Silicate as regulating nutrient in phytoplankton competition

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ABSTRACT· The development of phytoplankton communities was studied in floating enclosures. The enclosures were supplied with either surface water or water from 40 m depth. Nutrients with or without silicate were added in some of the experiments, while others recieved no artificial fertilization. It is shown that diatom dominance occurred irrespective of season if silicate concentration exceeded a threshold of approximately 2 µM. Flagellate dominance changed to diatom dominance within a few days after nutrient addition resulting in silicate concentrations above this threshold. Dominance of *Phaeocystis* sp. appeared on several occasions after the bloom of another species, but never at high silicate concentrations. The success of the diatom group seemed to be due to a high inherent growth rate at non-limiting silicate concentrations. Calculations indicated that the inherent growth rate for the diatom group had to be 5 to 50 % higher than for the flagellate group in order to explain the outcome of our experiments.

INTRODUCTION

Human activities have increased the input of nitrogen and phosphorus nutrients to estuarine and coastal waters. Eutrophication and construction of artificial lakes, however, have led to decreased silicate input into the sea (Bennekom & Salomons 1981). Furthermore, nitrogen and phosphorus are recycled more rapidly in the water column than is silicon. Thus, along with increased eutrophication in coastal areas, increased N : Si and P : Si nutrient ratios should be expected. As postulated by Officer & Ryther (1980), a change in the nutrient composition should also affect the phytoplankton composition. According to Smayda (1990), measurements from central North Sea and Elbe-influenced water masses show significant increases in nitrate and phosphorus in recent decades, while silicate is constant or decreasing. Over the same period, the biomass of flagellates has increased by a factor of 6 to 16 while the biomass of diatoms has been constant or decreasing.

When environmental quality is reduced as a result of altered phytoplankton composition, rather than by biomass, a sound strategy may be to modify the nutrient composition rather than to reduce the magnitude of the discharge. This assumes, however, that the influence of nutrient composition on phytoplankton composition is predictable. As postulated by Officer & Ryther (1980) it

is conceivable that the N : Si ratio influences the composition of phytoplankton as phytoplankton communities may be divided into 2 basic categories: those dominated by diatoms and those dominated by flagellates or non-diatomaceous forms. Growth of diatoms depends on the presence of silicate while growth of the non-diatomaceous forms normally does not. Officer & Ryther (1980) point out that flagellate communities are often associated with undesirable effects of eutrophication while diatoms are not.

The present paper reports on the effect of silicate on phytoplankton composition in 14 mesocosm experiments. Experiments were conducted in spring, summer and autumn when quite different environmental forces were acting. Despite this environmental variability, our data indicate that diatoms dominate as long as silicate concentration is held above 2 µM.

MATERIALS AND METHODS

Four experiments with and without silicate addition. The enclosure experiments were carried out in the period April to July 1988 in Bergen, Norway. The enclosures were 4 m deep plastic bags with a volume of 11 m³ and 90 % light penetration (Fig. 1, Table 1). Enclosures 1 and 2 (E1 and E2) were supplied by water from 40 m depth while E3 and E4 were supplied with
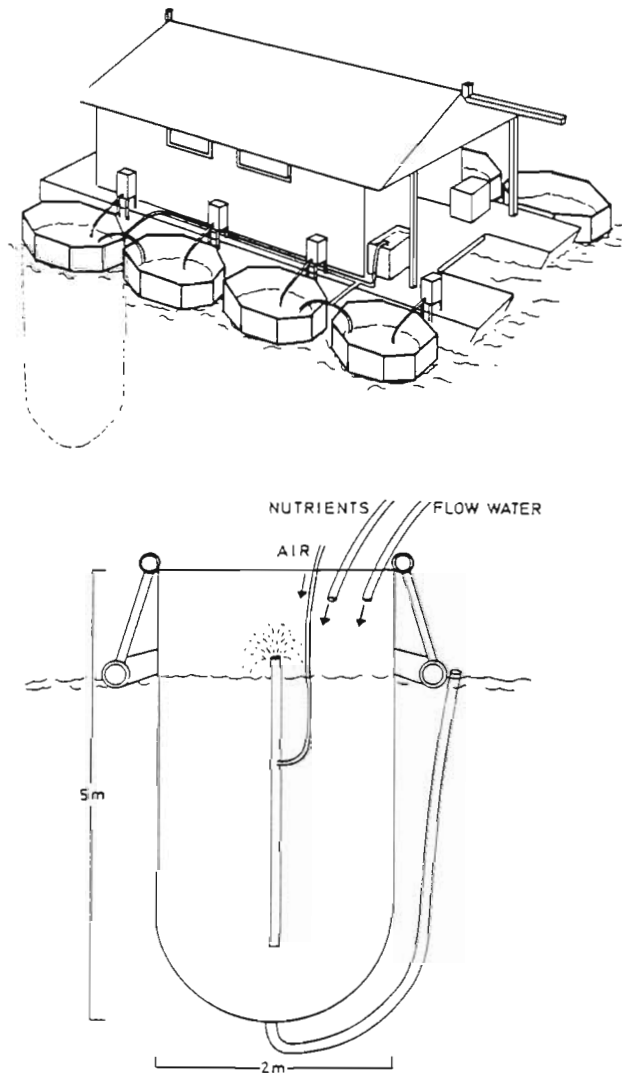
Fig. 1 The floating laboratory with the sea enclosures

