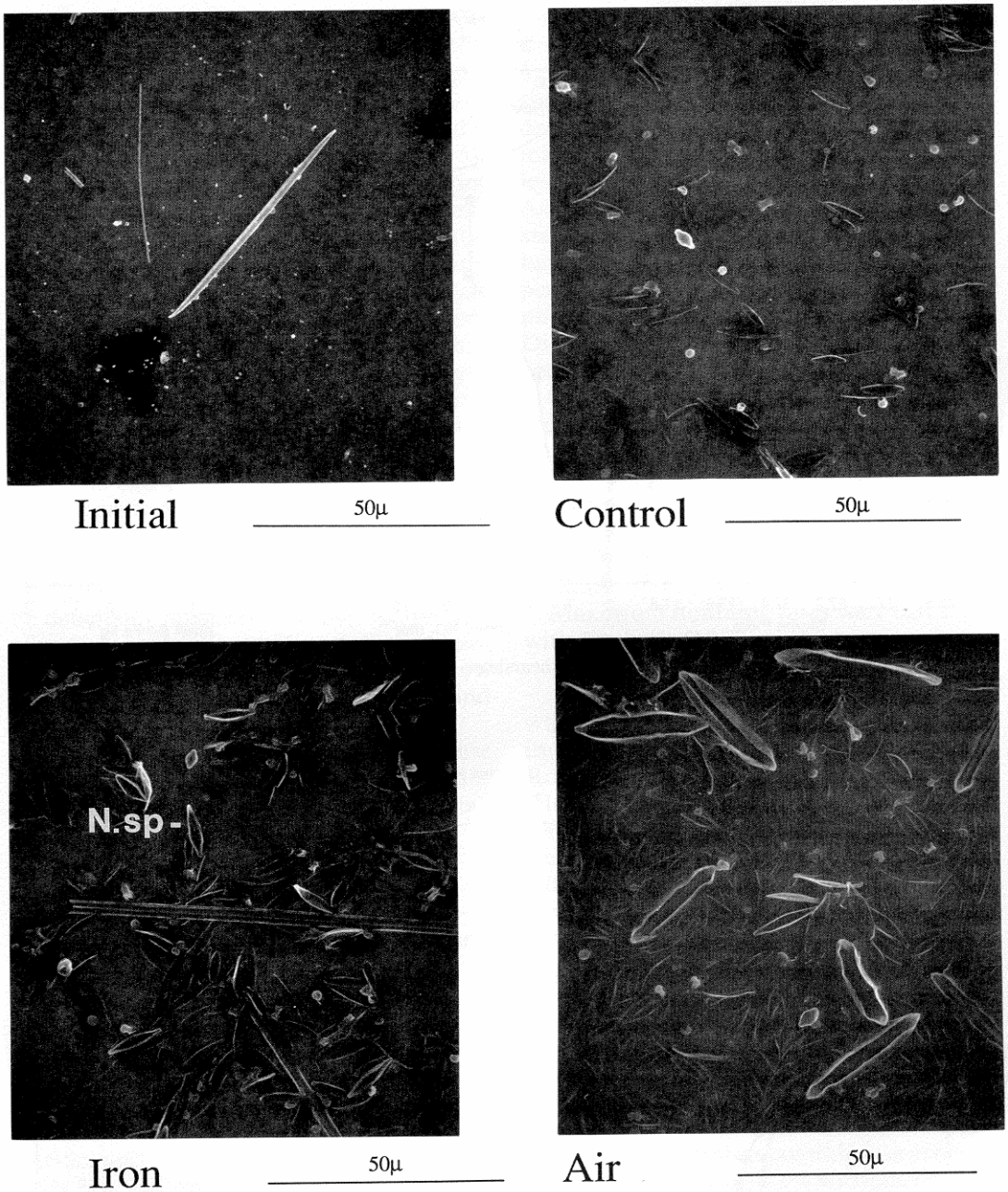

Fig. 3. Scanning electron microscope photographs of phytoplankton in equatorial Pacific enrichment experiments; water from 60 m. N. sp—*Nitzschia* sp.; air—aerosol-Fe added.

