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Limitation of algal growth by iron deficiency in the Australian Subantarctic region

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Abstract. In March 1998 we measured iron in the upper water column and conducted iron- and nutrient-enrichment bottle-incubation experiments in the open-ocean Subantarctic region southwest of Tasmania, Australia. In the Subtropical Convergence Zone (~42°S, 142°E), silicic acid concentrations were low (< 1.5 μM) in the upper water column, whereas pronounced vertical gradients in dissolved iron concentration (0.12-0.84 nM) were observed, presumably reflecting the interleaving of Subtropical and Subantarctic waters, and mineral aerosol input. Results of a bottle-incubation experiment performed at this location indicate that phytoplankton growth rates were limited by iron deficiency within the iron-poor layer of the euphotic zone. In the Subantarctic water mass (~46.8°S, 142°E), low concentrations of dissolved iron (0.05-0.11 nM) and silicic acid (< 1 μM) were measured throughout the upper water column, and our experimental results indicate that algal growth was limited by iron deficiency. These observations suggest that availability of dissolved iron is a primary factor limiting phytoplankton growth over much of the Subantarctic Southern Ocean in the late summer and autumn.

Introduction

The Subantarctic region of the Southern Ocean, between the Polar and Subtropical water masses, covers roughly one-tenth of the world ocean area [*Deacon*, 1984; *Banse*, 1996]. The region sustains a significant fraction of oceanic net primary production [*Field et al.*, 1998], and constitutes one of the strongest oceanic sinks for atmospheric CO_2, due in part to biological uptake [*Metzl et al.*, 1999]. Despite the potential importance of algal production in the Subantarctic waters to the global carbon budget, few studies have examined the factors which control primary production in this region [Boyd et al., 1999a]. The Subantarctic surface waters are generally replete with nitrate and phosphate, yet support relatively low algal biomass and production [*Comiso et al.*, 1993; *Banse*, 1996; *Boyd et al.*, 1999a]. Availability of light, iron and silicic acid [*Martin et al.*, 1990a; *Nelson and Smith*, 1991; *Dugdale et al.*, 1995; *Sedwick et al.*, 1997; *Sunda and Huntsman*, 1997; *Boyd et al.*, 1999a], and zooplankton grazing [*Cullen,* 1991; *Banse*; 1996] have been suggested as the major controls on algal production in the Subantarctic.

Low dissolved iron concentrations are thought to limit algal growth rates in much of the Southern Ocean [*Martin et al.*, 1990a; *de Baar et al.*, 1995], although this hypothesis remains largely untested within the Subantarctic region. Few iron measurements have been reported for this oceanic province, and these data are mostly from the area around the Polar Front [e.g., *Martin et al.*, 1990b; *de Baar et al.*, 1995; *Löscher et al.*, 1997]. *Sedwick et al.* [1997] reported dissolved iron concentrations of 0.14-0.33 nM for Subantarctic waters southwest of Tasmania in January 1995, and speculated that these concentrations were low enough to limit phytoplankton production. More recently, *Boyd et al.* [1999a] reported low concentrations of dissolved iron (~0.2 nM) in Subantarctic waters southeast of New Zealand, where flavodoxin assays and the results of bottle-incubation experiments suggested that algal growth was limited by the availability of iron and light.

Here we report dissolved iron concentrations for water-column samples collected from the Subantarctic region southwest of Tasmania, Australia in March 1998 (austral autumn), together with the results of iron- and nutrient-addition bottle-incubation experiments using resident plankton populations. These data suggest that low iron concentrations limit phytoplankton growth rates over much of the Subantarctic Southern Ocean during the late summer and autumn.

Results and Discussion

In March 1998, the RSV *Aurora Australis* was used in a biogeochemical study of the Subantarctic Southern Ocean southwest of Tasmania. This is an oceanographically-complex region, where the Subtropical and Subantarctic water masses mix over a broad zonal band [*Rintoul et al.*, 1997; *Griffiths et al.*, 1999]. We will describe surface waters in this region based on the salinity (S) of the upper mixed layer [*Griffiths et al.*, 1999]: the Subtropical water mass (S > 35.2), the Subtropical Convergence Zone (34.8 < S < 35.2), the Subantarctic water mass (34.2 < S < 34.8) and the Polar water mass (S < 34.2). Our cruise track included stations along 141-142°E, from the Subtropical Convergence Zone at 42°S to the Polar water mass at 55°S, crossing the Subantarctic Front near 51°S (Fig. 1). Surface-water concentrations of nitrate and silicic acid ranged from around 5 μM and 0.1 μM, respectively, near 42°S, to 25μM and 3 μM near 55°S. Here we present results from two 4-day process stations occupied during the cruise, Process Station 1 (42°04'S, 141°52'E, 1-5 March) and Process Station 2 (46°46'S, 142°E, 8-12 March), nominally located within the Subtropical Convergence Zone and the Subantarctic water mass, respectively (Fig. 1).

