NOTE

Consumption of silicic acid below the euphotic zone by sedimenting diatom blooms in the Barents Sea

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ABSTRACT: Massive sedimentation of spring phytoplankton blooms occurs in the Barents Sea as in many other shelf sea environments. Associated with this sedimentation there is a large decrease in concentration of dissolved silicic acid below the nitracline. This decrease is apparently related to resting spore formation of the dominant diatom species *Chaetoceros socialis*. The deep silicic acid consumption seems to be a regular and extensive phenomenon which results in a vertical separation of the silicic acid gradient from the nitracline. This will disfavour further growth of diatoms during the summer season due to reduced upward transport of silicic acid by vertical mixing.

Extensive sedimentation of organic material following phytoplankton blooms has been documented for both coastal and oceanic environments (Smetacek 1980, Bodungen et al. 1981, Peinert et al. 1982, Billett et al. 1983, Wassmann 1983, 1985, Davies & Payne 1984, Schnack et al. 1985). Diatoms are typically the bloom organisms and their sedimentation has great ecological consequences for both zooplankton and benthos (Walsh 1983, Smetacek 1984, 1985). Increased sinking rate due to nutrient limitation is probably involved (Bienfang et al. 1982, Bienfang & Harrison 1984), although mass sedimentation has been suggested to represent a seeding stage in the life cycle of bloom diatoms (Smetacek 1985). We present here field evidence for a large decrease in concentration of dissolved silicic acid below the euphotic zone associated with sedimentation of diatom blooms in the Barents Sea. This appears to be a regular and large-scale phenomenon which could be of great importance for the ecology in this sea area.

The Institute of Marine Research, Bergen, Norway, has since 1979 conducted biological oceanographical investigations in the Barents Sea with the aim of describing the feeding conditions of capelin *Mallotus villosus*. Our study area has mainly been the western and central part between 74° and 78° N, but since 1984 this was extended to include also the eastern part (Fig. 1).

Compared to other polar seas the Barents Sea is relatively poor in dissolved nutrients, particularly silicic acid (Sakshaug & Holm-Hansen 1984). During summer, the ice retreats ca 500 km northwards (Loeng 1979). A diatom bloom is associated with the retreating ice-edge and this causes depletion of silicic acid and nitrate from the upper water layer (Rey & Loeng 1985). Towards the end of the bloom, the nitracline is usually located around 40 m and deeper than the pycnocline (Rey & Loeng 1985).

This is exemplified in Fig. 2 which shows vertical profiles from a station sampled at a late phase of the phytoplankton spring bloom in the central Barents Sea (Fig. 1). Sampling and analytical procedures were as described by Rey & Loeng (1985) and Skjoldal & Wassmann (1986). A marked pycnocline at 25 to 30 m sepa-
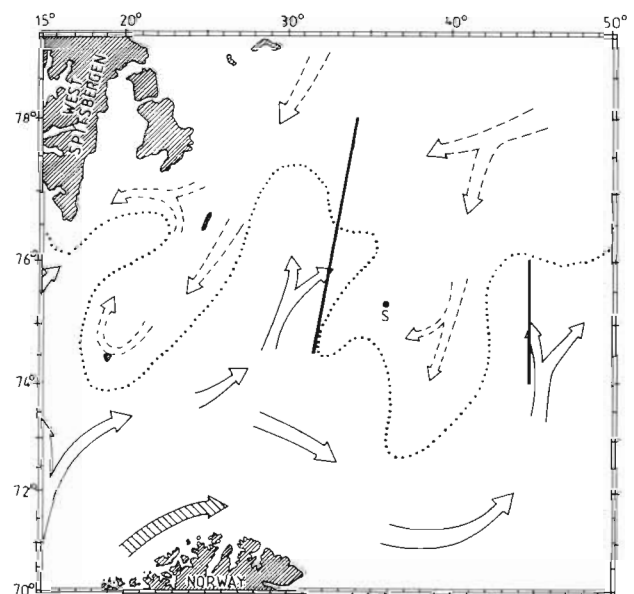

Fig. 1. Map of the Barents Sea showing the positions of the central and eastern transects (heavy lines) and Stn 713 (S), and a simplified current pattern (open arrows: Atlantic water; broken arrows: Arctic water; hatched arrow: coastal water). Dotted line: approximate position of the polar front

rated a top layer of slightly warmed meltwater from the core of cold Arctic water below (Fig. 2B). Nitrate and phosphate showed marked gradients between 45 and 60 m. Silicic acid, on the other hand, was depleted down to 75 m, with a marked gradient below (Fig. 2A). Ammonium exhibited a peak of 1.1 µM in the lower part of the nitracline at 60 m (Fig. 2A).

