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## SHORT COMMUNICATION

### Silicate and the functional geometry of marine phytoplankton

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**Abstract.** The impact of nutrient supply ratios on the functional geometry of phytoplankton has been studied by means of competition experiments with phytoplankton communities from the Arabian Sea. Cell length and deviation from spherical shape of dominant competitors increased with Si:N ratios. Surface:volume ratios were minimal at intermediate Si:N ratios. Grazing by the rotifer *Brachionus plicatilis* did not lead to a qualitative shift in the response of geometric properties to Si:N ratios; however, mean cell lengths increased while surface:volume ratios decreased.

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Form–function and, especially, size–function relationships have a great potential for establishing an intermediate resolution level of community and ecosystem analysis between trophic levels and species. This approach has been advocated for terrestrial plant communities (e.g. Gaudet and Keddy, 1988; Keddy, 1992), as well as for plankton communities (e.g. Gaedke, 1993, 1995). A recent book on phytoplankton ecology (Reynolds, 1997) relates most of the probability at which a phytoplankton species can thrive in a given environment to its cellular geometry. Still, it is controversial to what extent the geometric properties of phytoplankton (cell size, surface–volume ratios, shape) override the importance of phylogenetically acquired biochemical and physiological differences between higher taxa in the determination of ecophysiological and ecological properties. Strong cases have been made for the size dependency of nutrient-saturated growth rates (Schlesinger *et al.*, 1981; Banse, 1982; Blasco *et al.*, 1982; Sommer, 1989a), susceptibility to grazing (Burns, 1968; Gliwicz, 1977; Geller and Müller, 1981; Sommer, 1988; Sterner, 1989) and sinking (Walsby and Reynolds, 1980; Reynolds, 1989). Maximal growth rates have also been related to surface–volume ratios (Reynolds, 1989), and light-harvesting properties to the distortion from a spherical shape (Reynolds, 1989).

The case is more controversial for phytoplankton nutrient competition. Here, competitive ability will be used in the sense of Tilman (1982), i.e. as the ability to persist and to exclude competitors in a constant environment. Smith and Kalff (1983) provided an example for an inverse relationship between cell size and competitive ability (but cf. Sommer and Kilham, 1985), while Grover (1989) provided theoretical evidence for a competitive advantage of long, needle-shaped cells over much smaller spheres. In most of the numerous culture competition experiments with freshwater phytoplankton performed during the 1980s (summarized in Sommer, 1989b), there was no evident trend of smaller species becoming dominant over larger ones, but the needle-shaped freshwater diatom *Synedra* spp. became notorious as a winner at high Si:P ratios. Generally, phylogenetic relationship, as expressed by taxonomic position, seemed more important for competitive success in a given nutrient scenario than size. In accordance with

Tilman's (1982) competition theory, competitive dominance was controlled by ratios of limiting resources, with diatoms dominant at high Si:P ratios, green algae at low Si:P ratios and high N:P ratios, and cyanobacteria dominant at low Si:P ratios and low N:P ratios, respectively (Tilman *et al.*, 1986). Recent similar experiments with marine phytoplankton have shown a dominance of diatoms at high Si:N ratios (Sommer, 1994, 1996). There is, however, one remarkable difference between marine and lake phytoplankton: in the former, long and thin cells are found almost exclusively among diatoms, while in the latter they also occur in other higher taxa such as green algae and cyanobacteria. Therefore, it might be hypothesized that nutrient supply ratios have a major impact on the functional geometry of marine phytoplankton. This would be in contrast to Reynolds' (1997) phytoplankton life-form model which implies a selection in favour of strongly non-spherical geometries primarily for light-limited conditions, such as those realized in deeply mixed water columns.

