Persistence of phytoplankton responses to different Si:N ratios under mesozooplankton grazing pressure: a mesocosm study with NE Atlantic plankton

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ABSTRACT: We fertilised 12 mesocosms with NE Atlantic phytoplankton with different Si:N ratios (0:1 to 1:1). After 1 wk, we added mesozooplankton, mainly calanoid copepods at natural densities to 10 of the mesocosms; the remaining 2 mesocosms served as controls. A trend of increasing diatom dominance with increasing Si:N ratios and species-specific correlations of diatoms to Si:N ratios were not changed by the addition of mesozooplankton. Large unicellular and chain-forming diatoms, thin-walled dinoflagellates (Gymnodiniales) and ciliates were reduced by copepod grazing while armoured dinoflagellates remained unaffected. Nanoplanktonic flagellates and diatoms profited from the addition of copepods, probably through release from ciliate grazing.

KEY WORDS: Phytoplankton · Zooplankton · Nutrient ratios · Mesocosms

INTRODUCTION

Prediction of the specific composition of communities of primary producers from resource ratios is a core element of Tilman's (1982) mechanistic competition theory ('resource ratio hypothesis', RRH). The RRH has successfully been applied to laboratory competition experiments with limnetic and marine phytoplankton, and worked well in both pairwise competition experiments with algae from clonal cultures (Tilman 1977) and in multispecies competition experiments with natural assemblages (for review see Sommer 2002). Among others, an increase of diatom dominance with increasing Si:P (Sommer 1983, 1986, Tilman et al. 1986) and Si:N ratios (Sommer 1994, 1998) has been reported. In such laboratory experiments, competition for limiting nutrients is the only factor influencing species composition, while other potentially important factors, such as grazing, temperature changes and stratification of the water column, are excluded. Therefore, it is not clear to what extent the RRH can be applied to field situations. The applicability of the diatom-related

predictions is particularly important in biological oceanography, since the alternative to dominance by sinking diatoms is either dominance by motile flagellates or by picoplankton. Those alternatives have far-reaching consequences for biogeochemical cycles (sedimentation versus remineralisation in the surface layer) and for the efficiency of energy transfer in the food web (Sommer & Stibor 2002, Sommer et al. 2002).

Attempts to use field data on nutrients and phytoplankton to test the RRH have been partially successful, but are intrinsically problematic (for more detailed discussion see Sommer 1999). First, it is necessary to include only those situations in which there is actual nutrient competition. Second, it is important to understand which of the nutrient concentration parameters (dissolved, particulate, total) usually measured comprises the optimal proxy for nutrient supply rates. Third, in most field situations, different nutrient ratios are accompanied by differences in confounding factors that influence phytoplankton composition, such as grazing, temperature, and stratification of the water column. *In situ* mesocosms offer a unique opportunity

to manipulate nutrient ratios under semi-natural conditions while keeping the other potentially important factors relatively equal among treatments. In this study, we used mesocosms to test which phytoplankton responses to different Si:N supply ratios with no concurrent mesozooplankton grazing would persist after the addition of natural levels of herbivorous/omnivorous mesozooplankton.

MATERIALS AND METHODS

We installed 12 transparent mesocosms of 7 m depth and 1 m diameter in Hopavågn, a sheltered semi-enclosed marine lagoon near the outlet of the Trondheimsfjord, Norway. The mesocosms were filled with surface water from Hopavågn on 21 August 2003. Mesozooplankton were removed by 30 net tows with a 100 μm mesh-size plankton net. Nutrients were added daily at 6 different molar Si:N ratios (0:1, 0.125:1, 0.25:5, 0:5:1, 0.75:1, 1:1; each replicated twice). The N:P ratio was 16:1 in order to ensure a balanced supply of P over N. Silicate additions were variable between treatments, while N and P additions (0.5 μg P l^{-1} d^{-1}; ammonium:nitrate = 1:1) were constant to ensure that total biomass levels between treatments were as similar as possible. The daily N dosage was designed to balance the sedimentary losses of N found to be typical for similarly shaped mesocosms in Hopavågn during previous years (COMWEB 1999, Y. Olsen et al. unpubl.). On 28 August (Day 7), 10 enclosures received mesozooplankton from fresh net catches at natural densities (ca. 20 to 30 ind. l^{-1}, dominated by calanoid copepods); 2 mesocosms (Si:N = 0:1, 0.75:1) received no mesozooplankton additions (controls). The experiment was terminated on 4 September.

