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# The species composition of Antarctic phytoplankton interpreted in terms of Tilman's competition theory

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**Summary.** An attempt was made, to test for the impact of resource competition on Antarctic marine phytoplankton. According to theory, species composition near competitive equilibrium should be determined by the ratios of limiting resources. Enrichment bioassays identified silicon and nitrogen as limiting nutrients for some of the most important phytoplankton species during early austral summer in the region near the Antarctic Peninsula. Together with the generally acknowledged limiting resource light, this gave three meaningful ratios of essential resources (Si:N, Si:light, N:light) and one ratio of substitutable resources ($NO_3$:$NH_4$). Phytoplankton species assemblages were found to be well separated by the ratios of the essential resources and by mixing depth. Nine out of 12 individual species were found to be separated along at least one of the gradients of resource ratios. Where comparison with competition experiments was available, predicted and realized distributions of species were compatible.

**Key words:** Antarctic phytoplankton – Competition – Resource ratios – Nutrients

After ten years of successful application in phytoplankton culture eperiments, the time has come to examine the real world applicability of Tilman's mechanistic theory of resource competition (1977, 1982). The concept of resource competition as a major determining factor of species composition competes with other explanations, such as control by physical factors, control by higher trophic levels, allelopathic interactions, facilitation, colonisation history and randomness. Tilman's competition theory predicts that at or near competitive equilibrium species dominance and relative abundances are determined by the ratios of the limiting resources. This prediction is unique to competition theory. No other theory about the determination of the species composition of natural communities makes this prediction. Therefore, the existence of distribution patterns of species along resource ratio gradient has a highly diagnostic value for the underlying mechanisms of community regulation. I took it as a challenge to look for such patterns in Antarctic phytoplankton, where most colleagues would consider resource limitation and, hence, resource competition quite unimportant.

Extensive experimental research mainly with freshwater phytoplankton (cf. Tilman et al. 1982, 1986) but also with marine Antarctic phytoplankton (Sommer 1986) showed an inverse ranking of several species with respect to their competitive abilities for different limiting resources. This tradeoff enables species to coexist in equilibrium at those resource ratios where the coexisting species are limited by different resources. The tradeoff in competitive abilities further enables numerous species to share a gradient of the ratio of two limiting resources, being most dominant at their optimal resource ratio. If the temporal change of resource ratios is slow relative to competitively induced shifts in species composition (Tilman 1985) relative abundances should show clear patterns along resource ratio gradients: A positive correlation with resource ratios, if the optimal ratio is higher than the maximal one in the data set, a negative correlation if it is lower, and an A-shaped pattern if the optimal ratio is in the middle of the observed gradient.

The majority of researchers considers Antarctic marine phytoplankton to be light- but not nutrient-limited (Hayes et al. 1984) which would exclude the possibility of competition for more than one limiting resource. Light limitation is accepted because the usually high mixing depths of the water (around $10^2$ m) lead to a low average light exposure of algal cells circulated through the vertical light gradient. Nutrient limitation is denied because of high concentrations of dissolved silicate, nitrate and phosphate. However, Monod-type growth rate vs. nutrient concentration experiments at in situ temperatures have shown very high silicate and nitrate requirements of some important Antarctic diatoms, half saturation parameters being in the same order as the lower concentrations of silicate and nitrate encountered in the Bransfield Strait and adjacent regions of the Drake Passage during November/December 1984 (Sommer 1986; Sommer and Stabel 1986). During the expedition ANT VI-2 of the RV "Polarstern" from mid-October to mid-December in the same region, I made a follow up study, aimed at the identification of nutrient limitation of phytoplankton growth and at the identification of resource related patterns in the distribution of phytoplankton species. Here, I discuss the latter.

## Methods

Samples for chemical analyses and for phytoplankton counts were taken with a rosette-sampler from 10, 50, and 100 m depths at 48 stations (see map in Fig. 1). Dissovled nutrient concentrations (Si, P, $NO_3$, $NO_2$, $NH_4$) were measured by oceanographic standard methods (Strickland and Parsons 1972); phytoplankton was counted under the inverted microscope. About 400 individuals of the dominant species and a correspondingly lower number of the rare ones were counted. Species specific biomass was defined as cell-volume, which was calculated by approximation to the nearest standard geometric solid. Relative importance of a species is expressed as share of total phytoplankton biomass.