The impact of nutrient competition on cell size and shape was tested by semi-continuous competition experiments carried out during a summer monsoon cruise of the research vessel 'Sonne' in the Arabian Sea (SONNE 120, 12 June–12 July 1997). The culture medium consisted of filtered (0.2 µm) sea water from an oligotrophic station (10°N, 65°E) enriched with nutrients and unenriched sea water serving as a control. The enriched media received 30 µM N (15 µM NH<sub>4</sub> and 15 µM NO<sub>3</sub>), a variable dose of silicate (0, 3.75, 7.5, 15, 30 µM), and Provasoli's trace elements and vitamins enrichment (270 µl l<sup>-1</sup>); the final concentrations, as measured according to oceanographic standard methods (Strickland and Parsons, 1968) by an autoanalyser, are given in Table I. The experimental design consisted of two steps: phytoplankton bottles (250 ml culture volume) where algae competed for nutrients and grazing bottles where the rotifer *Brachionus plicatilis* fed on the algal assemblage resulting from nutrient competition. The phytoplankton bottles were diluted manually once per day with fresh medium corresponding to a dilution rate of 0.25 day<sup>-1</sup>. The inoculum was a natural phytoplankton assemblage collected from 20:30°N, 59:10°E on 13 July. Mesozooplankton were removed by sieving through a 200 µm screen; thus, microzooplankton were still present. Consequently, the competition experiments are expected to reveal competition between nano- and microphytoplankton species, while picoplankton are expected to be suppressed by microzooplankton grazing. The replaced algal suspension (62.5 ml day<sup>-1</sup>) was split into a 10 ml subsample and 50 ml food suspension for the grazing step. The food suspension was filled into a second bottle which received an inoculum of the rotifer zooplankton species

**Table I.** Final dissolved nutrient concentrations and nutrient ratios of experimental media

Medium	NH <sub>4</sub>	NO <sub>3</sub>	P	Si	Si:N	N:P
Control	0.08	0.23	0.07	1.58	5.10:1	4.4:1
Enrichment 1	15.08	15.23	2.07	1.58	0.05:1	14.6:1
Enrichment 2	15.08	15.23	2.07	5.33	0.18:1	14.6:1
Enrichment 3	15.08	15.23	2.07	9.08	0.30:1	14.6:1
Enrichment 4	15.08	15.23	2.07	16.58	0.55:1	14.6:1
Enrichment 5	15.08	15.23	2.07	31.58	1.04:1	14.6:1

*B.plicatilis*, to study the impact of grazing on the phytoplankton community prestructured by competition. The grazing bottles were diluted at a rate of 0.125 day<sup>-1</sup>. Direct sunlight was attenuated by a white veil that transmitted ~30% light.

Samples for algal cell counts and measurements were fixed with formaldehyde (2.5% final concentration). *Brachionus*, phytoplankton and protozoa >3 µm were counted by Utermöhl's inverted microscope technique (1958); smaller organisms by epifluorescence microscopy. Counting of 400 individuals per species gives a 95% confidence limit of ±10% (Lund *et al.*, 1958). The geometric properties used in the analysis are the same as in Reynolds (1997): cell length ( $L$ ; greatest axial linear dimension; in µm), cell surface ( $S$ ; in µm<sup>2</sup>), cell volume ( $V$ ; in µm<sup>3</sup>), surface:volume ratio ( $SV^{-1}$ ; in µm<sup>-1</sup>), and a dimensionless shape index which measures the distortion from a spherical shape as the product of the length and the surface:volume ratio ( $LSV^{-1}$ ). Measurements were made in the microscope on 40 cells per species. Surfaces and volumes were calculated according to the formula for the most similar standard geometric figure. Biomass was estimated as carbon on the basis of calculated cell volumes, using Strathmann's (1969) conversion equations for diatoms and non-diatom protists. The data were analysed by linear or, if appropriate, second-order polynomial regression analysis (Table II). Biomass and morphological parameters were log transformed. Si concentrations and Si:N ratios were log transformed as well because of the