In order to obtain a sample as soon as possible after the addition of mesozooplankton, samples for phytoplankton and protozoan counts were taken every second day, except for the samples on 28 and 29 August (Days 7 and 8). Samples for nanoplankton and microplankton counts were preserved with Lugol's iodine, samples for picoplankton counts were counted without preservation immediately after sampling with a flow-cytometer. The flow cytometer revealed 3 picoplankton clusters of equal size (1 to 3 μm), 1 containing chlorophyll *a* and phycoeythrin, the other 2 without phycoeythrin and with a different chlorophyll *a* content. As they were of equal size, the 3 clusters were combined for further analysis. Nano- and microplankton were counted according to Utermöhl's (1958) inverted microscope method. Phytopankton were identified mostly to species or genus level. In some cases, collective categories had to be used (unidentified, small Gymnodiniales and unidentified, naked

nanoflagellates). Ciliates were only distinguished according to size categories (small: <25 μm, medium: 25 to 50 μm, large: >50 μm). Where possible, 400 individuals per category were counted, giving a 95% confidence limit of ±10% when cells were randomly distributed (Lund et al. 1958). Biomass was estimated as cell volume (calculated as for standard geometric solids: Hillebrand et al. 1999) after microscopic measurements of 20 randomly selected cells of each category. Dissolved nutrients were measured according to standard oceanographic methods (Grasshoff et al. 1983) on 29 August (Day 8) and 4 September (Day 14).

The statistical analysis presented here was performed with the data from the last sample before the addition of mesozooplankton (28 August, Day 7) and with the data from the last sampling date (4 September). The nutrient ratio effect was analysed by linear regression of log absolute biomass ($\log^{10} B_{tot}$, original values replaced by B + 0.1 where there were zeros) and relative biomass ($p_i = B_{tot}/B_i$; arcsine-square-root-transformed) on Si:N ratios of the daily nutrient addition. If the data suggested a unimodal response, a second-order polynomial was used and the optimum ratio

Table 1. Protist species, individual cell volume and biomass on 21 August 2003 (Day 0). Totals for the functional groups in **bold**

Taxon	Volume cell^{-1} (μm^3)	Biomass (10^3 μm^3 ml^{-1})
Dinoflagellates		**53.94**
Ceratium tripos	90000	4.50
Ceratium fusus	60000	4.80
Gyrodinium fusiforme	21000	0.42
Prorocentrum micans	14000	5.32
Dinphysis spp.	8000	0.40
Gymnodinium spp.	5900	4.40
Scrippsiella trochoidea	5500	5.90
Small Gymnodiniales	1100	28.20
Diatoms		**265.06**
Rhizosolenia hebetata	6900	220.80
Thalassiosira sp.	3800	0.08
Guinardia delicatula	2000	1.40
Leptocylindrus minimus	480	41.76
Nitzschia acicularis	280	0.56
Pseudonitzschia pungens	250	0.15
Skeletonema costatum	130	0.13
Thalassiosira delicatula	80	0.08
Nitzschia delicatissima	50	0.10
Naked flagellates		**160.71**
Teleaulax acuta	190	33.44
Unidentified nanoflagellates	65	127.27
Picoplankton	**4**	**205.40**
Ciliates		**291.70**
Large (>50 μm)	50000	125.0
Medium (25–50 μm)	10700	139.10
Small (<25 μm)	2300	27.60

was estimated as the Si:N value at which the first derivative of the regression was zero. On 4 September (Day 14), the data from the mesocosms without mesozooplankton were excluded. The effect of mesozooplankton grazing was analysed by general linear models, with log-transformed biomass on 4 September as a dependent variable, mesozooplankton presence/absence as a categorial factor, and the Si:N ratio as a quantitative factor (Stagraphics).

RESULTS

The initial phytoplankton assemblage was fairly rich in species (Table 1). It had a moderate biomass level of ca. 685×10^3 µm^3 ml^{-1} comprised of 38.8% diatoms (mainly *Rhizosolenia hebetata*), 29.9% autotrophic picoplankton, 23.5% naked nanoflagellates, and 7.9% dinoflagellates. The ciliate biomass was ca. 290×10^3 µm^3 ml^{-1}. The abundance of other microzooplankton, including heterotrophic dinoflagellates, was negligible. Mixotrophic dinoflagellates were counted as phytopankton. Immediately after the onset of nutrient addition, the phytopankton community composition started to diverge between the different treatments, the most conspicuous response being the increase in *Rhizosolenia hebetata* in the high Si:N treatments (Fig. 1). On 28 August (Day 7), divergence in phytoplankton composition had proceeded sufficiently to allow us to begin the mesozooplankton treatment. The mesozooplankton community consisted almost entirely of copepods, with an abundance of ca. 20 to 30 ind. l^{-1}. About two-thirds of the biomass was comprised of the calanoids *Paracalanus* sp., *Pseudocalanus elongatus*, and *Acartia longiremis*. Other important taxa were the calanoids *Temora longicornis*, *Centropages* sp., *Calanus finnmarchicus*, and the cyclopoid *Oithona*
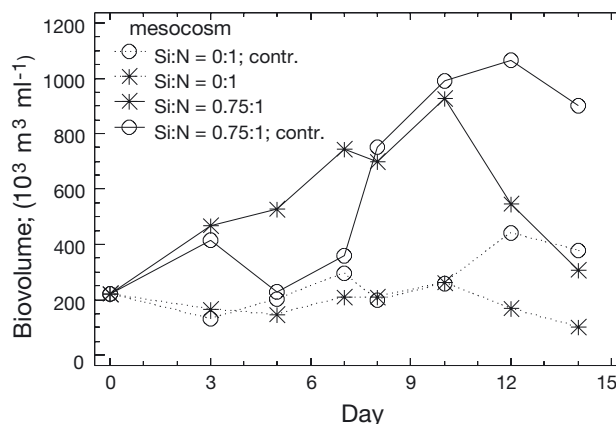

