

Vertical flux of phytoplankton and particulate biogenic matter in the marginal ice zone of the Barents Sea in May 1993

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ABSTRACT: Hydrography, nutrients, chlorophyll *a* (chl *a*), phaeopigments (phaeo) and phytoplankton abundance as well as the vertical flux of particulate organic carbon and nitrogen (POC and PON) and pigments in the upper 200 m were investigated at 4 stations along a north-south transect in the Barents Sea in May 1993. Two stations were located in Arctic water and 2 in Atlantic water. The northernmost station had a well-developed ice edge bloom with high abundance of *Fragilariopsis* sp., *Thalassiosira* spp. and *Chaetoceros* spp. The phytoplankton community at the ice edge and the northernmost Atlantic station was dominated by *Phaeocystis* sp. colonies in concert with *Chaetoceros* spp. and *Thalassiosira* spp. The phytoplankton community at the southernmost station was dominated by large *Chaetoceros* spp. cells. Vertical flux of biogenic matter in the upper water column (20–100 m) varied along the transect (2.1–13.3 mg chl *a* m⁻² d⁻¹, 0.6–11 mg phaeo m⁻² d⁻¹ and 409–1090 mg POC m⁻² d⁻¹), while vertical flux in the deeper water column (100–200 m) was less variable (0.7–2.9 mg chl *a* m⁻² d⁻¹, 1.5–6.5 mg phaeo m⁻² d⁻¹ and 200–300 mg POC m⁻² d⁻¹). Hydrographic conditions, nutrient status and species specific sinking rates did not have a profound influence on the vertical flux of phytoplankton. High daily loss rates of chl *a* (4 to 18 % d⁻¹ of standing stock chl *a*) and microplankton at 2 stations (southernmost and northernmost Atlantic) was probably caused by high production of extracellular carbon, increasing the aggregation potential of the phytoplankton community. Evidence of incomplete dissolution of *Phaeocystis* sp. colonies was observed to a depth of 200 m. Faecal matter and detritus were the main vehicles for the vertical export of organic matter to deeper water (below 100 m). Protozoan grazing was more important in retaining organic matter and nutrients in the upper water than mesozooplankton grazing.

KEY WORDS: Vertical flux · Phytoplankton · Spring bloom · Barents Sea

INTRODUCTION

Spatial and temporal patterns in the vertical flux of biogenic matter are central to the understanding of elemental dynamics and food-webs in the ocean (Smetacek et al. 1984, Legendre 1990, Wassmann 1991a). The dynamics of vertical flux of biogenic matter, and to a lesser extent the composition of exported matter, was investigated in the Barents Sea during the period 1984–1989 (Wassmann 1989, Wassmann et al. 1990, 1994, Wassmann & Slagstad 1993). The studies were part of the extensive oceanographic investigations carried out in the Barents Sea by the Norwegian

Research Programme for Marine Arctic Ecology (PRO MARE) (e.g. Sakshaug et al. 1991).

Previous studies of vertical flux in the Barents Sea had low vertical resolution and were only to a limited degree conducted in concert with studies of pelagic processes. Our knowledge of the relative contribution of algal groups to the vertical export of carbon and of the environmental and biological factors that control their abundance is therefore limited, in particular in the marginal ice zone (MIZ). Studies of vertical flux from the ice-covered waters east and north off Spitsbergen are even more scarce (Andreassen et al. 1996). Therefore, based on current knowledge, a field program to study phytoplankton abundance and vertical export of biogenic matter from the upper layers of the MIZ and the central Barents Sea was carried out in concert with

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studies of other pelagic processes (Hansen et al. 1996, Urban-Rich 1997, Vernet et al. 1998, Wassmann et al. 1998). A section ranging from 72° 30' N to 80° N in the central Barents Sea was emphasised in earlier studies (e.g. Skjoldal et al. 1987, Wassmann & Slagstad 1993) and the same section was chosen for this study. The transect crosses the zonal structure of the Barents Sea and its main water masses: Atlantic water, the Polar Front, the ice edge and Arctic water.

The Barents Sea is characterised by a complex hydrography with large regional differences in hydrographic conditions and ice coverage (Rey & Loeng 1985, Loeng 1991). The environment is highly dynamic both on a seasonal and interannual scale (Wassmann et al. 1996) and physical processes strongly influence the pelagic community both in terms of production and species composition. The magnitude of the vertical flux is determined by new production, phytoplankton bloom development and species composition as well as the impact of planktonic heterotrophs on algae. The physical oceanography may hence influence the dynamics of the vertical flux in the Barents Sea indirectly through its impact on ice coverage, ice melt, stabilisation, and through over-wintering, advection and retention of zooplankton (Wassmann et al. 1996).