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At these stations we collected seawater from the upper water column for iron measurements and iron- and nutrient-addition bottle-incubation experiments. Iron was determined by flow injection analysis in seawater collected and filtered (0.4 μm) using trace-metal clean techniques, as described by *Sedwick et al.* [1997]. Seawater for the bottle experiments was collected from ~20 m depth while underway at 1-2 knots, through acid-cleaned polyethylene tubing using a Teflon diaphragm pump [*Hutchins et al.*, 1998]. The pumped seawater was discharged in a container van under Class-100 filtered air, where sample containers used in the experiments were rinsed and filled. The seawater was gently mixed in acid-cleaned 50-L polyethylene carboys, then transferred into acid-cleaned 2.7-L (Process Station 1) or 2.4-L (Process Station 2) polycarbonate bottles.

In the experiment at Process Station 1, these bottles were either (1) enriched with nutrients (10 μM nitrate, 1 μM phosphate, 10 μM silicic acid), (2) enriched with nutrients and iron (nutrients as described above plus 1.7 nM iron), or (3) left untreated as controls. In the experiment at Process Station 2, bottles were either (1) enriched with silicic acid (9 μM), (2) enriched with iron (1.9 nM), (3) enriched with iron and silicic acid (1.9 nM and 9 μM, respectively), or (4) left untreated as controls. Nitrate, phosphate and silicic acid were added as aqueous solutions of sodium nitrate, disodium hydrogen orthophosphate and sodium metasilicate, respectively, each purified (i.e., iron removed) using Chelex-100 ion-exchange resin. Iron was added as a solution of ferric chloride in dilute hydrochloric acid. After filling, the bottles were sealed and set in circulating surface seawater in deck incubators shaded to ~50% of incident irradiance. The temperature of seawater in the incubators varied to within ± 2°C of the initial *in situ* temperature of the seawater used in the experiments. Duplicate bottles for each treatment were harvested over an 8-day period, and sub-sampled for measurements of dissolved nutrients (by flow analysis), size-fractionated chlorophyll *a* (Chl *a*, by fluorometry), and other parameters. The detailed results of these experiments and concurrent large-volume iron/irradiance perturbation experiments are reported in *Hutchins et al.* [in prep.] and *Boyd et al.* [1999b].

Process Station 1: Subtropical Convergence Zone

The upper water column at Process Station 1 was weakly stratified, with a well-defined pycnocline evident at depths

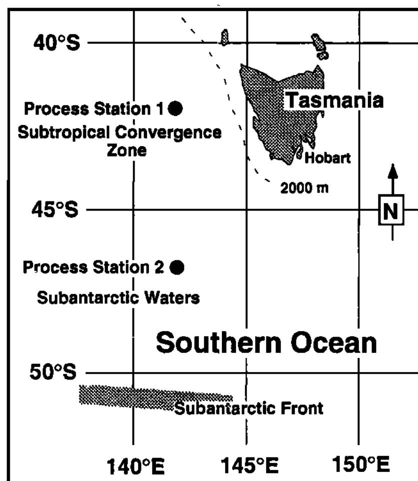

Figure 1. Location of the study area and Process Stations 1 and 2.