surface water (from 1 m depth). Homogeneous water-masses within the enclosures were ensured by pumping water from the bottom of the bag to the surface at a rate of 40 l min^{-1}. Nitrate and phosphate were added initially to all 4 enclosures. E2 and E4 were supplied with silicate while E1 and E3 were not. The water from 40 m (E1 and E2) contained, on average, 10.4, 1.0 and 8.6 µM nitrate, phosphate and silicate, while the surface water was nutrient depleted with average values of 0.3, 0.06 and 0.6 µM respectively. The enclosures were grown as batch cultures for about 1 wk. Inflow of water (from 1 or 40 m) was then initiated and the cultures run continuously with an average water renewal of 30 % d^{-1} during the experimental period. Nitrate, phosphate and silicate (E2 and E4), or just nitrate and phosphate (E1 and E3), were added to the enclosures every second day (after sampling) during the rest of the experimental period (26 d). Each nutrient

dose corresponded to an instantaneous final concentration of about 5.5 µM nitrate, 1.5 µM phosphate and 6 µM silicate within the enclosures.

Samples for chlorophyll (chl) a, nutrients, phytoplankton enumeration and identification were taken daily or every second day during the experiment. Samples were taken only at 1 m depth as the water column was homogeneous. Samples for pigment analysis were filtered through a Sartorius membrane filter (0.45 µm), and analyzed fluorometrically for chl a according to Holm-Hansen et al. (1965). Samples for nutrient measurements were preserved by adding chloroform, and determinations of nitrate, phosphate and silicate were performed on a Chemlab autoanalyzer. Enumeration and identification of phytoplankton were carried out on samples preserved by neutralized formalin and acid Lugol using the sedimentation method of Utermöhl (1931). Light conditions during the experiments were obtained as global radiation (MJ m^{-2}) from the Radiation observatory, University of Bergen, Norway, where measurements are made continuously.

Diatom abundance versus silicate concentration. Data on diatom abundance from the above 4 experiments together with data from an additional 10 enclosure experiments (Table 2) were plotted against silicate concentration. The purposes of these experiments were diverse. Some were aimed at the study of increased primary production by artificial upwelling (Aksnes et al. 1985), others at producing suitable food for scallops (Kaartvedt et al. 1987) and at the study of succession in enclosures (Harboe 1988). The experiments were carried out in different seasons and with different nutrient input. Measurements from the first week of all experiments were excluded. In this period high nutrient concentrations prevailed due to fertilization and low total nutrient uptake occurred due to low initial phytoplankton stock. Interspecific competition was presumably low during this period and species composition reflected initial dominance rather than competition for nutrients. Altogether, we obtained 98 records on diatom dominance versus silicate concentration from the non-initial phases.

RESULTS

Nutrients and biomass in E1 to E4

At the start of the experiments, nitrate and phosphate concentrations were high in all enclosures (Fig. 2). E2 and E4 also had high initial silicate concentrations. E1 was supplied with deep water containing about 8 µM silicate, while E3 was supplied with silicate-exhausted surface water. Thus, the difference in initial silicate

Table 1. Four 12 m^3 enclosure experiments conducted in 1988. Depth of water intake, artificial nutrient addition (P; phosphate, N; nitrate, Si; silicate), mean temperature and global radiation during the experiments are indicated. Dominant species of the seedling water masses (*) are given together with species dominating after 1 wk and during the rest of the experimental period. Names are given in order of appearance