The light climate was characterized by the quotient average light intensity in the mixed layer: surface light intensity ($\bar{I}/I_0$). This relative index was chosen instead of an absolute value because cloud cover and, hence, surface irradiance changed on a daily time scale which is much more rapid than shifts in species composition. The average light intensity ($\bar{I}$) of the mixed layer (depth: $z$) was calculated according to the equation (Riley 1957)

$$\bar{I} = I_0(1 - e^{\varepsilon z})/\varepsilon z.$$

The vertical extinction coefficient ($\varepsilon$) was calculated from chlorophyll concentrations according to an empirical formula which had been established for the same season and the same region:

$$\varepsilon = 0.027 * \mu g \text{ Chl.} l^{-1} + 0.06$$

(Tilzer et al. 1985).

Bioassays for the identification of nutrient limitation were performed on 11 occasions. Raw water from 10 m depth was diluted threefold with filtered water from the same depth. Large zooplankton was removed by a 500 μm mesh-size screen. The resulting plankton suspension was distributed into 9 bottles, from which two received no nutrient addition, 3 received individual addition of Si, P, and N (ammoniumnitrate), 3 received the pairwise combinations and one bottle received the triple combination of nutrient additions. The bottles were incubated at the ambient light:dark cycles at 160 $\mu E\ m^{-2}\ s^{-1}$ light intensity and 0° C temperature. Growth rates were calculated after cell counts performed on days 0, 2, and 5. Nutrient limitation was accepted, if the growth rate in the bottles supplemented with the limiting nutrient was significantly higher than in the bottles without (ANOVA, $P < 0.05$).

## Results

### *Limiting resources*

The bioassay experiments showed a significant nutrient effects in 42 out of 89 cases, one species per one experiment constituting one case. In all cases, either N (28 cases) or Si (14 cases) were the limiting nutrient. Nutrient limitation was never strong. In most cases the growth rate in the unenriched bottles was >70% of the growth rate in the enriched bottles. Most species behaved consistently, being limited always by the same nutrient, if nutrient limited at all. The diatoms *Corethron criophilum* and *Nitzschia kerquelensis* tended to be Si-limited; the diatoms *Nitzschia cylindrus, N. seriata, Thalassiosira subtilis,* the Prymnesiophyceae *Phaeocystis pouchetii*, the Prasinophyceae *Pyramimonas* sp. and the Cryptophycean flagellates tended to be N-limitated. Only *Thalassiosira antarctica* was three times N-limited, once Si-limited and showed no nutrient limitation in 3 further cases.

Light limitation was not tested experimentally during this expedition. However, the photosynthetic parameters published by Tilzer et al. (1985) for the same region and season together with the $\bar{I}/I_0$ index permit a rough estimate of the strength of light limitation. Tilzer et al. give an average saturation intensity ($I_k$) of 86±42 (SD) $\mu E\ m^{-2}\ s^{-1}$ and an average $I_0$ of 673±194 $\mu E\ m^{-2}\ s^{-1}$ around noon. During this cruise, the $\bar{I}/I_0$ index varied between 0.071 and 0.438. For an average surface irradiance and an average $I_k$ this implies between ca. 55 and 100% of the light saturated photosynthesis. Potential light limitation is, therefore, about as strong as potential nutrient limitation, which makes it possible that light- and nutrient limited algal species coexist.

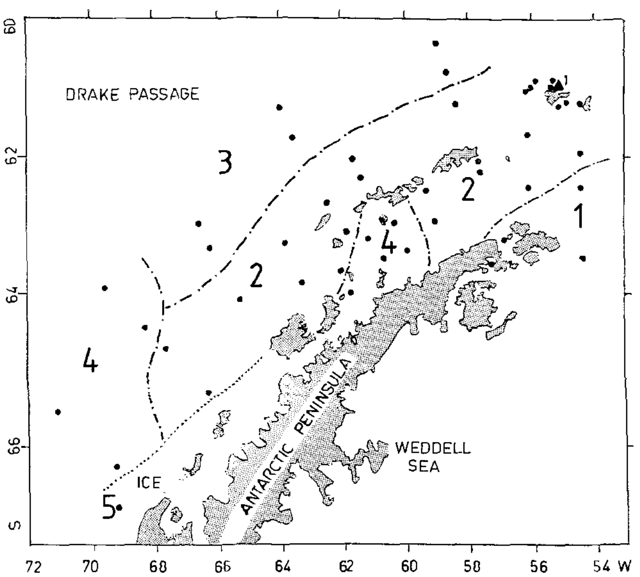

**Fig. 1.** Geographic distribution of the different phytoplankton communities in the period 28 October to 16 December 1987