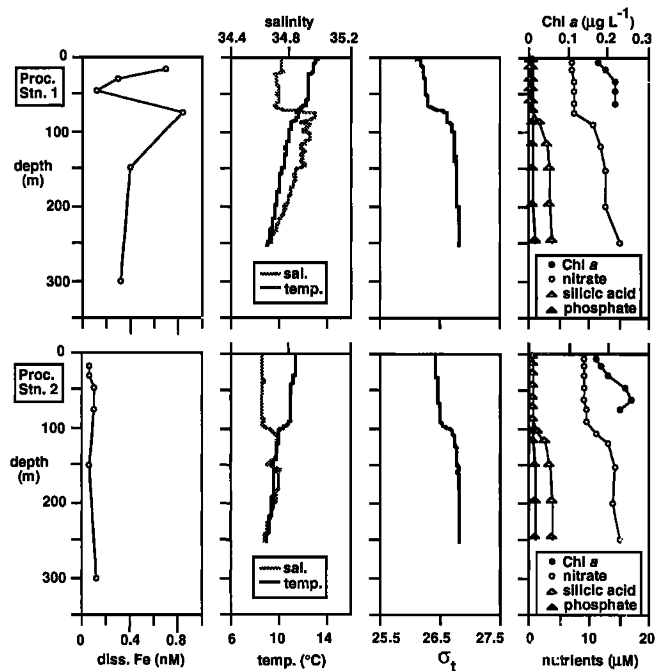

Figure 2. Vertical profiles of dissolved iron, temperature, salinity, σ_t, macronutrients and fluorometric chloropyll a from Process Stations 1 (upper panels) and 2 (lower panels).

ranging from 60 to 90 m. The depth of 1% of surface irradiance was 84 m. Hydrographic structure within the euphotic zone was complex, reflecting the interleaving of high-salinity Subtropical Convergence Zone waters (S > 34.8) with lower-salinity Subantarctic waters (S < 34.8), and there was considerable variation in this salinity structure during the 4-day site occupation. Figure 2 (upper panels) shows water-column profiles of dissolved iron, temperature, salinity, σ_t, nutrients and Chl *a* from Process Station 1. An intrusion of low-salinity Subantarctic water is evident between depths of ~20 and 70 m (S < 34.75). The iron profile is consistent with this hydrographic layering, with relatively high dissolved iron concentrations (> 0.7 nM Fe) typical of the Subtropical waters observed at depths of 15 m and 75 m, and lower concentrations (< 0.3 nM Fe) typical of Subantarctic waters observed at depths of 30 m and 45 m [cf. *Sedwick et al.*, 1997]. Given the proximity of this site to the Australian continent, the relatively high dissolved iron concentration at 15 m depth may also reflect mineral aerosol input at the sea surface, as observed in the central North Pacific [*Bruland et al.*, 1994].

Algal biomass was relatively low throughout the upper mixed layer (0.18-0.22 μg L^{-1} Chl *a*), as were modelled algal production rates derived from ^{14}C incubations (~500 mg C m^{-2} d^{-1}; F. B. Griffiths, unpublished data). Major phytoplankton taxa at this station included dinoflagellates, diatoms, flagellates, coccolithophorids, and cyanobacteria (R. van den Enden and S. Wright, pers. comm.). Seawater collected for the bottle experiment contained 6.7 μM nitrate+nitrite, 0.60 μM phosphate, 1.0 μM silicic acid, 0.20 nM dissolved iron and 0.17 μg L^{-1} Chl *a* (> 0.2 μm size fraction). The bottles were amended with nitrate, phosphate and silicic acid because low nutrient concentrations (< 5 μM nitrate, < 0.5 μM phosphate, < 2 μM silicic acid) were anticipated, based on previous field observations [*Sedwick et al.*, 1997; *Griffiths et al.*, 1999]. However, subsequent analyses revealed relatively high concentrations of nitrate (~7-8 μM) and phosphate (~0.6-0.7

μM), presumably reflecting the high proportion of nutrient-rich Subantarctic water in the euphotic zone; only silicic acid was present at relatively low concentrations (0.2-1.5 μM). Nevertheless, the results of this experiment allow us to evaluate the nutritional status of the algal community at ~20 m depth with respect to iron and silicic acid.