Fig. 1. *Rhizosolenia hebetata*. Time-course of biomass in 4 selected mesocosms: Si:N = 0:1, without mesozooplankton; Si:N = 0:1, with mesozooplankton; Si:N = 0.75:1, with mesozooplankton; Si:N = 0.75:1, without mesozooplankton. contr.: control

similis. For some species clear differences between mesozooplankton and control treatments emerged as early as 31 August (Day 10), for other species on 2 September (Day 12). These patterns persisted until the end of the experiment. Ciliates showed little response to Si:N treatments and declined slowly in abundance until 28 August. During the second phase of the experiment, this decline accelerated in those mesocosms that had received the mesozooplankton addition, and continued slowly in the control mesocosms.

On 28 August (Day 7), the response of total phytoplankton biomass to Si:N treatment was only weak ($\log^{10} B = 3.08 + 0.71$ Si:N; Fig. 2) and not statistically significant (p = 0.0755). Therefore, the responses of B_i and p_i had the same sign in most species (Tables 2 & 3, Figs. 3 & 4). Most diatoms responded positively to increasing Si:N. A marginally nonsignificant (p =

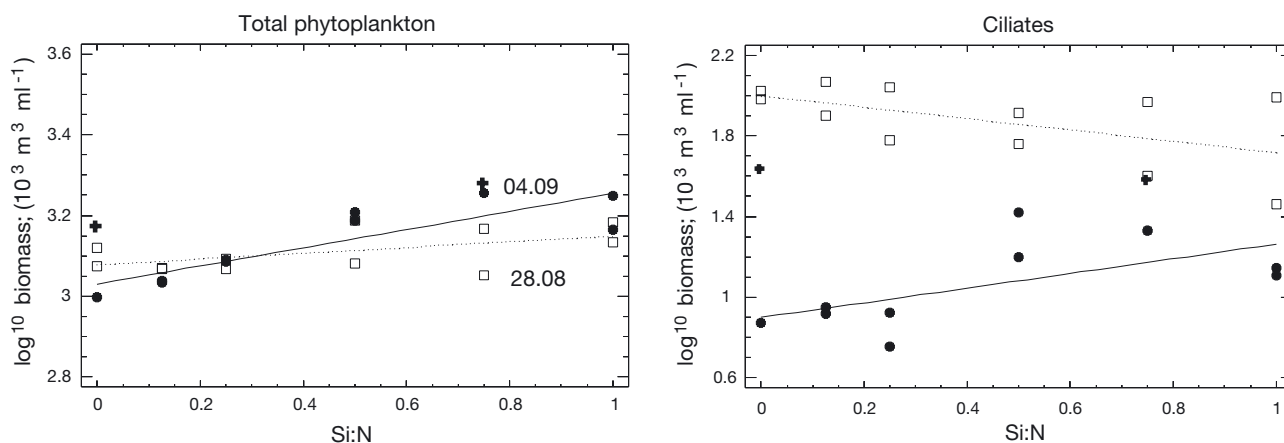
Fig. 2. Biomass of total phytoplankton and ciliates as a function of Si:N loading ratios and copepod addition on 28 August (Day 7, dashed line, □) and 4 September (Day 14, continuous line, ●). ✚: September controls

Table 2. Regressions of $\log^{10} B_i$ (specific, absolute biomass) on Si:N ratios (linear or second-order polynomial) on 28 August (Day 7). Higher taxa in **bold**

Taxon	a	b	c	r^2	p
Dinoflagellates	**2.22**	**−0.24**		**0.604**	**0.0029**
Ceratium tripos	0.86	0.46		0.018	0.671
Ceratium fusus	0.72	0.34		0.28	0.077
Gyrodinium fusiforme	0.73	0.31		0.680	0.001
Prorocentrum micans	0.99	−0.066		0.016	0.699
Dinophysis spp.	0.77	−0.172		0.175	0.177
Gymnodinium spp.	1.54	−0.211		0.225	0.124
Scrippsiella trochoidea	1.02	−0.356		0.191	0.156
Small Gymnodiniales	1.91	−0.52		0.586	0.0037
Diatoms	**2.39**	**0.49**		**0.822**	**<0.0001**
Rhizosolenia hebetata	2.39	0.41		0.769	0.0002
Guinardia delicatula	−0.88	2.33		0.700	0.0007
Leptocylindrus minimus	−0.33	2.12		0.539	0.0065
Pseudonitzschia pungens	−0.94	1.97		0.750	0.0003
Skeletonema costatum	−1.30	3.03		0.916	<0.0001
Thalassiosira delicatula	0.28	2.09	−1.88	0.401	0.0403
Nitzschia delicatissima	−0.77	1.06		0.891	<0.0001
Naked flagellates	**2.45**	**−0.62**		**0.913**	**<0.0001**
Teleaulax acuta	1.72	−0.70		0.841	<0.0001
Unidentified nanoflag.	2.36	−0.60		0.892	<0.0001
Picoplankton	**2.18**	**0.011**		**0.003**	**0.867**
Total phytoplankton	**3.08**	**0.071**		**0.282**	**0.0755**
Ciliates	**2.00**	**−0.28**		**0.302**	**0.0644**