Three limiting essential resources (light, N, Si) give three meaningful resource ratios along which species can be sorted: Si:N, Si:light, N:light. Concentrations of dissolved nitrogen were expressed as the sum of all inorganic N-ions ($NO_3$, $NO_2$, $NH_4$), among which $NO_3$ always comprised >85%. In addition to the ratios of the non-substitutable resources, the ratio of the physiologically substitutable resources $NO_3$ and $NH_4$ was taken into consideration.

### *Distribution of algal communities*

Phytoplankton species composition, as defined by the relative contribution of species to the total cell-volume, showed five fairly distinct types within the study region (Fig. 1). At the northern margin of the Weddell Sea and at a few scattered stations elsewhere phytoplankton was dominated by large *Thalassiosira* spp., mainly *T. antarctica* (Type 1). Phytoplankton biomass was relatively low (median of chlorophyll concentrations: 0.225 $\mu g \cdot l^{-1}$; interquartile range from 0.107 to 1.214 $\mu g \cdot l^{-1}$; $n = 7$). Nitrogen concentrations (median 20.5 μM; interquartile range from 19.1 to 44.8 μM) and silicate concentrations (median 69 μM; interquartile range from 63.6 to 75.6 μM) in those waters were high. At most stations in the Bransfield Strait and at the nearshore stations of the Drake Passage phytoplankton biomass was dominated by *Corethron criophilum* (type 2). Here, chlorophyll concentrations were again quite low (median 0.275 $\mu g \cdot l^{-1}$; interquartile range 0.202 to 0.378 $\mu g \cdot l^{-1}$, $n =$ 24); silicate concentrations were high (median 71.6 μM; interquartile range 66.3 to 75.5 μM), but nitrogen concentrations were low (median 13.6 μM; interquartile range 10.95

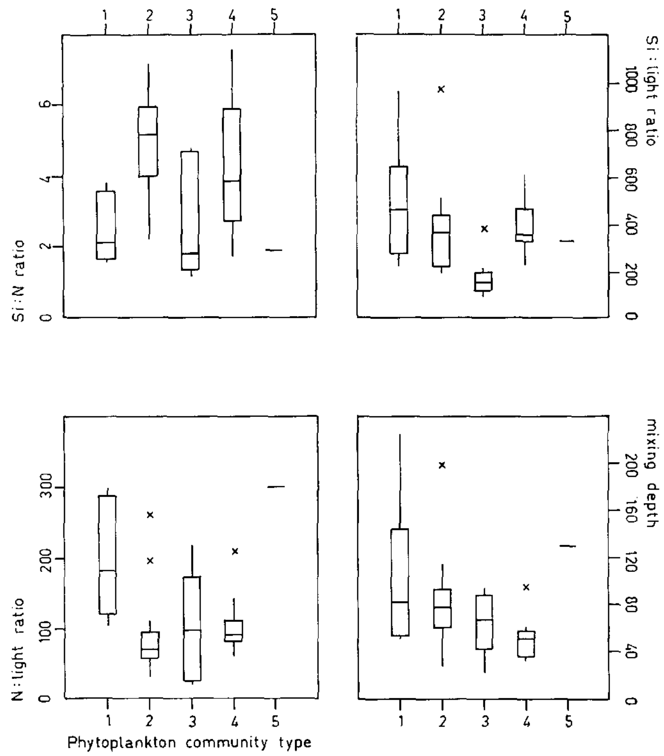

**Fig. 2.** Box- and Whisker-Plots showing medians, quartiles, minimum to maximum-ranges and outliers for the Si:N ratios, Si:light ratios, N:light ratios and mixing depths for the waters occupied by the five different phytoplankton communities