Enclosure	Water intake	Period	Artificial fertilization	Temp. (°C)	Global radiation (MJ m^{-2} d^{-1})	Dominant species
E1	40 m	20 Apr–15 May	N, P	7.9	14.6	*Flagellates indet. Skeletonema costatum Phaeocystis sp.
E2	40 m	30 Jun–24 Jul	N, P, Si	14.2	12.6	*Skeletonema costatum Skeletonema costatum Chaetoceros sp.
E3	1 m	30 Jun–24 Aug	N, P	14.2	12.6	*Skeletonema costatum Emiliania huxleyi Phaeocystis sp.
E4	1 m	8 Jul–1 Aug	N, P, Si	15.8	12.5	*Flagellates indet. Skeletonema costatum Chaetoceros sp. Nitszschia delicatissima

Table 2. Experiments conducted in 1983 (Aksnes et al. 1985), 1986 (Harboe 1988), 1987 and 1988 (Egge unpubl.). Depth of water intake, indication of artificial nutrient addition (P; phosphate, N; nitrate, Si; silicate), mean dilution rate, mean temperature, mean global radiation, and dominant species (>50% of total cell numbers) are given. * Dilution rate (0 to 100%) was automatically controlled by the chlorophyll content in the enclosures. All experiments were mixed by airlift (Fig. 1), except the two conducted in 1983

Time	Water intake	Artificial fertilization	Dilution rate (%)	Temp. (°C)	Global radiation (MJ m^{-2} d^{-1})	Dominant species
1983 Jul	34 m & 0.5 m	–	8	12.4	16.8	Chaetoceros compressus Leptocylindrus danicus
1983 Jul	34 m & 0.5 m	–	4	12.4	16.8	Chaetoceros compressus Leptocylindrus danicus
1986 Apr	40 m	N, P	23	8.2	13.1	Phaeocystis pouchetii Skeletonema costatum
1986 Apr	40 m	N, P	23	8.2	13.1	Phaeocystis pouchetii Skeletonema costatum
1986 Apr	40 m & 0.5 m	N, P	23	8.2	13.1	Phaeocystis pouchetii
1986 Apr	40 m & 0.5 m	N, P	23	8.2	13.1	Phaeocystis pouchetii
1987 Jun	40 m	N, P	*		14.2	Flagellates indet.
1987 Sep	40 m	N, P	*	12.8	7.2	Flagellates indet.
1988 Apr	40 m	N, P, Si	30	8.7	15.5	Skeletonema costatum
1988 Sep	40 m	N, P, Si	30	17.0	5.4	Skeletonema costatum

concentrations in E1 and E3 reflects the composition in 2 different water masses.

Nitrate became almost exhausted in all experiments (Fig. 2). Despite a daily nitrate-supply, nitrate concentrations fell below 0.5 µM and nitrate probably became limiting. Phosphate concentrations were always higher than 0.6 µM and were probably not limiting. In E1, silicate concentrations fell below 2 µM after the sixth day, E2 had no values below 3.2 µM, E3 had no values higher than 0.6 µM, and the concentrations in E4 were higher than 2 µM except for the last 5 d.