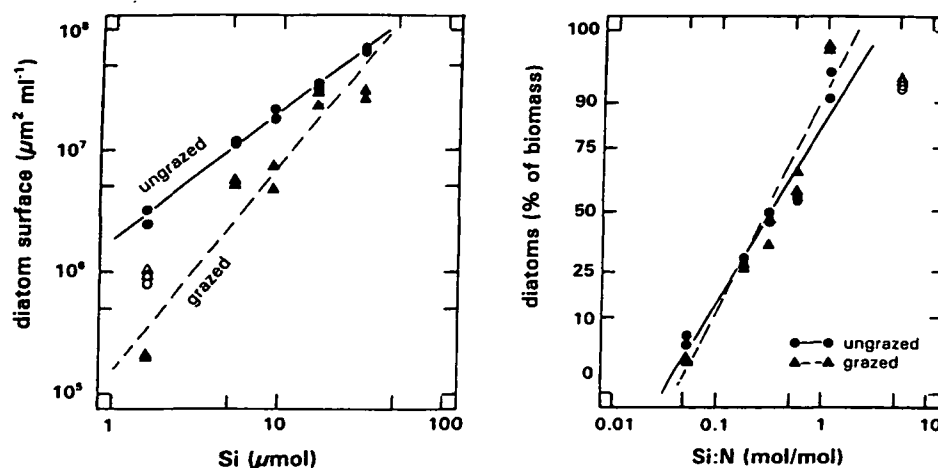
**Table II.** Regressions of biological response variables on silicate concentration (µm) or Si:N ratios (mol/mol)

Equation	$r^2$	$P$
<i>Without grazing</i>		
Diatom cell surface ( $S_D$ ; 10 <sup>3</sup> µm <sup>2</sup> ml <sup>-1</sup> )		
$\log_{10} S_D = 3.25 + 1.07 \log_{10} \text{Si}$	0.99	<0.00001
Diatom biomass ( $B_D$ ; µg C l <sup>-1</sup> )		
$\log_{10} B_D = 1.87 + 1.39 \log_{10} \text{Si}$	0.83	<0.00005
Contributions of diatoms to phytoplankton biomass ( $p_D$ )		
$\arcsin \sqrt{p_D} = 1.17 + 0.78 \log_{10}(\text{Si:N})$	0.93	<0.00005
Mean cell length ( $L$ ; µm)		
$\log_{10} L = -1.94 + 0.68 \log_{10}(\text{Si:N})$	0.81	<0.005
Mean surface:volume ratio ( $SV^{-1}$ ; µm <sup>-1</sup> )		
$\log_{10}(SV^{-1}) = -0.009 + 0.66 \log_{10}(\text{Si:N}) + 0.45(\log_{10}(\text{Si:N}))^2$	0.74	<0.005
Mean shape index ( $LSV^{-1}$ ; dimensionless)		
$\log_{10}(LSV^{-1}) = 1.89 + 1.84 \log_{10}(\text{Si:N}) + 0.84(\log_{10}(\text{Si:N}))^2$	0.86	<0.0005
<i>With grazing</i>		
Diatom cell surface ( $S_D$ ; 10 <sup>3</sup> µm <sup>2</sup> ml <sup>-1</sup> )		
$\log_{10} S_D = 2.21 + 1.67 \log_{10} \text{Si}$	0.91	<0.00005
Diatom biomass ( $B_D$ ; µg C l <sup>-1</sup> )		
$\log_{10} B_D = 1.39 + 1.50 \log_{10} \text{Si}$	0.87	<0.00005
Contributions of diatoms to phytoplankton biomass ( $p_D$ )		
$\arcsin p_D = 1.24 + 0.96 \log_{10}(\text{Si:N})$	0.96	<0.00005
Mean cell length ( $L$ ; µm)		
$\log_{10} L = -2.26 + 0.90 \log_{10}(\text{Si:N})$	0.80	<0.005
Mean surface:volume ratio ( $SV^{-1}$ ; µm <sup>-1</sup> )		
$\log_{10}(SV^{-1}) = -0.16 + 0.77 \log_{10}(\text{Si:N}) + 0.47(\log_{10}(\text{Si:N}))^2$	0.93	<0.0001
Mean shape index ( $LSV^{-1}$ ; dimensionless)		
$\log_{10}(LSV^{-1}) = 2.23 + 2.68 \log_{10}(\text{Si:N}) + 1.25(\log_{10}(\text{Si:N}))^2$	0.88	<0.0005