The spring bloom in the MIZ of the Barents Sea usually starts in April/May, when the ice begins to retreat (Rey & Loeng 1985). Normally, the bloom takes place earlier and develops more rapidly in the MIZ than in the central Barents Sea, which is dominated by Atlantic water. Bloom development in the central part of Barents Sea usually takes place in May/June. Phytoplankton growth starts earlier, but stabilisation of the water column by solar radiation is slow, and hence the increase in phytoplankton biomass is correspondingly delayed (Rey & Loeng 1985).

Lack of a strong grazing impact by herbivorous mesozooplankton during spring in the Barents Sea gave rise to the hypothesis that extensive sedimentation of ungrazed phytoplankton and phytodetritus may take place at the end of the spring bloom (Eilertsen et al. 1989, Wassmann et al. 1990, Wassmann & Slagstad 1993). An increase in herbivorous mesozooplankton standing stock, due to advection of copepodites from the Norwegian Sea (Pedersen et al. 1995), is believed to reduce the pulse of spring sedimentation, compared to years with less herbivores (Wassmann & Slagstad 1993). Macrozooplankton such as euphausiids are important in the Barents Sea (Dalpadado & Skjoldal 1991), but little is known of their impact on the phytoplankton dynamics in the area. Recently, microzooplankton grazing has also been shown to be important and may exceed the grazing pressure of copepods during spring in the central and northern Barents Sea (Hansen et al. 1996).

A detailed description of hydrography, nutrient concentrations and phytoplankton community along the transect about 1 wk prior to this study is presented in (Wassmann et al. 1998). Primary production, grazing, faecal pellet production and faecal pellet vertical flux investigated parallel to this study are presented elsewhere (Hansen et al. 1996, Urban-Rich 1997, Vernet et al. 1998). Here we present information on the hydrography, nutrients, phytoplankton community and vertical flux of biogenic matter and microplankton at 4 stations in the northern and central Barents Sea. The intention of this investigation is to increase knowledge about the relative contribution of algal groups to the vertical export of carbon and to address possibly important processes in the regulation of vertical flux of phytoplankton and biogenic matter in the Barents Sea.

MATERIAL AND METHODS

Data were collected during a cruise to the Barents Sea onboard RV 'Jan Mayen' during spring 1993. The sampling period was May 19–26; data was collected while returning southward along a transect in the central Barents Sea (described by Wassmann et al. 1998). The sampling area was from 76° 22' N, 32° 44' E to 73° 40' N, 30° 35' E (Fig. 1).

Vertical flux data were collected using drifting sediment traps. In ice-covered areas it was necessary to anchor the drifter to ice floes to prevent the surface buoy from submerging under the ice during the drift. Free drifting sediment traps are convenient tools for short studies (1 to 2 d) of vertical flux since they are easily deployed and allow to some extent tracking of water masses. Turbulence around the opening of the trap due to strong currents may severely bias the estimation of both quality and quantity of settling matter. This problem is reduced when sediment traps are allowed to drift (Staresinic et al. 1978, GOFs 1989, Bloesch 1997). However, ice drift and surface currents may have different directions than deeper water currents. Sampling of vertical flux at all stations may thus be biased by current shear.

Sediment traps were deployed at 4 stations along the transect (Table 1). Vertical flux of particulate organic material was collected with 9 sediment traps between 20 and 100 m and 5 sediment traps every 20 m between 100 and 200 m. The sediment traps (KC maskiner og laboratorieudstyr, Denmark) were parallel cylinders mounted in a gimbaled frame equipped with a vane to ensure that the cylinders were always positioned vertically and never shaded each other. The traps were 0.072 m in diameter and 0.45 m high (H/D ratio = 6.25). The traps were deployed for 36 to 38 h.

