

Production of biogenic silica by spring diatoms

Abstract—The radioactive isotope ^{32}Si was used to measure Si uptake during a spring bloom dominated by the diatom *Thalassiosira nordenskiöldii*. The diatoms converted virtually all dissolved silicic acid in the surface layer into biogenic silica. The rate of Si uptake was unsaturated in all the experiments conducted during the bloom. The half-saturation constant for Si uptake declined from 6–12 mmol m^{-3} early in the bloom to 2 mmol m^{-3} when dissolved silicic acid concentration was low. The highest specific Si-uptake rates measured (ca. 0.3 d^{-1}) were comparable to average net growth rates calculated from cell abundance measurements.

Phytoplankton spring blooms in coastal waters are intense and short lived (a few weeks) and are usually dominated by diatoms. Silicic acid concentrations are greatly reduced during the bloom, and diatoms may show morphological signs of Si depletion later in the season (Paasche 1980a; Paasche and Østergren 1980). Rates of Si uptake as a function of silicic acid concentration by natural phytoplankton communities and by diatoms in culture fit reasonably well to Michaelis-Menten saturation curves (Paasche 1980a; Nelson and Tréguer 1992; Nelson and Dortch 1996), but published half-saturation constants for Si uptake are highly variable. Until recently, suitable radioactive Si isotopes have not been available, and only stable Si isotopes have been used in tracer studies (Brzezinski and Phillips 1997). Si-uptake rates are lacking from eastern North Atlantic waters, and only a limited number of biogenic silica production estimates from laboratory-incubated water samples are available from this area (Paasche and Østergren 1980).

Our main objectives were to measure Si uptake and Si-uptake kinetics during a spring bloom. We address the following questions: How did the Si-uptake rates vary during the bloom? Did the uptake kinetics change during the bloom? This is also the first study of Si-uptake kinetics during a spring bloom using radioactive Si and the first Si-tracer experiments published from North European waters.

We used both natural samples and cultures with diatoms isolated during the bloom. Samples were collected at 1-m depth from a pier in the Drøbakfjord, a narrow neck of the Oslofjord, Southern Norway. Nine samples were collected from 27 February–26 March 1996 using a nontoxic water sampling bottle. The diatoms *Thalassiosira nordenskiöldii* Cleve and *Detonula confervacea* (Cleve) Gran, isolated from the fjord samples, were cultivated at 3°C under $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ from daylight fluorescent tubes and a 12:12 light:dark (LD) cycle. The medium was standard enriched seawater medium with reduced silicic acid concentration made from nutrient-depleted seawater from the Norwegian Sea (Table 1). Silicic acid concentrations and in vivo fluorescence (Turner Designs fluorometer) were monitored daily in the cultures.

Uptake rates of Si were measured using ^{32}Si -labeled silicic acid of high specific activity ($52,000 \text{ Bq } \mu\text{g}^{-1}$) from

Los Alamos National Laboratory (Brzezinski and Phillips 1997). Usually $100 \mu\text{l}$ of a diluted and rinsed ^{32}Si solution (0.7 kBq) was added to 250-ml polycarbonate incubation bottles (only natural samples). The bottles were incubated for 5–6 h (starting 10 h local time) at in situ temperature (between -1 and 0°C) and exposed to 50% of surface irradiance. The incubations were terminated by filtering $3 \times 80\text{-ml}$ subsamples from each incubation bottle onto $0.6\text{-}\mu\text{m}$ polycarbonate filters. The funnels and filters were rinsed with 5–10-ml filtered seawater ($0.6\text{-}\mu\text{m}$ polycarbonate filters), the filters were dried overnight at 60°C and stored in polyethylene vials at room temperature. Uptake kinetic experiments (both natural samples and cultures) were performed by adding $400 \mu\text{l}$ of the ^{32}Si solution (2.8 kBq) to a 500-ml sample, mixing, gently pouring 50-ml subsamples into 7–8 polycarbonate tubes, adding cold $\text{Si}(\text{OH})_4$ to the tubes [final concentrations of added cold $\text{Si}(\text{OH})_4$ in the tubes were $0\text{--}10 \text{ mmol m}^{-3}$], and incubating the tubes as described above. The ^{32}Si activity was measured as ^{32}P activity at secular equilibrium (^{32}Si activity = ^{32}P activity) using Cerenkov counting and a Packard Tri-Carb 1500 liquid scintillation analyzer (Tréguer et al. 1991). Counting efficiency was 53%, and the values have been corrected for color quench using a quench curve made from carrier-free $^{32}\text{PO}_4$ (Amersham) and Irgalan Black (Ciba-Geigy) as a color quencher. Analysis 2 weeks apart in June and again in November showed that secular equilibrium was already established in June. Coefficients of variation of Cerenkov counts from eight sets of samples were $<7\%$. The uptake rates were calculated according to Brzezinski and Phillips (1997), their eqs. 18 and 22. Uptake rates from the kinetic experiments were fitted to a Michaelis-Menten hyperbola by nonlinear procedures using the Marquardt's algorithm, and the parameters V_{max} (maximum specific Si-uptake rate in h^{-1}) and K_m (half-saturation constant in mmol m^{-3}) were calculated. The affinity for nutrient uptake depends on both K_m and V_{max} , and the ratio $0.5V_{\text{max}}/K_m$ (initial slope of the uptake curve versus concentration) can be used as an indicator of nutrient affinity (Healey 1980; Harrison et al. 1989). Maximum ^{32}Si added to our samples was $2.8 \text{ kBq (500 ml)}^{-1}$ or $4 \mu\text{mol m}^{-3}$, which is $<10\%$ of the lowest ambient silicic acid concentration measured. Silicic acid concentration was also measured in the incubation bottles before and after addition of the isotope, and no significant increase was found ($<0.05 \text{ mmol m}^{-3}$). It can thus be assumed that addition of ^{32}Si did not perturb the silicic acid uptake system.