Figure 3 (upper panels) shows the concentrations of nitrate+nitrite (N+N) and Chl *a* in the incubation bottles as a function of time. We assume that decreases in N+N and increases in Chl *a* provide measures of net accumulation of algal biomass in the bottles, thus relative measures of algal growth rates [*Martin et al.*, 1991]. After 8 days, there were no significant differences in N+N drawdown (p = 0.75, unpaired Student's t-test) and Chl *a* increase (p = 0.82) between the nutrient-amended (ΔN+N = -2.3 μM, ΔChl *a* = 0.39 μg L^{-1}) and control bottles (ΔN+N = -2.7 μM, ΔChl *a* = 0.44 μg L^{-1}). However, there was a significantly greater drawdown in N+N (ΔN+N = -6.3 μM, p = 0.001) and increase in Chl *a* (ΔChl *a* = 1.8 μg L^{-1}, p = 0.001) in the iron+nutrient-amended bottles relative to the nutrient and control treatments. Around 50% of the Chl *a* increase in the iron+nutrient-treated bottles was in the > 5 μm size fraction (Fig. 3). Table 1 presents Chl *a*-specific net growth rates, calculated assuming exponential growth between days 2 and 8. These and the results of flow cytometric analyses and microscopic cell counting [*Hutchins et al.*, in prep.] indicate that addition of iron+nutrients favoured the growth of diatoms relative to smaller (< 5 μm) algal species, a trend observed in iron-addition experiments in other iron-poor oceanic regions [e.g., *Martin et al.*, 1991; *Coale et al.*, 1996; *Hutchins et al.*, 1998; *Boyd et al.*, 1999a].

Given that nitrate and phosphate concentrations were sufficient for algal growth during the course of the experiment (N+N > 2.7 μM, N/P < 12), our results suggest that addition of iron and silicic acid, but not silicic acid alone, mediated a significant increase in the growth rate of the algal community, particularly diatoms. From this we infer that algal community growth rate at ~20 m depth was limited by the low ambient concentrations of dissolved iron (~0.2 nM), although our experimental design does not allow us to eliminate the possibility of co-limitation of algal growth by availability of iron and silicic acid. However, it is unlikely that algal growth rates were limited by iron deficiency throughout the euphotic zone, given the significantly higher dissolved iron concentrations (> 0.7 nM) measured at depths of 15 m and 75 m.

Table 1. Chlorophyll *a*-Specific Net Growth Rates

Stn.	Treatment	Growth Rate (d^{-1})* > 0.2 μm Fraction	Growth Rate (d^{-1})* > 5 μm Fraction
1	control	0.13 ± 0.06	0.25 ± 0.06
1	nutrients	0.17 ± 0.03	0.19 ± 0.01
1	nutrients+Fe	0.31 ± 0.03	0.49± 0.03
2	control	0.09 ± 0.03	0.14 ± 0.03
2	Si	0.13 ± 0.02	0.10 ± 0.03
2	Fe	0.24 ± 0.04	0.30 ± 0.04
2	Fe+Si	0.29 ± 0.04	0.38 ± 0.03

*estimated from slope ± standard error on slope of the linear regression fit to ln(Chl *a*) *vs* time between days 2 and 8.

Process Station 2: Subantarctic Water Mass

Process Station 2 was characterised by a shallow surface mixed layer of 20-50 m depth, and a second, well-defined pycnocline at 80-100 m depth. The depth of 1% of surface irradiance was again at 84 m. Salinity of the upper water column (34.6-34.7) was characteristic of the Subantarctic water mass, and nitrate and phosphate concentrations were relatively high (> 8 μM and 0.6 μM, respectively), whereas silicic acid concentrations were low (< 1 μM). Figure 2 (lower panels) shows water-column profiles of dissolved iron, temperature, salinity, σ_t, nutrients and Chl *a*. Dissolved iron concentrations were low throughout the euphotic zone, ranging from 0.05 to 0.11 nM. Water-column Chl *a* concentrations and modelled algal production rates were generally low and similar to those at Process Station 1. Predominant phytoplankton taxa included dinoflagellates, diatoms, coccolithophorids and cyanobacteria (R. van den Enden and S. Wright, pers. comm.).

Seawater used in the bottle experiment at Process Station 2 contained 9.4 μM nitrate+nitrite, 0.74 μM phosphate, 0.66 μM silicic acid, 0.07 nM dissolved iron and 0.21 μg L^{-1} Chl *a*.

