

## Nitrate- and silicate-competition among antarctic phytoplankton

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### Abstract

Natural phytoplankton from antarctic waters in the Drake Passage were used for competition experiments in semi-continuous cultures. The outcome of interspecific competition for silicate and nitrate was studied at a range of Si:N ratios (from 2.6:1 to 425:1) and at three different dilution rates. For five species Monod kinetics of silicate- and nitrate-limited growth has been established. Comparison between theoretical predictions derived from Monod kinetics and the outcome of competition experiments showed only minor deviations. Contrary to literature data, considerable depletion of nitrate was found in antarctic seawater. Both the concentrations of soluble silicate and of nitrate were too low to support maximum growth rates of some of the diatom species under investigation.

### Introduction

One of the main goals of phytoplankton ecology is the prediction of species composition from environmental data. A number of factors, e.g. temperature, stratification, turbulence, light, nutrient availability, sinking, and zooplankton grazing, have the potential to structure phytoplankton communities by influencing either the rate of reproduction or the loss rate in a species specific way. During recent years considerable progress has been made in explaining species replacements by competition for limiting nutrients (Tilman, 1982). Experimental results obtained by continuous culture techniques (Tilman, 1977, 1981; Sommer, 1983; Kilham, 1984) have been consistent with Tilman's theory, and examples of field data consistent with these experimental results have also been presented (Tilman, 1977; Tilman *et al.*, 1984).

In antarctic phytoplankton, however, nutrient limitation is considered to be nearly absent. Nutrient concen-

trations in antarctic waters belong to the highest found in the sea. Nutrients are not even exhausted during blooms. Bioassays (Hayes *et al.*, 1984) have failed to show growth enhancement following nutrient enrichment. The only exception seems to be silica limitation of at least some diatom species immediately south of the Polar Front (Jacques, 1983). Jacques' conclusion is based on Si-uptake kinetics of *Nitzschia turgiduloides* and *Nitzschia* (= *Fragilariopsis*) *kerguelensis* measured at +5 °C. As far as I am aware, there have been no experiments on nutrient-limited uptake and growth kinetics at extremely low ambient temperatures (-1° to +1°C) available. It could still be possible that the initial slopes of the saturation curves for nutrient uptake and growth at those temperatures are considerably higher than under moderately cold temperatures. In this case, even high nutrient concentrations might be limiting. Therefore, I used the opportunity to participate in the second section of the 1984/85 expedition of RV "Polarstern" to perform phytoplankton competition experiments with natural phytoplankton collected from the Drake Passage. The species enriched during the course of the competition experiments were then used for analyses of Monod-type growth kinetics.

### Theory

Since the theory of steady-state competition has been presented in detail by Tilman (1982), only a short outline will be given here. Under steady-state conditions the per capita reproduction rate ( $\mu$ ) of an algal population is related to the ambient concentration of the limiting nutrient according to the Monod (1950) equation.

$$\mu = \frac{\mu_{\max} \cdot S}{S + k_s}, \quad (1)$$

where S = concentration of the limiting nutrient,  $\mu_{\max}$  = maximal growth rate, and  $k_s$  = half-saturation constant.

It is important to note that substrate affinity is not expressed by  $k_s$ , but rather by the initial slope of the saturation curve ( $\mu/k_s$ ).

At a given equilibrium turnover rate (reproduction rate=loss rate; in chemostat culture given by the dilution rate), a single species will deplete the external concentration of the limiting nutrient to the corresponding level:

$$R_1^* = \frac{\mu \cdot k_{s1}}{\mu_{\max 1} - \mu} \quad (2)$$

$R_1^*$  = residual equilibrium nutrient concentration for Species 1.

If a second species has a lower value of  $R^*$  it will deplete the limiting nutrient to  $R_2^*$ , which in turn will cause the reproduction rate of Species 1 to fall below the loss rate. As a consequence, Species 1 will be displaced (competitive exclusion). Competitive exclusion can be prevented if Species 2 is limited by another nutrient (or light) to such a degree that it is not able to deplete the nutrient limiting for Species 1 to a level beneath  $R_1^*$ . This possibility of coexistence can be expressed as a region along the resource ratio gradient (Nutrient 1:Nutrient 2) confined by the "optimum" ratios of the two species. The optimum ratio is the switch point from limitation by Nutrient 1 to limitation by Nutrient 2. This is identical to the ratio of the  $R^*$  values of the two nutrients: i.e. the ratio of the  $k_s$  values or the inverse ratio of the initial slopes of the saturation curves. The main attraction of this concept lies in the fact that it permits the prediction of the outcome of interspecific competition based on the knowledge of a few physiological parameters of the species involved.