0.093) unimodal response was found for *Thalassiosira delicatula* (calculated optimum 0.56:1 for B_i and 0.53 for p_i). Non-silicified algae responded either neutrally or negatively to increased Si:N ratios, with 1 notable exception. The dinoflagellate *Gyrodinium fusiforme* showed a significantly positive (B_i: $p = 0.001$; $p_i = 0.009$) response to increased Si:N ratios. Ciliate biomass did not respond significantly to increased Si:N ratios, and on Day 7 it was less than half that at the start of the experiment (Fig. 2).

On September 4 (Day 14), total phytoplankton biomass showed a significantly positive correlation to Si:N ratios, but the response was much weaker than the response of the diatoms (Table 4). The taxon-specific response patterns to Si:N ratios remained unchanged during the second phase of the experiment (Figs. 3 & 4, Tables 4 & 5). Relative and absolute biomasses of most diatom species increased significantly with increasing Si:N ratios, while a unimodal response was found for *Thalassiosira delicatula*, with calculated optimum Si:N ratios almost identical to those during the first phase (0.54:1 for B_i and 0.54 for p_i). Again, the dinoflagellate *Gyrodinium fusiforme* responded positively to in-

creasing Si:N ratios. The other non-silicified phytoplankton showed some shifts between negative and neutral responses, but the gross taxonomic patterns of relative biomass remained unaltered, except for a decline in autotrophic picoplankton biomass with increasing Si:N ratios as opposed to their neutral response on August 28 (Day 7). Dinoflagellates and naked flagellates responded negatively to increasing Si:N ratios on both dates.

The phytoplankton response to mesozooplankton addition differed strongly between taxa (Figs. 3 & 4, Table 4). Naked nanoflagellates and single-celled nanoplankton diatoms (*Nitzschia delicatissima*, *Thalassiosira delicatula*) profited from the addition of mesozooplankton, while large-celled diatoms (*Rhizosolenia hebetata*, *Thalassiosira* sp.) and small-celled, chain-forming diatoms (*Leptocylindrus minimus*, *Pseudonitzschia pungens*, *Skeletonema costatum*), dinoflagellates of the order Gymnodiniales (*Gyrodinium fusiforme*, *Gymnodinium* spp., unidentified small Gymnodiniales), and ciliates (Fig. 2) responded negatively to the addition of mesozooplankton. No response was found for thecate dinoflagellates (*Ceratium* spp., *Prorocentrum micans*, *Dinophysis trochoidea*) or picoplankton.

Table 3. Regressions of arcsin $\sqrt{p_i}$ (relative biomass, B_i/B_{tot}) on Si:N ratios (linear or second-order polynomial) on 28 August (Day 7). Higher taxa in **bold**

