Effects of iron stress on chromatic adaptation by natural phytoplankton communities in the Southern Ocean

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ABSTRACT: Effects of iron stress on chromatic adaptation were studied in natural phytoplankton communities collected in the Pacific region of the Southern Ocean. Iron enrichment experiments (48 to 72 h) were performed, incubating plankton communities under white, green and blue light respectively, with and without addition of 2 nM Fe. Pigment ratios were affected by iron addition only to a minor extent. The pigment composition as dictated by the light conditions was similar for both the iron-enriched and the unamended bottles. Upon iron addition, phytoplankton auto-fluorescence, as estimated by flow cytometry, decreased markedly, indicating iron stress of the endemic phytoplankton community. It was concluded that iron did not control chromatic adaptation via the pigment composition, but exerted a clear effect on the efficiency of electron transfer

KEY WORDS: Iron · Chromatic adaptation · Antarctic phytoplankton

INTRODUCTION

Phytoplankton in the open Pacific region of the Southern Ocean has to maintain growth under conditions of a dynamic light regime. Due to prevalent strong winds, the plant cells are frequently mixed through the water column, down to depths of more than 100 m (Mitchell & Brody 1991). Light conditions thus change not only in intensity but also in spectral composition. With depth, light is increasingly attenuated towards shorter wavelengths, eventually leaving only blue light deep in the water column. Studies that address the photoadaptation response of phytoplankton towards light quantity and quality have a long history (e.g. Wallen & Geen 1971, Richardson et al. 1983, Glover et al. 1987, Rivkin 1989, Aidar et al. 1994). Light quality affects photosynthesis. Relative to phytoplank-

ton cells cultured under white and red light conditions, cells grown under blue light conditions show a more efficient functioning of the photosynthetic apparatus (Glover et al. 1987, Grotjohann et al. 1992). Chromatic adaptation does not necessarily involve adaptation of the pigment composition (Holdsworth 1985, Schofield et al. 1990). However, photosynthetic energy conversion and subsequent incorporation of carbon strongly depend on light quality. Cells grown under blue light may contain increased numbers of reaction centers per total chlorophyll (Voskresenskaya 1984). In its turn, the functioning of the reaction centers is also wavelength-dependent with respect to the quantum yield of photosynthesis (Kroon et al. 1993). Indirectly, blue light exerts its effects on photosynthesis via various enzyme systems, e.g. ribulose bisphosphate carboxylase, controlling the Calvin cycle (Ruyters 1984).

The photosynthetic apparatus requires iron to function. The quantum yield of photosynthesis is reduced under iron-limited conditions, resulting from a decrease in efficiency of electron transfer through the photosystems (Greene et al. 1991, 1992). In addition,

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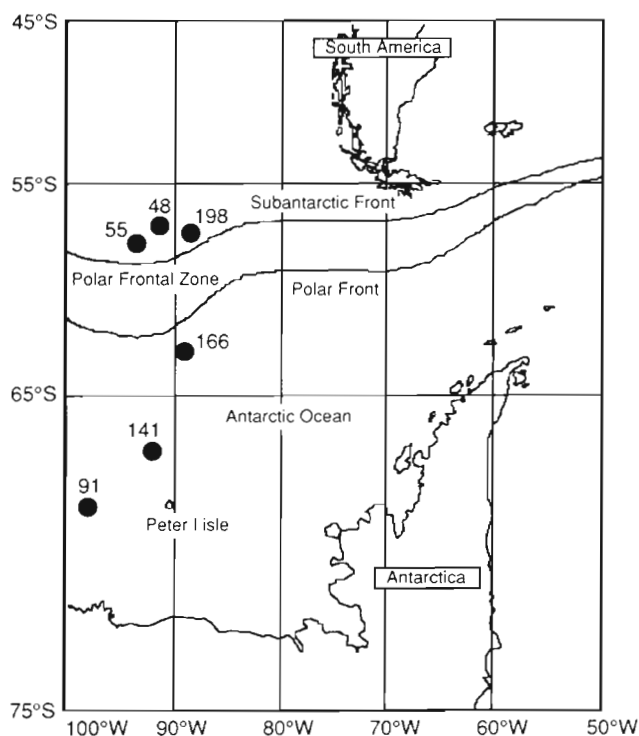
Fig. 1. Study area of cruise Ant XII/4 of the RV 'Polarstern' in April/May 1995 showing stations (48, 55, 91, 141, 166 and 198) where water was sampled for this study

