On iron limitation of the Southern Ocean: experimental observations in the Weddell and Scotia Seas

Hein J. W. de Baar[1], Anita G. J. Buma[1], Rob F. Nolting[1], Gerhard C. Cadée[1], Guy Jacques[2], Paul J. Tréguer[3]

[1] Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
[2] Laboratoire Arago, Université Pierre et Marie-Curie, CNRS, F-66650 Banyuls-sur-Mer, France
[3] Institut d'Etudes Marines, F-28287 Brest, France

ABSTRACT: Shipboard studies were performed for testing the classical hypothesis that Antarctic phytoplankton suffers from a deficiency of Fe. In a suite of 5 experiments over 8 to 12 d periods and encompassing different water masses (Weddell Sea water proper, Weddell-Scotia Confluence water, Scotia Sea water), and various plankton communities, biomass and dynamic spring/summer (ice) conditions, we always observed Fe to stimulate chlorophyll a synthesis and nutrient assimilation. In 3 out of 5 experiments there was an immediate response to added Fe, while in the other 2 experiments an effect was observed after 3 to 6 d. In 4 out of 5 experiments final particulate organic carbon (POC) levels were also higher in Fe-enriched cultures compared to controls. However the controls were also found to outgrow steadily typical chlorophyll a and POC levels found in ambient waters. This strongly suggests that the in situ Fe concentration in itself does not hamper build-up of high biomass levels. Extrapolation to the in situ ecosystem therefore suggests that, despite enhancement of phytoplankton growth, Fe is not the major factor controlling phytoplankton in the Weddell/Scotia Seas. Marginal sediments appear to supply adequate dissolved Fe for supporting at least minimum growth of phytoplankton. More remote sectors of the Southern Ocean might be more likely candidates for occasional limitation by Fe alone.

INTRODUCTION

Illusions about the fertility of the Southern Ocean are no longer in fashion (Fogg 1977, El-Sayed 1984, Tréguer & Jacques 1986). The Southern Ocean has very high nutrient levels in the surface waters while only low standing stocks of phytoplankton are found (Holm-Hansen 1985). Utilization of nutrients appears to be less efficient than in the coastal upwelling and oligotrophic ecosystems of temperate zones. Even during austral spring the phytoplankton biomass in the most productive regions, notably frontal systems (e.g. the Weddell-Scotia Confluence) and the seasonally receding ice-edge zones, remains relatively modest (Sullivan et al. 1988). Spring levels of nutrients, although depressed, are still well above depletion (Hayes et al. 1984). This apparent 'Antarctic Paradox' (Tréguer & Jacques 1986) is governed by a combination of physical, biological and chemical factors. Intense grazing pressure (Holm-

Hansen & Huntley 1984) undoubtedly plays an important role, whereas light limitation within the mixed layer (Jacques & Minas 1981, Priddle et al. 1986) has also been advocated. Whenever a single limiting factor such as temperature or light has been hypothesized, field measurements and experiments have provided contradicting results (Marra 1978, Jacques & Minas 1981, Priddle et al. 1986, Quéguiner & Legendre 1986). At a given point in time and space a plankton bloom may eventually succumb for just one reason, e.g. a shortage of either nitrate, a trace element or light, or intense grazing pressure. However for the many and various ecosystems integrated over time and space in the vast overall Southern Ocean control by just one *single* factor would appear most unlikely.

There has long been speculation about possible deficiency of a biolimiting trace chemical constituent in the Weddell Sea region, notably Fe. Gran (1931, p. 43) reflects on high nutrient levels in the Weddell/Scotia

Seas reported by Ruud (1930) by stating 'that the growth of the plankton diatoms is determined by other factors than the concentration of phosphates and nitrates besides light and temperature' and hints at his own experiments on Fe limitation. The balanced and scholarly overview by Hart (1934, p. 186) more explicitly briefly mentions Fe deficiency as one of *many possible* limiting factors in the Weddell Sea, Bransfield Strait and Bellingshausen Sea. Since then the possible lack of essential trace elements in the overall Southern Ocean has remained a subject of speculation (Martin & Fitzwater 1988). Thus far there is however a paucity of data on their Antarctic distribution (Orren & Monteiro 1985) whereas studies of their interaction with biota have also been frustrated by contamination problems (Hayes et al. 1984, Jacques et al. 1984). Carlucci & Cuhel (1977) investigated the distribution and biological effects of vitamin B_{12} in the Southern Ocean, indirectly hinting at the possible limiting role of Co, a major constituent of vitamin B_{12}.

The original mention (Gran 1931, Hart 1934) of Fe as one among several possible limiting factors specifically for the Southern Ocean was inspired by experiments of Gran (1931, 1932) on phytoplankton in temperate waters. These and subsequent studies in various regions (Harvey 1933, 1937a, b, Thompson & Bremner 1935, Menzel & Ryther 1961) may, in retrospect, not have been executed with the ultraclean techniques which are now considered necessary for trace metal studies. For example, reported Fe:P ratios in seawater and phytoplankton have decreased from about 4:1 (Harvey 1937a) to about 0.1:1 (Johnston 1964) to modern values around or below 0.001:1 (see Table 5). Only very recently, more than 50 yr after the Gran (1931) hypothesis, 2 simultaneous (August 1987), yet independent, studies (Martin & Fitzwater 1988, Coale 1988) convincingly demonstrated with clean methods the stimulation of phytoplankton by realistic Fe concentrations in the Subarctic North Pacific, an area also characterized by elevated levels of macronutrients in the surface waters. Both for the Pacific area of actual investigation as well as the Antarctic region Fe was speculated to be the *single* growth limiting factor (Martin & Fitzwater 1988, Martin & Gordon 1988, Martin et al. 1989, Martin 1990).

Here we report on the first reliable Antarctic experiments in conjunction with a field survey (Nolting & De Baar 1990), employing clean techniques throughout during the EPOS program. The European Polarstern Study (EPOS) was organized by the European Science Foundation, stimulating a joint effort between scientists from various disciplines and countries of origin. A suite of 3 expeditions was executed with RV 'Polarstern' in the 1988/1989 austral spring and summer seasons. Inspired by the pioneering 'Discovery' expeditions (Hart 1934) the Weddell/Scotia Seas were chosen as the study site of EPOS Leg 2 (Fig. 1). The comprehensive EPOS program was designed for investigating the interaction of physical, chemical and biological processes in the surface ocean at and around the receding ice-edge, with an eye towards unraveling the aforementioned 'Antarctic Paradox' (Hempel et al. 1989). Initial results of our study have already been reported (De Baar et al. 1989a) and presented (Buma et al. 1990).
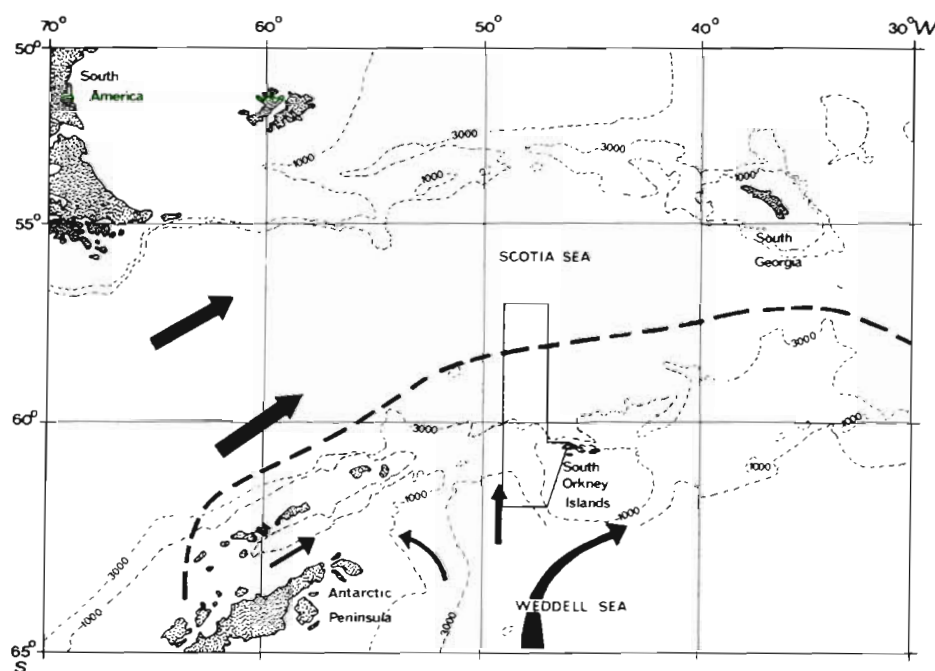

Fig. 1. General area with research rectangle stretching from North to South largely along the 49°W section

MATERIALS AND METHODS

Sampling relied on 12 to 17 modified Teflon-coated Go-Flo bottles on an all-Teflon-coated stainless steel CTD/Rosette frame, as used successfully for studies of nanomolar Fe and Mn distributions (Saager et al. 1989). The package was sent down to 500 m to flush out any possible remaining contamination, and the samplers were closed during the upcast at 30 to 50 m depth in order to avoid contamination from the ship. Upon recovery the bottles were mounted outside a Class-100 clean air laboratory van, then the water was led through all-Teflon (PTFE, FEP) lines into 20 l polycarbonate vessels (Coale 1988) within the clean van. Dissolved Fe, Fe+EDTA, EDTA and Mn were added from analytical stock solutions. The final physico-chemical state (valency, complexation) within the seawater is predicted from thermodynamics to be finely dispersed amorphous $Fe(III)(OH)_3$ in equilibrium with about 0.1 nM dissolved Fe(III) and negligible levels (ca 10^{-10} nM) of dissolved Fe(II) (Byrne et al. 1988). However slow kinetics in combination with occurrence of colloids as well as organic complexes would probably yield higher abundance of both dissolved species Fe(III) and Fe(II); the latter have also been reported from direct determination (Waite & Morel 1984, Hong & Kester 1986, Millero et al. 1987). Our measurements of total Fe concentrations at the beginning and end of the experiments showed that no significant Fe losses occurred due to wall adsorption. The culture vessels were then moved inside a second, refrigerated, container van. During the experiments the sealed vessels were slowly revolving (1.0 rpm) under artificial light at the prescribed saturation level (100 μE m^{-2} s^{-1} on a 16/8 light/dark cycle) for plankton communities encountered during the EPOS 2 cruise (Lancelot & Mathot 1989). Vessels were brought into the Class-100 van daily in order to sample for shipboard determinations of nutrients (nitrate, phosphate, silicate) and chlorophyll a (Neveux & Panouse 1987). Samples were also taken and stored for analyses in the shore laboratory of species composition and abundance, particulate organic carbon (POC), pigments (by HPLC) and trace metals.