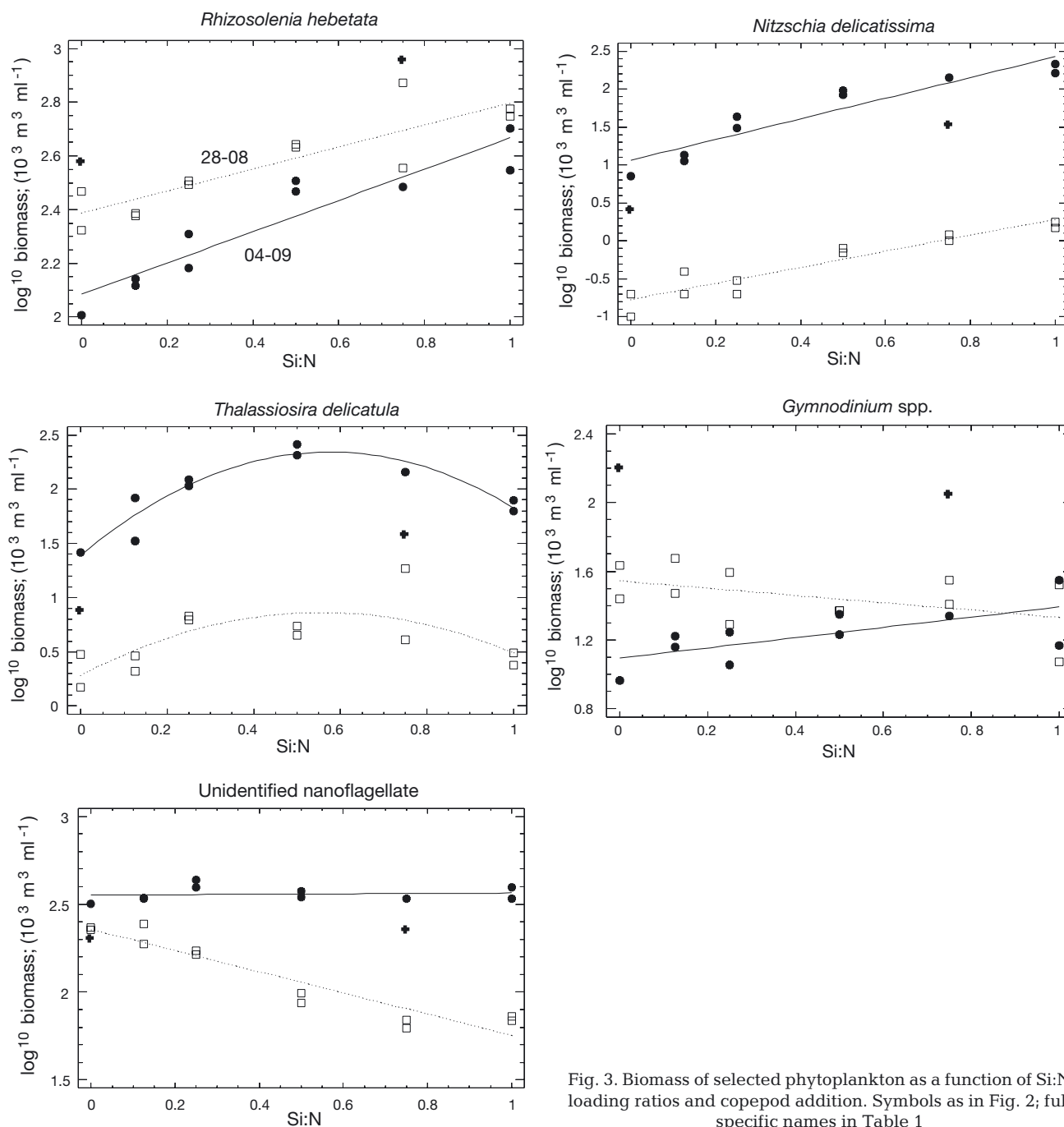| Taxon	a	b	c	r^2	p
Dinoflagellates	**21.9**	**−7.08**		**0.699**	**0.0007**
Ceratium tripos	4.52	−0.12		0.004	0.840
Ceratium fusus	3.96	1.20		0.196	0.148
Gyrodinium fusiforme	3.88	1.13		0.511	0.0009
Prorocentrum micans	5.26	−0.68		0.055	0.461
Dinophysis spp.	4.08	−1.07		0.331	0.050
Gymnodinium spp.	9.85	−2.67		0.339	0.047
Scrippsiella trochoidea	5.48	−2.11		0.306	0.062
Small Gymnodiniales	15.3	−8.05		0.650	0.0015
Diatoms	**26.7**	**19.5**		**0.821**	**<0.0001**
Rhizosolenia hebetata	26.6	16.7		0.750	0.0003
Guinardia delicatula	0.218	5.94		0.684	0.0009
Leptocylindrus minimus	2.05	6.68		0.393	0.0291
Pseudonitzschia pungens	−0.054	4.26		0.812	0.0001
Skeletonema costatum	−1.39	10.5		0.835	<0.0001
Thalassiosira delicatula	2.19	7.98	−7.36	0.278	0.0930
Nitzschia delicatissima	0.63	1.33		0.915	<0.0001
Naked flagellates	**28.4**	**−16.7**		**0.891**	**<0.0001**
Teleaulax acuta	11.76	−7.25		0.837	<0.0001
Unidentified nanoflagellates	25.4	−14.7		0.861	<0.0001
Picoplankton	**41.7**	**−2.9**		**0.071**	**0.399**

Fig. 3. Biomass of selected phytoplankton as a function of Si:N loading ratios and copepod addition. Symbols as in Fig. 2; full specific names in Table 1

Nutrient concentrations (Table 6) showed the following trends: PO_4 dropped from measurable concentrations (0.21 to 0.28 µmol l^{-1}) on 29 August (Day 8) to the detection limit (0 to 0.4 µmol l^{-1}) in the enclosures with copepods, and displayed slightly higher concentrations (0.04 to 0.08 µmol l^{-1}) in the enclosures without copepods on 4 September. There was no trend along the Si:N gradient. Dissolved inorganic nitrogen concentrations (NO_3 + NH_4) ranged from 0.13 to 0.77 µmol l^{-1} on 29 August and from 0.10 to 0.54 µmol l^{-1} on 4 September. On both dates, there was