iron stress may affect pigment synthesis (e.g. Geider et al. 1993, Pascal et al. 1995). Phytoplankton biomass in large parts of the Southern Ocean is often very low, whereas concentrations of major nutrients are high; at the same time, ambient iron concentrations are very low, <1 nM (Nolting et al. 1991, Westerlund & Öhman 1991, de Baar et al. 1995). Because of this, it has been suggested that iron limits growth of the existing phytoplankton community (Martin et al. 1990). This hypothesis was first proposed and tested in the Subarctic Pacific by Martin & Fitzwater (1988). In several incubation experiments in the Southern Ocean (de Baar et al. 1990, Buma et al. 1991, van Leeuwe et al. 1997) a response of the phytoplankton community upon the addition of iron was observed. Only since the application of sensitive fluorescence techniques that can measure *in situ* photosynthetic energy conversion (e.g. Kolber et al. 1994) has direct evidence for iron stress of endemic phytoplankton communities been provided.

Taking into account the dynamic light regime, which by itself imposes considerable stress upon the phytoplankton community (Sakshaug & Holm-Hansen 1986, Mitchell & Brody 1991), and the importance of iron in the process of photosynthesis, interaction of iron limitation with light limitation can be envisioned. During a cruise (Ant XII/4, RV 'Polarstern') in the Southern

Ocean (ca 90° W) in April/May 1995, experiments were performed to study the role of iron in phytoplankton physiology. On board measurements confirmed that iron concentrations in the eastern section of the Southern Pacific Ocean were low (ca 0.2 to 0.3 nM; H. de Baar, J. de Jong, R. Nolting, M. van Leeuwe & K. R. Timmermans unpubl.). To test whether the endemic phytoplankton community was adapted to the ambient spectral composition, natural plankton communities sampled at different locations were incubated under 1 of 3 different light spectra: white light, mimicking the entire light spectrum as encountered near the sea surface, and green and blue light, mimicking the light prevailing at the deeper layers of the euphotic zone. The aim of the experiments was to study the control of iron on pigment synthesis and photosynthetic efficiency, in relation to changes in the photosynthetic apparatus required for chromatic adaptation. Pigment composition and fluorescence of phytoplankton cells were analysed. The phytoplankton distribution pattern in the study area is described elsewhere (van Leeuwe et al. 1998). Effects of iron stress on the nitrogen metabolism are described in an accompanying article by Timmermans et al. (1998, in this issue).

METHODS

Experimental procedures. During the ANT XII/4 cruise aboard the RV 'Polarstern', seawater for incubations was collected at 8 different stations, north and south of the Polar Front (Fig. 1). Dissolved iron concentrations in the seawater were low for all studies (Table 1: experimental series 48, 55, 91, 141, 166 and 198). In order to prevent contamination with iron, all procedures were performed under ultraclean conditions using acid-cleaned Teflon or polycarbonate material. Seawater was collected using acid-cleaned Go-Flo samplers fixed on a polyurethane coated titanium frame. Upon recovery of the frame, the Go-Flos were mounted to the outside wall of a specially designed, clean cool container. Tubes leading through the wall were connected to the Go-Flos, by which means it was possible to tap the seawater, leading it into 10 or 20 l polycarbonate bottles (Nalgene) inside the container, without having to expose the seawater to the outside air. For each control bottle, an additional bottle was enriched with 2 nM $FeCl_3$. The bottles were placed on rollers, and were rotated at 1 to 2 rpm at ambient temperatures (1 to 5°C). For each experimental series, 3 sets of 2 bottles (i.e. a control and an iron-enriched bottle) were exposed to white, green or blue light respectively (PAR 70 to 80 µmol photons m^{-2} s^{-1}, light source: Philips TLD 36W/54), using Lee Flashlight filters for the blue and green treatments (Dark Green, HT 124,

Table 1. Date, station, location, depth of collection (m), water temperature (°C) initial dissolved iron concentration (nM), dominant phytoplankton and light incubation and analyses carried out for samples collected in the Southern Ocean (April/May 1995). SAF: Subantarctic Polar Frontal zone; ACC: Antarctic Circumpolar Curent (after Read et al. 1995). (+) carried out; (–) not carried out