Two factors can be manipulated in order to select species in continuous culture competition experiments: the ratio of the limiting nutrients in the inflow medium or the dilution rate. Unfortunately it is technically impossible to impose different loss rates for competing species in continuous cultures, although differential loss rates are probably important in nature.

## Materials and methods

### Competition experiments

All experiments were carried out on board the RV "Polarstern" in an incubator (Rubarth, Hannover) which provided light ( $320 \mu\text{E m}^{-2} \text{s}^{-1}$ , 16 hL:8 hD cycle), constant temperature ( $0^\circ$  to  $0.5^\circ\text{C}$ ), and gentle shaking of the cultures. The cultures were maintained in 500-ml polycarbonate Erlenmeyer flasks (200 ml culture volume). In order to avoid wall growth, cultures were transplanted into new bottles at 3-d intervals. For the sake of technical simplicity dilution of the cultures was performed semi-continuously at 12-h intervals.

Sterile filtered seawater, either unenriched or enriched by silicate or by phosphate and nitrate, was used as medium. Seawater A was taken on 17 November 1984

from Lat.  $59^\circ 39' 85''\text{S}$ , Long.  $59^\circ 06' 50''\text{W}$  (Drake Passage, first station south of the Polar Front); Seawater B on 20 November from Lat.  $63^\circ 28' 06''\text{S}$ , Long.  $54^\circ 17' 55''\text{W}$  (northern Weddell Sea). Natural phytoplankton was taken from both locations and concentrated about tenfold to serve as inoculum. Before inoculation, zooplankton were killed by bubbling nitrogen through the inoculum and thus removing the oxygen. Inoculum A was dominated by *Corethron croiphilum* (80% of total cell volume); Inoculum B by *Thalassiosira antarctica* (75%). In spite of high dominance by single species, both inocula were rich in species number of diatoms (over 30), but other taxa were only poorly represented (1 silicoflagellate, few dinoflagellates, no *Phaeocystis* spp.).

Samples for cell counts (on membrane filters made transparent by immersion oil) were taken daily. The daily cell counts performed on shipboard were only rough estimates, because the small volume available for samples did not permit satisfactory counts of many of the larger algae. However, the final samples at the end of the experiments were counted according to the Utermöhl standard technique (sedimentation, inverted microscope) at the home institute. Four hundred individuals of each important species were counted, thus giving a  $\pm 10\%$  precision within 95% confidence limits. Cell volume was based on microscopic measurements; no attempt was made to correct for vacuole volume. Samples for chemical analyses (nitrate, ammonium, soluble reactive phosphorus, soluble silicate) were taken from the fresh media at the end of the experiments and deep frozen after filtration ( $0.1 \mu\text{m}$ ). Nutrient analyses were performed with a Technicon-autoanalyser using the methods according to Strickland and Parsons (1972).

Three series of experiments were performed. In Series 1 (Seawater A, Inoculum A) and Series 2 (Seawater A, Inoculum B) three different dilution rates ( $0.1$ ,  $0.25$ ,  $0.5 \text{ d}^{-1}$ ) and three different nutrient treatments (Si-enriched with a molar Si:N ratio of 425:1, unenriched with a Si:N ratio of 14:1, N and P-enriched with a Si:N ratio of 2.6:1) were used. The Si:N ratios were higher than initially planned, because nitrate concentrations of the seawater were unexpectedly low. There was a total of nine

**Table 1.** Nutrient concentration ( $\mu\text{M}$ ) in the experimental media (ammonium was always undetectable)

	Silicate	Nitrate	Phosphate	Si:N
Seawater A	29.4	2.1	1.7	14:1
Seawater B	37.7	3.0	2.0	13:1
Series 1 and 2				
N- and P-enriched	29.4	11.3	7.0	2.6:1
Unenriched	29.4	2.1	1.7	14:1
Si-enriched	892.5	2.1	1.7	425:1
Series 3				
1	37.7	5.8	2.2	6.5:1
2	137.7	5.1	2.15	27:1
3	268.5	4.4	2.1	61:1
4	470.0	3.7	2.05	127:1
5	942.0	3.0	2.0	314:1

experiments per series. In Series 3 (Seawater B, Inoculum B) only one dilution rate ( $0.25 \text{ d}^{-1}$ ) but a more refined gradient of Si:P ratios (6.5:1, 27:1, 61:1, 127:1, 317:1) were employed. Due to the high concentration of P relative to N in the original seawater (Table 1), P could be excluded as a potentially limiting factor (the maximum N:P was 2.6:1).