At the beginning of the experiments, phytoplankton biomass was lower than 2 mg chl a m^{-3} in all 4 enclosures (Fig. 3). Highest chl a concentrations were observed in the enclosures with artificial silicate addition. Here average values during the experimental period were 49.9 (E2) and 31.7 (E4) mg chl a m^{-3}, while corresponding values were 24.5 (E1) and 14.6 (E3) mg
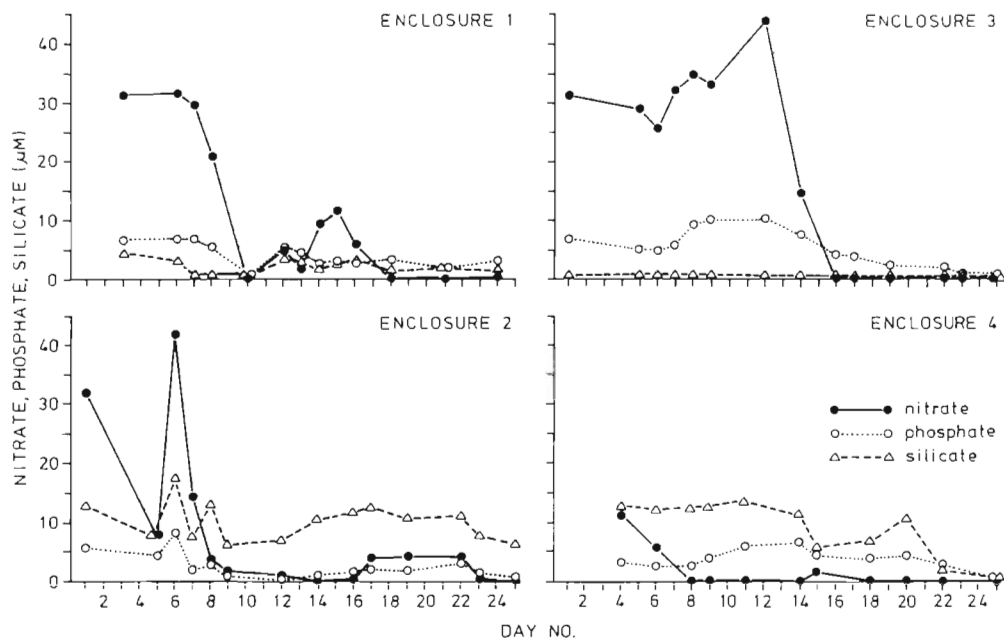
Fig. 2. Nitrate, inorganic phosphate and nitrate concentrations during the 4 enclosure experiments in 1988 (E1 and E3 without artificial silicate addition, E2 and E4 with artificial silicate addition. E1 and E2 also received some silicate through the 40 m depth water supply)
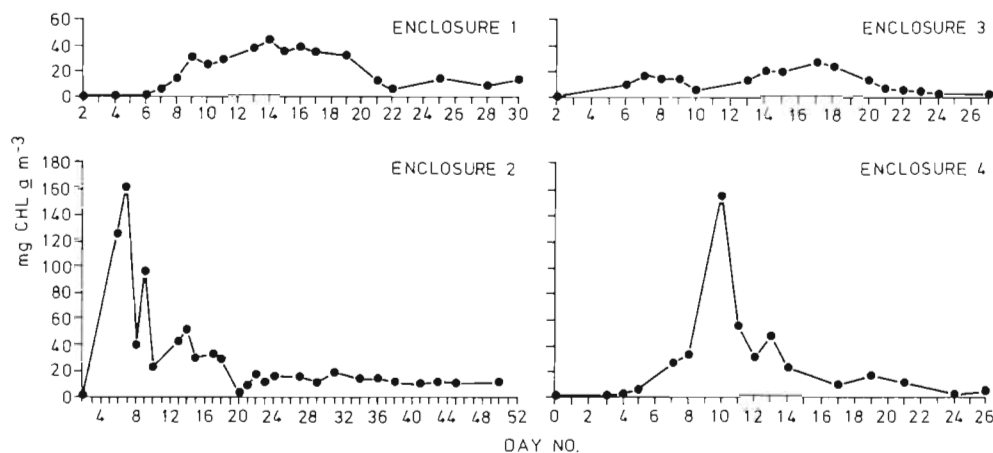

Fig. 3. Chlorophyll a concentration during the 4 enclosure experiments in 1988 (E1 and E3 without artificial silicate addition, E2 and E4 with artificial silicate addition. E1 and E2 also received some silicate through the 40 m depth water supply)

chl a m^{-3} in the 2 enclosures without artificial silicate fertilization (Table 1). E1 received some additional silicate with the deep water and this may explain the higher chl a content in this enclosure when compared to E3.

Species dominance in E1 to E4

Water from 40 m depth supplied with N and P (E1). The initial phytoplankton community of E1 was dominated by diatoms, mainly *Skeletonema costatum* (Grev.) Cleve (Table 1, Fig. 4). The highest concen-