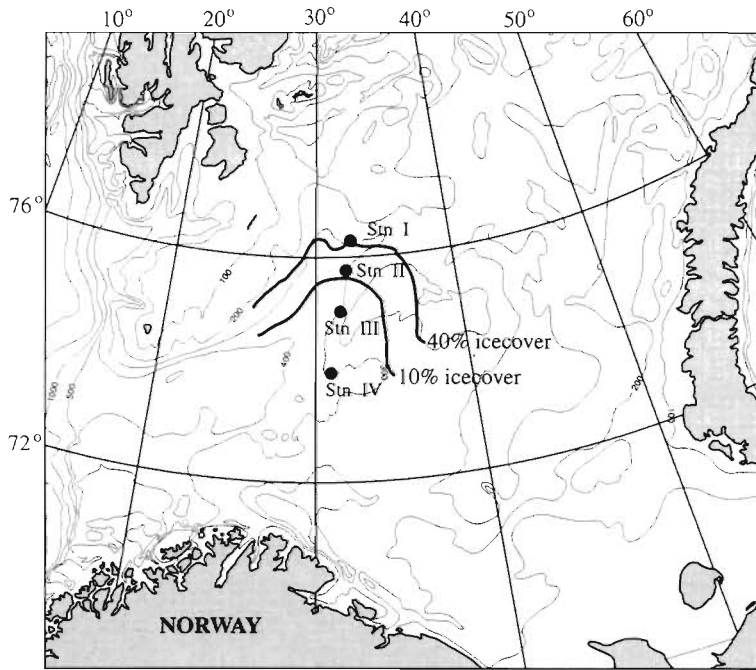


Fig. 1. Map of the sampling area in the Barents Sea with positions of stations and ice coverage in the area

Poison was not applied and, therefore, grazing and bacterial decomposition could have taken place in the sediment traps during the deployment.

While following the drifter, CTD profiles and samples for pigment analysis were taken every 6 h. Hydrographic profiles were obtained by means of a Neil Brown Mk III CTD profiler mounted together with a SeaTech fluorometer, and a General Oceanic Rosette Sampler equipped with 5 l Niskin bottles. Samples for nutrients, chlorophyll *a* (chl *a*) and phaeopigments (phaeo) and microscopic examination of phytoplankton were taken at selected depths based on irradiance (50, 30, 10, 1 and 0.1% surface irradiance) and the structure of other physical or biological parameters of the water column (e.g. fluorescence maximum or stratification). Samples for chl *a* and phaeo were filtered on precombusted Whatman GF/F filters. Samples for microscopic examination were fixed with an ethanol-glutaraldehyde-Lugol solution (Rousseau et al. 1990)

Table 1. Date of deployment and positions of deployment and recovery of drifting sediment traps in May 1993 in the Barents Sea

Stn	Date	Deployment	Recovery
I	May 19	32°44'E, 76°22'N	31°26'E, 76°20'N
II	May 21	32°30'E, 75°58'N	31°58'E, 75°53'N
III	May 23	31°42'E, 74°58'N	31°31'E, 75°04'N
IV	May 25	31°00'E, 73°44'N	30°35'E, 73°40'N

especially designed to preserve *Phaeocystis* sp. colonies. Samples for nitrate, silicate and phosphate were handled and analysed by a Technicon autoanalyser as described by Wassmann (1991b) at the Institute of Marine Research, Bergen, Norway.

After recovery, contents of the sediment traps were transferred to bottles and kept cold and dark. Samples were never kept more than 6 h before subsampling. Each sample was thoroughly mixed and a bird pipette was used for subsampling. Duplicate samples (200 to 300 ml) from each cylinder were taken and filtered for analysis of particulate organic carbon and nitrogen (POC and PON), chl *a* and phaeo on precombusted Whatman GF/F filters. On all filters, swimmers were removed by means of forceps. Samples for microscopic examination were taken from the traps deployed at 60, 100 and 200 m.

Samples for chl *a* and phaeo were analysed immediately after subsampling using a Turner Design AU-10 fluorometer according to Holm-Hansen et al. (1965).

POC and PON samples were stored in a freezer (−18°C) and were later analysed on a Leeman Lab CEC 440 CHN analyser after removal of carbonate with fumes of concentrated HCl.

Aliquots of 10 ml for sediment trap samples and 25 ml for water samples were allowed to settle for 24 h, before examination in a Leitz DM IL inverted microscope. A minimum of 50 to 100 cells of the dominant phytoplankton species or groups in the samples were counted. When one or a few species dominated the sample, cells were quantified at a species level, but most cells were counted in classes at higher taxonomic levels. Average cell size of each group was measured to calculate the carbon content of the cells (PPC), according to Strathmann (1967). The carbon content of colonial *Phaeocystis* sp. was calculated in 2 steps. The carbon content of the colonial matrix was calculated according to Rousseau et al. (1990). Carbon content of the cells in the colonies was calculated by using average cell numbers for different size classes of colonies (estimated by counting colonial cells in 10 colonies from each size class). Diatoms are presented in groups of families, other groups at a class or subclass level. It was not always possible to distinguish between autotrophic and heterotrophic dinoflagellates and flagellates, which implies that groups of autotrophic dinoflagellates and flagellates also included heterotrophic cells.