Five experimental series, each comprising 2 to 7 cultures simultaneously, were run over periods of 8 to 12 d (Table 1). The initial phytoplankton populations were taken from stations (Fig. 2) located in the Scotia Sea (EPOS 159 and 182), in the Weddell-Scotia Confluence (EPOS 145 and 158) and in the Weddell Sea proper under more than 90 % ice cover (EPOS 169). The overall research area stretched from North to South largely along the 49°W section (Figs. 1 and 2). The general eastward drift (Fig. 1) of the Antarctic Circumpolar Current is augmented by waters from the Bellingshausen Sea and Bransfield Strait which also flow eastward, the latter passing over the various shelves of the archipelago. Different plankton communities were encountered. EPOS 145 was dominated by the diatom *Corethron criophilum* and nanoflagellates (mainly cryptomonads). EPOS 158 consisted largely of nanoflagellates (mainly cryptomonads). EPOS 159 and 182 from the Scotia Sea were dominated by the diatoms *C. criophilum*, *Chaetoceros dichaeta* and *Chaetoceros neglectus*. Finally EPOS 169 was dominated by *C. criophilum* and various nanoflagellates. Preliminary shipboard microscopic inspection during the course of the experiments revealed some changes in relative species composition, but no complete take-over by a single species, and generally excellent physiological condition, the latter also monitored by the ratio chlorophyll a / phaeophytin (mostly higher than 10, never below 2) during shipboard inspection. In total 8 cultures ran with Fe additions, 4 with Fe and EDTA additions and 4 with Mn additions (Table 1). Simultaneous experiments with additions of EDTA with Cu or Zn (EPOS 182; Table 1), as well as results for orthosilicic acid, and information on phytoplankton community structure (cell counts and HPLC pigment data) will be reported elsewhere (Buma et al. unpubl.)

RESULTS

Addition of iron versus untreated controls

In all 5 experiments the Fe-enriched bottles as well as the control bottles showed rapid growth eventually leading to high levels of chlorophyll a and low nutrient concentrations (Figs. 3 to 7; Tables 2 and 3). EPOS 159 and 182, originating from the Scotia Sea proper, showed rapid response (within 2 to 5 d, Fig. 8) to Fe additions, with the most pronounced effect in EPOS 159 (Fig. 9). In the second experiment (EPOS 158) metal was added only after 2 d (t = 2), and 3 d later (t = 5) a similar distinct response was observed (Figs. 4 and 8). However experiments started with Weddell-Scotia Confluence water and Weddell Sea water (EPOS 145, 169) showed no response to the metal enrichment during an initial period of 3 to 6 d (Figs. 3, 6 and 9). Initial effects of metal additions can be demonstrated by calculating linear regression coefficients over the initial period (3 to 6 d) between chlorophyll a (Control) and chlorophyll a (Fe = 10 nM) (Fig. 9). Only Fe = 10 nM additions are plotted and shown. The other Fe additions show comparable trends, as can be seen from Figs. 3 to 7.

During the second phase of the incubations (beyond 3 to 6 d after start of the experiment) all 5 enriched cultures clearly started to outgrow the controls (Figs. 3 to 7 and 9). Regression coefficients of chlorophyll a

Table 1. General information on the 5 culture series. Number of untreated controls and nominal concentrations (nM) of trace metals and EDTA in the culture solutions. Metal additions usually at t = 0, except for EPOS 158 at t = 2 d and for EPOS 145 second additions of 10 nM and 20 nM at t = 7 d. The 4 small-volume (2.5 l) cultures of EPOS 182 showed consistent trends for Fe and Mn, but will otherwise be reported elsewhere (Buma et al. unpubl.)

| | EPOS experiment (Station) | | | | |
	145	158	159	169	182
Region or sea	Confluence	Confluence	Scotia sea	Weddell Sea	Scotia Sea
Latitude °S	58	59	57	62	57
Longitude °W	49	49	49	47	49
Date (1988)	27 Nov	8 Dec	12 Dec	17 Dec	27 Dec
Ice cover	–	–	–	over 90 %	–
Sampling depth (m)	35	20	50	40	40
Temperature (°C)	–0.6	–1.3	0.08	–1.77	1.62
No. of cultures (20 l)	4	7	2	6	7
(2.5 l cultures)					(4)
Controls	2	2	1	1	1
Fe (nM)	10	1 at t = 2	–	–	–
	20	10 at t = 2	10	10	10
		1 at t = 2[a]			
Fe + EDTA	–	–	–	10 + 15	10 + 30 at t = 0
					10 + 30 at t = 4
Fe + EDTA + Mn					1 + 30 + 1 at t = 4
EDTA (nM) control				15	30
Mn (nM)	–	1 at t = 2[a]			1
			–	–	
Mn		10	–	10	
Untreated control (2.5 l)					1
Fe + EDTA (2.5 l)					1 + 30 at t = 0
Fe + EDTA + Cu (2.5 l)					1 + 30 + 1 at t = 0
Fe + EDTA + Zn (2.5 l)					1 + 30 + 1 at t = 0
End: Time (d)	10	8	12	9	8
Temperature (°C)	3.5	3.5	3.5	3.5	3.5
Depletion of:	NO_3	NO_3	(NO_3)	(NO_3)	Si

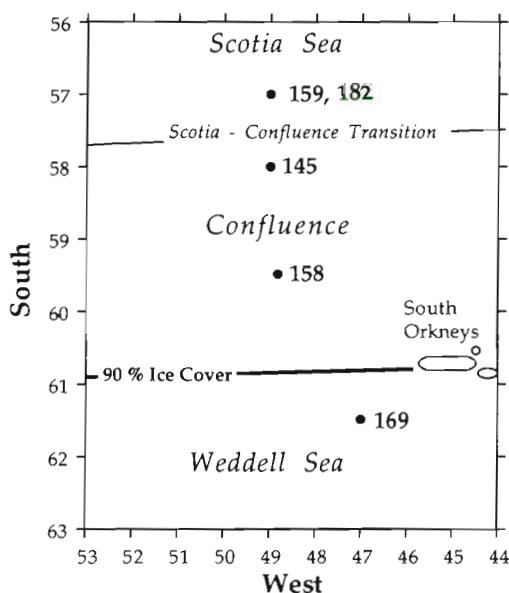[a] With daily 1 nM addition until 6 nM at t = 8 d

Fig. 2. Station locations in the Scotia Sea, the Scotia-Weddell Confluence and the Weddell Sea where waters were collected for starting the experiments

(Control) plotted against chlorophyll a (Fe = 10 nM) from this second phase show ratios far above 1 (Fig. 9). At the point in time (3 to 6 d) where this secondary yet more distinct Fe effect started, the levels of chlorophyll a and nutrients in both the control and the Fe-enriched bottles had developed near the highest and lowest levels respectively found in the ambient surface waters. During the cruise the highest in situ chlorophyll a values measured were about 4.5 µg l^{-1}, consistent with earlier reported maximum values (Sullivan et al. 1988). Spring or summer values for nitrate and phosphate rarely drop below 20 and 1.5 µM respectively, only about 25 % below the winter values of 25 to 30 µM and 2 µM respectively. Silicate levels (not shown) in the Weddell Sea and Scotia Sea rarely drop more than 25 % below their respective winter values of about 80 and 25 µM (Van Bennekom pers. comm.). So the more pronounced effects of Fe in the second phase of the experiments took place under conditions (chlorophyll a, nutrients, community structure) no longer comparable with the in situ situation.
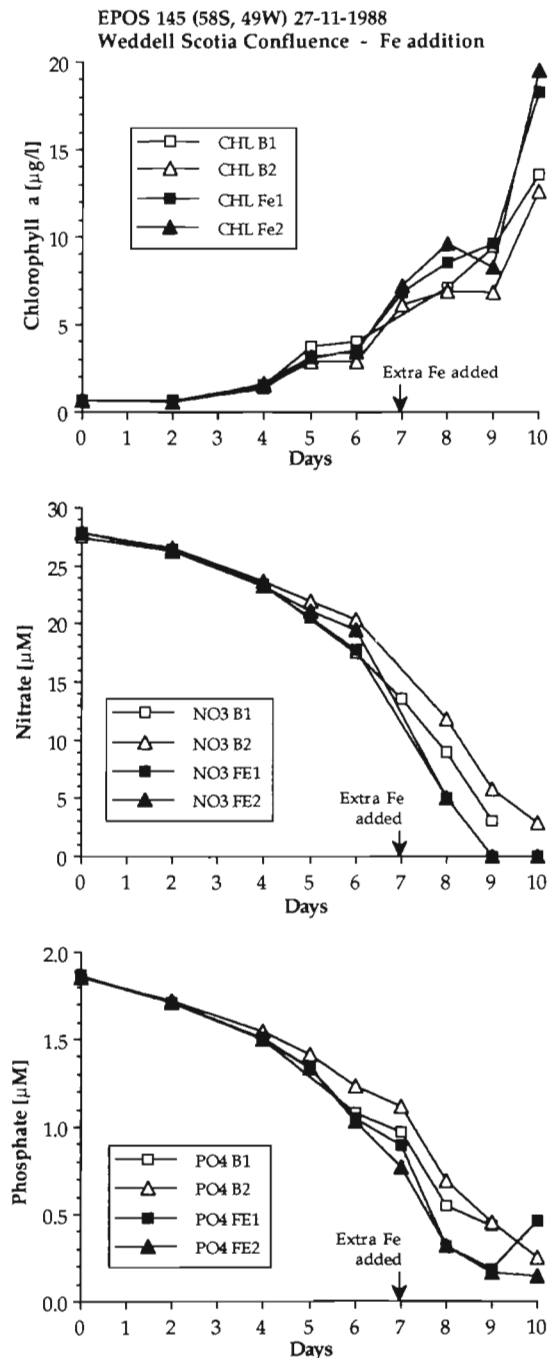
Fig. 3. Expt 145, Confluence. Concentrations of chlorophyll *a* (µg l^{-1}), dissolved nitrate (µM) and phosphate (µM) versus time (d). At t = 0 nominal Fe = 1 nM was added, at t = 7, another nominal Fe = 10 nM and Fe = 20 nM in Fe1 and Fe2 respectively. Controls are B1 and B2

Most experiments (EPOS 145, 158 and 182) were run until nutrient exhaustion of the metal-enriched vessels was reached, at which time the chlorophyll *a* stock in Fe 10 nM enriched bottles was 1.5 to 2.1 times that in the controls. In general nitrate was the first nutrient to

be completely (EPOS 145 and 158) or largely (EPOS 159 and 182) depleted. In the Scotia Sea with lower initial levels of orthosilicic acid the latter was exhausted first for the Fe 10 nM culture in the final bloom experiment EPOS 182. (J. van Bennekom pers. comm., EPOS 159 not measured). Levels of ammonia remained fairly constant around their low starting values (ranging from 0.1 to 0.5 µM) in most experiments. Only in the third experiment did ammonia gradually decrease from 0.47 to 0.08 µM, presumably due to unbalance in phytoplankton uptake and ammonia regeneration through grazing.

In all cases where only Fe was added we eventually observed enhanced chlorophyll *a* levels and more rapid utilization of available nutrients (Figs. 3 to 7). For the Fe 10 nM additions the net increase of chlorophyll *a* was 31 to 110 % higher than in controls, as assessed from simple linear regression throughout the duration of the experiment (Table 4). At close inspection most of this Fe-stimulated increase took place in the second stage of each experiment (Fig. 9). Curiously enough the level of added Fe (1 nM or 10 nM) did not appear to make much difference (Fig. 4), in contrast with at least one experiment in the North Pacific study of Martin & Fitzwater (1988). In EPOS 158 (Weddell-Scotia Confluence) the metals were added only after 2 d, for Fe at 1 nM and at 10 nM, as well as at 1 nM (t = 2) with daily extra 1 nM additions up to 6 nM at t = 8 d (Table 1). For all 3 cases similar chlorophyll *a* enhancement was observed (Fig. 4). In all 5 experiments the uptake of nitrate and phosphate was enhanced: 20 to 60 % and 4 to 70 % respectively (Table 4), demonstrated by regression plots representing the complete experimental period (e. g. EPOS 159 in Fig. 10).