Station 4 is in deep water (3,200 m), ~500 km east of Cape Adare and 650 km north of the Ross Ice Shelf, i.e. far from shallow-bottom Fe sources (Fig. 5). Although the waters were ice-free on the day we sampled, ice was reported in the area ~3–4 d before (D. M. Nelson pers. comm.). This ice was evidenced by lower salinities that resulted in water column stability second only to that at Sta. 1 (*see Fig. 4*). Light levels were also

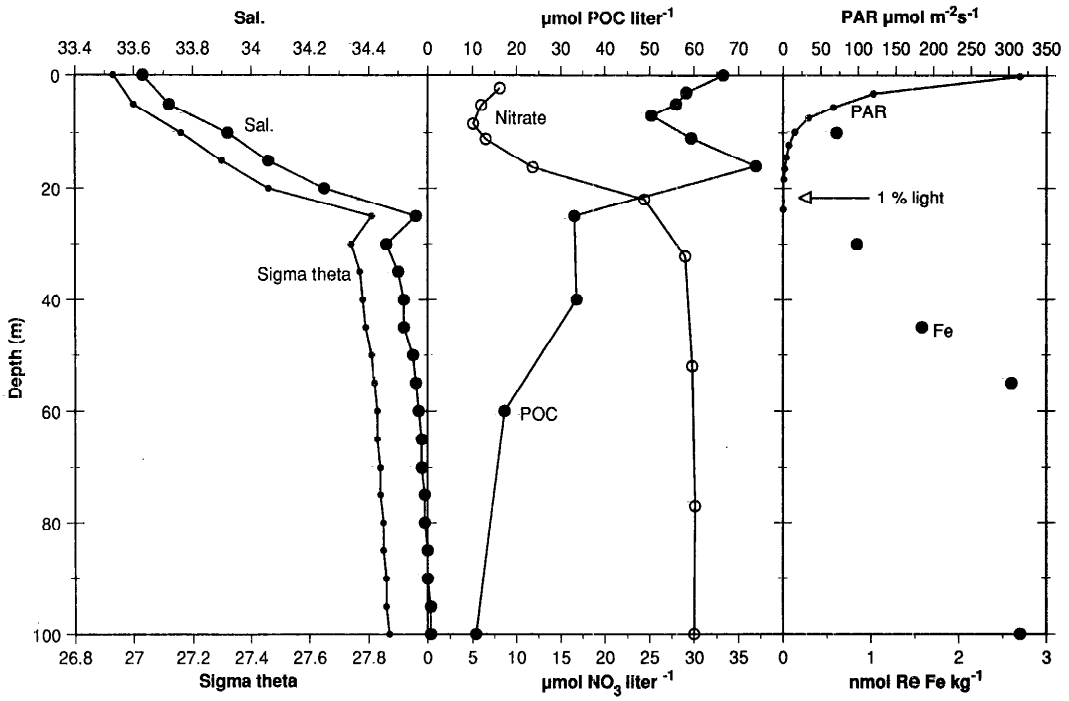

Fig. 4. Data from Ross Sea water column for nearshore (76°33′S, 167°37.5′E) Sta. 1 sampled 13 January 1990.