### Monod experiments

Monod growth kinetics for nitrate and silicate were established by short-term batch culture experiments for five species enriched by the competition experiments: *Corethron criophilum*, *Nitzschia kerguelensis*, *Nitzschia cylindrus*, *Thalassiosira subtilis*, *Chaetoceros neglectum*. Small (1 ml) inocula were taken from the competition experiments and grown in 1 l of experimental medium for four days, then 10 ml of this culture were transplanted into 1 l of fresh medium and grown for three days. The latter procedure was repeated once. Growth rates were estimated for the second and third cultures. It is assumed that by this procedure the steady-state conditions required for the application of the Monod equation are sufficiently approximated. Use of very dilute algal cultures for short periods does not lead to significant nutrient depletion in the medium, and successive transplantations prevent the results from being biased by carry-over of cells with non-equilibrated cell quota.

In order to obtain a base medium of sufficiently low nutrient concentrations, Seawater B was inoculated by a dense suspension of phytoplankton, which was then grown until the onset of the stationary phase. The filtrate of these cultures was sufficiently low in N (nitrate, ammonium, and dissolved organic nitrogen were not detectable) and Si ( $10 \mu\text{M}$ ) to serve as a base medium. Experimental media were prepared by addition of silicate, nitrate, phosphate, and trace elements.

## Results

### Competition experiments

The 36 (Series 1) or 27 (Series 2 and 3) days available for the competition experiments were not always sufficient to obtain complete competitive exclusion. However, in all cases it was evident that either one or two species approached steady state, whereas all other species exhibited a continuous decline over at least the final 5 d (Fig. 1). There was one case, (dilution rate  $0.5 \text{ d}^{-1}$ , Si:N=14:1) both in Series 1 and 2, where the growth rate of any species could not cope with the dilution rate. In Series 1 *Nitzschia cylindrus* and *Chaetoceros neglectum* came closest to withstanding dilution ( $\mu=0.42 \text{ d}^{-1}$ ), in Series 2 only *N. cylindrus* dominated during the final phase.

In spite of strong differences in inoculum species composition, Series 1 and 2 yielded almost identical final

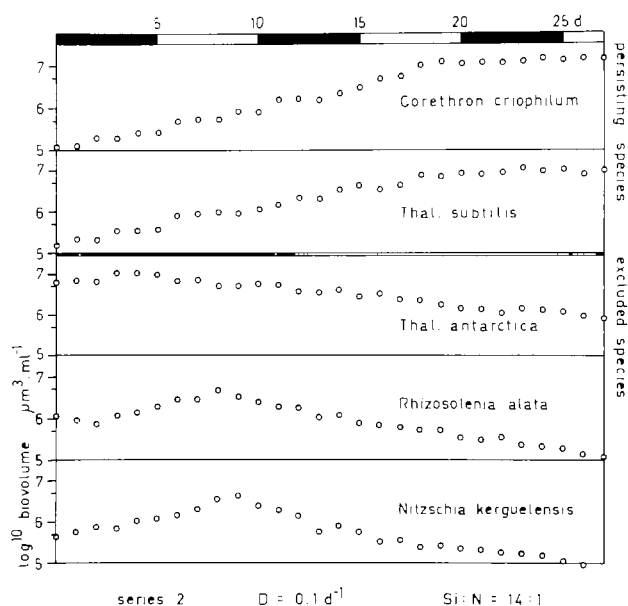


Fig. 1. Example for the time course of competition experiments (Series 2, Si:N=14:1,  $D=0.1 \text{ d}^{-1}$ ); biovolume of important species in log-scale