tration of this species was 35×10^6 cells l^{-1}. Silicate, which had initial concentration above 4 μM, decreased throughout the experiment and from Day 7 concentrations fell below 1 μM. At this time *Phaeocystis* sp. appeared, and constituted 6 to 64 % of the total cell number for the rest of the experiment (Fig. 4). *Phaeocystis* colonies $\leqslant$ 2 mm were lobe-formed, indicating that the species was *P. pouchetii*. A temperature of 14 °C has been reported as the upper temperature limit for *P. pouchetii*, while in E3, where *Phaeocystis* also dominated, the temperature was in the range 14 to 16 °C. This range has been reported to be the temperature optimum for *P. globosa* (Jahnke & Baumann 1987).
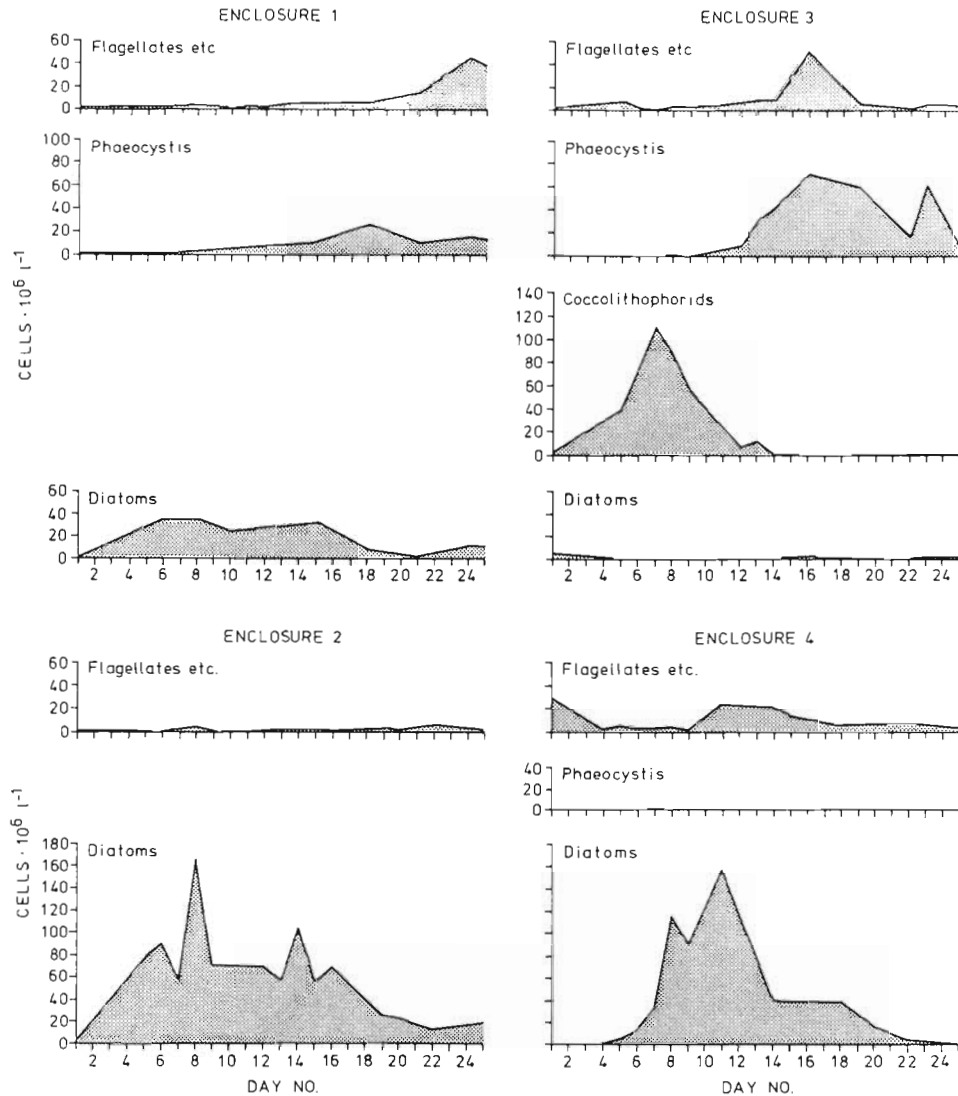
Fig. 4. Taxonomical composition during the 4 enclosure experiments in 1988 (E1 and E3 without artificial silicate addition, E2 and E4 with artificial silicate addition. E1 and E2 also received some silicate through the 40 m depth water supply)

Accordingly, we prefer to use the term *Phaeocystis* sp. in this report. *S. costatum* was never entirely outcompeted by *Phaeocystis* sp., and remained in low numbers throughout the experiment. After Day 21 small unidentified flagellates dominated the phytoplankton assemblage.

Water from 40 m depth supplied with N, P and Si (E2). Diatoms dominated E2 during the entire experimental period (Fig. 4). Silicate concentrations were high, varying between 3 and 10 μM. The initial concentration of *Skeletonema costatum* was 1.88×10^6 cells l^{-1} and the highest number was reached on Day 8 with 163×10^6 cells l^{-1}. *S. costatum* was replaced by small *Chaetoceros* spp. which dominated until the termination of this experiment after 52 d (not shown in Figs. 2, 3 & 4). The maximum concentration of the latter species was 39×10^6 cells l^{-1}.

Water from 1 m depth supplied with N and P (E3). The initial community of E3 was dominated by *Skeletonema costatum* (4.4×10^6 cells l^{-1}) and *Emiliania huxleyi* (Lohm.) Hay & Mohler (1.8×10^6 cells l^{-1}). *Phaeocystis* sp. had a concentration of 0.14×10^6 cells l^{-1}. Silicate values were lower than 0.6 μM during the experiment, and *E. huxleyi* outcompeted *S. costatum*. An extensive *E. huxleyi* bloom was observed during the next weeks with the highest cell number, 111×10^6 cells l^{-1}, occurring after 8 d (Fig. 4). After the decline of *E. huxleyi*, *Phaeocystis* sp. became dominant for the rest of the experiment with a maximum concentration of 71×10^6 l^{-1} on Day 16.