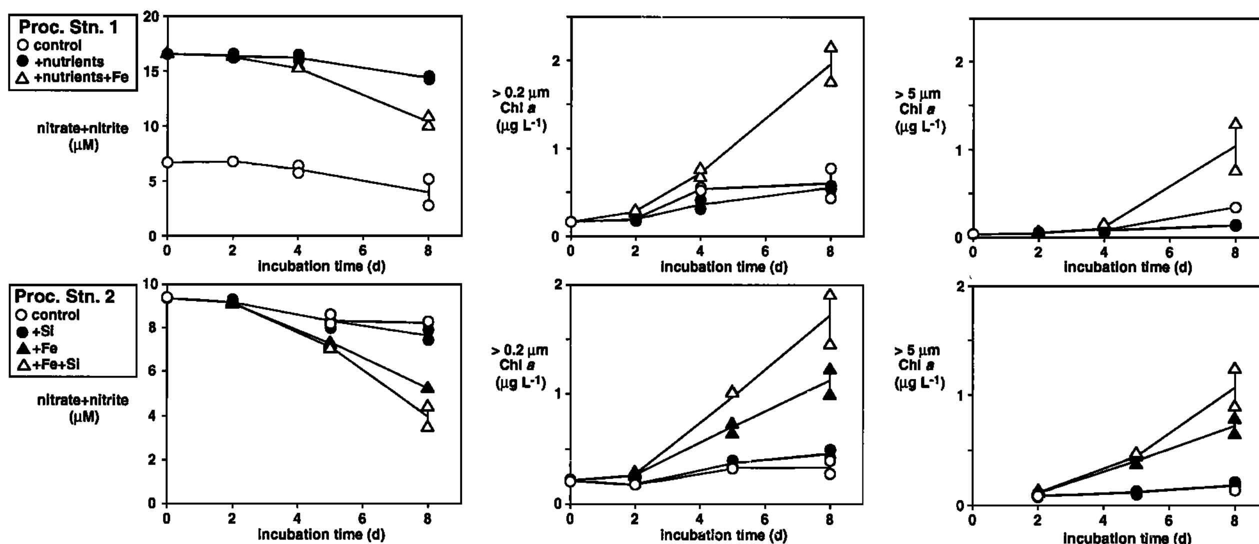

Figure 3. Concentrations of dissolved nitrate+nitrite and particulate chlorophyll *a vs* incubation time for experiments at Process Stations 1 (upper panel) and 2 (lower panel).

Given the low ambient concentrations of iron and silicic acid, we sought to examine the nutritional status of the algal community with respect to both these chemical species, so bottles were amended with either iron, silicic acid, or iron+silicic acid. Figure 3 (lower panels) shows the N+N and Chl *a* concentrations in the incubation bottles *vs* time. There were no statistically significant differences in N+N drawdown ($p = 0.12$) or Chl *a* increase ($p = 0.21$) between the control treatments (ΔN+N = -1.1 µM, ΔChl *a* = 0.13 µg L^{-1}) and silicic acid treatments (ΔN+N = -1.7 µM, ΔChl *a* = 0.26 µg L^{-1}). However, after 8 days there were significantly greater decreases in N+N ($p < 0.01$) and increases in Chl *a* ($p < 0.01$) in bottles amended with iron (ΔN+N = -4.2 µM, ΔChl *a* = 0.90 µg L^{-1}) and iron+silicic acid (ΔN+N = -5.4 µM, ΔChl *a* = 1.5 µg L^{-1}) relative to control and silicic acid treatments. The differences in N+N drawdown and Chl *a* increase between the iron and iron+silicic acid treatments were not significant ($p > 0.1$).

As in our first experiment, around half of the Chl *a* increases in the iron- and iron+silicic acid treatments were in the > 5 µm size fraction. The calculated Chl *a*-specific net growth rates between days 2 and 8 (Table 1) and the results of microscopic cell counts and radiocarbon pigment labelling [*Hutchins et al.*, in prep.] indicate that addition of iron and iron+silicic acid favoured the growth of diatoms, mainly small pennate diatoms and some larger centric species, relative to smaller algal species. These observations and the low concentrations of dissolved iron measured throughout the upper water column suggest that algal production at this station was limited by iron deficiency. The N+N and Chl *a* data provide no statistically significant evidence for higher growth rates in the silicic acid treatments relative to the controls, nor in the iron+silicic treatments relative to the iron treatments. However, there is some evidence for co-limitation of algal growth at this station by iron *and* silicic acid in other results from this experiment (flow cytometry, microscopic cell counts, taxon-specific growth-rate measurements), which are presented and discussed by *Hutchins et al.* [in prep].

In conclusion, our water-column measurements and experimental results from these two stations in the Australian Subantarctic region indicate that algal growth rates are limited by iron deficiency in this oceanic province during the late summer and autumn. To our knowledge, these are the most northerly locations in the Southern Ocean where limitation of algal growth by iron deficiency has been demonstrated. However, the relative importance of iron, silicic acid, light and grazing in controlling phytoplankton production in this region remains to be established.

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