to 18.85 µM). In the offshore region of the Drake Passage phytoplankton was more diverse, being dominated by *Nitzschia* spp. with seriate colony morphology (*N. seriata, N. barclayi* etc.), narrow-celled *Rhizosolenia* spp. and the silicoflagellate *Distephanos speculum* (type 3). Chlorophyll concentrations were quite variable (median 0.467 µg·l$^{-1}$; interquartile range 0.281 to 0.829 µg·l$^{-1}$, $n=6$); N-concentrations varied over a wide range (median 18.3 µM; interquartile range from 7.9 to 34.1 µM); silicate concentrations were quite low (median 37.1 µM; interquartile range 30.1 to 38.4 µM). In two areas (western Bransfield Strait, Drake Passage near the ice edge) extended *Phaeocystis pouchetii* blooms (type 4) were encountered, with high chlorophyll concentrations (median 2.28 µg·l$^{-1}$; interquartile range 1.066 to 2.605 µg·l$^{-1}$, $n=10$), low N-concentrations (median 17.55 µM; interquartile range 13 to 16.9 µM), and high Si-concentrations (median 70.2 µM; interquartile range 51.2 to 75.7 µM). Type 5 phytoplankton community was found only once within a polynia. The sparse plankton (mainly *Nitzschia* sectio *Fragilariopsis*) of this station was obviously not autochthonous in the free water, but was seeded from the ice-flora. Therefore, it will be excluded from further discussions.

In accordance with competition theory, the different algal communities were more clearly separated from each other by resource ratios (Fig. 2) than by absolute resource levels. The non-parametric Kruskal-Wallis analysis with the resource ratios as data values and the community types as level codes showed significant differences in the Si:N ratios ($Z=17.26$; $p=0.0017$), in the Si:light ratios ($Z=$

**Table 1.** Results of multiple correlation analysis (forward stepwise variable selection, $F$-to-enter $=4$) of relative importance of algal taxa ($p_i$) on resource ratios and mixing depth. $y=\arcsin\sqrt{p_i}$; $x_1=\log^{10}(\mathrm{Si:N})$, $x_2=\log^{10}(\mathrm{Si:light})$; $x_3=\log^{10}(\mathrm{N:light})$; $x_4=\log^{10}(\mathrm{NO_3:NH_4})$; $x_5=\log^{10} z_{\mathrm{mix}}$

| *i* | Equation<br>$y=$ |
|---|---|
| *Corethron criophilum* | $-0.82+1.2x_1+0.44x_4$<br>$r=0.65$; $F=16.0$; $p<0.0001$ |
| *Thalassiosira antarctica* | $0.051+0.074x_3$<br>$r=0.45$; $F=11.5$; $p=0.0015$ |
| *Th. subtilisis* | $0.47-0.195x_5$<br>$r=0.36$; $F=6.66$; $p=0.013$ |
| *Nitzschia kerquelensis* | $0.32-0.14x_1-0.076x_4$<br>$r=0.44$; $F=5.46$; $p=0.0076$ |
| *N. cylindrus* | $0.71-0.27x_1-0.26x_4$<br>$r=0.43$; $F=4.96$; $p=0.0113$ |
| *N. seriata* | $1.02-0.81x_1+0.59x_1^2-0.34x_2-0.05x_4^2-0.2x_5$<br>$r=0.77$; $F=12.0$; $p<0.0001$ |
| *Rhizosolenia alata* | $0.22-0.19x_1^2$<br>$r=0.35$; $F=6.21$; $p=0.016$ |
| *R. hebetata* f. *semispina* | $0.3-0.2x_2+0.15x_5$<br>$r=0.62$; $F=13.9$; $p<0.0001$ |
| *Distephanos speculum* | $3.93-3x_2+0.53x_2^2+0.15x_5$<br>$r=0.70$; $F=14.2$; $p<0.0001$ |
| *Phaeocystis pouchetii* | $-1.35-0.55x_1^2+1.35x_2-0.094x_4^2-0.41x_5^2$<br>$r=0.67$; $F=10.3$; $p<0.0001$ |
| *Pyramimonas* sp. | no correlation |
| Cryptophycean flagellates | no correlation |

11.4; $p=0.022$), and in the N:light ratios ($Z=15.83$; $p=0.0032$). Community type 1 was characterized by low Si:N ratios and high N:light ratios, type 2 by high Si:N ratios and low N:light ratios, type 3 by low Si:N ratios, low Si:light ratios and low N:light ratios. Type 4 was not well separated from other communities by resource ratios (it behaved quite similar to type 2) but was separated from all other communities by low mixing depths. There was no significant separation of algal communities along the gradient of $NO_3$:$NH_4$ ($Z=5.67$; $p=0.225$).