Chlorophyll in vivo fluorescence (Fig. 2C) showed a maximum at the top of the nitracline (45 m) where POC and PON also had their maxima (Fig. 2D). The highest chlorophyll a concentrations were found deeper (60 to 75 m), but this probably reflected an increase in chlorophyll due to photoadaptation (Bienfang et al. 1983) rather than a maximum in phytoplankton biomass. Particulate silicon increased steadily with depth to 1.5 µM at 100 m (Fig. 2D). The content of particulate silicon was low compared to the amount of dissolved silicic acid depleted between 45 and 75 m. We therefore conclude that the majority of diatoms, which we suggest are responsible for this depletion, had already sedimented out from the investigated part of the water column. Species-specific differences in sinking rate (Malone et al. 1983) or seeding of resting stages

(Smetacek 1985) are possible mechanisms behind such a sink-out.

Massive reduction of the silicic acid content below the nitracline is not an isolated phenomenon, but has been observed regularly over extensive areas of the Barents Sea. Fig. 3 shows isopleth diagrams of silicic acid concentrations in summer along a north-south section in the central Barents Sea (Fig. 1). Isolines for 1 and 8 µM nitrate are shown superimposed on these isopleths. The June 1983 section extended 130 km into ice-covered waters where a pre-bloom plankton situation occurred. Silicic acid (about 4 µM) and nitrate (about 8 µM) occurred here in the typical 1:2 molar ratio (Ellertsen et al. 1982, Sakshaug & Holm-Hansen 1984). South of 77° N, however, nutrients were virtually depleted from the surface layer and silicic acid concentrations at the depth of 8 µM NO_3 were from 1 to 3 µM (Fig. 3A). Similarly, low silicic acid concentrations were found at the 8 µM nitrate depth in June 1984 both along the central section (Fig. 3B) and a section along 45° E. A plot of silicic acid vs nitrate concentrations for sampling depths of 50 m and deeper from this eastern section reveals that the majority of samples from all
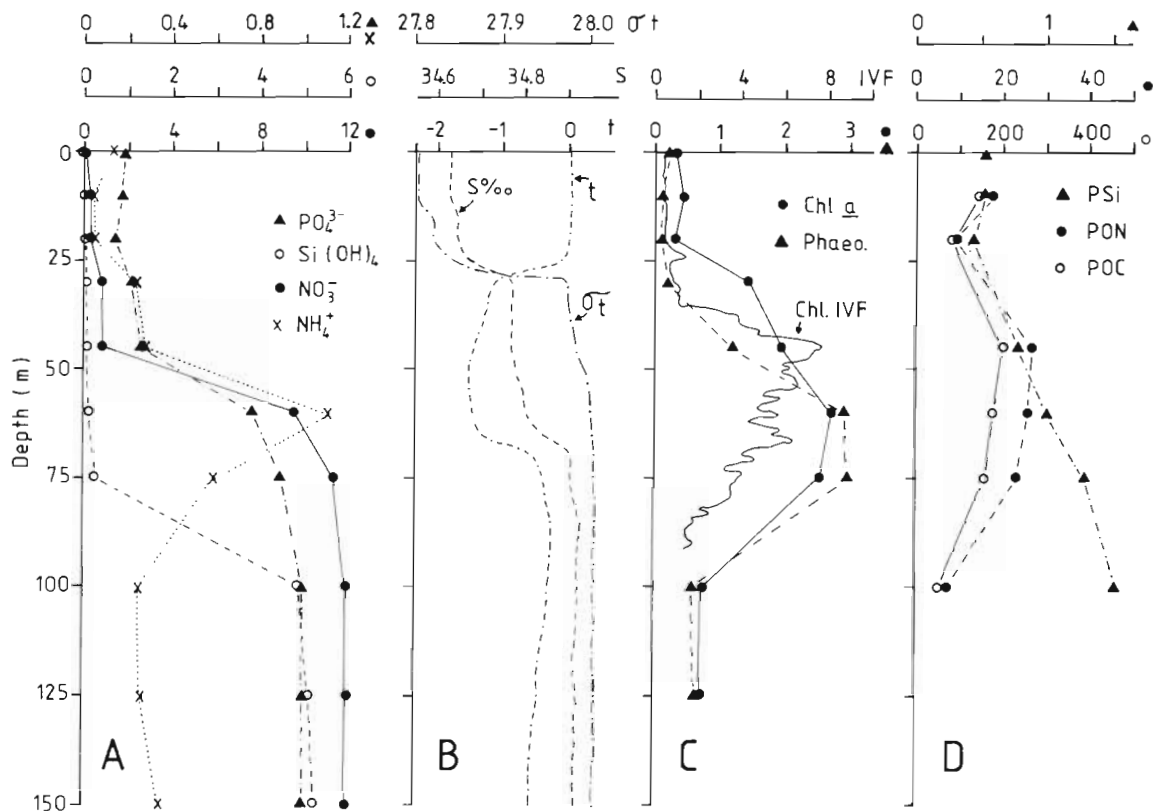