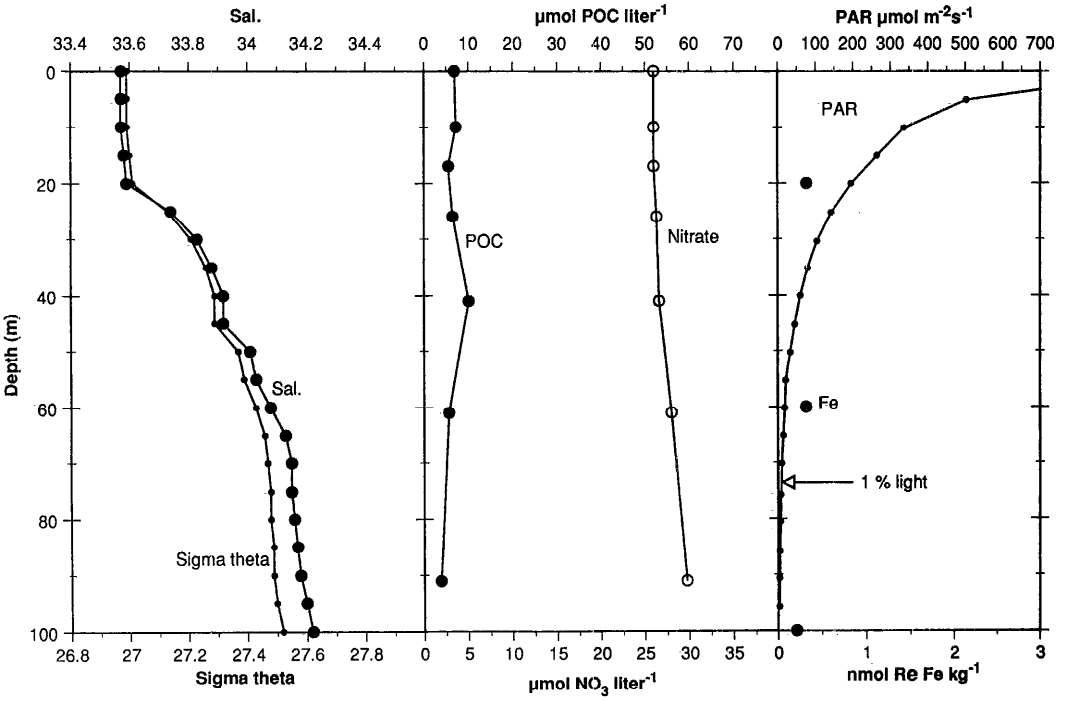

Fig. 5. As Fig. 4, but for offshore (72°30′S, 173°59.7′W) Sta. 4 sampled 26 January 1990.

high; i.e. the 1% light level (75 m) was 60 m deeper than at St. 1. Nevertheless, in spite of the stable water column and high light levels, Chl and POC concentrations were both relatively low and little, if any, of the major nutrients had been removed (Fig. 5).

In view of the offshore location it was not surprising that particulate Fe concentrations were very low (Fig. 5), and apparently little Fe had been released from the recently melted ice. Evidence of Fe deficiency was also found in the enrichment experiment performed here. Without added Fe, the phytoplankton were removing only 0.58 and 0.57 μmol NO_3 kg^{-1} d^{-1} in the control and Mn-added bottles. With Fe, NO_3 uptake rates were an order of magnitude higher toward the end of the experiment (*see* figure 2 of Martin et al. 1990*a*). All in all, the combined Fe distribution and experimental evidence indicate classic Fe deficiency. We also point out that in all likelihood similar Fe deficiency must exist for the ~2,400 km of ocean equatorward of Sta. 4; Fe does not become abundant again until the shallow shelf waters of Australia and New Zealand are reached.

Growth rates—Per the suggestion of Banse (1991*b*) we have estimated instantaneous "growth" rates k (d^{-1}) calculated on the basis of the model,

$$C_t = C_0 \exp[k(t_2 - t_1)]$$

where C_t is concentration after time $t_2 - t_1$ with $t_2 > t_1$, and C_0 the initial concentration. Linear regression analysis is used on log-transformed C data where k is the slope of the line. Doubling rates are estimated by dividing k by ln 2 (0.693). Here we compare three data sets (Table 2): those for the three Gulf of Alaska stations (Martin et al. 1989), the four experiments from the equatorial Pacific, and those from Sta. 3 and 4 in the Ross Sea. All are compared with the maximum rates (Eppley 1972) that can be obtained under various temperature and light conditions.

