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Comparative nutrient status and competitive interactions of two Antarctic diatoms (*Corethron criophilum* and *Thalassiosira antarctica*)

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Abstract. The nutrient status of two common Antarctic diatoms (*Corethron criophilum* and *Thalassiosira* cf. *antarctica*) was analysed by studying the growth response in enrichment bioassays and by estimates of the cell quotas of Si, N and P after size-fractionation of net plankton samples *Corthron* had higher biomass-specific N-quotas; Si- and P-quotas were quite similar between both species. *Corethron* was Si-limited in five enrichment experiments and not nutrient limited in five experiments. *Thalassiosira* was not nutrient limited in six experiments, N-limited in four experiments and Si-limited in one experiment Droop-kinetics of Si-limited growth of *Corethron* and of N-limited growth of *Thalassiosira* were obtained by combining the growth rates in the bioassays and the cell quotas from the natural populations. The minimal Si-quota of *Corethron* was 0 041 mol Si/mol C, the saturating cell quota was 0.158 mol Si/mol C respectively The minimal N-quota of *Thalassiosira* was 0 0223 mol N/mol C, the saturating cell quota was 0.208 mol N/mol C *Corethron* was N-saturated at cell quotas of >0 106 mol N/mol C; *Thalassiosira* was Si-saturated at cell quotas of >0 132 mol Si/mol C. As the better competitor for N and the poorer one for Si, *Corethron* became more important with increasing Si N ratios, while *Thalassiosira* became more important with decreasing Si:N ratios in the water

Introduction

Antarctic waters are unusually rich in conventional nutrients (P, N and Si). Therefore, most authors have ruled out the possibility of nutrient limitation of phytoplankton. This conclusion was made before Jacques (1983) and Sommer (1986) published half-saturation constants at 0°C temperatures which were much higher than half-saturation constants at temperatures >0°C, the highest being a k_{Si} of 88.7 μM for *Nitzschia kerguelensis* and a k_N of 4.2 μM for *Nitzschia cylindrus*. Such high concentrations would not be limiting under warmer conditions. The suggestion of potential nutrient limitation in the Antarctic Sea by Jacques (1983) and Sommer (1986) was based on the Monod model, which makes the growth rate a function of the dissolved nutrient concentration. This model has frequently been criticized because of its dependence of chemostat-like equilibrium conditions (Goldman *et al.*, 1979; Harris, 1986). Therefore, it seems wise to test for nutrient limitation also by the more generally accepted Droop-model.

The potential of resource competition in shaping the taxonomic composition of phytoplankton has been repeatedly shown in culture experiments (Tilman, 1982) (for Antarctic phytoplankton: Sommer, 1986). However, the 'real world' application of these experimental results, is still debated. Objections against the applicability fall into two categories. First, the occurrence of resource limitation of growth rates and, by implication, of nutrient competition under natural conditions is doubted (Goldman *et al.*, 1979; Harris, 1986). Second, it is doubted whether competition proceeds for long enough to replicate the taxonomic

patterns found in the equilibrium phase of chemostat cultures. In order to reject the first objection evidence for resource limitation has to be provided. In order to reject the second objection it has to be shown that the relative abundance of species follows the ratio of limiting resources (Tilman, 1982). In this study it is attempted to use distribution, chemical composition and growth rates of two Antarctic diatoms to test the 'real world' application of Tilman's experimentally successful competition theory.

Corethron criophilum Castracane and *Thalassiosira antarctica* Comber (plus similar *Thalassiosira* spp. which cannot be distinguished during routine counts) are important components of the early summer phytoplankton around the Antarctic Peninsula. In a previous chemostat study (Sommer, 1986) *Corethron* was a successful competitor at high Si:N ratios and *Thalassiosira* at average Si:N ratios in the medium. During the *Polarstern* expedition ANT VI-2 from mid-October to mid-December 1987, both species showed quite different distribution patterns. In a first publication of the results from ANT VI-2 (Sommer, 1988a), the taxonomic composition of the entire phytoplankton community has been interpreted in terms of Tilman's (1982) competition theory by multiple regression of the relative abundances on the ratios of the potentially limiting resources. The relative importance of *Corethron* has been shown to correlate positively with Si:N and with NO_3:NH_4 ratios, while the relative importance of *Thalassiosira* correlated positively with N:light ratios.

In this article the emphasis is put on the nutritional status of the early summer (October–December) populations of both species. Nutrient limitation of growth rates was tested for by enrichment bioassays. Two models of nutrient-limited growth were fitted (Monod, 1950; Droop, 1973) to the growth rates determined in the bioassays. Both models rest on different independent variables. The Monod model requires dissolved nutrient concentrations which can easily be measured. The Droop model requires intracellular nutrient concentrations ('cell quotas') which cannot be directly measured in natural plankton samples consisting of different phytoplankton species, small zooplankton, bacteria and detritus. It was attempted to obtain estimates of the cell quotas by size fractionation and subsequent chemical analysis of those fractions which most closely approximated the ideal of monospecific purity.

If both species compete for nutrients the experimental results in Sommer (1986) suggest the following predictions: *Corethron* should be more often Si-limited than *Thalassiosira*. *Thalassiosira* should be more often N-limited than *Corethron*. *Corethron* should be more dominant at high Si:N ratios. *Thalassiosira* should be more dominant at low Si:N ratios.