Upon completion we also measured 14 to 115 % higher POC in the Fe-enriched versus the control incubations, except for identical levels in EPOS 182 (Scotia Sea; Table 4). In EPOS 158 the final POC level for the daily Fe addition was slightly higher (145 µM as compared to 138 and 126 µM for Fe = 10 and Fe = 1 nM respectively) despite the observation that no differences in chlorophyll *a* levels were observed between these bottles. In EPOS 182 (Scotia Sea) chlorophyll *a* and phosphate showed a subtle but distinct Fe stimulation right from the start (Figs. 7 and 9), which however was not found for nitrate until t = 7 d, whereas the final (t = 8 d) POC values were virtually identical at 160 µM for Fe = 10 nM and control alike (Table 4). Stimulation of POC levels in Fe-enriched bottles did not keep up completely with the enhancement of chlorophyll *a* synthesis which is reflected in the ratio POC:chlorophyll *a* (µM:µM; Table 4). In general this ratio was high, between 77 and 320. Obviously non-autotrophic biomass was considerable during the cruise, both in the field and in our experiments, as
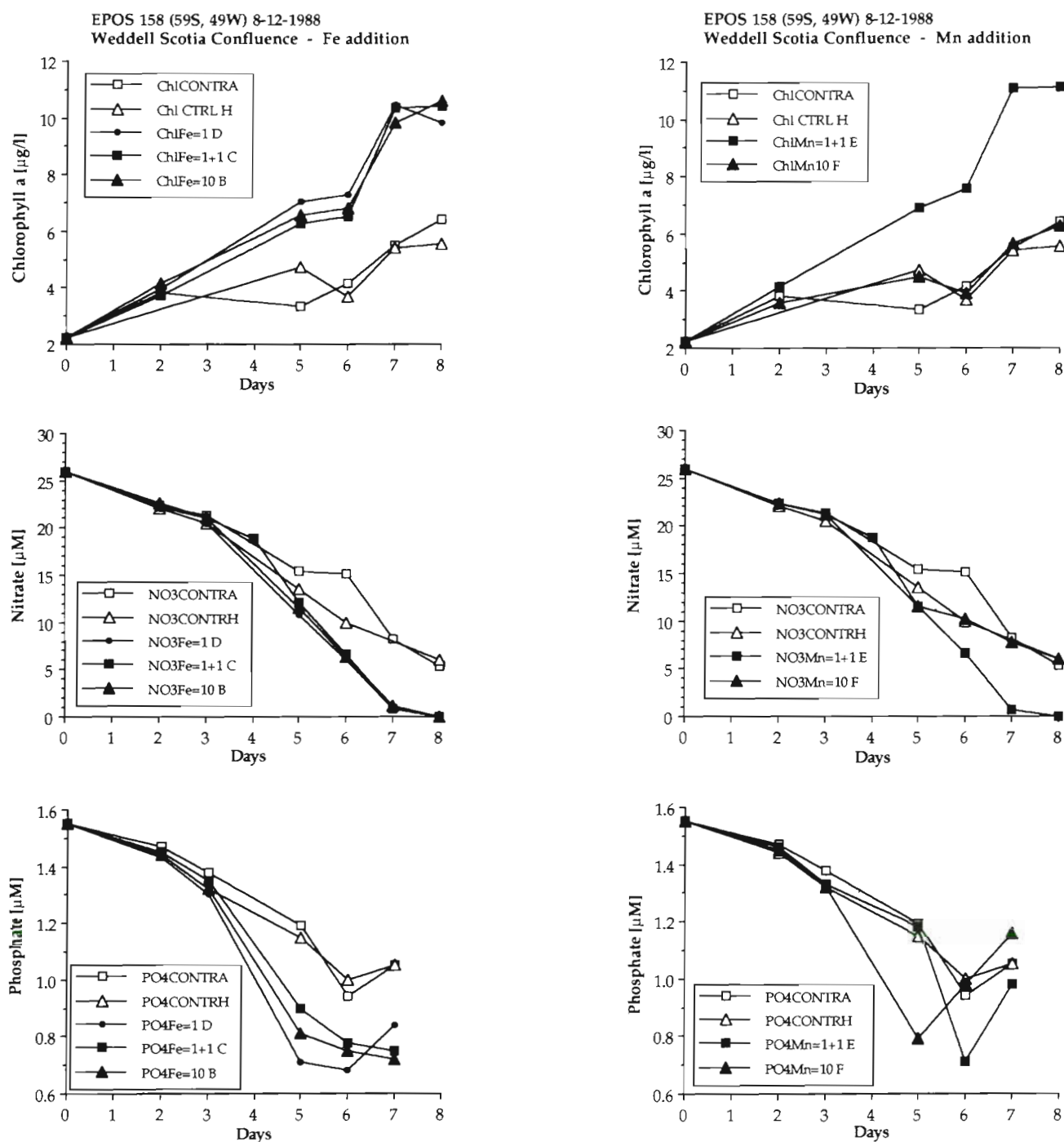
Fig. 4. Expt 158, Confluence. Concentrations of chlorophyll *a* (µg l⁻¹), dissolved nitrate (µM) and phosphate (µM) versus time (d). Left: Fe additions (D = 1 nM, B = 10 nM, C = 1 nM with daily 1 nM extra) and controls A and H. Right: Mn additions (E = 1 nM with daily 1 nM extra, F = 10 nM) and controls A and H. All additions only after 2 d (t = 2); in 2 cultures daily extra dose of 1 nM (Fe in C and Mn in F)

supported by cell numbers and calculated biomass of heterotrophs in the experimental bottles (Buma et al. unpubl.). During the course of the experiments the ratio POC : chlorophyll *a* varied but was always lower in the Fe-enriched samples as compared to the controls (Table 4).

Table 2. Daily values of chlorophyll a ($\mu g\ l^{-1}$), nitrate (NO_3) (μM) and phosphate (PO_4) (μM). In EPOS 145 Fe additions were nominal 1 nM at t = 0 d; another nominal 10 nM and 20 nM respectively at t = 7 d. In EPOS 158 no additions were made during the first 48 h, then at t = 2 d additions of Fe of nominally 1 nM, 10 nM and daily 1 nM (i.e. [Day −2] nM) until 6 nM at t = 8 d. Similarly at t = 2 d additions of Mn of nominally 10 nM and daily 1 nM (i.e. [Day −2] nM) until 6 nM at t = 8 d

EPOS 145 (58 °S, 49 °W) Confluence

Day	Control Fe = 0 nM			Control Fe = 0 nM			Added Fe = 1 nM			Added Fe = 1 nM		
	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄
0	0.63	27.9	1.86	0.63	27.9	1.86	0.63	27.9	1.86	0.63	27.9	1.86
2	0.68	26.2	1.71	0.62	26.6	1.72	0.62	26.4	1.71	0.58	26.2	1.71
4	1.57	23.3	1.50	1.58	23.7	1.55	1.39	23.2	1.51	1.66	23.2	1.50
5	3.78			2.85	20.3	1.41	3.10	20.5	1.34	3.21	21.0	1.34
6	4.01	17.5	1.08	2.92		1.23	3.53	17.8	1.05	3.42	19.5	1.03
7		13.5	0.97	6.12		1.12	6.80		0.89	7.20		0.77
							Added Fe = 11 nM			**Added Fe = 21 nM**		
8	7.11	8.9	0.55	6.88	11.8	0.69	8.51	5.10	0.32	9.65	5.1	0.32
9	9.42	3.1	0.43	6.80	5.70	0.45	9.58	0.0	0.18	8.25	0.0	0.16
10	13.54			12.59	2.9	0.25	18.24	0.0	0.46	19.54	0.0	0.14

EPOS 158 (59 °S, 49 °W) Confluence: Fe experiments

Day	Control Fe = 0 nM			Control Fe = 0 nM			Various additions of Fe were made only after 2 d (48 h)								
	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄
0	2.24	26.0	1.55	2.24	26.0	1.55	2.24	26.0	1.55	2.24	26.0	1.55	2.24	26.0	1.55
2	3.81	22.4	1.47		22.1	1.44	3.96	22.1	1.43	3.72	22.2	1.45	4.17	21.0	1.44
							Added Fe = 1 nM			**Fe = (Day −2) nM**			**Added Fe = 10 nM**		
3		21.3	1.38		20.5	1.32		20.5	1.30		21.0	1.35		21.0	1.32
4											18.9				
5	3.35	15.5	1.19	4.73	13.5	1.15	7.03	10.8	0.71	6.29	12.1	0.90	6.57	11.5	0.81
6	4.16	15.2	0.94	3.66	10.0	1.00	7.27	6.1	0.68	6.51	6.6	0.78	6.79	6.3	0.75
7	5.51	8.2	1.05	5.41		1.05	10.46	0.9	0.84	10.36	0.9	0.75	9.83	1.1	0.72
8	6.40	5.3		5.58	6.1		9.82	0.0		10.43	0.0		10.61	0.0	

EPOS 158 (59 °S, 49 °W) Confluence; Mn experiments (controls same as for Fe of EPOS 158)

Day	Control Mn = 0 nM			Control Mn = 0 nM			Additions of Mn only after 2 d (48 h)					
	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄	Chl a	NO₃	PO₄
0	2.24	26.0	1.55	2.24	26.0	1.55	2.24	26.0	1.55	2.24	26.0	1.55
2	3.81	22.4	1.47		22.1	1.44	4.14	22.4	1.46	3.60	22.4	1.45
							Mn = (Day −2) nM			**Added Mn = 10 nM**		
3		21.3	1.38		20.5	1.32		21.2	1.33		21.2	1.32
4								18.7				
5	3.35	15.5	1.19	4.73	13.5	1.15	6.88	11.5	1.18	4.5	11.6	0.79
6	4.16	15.2	0.94	3.66	10.0	1.00	7.59	6.7	0.71	3.91	10.2	0.98
7	5.51	8.2	1.05	5.41		1.05	11.07	0.7	0.98	5.64	7.8	1.16
8	6.40	5.3		5.58	6.1		11.15	0.0		6.3	6.1	

Additions of iron and EDTA

In 2 series (EPOS 169 and 182) we also added a prepared stock of Fe with EDTA, and a separate EDTA control (Figs. 6 and 7). These Fe+EDTA enriched and EDTA control cultures by and large exhibited the same trends as for the Fe-enriched and untreated control cultures respectively.