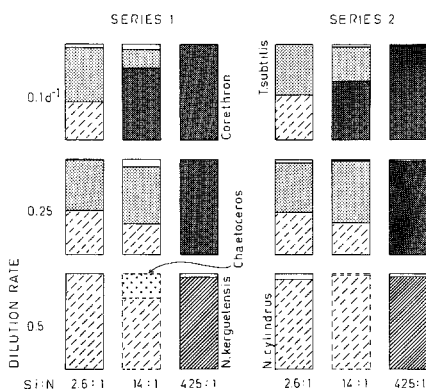
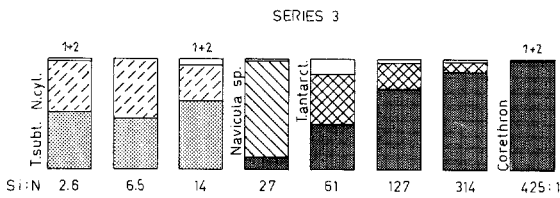


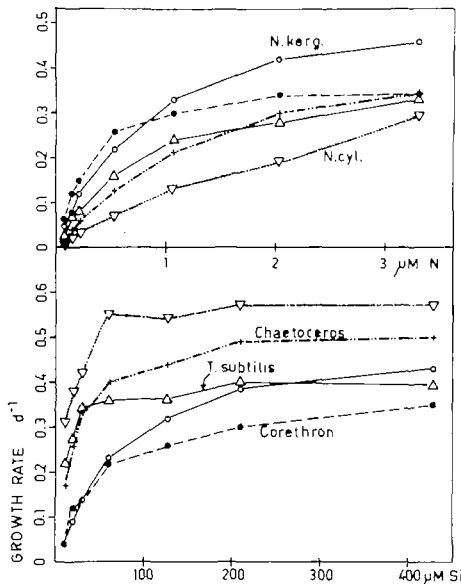
Fig. 2. Species composition of biomass at the end of competition experiments of Series 1 and 2; species indicated by different shading

results (Fig. 2). At the highest Si:N ratios the large ( $100\,000 \mu\text{m}^3$ ) centric diatom *Corethron criophilum* dominated at the low and medium dilution rates. The medium-sized ( $2\,000 \mu\text{m}^3$  cell volume, ribbon like colonies) diatom *Nitzschia kerguelensis* was the superior competitor at the high dilution rates. At the Si:N ratio 14:1, *Corethron criophilum* and *Thalassiosira subtilis* ( $2\,000 \mu\text{m}^3$ , colonies of numerous cells in a common mucilage) coexisted at the dilution rate of  $0.1 \text{ d}^{-1}$ , whereas at the dilution rate of  $0.25 \text{ d}^{-1}$ , *T. subtilis* and *N. cylindrus* (very small:  $8 \mu\text{m}^3$ ) coexisted. At the Si:N ratio 2.6:1, *T. subtilis* and *N. cylindrus* coexisted at the low and the medium dilution rates. *Nitzschia cylindrus* was the only successful competitor at the high dilution rate (Fig. 2).

Series 3 cannot be directly compared with Series 1 and 2, because nutrient ratios were not identical. However, Fig. 3 shows that the results fall on the same continuum, with *Nitzschia cylindrus* and *Thalassiosira subtilis* coexisting



**Fig. 3.** Species composition of biomass at the end of competition experiments of Series 3. Corresponding experiments (dilution rate  $0.25 \text{ d}^{-1}$ ) of Series 1 and 2 (averages) have been added to show the continuity along resource ratio gradient



**Fig. 4.** Nitrate (top panel) and silicate (lower panel) limited growth of *Corethron criophilum*, *Nitzschia kerguelensis*, *N. cylindrus*, *Chaetoceros neglectum*, *Thalassiosira subtilis*

**Table 2.** Monod kinetics for five antarctic diatoms at  $0^\circ\text{C}$  for silicate- and nitrate-limited growth. Maximum growth rate ( $\text{d}^{-1}$ ), half-saturation constant ( $\mu\text{M}$ ), initial slope ( $\mu_{\text{max}}/k_s$ )