a tendency towards lower concentrations in the higher Si treatments. On both dates, the concentrations were highest in the Si:N = 0:1 treatment without copepods, while they were low in the Si:N 0.75:1 treatment without copepods. Dissolved silicate concentrations varied between 0.20 and 0.31 µmol l^{-1} on 29 August and between 0.10 and 0.22 µmol l^{-1} on 4 September, except for an exceptionally high value (0.54 µmol l^{-1}) in the Si:N = 0:1 treatment without copepods. Interestingly, there was no tendency of increasing Si concentrations with increasing Si addition.
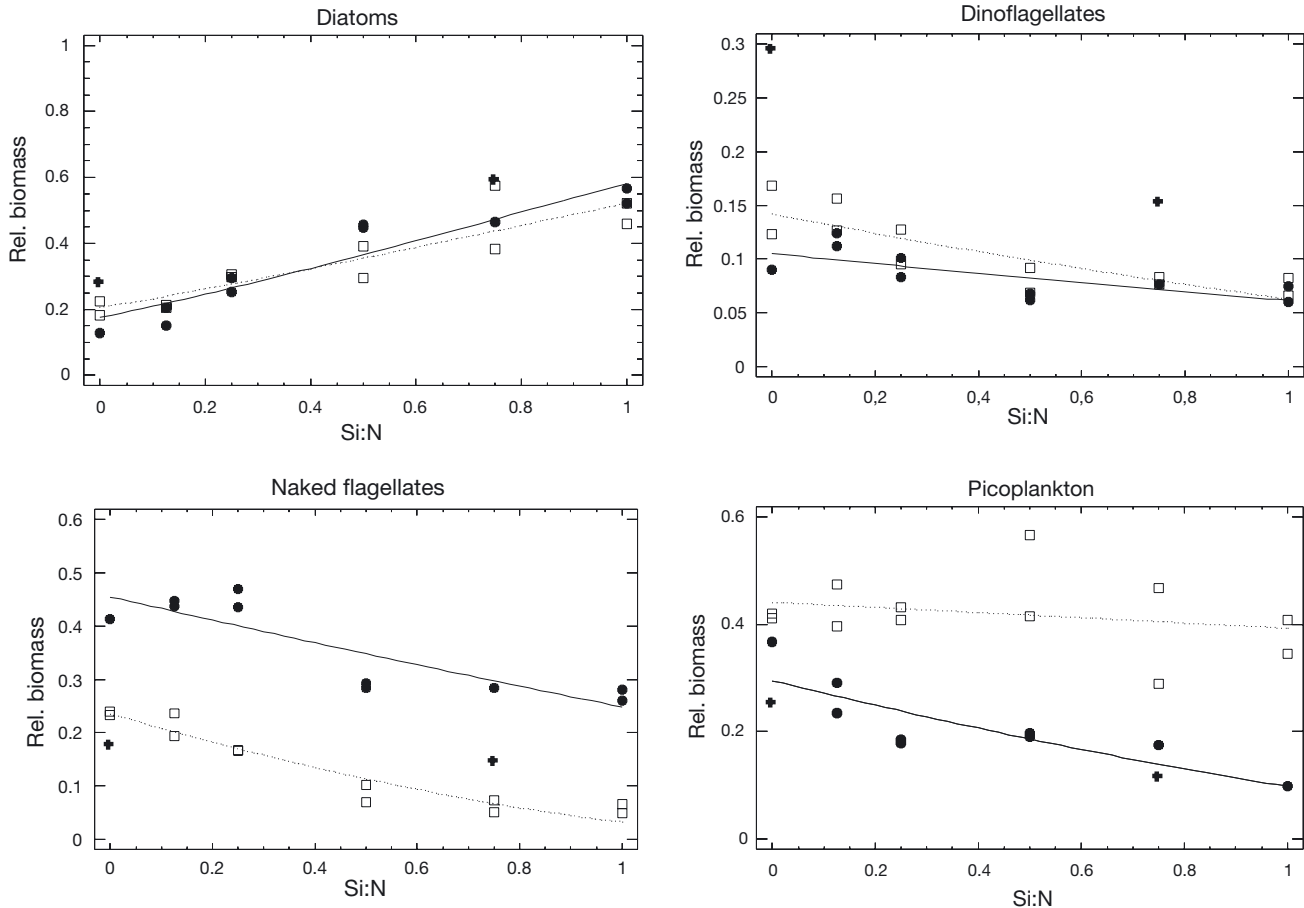
Fig. 4. Relative biomass (p_i = B_i/B_{tot}) of selected phytoplankton as a function of Si:N loading ratios and copepod addition. Symbols as in Fig. 2