Daily loss rates (%) were calculated using integrated concentrations of chl *a* from 0 to 30 m and 0 to 60 m

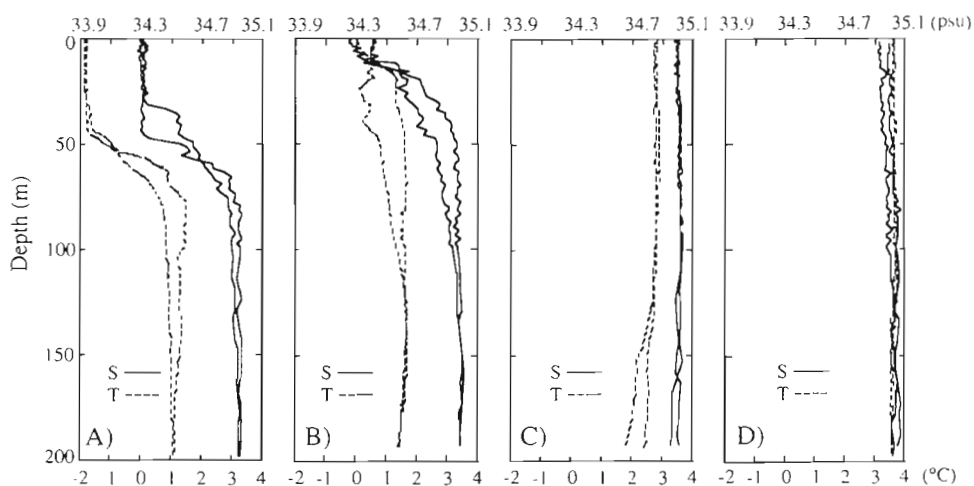


Fig. 2. Vertical profiles of temperature (T) and salinity (S) at the time of deployment and recovery of sediment traps at (A) Stn I, (B) Stn II, (C) Stn III, (D) Stn IV

(averages based on 4 to 6 profiles taken during drift) and PPC from 0 to 60 m divided by the vertical fluxes of chl *a* at 30 and 60 m depth and PPC at 60 m.

RESULTS

Ice coverage and hydrography

Stns I and II were located in the MIZ close to the Polar Front. Stn I had 40 to 60 % ice coverage (Fig. 1) and the surface water was characterised by fresh and cold Arctic water (34.32 psu and $<-1.7^{\circ}\text{C}$) down to 40–50 m (Fig. 2A). Below 50 m warmer and more saline water (34.60 to 34.95 psu and 1 to 1.5°C) of probable Atlantic origin dominated. The depth of the halocline varied during the time of drift. Stn II had ~40% ice coverage (Fig. 1) at the time when the sediment trap was deployed, but the ice coverage was reduced during the time of deployment to ~20%. The surface water at Stn II was characterised by warmer water (0 to 1.5°C) with a similar salinity (34.33 psu) as Stn I (Fig. 2B). The upper layer was thinner (20 to 40 m) than at Stn I. Profiles of salinity and temperature changed during the period of drift. The upper 10 to 15 m became more homogeneous and the water below the pycnocline showed a decrease in temperature and salinity during this period, indicating vertical mixing.

Stns III and IV were not influenced by sea ice and were dominated by Atlantic water (2.5 to 3°C and ~35 psu). The water column of the 2 stations did not have any distinct stratification, but both stations had a slight increase of density from surface to 100 m (Fig. 2C, D). While there was no significant change in the temperature and salinity during the drift at Stn III, a slight increase of salinity during the drift at Stn IV was recorded (Fig. 2D).