Species	$\mu_{\text{max}}$	$\mu_{\text{max}}/k_{\text{N}}$	$k_{\text{N}}$	$\mu_{\text{max}}/k_{\text{Si}}$	$k_{\text{Si}}$
<i>Corethron criophilum</i>	0.39	1.30	0.3	0.0065	60.1
<i>Nitzschia kerguelensis</i>	0.56	0.70	0.8	0.0063	88.7
<i>Thalassiosira subtilis</i>	0.40	0.44	0.9	0.071	5.7
<i>Chaetoceros neglectum</i>	0.52	0.37	1.4	0.024	21.7
<i>Nitzschia cylindrus</i>	0.59	0.14	4.2	0.070	8.4

in the range from Si:N=2.6:1 to 14:1, a small *Navicula* sp. ( $300 \mu\text{m}^3$ ) and *Corethron criophilum* coexist at 27:1; from 27:1 to 425:1 the importance of *C. criophilum* steadily increases; at the Si:N ratios from 61:1 to 314:1 the large *Thalassiosira antarctica* ( $40\,000 \mu\text{m}^3$ ) is the second persisting species.

## Monod-experiments

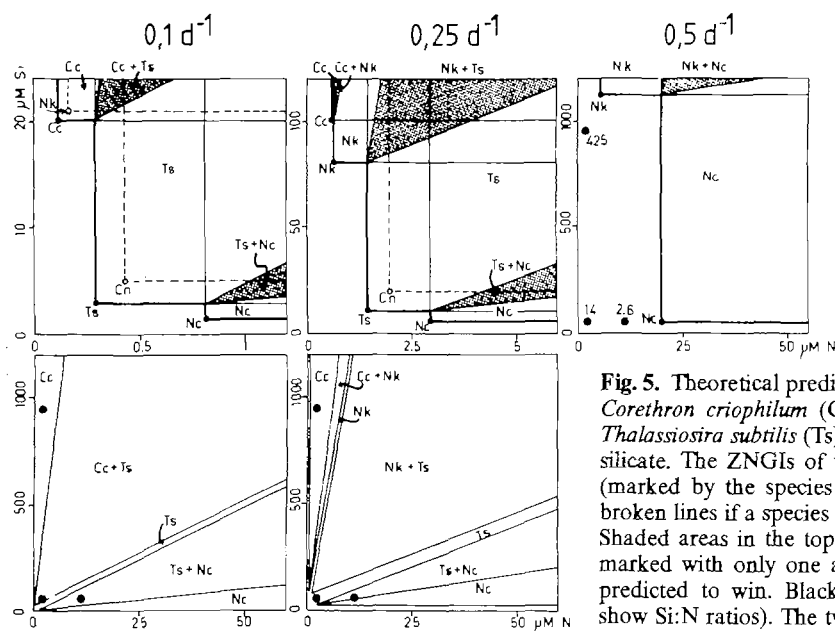
Monod type saturation curves for nitrate- and silicate-limited growth were obtained for all five species tested (Fig. 4). Unfortunately the lowest concentration of Si ( $10 \mu\text{M}$ ) was already beyond the region of serious limitation for some of the species. Monod parameters estimated according to Li (1983) are given in Table 2. Species with a high initial slope of the saturation curve for Si tend to have a high one for N and vice versa. Half-saturation constants of silicate-limited growth for two species are higher than the soluble Si concentrations found in Seawaters A and B, and the half-saturation constants of nitrate-limited growth of one species is higher than the nitrate concentration in Seawaters A and B (ammonium was undetectable).

## Discussion

### Internal consistency of experiments and theory

The replication between the competition experiments showed that the outcome of interspecific competition depends only on nutrient kinetics and not on the initial abundance of competitors. The independence from starting conditions is a common feature of all published chemostat competition experiments (e.g. Sommer, 1983, 1985; Tilman and Sterner, 1984). This behavior is predicted by the resource based competition theory developed by D. Tilman, S. Kilham, P. Kilham and their co-workers (Tilman, 1982; Tilman *et al.*, 1982). This theory assumes depletion of common resources to be the only interaction between competing species.

The resource based competition theory implies that the outcome of competition can be predicted from the Monod parameters of the competing species. Since the kinetic parameters of the successful competitors of Series 1 and 2 experiments are available (Table 2), this test can be performed here. Tilman (1982) developed a simple graphic technique to predict the outcome of interspecific competition for two potentially limiting nutrients: (1) Calculate the equilibrium (reproduction rate = dilution rate) concentration of the limiting nutrients [ $R^*$  in Eq. (2)]. (2) If limitation by two nutrients follows Liebig's "law of the minimum" (usually it does, Rhee and Gotham, 1980), a rectangular zero-net-growth-isocline (ZNGI) can be drawn in a field where the two axes represent the concentrations of the two nutrients. Any point on the ZNGI represents a combination of nutrient concentrations, at which the  $\mu$  equals the dilution rate. The nutrient concentrations of the inflow medium can be represented by a "resource supply point". If the resource supply point is nearer to the origin than the ZNGI, the species will be washed out, even in the absence of competitors. If the resource supply point is beyond the ZNGI, it will survive and depress the combined concentrations of both nutrients to a point on the ZNGI. (3) If two or more species