In the first 4 d of EPOS 169 all developed very simi-larly; at t = 6 d the Fe+EDTA picked up at enhanced rate, yet eventually both Fe-enriched and both control cultures ended up at the same levels of chlorophyll a, nitrate and phosphate, notwithstanding the EDTA (Fig. 6). The final POC = 98 μM for Fe+EDTA was somewhat above the 91 μM for the pure Fe addition, both being 10 to 20 % above the POC = 77 and 80 μM in the control and EDTA control respectively. In this experiment the EDTA might eventually (t = 6 d) have

Table 3. Daily values of chlorophyll *a* (µg l^{-1}), nitrate (µM) and phosphate (µM) for EPOS 159, 169, 182. Values for experiments with Fe addition of nominally 10 nM and Mn of 10 nM or 1 nM at t = 0 d, and controls. Data for simultaneous experiments with Fe/EDTA available upon request (overview in Table 1)

EPOS 159 (57 °S, 49 °W) Scotia Sea

Day	Control Fe = 0 nM			Added Fe = 10 nM		
	Chl *a*	NO$_3$	PO$_4$	Chl *a*	NO$_3$	PO$_4$
0	0.15	29.8	1.81	0.15	29.8	1.81
1	0.30	27.8	1.72	0.21	27.6	1.72
2	0.27	27.2	1.71	0.36	26.8	1.65
3	0.61	26.1	1.74	0.60	26.1	1.83
5	0.88	25.4		0.98	25.5	
7	1.64	25.6	1.48	2.17		1.51
8	2.79		1.31	3.38		1.37
9	2.69	22.0	1.38	4.39	20.8	1.30
10	4.63	18.8	1.14	7.81	15.6	0.98
11	5.635	17.4	0.94	12.42	11.2	0.66
12	5.10	16.4	0.79	10.66	7.2	0.30

EPOS 169 (62 °S, 47 °W) Weddell Sea

Day	Control Fe = 0 nM			Added Fe = 10 nM			Added Mn = 10 nM		
	Chl *a*	NO$_3$	PO$_4$	Chl *a*	NO$_3$	PO$_4$	Chl *a*	NO$_3$	PO$_4$
0	0.83	28.1	1.89	0.83	28.1	1.89	0.83	28.1	1.89
2	0.70	30.8	1.86	0.69	30.8	1.79	0.63	30.3	1.86
4	1.71	28.5	1.87	1.60	28.7	1.87	1.63	28.3	1.82
6	3.30	27.2	1.54	3.28	26.7	1.58	3.16	27.0	1.66
8	6.26	20.3	1.13	8.80	19.1	1.10	6.89	23.6	1.39
9	7.57	18.5	0.91	11.97	15.8	0.73	8.32	21.2	1.14

EPOS 182 (57 °S, 49 °W) Scotia Sea

Day	Control F = 0 nM			Added Fe = 10 nM			Added Mn = 1 nM		
	Chl *a*	NO$_3$	PO$_4$	Chl *a*	NO$_3$	PO$_4$	Chl *a*	NO$_3$	PO$_4$
0	0.89	27.9	1.74	0.89	27.9	1.74	0.89	27.9	1.374
0.37	0.85	26.0		1.084	27.3				
1.10	1.22	25.7		1.26	27.0				
2	1.74	24.3	1.36	1.97	24.1	1.2	1.70	23.9	1.20
3	2.49	24.7	1.12	2.83	24.5	1.00	2.58	25.1	1.18
4	3.64	22.8	1.10	4.38	21.3	1.03	3.45	22.1	1.06
5	5.75	15.4	0.83	7.39	17.2	0.61	6.06	15.7	0.64
6	6.45	16.0	0.75	6.06	14.4	0.62	6.09	15.7	0.64
7	8.28	11.6	0.38	12.26	8.7	0.25	9.72	9.9	0.28
8	10.59	7.3	0.18	13.89	4.5	0.10	12.34	6.2	0.22

made the Fe slightly more readily available. Detoxification (Barber & Ryther 1969) of high levels (in keeping with high ambient nutrients; Nolting & De Baar 1990) of adversely acting metals like Cd or Cu (Brand et al. 1986) would have been an alternative mechanism but is not supported by the identical development of untreated and EDTA controls.

In EPOS 182 the added EDTA led to about 20 % lower chlorophyll *a* synthesis, with or without Fe 10 nM. Otherwise the chlorophyll *a* for Fe+EDTA was still about 75 % higher than in the EDTA control (Fig. 7), but both were distinctly below the chlorophyll *a* level in the Fe 10 nM and untreated control culture.

The final POC = 117 µM for Fe+EDTA was also above that (98 µM) in the EDTA control, but both are again below the POC = 160 µM for Fe 10 nM and untreated culture alike.

Summarizing we found either a slight enhancement (EPOS 169) or modest reduction (EPOS 182) of chlorophyll *a* and POC upon addition of EDTA. In these surface waters with, as has now been determined, relatively high ambient concentrations of trace metals (several nM for Fe, Cu, Cd, Ni, Zn; Nolting & De Baar 1990) the added level of EDTA (15 or 30 nM) may in retrospect have been inadequate for EDTA to cause a distinct effect.

Table 4. Initial and final values of particulate organic carbon (POC) for untreated controls and Fe = 10 nM incubations. Final POC values for Mn additions are mentioned in the text. Complete datasets available from principal authors, including the t = 4 d additions and 4 small-volume incubations of EPOS 182, are not dealt with here but otherwise show consistent trends for Fe and Mn. Relying also on data listed in Tables 2 and 3 various relations were calculated: (1) The ratio POC/chl at the end of the experiments is systematically lower in the Fe-enriched cultures, indicating that Fe stimulates chl synthesis more strongly than carbon fixation. (2) Slopes of linear regression (with correlation coefficient for given number of data points) of chl versus NO_3 are systematically higher in the Fe = 10 nM versus controls. The ratio $\Delta C/\Delta N$ for difference Δ over time interval t = 0 to t = end is also systematically higher in Fe = 10 nM versus controls. (3) The slope of linear regression chl/chl for Fe = 10 nM and control respectively is systematically steeper than corresponding slope of NO_3/NO_3 regression. The latter slope is steeper than for PO_4/PO_4 of Fe = 10 nM and control respectively. The ratio $\Delta C/\Delta C$ has values in between slopes of chl/chl and NO_3/NO_3. Summarizing, Fe appears to stimulate (i) chl synthesis, (ii) carbon fixation, (iii) NO_3 assimilation and (iv) PO_4 assimilation in that order Separate regressions for the first (3 to 6 d) and second periods of the experiments are shown in Fig. 9
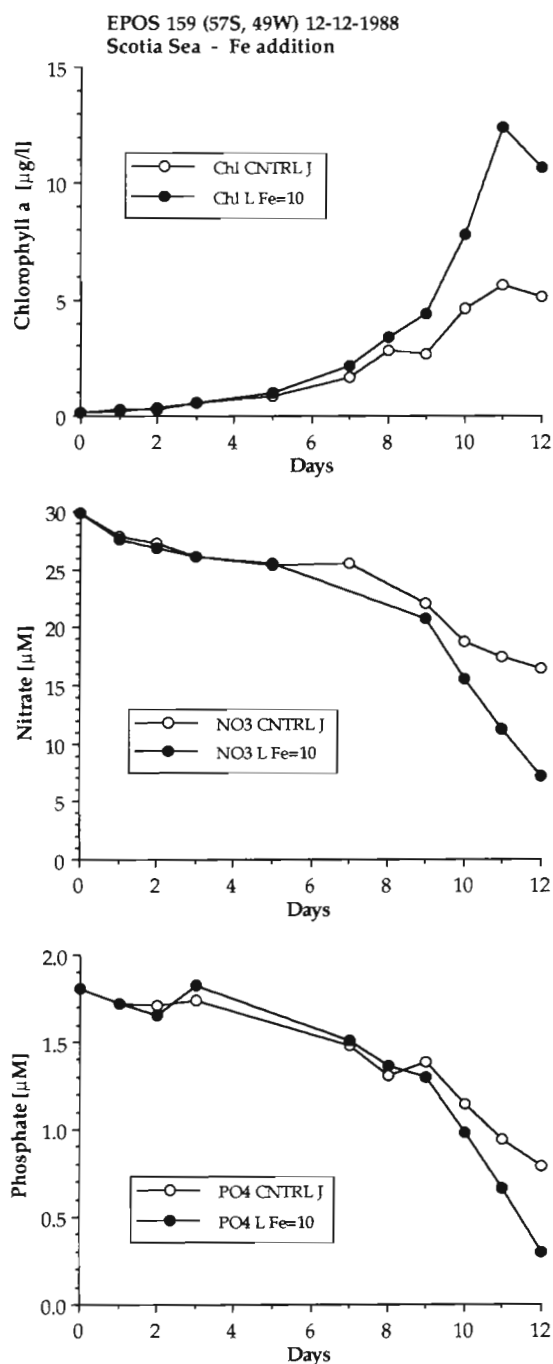
		EPOS station										
		145			158			159		169		182
Time (d)	0	10	10	0	8	8	0	12	0	9	0	8
					Untreated control cultures							
POC (μM)	12.5	136.7	135.0	15.0	95.0	84.2	4.2	89.3	5.0	80.0	10.8	160.0
POC/chl	238	212	129	82	178	181	320	231	77	127	148	181
Overall slopes of regression of 2 different properties throughout the control experiments:												
Chl/NO_3		−0.37	−0.41		−0.17	−0.15		−0.45		−0.57		−0.48
Regress. coeff.		1.00	0.95		0.93	0.87		0.98		0.98		0.99
Datapoints		6	7		6	5		10		6		10
NO_3/PO_4		16.2	15.7		23.0	29.4		12.8		11.3		13.8
Regress. coeff.		0.99	1.00		0.89	0.99		0.98		0.97		0.97
Datapoints		7	8		6	5		9		6		8
$\Delta C/\Delta N$		4.96	nd		3.7	3.5		7.0		7.8		7.23
					Cultures with 10 nM Fe additions							
POC (μM)	12.5	192.5	nd	15.0	138.3		4.2	191.7	5.0	90.8	10.8	160.8
POC/chl	238	118		82	156		320	216	77	91	148	139
Overall slopes of regression of 2 different properties throughout Fe-enriched experiments:												
Chl/NO_3		−0.48	−0.48		−0.29			−0.59		−0.78		−0.56
Regress. coeff.		0.91	0.88		0.97			0.98		0.99		0.98
Datapoints		8	8		6			9		6		10
NO_3/PO_4		17.3	16.3		25.4			14.4		12.2		14.6
Regress. coeff.		0.98	0.99		0.97			0.99		0.97		0.91
Datapoints		8	8		6			8		6		8
$\Delta C/\Delta N$		6.52	nd		4.73			8.29		6.95		6.40
					Comparison of Fe-enriched versus control experiment							
Overall ratios of the same properties in the Fe-enriched versus the control experiment:												
Chl/chl		1.31	1.53		2.00			2.10		1.60		1.40
Regress. coeff.		0.98	0.98		0.94			0.98		0.99		0.98
Datapoints		7	8		6			11		6		10
$\Delta C/\Delta C$		1.41	nd		1.54			2.14		1.14		1.01
NO_3/NO_3		1.20	1.21		1.33			1.60		1.20		1.15
Regress. coeff.		0.99	0.99		1.00			0.98		1.00		0.99
Datapoints		14	14		12			9		6		10
PO_4/PO_4		1.04	1.16		1.67			1.42		1.11		1.04
Regress. coeff.		0.96	0.99		0.98			0.98		0.99		0.99
Datapoints		16	16		12			10		6		8

nd: no data

EPOS 159 (57S, 49W) 12-12-1988
Scotia Sea - Fe addition

Fig. 5. Expt 159, Scotia Sea. Concentrations of chlorophyll a (µg l⁻¹), dissolved nitrate (µM) and phosphate (µM) versus time (d) for Fe = 10 nM addition (L) and control (J)

Addition of manganese

Manganese was added in EPOS 158 (Weddell-Scotia Confluence) at t = 2 d to a level of 10 nM, as well as to 1 nM at t = 2 d with daily additions of 1 nM up to 6 nM in total at the end (Fig. 4). Controls were identical to those for the simultaneous Fe study. The daily Mn addition led to distinctly more chlorophyll a than the control, the final POC = 144 µM virtually identical to POC = 145 µM for daily Fe addition and well above POC = 84 µM in the untreated control. Curiously enough the higher addition of 10 nM showed very little effect, both for chlorophyll a and for final POC = 78 µM, slightly below the untreated control. Removal of Mn, for example by slow oxidation or wall adsorption, might negate any possible effect in the 10 nM culture, whereas the daily addition of fresh Mn in the other would sustain enhanced growth. Future analyses of Mn levels in stored samples may provide the answer here. Another run with a 10 nM addition (EPOS 169, Weddell Sea; Fig. 6) showed little effect, only at the end of the run was chlorophyll a enhanced although nutrient uptake was slightly less (Fig. 6). POC = 77 µM was identical to 80 µM in the untreated control. In the final study (EPOS 182, Scotia Sea) the Mn = 1 nM addition at t = 0 eventually led to a 15% enhancement of chlorophyll a and similar decrease of nutrients; however POC = 128 µM of the Mn addition was well below 160 µM in the untreated control (Fig. 7). In summary we found a distinct effect for Mn in 1 out of 5 experiments, the other 4 only exhibiting modest trends as also reported for one Mn experiment in the North Pacific (Coale 1988).