Recently, Martin *et al.* (1990) suggested iron as a potentially limiting nutrient. I became aware of this study some time after the experiments published here were finished. Therefore tests for iron limitation are not included. The potential impact of this omission will be dealt with in the Discussion.

Methods

Water samples were taken with a rosette sampler from 10 and 50 m depths at 48

stations between October 26 and December 17, 1987 for dissolved nutrient analyses and phytoplankton cell counts. At 11 of the 48 stations a larger amount of water was taken for the enrichment bioassays. At all 48 stations a net sample was taken from 50 m depth to the surface (Apstein net with cowl, 50 cm diameter, 20 μm mesh size, tow velocity ~10 m min^{-1}).

Subsamples for dissolved nutrient analyses were filtered immediately (0.2 μm pore size, cellulose nitrate membrane filters) and samples for phytoplankton counts were fixed with Lugol's iodine solution. Dissolved nutrient analysis (dissolved silicate, dissolved molybdenum blue reactive phosphorus, nitrate, nitrite and ammonium) was performed according to oceanographic standard techniques (Strickland and Parsons, 1986) on shipboard.

Phytoplankton counts were performed according to the Utermöhl settling technique for the nanoplankton algae and for the most-common large algae. If possible, ~400 individuals of the most important species and a correspondingly lower number of the rare ones were counted. If cells are randomly distributed 400 counted individuals give 95% confidence limits of ~10% (Lund *et al.*, 1958). In most cases the settling volume (50 ml) was insufficient to reach satisfactory counts of the majority of the large (netplankton) species. To obtain an approximate estimate of their abundance, they were counted in the net samples from the same station. The absolute abundance of the rare net species was estimated by calculating the abundance of the most-common net plankton species from the settling chamber counts and from the proportions of this species to the rare ones in the net samples. It was assumed that the net samples did not bias the relative abundances of species exceeding the mesh-size in at least two linear dimensions. Cell volumes were calculated by approximation to the nearest standard geometric solid after microscopic measurements of at least 20 individuals. The relative importance of a species is expressed as its share of the total phytoplankton cell volume.

The cell quotas of Si and N were obtained from the fractionated net samples. First, net samples were fractionated by netting of different mesh size: 20, 30, 105, 250 and 500 μm. Then the size fractions were examined microscopically. Fractions were considered 'satisfactory' if one species comprised >90% of total biovolume of all organisms, and detrital material could not be found by examination in phase contrast. Alternatively, fractions were also accepted if two species together comprised >90% in at least two fractions ('detritus free' according to microscopic examination) and showed different relative abundances in both. In this case, cell quotas could be recalculated by solving two equations with two unknown variables. 'Satisfactory' size fractions were divided into three subsamples. The subsample for particulate silicate analysis was filtered onto Nucleopore filters, the subsample for particulate P analysis onto cellulose nitrate membrane filters and the subsample for particulate C and N analysis was filtered onto precombusted glass-fibre filters. The filters were deep frozen and stored for analysis after the expedition.

Enrichment bioassays were performed in a shaking incubator (Rubarth, Hannover) at 0°C, in a 20:4 h light–dark cycle (near to ambient conditions) and with 160 μE m^{-2} s^{-1} photosynthetically active radiation. To prevent algae from

entering the stationary phase during the incubation, raw water from 10 m depth was diluted 3-fold with filtered water from the same sample. Large zooplankton were removed by a 500 μm mesh size screen. Two bottles received no nutrient addition, three bottles received addition of a single nutrient (180 μM Si, 45 μM NH_4NO_3, 3 μM P), three bottles received the three possible pairwise combinations and one bottle received the triple combination. Growth rates (μ) were calculated after cell counts performed on days 0, 2 and 5 according to the equation

$$\mu = \ln (N_2/N_1)/(t_2 - t_1). \quad (1)$$

For the statistical treatment all bottles enriched with the nutrient in question were considered as 'treatment' and all bottles not enriched by that nutrient as 'control'. This means five 'control' bottles versus four 'treatment' bottles, if growth rates responded to single-nutrient addition, and seven 'control' bottles versus two 'treatment' bottles, if growth rates responded to double-nutrient limitation. A nutrient was considered limiting if Tukey's nonparametric test showed a significant difference between treatment and controls at $P < 0.05$. Lumping different enrichment regimes into the categories 'control' and 'treatment' is justified by Liebig's principle of the minimum, from which it follows that addition of a non-limiting nutrient is equivalent to no nutrient addition at all. Liebig's principle is widely accepted for nutrient-limited growth kinetics of phytoplankton. Experimental attempts to falsify Liebig's principle have repeatedly failed (e.g. Rhee, 1978) and the results of the enrichment experiments here have never suggested a violation of Liebig's principle.

It is a frequent critique of enrichment bioassays that enclosing water exaggerates the extent of nutrient limitation in the controls because protection from several loss factors (e.g. sinking and grazing) would lead to a higher accumulation of biomass than *in situ*. In order to minimize this artefact the natural plankton density has been decreased by dilution with filtered seawater prior to the beginning of the bioassays. An artificially exaggerated extent of nutrient limitation in the control bottles would have been recognized by a decrease in growth rates from the first (day 0–2) to the second interval (day 2–5). This did not happen in a single case.