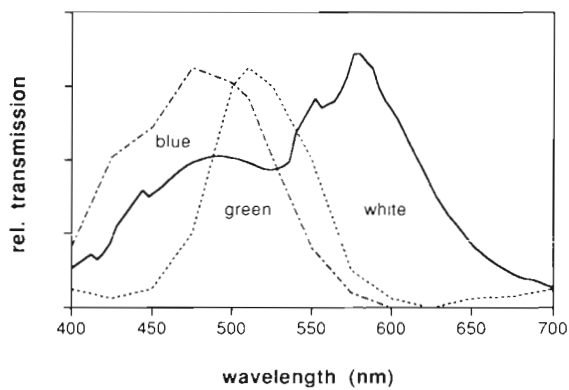| Series	Date	Stn	Latitude, longitude	Water body	Depth	Temp	[Fe]	Dominant phytoplankton	Light			Analyses	
									Blue	Green	White	Fluor.	Pigments
48	1 Apr	048	57° 15' S 91° 14' W	SAF	60	4	0.36	Flagellates, small dinoflagellates	+	+	+	+	+
55	4 Apr	055	57° 53' S 93° 32' W	SAF	40	4	0.43	Flagellates, small dinoflagellates	+	+	+	+	+
91	9 Apr	091	68° 31' S 97° 10' W	ACC	60	1.5	–	Diatoms	+	+	+	+	+
141	21 Apr	141	67° 13' S 91° 50' W	ACC	40	1.5	0.53	Diatoms	+	+	+	+	–
166	26 Apr	166	62° 60' S 89° 30' W	ACC	35	1.5	0.33	Flagellates	+	–	+	+	–
198	2 May	198	57° 31' S 89° 02' W	SAF	35	5	0.26	Flagellates, small dinoflagellates	+	+	+	+	–

Fig. 2. Transmission spectra of the cool-white light source (—— white) and of the colours of the 2 Lee Flashlight filters used in the experiments (-·--- blue; ----- green)
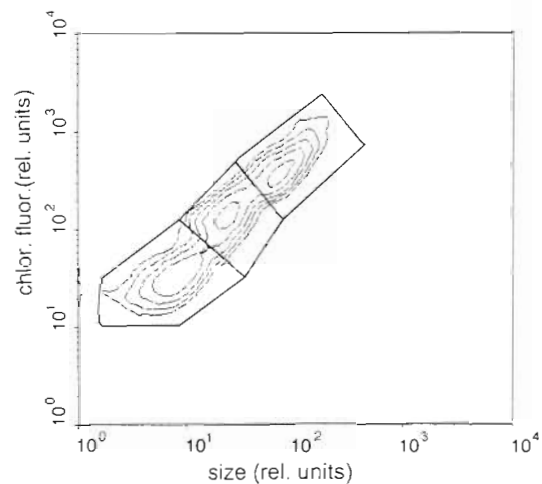

Fig. 3. Diagram of clusters as detected by the flow cytometer (Series 166, at $t = 0$). The horizontal axis displays Forward Scatter (FS), as an indication of cell size, and the vertical axis displays autofluorescence (FL3: red fluorescence), indicating cellular chl a content. Values for FL3 were typically based on 1000 to 2000 observations, with a typical SD of 30 to 50%

and Lagoon Blue, HT·172; Fig 2). The plankton was incubated under an 8 h light:16 h dark regime. At $t = 0$, samples were taken for direct analysis of cell number and auto-fluorescence (applying flow cytometry), community structure (microscopy), and initial dissolved Fe concentrations. In order to follow the development of biomass, samples were taken for flow cytometry every 12 h, until $t = 72$ h, with intensified sampling from $t = 48$ h onwards. At $t = 48$ h, samples were taken for pigment analyses and cellular fluorescence. In addition, iron levels were followed throughout the experiments. The results on iron and nutrient analyses are described elsewhere (Timmermans et al. 1998).

Analytical procedures. *Flow cytometry:* Cells were collected every 12 h. Cell numbers were determined by counting 1 ml samples using a flow cytometer (Epics XL MCL, 488 nm laser, size range <40 µm). Different clusters were distinguished on the basis of cell size

(Forward Scatter) and cellular fluorescence (Fig. 3). Red fluorescence (FL3) and orange fluorescence (FL2) were recorded using emission wavelengths between 656 and 700 nm and between 530 and 590 nm respectively. FL3 is a measure for chlorophyll a (chl a) fluorescence and FL2 a measure for phycoerythrin fluorescence. The flow rate and fluorescence signals were calibrated daily using fluorescence beads (EPICS). The cell samples were kept in the dark at least 20 min before analysis.

Pigments: Samples taken for pigment analyses (minimum 4 l) were filtered gently (pressure <0.15 bar) over GF/F Whatman filters. The filters were flash-

cooled by dipping in liquid nitrogen and subsequently stored at –20°C until analysis at the home laboratory. Pigments were extracted in 90% methanol (2% ammonium buffered). The pigment composition was determined by HPLC analysis according to Kraay et al. (1992) using a C18 column.

Community structure: The composition of the phytoplankton community was determined qualitatively by an inverted microscope after fixation with an acid Lugol's solution.