DISCUSSION

Initial response

For plankton communities taken from waters of the Scotia Sea and the Confluence we found virtually immediate (within 2 to 5 d) stimulation by Fe of the synthesis of chlorophyll a and assimilation of nutrients (EPOS 158, 159, 182). For another experiment in the Confluence (145) and an experiment started with Weddell Sea water proper (169) no immediate response was observed. Two of the experiments of Martin et al. (1989) in the North Pacific Ocean showed an immediate response to added Fe, in contrast with the 2 controls which initially showed a net drop in chlorophyll a contents, possibly as a result of initial handling (Fig. 8). The third experiment of Martin et al. (1989) exhibited an immediate steady growth of both control and Fe-enriched cultures – initially the control actually exhibits the largest net increase of chlorophyll a (Fig. 8). The one Fe-enrichment experiment by Coale (1988) at the same North Pacific site shows an immediate and steady response (not shown here). Summarizing, for a total of 9 of this type of experiments in both Pacific and Southern Ocean there was an immediate response to Fe in 6 of them (EPOS 158, 159, 182; VERTEX T-7, T-8; Coale).
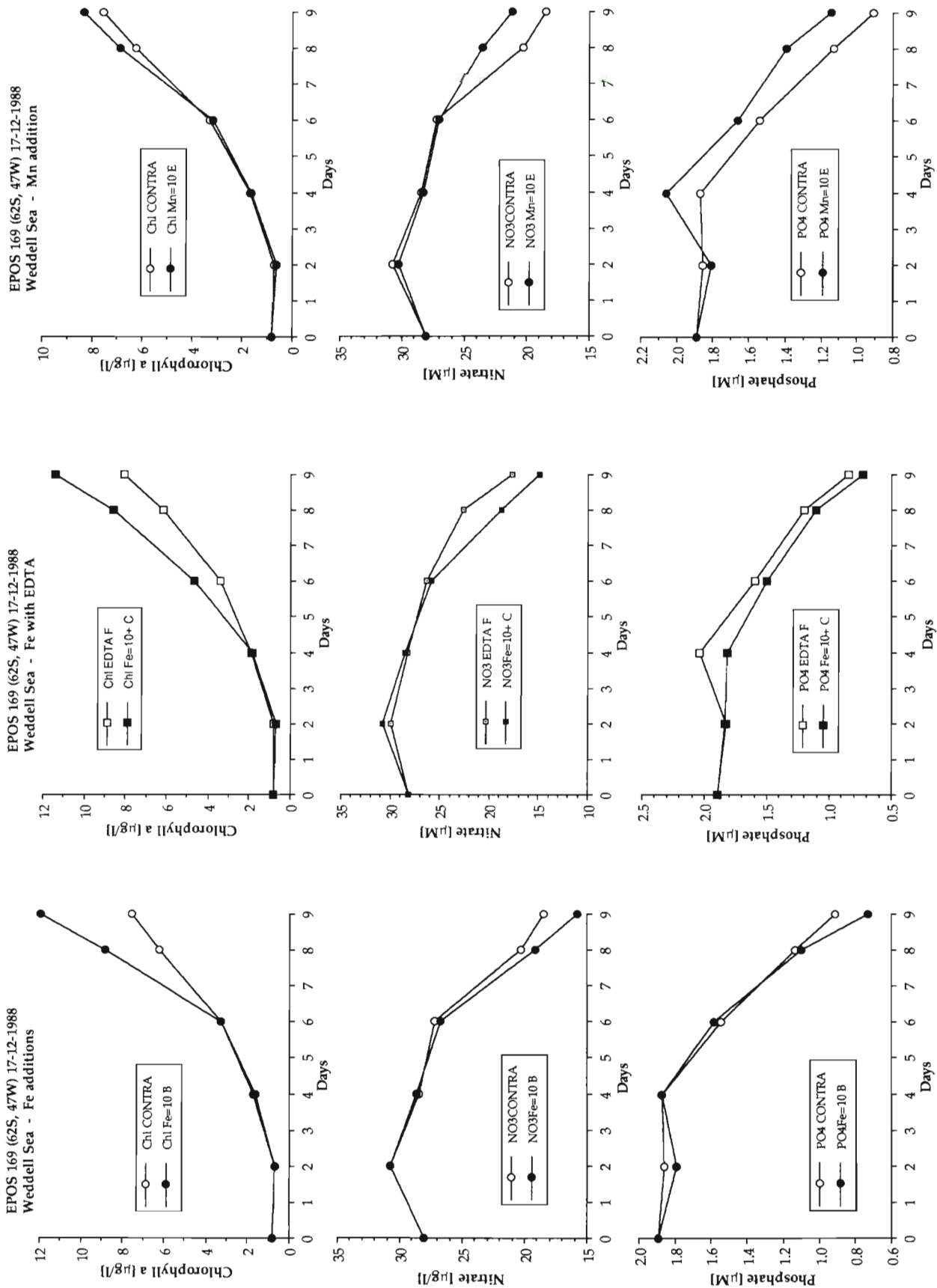
Fig. 6. Expt 169, Weddell Sea. Concentrations of chlorophyll a ($\mu g\,l^{-1}$), dissolved nitrate (μM) and phosphate (μM) versus time (d). Left: Fe = 10 nM (B) and control (A). Middle: Fe = 10 nM + EDTA = 15 nM and EDTA = 15 nM control. Right: Mn = 10 nM (E) and control (A). All additions at t = 0, versus controls
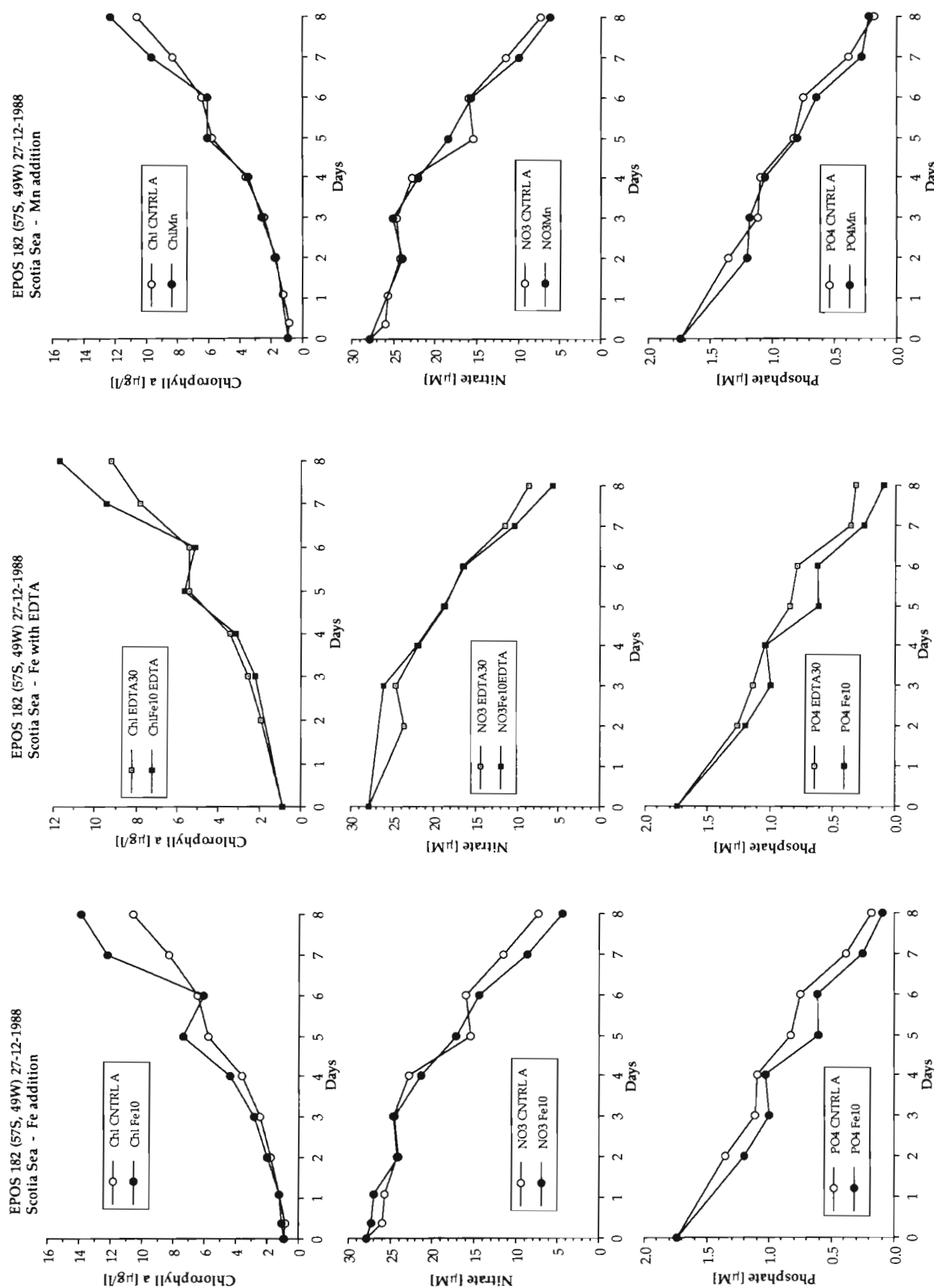
Fig. 7. Expt 182. Scotia Sea. Concentrations of chlorophyll *a* (µg l⁻¹), dissolved nitrate (µM) and phosphate (µM) versus time (d). Left: Fe = 10 nM and control (A). Middle: Fe = 10 nM + EDTA = 30 nM and control EDTA = 30 nM. Right: Mn = 1 nM and control (A). Not shown are the two t = 4 additions and the 4 small-volume (2.5 l) incubations
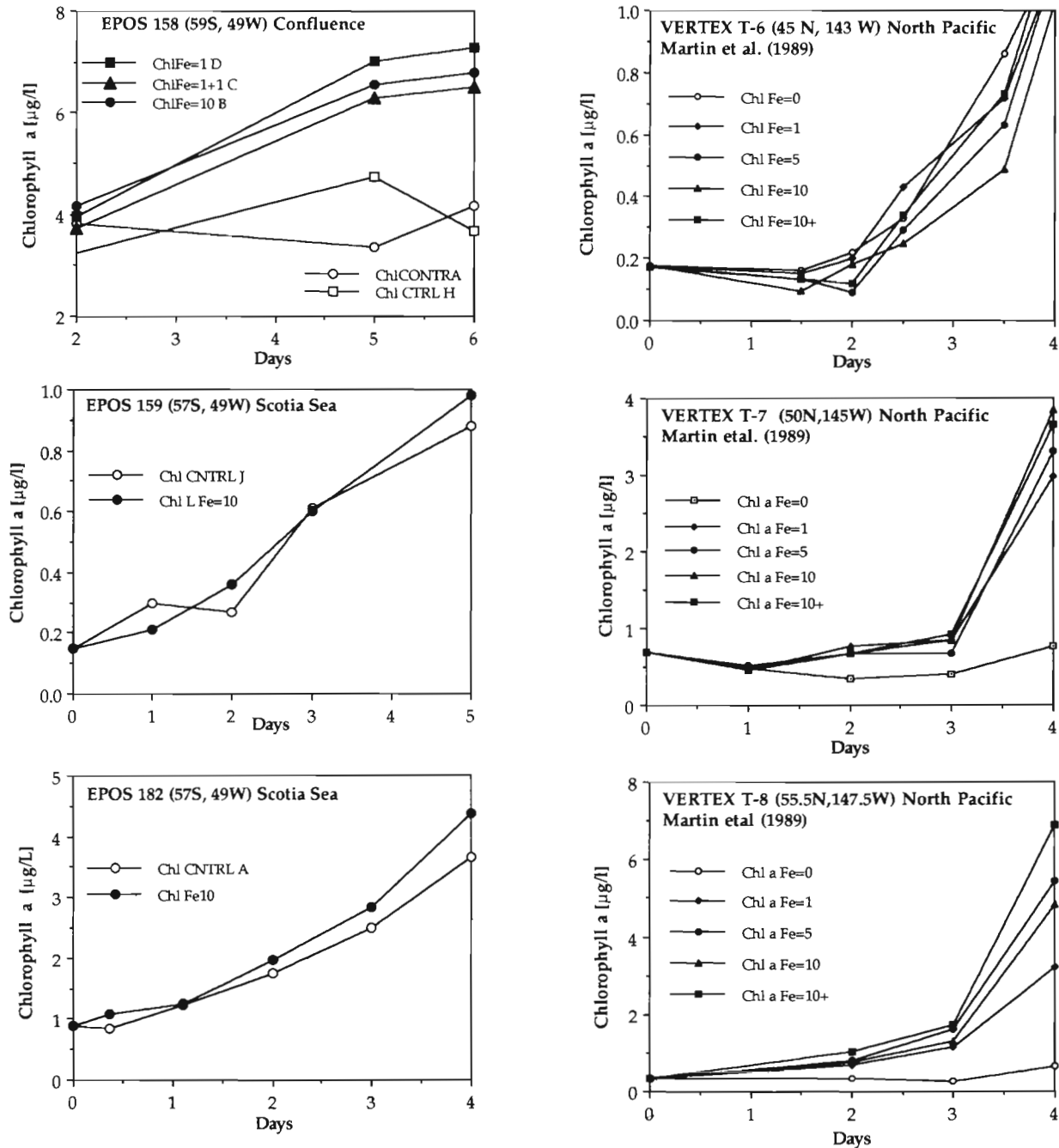
Fig. 8. Immediate response of chlorophyll a (μg l^{-1}) to Fe addition at expanded scale in the initial 4 to 5 d of Expts 158, 159, 182 and the 3 experiments of Martin et al. (1989). (All Fe additions at t = 0 d except at t = 2 d for EPOS 158)