Results

Distribution of Corethron and Thalassiosira

There were only minor differences in phytoplankton species composition and biomass between the 10 and the 50 m samples. Therefore, only averages between both samples are considered here. An exception to that were the *Phaeocystis pouchetii* Langerheim blooms in the western Bransfield Strait and near the ice edge in Drake passage. Here, biomasses were much higher at 10 than at 50 m depths, though species composition did not change with depth. *Corethron criophilum* and *T.antarctica* showed quite opposing distribution patterns, in spite of the fact that both were most prominent at stations with low

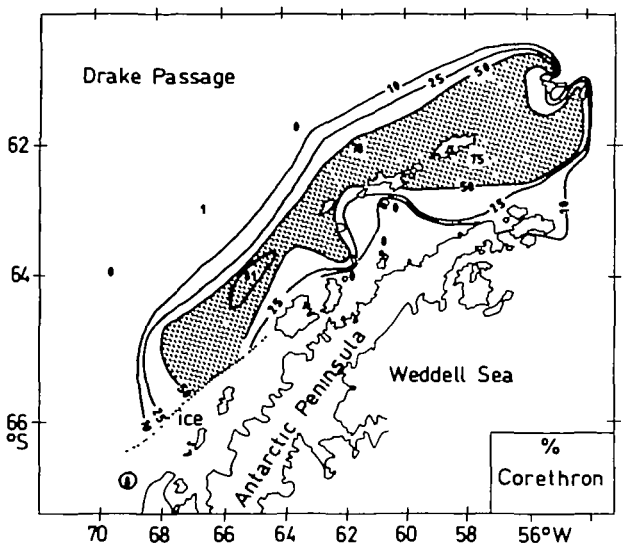

Fig. 1. Percentage contribution of *C criophilum* to total phytoplankton biomass; isolines for 10, 25, 50 and 75%, local minima and maxima shown by numbers; regions with >50% *Corethron* shown by shading.

phytoplankton biomass. *Corethron* (Figure 1) attained both maximal absolute and maximal relative abundances at the southern margin of Drake Passage and parts of Bransfield Strait. In these regions *Corethron* was the dominant species in terms of biomass with often >50% of total cell volume. Total biomass in this region was quite low, with average chlorophyll concentrations of 0.275 μg l^{-1} (lower quartile, 0.202; upper quartile, 0.378). *Corethron* was rare to absent in those parts of Bransfield Strait where there were blooms of *Phaeocystis* (average chlorophyll 2.28 μg l^{-1}; lower quartile, 1.07; upper quartile, 2.605).

Thalassiosira cf. *antarctica* (Figure 2) had its maximal absolute and relative abundances at the northern margin of the Weddell Sea, at one station north-east of Elephant Island and at some offshore stations in Drake Passage. It never contributed >50% to total cell volume. Most stations with important contributions of *Thalassiosira* had low chlorophyll concentrations (median 0.225 μg l^{-1}; lower quartile, 0.107; upper quartile, 1.214).

Nutrient concentrations

Soluble reactive phosphorus (SRP) was the least variable nutrient (minimum, 1.58 μM; maximum, 2.32 μM; average, 2.17 μM). Silicate showed more variability (minimum, 26 μM; maximum, 93 μM; average, 69 μM). There was an apparent geographic pattern (Figure 3) with the highest concentrations in Bransfield Strait and a gradual decrease towards the offshore regions of Drake passage. Nitrogen concentrations showed the biggest degree of variability, with minimal concentrations of dissolved inorganic nitrogen (DIN) of 7.5 μM and maximal values of 35 μM. The average concentration was 16.3 μM. Most of the

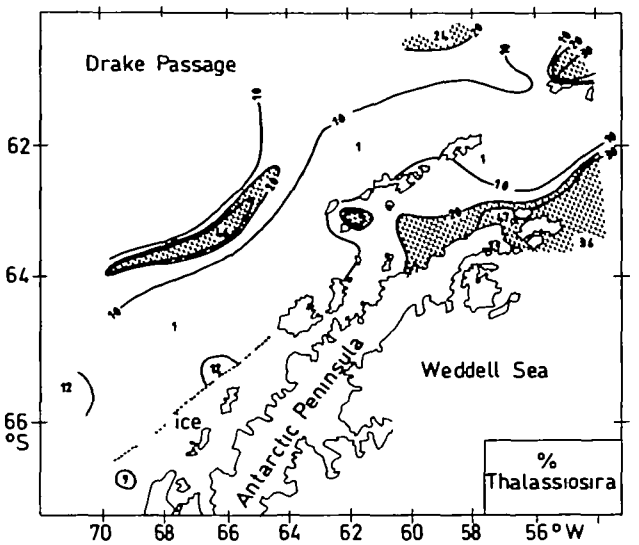

Fig. 2. Percentage contribution of *T. antarctica* to total phytoplankton biomass, isolines for 10, 20 and 30%; local minima and maxima shown by numbers; regions with >20% *Thalassiosira* shown by shading