Concentration of chlorophyll *a* (Chl *a*) was immediately measured in acetone extracts on fresh samples using a calibrated Turner Designs fluorometer (Sigma Chl *a*), and silicic acid concentration was measured according to Strickland and Parsons (1972). Samples for biogenic silica (BSi) were filtered onto $0.6\text{-}\mu\text{m}$ polycarbonate filters as described above and subsequently analyzed using soda hydrolysis according

Table 1. Salinity and concentrations of silicic acid, biogenic silica (BSi, both in mmol m^{-3}), and chlorophyll *a* (Chl *a* in mg m^{-3}) during the spring bloom and in the culture experiments with *Detonula confervacea* and *Thalassiosira nordenskiöldii*.

Date or species	Salinity	Silicic acid (mmol m^{-3})	BSi (mmol m^{-3})	Chl <i>a</i> (mg m^{-3})
Oslofjord samples				
27 Feb	—	7.6	1.5	4.9
29 Feb	25.78	6.3	3.2	12.2
5 Mar	26.12	4.6	6.0	22.7
8 Mar	27.89	3.6	7.9	27.3
12 Mar	28.25	3.5	8.6	27.2
15 Mar	27.80	2.6	9.7	32.3
19 Mar	28.40	0.5	9.8	37.5
22 Mar	28.23	<0.1	9.4	23.9
26 Mar	25.71	0.4	4.4	4.1
Cultures				
<i>D. confervacea</i>	26	0.75	5.3	49.0
<i>T. nordenskiöldii</i>	26	0.50	10.9	17.0

to Paasche (1980b). He also tested the method for interference from silicate minerals and found it specific for BSi. The freshwater discharge into the fjord is low during the spring bloom (no major rivers and reduced freshwater discharge). The lithogenic silica component was therefore low in our samples and did not significantly bias our BSi values. The concentrations were all measured in triplicates, and the coefficients of variation were <10% for Chl *a*, <8% for silicic acid, and <7% for BSi. Quantitative phytoplankton samples were preserved with neutralized formaldehyde and later counted in a microscope using 2-ml chambers. More than 150 cells of the dominating species were counted. Average cell dimensions were determined by measuring >50 cells of the dominating species from three different dates (29 February, 15 and 26 March). No significant differences in size distribution of single species were found between the samples. Average cell dimensions (all three dates) were thus used to calculate cell volumes and cell surface areas. Empty frustules were included in the cell surface estimates. Species with pronounced setae were not abundant; thus setae are not included in the cell volume and cell surface-area estimates. Phytoplankton cell carbon was calculated using the equations given by Strathmann (1967).

The fjord was partly covered by ice in February–March

Table 2. Biogenic silica per diatom surface area ($\text{pg } \mu\text{m}^{-2}$), and ratio between chlorophyll *a* and biogenic silica (g g^{-1}).

Date	Surface BSi ($\text{pg } \mu\text{m}^{-2}$)	Chl <i>a</i> /BSi (g g^{-1})
27 Feb	0.043	0.11
29 Feb	0.054	0.13
5 Mar	0.049	0.13
8 Mar	0.049	0.12
12 Mar	0.051	0.11
15 Mar	0.051	0.12
19 Mar	0.053	0.13
22 Mar	0.057*	0.09
26 Mar	0.027*	0.03

* Corrected for detrital Si, uncorrected values were 0.084–0.085.