Nutrients and pigments

The lowest nutrient concentrations during this investigation were found in the upper 40 m at Stn I (Fig. 3B). The concentration of $\text{Si}(\text{OH})_4$ was close to detection limit ($\sim 0.1\ \mu\text{M}$), while nitrate and phosphate concentrations were higher ($>2\ \mu\text{M}\ \text{NO}_3$ and $>0.3\ \mu\text{M}\ \text{PO}_4$). Below the pycnocline nutrients were close to winter concentrations (about 10, 5 and $0.8\ \mu\text{M}$ of NO_3 , $\text{Si}(\text{OH})_4$ and PO_4 , respectively). High concentrations of chl *a* (12.6 to $14.6\ \text{mg m}^{-3}$) were also observed in the upper 40 to 50 m at Stn I (Fig. 3C). Stn II had much lower chl *a* concentrations and a sub-surface maximum (2.7 to $3.3\ \text{mg m}^{-3}$) at the depth of the pycnocline (Fig. 4A, C) was observed. Nutrient concentrations at Stn II [data from the start of the drift: $>4\ \mu\text{M}\ \text{NO}_3$ and $>2.6\ \mu\text{M}\ \text{Si}(\text{OH})_4$; Fig. 4B] were higher in the upper water column compared to Stn I, but nutrient concentrations were reduced during the drift [2 to $3\ \mu\text{M}\ \text{NO}_3$ and 0.8 to $2.1\ \mu\text{M}\ \text{Si}(\text{OH})_4$]. Nutrient concentrations below the pycnocline at Stn II (35 to 45 m) were also reduced compared to winter values (Fig. 4B). The highest nutrient concentrations in the upper water column during this investigation were observed at Stn III [$>6\ \mu\text{M}\ \text{NO}_3$ and $>3\ \mu\text{M}\ \text{Si}(\text{OH})_4$; Fig. 5B]. Stn IV had lower nutrient concentrations [3.8 to $6\ \mu\text{M}\ \text{NO}_3$ and 0.9 to $1.4\ \mu\text{M}\ \text{Si}(\text{OH})_4$; Fig. 6B]. The chl *a* profiles showed modest concentrations (1.1 to $2.4\ \text{mg m}^{-3}$) above 50 m at both Stns III and IV (Figs. 5C & 6C).

Suspended phytoplankton

The phytoplankton community of Stn I (Fig. 7A) was characterised by high abundance of pennate ribbon-forming species (*Fragilariopsis* sp. and *Navicula* spp., total: 3×10^5 to 1.1×10^6 cells l^{-1}) and colony-forming

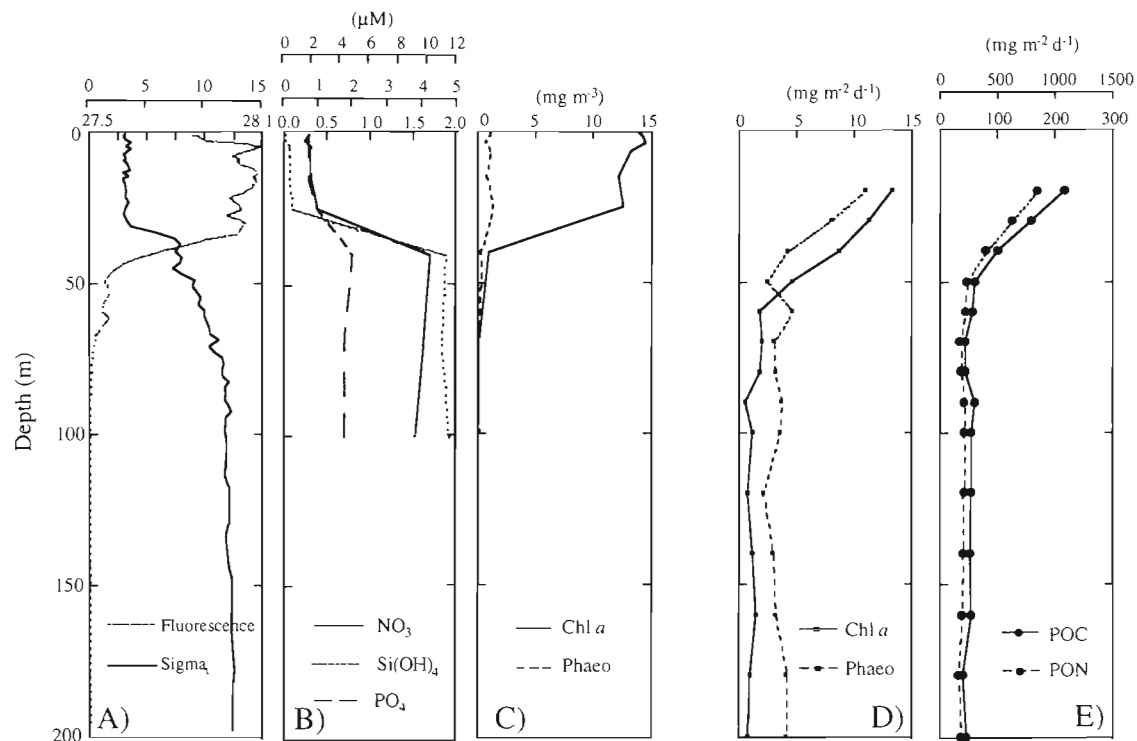


Fig. 3. Profiles from Stn I of (A) fluorescence (upper axis) and sigma-t (lower axis); (B) nutrient concentrations of NO_3 (upper axis), Si(OH)_4 (middle axis) and PO_4 (lower axis); (C) suspended chl *a* and phaeopigment; (D) vertical flux of chl *a* and phaeopigment and (E) vertical flux of POC (upper axis) and PON (lower axis). Profiles in A to C are representative of average conditions