Secondary and overall response

During the second stages of all 5 of our experiments the stimulation by Fe became distinctly apparent (Figs. 3 to 7 and 9). However the controls also exhibited steady growth. The 3 experiments of Martin et al. (1989) also showed more pronounced response in their second stage, starting after about 4 d. In their experi-

ment VERTEX T-6 the control however also exhibited steady growth. Controls in their other 2 experiments (VERTEX T-7 and T-8) exhibited no net chlorophyll a increase, at best a recovery after the initial drop. The control of Coale (1988) also barely showed a net increase of chlorophyll a. Summarizing one finds a final response to Fe in all 9 experiments. However in only 3 of them does the control truly appear to be limited
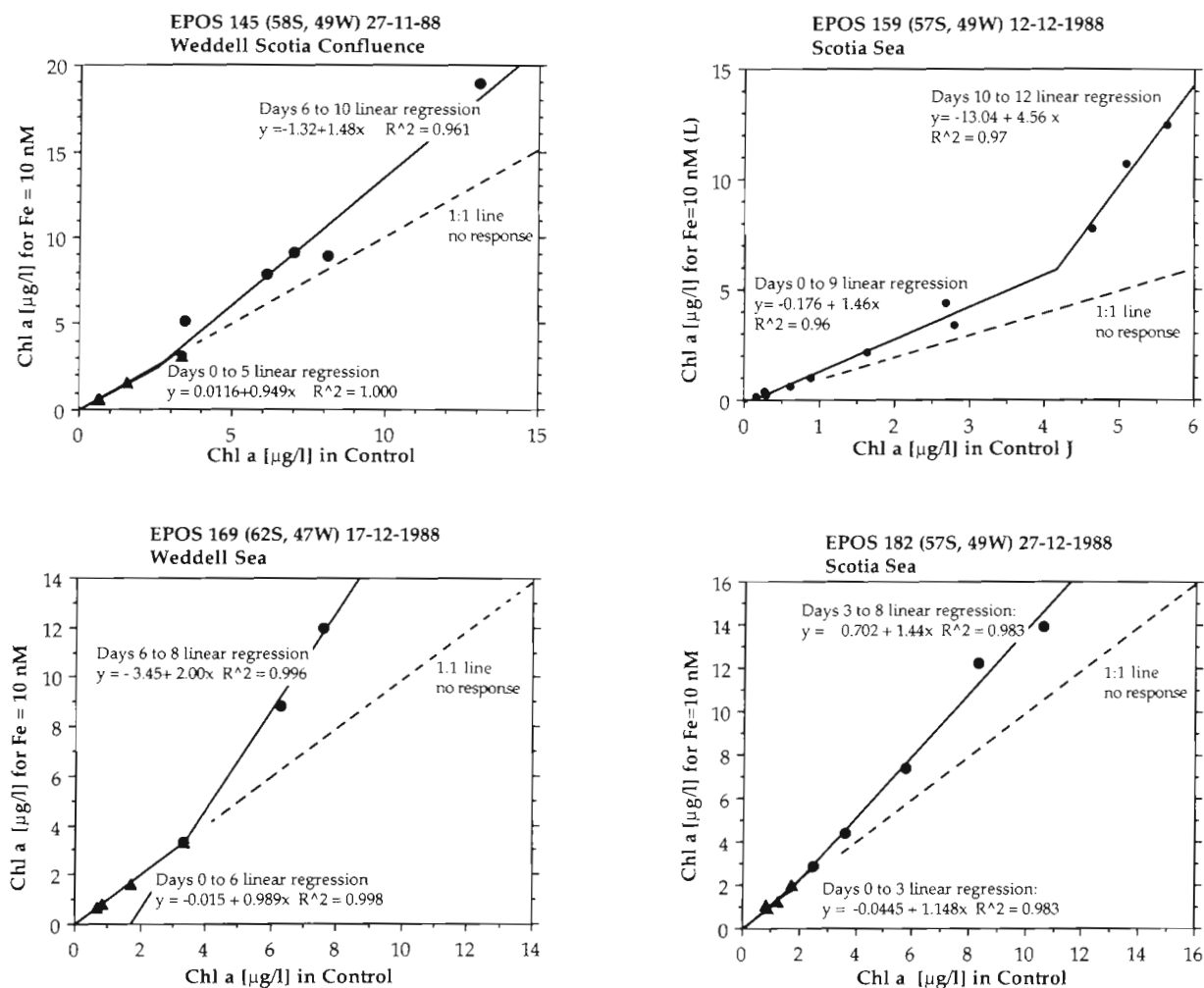
Fig. 9. Enhancement by Fe of net chlorophyll *a* (µg l⁻¹) during the first (3 to 6 d) and second stages of Expts 145, 159, 169, 182. Separate linear regression over the first and second stages. Dashed line represents 1 : 1 ratio of no-response to Fe addition. Note the distinctly stronger effect in the second stage

throughout (VERTEX T-7, T-8; Coale). This overall trend is largely in keeping with observed ambient Fe levels below and above 1 nM in the North Pacific Ocean (Martin et al. 1989) and our research area (Nolting & De Baar 1990) respectively.

With the key role of Fe in the biochemical synthesis of chlorophyll *a* it is not surprising that Fe addition enhances the net increase of chlorophyll *a* throughout the experiments. Several other pigments are also affected (Buma et al. unpubl.), as well as the assimilation of nitrate and phosphate (Figs. 3 to 7). This clearly relates with true net growth as assessed from cell counts (Buma et al. unpubl.) as well as overall POC levels. In 4 out of 5 EPOS experiments the final POC values of the Fe-enriched cultures are slightly or considerably higher than final POC values in the controls. Coale (1988) also reported enhanced carbon uptake as determined in various ways.

Physiology

With regard to the underlying physiology it is well known that Fe plays an important role in the plant cell (Glover 1977). Chlorophyll synthesis depends on Fe, and Fe-limited algae have low concentrations of this pigment (Brand et al. 1986, Rueter & Ades 1987). Fe occurs in ferredoxines and in both nitrate- and nitrite-reductase. Fe starvation has been reported to decrease the level of nitrite reductase in the cell (Verstraete et al. 1980).