Water from 1 m depth supplied with N, P and Si (E4). The initial phytoplankton community of E4 differed from E3 in that small unidentified flagellates dominated rather than diatoms. Low concentrations of

Emiliania huxleyi (0.7×10^6 l^{-1}) and *Phaeocystis* sp. (0.1×10^6 l^{-1}) were also observed while diatoms were not found in the 10 ml sample (which indicates a concentration of less than 100 ind. l^{-1}). Despite these unfavourable initial conditions for diatoms, they dominated within a few days with a concentration of 120×10^6 l^{-1}. This increase amounts to a growth rate higher than 1.7 d^{-1} (corresponding to a doubling time of 10 h). Diatoms remained dominant as long as silicate concentrations were high (Figs. 2 & 4). The main diatom species were small *Chaetoceros* spp., *Pseudonitzschia delicatissima* (Cleve) Haiden, and *Skeletonema costatum*. At the end of the experiment, silicate and diatom concentrations dropped to low levels and flagellates became dominant.

Diatom dominance versus silicate concentration

Fig. 5 is based on the experiments listed in Tables 1 & 2 and indicates that diatoms always dominate the phytoplankton at high silicate concentrations. When silicate concentrations are below approximately 2 µM this dominance seems to cease. In some cases, diatom dominance was also found at concentrations below 2 µM. This dominance, however, was transitional and established in periods with high silicate concentrations. Diatom dominance ceased when concentrations remained below 2 µM.
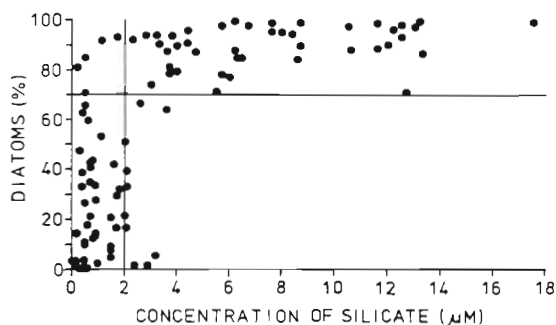

Fig. 5. Diatom dominance (given as percentage of total cell counts) versus silicate concentration. Data were obtained from the 14 enclosure experiments listed in Tables 1 & 2

DISCUSSION

Our experiments indicate that diatoms dominate when silicate concentration is above 2 µM. This seems to apply over a wide range of environmental conditions. The range of the average temperature in the experiments was 7 to 17 °C, and average surface radiation ranged from 5.42 to 16.84 MJ m^{-2} d^{-1} (unfortunately, the radiation measurements can only be approximated in terms of µE m^{-2} s^{-1}; the above range

is within 10^2 to 10^3 µE m^{-2} s^{-1} during the daylight period). The water masses studied originated from the surface, from 30 to 40 m, or from mixtures of the two. Finally, both nutrient-enriched and non-enriched experiments were carried out. The heterogeneous experimental design does not allow ordinary statistical comparisons between experiments. A balanced experimental design with respect to such factors as season, temperature, radiance, watermass, nutrient composition and nutrient loading would require an unmanageable amount of experiments. Thus, our limited number of mesocosm experiments should be interpreted more as traditional 'field' results rather than as strictly experimentally derived results. The heterogeneous environmental conditions under which the results were obtained, however, strengthen rather than weaken the conclusion about the strong influence of silicate concentration on phytoplankton species composition. The results obtained in E4 versus E3 clearly demonstrate the major influence of silicate concentration. Both experiments were run with silicate-depleted surface water. The initial community of E3 was dominated by diatoms, while E4 had initial flagellate concentrations (*Emiliania huxleyi* and *Phaeocystis* sp.) 10000 times higher than the diatom concentration. In less than 1 wk (before water renewal was initiated), however, *Skeletonema costatum* became dominant in E4 while the initial diatom dominance of E3 ceased. It is very unlikely that any other factor than the silicate enrichment of E4 could be responsible for the dramatic difference in species succession in the 2 enclosures.

Phaeocystis sp., *Emiliania huxleyi*, and diatoms

In the silicate-depleted E3, *Phaeocystis* sp. became dominant after an *Emiliania huxleyi* bloom (Fig. 4). For a short period, *Phaeocystis* sp. also became dominant in E1 (Fig. 4) which was moderately silicate depleted. Here, silicate was not added, but present in the deep water. In the silicate-enhanced E4, however, *Phaeocystis* sp. was not able to compete at any time although the environmental conditions were similar to those of E3, and *Phaeocystis* sp. was present at the start of the experiment.