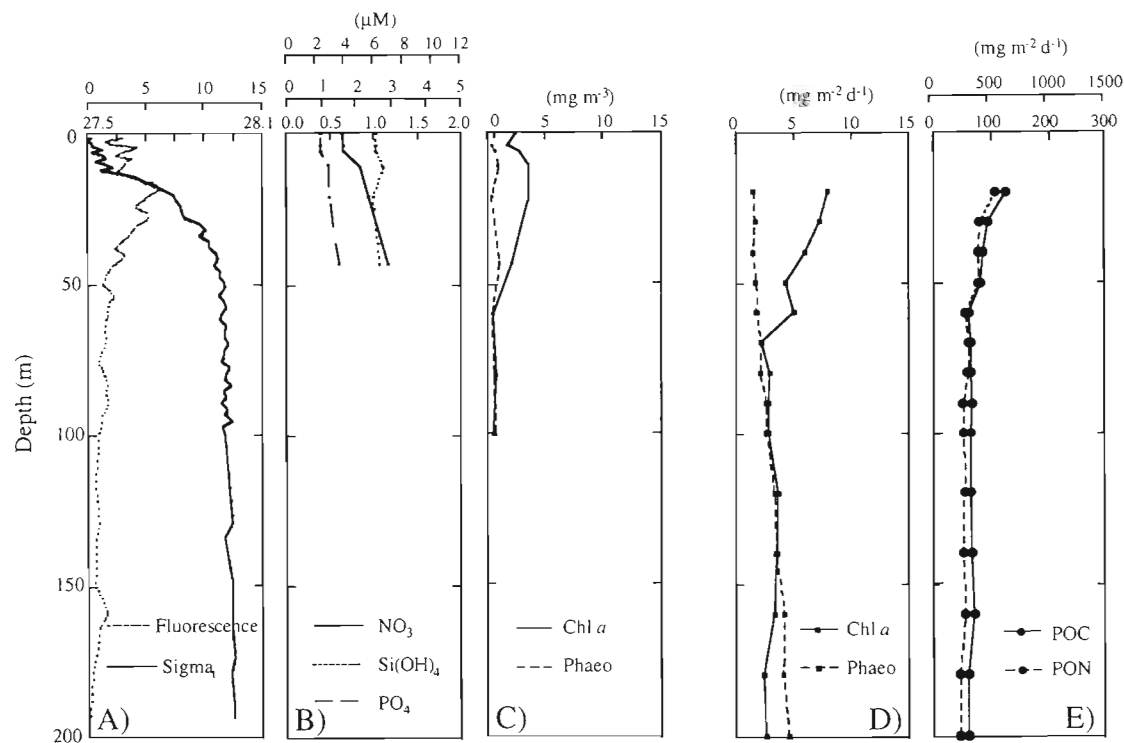


Fig. 4. Profiles from Stn II of (A) fluorescence (upper axis) and sigma-t (lower axis); (B) nutrient concentrations of NO_3 (upper axis), Si(OH)_4 (middle axis) and PO_4 (lower axis); (C) suspended chl *a* and phaeopigment; (D) vertical flux of chl *a* and phaeopigment and (E) vertical flux of POC (upper axis) and PON (lower axis). Profiles in A to C are representative of average conditions