Not all parameters described were determined for all experimental series as large volumes of seawater were required for the different analyses.

RESULTS

Community structure of the experiments

Phytoplankton biomass was generally low, chl a levels never exceeding 0.3 µg l^{-1}. Chlorophyll concentrations of the northernmost stations (north of the Subantarctic Front), covering Series 48, 55 and 198, averaged 0.28 µg chl a l^{-1}. These chlorophyll levels coincided with total cell numbers averaging between 5000 and 7000 cells ml^{-1}. Series 91, 141 and 166, with samples taken at stations in the Antarctic Circumpolar Current, contained cell numbers around 3000 cells ml^{-1}, with lowest chl a values (ca 0.1 µg l^{-1}) for Series 166. Series 91 and 141 had chl a levels of ca 0.3 µg l^{-1}, and were dominated by large diatoms (>25 µm) (40 to
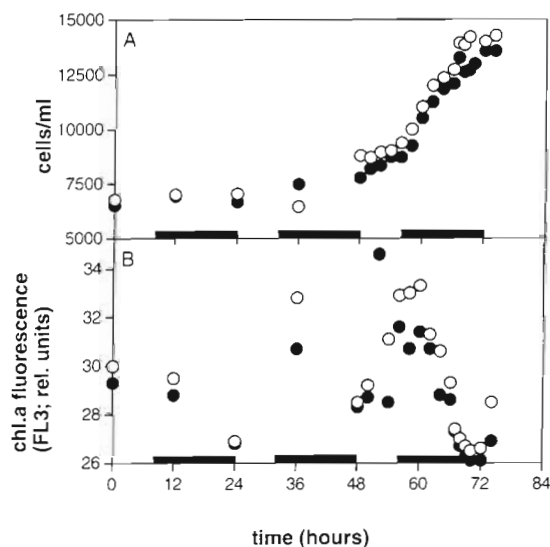

Fig. 4. Development of (A) cell numbers (cells ml^{-1}) and (B) red fluorescence (arbitrary units) as recorded by flow cytometry for both a representative cluster from a control bottle (O) and an iron-enriched bottle (●). Dark bars represent the dark periods

60% of total chl a) which could not properly be quantified by the flow cytometer (Table 1). These stations contained high numbers of *Fragilariopsis kerguelensis*; several (unidentified) *Coscinodiscus* and *Thalassiosira* species were also observed. The diatom communities consisted furthermore of small pennates and various *Chaetoceros* species (Series 141). Various dinoflagellates were also present. The phytoplankton communities analysed for Series 48, 55 and 198 were composed mainly of small flagellates (ca 90% of chl a), typically Chrysophyceae (characterised by 19'butanoyloxyfucoxanthin, BUTA) and Prymnesiophyceae (19'hexanoyloxyfucoxanthin, HEXA). In addition, elevated levels of chl b, indicating the presence of Prasinophyceae, were observed in Series 48 and 55 (ca 10%) and 198 (ca 20%) respectively. Series 166 was characterised by an enhanced ratio of fucoxanthin (FUCO) to HEXA, suggesting (in the absence of diatoms) the presence of *Phaeocystis* sp.

Growth response

For all experimental series a distinct lag phase in growth response was observed. Following a slight increase in cell number over the first 2 d of incubation, cell numbers did not increase again until after 48 h (Fig. 4A). Apparently, the structure of the phytoplankton community was no different at $t = 0$ than at $t = 48$ h. A clear diurnal signal was observed for chl a fluorescence (FL3, Fig. 4B). Growth patterns as depicted in Fig. 4 were identical for all experiments, irrespective of light quality. No significant differences between control bottles and iron-enriched bottles were observed.

Pigments

Experimental Series 48 and 55 consisted mainly of flagellates, and contained elevated levels of HEXA and BUTA. Part of the phytoplankton community was formed by green algae, as reflected in the presence of chl b (Table 2, Fig. 5). Series 91 contained HEXA and FUCO, and elevated levels of chl c_2, which characterise a mixed population of diatoms and flagellates (Table 2).