**Fig. 5.** Theoretical prediction of the outcome of Si and N competition among *Corethron criophilum* (Cc), *Nitzschia kerguelensis* (Nk), *N. cylindrus* (Nc), *Thalassiosira subtilis* (Ts), *Chaetoceros neglectum* (Cn). x-axis: nitrate, y-axis: silicate. The ZNGIs of the five species are shown by the rectangular lines (marked by the species abbreviation at the corner). ZNGIs are shown by broken lines if a species is predicted to be outcompeted at any nutrient ratio. Shaded areas in the top three diagrams are regions of coexistence. Regions marked with only one abbreviation are regions, where only one species is predicted to win. Black circles indicate resource supply points (numbers show Si:N ratios). The two bottom diagrams indicate the predictions for the two lower dilution rates in different scale; only regions of predicted coexistence and single species dominance are shown

compete for the two nutrients, there are two possibilities: If the ZNGIs do not intersect, the species with the ZNGI closer to the origin will exclude the other. If the ZNGIs intersect, there will be a region of coexistence. It is confined by the intersection point of the ZNGIs and two vectors with slopes equal to the "optimal" nutrient ratios for the two species. If the resource supply point falls into that sector, both species will coexist. If the resource supply point lies to the left of it, the species with the ZNGI closer to the y-axis will win; if it lies to the right, the species with the ZNGI closer to the x-axis will win.

Figure 5 shows the predictions for the experiments of Series 1 and 2. The graphs for the lower dilution rates are shown in two different scales in order to show the resource supply point in one graph and the region near the origin in greater detail in the other graph. The predictions for a dilution rate of  $0.1 \text{ d}^{-1}$  are: at Si:N=425:1 only *Corethron criophilum* should win, and it did. At 14:1 *C. criophilum* and *Thalassiosira subtilis* should coexist, and they did. At 2.6:1 *Nitzschia cylindrus* should coexist with *T. subtilis*, but in fact only *N. cylindrus* persisted. The predictions for a dilution rate of  $0.25 \text{ d}^{-1}$  are: At the highest Si:N ratio *C. criophilum* should win, and it did. At the medium ratio *T. subtilis* should win; in the experiments *N. cylindrus* coexisted with *T. subtilis* with an apparently stable 32 to 33% contribution to total biomass. Note that the resource supply point is in the region of pure *T. subtilis* dominance, but it closely neighbours the region of *T. subtilis*–*N. cylindrus* coexistence. At the lowest Si:N ratio the coexistence of *T. subtilis* and *N. cylindrus* again followed the prediction. Washout of all species under all nutrient conditions is expected theoretically for the highest dilution rate. However, in the Si-enriched cultures *N. kerguelensis* and in the N-enriched cultures *N. cylindrus* seemed to persist, although the biomass levels were only about 5% of those in

the experiments with low or medium dilution rates. Fig. 5 shows that the resource supply points are not very distant from the ZNGIs of the respective species.

In summary, the deviations of the results of competition experiments from predictions based on Monod kinetics are only minor. The trade-off between Si-competition and N-competition closely resembles an analogous trade-off between Si- and P-competition in freshwater diatoms (Tilman, 1981, 1982). Additionally a trade-off in competition for one nutrient at different dilution rates has been found. In the absence of Si-limitation, e.g. *Corethron criophilum* was the best competitor for N at the low and the medium dilution rate and *Nitzschia kerguelensis* at the high dilution rate. This is contrary to the opinion of Smith and Kalff (1983) who denied the existence of this type of specialisation (but cf. Sommer and Kilham, 1985).