1996, and the spring bloom started in leads between broken ice. The variable salinity (25.71–28.40) shows that water masses changed through the sampling period (Table 1). The ice disappeared during the last week of March, and no ice was observed in the sampling area on the last sampling day (26 March). Summed silicic acid and BSi increased from 9.1–12.3 mmol m^{-3} during the first 2–3 weeks, which indicates that the changing water masses did not have any profound effects on nutrient concentrations or phytoplankton abundance. Silicic acid concentration was very low on the last three sampling dates (0.05–0.35 mmol m^{-3}), and >93% of the silicon was found as BSi. During the last 4 d BSi dropped from 9.4 to 4.4 mmol m^{-3} , probably because of massive sedimentation of BSi out of the surface layer. The Chl *a*:BSi ratio was almost constant until 19 March (0.11–0.13 g g^{-1}) and then decreased to 0.03 on 26 March (Table 2). BSi per diatom surface area ($\text{pg } \mu\text{m}^{-2}$) showed an opposite trend, varying from 0.043–0.054 $\text{pg } \mu\text{m}^{-2}$ until 19 March and then increasing to 0.085 on 26 March.

Diatoms dominated the phytoplankton community (Table 3), accounting for 94–99% of the autotrophic C biomass. The most abundant species were *T. nordenskiöldii* and *Chaetoceros socialis*, and few empty frustules of the dominating species were found (usually <5%). The last sample collected contained significant fractions of empty frustules of two nondominant species (33% of *D. confervacea* and 88% of *Chaetoceros decipiens*). Linear regression analyses of BSi versus Chl *a* and of BSi versus diatom surface area, omitting the last two samples (22 and 26 March), both indicate that most BSi was in diatom frustules and that diatom surface area was a reasonable estimate of BSi ($\text{BSi} = 2.35 + 7.91 \text{ Chl } a$; $r^2 = 0.968$ and $\text{BSi} = -5.61 + 52.2 \text{ area}$; $r^2 = 0.994$; BSi and Chl *a* in mg m^{-3} , diatom surface area in $\text{mm}^2 \text{ ml}^{-1}$). The two last samples were not included in the regression analyses because the spring bloom was declining and the particulate ratios differed (Tables 1, 2). Moreover, the cells in these two samples also looked stressed (reduced cellular content, more empty frustules and bacteria attached to the cell surfaces). A few resting spores were

Table 3. Species with cell abundances $>10^7$ cells m^{-3} identified in one or more of the samples. Average cell dimension (width \times length), maximum cell abundances, and dates maximum cell abundances found are given.

Species	Cell dimensions (μm)	Max. cell abundances (10^9 cells m^{-3})	Date
<i>Chaetoceros compressus</i> Lauder	21 \times 16	0.04	5 Mar
<i>C. debilis</i> Cleve	15 \times 13	0.60	22 Mar
<i>C. decipiens</i> Cleve	38 \times 25	0.01	8 Mar
<i>C. diadema</i> (Ehrenberg) Gran	29 \times 15	0.27	19 Mar
<i>C. lacinosus</i> Schütt	16 \times 19	0.06	22 Mar
<i>C. socialis</i> Lauder	9 \times 7	1.22	19 Mar
<i>Chaetoceros</i> sp.	13 \times 20	0.23	8 Mar
<i>Detonula confervacea</i> (Cleve) Gran	8 \times 17	0.55	19 Mar
<i>Navicula</i> spp.	8 \times 42	0.07	8 Feb
<i>Pseudo-nitzschia</i> spp.	6 \times 100	0.01	22 Mar
<i>Skeletonema costatum</i> (Greville) Cleve	5 \times 12	0.03	29 Feb
<i>Thalassiosira nordenskiöldii</i> Cleve	29 \times 16	1.35	15 Mar
<i>Thalassiosira</i> sp.	10 \times 7	0.01	27 Feb
<i>Eutreptiella</i> cf. <i>braarudii</i>	21 \times 70	0.01	22 Mar

found in all the samples, thus the resting spore abundance did not change significantly during the sampling period. The BSi versus Chl *a* regression above indicated that there was very little BSi in the detrital fraction (0.08 $mmol m^{-3}$) until 22 March. BSi in the detrital fraction increased significantly in the last two samples. Based on a BSi versus Chl *a* plot, a reasonable estimate of detrital BSi is about 3 $mmol m^{-3}$ on 22 and 27 March. Detritus-corrected BSi per diatom surface area in these two samples decreased to 0.057 and 0.027 $pg \mu m^{-2}$, respectively (Table 2).