None of the different plankton communities incubated showed a significant response towards iron addition in their relative pigment patterns (Fig. 5). Only a small, but significant, decrease in the chl b concentration (expressed in percentage of the total pigment content) was observed following iron addition under white and blue light (ANOVA, $p < 0.05$) (Fig. 5). This change was not consistent for green light incubations. An increase in the ratio of chl c_2 to c_3 for iron-

Table 2. Chl c and fucoxanthins expressed as percentages of total chl a. Values are presented for Series 48, 55 and 91 for both the control bottles and the bottles enriched with iron ('2 nM Fe') under white, green and blue light conditions

Light	Series		Chl c_3	Chl c_2	Chl c_{2+3}	Chl c_2:chl c_3	BUTA	HEXA	FUCO
White	48	Control	2.64	4.54	7.18	1.72	3.45	11.61	2.81
		2 nM Fe	2.67	5.17	7.84	1.93	3.68	11.82	2.81
	55	Control	2.63	3.96	6.59	1.51	3.24	11.81	2.85
		2 nM Fe	2.42	4.38	6.80	1.81	3.66	12.62	3.14
	91	Control	3.62	8.18	11.80	2.26	1.42	5.66	22.60
		2 nM Fe	3.75	8.44	12.19	2.25	0.87	2.70	23.39
Green	48	Control	4.07	6.24	10.31	1.53	5.40	13.25	6.28
		2 nM Fe	3.97	5.74	9.71	1.45	5.23	14.62	6.13
	55	Control	3.64	5.17	8.81	1.42	4.90	11.68	6.77
		2 nM Fe	4.76	5.40	10.16	1.13	3.75	13.81	5.95
	91	Control	4.95	8.09	13.04	1.64	1.25	2.75	25.39
		2 nM Fe	5.52	8.02	13.54	1.45	1.16	3.48	23.99
GBlue	48	Control	3.62	5.98	9.60	1.65	5.28	10.85	3.30
		2 nM Fe	3.89	6.40	10.29	1.64	5.28	12.63	3.84
	55	Control	3.38	5.55	8.93	1.64	4.39	10.24	3.92
		2 nM Fe	3.24	5.16	8.40	1.59	5.36	12.66	4.78
	91	Control	4.26	8.18	12.44	1.92	1.00	4.47	22.30
		2 nM Fe	4.40	7.87	12.27	1.79	1.13	4.66	22.73

enriched bottles was observed under white light only (Table 2). No changes were observed within the pool of fucoxanthins in relation to iron addition (Table 2).

Iron addition resulted in a decrease in the ratio of chl b to chl a (ANOVA, $p < 0.05$). For the total pool of chl c (c_1, c_2, c_3) as well as for the carotenoids, the ratio to chl a was not affected by the iron conditions. Neither the differences in pigment content nor the pigment ratios to chl a (as they were affected by light quality) were found to be significant (Fig. 6).

Cellular fluorescence

For each experimental series different numbers of cell clusters with variable values for chl a fluorescence could be distinguished (FL3) (see Fig. 3). In addition to responses described for the phytoplankton community as a whole (i.e. considering the total community as one cluster), effects of iron stress were revealed by study of these clusters separately. Consistent with the decrease in cellular fluorescence observed for the total community upon iron addition, FL3 decreased for nearly all individual clusters. Under white light, a general decrease ranging from 2 to 20% was recorded (Fig. 7). Changes in FL3 recorded for green and blue light were highly variable, and did not show a clear trend (data not shown).

Orange fluorescence induced by phycoerythrin (FL 2) was detected for Series 48, 55 and 198 (Table 3). Values for FL2 were highest under

green light. In response to iron addition, FL2 generally decreased (Fig. 7). Only under white light did FL2 not change for Series 198. The ratio of FL2 to FL3
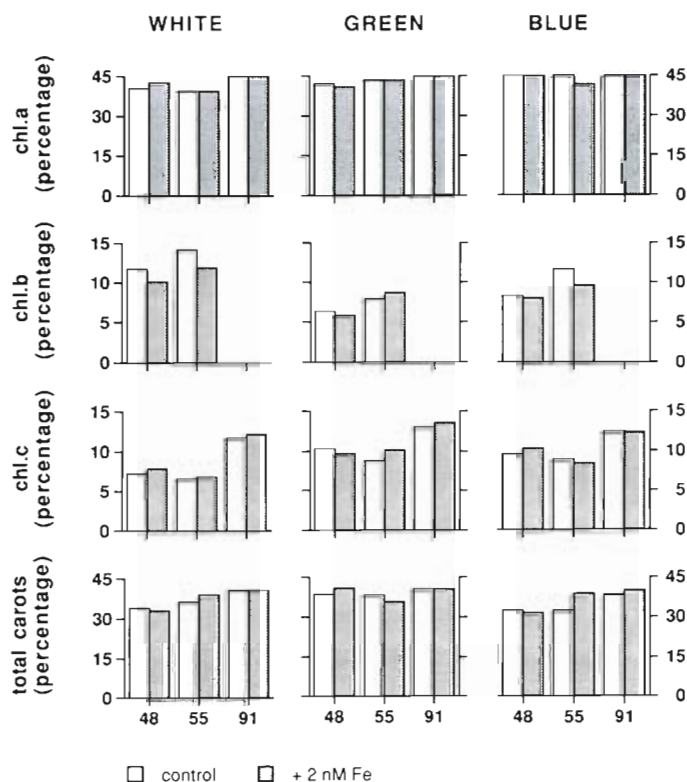