Fig. 2. Vertical structure of physical, chemical and biological properties of the water column at a station sampled at a late phase of the spring bloom in the Barents Sea (75° 20′ N, 36° 00′ E; R/V G. O. Sars, Stn 713; 7 Jun 1984). (A) Concentrations of nitrate, phosphate, silicic acid and ammonium (µM). (B) Temperature (°C), salinity (‰) and water density (σ_t). (C) Chlorophyll a, phaeopigments (mg m⁻³), and chlorophyll in vivo fluorescence measured in situ (IVF; relative units). (D) Particulate organic carbon (POC), organic nitrogen (PON) (mg m⁻³) and biogenic silicon (PSi) (µM)

stations north of 74°30′ N were poor in silicic acid relative to nitrate (Fig. 4).

Positioning of the silicic acid gradient deeper than the nitracline has been reported for only a few other environments, e.g. a land-locked fjord in Norway (Skjoldal & Wassmann 1986) and subtropical water off Hawaii (Bienfang et al. 1984). For the world oceans there seems to be great variation with respect to nitrate
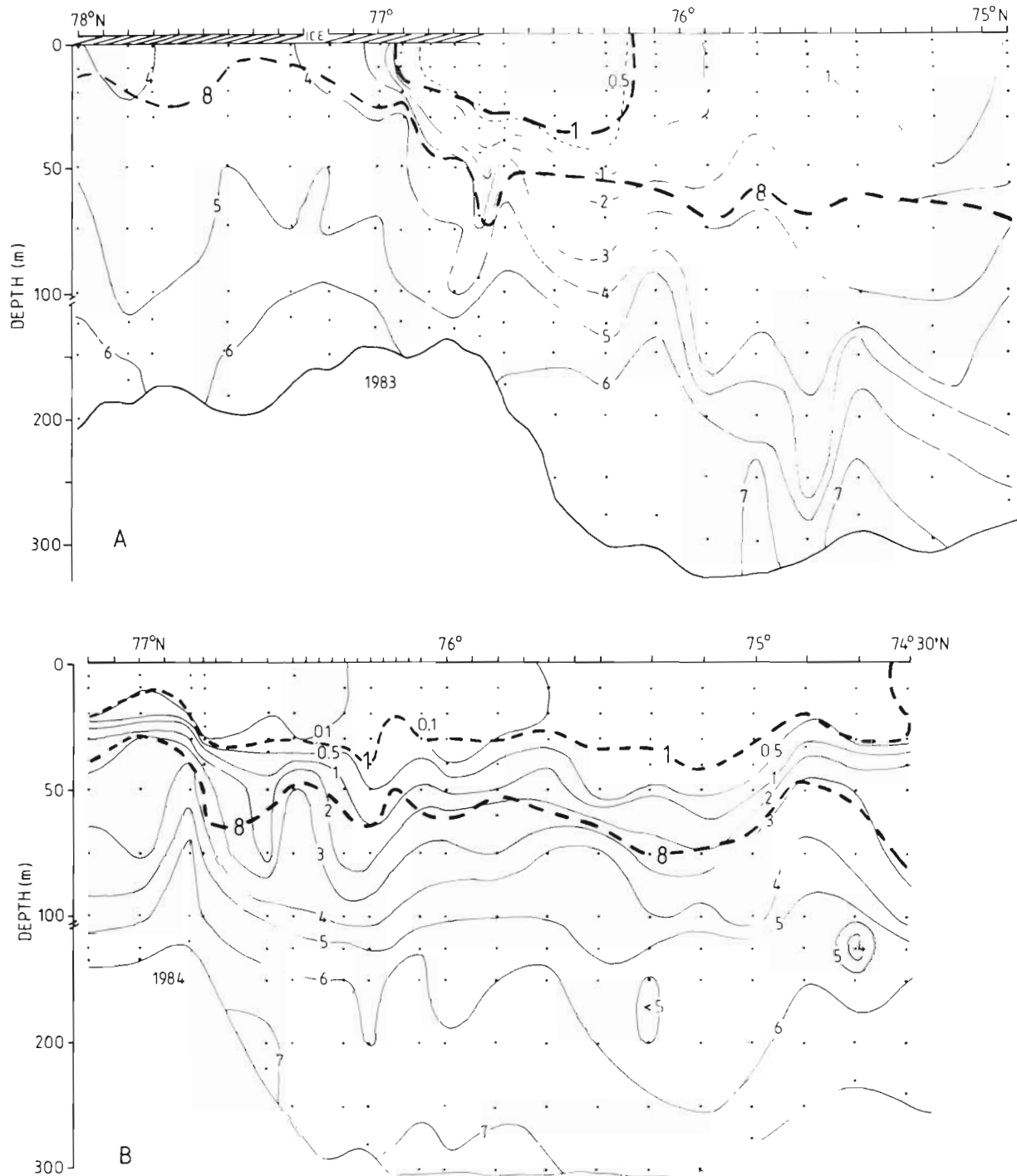