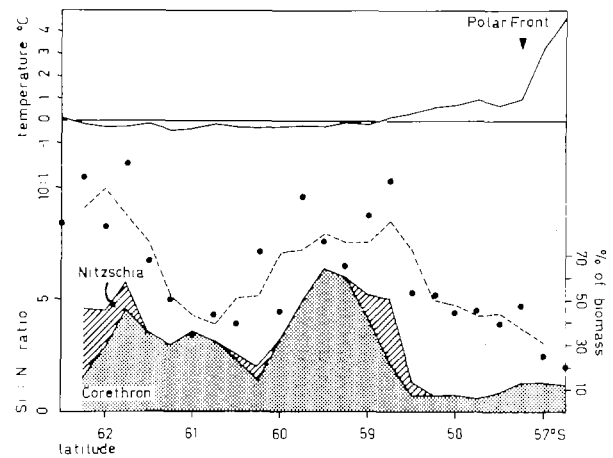
#### "Real world" application

The internal consistency of competition theory and of competition experiments in cultures does not yet permit any conclusion on the importance of nutrient competition in nature. Other factors, e.g. grazing, sinking, and light limitation, might be equally or more influential in the determination of the phytoplankton species composition. This seems especially probable for the Antarctic Ocean, where most of the literature doubts the existence of nutrient limitation (except for Si). There cannot be nutrient competition without nutrient limitation. On the other hand, competition can be inferred if nutrient limitation can be demonstrated, as long as it can be assumed that uptake by phytoplankton is the major sink of nutrients.

The results presented here offer two pieces of evidence in favor of nutrient limitation in antarctic waters. First, the

unenriched Seawater A did not permit any species to withstand a dilution rate of  $0.5 \text{ d}^{-1}$ , although some had a higher maximum growth rate. In the enriched media survival of two species at this dilution rate became possible. In my opinion, these experiments are a more powerful test for nutrient limitation than short-term enrichment bioassays (Hayes *et al.*, 1984), where some (unknown) time lag has to be considered, until a response of the growth rate or photosynthesis can be expected.

Second, Seawaters A and B had Si-concentrations clearly below the half-saturation constants of two species and N-concentrations below the half-saturation constant of one species. Ambient nutrient concentrations, however, are only indicative of nutrient limitation if they are steady-state concentrations. Transient minima of nutrient concentrations do not necessarily lead to the corresponding decline of growth rates if faster growth can be maintained at the expense of a previously built-up intracellular pool (Droop, 1973, 1983). To obtain information on the large scale spatial nutrient distribution a gradient analysis was performed from the end of Bransfield Strait (Lat.  $62^{\circ}30'S$ , Long.  $58^{\circ}22'04''W$ ) to the Polar Front in the Drake Passage (Lat.  $56^{\circ}45'S$ , Long.  $61^{\circ}50'20''W$ ) during the northward trip of RV "Polarstern" from 4 to 6 December 1984 (Sommer and Stabel, in preparation). Samples for dissolved nutrient analyses and cell counts were taken from the seawater pump (inlet at about 10-m depth) at intervals of 15 latitudinal minutes. Nitrate concentrations were consistently low and slowly declining northwards (from  $3.35$  to  $2.2 \mu\text{M}$ ), indicating that the concentrations in Seawaters A and B had not been abnormal for that period and region. Phosphate concentrations were consistently high ( $1.8$  to  $2.35 \mu\text{M}$ ). Silicate concentrations fluctuated more irregularly, but high values occurred more often in the South (up to  $32 \mu\text{M}$ ) and the lowest values were found near the Polar Front ( $4.3 \mu\text{M}$ ). Our P and Si data are in the same range as literature data (El Sayed *et al.*, 1983; Jacques, 1983; Le Jehan and Treguer, 1983). Our N data, however, are nearly one order of magnitude lower than the usual literature data. Re-analysis of the samples has confirmed the low nitrate concentrations and there is no difference in methods to the papers cited above (nitrate analysis according to Strickland and Parsons, 1972). At present, there is no way to judge whether such low N concentrations are an extremely rare event in antarctic waters or a recurring seasonal pattern, which is overlooked if temporal resolution of the sampling regime is insufficient. Unfortunately we do not know the pre-history of the water body sampled; e.g. we do not know whether a nitrate depleting bloom subsequently eliminated by sedimentation preceded our sampling. The lowest nitrate concentrations encountered would permit growth of *Nitzschia cylindrus* at 35% of its maximum growth rate, of *Chaetoceros neglectum* at 56%, *Thalassiosira subtilis* at 73%, *Nitzschia kerguelensis* at 75%, *Corethron criophilum* at 88%. *In situ*, however, the availability of light might have imposed an even stronger limitation on population growth.