Fig. 5. Pigments expressed as a percentage of total pigments for phytoplankton cultured under white, green and blue light conditions with (2 nM Fe) and without (control) iron addition. Pigments were measured in Series 48, 55 and 91. Carots: carotenoids

decreased for iron-enriched bottles relative to the control bottles under white and green light conditions (Table 3). Data recorded under blue light were again variable (data not shown).

DISCUSSION

Development of the phytoplankton communities

Open ocean areas are generally dominated by nanoplankton (3 to 10 µm; green algae, Prymnesiophyceae, Cryptophyceae). The pigment composition of these species is characterised by chl b and/or chl c_2 and chl c_3. When mixed through the water column, and hence experiencing predominantly blue-green light, these species are considered to be best adapted by their pigment composition to the ambient light spectrum (Richardson et al. 1983, Bidigare et al. 1990). The phytoplankton communities encountered during the cruise confirmed this concept, although at 2 stations diatoms dominated. During incubation, the various phytoplankton communities behaved fairly similarly. A lag phase of 48 h, as is generally observed during incubation experiments (e.g. Scharek et al. 1997), indicated that the observations described in this study largely concerned the cells of the initial plankton population, although a small increase in cell number was observed over the first 2 d (Fig. 4). Neither can we exclude the selective effect of grazers on the community structure. A general feature observed was the clear diurnal pattern in cellular fluorescence, with a maximum early in the dark period. A diurnal rhythm has previously been described, and may be ascribed to changes in the membrane configuration of the chloroplast (Prézelin & Ley 1980). The magnitude of the fluorescence rhythm may form a serious bias if the fluorescence signal is directly correlated with phytoplankton biomass. This daily variation may also affect phytoplankton physiology. In order to avoid deviation due to cellular rhythm, samples from the incubations were taken at fixed hours.

Fig. 6. Pigment to chl a ratios (avg ± SD, n = 2 or 3) for phytoplankton cultured under white, green and blue light conditions with (2 nM Fe) and without (control) iron addition

Pigments

Iron is essential for pigment synthesis, as the synthesis of both chlorophyll (Guikema & Sherman 1983, Greene et al. 1991) and carotenoids (Terry 1980, Geider et al. 1993, Morales et al. 1994, Pascal et al. 1995) requires iron. An increase in pigment content follow-
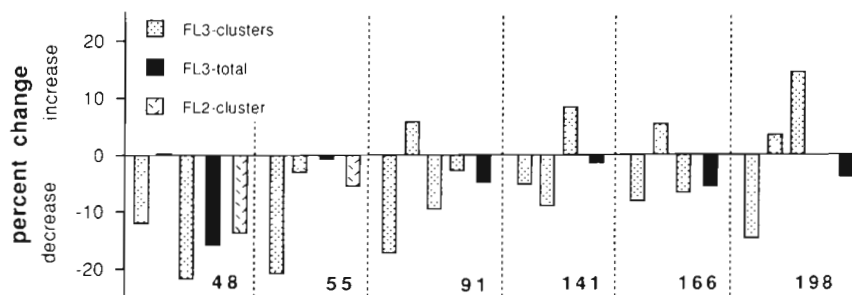