The relative importance of Fe for these biochemical processes is demonstrated through linear regression analysis of our data. The negative correlation between increasing chlorophyll *a* versus decreasing nitrate varied from one experiment to the other, ranging from -0.17 to -0.78 (Table 4). Yet for each individual experiment a systematic offset was observed, such that upon
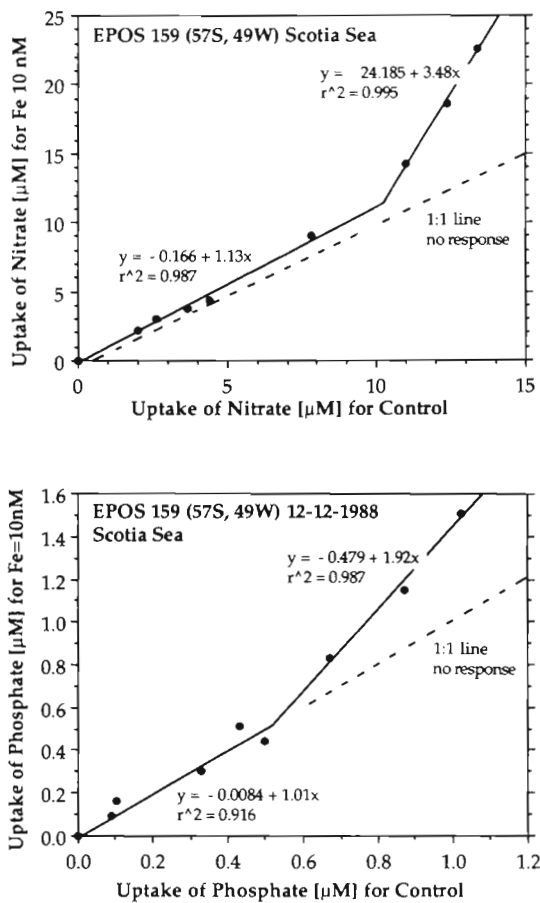
Fig. 10. More rapid utilization $(\mu M_{(t=0)} - \mu M_{(t=t)})$ of the nutrients nitrate (upper) and phosphate (lower graph) in the Fe-enriched culture versus control in Expt 159 (Scotia Sea). Linear regressions over the first and second period of the experiment. Dashed line represents 1:1 ratio of no-response to Fe addition

Table 5. The ratio Fe:P:N of dissolved nutrient elements, adapted after Redfield et al. (1963). Dissolved Fe values of Nolting & De Baar (1990), VERTEX data from Martin & Gordon (1988). Regional variation within our study area is consistent with occurrence or lack of initial response. Also both absolute and relative Fe values are high compared to those reported for waters the North Pacific Ocean. Cellular ratios (Anderson & Morel 1982) also suggest ambient Fe levels to be adequate in our study area

Experiment	Location	Fe	:	P	:	N
EPOS 159	Scotia Sea	0.001	.	1.0	:	16.5
EPOS 182	Scotia Sea	0.002	:	1.0	:	16.0
EPOS 158	W/S Confluence	0.003	:	1.0		16.8
EPOS 169	Weddell Sea	0.002	:	1.0	:	14.9
VERTEX	North Pacific	0.0004	.	1.0	:	19.0
Cellular ratio	Laboratory	0.0008	:	1.0	:	16.0

Fe addition the synthesis of chlorophyll a was stimulated more strongly than nitrate assimilation. When plotting the results of the recently reported Subarctic North Pacific study (Martin & Fitzwater 1988) the same systematic trend was found (not shown). Another way to look at this is by comparison of the slopes of $chl_{(Fe=10)} : chl_{(Control)}$ and $NO_{3(Fe=10)} : NO_{3(control)}$ (Table 4). These range from 1.31 to 2.10 and 1.20 to 1.60 respectively (chlorophyll a relation here calculated over the whole experiment period), yet in each individual experiment the slope for chlorophyll a synthesis is systematically steeper than for NO_3 assimilation (Table 4). The same was found again upon plotting the results of the North Pacific study (Martin & Fitzwater 1988) (not shown). In other words Fe most strongly stimulates chlorophyll a synthesis. This is also reflected in the final $POC : chl\ a$ ratio, being consistently lower in the Fe-enriched cultures (Table 4).

The measured POC at $t = 0$ and $t = $ end also allows calculation of overall $\Delta C : \Delta N$ ratios ranging from 3.5 to 8.3, values near or around the presumed Antarctic ratio (Jennings et al. 1984) of 5.6. In 4 out of 5 experiments this ratio was higher for Fe additions versus controls (Table 4). This suggests that Fe affects C fixation more strongly than nitrate assimilation, presumably due to the aforementioned strong stimulation of chlorophyll a, the neccessary prerequisite for carbon fixation.

Linear regression of NO_3 versus PO_4 yield ratios varying from 11 to 29, nutrient assimilation apparently fluctuating arount the Redfield value of 16:1 or a 'typical' Antarctic ratio (Jennings et al. 1984) of about 11:1. For each individual experiment $NO_3 : PO_4$ was found to be systematically higher upon Fe addition, i.e. Fe stimulates NO_3 uptake more than PO_4 uptake. Summarizing, Fe was found to stimulate net chlorophyll a increase, carbon build-up, nitrate uptake and phosphate uptake, in that order. This apparent ranking is in itself quite remarkable yet also underlines the importance of the simultaneous determination of these variables. However definite statements on the effect of Fe on plant cell physiology through these type of experiments is difficult especially when little information is available on the effect of Fe addition on heterotrophic activity. First of all a direct inhibiting effect of Fe on grazing activity would result in enhanced phytoplankton stock and a shift in the species composition. Secondly one could expect an increase in activity caused by Fe-stimulated primary production, thereby resulting in higher POC levels of heterotrophs as well as underestimation of Fe-stimulated phytoplankton parameters. The impact of grazing activity will be discussed elsewhere since it essentially does not change interpretation of the data set within the scope of this paper (Buma et al. unpubl.)

Implications for the field

When extrapolating results of the above shipboard laboratory experiments to the in situ ecosystem it appears conceivable that Fe may occasionally stimulate phytoplankton growth and utilization of macronutrients in Scotia/Weddell Sea waters, since addition of Fe did indeed enhance phytoplankton biomass in comparison with the control experiments. However, there was a steady increase of chlorophyll *a* in the control bottles as well, reaching concentrations higher than ambient chlorophyll *a* levels. This was also found in one of the 3 Subarctic North Pacific experiments (Martin & Fitzwater 1988). Such findings suggest that experimental conditions in the controls were more favourable for phytoplankton growth than conditions in the field, obviously eliminating one (or more) growth suppressing factor which only exists in the field. Here we think of the turbulence regime or the remarkably intense grazing pressure by large herbivores such as *Euphausia superba* (Hempel et al. 1989). Also the constant light at the prescribed saturation level could benefit the steady build-up of phytoplankton biomass. The experimental approach of studying one limiting factor (Fe) dictates ruling out other limiting factors (light, large grazers). Inevitably the adopted experimental conditions will always deviate from the complicated and dynamic in situ conditions.

Ambient levels of dissolved iron

It is interesting to note that in Weddell Sea water and Weddell-Scotia Confluence water the added Fe only showed a pronounced effect after several days, once the cultures had reached levels of chlorophyll *a* and nutrients comparable to the maximum and minimum levels observed respectively in the real field situation during the cruise. This would suggest that there is adequate Fe in Antarctic waters to support modest growth and biomass, but not enough for efficient utilization of macronutrient resources. In those instances where phytoplankton growth is not limited by light, and stocks not depleted through intense grazing, Fe might become a limiting factor in these areas.

The experiments from the Scotia Sea (EPOS 159, 182) showed a more pronounced Fe effect right from the start (Table 2, Fig. 9). Here Fe-stimulated growth occurred at high nutrient levels, comparable with the field situation. However, in these waters too the hypothesis of Fe limitation does not receive full support when phytoplankton growth in the control bottles is considered. Our recent analyses (Nolting & De Baar 1990) of filtered seawater collected during the same expedition yielded ambient Fe levels of about 2 to 4 nM

in the Scotia Sea. Higher levels of about 5 to 7 nM in the Confluence and Weddell Sea are consistent with the initial no-response period for the corresponding EPOS 145 and 169. These Fe levels are quite low but still an order of magnitude above those reported for surface waters in the North Pacific Ocean (Martin & Gordon 1988). Upon addition of 1 nM Fe the effect was indeed less dramatic in our experiments as compared to the one North Pacific experiment of Coale (1988) and 2 of the 3 North Pacific experiments of Martin & Fitzwater (Martin & Fitzwater 1988; their third experiment with steady growth of the control being remarkably similar to ours). When comparing our data on extended Fe:nutrient ratios with other areas (Table 5) it is obvious that Fe was relatively high in the EPOS study area. Moreover Fe:P:N ratios match with a cellular ratio given by Anderson & Morel (1982) consistent with our findings that in situ Fe concentrations can support phytoplankton growth adequately.

On the other hand surface water levels of Cd and Cu were about 0.4 to 0.8 and 3 to 4 nM respectively (Nolting & De Baar 1990), in keeping with the higher nutrient levels. Both Cd and Cu are known to be mostly toxic (Brand et al. 1986) and at the high levels encountered may suppress rather than limit Antarctic phytoplankton growth. In one experiment concurrent with EPOS 182 the added 1 nM of Cu did indeed yield slightly lower growth (Buma et al. unpubl.) (not shown, small 2.5 l experiments listed in Table 1).

Possible sources of dissolved iron

Assuming steady state it appears that either the surface waters recycle their Fe resources quite efficiently, or there is an adequate supply from external sources. Here we observe that ice zone blooms (Sullivan et al. 1988) are associated with less saline meltwater, which may also carry an elevated Fe (Mn) signal from dust input. The EPOS Leg 2 study site, downwind and downstream from relatively nearby landmasses (America, Antarctic Peninsula) may receive adequate inputs from both aeolian and continental shelf sources. Nolting & De Baar (1990) report very high dissolved Fe levels of about 60 nM for a station on the shelf of the nearby South Orkney Islands. With similarly high dissolved Fe over the shelves around the Antarctic Peninsula and the general eastward flow of waters along the peninsula into our research area (Fig. 1) the supply of dissolved Fe would be adequate. In this respect the remote Indian and Pacific sections of the Southern Ocean might be more likely candidates for occasional limitation by Fe alone. Nevertheless the importance of our Weddell-Scotia Sea study area for the overall Southern Ocean cannot be ignored. On the other hand one

cannot avoid observing the many 'dirty' icebergs which slowly melt while drifting away from the Antarctic continent. They are literally carrying along dirt – weathered material rich in Al and Fe – of which at least a portion would dissolve and become available for plant uptake. These icebergs exist not only in the Weddell Sea but all around the Antarctic continent and might well be the missing source for the Fe budget (Martin & Fitzwater 1988) of the Southern Ocean, as actually already suggested by Hart (1934, p. 186).

CONCLUSIONS

From this and other studies (Martin & Fitzwater 1988, Martin & Gordon 1988, Coale 1988) it appears that Fe deficiency may occur once surface water levels are around or below the 0.1 to 1 nM range, presumably also depending on such factors as phytoplankton species and abundance, grazing, light and availability of other nutrients (Table 5). The limited available data indicate Fe in oceanic surface waters to range from about 0.05 to 5 nM (Symes & Kester 1985, Hong & Kester 1986, Landing & Bruland 1987, Martin & Fitzwater 1988, Martin & Gordon 1988, Saager et al. 1989, Nolting & De Baar 1990, Nolting et al. 1990) and Fe deficiency may occur more commonly than hitherto acknowledged. The role of Fe and other trace elements in affecting oceanic productivity deserves considerable attention (Martin & Fitzwater 1988, Martin & Gordon 1988), notably in current programmes like the Joint Global Ocean Flux Study (De Baar et al. 1989b) which focus on past and present ocean/atmosphere exchange of CO_2 as one of the controls (Broecker & Denton 1989, De Baar & Stoll 1989) on the global carbon cycle.

The results of our study within the larger EPOS context (Hempel et al. 1989) confirm for the first time the original suggestion (Hart 1934) that Fe is one of *several* chemical and physical factors affecting phytoplankton production in the Weddell-Scotia Sea.