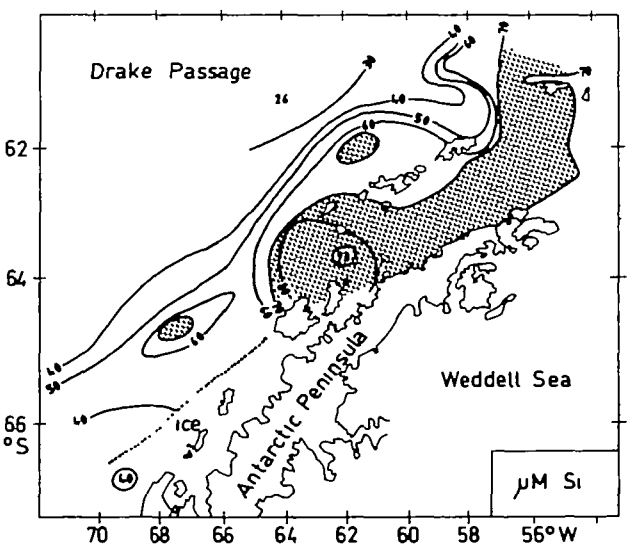

Fig. 3. Concentration of dissolved silicate (µM, average between 10 and 50 m); isolines at 30, 40, 50, 60, 70, 80 and 90 µM, concentrations >70 µM shown by shading.

variability of DIN was due to NO_3 which always contributed >87%, and in 75% of the cases >96% to DIN. Contrary to silicate, the geographic variation of DIN concentrations had no geographic pattern (Figure 4) and was more related to the distribution of phytoplankton biomass. The expected negative correlations

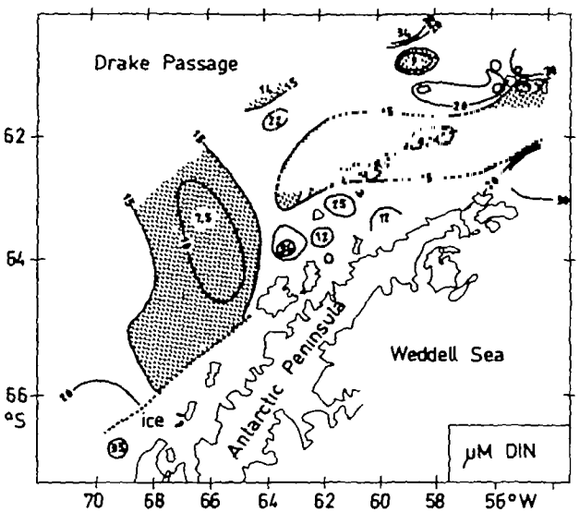

Fig. 4. Concentrations of DIN (μM, average between 10 and 50 m); isolines at 10, 15, 20 and 30 μM; concentrations <15 μM shown by shading.

(Spearman's rank correlation coefficient, r_S) between dissolved nutrient concentrations and algal biomass showed up for DIN and SRP, but not for Si, even when diatoms alone were considered. This implies that variation by biotic consumption was probably overrun by geographic variation, or that the regional minima of Si-concentrations were consequences of earlier diatom blooms, which had been eliminated by subsequent sinking. Biomass was negatively correlated with mixing depth (z_m).

DIN with chlorophyll:	$r_s = -0.31$,	$P < 0.005$
DIN with cell volume:	$r_s = -0.44$,	$P < 0.005$
SRP with chlorophyll:	$r_s = -0.67$,	$P < 0.0001$
SRP with cell volume:	$r_s = -0.67$,	$P < 0.0001$
chlorophyll with z_m:	$r_s = -0.61$,	$P < 0.0001$
cell volume with z_m:	$r_s = -0.65$,	$P < 0.0001$

Cellular chemistry

Cellular carbon content of both species varied within wide limits (Figure 5). *Corethron* had 1290–25 400 pg C cell^{-1}, with a median value of 6325 pg C cell^{-1} (n = 36). The corresponding cell volumes varied between 32 000 and 817 000 μm^3 (average, 192 000 μm^3). On the other hand, carbon contents of the cell volume were quite invariant (0.031–0.04 pg C μm^{-3}). The cellular carbon content of *Thalassiosira* varied between 1230 and 16 400 pg C cell^{-1}, with an average of 2755 pg C cell^{-1} (n = 42). Cell volumes varied from 14 000 to 219 000 μm^3 (average, 33 700 μm^3). The carbon content per volume was higher