The measured BSi per diatom surface-area ratios fit very well with similar ratios from culture experiments with *T. nordenskiöldii* grown in silicic acid rich media at 0°C (0.04–0.08 $pg \mu m^{-2}$; Durbin 1977). A somewhat wider range of this ratio (0.02–0.13 $pg \mu m^{-2}$) has been found in other diatoms isolated from Norwegian fjords and also grown in silicic acid rich media (Paasche 1973, 1980b). Diatoms may produce thinner frustules when exposed to lim-

iting silicic acid concentrations (Paasche 1980a; Brzezinski et al. 1990), and a twofold variation in BSi per diatom surface area as in Table 2 is realistic. Relative diatom surface area (surface area of individual species as percentage of summed diatom surface area) can thus be used as relative BSi concentration. Under this assumption, *T. nordenskiöldii* accounted for $>56\%$ of BSi until 19 March (Fig. 1). On 26 March, the community was dominated by a mixture of four diatoms (*T. nordenskiöldii* and three *Chaetoceros* species). The species in Table 3 are common in the area (Lange et al. 1992), and *T. nordenskiöldii* often dominates the spring bloom in the fjord (Hasle and Smayda 1960; Kristiansen 1987).

Absolute Si-uptake rate increased from 13–82 $\mu mol m^{-3} h^{-1}$ during the first 2 weeks of the bloom (27 February–15 March) and then decreased as dissolved silicic acid was depleted (Table 1; Fig. 2). Specific Si-uptake rate was about 0.2–0.3 d^{-1} during the same 2 weeks, and then decreased abruptly as the absolute rate did. The measured Si-uptake rates are confirmed both by the silicic acid concentrations and the cell abundances in the samples. Assuming that the Si-uptake rate is constant for 24 h, diatoms in the surface layer used 1–2 $mmol Si m^{-3} d^{-1}$ during the most intense part of the bloom. The drop in ambient concentration of silicic acid and increase in BSi (Table 1) both agree with the measured absolute Si-uptake rates given in Fig. 2. Diatom cell abundances increased exponentially during the first 1–2 weeks of the bloom, and average net growth rates of the dominating species, calculated by regression analyses, were in the range 0.1–0.2 d^{-1} (Table 4; Fig. 2). Net growth rates from 27–29 February were much higher (1.1 d^{-1}) than average net growth rates for two of the diatoms (*C. socialis* and *D. confervacea*). Cell abundances from the first sampling are therefore not included in the average net growth rates of these species. Growth-rate estimates based on natural cell abundances are questionable for several reasons (e.g., patchiness, sedimentation, and grazing). Nevertheless, the growth rates support the specific Si-uptake rates

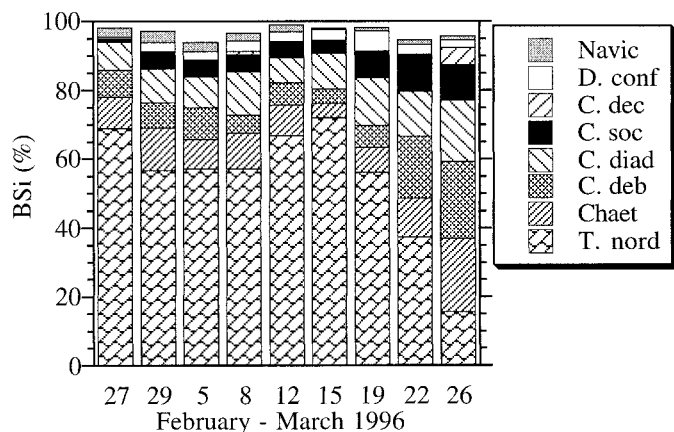


Fig. 1. Dominating diatoms as percentage of biogenic silica (BSi). The species are *Navicula* spp., *Detonula confervacea*, *Chaetoceros decipiens*, *C. socialis*, *C. diadema*, *C. debilis*, *Chaetoceros* sp., and *Thalassiosira nordenskiöldii*.