In the case of the four equatorial Pacific experiments and the Ross Sea Sta. 4 experiment, we first estimated POC formed from NO_3 taken up (e.g. Fig. 2). With the resulting regressions we then estimated cumulative POC based on the NO_3 removed at various times. Plots of log-transformed cumulative C vs. day for the equator are shown in Fig. 6. We did not use Chl data for two reasons: since we used only ~150 ml of water, Chl detection limits were only 0.2 μg $liter^{-1}$; many of the values were at or below this level in the early stages of the experiments. As in other experiments, we observed substantial Chl losses as soon as NO_3 was exhausted. We do not know why this happened but it was not from grazing because pheophorbide levels did not increase (G. R. DiTullio pers. comm.) and POC and PON concentrations did not decrease.

Gulf of Alaska data (Martin et al. 1991) are also included (Table 2). In view of Banse's (1991*a*) criticism, the data are based on PON buildup as estimated from NO_3 uptake rather than NO_3 uptake alone; the initial PON was estimated to be 1 μmol PON $liter^{-1}$ (N. A. Welschmeyer pers. comm.).

Maximum doubling rates were calculated with Eppley's (1972) formula,

$$\log_{10}\mu = 0.0275T - 0.070,$$

where T is temperature in °C (Fig. 7). Maxima expected are 0.85 doublings d^{-1} for the Ross Sea, 1.2 doublings d^{-1} for the Gulf of Alaska, and 2.5 doublings d^{-1} for the equator. In the Antarctic, doubling rates with Fe were 45–79% of the maximum; controls without Fe were 21–35%. In the Gulf of Alaska, doubling rates at Sta. T-8 approached maximum, while in the control the doubling rate was 38% of maximum. At Sta. T-7 rates with and without Fe were 55 and 26%; at T-6 rates with and without added Fe were about the same, 64 and 54%. In the equatorial Pacific, doublings d^{-1} were 2–3 times higher with Fe than those measured in the controls without Fe. With Fe, 42–66% of the maximum possible was achieved in comparison to 11–31% without Fe. Thus these findings indicate that the addition of minute quantities of Fe will not only lead to accumulation of Chl and biomass and depletion of major nutrients but growth rates will increase as well.

Discussion

The data in Fig. 7 illustrate that Fe deficiency is a common problem in three very

Table 2. Doubling rates for experiments performed in the Gulf of Alaska, the equatorial Pacific, and Ross Sea estimated with the method recommended by Banse (1991*a*). After converting to natural logs, cumulative C, and(or) N, and(or) chlorophyll values were plotted vs. day; linear regressions give intercept and slope of line that equals instantaneous growth rate, *k*. The latter is divided by ln 2 to give doubling rates d^{-1} (μ). Percent of maximum growth rates at various temperatures and hours of light are also shown.

	Days	Intercept	*k*	*n*	*r*	μ	% max
Gulf of Alaska* (13°C, 15-h light, max μ = 1.21)							
T-6 control	2.5–5.5	−0.83	0.45	4	1.00	0.66	54
1 nm Fe		−1.06	0.53	4	1.00	0.77	64
T-7 control	2–5	0.07	0.22	4	1.00	0.31	26
5 nm Fe		−0.20	0.46	4	1.00	0.67	55
T-8 control	2–4	−0.55	0.34	3	1.00	0.49	40
1 nm Fe		−1.28	0.84	3	1.00	1.21	100
Equatorial Pacific† (28°C, 12-h light, max μ = 2.5)							
20-m control	2, 3, 5	1.028	0.197	3	0.974	0.28	11
aer Fe		0.325	0.720	3	0.854	1.04	42
40-m control	2, 3, 5	0.866	0.329	3	0.986	0.47	19
aer Fe		−0.043	0.803	3	0.998	1.16	46
60-m control	4, 5, 6, 7	−0.498	0.386	4	0.984	0.56	22
aer Fe		−3.475	1.140	4	0.941	1.64	66
80-m control	2, 4, 5, 6	−0.736	0.540	4	0.976	0.78	31
aer Fe		−1.670	1.070	4	0.985	1.54	62
Ross Sea‡ (0°C, 24-h light, max μ = 0.85)							
Sta. 4 cum. C							
control 2 Mn	6, 9, 11	1.15	0.208	6	0.975	0.30	35
5 Fe		0.366	0.412	3	1.000	0.59	69
Sta. 4 Chl							
control	6, 9, 11	−1.33	0.148	3	0.997	0.21	25
5 Fe		−2.60	0.463	3	0.999	0.67	79
Sta. 3 Chl							
control	6, 9, 10, 11	−0.023	0.128	4	1.000	0.18	21
5 Fe		−0.666	0.263	4	0.991	0.38	45