DISCUSSION

While a negative response of phytoplankton species to the addition of a grazer guild results from grazing, positive responses can have 2 causes: recycling of nutrients (Sterner 1986) or release from grazing pressure by intermediate consumers, such as microzooplankton (Sommer et al. 2003). In our case, mesozooplankton was almost exclusively represented by copepods and microzooplankton by ciliates. In our experiment, the response of phytoplankton species to grazing can be explained by 2 relatively simple attributes: size and armour. Species with a positive response to copepod addition were unicellular nanoplankton of <200 µm³ cell volume and <20 µm cell length. The long, spindle-shaped diatom *Nitzschia acicularis* (280 µm³ volume, 30 to 50 µm length) showed a marginally non-significant (p = 0.056) negative response to copepods, while the larger diatoms (including chain-forming species with small cells) and the thin-walled dinoflagellates (order Gymnodiniales) showed a significantly negative response. Dinoflagellates with cell walls consisting of thick cellulose plates or shells (orders Peridiniales, Prorocentrales, Dinophysales) were neither favoured nor harmed by the addition of copepods. This relatively simple pattern can be most easily explained by ciliates feeding on nanoplankton, and copepods on microplankton except armoured dinoflagellates. This agrees with previous findings that omnivorous copepods feed primarily on microplankton (phytoplankton and protozoans), if the natural plankton community offers sufficient choice (Burns & Schallenberg 1996, Granéli & Turner 2002, Katechakis et al. 2002, Sommer et al. 2002, 2003). This feeding pattern contrasts with findings from food monocultures, whereby copepods have been successfully reared with nanophytoplankton (e.g. *Isochrysis*) and with armoured dinoflagellates (e.g. *Prorocentrum minimum*) (Kleppel 1993, Uye 1996). The neutral response of autotrophic picoplankton to mesozooplankton addition can most easily be explained by a compensation between ciliate grazing on picoplankton and release from grazing by heterotrophic nanoflagellates suppressed by ciliates.

Table 4. Regressions $\log^{10}$ B on Si:N ratios (linear or second-order polynomial) and mesozooplankton effect (Z: sign; p_z: probability of error) on 4 September (Day 14). Higher taxa in **bold**

Taxon	a	b	c	r^2	p	Z	p_z
Dinoflagellates	**2.05**	**0.010**		**0.003**	**0.889**	**–**	**<0.0001**
Ceratium tripos	1.15	–0.084		0.129	0.307	0	0.527
Ceratium fusus	1.38	–0.037		0.045	0.555	0	0.269
Gyrodinium fusiforme	0.27	0.50		0.71	0.0022	–	0.0001
Prorocentrum micans	1.16	–0.29		0.120	0.326	0	0.924
Dinophysis spp.	0.150	–0.07		0.013	0.755	0	0.991
Gymnodinium spp.	1.09	0.30		0.447	0.0345	–	<0.0001
Small Gymnodiniales	1.58	–0.022		0.067	0.816	–	<0.0001
Diatoms	**2.26**	**0.80**		**0.820**	**0.0003**	**–**	**0.0408**
Rhizosolenia hebetata	2.08	0.55		0.872	0.0001	–	<0.0001
Thalassiosira sp.	–0.82	1.08		0.665	0.0040	–	0.0019
Leptocylindrus minimus	–0.75	1.51		0.683	0.0032	–	0.0059
Nitzschia acicularis	–0.22	1.21		0.562	0.0125	(–)	0.0565
Pseudonitzschia pungens	–0.72	1.33		0.620	0.0069	–	0.0061
Skeletonema costatum	–0.68	1.34		0.569	0.0117	–	0.0046
Thalassiosira delicatula	1.27	3.49	–3.04	0.573	0.0088	+	0.0196
Nitzschia delicatissima	1.06	1.36		0.881	0.0001	+	0.0019
Naked flagellates	**2.69**	**–0.028**		**0.048**	**0.540**	**+**	**0.0001**
Teleaulax acuta	2.13	–0.19		0.262	0.130	+	0.0092
Unidentified nanoflag.	2.55	0.011		0.010	0.781	+	0.0001
Picoplankton	**2.51**	**–0.188**		**0.411**	**0.0246**	**0**	**0.820**
Total phytoplankton	**3.03**	**0.220**		**0.750**	**0.0012**	**–**	**0.0207**
Ciliates	**0.90**	**0.36**		**0.386**	**0.055**	**–**	**0.0032**

While nutrient recycling by copepods most probably took place, it does not seem to be an an important factor influencing phytoplankton species composition. Nutrient recycling by zooplankton would bias the nutrient supply ratios, because N and P are excreted in bio-available forms (ammonium, orthophosphate), while diatom silicate is excreted as particulate debris. Had nutrient recycling by copepods comprised a major component of the nutrient supply for phytoplankton, Si:N supply ratios in the mesocosms with copepods would have been lower than the Si:N ratios of the external supply, which would have resulted in a rightward displacement of the diatom response curves of phytoplankton taxa to Si:N ratios, as has been shown in closed experimental systems for Si:P ratios (Sommer 1988). There was no indication for any such rightward shift of the response curve in our data. Even the Si:N optimum of *Thalassiosira delicatula* remained remarkably constant between both phases of the experiment. Moreover, the concentrations of dissolved nutrients did not indicate a positive impact of copepod presence on nutrient supply; indeed the reverse occurred on 4 September at the low Si:N end of the gradient, where dissolved nutrient concentrations were higher in the enclosures without copepods than in those with copepods.