Fe is not the *single* limiting factor (Martin & Fitzwater 1988, Martin & Gordon 1988, Martin et al. 1989, Martin 1990) for the biota in the Scotia-Weddell-Sea, although stimulation of phytoplankton growth can be achieved by addition of Fe, especially in the Scotia Sea region. Marginal sediments may provide ample dissolved Fe supporting at least minimum growth of phytoplankton (Nolting & De Baar 1990). More remote sectors of the Southern Ocean might in the future be demonstrated to be a more likely site for occasional Fe limitation. Limitation of the vast assemblage of various Antarctic ecosystems by just one single factor, e.g. Fe, would appear unlikely. In the Weddell-Scotia Seas, an important and well-studied (Hart 1934, Hempel et al. 1989) sector of the overall Southern Ocean, Fe deficiency can only be partly responsible for the Antarctic Paradox 'that the growth of the plankton diatoms is determined by other factors than the concentration of phosphates and nitrates besides light and temperature' (Gran 1931).

LITERATURE CITED

Barber, R. T., Ryther, J. H. (1969). Organic chelators: factors affecting primary production in the Cromwell Current upwelling. J. exp. mar. Biol. Ecol. 3: 191–193

Anderson, G. C., Morel, F. M. M. (1982). The influence of aqueous iron chemistry on the uptake of iron by the coastal diatom *Thalassiosira weissflogii*. Limnol. Oceanogr. 27: 789–813

Brand, L. E., Sunda, W. G., Guillard, R. R. L. (1986). Reduction of marine phytoplankton reproduction rates by copper and cadmium. J. exp. mar Biol. Ecol. 96: 225–250

Broecker, W. S., Denton, G. H. (1989). The role of ocean-atmosphere reorganizations in glacial cycles. Geochim. Cosmochim. Acta 53: 2465–2501

Buma, A. G. J., Nolting R. F., De Baar, H. J. W., Cadée, G. C., Jacques, G., Treguer, P. (1990). Testing the iron limitation hypothesis for phytoplankton from the Southern Ocean. EOS (Trans. Am. Geophys. Un.) 71: 67 (Abstract)

Byrne, R. H., Kump, L. R., Cantrell, K. J. (1988). The influence of temperature and pH on trace metal speciation in seawater. Mar. Chem 25: 163–181

Carlucci, A. F., Cuhel, R. L. (1977). Vitamins in the south Polar Seas: distribution and significance of dissolved and particulate vitamin B_{12}, thiamine, and biotin in the Southern Indian Ocean. In: Llano, G. A. (ed.) Adaptations within marine ecosystems. Smithsonian Institute, Washington, D. C., p. 115–128

Coale, K. H. (1988). Effects of iron, manganese, copper and zinc enrichments on productivity and biomass in the Subarctic Pacific. In: Copper complexation in the North Pacific Ocean. Ph. D. dissertation, Univ. of California, Santa Cruz, Chap. 3, p. 148–199

De Baar, H. J. W., Buma, A. G. J., Jacques, G. Nolting, R. F., Tréguer, P. J. (1989a). Trace metals – iron and manganese effects on phytoplankton growth. Ber. Polarforsch. 65: 34–44

De Baar, H. J. W., Fransz, H. G., Ganssen, G. M., Gieskes, W. W. C., Mook, W. G., Stel, J. H. (1989b). Towards a joint global ocean flux study: rationale and objectives. In: Ayala-Castanares, A., Wooster, W. A., Yanez-Arancibia, A. (eds.)

Oceanography 1988, Proceedings Joint Oceanographic
Assembly. Acapulco, Mexico p. 11–33

De Baar, H. J. W., Stoll, M. H. C. (1989). Storage of carbon
dioxide in the oceans. In: Okken, P. A., Swart, R. I.,
Zwerver, S. (eds.) Climate and energy: the feasibility of
controlling CO₂ emissions. Kluwer Acad. Publ., London,
p. 143–177

El-Sayed, S. Z. (1984). Productivity of the antarctic waters – A
reappraisal. In: Holm-Hansen, O., Bolis, L., Gilles, R. (eds.)
Marine phytoplankton and productivity. Springer-Verlag,
Berlin, p. 19–34

Fogg, G. E. (1977). Aquatic primary production in the Antarctic.
Phil. Trans. R. Soc. 279: 27–38

Glover, H. E. (1977). Effect of iron-deficiency on *Isochrysis
galbana* (Chrysophyceae) and *Phaeodactylum tricornutum*
(Bacillariophyceae). J. Phycol. 13: 208–212

Gran, H. H. (1931). On the conditions for production of plank-
ton in the sea. Rapp. P.-v. Cons. perm. Explor. Mer 75:
37–46

Gran, H. H. (1932). Phytoplankton. Methods and problems. J.
Conseil VII: 343–358

Hart, T. J. (1934). On the phytoplankton of the Southwest
Atlantic and the Bellinghausen Sea 1929–1931. 'Discovery'
Rep. 8: 1–268

Harvey. H. W. (1933) On the rate of diatom growth. J. mar. biol.
Ass. U. K. 19: 253–276

Harvey, H. W. (1937a). The supply of iron to diatoms. J. mar. biol.
Ass. U. K. 22: 205–219

Harvey, H. W. (1973b). Note on colloidal ferric hydroxide in sea
water. J. mar. biol. Ass. U. K. 22: 221–225

Hayes, P. K., Whitaker, T. M., Fogg, G. E. (1984). The distribution
and nutrient status of phytoplankton in the Southern Ocean
between 20 and 70 °W Polar Biol. 3: 153–165

Hempel, I., Schalk, P. H., Smetacek, V (1989). The expedition
Antarktis VII/3 (EPOS LEG 2) of RV 'Polarstern' in 1988/
1989. Ber Polarforsch. 65: 1–199

Holm-Hansen, O. (1985). Nutrient cycles in the marine ecosys-
tems. In: Siegfried, W. R., Condy, P. R., Laws, R. M. (eds.)
Antarctic nutrient cycles and food webs. Springer-Verlag,
Berlin, p. 6–10

Holm-Hansen, O., Huntley, M. (1984). Feeding requirements of
krill in relation to food sources. J. Crust. Biol. 4(1): 156–173

Hong, H., Kester, D. R. (1986). Redox state of iron in the offshore
waters of Peru. Limnol. Oceanogr. 31(3): 512–524

Jacques, G., Minas, M. (1981). Production primaire dans le
secteur indien de l'ocean Antarctique en fin d'été.
Oceanologica Acta 4: 33–41

Jacques, G., Fiala, M., Oriol, L. (1984). Demonstration, a partir
de tests biologiques, de l'effet négligeable des elements
traces sur la croissance du phytoplancton antarctique. C.-r.
Acad. Sci. Paris 298: 527–530

Jennings, Jr. J. C., Gordon, L. I., Nelson, D. H. (1984). Nutrient
depletion indicates high primary productivity in the Weddell
Sea. Nature, Lond. 309: 51–54

Johnston, R. (1964). Sea water, the natural medium of phyto-
plankton. J. mar biol. Ass. U. K. 44: 87–109

Lancelot, C., Mathot, S. (1989). Phytoplankton: photosynthesis,
growth and respiration. Ber. Polarforsch. 65: 78–86

Landing, W. M., Bruland, K. W. (1987). The contrasting
biogeochemistry of iron and manganese in the Pacific
Ocean. Geochim. Cosmochim. Acta 51: 29–43

Marra, J. (1978). Effect of short term variations in light intensity
on photosynthesis of a marine phytoplankter; a laboratory
simulation study. Mar Biol. 46: 191–202

Martin, J. H. (1990). Glacial-interglacial CO₂ change: the iron
hypothesis. Paleoceanography 5: 1–13

Martin, J. H., Fitzwater, S. E. (1988). Iron deficiency limits
phytoplankton growth in the north-east Pacific subarctic.
Nature, Lond. 331: 341–343

Martin, J. H., Gordon, R. M. (1988). Northeast Pacific iron
distributions in relation to phytoplankton productivity. Deep
Sea Res. 35: 177–196

Martin, J. H., Gordon, R. M., Fitzwater, S. (1989). VERTEX:
phytoplankton/iron studies in the Gulf of Alaska. Deep Sea
Res. 35 (5): 649–680

Menzel, D. W., Ryther, J. H. (1961). Nutrients limiting the
production of phytoplankton in the Sargasso Sea, with
special reference to iron. Deep Sea Res 7: 276–281

Millero, F. J., Sotolongo, S., Izaguirre, M. (1987). The oxidation
kinetics of Fe (II) in seawater. Geochim. Cosmochim. Acta
51: 793–801

Neveux, J., Panouse, M. (1987). Spectrofluorometric determina-
tion of chlorophylls and pheophytins. Arch. Hydrobiol. 109:
567–581

Nolting, R. F., De Baar, H. J. W. (1990). Dissolved Fe, Cu, Zn and
Cd in the Weddell and Scotia Seas of the Southern Ocean.
EOS (Trans. Am. Geophys. Un.) 71: 67 (Abstract)

Nolting, R. F., De Baar, H. J. W., De Jong, J. T. M. (1990). JGOFS
North Atlantic Pilot Study: trace metal distributions. In: De
Baar, H. J. W. Data Report of RV TYRO JGOFS, 1989 Leg I.
Netherlands Institute for Sea Research (NIOZ) Report 1990-X

Orren, M. J., Monteiro, P. M. S. (1985). Trace element
geochemistry in the Southern Ocean. In: Siegfried, W. R.,
Condy, P. R., Laws, R. M. (eds.) Antarctic nutrient cycles and
food webs. Springer-Verlag, Berlin, p. 30–37

Priddle, J., Hawes, I., Ellis-Evans, J. C., Smith, T. J. (1986).
Antarctic aquatic ecosystems as habitats for phytoplankton.
Biol. Rev. 61: 199–238

Quéguiner, B., Legendre, L. (1986). Phytoplankton photo-
synthetic adaptation to high frequency light simulating
those induced by sea surface waves. Mar. Biol. 90: 483–491

Rueter, J. G., Ades, D. R. (1987). The role of iron nutrition in
photosynthesis and nitrogen assimilation in *Scenedesmus
quadricauda* (Chlorophycea). J. Phycol. 23: 452–457

Ruud, J. T. (1930). Nitrates and phosphates in the Southern Seas.
J. Conseil V: 347–360

Redfield, A. C., Ketchum, B. H., Richards, F. A. (1963). The
influence of organisms on the composition of seawater. In:
Hill, M. N. (ed.) The sea. Wiley Interscience, New York,
p. 26–77

Saager, P. M., De Baar, H. J. W., Burkill, P. H. (1989). Manganese
and iron in Indian Ocean waters. Geochim. Cosmochim.
Acta 53: 2259–2267

Sullivan, C. W., McClain, C. R., Comiso, J. C., Smith, W. O. Jr.
(1988). Phytoplankton standing crops within an antarctic ice
edge assessed by satellite remote sensing. J. Geophys. Res.
93: 12 487–12 498

Symes, C. J., Kester, D. R. (1985). The distribution of iron in the
Northwest Atlantic. Mar Chem 17: 57–74

Thompson, T. G., Bremner, R. W. (1935). The occurrence of iron
in waters of the northeast Pacific Ocean. J. Conseil 10: 39–47

Tréguer, P. J., Jacques, G. (1986). L'Ocean Antarctique.
Recherche 178: 746–755

Verstraete, D., Storch, R., Dunham, V. L. (1980). A comparison of
the influence of iron and nitrate metabolism of *Anabaena*
and *Scenedesmus*. Physiol. Plant 50: 47–51

Waite, T D., Morel, F. M. M. (1984). Coulometric study of the
redox dynamics of iron in seawater. Analyt. Chem. 56:
787–792

This article was submitted to the editor