### *Distribution of individual taxa along resource ratio gradients*

The distribution of individual taxa along resource ratio gradients was examined by multiple correlation analysis with the relative contribution of individual species ($p_i$) as dependent variable. In order to normalize the distributions, $p_i$ values were arcsine-squareroot transformed, which is a commonly used transformation for data bound between 0 and 1. The four ratios of limiting resources (Si:N, Si:light, N:light, $NO_3$:$NH_4$) and the physical parameter mixing depth ($z_{mix}$) were used as independent variables in logarithmic transformation. In order to account for non-linearities and for unimodal response, also quadratic terms of the independent variables were included. The numbers of independent variables was reduced by automatic stepwise variable selection (forward procedure; $F$-to-enter = 4). Nine of the 12 species under investigation showed a significant correlation of $p_i$ with one or more resource ratios; 4 of them also showed a correlation with $z_{mix}$, one with $z_{mix}$ alone, and two species showed no correlation with any of the dependent variables (Table 1).

## Discussion

Contrary to fresh waters, experimental analysis of the competitive performance of marine algae is scarce. For Antarctic phytoplankton, only one series of competition experiments is available (Sommer 1986). Those competition experiments were semicontinuous cultures with different Si:N ratios and dilution rates. The inocula consisted of natural phytoplankton assemblages from the same region and season as in this study. Fortunately, the experiments and this analyses have several important species in common. Among all species, *Corethron criophilum* was the one, which became dominant at the highest Si:N ratios at low and intermediate dilution rates; i.e. it was the best competitor for N and the poorest for Si. Its optimal Si:N ratio (200) is far beyond the range of Si:N encountered during this study. Its positive correlation (quadratic term insignificant) with the ambient Si:N ratios is therefore consistent with its experimentally determined competitive abilities.

On the other hand, *Nitzschia cylindrus* had been the alga which became dominant at the lowest Si:N ratios (optimal ratio 2.0). It shows a negative correlation with ambient Si:N ratios here. Those species, which had been dominant in the experiments at intermediate Si:N ratios (*Thalassiosira antarctica, T. subtilis*) showed no significant correelations with Si:N ratios here. Similar comparisons for Si:light, N:light, and $NO_3$:$NH_4$ are not yet possible. Further experimental research is needed.

It should be mentioned, that this study is not the only one where resource ratios have been found important in the determination of the species composition of Antarctic phytoplankton. Priddle et al. (1986) report a significant influence of Si:P ratios in the region around South Georgia during early austral summer. Together with Jaques' (1983) finding of silicate limitation of some diatoms near the Antarctic Convergence, this makes the dogma of always saturating nutrient concentrations in the Antarctic marine habitats at least a premature conclusion.

Exploitative competition occurs by definition, if consumption by organisms reduces the availability of resources sufficiently to be limiting for the reproductive rates (Tilman 1982). Therefore, the bioassays alone are a sufficient demonstration of competition for Si and N. The distribution of species along resource ratio gradients requires more than simple occurence of resource competition. It requires, that competition proceeds under relatively invariable boundary conditions for long enough time, to permit the superior competitors to become dominant in terms of number and biomass. This does not necessarily imply perfect competitive equilibrium, but it implies that the change of limiting resource ratios is slow realative to the change in species composition (Tilman 1985). Obviously, it is impossible to prove such a premise on the basis of a snapshot in time. The combination of evidence for nutrient limitation and of correlations between species composition and limiting resorce ratios, however, make it at least a strong case for the importance of competition as a major structuring force in the determination of species composition even in the physically harsh and nutrient-rich environment of the Antarctic Sea.

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