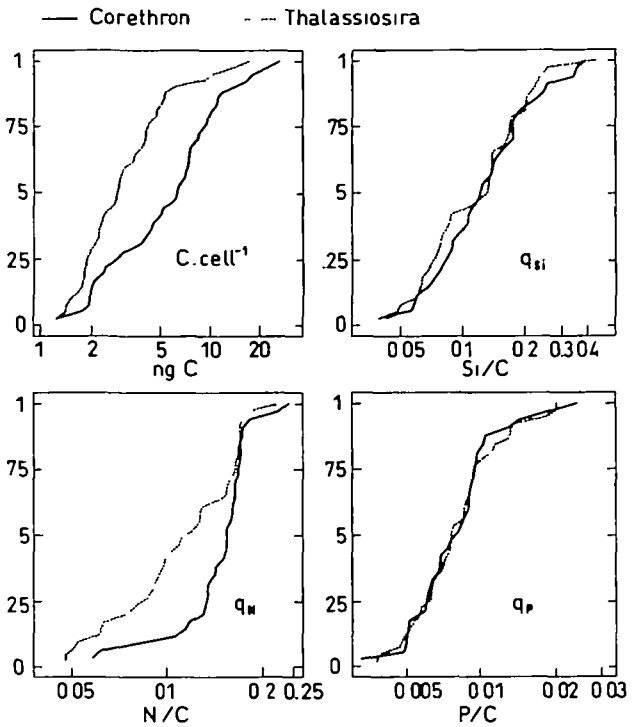

Fig. 5. Cumulative relative frequency plots of the chemical composition of *Corethron* (continuous line) and *Thalassiosira* (dotted line) with logarithmically scaled x axis. **Upper left**, cellular carbon content (ng cell^{-1}), **upper right**, silcon quota (mol Si/mol C); **lower left**, nitrogen quota (mol N/mol C); **lower right**, phosphorus quota (mol P/mol C)

than for *Corethron* (0.075–0.088 pg C μm^{-3}). Interspecific differences in the carbon content per cell were significant (Kolmogorov–Smirnov two-sample test; DN = 0.44; $P < 0.001$).

Because of the big variation in cell size biomass-specific cell quotas were used instead of cell-number-specific ones. They were expressed as stoichiometric quotients of particulate nutrient/carbon (Figure 5). Only nitrogen quotas (q_N) showed significant interspecific differences (Kolmogrov–Smirnov two-sample test; DN = 0.43; $P < 0.002$). *Corethron* had the higher nitrogen quota at 26 of the 33 stations, where both species could be analysed. Its q_N varied between 0.057 and 0.238 N/C ($n = 34$), with an average of 0.152. The q_N of *Thalassiosira* varied between 0.039 and 0.217 N/C, with an average value of 0.118 ($n = 41$). No significant interspecific differences showed up in the silicon quotas (q_{Si}) and phosphorus quotas (q_P). The q_{Si} of *Corethron* varied between 0.042 and 0.385 Si/C, with an average of 0.122 ($n = 34$); the q_{Si} of *Thalassiosira* varied between 0.039 and 0.417 Si/C, with an average of 0.131 ($n = 38$). The q_P of *Corethron* varied between 0.0033 and 0.024 P/C, with an average of 0.0102 ($n = 33$); the q_P of *Thalassiosira* varied between 0.0038 and 0.0196 P/C, with an average of 0.0086 ($n = 39$).

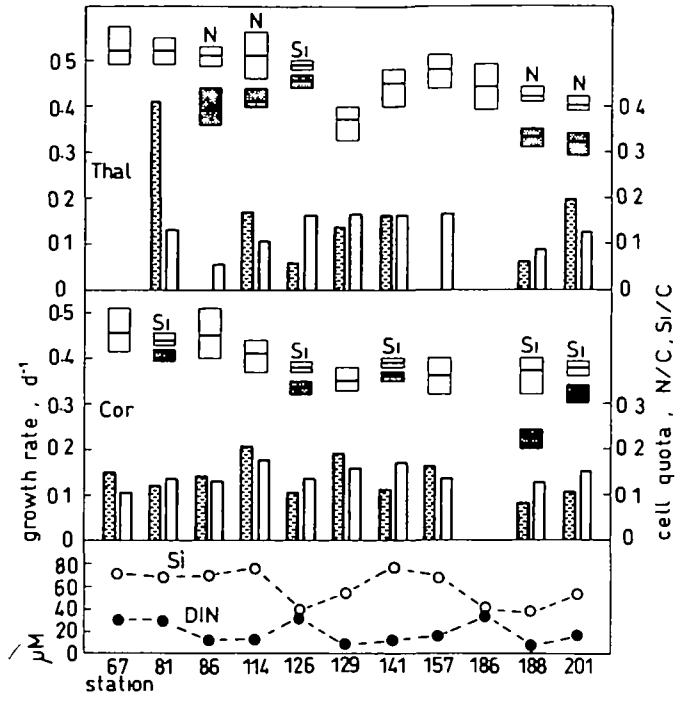

Fig. 6. Results of enrichment bioassays **Top**, response of *Thalassiosira*, **centre**, response of *Corethron*; **bottom**, dissolved nutrient concentrations (Si and DIN) Growth rates indicated by boxes (minimum to maximum with mean shown as a thick horizontal line; single box, no significant nutrient limitation; two boxes, significant nutrient limitation; shaded box, bottles without addition of limiting nutrient. Cell quotas indicated by bars (Si, stippled, N, open)

Enrichment bioassays (Figure 6)