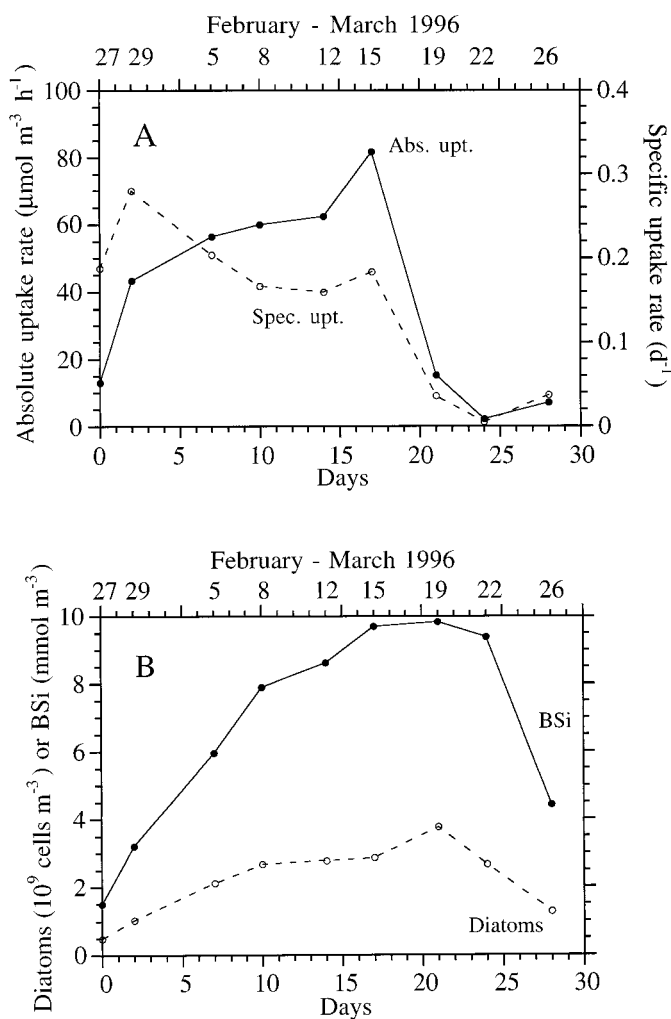


Fig. 2. (A) Absolute ($\mu\text{mol m}^{-3} \text{h}^{-1}$) and specific Si-uptake rates (d^{-1}). (B) Diatom abundance ($10^9 \text{ cells m}^{-3}$) and biogenic silica concentration (BSi in mmol m^{-3}). Number of days from 27 February (the first sampling) are given below each figure and the sampling dates are given above each figure.

in Fig. 2. Consequently, ^{32}Si seems to be a suitable tracer for Si-uptake measurements. This confirms the work by Brzezinski and Phillips (1997), who tested ^{32}Si and the stable ^{30}Si in samples from Monterey Bay and did not observe any bias between Si-uptake rates obtained with the two tracers.

In situ Si-uptake rate was $\leq 62\%$ of maximum measured uptake rate (Fig. 3; Table 5) and $\leq 41\%$ of calculated V_{max} . Despite the large statistical variation, the uptake versus concentration curves and the kinetic parameters (K_m and V_{max}) obtained from the fjord samples can be divided into two groups. The group from 29 February–19 March had high K_m and V_{max} ($5.5\text{--}11.5 \text{ mmol m}^{-3}$ and $0.018\text{--}0.027 \text{ h}^{-1}$, respectively); the other group from 22 and 26 March had low K_m and V_{max} ($1.7\text{--}2.1 \text{ mmol m}^{-3}$ and $0.007\text{--}0.009 \text{ h}^{-1}$, respectively). The measured maximum uptake rates from the two groups were significantly different (ANOVA, $P < 0.001$). However, the affinity indicator ($0.5V_{\text{max}}/K_m$) was not significantly different in the two groups (propagation of errors; Bevington and Robinson 1992). Thus, the only significant difference between the two groups was the V_{max} values; the affinity indicator shows that the ability to take up silicic acid at low and high concentration was the same. The phytoplankton community responsible for the first group was dominated by *T. nordenskiöldii*, whereas a mixture of *T. nordenskiöldii* and three *Chaetoceros* species dominated in the second group. The latter group represented the later phase of the bloom, when the cell abundance of all the species decreased (Fig. 1; Table 3).

Uptake kinetics in the culture experiments with *T. nordenskiöldii* and *D. confervacea* isolated during the bloom were almost identical (Fig. 3C; Table 5). In the cultures V_{max} ($0.070\text{--}0.071 \text{ h}^{-1}$) was 3 times higher than the highest V_{max} found in the fjord samples, although K_m in the cultures ($2.7\text{--}2.9 \text{ mmol m}^{-3}$) was close to the lowest K_m found in the fjord samples ($1.7\text{--}2.1 \text{ mmol m}^{-3}$). The affinity indicator was an order of magnitude higher in the two cultures ($12\text{--}13 \text{ mM}^{-1} \text{ h}^{-1}$) than in the fjord samples, mainly because of increased V_{max} in the cultures. The cultures were growing at $0.7\text{--}0.8 \text{ d}^{-1}$, which is close to maximum growth rates at the ambient conditions (Suzuki and Takahashi 1995). Irradiance was low in the lower part of the mixed layer at our station (daily maximum irradiance, PAR, was $50\text{--}100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 5-m depth, and the day length was 10–13 h); thus phytoplank-

Table 4. Net growth rates (d^{-1}) of dominating species during early bloom (27–29 February) and average net growth rates $\pm 1 \text{ SE}$ (d^{-1}) the first 1–2 weeks of the bloom. Dates and r^2 are given for average growth rates.