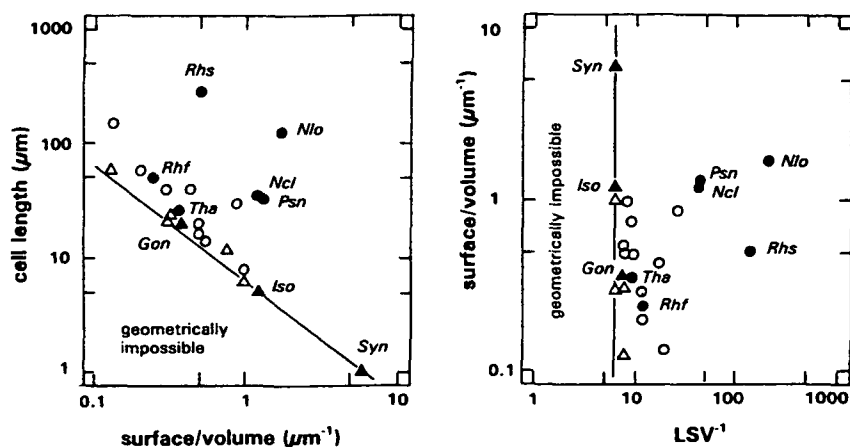
logarithmic scaling of the Si dosage. Because of the differences in N, P and trace element concentrations, the unenriched cultures are not included in the regressions, but are shown either at the lower end of the Si gradient or at the upper end of the Si:N gradient in the figures. Geometric community properties are biomass (carbon) weighted mean values for the entire phytoplankton community.

At the end of the experiments, algal biomass in the phytoplankton bottles was controlled by nitrogen (C:N from 11 to 17.5:1, atoms). The diatom biomass was significantly correlated ( $r^2 = 0.83$ ) with the log Si concentration in the supply medium, but the diatom surface area showed an even higher and virtually linear correlation with Si ( $r^2 = 0.99$ ;  $P < 0.00001$ ; Figure 1, left; Table II). The outcome of competition was analysed after 20 days of cultivation, which, according to previous experiments (Sommer, 1989b, 1994), was probably insufficient for complete competitive exclusion. However, the number of species had already been reduced from 23 initially to a maximum of five detectable species and three species with >10% of total biomass per treatment. As in comparable experiments with North Sea algae (Sommer, 1996), the relative biomass of diatoms increased with Si:N ratios and exceeded 90% at ratios >1:1 (Figure 1, right).

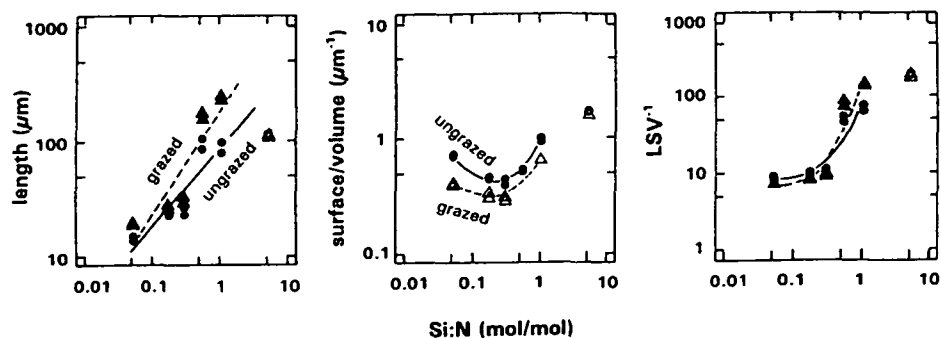
The phytoplankton species of the inoculum spanned almost three orders of magnitude of  $L$ , four and a half orders of magnitude of  $V$ , and two orders of magnitude of  $SV^{-1}$  and  $LSV^{-1}$ , respectively (Figure 2). The non-siliceous species were nearly spherical ( $LV^{-1} = 6$ ) or slightly subspherical ( $LSV^{-1} < 8$ ). The diatoms were morphologically more diverse. Four of the six successful diatom competitors at one or several Si:N ratios had very elongate shapes: the long, slim cylindrical *Rhizosolenia setigera* (subdominant at Si:N = 0.55:1 and Si:N = 1.04:1;  $LSV^{-1} = 141$ ) and the needle-shaped *Nitzschia longissima* (dominant at Si:N = 5.1:1;  $LSV^{-1} = 211$ ), *Nitzschia closterium* (rare at all Si:N ratios;  $LSV^{-1} = 41$ ) and