Thalassiosira did not respond to nutrient addition with increased growth rates in six of eleven experiments, in four experiments it responded to nitrogen addition and in one experiment it responded to silicate addition. *Corethron* did not respond to nutrient addition in five experiments and responded to silicate addition in five experiments. In the experiments with material from station 186 its density was insufficient for reliable counts. Nutrient limitation was never strong, growth rates in the controls being always more than half of the growth rates in the enriched treatments. The same holds for the other species which were analysed (Sommer, 1988a). Phosphorus limitation was never found. When there was nutrient limitation, the increase in growth rates usually was immediate, i.e. already during the interval from day 0 to 2 the full response was reached. Only in a few cases (*Corethron*, station 188; *Thalassiosira*, station 86) was the full response reached in the time interval from day 2 to day 5. Growth rates in the controls showed no decline from the first to the second interval. This indicates that the experimental treatment did not artificially exaggerate the

extent of nutrient limitation. It seems justified to assume that growth rates in the experiments without nutrient limitation and growth rates in the enriched treatments are close to true nutrient-saturated growth rates (μ_{max}). The nutrient saturated growth rates of *Thalassiosira* were slightly higher (0.47 day^{-1} ± 0.06) than the μ_{max} of *Corethron* (0.40 day^{-1} ± 0.03).

Droop kinetics

The Droop equation predicts the growth rate (μ) as a function of the cell quota of the limiting nutrient (q):

$$\mu = \hat{\mu}_{max} \cdot (1 - q_0/q) \quad (2)$$

where q_0 is the minimal cell quota and where $\hat{\mu}_{max}$ is a hypothetical maximal growth rate, which could only be attained at an infinite cell quota. The real maximal growth rate (μ_{max}) is lower. It is attained at the saturating cell quota (q_S). The value of q_S can be obtained by substituting μ_{max} for μ and solving equation (2) for q. Equation (2) could be fitted directly (nonlinear regression, Statgraphics) to the Si-limited growth rates of *Corethron*:

$$\begin{aligned} q_0 &= 0.041 \text{ (SE = 0.01) Si/C} \\ \mu_{max} &= 0.54 \text{ (SE = 0.006) } day^{-1} \\ r^2 &= 0.49 \end{aligned}$$

If μ_{max} = 0.4 day^{-1}, then q_S = 0.158 Si/C.

The N-limited growth kinetics of *Thalassiosira* could not be obtained in this way. Because of some unknown reasons there was too much variability in the values of μ_{max}. It can be seen from Figure 6, for example, that at station 86 a growth rate of 0.39 day^{-1} was clearly N-limited, while at station 129 a growth rate of 0.37 day^{-1} appeared to be nutrient saturated. As would have been expected from the finding of nutrient limitation, but not from the absolute magnitude of the growth rates, the N-quota at station 86 was quite low (0.063 N/C) while the N-quota at station 129 was quite high (0.167 N/C). Therefore, the variability in μ_{max} was cancelled out by calculating relative growth rates *sensu* Goldman *et al.* (1979).

$$\mu_{rel} = \mu/\mu_{max} \quad (3)$$

Assuming that $\hat{\mu}_{max}$ and μ_{max} remain proportional, μ_{rel} remains a linear function of $1/q$: if

$$\hat{\mu}_{max}/\mu_{max} = a \quad (4)$$

then

$$\mu_{rel} = a.\mu/\mu_{max} \quad (5)$$

Substituting this into equation (2) gives:

$$\mu_{rel} = a - a.q_0/q \quad (6)$$

The saturating cell quota can then be calculated as:

$$q_S = a.q_0/(a - 1) \quad (7)$$

By this approach a q_0 of 0.0223 C/N and a q_S of 0.208 C/N could be estimated for *Thalassiosira* ($r^2 = 0.61$; $P = 0.022$). In order to check, whether this approach distorts the results it was also applied to the Si-limited growth of *Corethron*. The results were extremely close to the direct fit of equation (2): $q_0 = 0.039$ Si/C; $q_S = 0.163$ Si/C; $r^2 = 0.76$; $P = 0.00097$).

Because there was only one occasion of Si-limitation of *Thalassiosira* and no occasion of N-limitation of *Corethron*, it was impossible to establish complete growth kinetics for those nutrients. However, it can be stated that q_S for silicate limitation of *Thalassiosira* must be <0.132 Si/C, because this was the lowest Si-quota at which it still grew at μ_{max} in the unenriched bottles. Similarly it can be assumed that the q_S for N-limited growth of *Corethron* must be <0.106 N/C. Based on the same reasoning, the saturating cell quotas of P must be <0.0062 P/C for *Thalassiosira* and <0.0051 for *Corethron* respectively.

Monod kinetics

The dependence of growth rates on external nutrient concentrations could be described with the Monod equation (nonlinear regression):

$$\mu = \mu_{max}.S/(k_s + S) \quad (8)$$

For *Thalassiosira* a μ_{max} of 0.54 (SE = 0.07) day^{-1} and a k_s of 4.2 (SE = 2.3) μM DIN were estimated ($r^2 = 0.40$). For *Corethron* an unrealistically high μ_{max} of 0.87 (SE = 0.37) day^{-1} and a k_s of 81.2 (SE = 61.1) μM Si were obtained ($r^2 = 0.63$). In a previous study (Sommer, 1986) a μ_{max} of 0.39 day^{-1} and a k_s of 60.1 μM Si had been obtained from cultures of *Corethron*. Better agreement can be obtained, if instead of the curvilinear Monod model a rectilinear ('Blackman'-type) model is fitted to the Si-limited data. The slope of 0.0058 (SE = 0.00055; $r^2 = 0.96$; $P = 0.0005$) permits the calculation of a k_s of 34.5 μM, if 0.2 day^{-1} is considered to be half μ_{max}.