Species	Growth rates 27–29 Feb	Average growth rates	Dates	r^2
<i>Chaetoceros debilis</i>	0.26	0.20 ± 0.02	27 Feb–5 Mar	0.994
<i>C. diadema</i>	0.31	0.18 ± 0.02	27 Feb–8 Mar	0.983
<i>C. socialis</i>	1.14	0.13 ± 0.01	29 Feb–8 Mar	0.987
<i>Chaetoceros</i> sp.	0.40	0.10 ± 0.02	29 Feb–8 Mar	0.955
<i>Detonula confervacea</i>	1.07*	0.14 ± 0.01	29 Feb–8 Mar	0.994
<i>Thalassiosira nordenskiöldii</i>	0.16	0.14 ± 0.01	27 Feb–8 Mar	0.993
<i>Eutreptiella cf. braarudii</i>	0.27*	NS†	—	—

* Less than 50 cells counted.

† NS, no significant average net growth rate ($P > 0.05$).

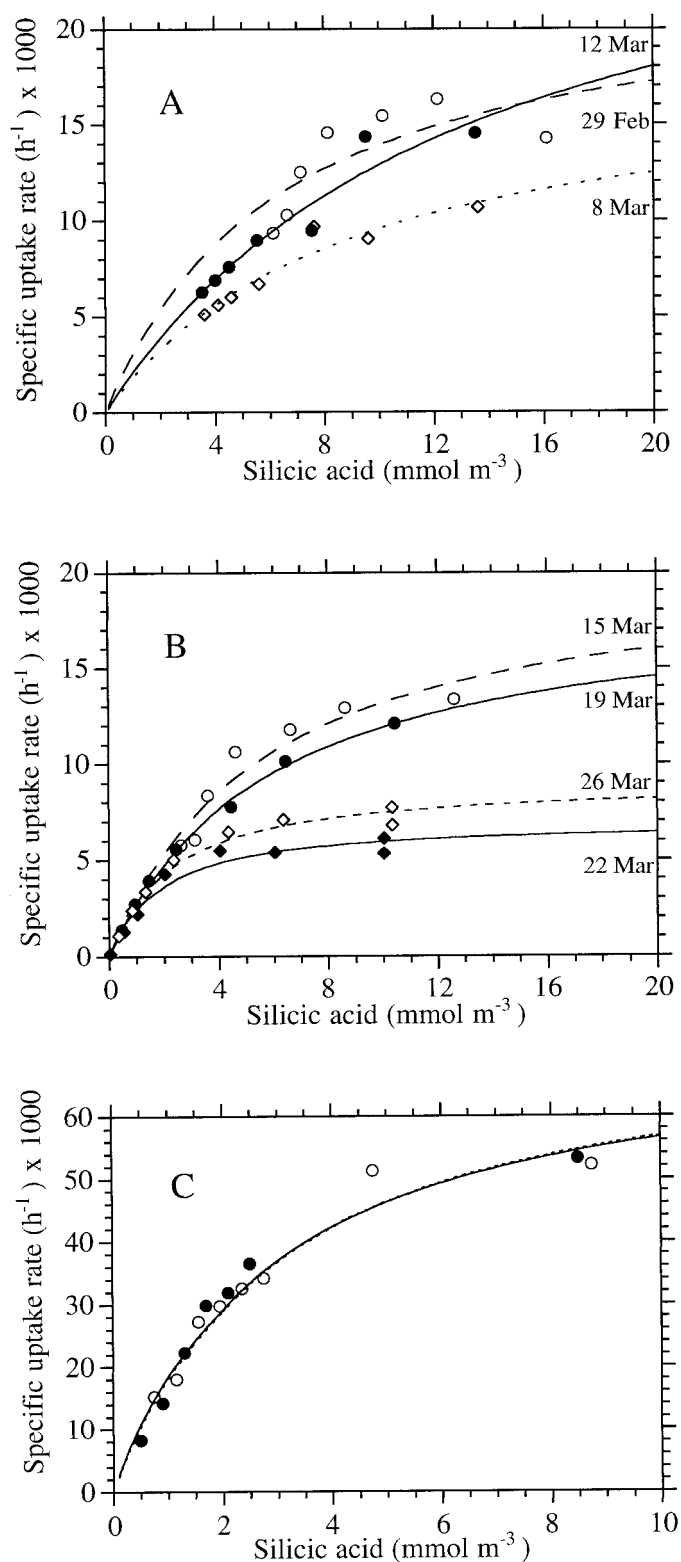


Fig. 3. Si-uptake kinetic experiments from (A) 29 February, 8 and 12 March; (B) 15, 19, 22, and 26 March; (C) culture experiments with *Detonula confervacea* (open symbols and broken line) and *Thalassiosira nordenskiöldii* (filled symbols and solid line).