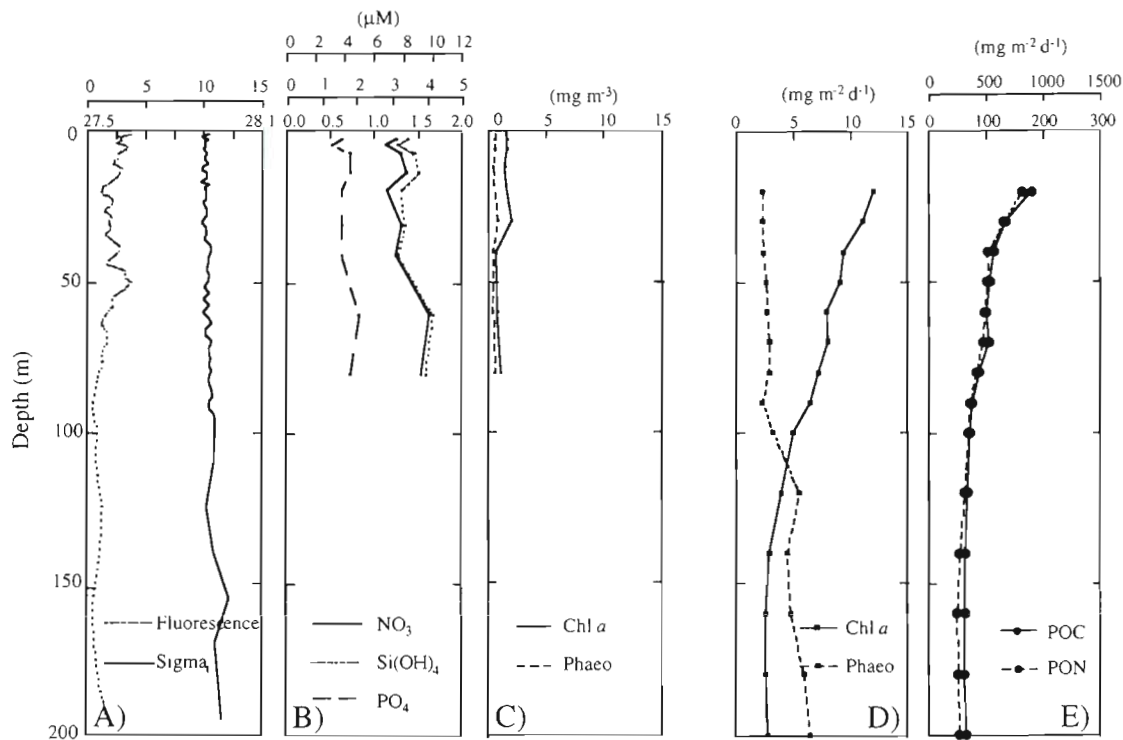


Fig. 5. Profiles from Stn III of (A) fluorescence (upper axis) and sigma-t (lower axis); (B) nutrient concentrations of NO_3 (upper axis), Si(OH)_4 (middle axis) and PO_4 (lower axis); (C) suspended chl *a* and phaeopigment; (D) vertical flux of chl *a* and phaeopigments and (E) vertical flux of POC (upper axis) and PON (lower axis). Profiles in A to C are representative of average conditions