In the North Sea it is well known that *Phaeocystis* sp. blooms may follow the spring diatom blooms (Gieskes & Kraay 1977, Cadee & Hegemann 1986, Veldhuis et al. 1986). Weisse et al. (1986) speculate whether diatoms excrete a substance which prevents *Phaeocystis* sp. blooming, or whether *Phaeocystis* sp. needs dissolved organic compounds from diatom blooms for growth stimulation. In E1, *Phaeocystis* sp. appeared after a bloom of diatoms and in E3 after an *Emiliania huxleyi* bloom. Harboe (1988) reported *Phaeocystis*

pouchetii dominance after blooms of diatoms (enclosure experiments conducted in 1986; Table 2). In later unpublished experiments in 1989 *Phaeocystis* sp. again followed blooms of *E. huxleyi.* In these experiments it is not possible to conclude whether the earlier blooms influenced *Phaeocystis* sp. growth in any way. Nevertheless, *Phaeocystis* sp. has never become dominant in these experiments unless the silicate concentration has dropped to levels below 2 μM. It has co-occurred with diatoms at silicate concentrations slightly above 2 μM. This is in close agreement with Verity et al. (1988) who also found co-occurrence at such concentrations. Bennekom et al. (1975) also report that *Phaeocystis* blooms coincide with silicate limitation in coastal water. On the coast of northern Norway *P. pouchetii* has been reported to occur early in the spring bloom (Gaarder 1938, Heimdal 1974, Eilertsen et al. 1981). These observations, however, were not accompanied by silicate measurements, but it is likely that these were higher than 2 μM. Skreslet (1988) has observed positive buoyancy in *P. pouchetti* and speculate that this may facilitate a competitive advantage under light limitation and weak stratification of the water column.

Emiliania huxleyi was found in the initial community in E4 (high silicate concentration), but was out-competed by diatoms. In E3 (low silicate concentration) *E. huxleyi* became dominant after 5 d. Eppley et al. (1969) report that *E. huxleyi* may compete with diatoms at low irradiance and low nitrogen concentration, but silicate conditions were not reported in their study.

Possible influence of experimental conditions

Eppley et al. (1978) found mechanical stirring to be a useful technique for manipulating the phytoplankton species composition. Pumping of water from the bottom of the bag to the surface in our experiments was done in order to make the water column homogeneous (Fig. 1). This is preferable, as sampling efforts are minimized and the results more easily interpretable. In contrast, the huge amount of data obtained in experiments involving vertical gradients (which are time-depth dependent) with physical, chemical and biological variables is extremely difficult to interpret. Furthermore, vertical gradients created in enclosure experiments are probably as artificial as the water renewal made in such experiments. Use of internal water renewal in our experiments, however, may have favoured diatoms in several ways. Resuspension of sinking individuals may have been most important. However, internal water renewal was not used in the experiments conducted in 1983 (Table 2), and diatom dominance was also observed in these experiments (Aksnes et al. 1985).

Several authors have reported mass aggregation of phytoplankton during diatom blooms (Alldredge & Gotschalk 1989, Riebesell 1989, 1991a, b). Physical coagulation is likely to be an important process leading to flocculation of algal biomass (Jackson 1990). Although aggregates of phytoplankton were not observed in our experiments, the artificial mixing may have led to aggregation, and thereby influenced competitive relationships between species. In a mixed mesocosm experiment Riebesell (1989) found that *Skeletonema costatum,* which was frequently found in sediment aggregates, had a higher sinking rate than *Chaetoceros* spp. This may have contributed to the replacement of *S. costatum* with *Chaetoceros* spp. in our experiment (E2).