* Based on cumulative PON, assumes PON = NO_3 utilization, initial PON = 1 μmol $liter^{-1}$.
† Based on cumulative POC and relationship between POC found and NO_3 taken up.
‡ Same as above for cumulative C; Chl based on direct observation.

different oceanic environments ranging from the polar Ross Sea to the tropical equatorial Pacific, which is not to say that phytoplankton do not grow in these environments. Obviously there are communities of organisms that do very well with the small amounts of Fe available. High productivity rates (>500 mg C m^{-2} d^{-1}) are regularly reported (e.g. *see* Miller et al. 1988; Chavez et al. 1990); NH_3 is the preferred N source and grazing undoubtedly keeps the population in check. Nevertheless, we argue that there is not sufficient Fe to produce the Chl and nitrate reductase that would enable the phytoplankton (primarily diatoms) to bloom and deplete the ambient nutrients, as is exemplified by the Ross Sea data. Even though light levels were extremely low in the turbid nearshore waters, the Fe-replete phytoplankton had removed most of the NO_3 and PO_4 (Fig. 4). In contrast, the Fe-depleted phytoplankton in the stable well-lit offshore waters were not able to affect amounts of major nutrients with their very slow Fe-limited uptake rates (Fig. 5).

Others argue (Mitchell et al. 1991) that lack of stability and resulting low light levels are primarily responsible for nonuse of the nutrients. We agree that light levels play an important role in regulating phytoplankton growth in the Southern Ocean. Nevertheless, light is a secondary factor. Even if the water column is stabilized and the sun shines brightly, offshore Southern Ocean phytoplankton can scarcely grow at all with the Fe available to them (*see open-ocean Ross Sea data in Fig. 5*).

We also contend that phytoplankton do

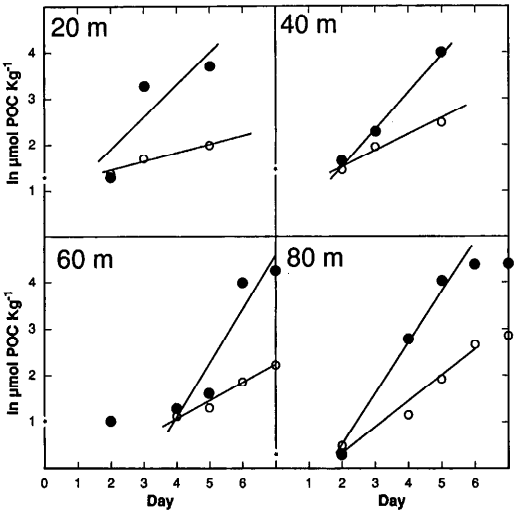

Fig. 6. Equatorial Pacific ln cumulative C estimated from NO_3 uptake (*see Fig. 2*) vs. day. Regression and doubling rate data are shown in Table 2.