**Fig. 6.** %-contribution to total phytoplankton biomass by *Corethron criophilum* (shaded) and *Nitzschia kerguelensis* (hatched) along the S-N transect in comparison to the Si:N ratios (circles: actual data; broken line: smoothed by using the running mean). Top panel: water temperatures

The results of the cell counts from the South-North gradient also permit interpretation with respect to two of the important species of the competition experiments: *Corethron criophilum* and *Nitzschia kerguelensis* (the two indicators of high Si:N ratios). The other species of the experiments were too rare in the samples to permit reliable counts. Figure 6 shows that the maxima of their cumulative relative biomass roughly coincide with the maxima of the Si:N ratio.

This paper is not meant to infer that nutrient limitation and competition are dominant forces in the determination of phytoplankton species composition in the Antarctic Ocean. The data, however, demonstrate that nutrient competition cannot be ruled out completely. Its relative importance in comparison to other selective forces and its commonness in time and space can only be evaluated by further research. Time-series analyses from the same water body are especially lacking at present.

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#### Literature cited

- Droop, M. R.: Some thoughts on nutrient limitation in algae. *J. Phycol.* 9, 264–272 (1973)
- Droop, M. R.: 25 years of algal growth kinetics. *Bot. mar.* 26, 99–112 (1983)
- El Sayed, S. Z., D. C. Biggs and O. Holm-Hansen: Phytoplankton standing crop, primary productivity, and near surface nitrogenous fields in the Ross Sea. *Deep-Sea Res.* 30, 871–886 (1983)
- Hayes, P. K., T. M. Whitaker and G. E. Fogg: The distribution and nutrient status and phytoplankton in the southern Ocean between  $20^{\circ}$  and  $70^{\circ}$  W. *Polar Biol.* 3, 153–165 (1984)

- Jacques, G.: Some ecophysiological aspects of the antarctic phytoplankton. *Polar Biol.* 2, 27–33 (1983)
- Kilham, S. S.: Silicon and phosphorus growth kinetics and competitive interactions between *Stephanodiscus minutus* and *Synedra* sp. *Verh. int. Ver. Limnol.* 22, 435–439 (1984)
- Le Jehan, S. and P. Treguer: Uptake and regeneration  $\Delta\text{Si}/\Delta\text{N}/\Delta\text{P}$  ratios in the Indian sector of the southern Ocean. *Polar Biol.* 2, 127–136 (1983)
- Li, W. K. W.: Consideration of errors in estimating kinetic parameters based on Michaelis-Menten formalism in microbial ecology. *Limnol. Oceanogr.* 28, 185–190 (1983)
- Rhee, G. Y. and I. S. Gotham: Optimum N:P ratios and the coexistence of planktonic algae. *J. Phycol.* 16, 486–489 (1980)
- Smith, R. E. and J. Kalf: Competition for phosphorus among co-occurring freshwater phytoplankton. *Limnol. Oceanogr.* 28, 448–464 (1983)
- Sommer, U.: Nutrient competition between phytoplankton species in multispecies chemostat experiments. *Arch. Hydrobiol.* 96, 399–416 (1983)
- Sommer, U.: Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. *Limnol. Oceanogr.* 30, 335–346 (1985)
- Sommer, U. and S. S. Kilham: Phytoplankton natural community competition experiments. A reinterpretation. *Limnol. Oceanogr.* 30, 436–440 (1985)
- Strickland, J. D. H. and T. R. Parsons: A practical handbook of seawater analysis. *J. Fish. Res. Bd Can. Bull.* 167, 1–310 (1972)
- Tilman, D.: Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58, 338–348 (1977)
- Tilman, D.: Test of resource competition theory using four species of Lake Michigan algae. *Ecology* 62, 802–815 (1981)
- Tilman, D.: Resource competition and community structure, 296 pp. Princeton: Princeton University Press 1982
- Tilman, D., S. S. Kilham and P. Kilham: Phytoplankton community ecology: the role of limiting nutrients. *A. Rev. Ecol. Syst.* 13, 349–372 (1982)
- Tilman, D. and R. W. Sterner: Invasions of equilibria: test of resource competition using two species of algae. *Oecologia* 61, 197–200 (1984)

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