Table 5. Kinetic experiments in the fjord samples and in cultures of *Detonula confervacea* and *Thalassiosira nordenskiöldii* isolated during the spring bloom. $K_m \pm 1$ SE (mmol m⁻³), $V_{max} \pm 1$ SE (h⁻¹ × 1,000), and in situ Si uptake rate as % of measured maximum Si uptake rate. Number of subsamples in each experiment was 7–8.

Date or species	K_m (mmol m ⁻³)	V_{max} (h ⁻¹ × 1,000)	% of measured max. rate
Oslofjord samples			
29 Feb	6.2 ± 4.1	22.4 ± 5.9	62
8 Mar	8.7 ± 2.5	17.8 ± 2.7	48
12 Mar	11.5 ± 2.1	26.7 ± 3.0	44
15 Mar	5.5 ± 1.7	20.3 ± 2.9	44
19 Mar	5.7 ± 0.5	18.6 ± 0.8	11
22 Mar	1.7 ± 0.5	6.9 ± 0.5	2
26 Mar	2.1 ± 0.4	9.0 ± 0.5	15
Cultures			
<i>D. confervacea</i>	2.9 ± 0.5	70.6 ± 6.0	30
<i>T. nordenskiöldii</i>	2.7 ± 0.5	70.0 ± 5.7	16

ton growth in the mixed layer was probably light limited during the spring bloom (personal observations). Light-limited phytoplankton growth may explain the low net growth rates and the low V_{max} in the fjord. Values from the culture experiments are not directly comparable with values from the multispecies fjord communities. The kinetic parameters may also vary through the cell cycle and with nutrient status of the cells (Brzezinski 1992). Our experiment was designed to give the cultures realistic growth conditions: the light regime was 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and the LD cycle was 12:12; these are reasonable surface values during the spring bloom. The Si concentrations (silicic acid and BSi) in the cultures and during parts of the bloom were also similar. The isotope was added 2–3 h into the light period, and the samples were incubated for 5–6 h. The following conclusions can therefore be made from the comparisons above. Si-uptake rates were substrate limited during the spring bloom. The shift in K_m for Si uptake during the bloom (from high to low) was not caused by changes in the species composition. K_m decreased when V_{max} decreased, which resulted in a near constant affinity indicator throughout the bloom. Close to maximum growth rates in the cultures resulted in high V_{max} and high affinity.

Despite similar affinity for Si uptake, *D. confervacea* accounted for only a minor fraction (1–6%) of BSi, whereas *T. nordenskiöldii* accounted for 16–72% of BSi in the fjord samples. This is partly explained by differences in cell dimensions. *T. nordenskiöldii* is a large cell (Table 3), and in our fjord samples its average cell surface area was 5.2 times larger than for *D. confervacea*. However, cell abundance of *D. confervacea* was lower than for *T. nordenskiöldii* in all the fjord samples, increasing from 4% (27 February) to 53% (19 March) of that of *T. nordenskiöldii*. Average net growth rates of the two diatoms were similar during the first 2 weeks of the bloom (0.14 d⁻¹; Table 4). Cell abundance of *T. nor-*

Table 6. Half-saturation constants for Si uptake (K_m) and for Si-limited growth (K_s , both in mmol m^{-3}) from culture studies (genera given) and from natural phytoplankton assemblages retrieved from the literature. Ambient silicic acid concentrations are given for comparisons. Sat. and unsat.: Saturated and unsaturated uptake rate.

Genera/area	Si(OH) ₄	K_m	K_s	Refs.
Southern Ocean				
<i>Nitzschia</i>	2–10	12–22	—	1
Diatom*	>10	—	4–88	1
Ross Sea	6–7	1.1–4.6	—	1
Arctic, temperate and tropical oceans and coastal waters				
Diatoms†	iii‡	0.4–5	0.02–1.4	1, 2, 3
<i>D. confervacea</i>	0.75	2.9 ± 0.5	—	This study
<i>T. nordenskiöldii</i>	0.5	2.8 ± 0.5	—	This study
Mexico & California coast	1–3.6	1.6 ± 2.5	—	4, 5
Mexico coast	5–19	Sat.	—	4
Gulf Stream ring	<0.2	0.5–0.9	—	6
Gulf Stream ring	2.5–2.9	Sat.	—	6
Mississippi plume	0.1–5.4	0.5–sat.	—	7
Mississippi plume	0.9–3.5	5.3–sat.	—	7
Peru upwelling	1.6–5.5	1.8–3.7	—	8
Sargasso Sea	<1.0	1.6–unsat.	—	9
North Pacific	1–3	0.6–sat.	—	10
Oslofjord	9	Sat.?	—	11
Oslofjord	<2.3	Unsat.	—	11
Oslofjord	0.5–7.6	5.8–11.7	—	This study
Oslofjord	<0.4	1.7–2.1	—	This study

* *Chaetoceros*, *Corethron*, *Nitzschia*, and *Thalassiosira*.