Fig. 3. Isopleth diagrams of the distribution of silicic acid along a section in the central Barents Sea. Superimposed are the 1 µM and 8 µM isolines for nitrate (thick, broken lines). (A) Section extending from 75°00′ N, 31°50′ E to 78°04′ N, 34°26′ E, covered on 4 to 8 Jun 1983 during cruise with M/S *Lance*. (B) Section extending from 74°30′ N, 31°29′ E to 77°10′ N, 33°29′ E, covered on 3 to 6 Jun 1984 during cruise with R/V *G. O. Sars*

vs silicic acid depletion, certain regions being charac-
terized by nitrate excess and others by silicic acid
excess (Kamykowski & Zentara 1985).

Nitrogen recycling can influence the phytoplankton
consumption ratio of nitrate to silicic acid (Kamy-
kowski & Zentara 1985). Utilization of recycled
ammonium in the absence of any substantial
remineralization of Si may have contributed to the
discrepancy in the silicic acid vs nitrate depletion
relation below the nitracline. The elevated ammonium
concentrations in this depth interval (Fig. 2A) suggest
that nitrogen remineralization occurred. We consider,
however, that any such influence was of limited mag-
nitude. Concentrations of nitrate and silicic acid below
their respective gradients were typical for winter nu-
trient levels (Hassel et al. 1986). Spring bloom
development in melt-water regions is a fairly rapid
process (Rey & Loeng 1985, Slagstad 1985), as is also
generally the sedimentation of spring diatom blooms
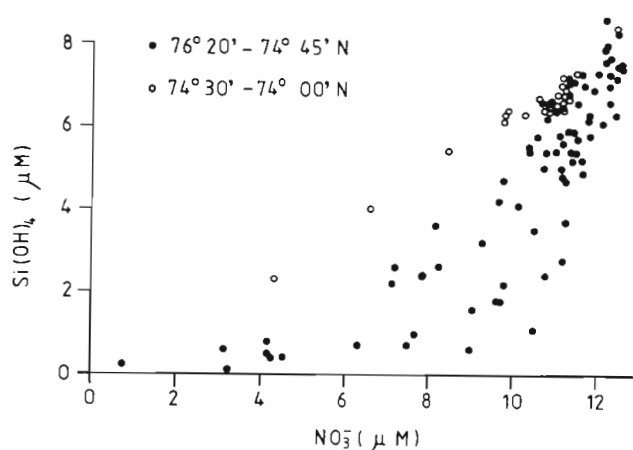following nutrient depletion (Smetacek 1984, 1985).

Fig. 4. Relation between concentrations of silicic acid and
nitrate in samples from 50 m and deeper at stations from a
section extending from 74°00′N to 76°20′N along 45°E,
covered on 10 to 12 Jun 1984 with R/V *G. O. Sars*

Substantial reutilization of remineralized N in the
deeper part of the euphotic zone towards the end of the
bloom is therefore unlikely (cf. Lännergren & Skjoldal
1976, Pomeroy & Deibel 1986).

Horizontal advection is another factor that can influ-
ence the pattern of vertical nutrient distributions by
disrupting the vertical continuity of properties and
processes. The uniform pattern of vertical distributions
of nitrate and silicic acid over vast areas of the Barents
Sea (Fig. 3) suggests, however, that advection did not
play a major role in this respect.

The diatom *Chaetoceros socialis,* which together
with the colony-forming flagellate *Phaeocystis
pouchetii* is usually the dominant component of the
ice-edge bloom (Rey & Loeng 1985), occurred at 1 to 4
$\times$ 10^6 cells l^{-1} from 45 to 100 m at Stn 713 (Table 1).
There was a dramatic increase in the proportion of
resting spores of *C. socialis* (as identified by light
microscopy), from none at 60 m to 100 % at 100 m. It
appears therefore that formation of resting spores took
place at the top of the silicic acid gradient (Fig. 2A) and
that these spores subsequently sedimented out. Spores
of *C. socialis* have been shown to sink about 5 times as
fast as vegetative cells (Bienfang 1981) and their for-
mation seems to be triggered by nutrient limitation
(Davis et al. 1980).