Fig. 7 Changes in cellular fluorescence upon iron addition (red = FL3, orange = FL2), calculated as a percentage of fluorescence recorded for the control bottles [(iron-enriched-control)/control] × 100. FL2 always consisted of single clusters. FL3 is presented for separate clusters and for the community as a whole. Data are presented only for phytoplankton cultured under white light
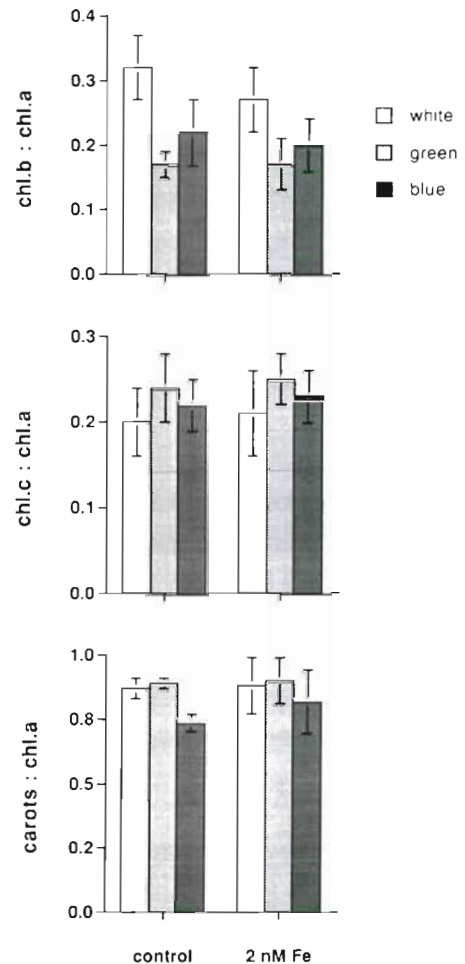
Table 3. Phycoerythrin fluorescence (FL2) and ratio of FL2 to FL3 (chlorophyll fluorescence) for phytoplankton communities exposed to white and green light

Series			White	Green
FL2	48	Control	24.1	27.9
		2 nM Fe	20.8	24.8
	55	Control	23.6	25.1
		2 nM Fe	22.3	24.3
	198	Control	28.6	35.9
		2 nM Fe	28.6	35.2
FL2:FL3	48	Control	2.71	3.05
		2 nM Fe	2.66	2.96
	55	Control	3.29	3.39
		2 nM Fe	3.21	3.38
	198	Control	3.76	3.74
		2 nM Fe	3.66	3.72

ing iron addition has generally been observed. Due to the short period of incubation applied in our experiments (all samples were taken at $t = 48$ h) in relation to low initial biomass, and the possible interfering effects of grazing, a response to iron addition in terms of absolute concentrations could not be determined accurately. The relative pigment composition examined for different plankton communities was, in general, similar for the control and the iron-enriched bottles. Iron stress apparently did not affect the response of pigment synthesis to light quality. This showed that the different pathways of pigment synthesis (Terry 1980, Morales et al. 1990, Pascal et al. 1995) are in balance even under conditions of iron stress.

Minor changes were only observed in the relative proportions of chlorophyll. Upon iron addition, the proportion of chl a decreased under white and blue light, relative to the accessory pigments. This resulted in a decrease in the chl b to chl a ratio for phytoplankton incubated under white light. Possibly, the decrease in chl b was related to a shift in species composition. The differences in the pigment concentrations between the control and the iron-enriched bottles were only very small, and little growth may have been required to induce the observed changes. In fact, under white light the ratio of chl c_2 to chl c_3 increased for iron-enriched bottles (Table 2). Overall, the data indicate an increased contribution of diatoms for iron-enriched bottles under white light conditions. It appears that white light induced an enhanced growth response by diatoms relative to flagellates. This may be explained by the difference in pigment composition between the 2 groups. Diatoms contain elevated levels of fucoxanthin, which has an absorption maximum at 475 nm (e.g. Jeffrey 1980) and, upon iron addition, allows better use of available light, as compared to flagellates, which lack this carotenoid.

Cellular fluorescence

An important consequence of iron limitation is a decrease in efficiency of electron transfer due to a decrease in structural proteins associated with the PS II reaction centers (Greene et al. 1991, 1992, Geider et al. 1993). If the integrity of the photosynthetic membranes is restored as a result of iron addition, energy transfer within the photosystems may be enhanced. Direct indications of the recovery of the photosynthetic membranes can be acquired by examining cellular fluorescence. In response to iron addition, decreased cellular fluorescence was measured for the iron-enriched bottles relative to control bottles (Fig. 7). Since fluorescence signals were obtained by flow cytometry (F_{cyt}), interpretation may not be straightforward. As thoroughly discussed by Neale et al. (1989), F_{cyt} values are probably intermediate between minimal fluorescence (F_0) and a maximum fluorescence signal (F_{max}), as is obtained after complete saturation of the primary electron acceptor Q_a in PS II. F_{max} is most sensitive to the activity of PS II, and thus best records changes in efficiency of light transfer through the photosystems. The merits of fluorescence data obtained by flow cytometry are illustrated by Fig. 7. Trends observed for FL3 and FL2 (Appendix 1), indicating chl a and phycoerythrin fluorescence respectively, were reproducible, generally decreasing upon iron addition. This suggests that the fluorescence signal as recorded by flow cytometry was most sensitive to changes in the photochemistry of PS II. Upon iron addition, light is used more efficiently in the photosystems, and less light energy is spilled as fluorescence (Greene et al. 1992). Hence, the decrease in cellular fluorescence recorded for the phytoplankton population must be considered as a sign of iron stress of the original phytoplankton population.