† *Ditylum*, *Nitzschia*, *Skeletonema*, and *Thalassiosira*.

‡ Cells from Si-depleted and Si-replete cultures giving no clear differences in K_m .

|| References: 1, Nelson and Tréguer (1992); 2, Paasche (1980a); 3, Olsen and Paasche (1986); Stapleford and Smith (1996); 4, Azam and Chisholm (1976); 5, Brzezinski and Phillips (1997); 6, Nelson and Brzezinski (1990); 7, Nelson and Dortch (1996); 8, Goering et al. (1973); Nelson et al. (1981); 9, Brzezinski and Nelson (1996); 10, Brzezinski et al. (1998); 11, Paasche and Østergren (1980).

denskiöldii declined after 15 March, whereas cell abundance of *D. confervacea* increased until 19 March and then decreased. Previous data from the Oslofjord also identify *T. nordenskiöldii* as a dominant diatom during early spring bloom (Hasle and Smayda 1960, and references therein). The culture experiments imply that growth rates of the two species in the fjord were similar, which was confirmed by the average net growth rates in Table 4. The kinetic experiments can neither explain why *T. nordenskiöldii* dominated the spring bloom nor why this species declined before *D. confervacea* did.

Published K_m values for Si uptake are few and variable (Table 6). Apparently K_m is lower ($<1 \text{ mmol m}^{-3}$) in silicic acid depleted water than in silicic acid rich water ($K_m > 1 \text{ mmol m}^{-3}$). The affinity indicator calculated from Table 6 is also variable ($0.3\text{--}22 \text{ mM}^{-1} \text{ h}^{-1}$). It tends to be lower in the Southern Ocean ($0.3\text{--}1.0 \text{ mM}^{-1} \text{ h}^{-1}$) than in temperate and tropical waters ($1\text{--}22 \text{ mM}^{-1} \text{ h}^{-1}$), which may be a temperature effect. In this study, both K_m and V_{\max} decreased with decreasing ambient silicic acid concentration, and the lowest K_m values in the fjord samples were similar to the culture values (*D. confervacea* and *T. nordenskiöldii*). The corresponding affinity indicators in the fjord samples were low ($1.0\text{--}2.2 \text{ mM}^{-1} \text{ h}^{-1}$) and comparable to the low values from the Southern Ocean given above. The lowest K_m in Table 6 is one order of magnitude higher than K_m for nitrate and ammonium uptake in oligotrophic oceans (Harrison et

al. 1996). Similar grouping of the affinity indicator is not possible because there are few and variable values. However, severe depletion of silicic acid will occur where diatoms bloom, usually in near-shore areas of high productivity (Levitus et al. 1993). The distribution of silicic acid in the world oceans is therefore slightly different from that of nitrate and phosphate. The first will show most severe depletion in near-shore areas, whereas the two latter may show severe depletion both in near-shore areas and in oligotrophic oceans.

Diatom morphology has been reported to change (thin cell walls, reduced spines, unusual shapes) in Si-deficient populations (Paasche 1980a; Paasche and Østergren 1980). Measured BSi per diatom surface area was reduced to almost one half in our last sample (Table 2). However, microscopic examination did not reveal any such morphological changes in our multispecies diatom communities. Cellular Si content will vary with ambient silicic acid concentrations (Paasche 1980a), and a reduced Si-uptake rate does not necessarily imply a reduced diatom growth rate. This is illustrated by the very low half-saturation constant for Si-limited growth (K_s) found in some diatoms (including *T. nordenskiöldii*, Table 6). It is still an open question whether diatoms growing in waters severely depleted in silicic acid have even lower K_m for Si uptake than those in Table 6.

This is the first study to track changes in Si production through a diatom bloom. The specific Si-uptake rates de-

clined, whereas the absolute uptake rates increased until both rates abruptly declined and the diatom bloom collapsed. Nitrogen and silicic acid dynamics will be discussed in a subsequent paper.

Svein Kristiansen¹

Tove Farbrot

Lars-Johan Naustvoll

Department of Biology
University of Oslo
P.O. Box 1069 Blindern,
N-0316 Oslo, Norway

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¹ Present address: NFH, University of Tromsø, Breivika, N-9037 Tromsø, Norway.

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