The positive response of the dinoflagellate *Gyrodinium fusiforme* to increasing Si:.N ratios during both phases of the experiment was surprising, and cannot be explained by physiological Si requirements. At present we can only speculate this mixotrophic dinoflagellate may feed on nanoplanktonic diatoms or on bacteria associated with diatoms; if the diatoms release more DOC than their non-siliceous competitors and thus enhance bacterial production, a mixotrophic bacterivore could indirectly profit from higher Si supply. Similarly, there is no obvious explanation for the temporal shift in the response of autotrophic picoplankton to increasing Si:N ratios (28 August no correlation; 4 September negative correlation).

While the increase in diatom abundance with increasing Si:N ratios in the absence of copepod grazing was not surprising, the robustness of this trend against the top-down impact of copepods has major implications. The copepod addition (ca. 20 to 30 ind. l^{-1}) corresponded not only to

Table 5. Regressions of arcsin $\sqrt{p_i}$ (relative biomass, B_i/B_{tot}) on Si:N ratios (linear or second-order polynomial). Higher taxa in **bold**

Taxon	a	b	c	r^2	p
Dinoflagellates	**18.81**	**–4.32**		**0.530**	**0.0170**
Ceratium tripos	6.59	–2.03		0.614	0.0073
Ceratium fusus	8.61	–2.25		0.771	0.0008
Gyrodinium fusiforme	2.41	0.90		0.457	0.0319
Prorocentrum micans	6.79	–2.98		0.276	0.1191
Dinophysis spp.	3.15	–0.90		0.208	0.1847
Gymnodinium spp.	6.19	0.60		0.070	0.461
Small Gymnodiniales	10.87	–2.79		0.392	0.0170
Diatoms	**23.9**	**26.0**		**0.885**	**<0.0001**
Rhizosolenia hebetata	19.4	10.9		0.841	0.0002
Thalassiosira sp.	0.27	1.48		0.610	0.0077
Leptocylindrus minimus	0.37	2.49		0.699	0.0026
Nitzschia acicularis	1.33	2.51		0.518	0.0190
Pseudonitzschia pungens	0.44	2.00		0.601	0.0084
Skeletonema costatum	0.55	2.05		0.529	0.0077
Thalassiosira delicatula	8.67	47.2	–44.2	0.752	0.0032
Nitzschia delicatissima	5.29	15.1		0.962	<0.0001
Naked flagellates	**42.2**	**–12.2**		**0.750**	**0.0012**
Teleaulax acuta	20.4	–7.8		0.645	0.0052
Unidentified nanoflag.	35.1	–8.46		0.667	0.0039
Picoplankton	**32.5**	**–13.7**		**0.709**	**0.0044**

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Table 6. Dissolved, inorganic nutrient concentrations (µmol l⁻¹) on 29 August (Day 8) and 4 September (Day 14). *Enclosures without copepod addition

Si:N	29 August			4 September		
	P	N	Si	P	N	Si
0:1*	0.25	0.77	0.30	0.08	0.89	0.54
0:1	0.26	0.38	0.31	0.00	0.66	0.11
0.125:1	0.27	0.57	0.24	0.00	0.51	0.13
0.125:1	0.23	0.47	0.34	0.04	0.38	0.11
0.25.1	0.25	0.24	0.30	0.04	0.28	0.10
0.25.1	0.25	0.27	0.28	0.03	0.35	0.07
0.5:1	0.28	0.20	0.30	0.04	0.31	0.13
0.5:1	0.25	0.18	0.20	0.04	0.30	0.10
0.75.1	0.27	0.27	0.24	0.03	0.44	0.22
0.75.1*	0.25	0.13	0.24	0.04	0.24	0.11
1.1	0.27	0.24	0.25	0.03	0.16	0.08
1:1	0.21	0.27	0.20	0.04	0.49	0.13

natural levels during the experimental period, but also to seasonal high levels (Saage 2003), being ca. one-half the maximum density observed during the last 8 yr (I. Gismervik pers. comm.). This suggests that nutrient ratios can successfully predict the gross taxonomic composition of phytoplankton even during periods of elevated copepod grazing. Consequently, nutrient competition among phytoplankton is not suspended by grazing. The persistence of nutrient competition under grazing pressure is probably due to the fact that copepods exert only a partial top-down control, while other portions of the phytoplankton size spectrum are released from protozoan top-down control by copepod grazing pressure. Thus, major depressions in total phytoplankton biomass by copepod grazing alone are rather the exception than the rule, and an increase in small phytoplankton will frequently compensate partially, fully, or even overcompensate, for the decline in edible phytoplankton (Sommer et al. 2003, Stibor et al. 2004). This compensation is reflected in the limited response of the total phytoplankton biomass (Fig. 2), which is probably even exaggerated by the use of biovolume as a measure of biomass (large diatoms contain a large vacuole and have thus a lower carbon content per cell volume than smaller diatoms or non-silicified algae of similar size: Strathmann 1967). Thus, both the increase in total biovolume with increasing Si:N ratios and the decrease in the copepod treatments relative to the controls could have been caused by *Rhizosolenia hebetata*, which was the most important food item of copepods in terms of biomass and the species increasing most strongly at high Si:N ratios. The use of other biomass measures might have diminished or even eliminated the response of total biomass to copepod grazing.

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