Most of the experiments (including E1 to E4) were operated as batch cultures the first week and thereafter as continuous cultures (see 'Materials and methods'). Hence, our results probably depend less on the initial conditions of the enclosures (data from the batch period are excluded in Fig. 5) than if the experiments were run entirely as batch cultures. Water renewal allows 'immigrating' species to compete with the established species, but under a nutrient regime controlled mainly by the artificial fertilization. The water renewal, however, also introduces a cell removal or 'mortality' factor influencing the net growth rate of the species. Theoretically, such mortality should move the growth isoclines in a resource (i.e. nutrients) space away from the resource axis as demonstrated by Tilman et al. (1982, Fig. 1D, p. 352). Although the dilution-mediated mortality, presumably, was the same for all species (at least in the stirred experiments), dilution rate may have altered the relative competitive ability among species as demonstrated by Mickelson et al. (1979) and De Pauw et al. (1983). At the extreme, species having a growth rate below the dilution rate would experience a negative realized growth despite other favourable environmental conditions. The external water renewal in E1 to E4 was about 30 %, while the experiments listed in Table 2 had renewal rates in the range 4 to 100 % d^{-1} (Table 2). Due to the many factors involved, however, our data are not suitable for assessing possible influences of the dilution rate on competitive relationships between flagellates and diatoms. It is possible that the critical concentration, interpreted as 2 μM silicate on the basis of our experiments (Fig. 5), depends on the actual dilution rate (external renewal) and perhaps also on the degree of stirring (internal renewal).

Considerations on the success of diatoms

The observed conditional competitive superiority of diatoms (Fig. 5) is in accordance with the extensive review of Furnas (1990) on growth rates in phytoplank-

ton. He concludes that there appears to be a broad dichotomy between the growth potential of diatom species and non-diatoms, with the highest growth potential among the diatoms. He reports that maximum in situ doubling rates between 2 and 4 d^{-1} have repeatedly been measured for diatoms, and that maximum growth rates for dinoflagellate, microflagellate and eukaryotic non-motile ultraplankton species or assemblages are generally below 2.5 d^{-1} When silicate concentration becomes limiting, however, the potential growth cannot be realized. The realized growth rate (μ_d) for diatoms may then be expressed:

$$\mu_d = \mu_{d\text{-}max}S/(K_s + S) \tag{1}$$

where K_s is the half-saturation constant for growth rate; and $\mu_{d\text{-}max}$ is the maximum growth rate under non-limiting silicate concentration (S) conditions. Our experiments indicate that diatoms, as a group, were outcompeted by the 'flagellate group' at silicate concentrations below a threshold of about 2 μM (Fig. 5). Then, we may postulate that the maximum flagellate growth rate ($\mu_{f\text{-}max}$), which is assumed not to be influenced by silicate concentration, equals the realized diatom growth rate at 2 μM silicate:

$$\mu_{f\text{-}max} = \mu_d = \mu_{d\text{-}max} \, 2/(K_s + 2)$$
$$\text{or } \mu_{d\text{-}max}/\mu_{f\text{-}max} = (K_s + 2)/2 \tag{2}$$

Here, it is assumed that the flagellates are not seriously limited by other factors, or more precisely that diatoms and flagellates are equally limited by all other factors except silicate. Inserting half-saturation constants for silicate-limited growth in the range 0.1 to 1 μM (Paasche 1980), it follows that a 5 to 50 % higher inherent growth for the diatom group may explain the outcome of our experiments (Fig. 5).

Several authors have speculated on why diatoms can grow at higher rates than other algae, and Thomas et al. (1978) stated that there must be reasons for the success of diatoms, but that these remain obscure. They hypothesized that diatoms might have a better ability to utilize low nitrogenous nutrient levels, i.e. that diatoms have lower half-saturation values (K_s) for nitrate and ammonium uptake. They pointed out, however, that this trend could not be statistically established on the basis of measured K_s values (Eppley et al. 1969). According to the nutrient uptake model of Aksnes & Egge (1991) (and references therein), however, the K_s value should not be taken as a measure of nutrient uptake efficiency. The affinity (α) is the significant uptake parameter at low nutrient concentrations, and it depends on both the maximum uptake rate and the half saturation parameter.

A higher photosynthetic capacity due to a higher chlorophyll content in diatoms (Langdon 1988) is also believed to be responsible for the higher inherent growth rate observed in diatoms. In our experiments too, the Si-fertilized bags (E2 and E4) had a much higher chlorophyll content than the two without artificial Si fertilization (E1 and E3). This undoubtedly contributed to a higher potential growth rate in these bags being dominated by diatoms. Our experiments, however, can hardly throw light onto mechanisms behind the success of diatoms. On the other hand, the important role of silicate concentration as a factor in competition is clearly demonstrated by the enclosure experiments, and gives strong support for Officer & Ryther's (1980) concern about the importance of silicon in marine euthrophication. Parsons et al. (1978) suggested a diatom 'corridor' (with respect to light and nutrient conditions) of maximum growth leading to diatom blooms in the ocean. Our experiments indicate that this corridor of diatom dominance may be generated under a wide range of environmental conditions as long as the silicate concentration is above approximately 2 μM. This is probably due to a higher maximum growth rate in diatoms being realized at non-limiting silicate concentrations.

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