Uptake of silicic acid in diatoms is usually a rapid
process, restricted to the stage in the cell cycle where
cell division occurs (Darley 1974, Paasche 1980, Sulli-
van & Volcani 1981). More than 90 % of the silicic acid
taken up is immediately deposited at the cell walls, the
rest being probably accumulated for use in metabolic
processes (Paasche 1980, Sullivan & Volcani 1981).
The silicification process requires little energy com-
pared to total cellular energy needs (Raven 1983).

Much of the phytoplankton biomass in the late
bloom situation was found below the euphotic zone
(1 % light level at about 50 m) (Fig. 2C). The algae
were apparently adapted to low light levels, as indi-

Table 1. Cell numbers of dominant species, light-saturated rate of photosynthesis, and chemical ratios for phytoplankton and
seston in and below the euphotic zone at Stn 713 (see Fig. 2)

Variable	Depth				
	10 m	45 m	60 m	75 m	100 m
Phaeocystis pouchetii (cells l^{-1})	4.0×10^4	3.9×10^6	4.1×10^6	2.9×10^6	1.2×10^5
Chaetoceros socialis (cells l^{-1})	5.1×10^4	1.1×10^6	2.0×10^6	3.7×10^6	8.3×10^5
C. socialis, resting spores (%)	78	2	0	76	100
C assimilation (µg C l^{-1} h^{-1})	0.42	0.96	1.46	3.97	–
Assimilation number (µg C [µg Chl a]$^{-1}$ h^{-1})	0.98	0.56	0.54	1.58	–
Chl a/C (w/w)	0.0032	0.0087	0.0155	0.0161	0.0135
N/C (atomic ratio)	0.112	0.115	0.127	0.127	0.118
N/P (atomic ratio)	23.3	29.1	21.8	28.6	16.7
Si/C (atomic ratio)	0.047	0.047	0.069	0.096	0.338

cated by high chlorophyll *a*/C ratios at 60 and 75 m (Table 1). The phytoplankton at 75 m, with a high proportion of *Chaetoceros socialis* resting spores, showed higher capacity for light-saturated photosynthesis than the phytoplankton higher up in the water column (Table 1). The N/C and N/P atomic ratios of the particulate material showed little variation with depth, whereas the Si/C ratio increased with depth below 45 m (Table 1). This reflected the increasing dominance of *C. socialis* with depth, but probably also a higher silicon content per cell. Thus the Si/C ratio at 100 m (0.34) falls in the upper range of values reported for marine diatoms (Brzezinski 1985).

These results indicate that heavily silicified resting spores can have an important role in the life cycle and survival strategy of at least one centric diatom species in the Barents Sea. Resting spores appear to be specialized to persist in darkness or low light, and show high photosynthetic ability coupled with low rates of respiration (Hargraves & French 1983).

The fact that *Chaetoceros socialis,* a small diatom of about 7 to 8 µm in diameter, seems to be the main species responsible for the depletion of silicic acid in the Barents Sea is important in the light of other investigations which have shown small *Chaetoceros* species growing at very low silicic acid concentrations (Hargraves & French 1983). Silicic acid deprivation has been found to elicit the greatest sinking response in diatom populations (Bienfang et al. 1982, Bienfang & Harrison 1984), and it has been suggested that silica can act as a sinking device, its effect being relatively greater in small cells with their inherently slower sinking speeds (Walsby & Reynolds 1980). The apparently high consumption of silicic acid below the euphotic zone and the formation of resting spores are probably integrated parts of a survival strategy for *C. socialis.* It is interesting to note that the majority of the dominant diatom species in the Barents Sea are of the resting-spore-forming type. On the other hand, the typical forms with resting cells, such as *Skeletonema costatum,* are seldom found.

The marked consumption of silicic acid below the euphotic zone has consequences for the further development of phytoplankton during the summer. Melt-water and warming of the surface layer lead to a fairly stable upper water column over vast areas of the northern Barents Sea (Rey & Loeng 1985). The positioning of the silicic acid gradient well below the nitracline will inevitably result in proportionally less upwards transport of silicic acid than of nitrate and phosphate into the lower part of the euphotic zone by mixing processes. This will disfavour the growth of diatoms during the summer season.

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