Discussion

Nutrient versus light limitation

It is a widespread view that nutrient limitation plays no role in Antarctic phytoplankton except for Si-limitation of the most Si-demanding diatoms (Jaques, 1983). This view is based on high dissolved-nutrient concentrations even under bloom conditions and on the failure to detect nutrient limitation by

enrichment bioassays (Hayes *et al.*, 1984). However, ^{14}C-fixation is not necessarily depressed by nutrient limitation of growth rates (Harris, 1986) and bulk-fixation rates may be quite uninformative about the performance of individual species. Monod kinetics of five diatom species at 0°C (Sommer, 1986) have revealed much higher nitrate and silicate requirements of some species than usually encountered at higher temperatures. Silicate half-saturation constants ranged from 8.4 to 88.7 μM, nitrate half-saturation constants from 0.3 to 4.2 μM respectively. The former suggest some Si-limitation of the most fastidious species even in relatively Si-rich waters; the latter suggest at least a moderate extent of N-limitation of the most fastidious species at local nitrate minima. For the region and season covered in this study, local nitrate and DIN minima are in the range 7–10 μM (Tilzer *et al.*, 1985; this study).

My enrichment experiments have been conducted at a light intensity which, according to photosynthesis–irradiance curves obtained for the same region and season (Tilzer *et al.*, 1985, 1986), is most likely to exclude both light limitation and light inhibition. It is not the light intensity to which the algae have been exposed prior to sampling. Therefore, it might be argued that the experiments with significant nutrient effects demonstrate only undersaturation of the cell quota and not nutrient limitation of the growth rate. If light is more undersaturating for the growth rates than the cell quota of the limiting nutrient, the growth rate in the control might be higher than the growth rate *in situ*, but still lower than the growth rate after nutrient enrichment. It has been shown, however, in chemostat cultures that transition from nutrient limitation to light limitation at constant μ results in a cellular chemistry characteristic of nutrient sufficiency (Tett *et al.*, 1985). The simultaneous occurrence of light limitation and undersaturated cell quotas is only probable if light and nutrient availability are so balanced that algae fluctuate between light and nutrient limitation according to short-term changes in conditions. This can easily occur in rapidly mixing regions such as the Weddell Sea.

Unfortunately, light profiles were not measured during the cruise ANT VI-2. The data from the 56th Meteor expedition in November/December 1980 in the same region (Tilzer *et al.*, 1985) may be used as a surrogate. Afternoon surface irradiance (I_0) (13.30–19.30) was (673 ± 194 μE m^{-2} s^{-1} photosynthetically active radiation). Using the relationship of Tilzer *et al.* between the extinction coefficient (ε) and the concentration of chlorophyll and the chlorophyll concentrations of my own study an average ε of 0.136 ± 0.5 m^{-1} can be calculated. Substituting the mean values of I_0 and ε into Riley's (1957) equation the mean light intensity of the mixed layer can be calculated: 99 μE m^{-2} s^{-1} for 50 m mixing depth and 49 μE m^{-2} s^{-1} for 100 m mixing depth. This compares with a saturation light intensity (I_k) of 86 ± 43 μE m^{-2} s^{-1} (Tilzer *et al.*, 1985). Light availability in the mixed layer would therefore be around the margin between limitation and saturation. This is quite comparable with the nutrient status and makes short-term fluctuation between moderate light limitation and moderate nutrient limitation quite probable. If growth saturates at lower light intensities than photosynthesis, nutrient limitation would be relatively more important than light limitation. Elbrächter *et al.* (1985) found an I_k of only

10 μE m^{-2} s^{-1} for the mean division rates of Antarctic algae as opposed to an I_k of 50–100 μE m^{-2} s^{-1} for photosynthesis.

Iron limitation

Martin *et al.* (1990) suggested iron as a potentially limiting nutrient for Antarctic phytoplankton. This possibility was not tested in my study. Provided that the relationship between iron limitation and limitation by another nutrient follows Liebig's principle of the minimum, no response to Si- or N-enrichment would have been found and the growth rates in all bottles would have been below maximal ones. Therefore, an increase of growth rate upon Si- or N-enrichment rules out Fe-limitation. If an experiment showed no response to Si- or N-enrichment but growth rates similar to the ones achieved by enrichment in other experiments Fe-limitation can be ruled out as well. However, there is a suspicion of Fe-limitation (or limitation by some other element) if there is no response to Si- or N-addition, but growth rates are less than in the enriched bottles of other experiments. This could have happened with *Thalassiosira* from station 129.