These results are consistent with recent experiments performed in the eastern equatorial Pacific Ocean. Enrichment of natural phytoplankton with iron resulted in an immediate response in photosynthetic efficiency, leading to a reduction in variable fluorescence as recorded using a fast-repetition-rate fluorometer (Behrenfeld et al. 1996). An increase in the cellular concentrations of chlorophyll apparently followed at a slower pace. Cellular fluorescence measured after several days of incubating natural phytoplankton populations from the equatorial Pacific with and without iron addition reflected this increase in cellular pigment concentrations (Zettler et al. 1996). The fluorescence recorded by flow cytometry in this study showed an increase that could be attributed to increased cellular chl a concentrations.

Phycoerythrin-containing species were present in 3 of the 6 experimental series from stations sampled in Subantarctic waters. The FL2 signal was higher under

green light than under white light. This illustrated adaptation towards green light; green light had its maximum at 510 nm, which is near the absorption maximum of phycoerythrin (Vesk & Jeffrey 1977, Glover et al. 1987). The ratio FL2:FL3 decreased for iron-enriched bottles (Table 3). These changes indicate a higher susceptibility of chl a relative to phycoerythrin towards iron deficiency (cf. Rueter & Unsworth 1991 and Hardie et al. 1983). This may relate to the function of phycoerythrin in nitrogen storage (Boussiba & Richmond 1980, Wyman et al. 1985), implying possible secondary effects of iron stress on phycoerythrin concentrations via the effects of iron on the nitrogen metabolism rather than direct effects on the pathways of phycoerythrin synthesis (Wilhelm 1995).

ment ratio that did occur originated from changes in the phytoplankton community. Previous studies have already noted that the control on pigment synthesis is largely compensated for by a decrease in package effect, whereby the absorption cross section of phytoplankton cells increases under iron limitation (Greene et al. 1991). These processes are also of importance with regard to chromatic adaptation. It appears not so much that the constitution of the cellular pigment composition is responsible for the adaptation but that the quantum yield of photosynthesis is controlled by the efficiency of electron transfer. Thus, chromatic adaptation may be affected by iron stress predominantly in the functioning of the photosynthetic membranes, whereas pigment synthesis appears to be far less important.

Summary

Phytoplankton communities in the Pacific region of the Southern Ocean responded to the addition of iron mainly through a decrease in cellular fluorescence, suggesting iron stress in the original phytoplankton population. These experiments confirm the idea that within the process of photosynthesis, iron exerts its effect mainly on the efficiency of electron transfer, rather than on pigment synthesis. The changes in pig-

Appendix 1. Chlorophyll fluorescence (FL3) and phycoerythrin fluorescence (FL2), recorded at t = 48 h. Effects of iron stress were found significant at $p < 0.02$ (ANOVA)

Series		White		Green		Blue	
		Control	2 nM Fe	Control	2 nM Fe	Control	2 nM Fe
48	FL3	35.90	36.00	44.70	44.90	41.30	41.00
	FL3	10.00	7.83	9.93	9.50	9.17	9.13
	FL3	8.88	7.81	9.15	8.37	8.28	9.15
	FL2	24.10	20.80	27.90	24.80	23.90	26.80
55	FL3	8.43	6.68	7.70	7.85	7.46	7.33
	FL3	7.17	6.95	7.40	7.19	7.17	7.38
	FL2	23.60	22.30	25.10	24.30	23.30	24.20
91	FL3	62.40	51.70	59.60	58.30	56.80	47.20
	FL3	13.60	14.40	14.40	14.40	14.40	13.30
	FL3	221.50	200.30	247.00	243.30	193.40	129.50
	FL3	57.30	55.70	58.50	59.20	56.00	55.50
141	FL3	13.50	12.80	13.30	14.50	13.00	14.80
	FL3	52.20	47.50	52.30	54.40	53.60	50.40
	FL3	228.70	247.90	260.60	272.60	258.50	235.50
166	FL3	3.44	3.16			3.36	3.43
	FL3	14.60	15.40			14.70	15.60
	FL3	47.40	44.20			47.40	50.40
198	FL3	4.03	3.44	5.16	4.91	4.56	4.37
	FL3	11.50	11.90	15.00	14.30	14.40	12.90
	FL3	37.40	42.80	44.90	44.80	62.20	44.40
	FL3	7.61	7.82	9.61	9.46	8.68	8.79
	FL2	28.60	28.60	35.90	35.20	32.60	32.90

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