**Fig. 1.** Left: Total surface of diatoms as a function of Si in the medium; right: contribution of diatoms to total biomass as a function of Si:N ratios in the medium. Circles: competition bottles without grazing; triangles: bottles with grazing pressure; full symbols: included in regression; open symbols: not included.



**Fig. 2.** Geometric ordination of phytoplankton species. **Left:** cell length versus surface:volume ratio; **right:** surface:volume ratio versus shape index ( $LSV^{-1}$ ); circles: diatoms, triangles: non-siliceous algae; full symbols: persistent in competition experiments; open symbols: excluded from competition experiments. Species abbreviations: *Gon*: *Gonyaulax minima*; *Iso*: *Isochrysis* sp.; *Ncl*: *Nitzschia closterium*; *Nlo*: *Nitzschia longissima*; *Psn*: *Pseudonitzschia fraudulenta*; *Rhf*: *Rhizosolenia fragilissima*; *Rhs*: *Rhizosolenia setigera*; *Syn*: *Synechococcus* sp.; *Tha*: *Thalassiosira* sp.



**Fig. 3.** Mean geometric properties (**left:** cell length; **centre:** surface:volume ratio; **right:** shape index) as a function of Si:N ratios in the medium; circles: competition bottles without grazing, triangles: bottles with grazing pressure; full symbols: included in regression; open symbols: not included.

*Pseudonitzschia fraudulenta* (dominant at Si:N = 1.04:1;  $LSV^{-1}$  = 43). None of the excluded diatoms had  $LSV^{-1}$  values >26, i.e. there was no very elongate diatom species among the excluded ones.

The increasing proportion of thin, elongate diatoms with increasing Si:N ratios has a clear impact on the average geometry of the phytoplankton community. The mean cell length increased (Figure 3, left) by one order of magnitude over the range of experimental Si:N ratios. Mean surface:volume ratios showed a U-shaped response to Si:N ratios (Figure 3, centre). The minimum at Si:N = 0.18–0.3

was due to the diatoms *Rhizosolenia fragilissima* and *Thalassiosira* sp., which have a relatively stout morphology compared to the diatoms which were dominant at higher Si:N ratios. The shape index showed an increasing trend with increasing Si:N ratios (Figure 3, right).

Grazing within the second step of the cultures was highly selective and had a strong impact on the edible species *Isochrysis* sp., *N.closterium*, *P.fraudulentula* and *Thalassiosira* sp. There, biomass was reduced by about one order of magnitude relative to the first culture step, whereas the biomass of the other species was not reduced or even slightly enhanced. Nevertheless, the overall taxonomic pattern was unchanged (Figure 1, right) and morphological response curves were only displaced vertically in Figure 3. Grazing led to an increase in mean cell lengths and a decrease in mean surface:volume ratios, while the response to the Si:N ratio remained the same as without grazing. There was no detectable impact of grazing on the mean shape index.

In conclusion, these experiments do not support the assumption that nutrient competition would always select for small cell size irrespective of the particular nature of nutrient limitation (Smith and Kalff, 1983) and only light limitation for elongate, non-spherical shapes as postulated by Reynolds (1987). Evidently, competition under changed Si:N might also lead to changes in the selection for different functional geometries. It seems that under steady-state conditions, diatoms may build as large a cell surface as possible from the available silicate. The higher the Si:N ratio, the more needle shaped the competitively superior diatoms. This, in combination with the increased dominance of diatoms at increasing Si:N ratios, leads to a changed functional geometry of the entire phytoplankton community. Grover's (1989) hypothesis of a competitive superiority of long, elongated cells is thus supported under the restriction that Si:N ratios have to be sufficiently high.

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