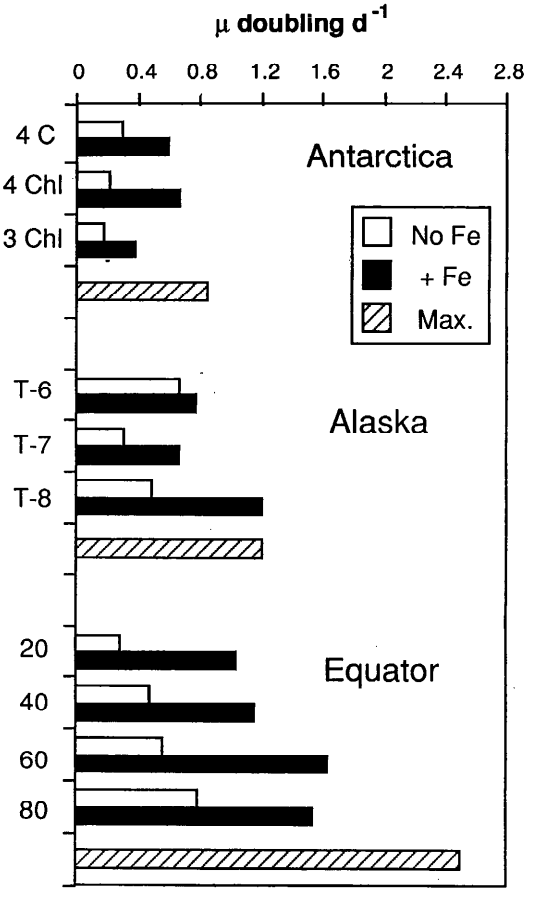

Fig. 7. A comparison of doubling rates from the Antarctic, Gulf of Alaska, and equatorial Pacific with and without added Fe (data from Table 2); theoretical maxima for various temperatures are also shown.

comparatively well under nonstable, low light conditions provided that Fe is available. Feldman's (1986) remotely sensed Southern Ocean pigment image (Lewis 1989) shows comparatively high levels of Fe in the Scotia Sea region between the Antarctic Peninsula and South Georgia. Although these waters are poorly lit and among the roughest in the world, de Baar et al. (1990) have shown them to be Fe-rich. We argue that this greater availability of Fe results in the elevated pigment concentrations observed there.

In summary, there is no doubt that Fe is absolutely essential for the synthesis of Chl and nitrate reductase, not to mention DNA (Weinberg 1989). It is also well established that Fe is insoluble (Stumm and Morgan 1981) and little will be found away from margins other than that advected away from Fe-rich shelves (Martin and Gordon 1988). It is also a fact that equatorial Pacific and Southern Ocean Fe levels in atmospheric dust are the lowest in the world (Uematsu et al. 1983; Prospero 1981). In view of these facts, very small amounts of Fe are to be expected in these remote offshore regions (e.g. <0.02 nmol diss. Fe kg^{-1} at 3°S, 140°W; Martin in press). And because of the scarcity, the acquisition of sufficient Fe for phytoplankton syntheses of Chl and nitrate reductase needed by them to use the abundant major nutrients must be a serious problem indeed.

Examining the opposite side of the coin, we also think it compelling that excess major nutrients are used up as Fe becomes available nearshore (e.g. *see* inshore-offshore Gulf of Alaska Fe/NO_3 data of Martin et al. 1989; cf. inshore-offshore Ross Sea Fe and NO_3 in Figs. 4, 5 of this paper), which also seems to be true for the equatorial Pacific. Large increases in Chl and decreases in NO_3 occur in the vicinity of the Galapagos Islands (*see* Barber and Chavez 1991; Chavez et al. 1991). This effect is observed hundreds of km "downstream" in the satellite ocean color images of Feldman (1986). Although we have no proof, we suspect that these increases in Chl are related to Fe input

from the Galapagos. We are confident that the case for Fe will be strengthened in coming years as more is learned about this essential element; eventually others will share the belief that Fe availability is the primary factor controlling phytoplankton production in nutrient-rich areas of the open sea.

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