Extent of nutrient limitation

Calculated q_0 values have to be taken with some caution, because they depend on extrapolation outside of the available data range. q_S values of N for *Thalassiosira* and of Si for *Corethron*, however, are more reliable because the original values entered into the regressions were in the upper half of the range of possible growth rates. The q_s values for the other nutrients are only maximal estimates. The available data on cell quotas permit a judgement about the nutrient status of the two diatom species also at those stations where enrichment experiments had not been performed. A nutrient can be considered limiting if the cell quota fulfills two criteria: it must be smaller than q_S and it must predict a smaller growth rate than the cell quota of other nutrients. The ratio of the cell quotas at which the switch of limitations takes place shall be called 'transition ratio' (TR). It depends on the magnitude of the growth rates and approaches the ratio of the minimal cell quotas at low growth rates and the ratio of the saturating cell quotas at high growth rates (Turpin, 1986). Because of the generally small extent of nutrient limitation in the study area q_S ratios can be used as a first approximation for TR: *Corethron*, $TR_{Si:N}$ >1.48; $TR_{Si\,P}$ ~31; $TR_{N:P}$ ~21; *Thalassiosira*, $TR_{Si:N}$ <0.64; $TR_{Si:P}$ ~21.4; $TR_{N:P}$ ~33.5.

Using the above criteria, limitation by N or P can be excluded for *Corethron*; at 12 stations the cell quotas suggest nutrient-saturated growth. Among the 22 stations where biomass is undersaturated with Si, only weak limitation (μ_{rel} = 0.75–1.0) is predicted for 12 stations, moderate limitation (μ_{rel} = 0.5–0.75) for seven stations and strong nutrient limitation (μ_{rel} <0.5) for four stations.

Thalassiosira appeared to be Si-limited at six stations; at one additional station the q_S:q_P ratio was quite similar to the transition ratio (22.5) and there were three more cases where it was difficult to decide between Si and N limitation (q_{Si}:q_N between 0.5 and 0.64). No case of saturation of all cell quotas was found. If the 31 cases of clear N-limitation and the three cases of Si–N-transition are

pooled, in 29 of them N-limitation was weak (μ_{rel} >0.75) and in four it was moderate (μ_{rel} = 0.5–0.75). There were no cases of strong N-limitation.

Competitive interactions

In spite of having the lower demand of nitrogen (lower q_S) *Corethron* usually was able to maintain a higher cellular N content than *Thalassiosira*. This implies that it must be the better competitor. In a previous experimental study in the same region (Sommer, 1985) *Corethron* (together with *Nitzschia kerguelensis*) had been one of the best competitors for nitrate and one of the poorest for silicate. *Thalassiosira* cf. *antarctica* had been an intermediate competitor for both. This conforms to the interspecific differences in the pattern of nutrient limitation found in this study. If a competitive community approaches equilibrium, relative abundances of competing species should depend on the ratios of the limiting resources for which competition occurs (Tilman, 1982). Here, the relative importance of *Corethron* should increase with Si:N ratios and the relative importance of *Thalassiosira* should decrease with Si:N ratios. This was the case; the relative contribution of *Corethron* to total biomass (p_{Cor}) had a positive correlation with dissolved Si:N ratios (Spearman's rank correlation coefficient r_s = 0.56, $P < 0.001$); p_{Thal} had a negative correlation with Si:N ratios ($r_s = -0.37$; $P < 0.01$) and the contribution of *Corethron* to the combined biomass of the two species under study [Cor/(Cor+Thal)] was positively correlated to Si:N ratios (r_s = 0.50; $P < 0.005$).

The agreement with the competition experiments in Sommer (1986) is only a qualitative one. In those experiments *Corethron* was the only persisting species at Si:N ratios of 425:1 at the intermediate dilution rate (0.25 day^{-1}) and at the low dilution rate (0.1 day^{-1}). At the low dilution rate it contributed ~70% total biomass at an Si:N ratio of 14:1 and was excluded at 2.6:1. At the medium dilution rate a finer gradient of Si:N ratios was used. Here, *Corethron* could not persist at 14:1, but contributed an increasing share to the biomass of the final equilibrium assemblage from 27:1 upwards. From 61:1 to 314:1 *T.antarctica* was the co-dominant species. The Si:N ratios encountered during this study were much lower (average, 4.25; minimum, 1.13; maximum, 7.7). Therefore, at first sight *Corethron* should have played a much less prominent role. However, it is known from competition experiments with different supply modes of limiting nutrients (continuous versus pulsed) that regions of competitive dominance may be displaced along resource ratio gradients by changing the supply mode, even if the qualitative patterns of species sequence along the gradient are quite stable (Sommer, 1985). Similarly it is possible that the presence of an additional trophic level (grazing zooplankton) leads to further displacements along resource ratio gradients (Sommer, 1988b).

In conclusion, it seems quite plausible that the contrasting distribution patterns of *C.criophilum* and *T.antarctica* during the early summer periods in the waters around the Antarctic Peninsula are partially caused by differences in their requirements for nutrients. *Corethron* has lower cellular requirements but higher cellular contents of N. Both species have quite similar contents of cellular

Si, but *Thalassiosira* has lower requirements for growth. As a consequence, *Thalassiosira* was more often N-limited, whereas *Corethron* was always Si-limited, if nutrient limited at all. As the better competitor for N and the poorer one for Si, *Corethron* tends to increase in relative importance with Si:N ratios while *Thalassiosira* as the poorer competitor for N and the better one for Si, tends to decrease in relative importance with Si:N ratios.

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