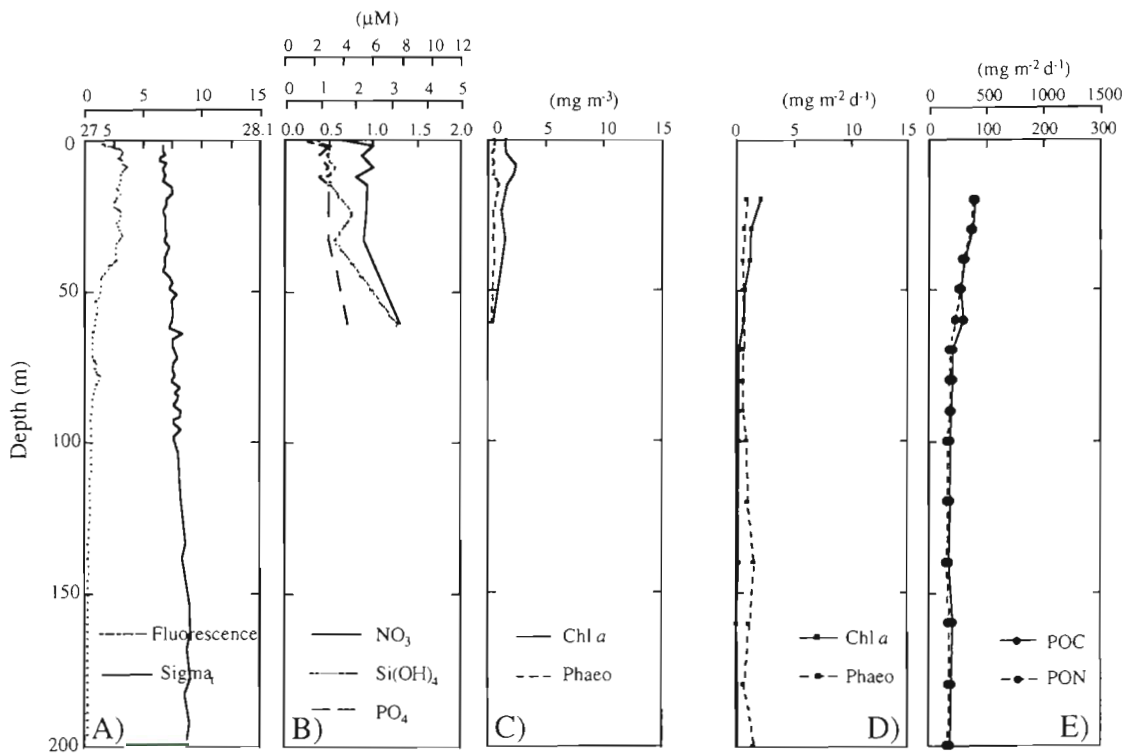


Fig. 6. Profiles from Stn IV of (A) fluorescence (upper axis) and sigma-t (lower axis); (B) nutrient concentrations of NO_3 (upper axis), Si(OH)_4 (middle axis) and PO_4 (lower axis); (C) suspended chl *a* and phaeopigment; (D) vertical flux of chl *a* and phaeopigments and (E) vertical flux of POC (upper axis) and PON (lower axis). Profiles in A to C are representative of average conditions

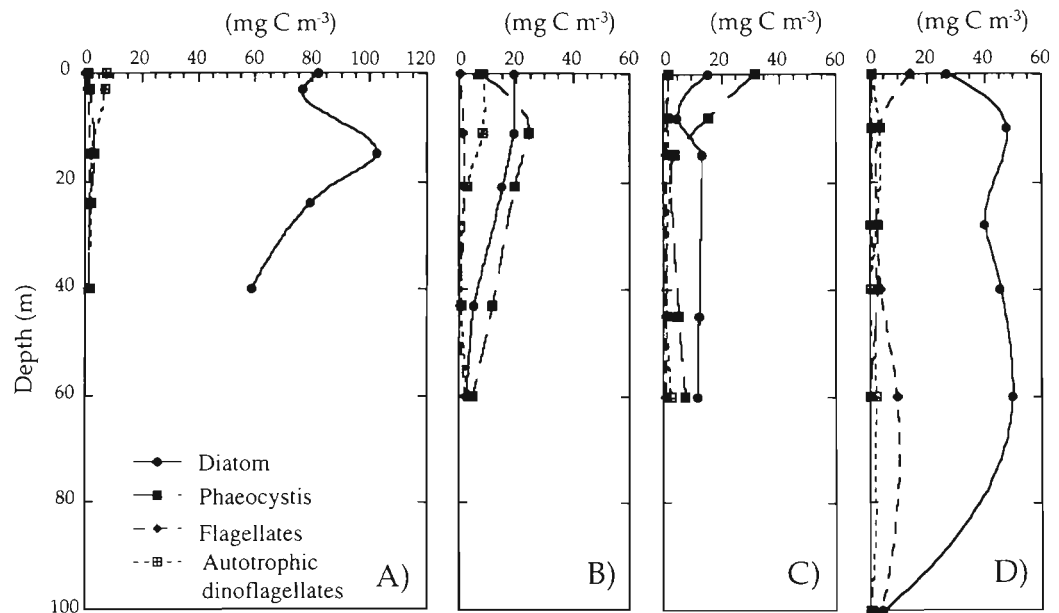


Fig. 7 Distribution of microplankton carbon at (A) Stn I, (B) Stn II, (C) Stn III, (D) Stn IV

centric diatoms (*Chaetoceros* spp. and *Thalassiosira* spp., total: $>4.2 \times 10^6$ cells l^{-1}). Only a few *Phaeocystis* sp. colonies were observed, equivalent to $<3\%$ of total PPC. Except for the surface water, *Phaeocystis* sp. ($\sim 4.3 \times 10^4$ colonies l^{-1}) dominated the water column at Stn II (Fig. 7B) and made up 38 to 67% of the PPC below 10 m. *Chaetoceros* spp. and *Thalassiosira* spp. were the dominant diatoms (total cell numbers: 1.5 to 2.0×10^6 cells l^{-1}) above 20 m at Stn II. At Stn III (Fig. 7C) the PPC maximum was found in the upper water column (0 to 8 m depth). *Phaeocystis* sp. colonies (1.2 to 2.9×10^3 colonies l^{-1}) provided $>60\%$ of PPC. Below 8 m, *Thalassiosira* spp. became the dominant phytoplankton group in terms of biomass at Stn III. The phytoplankton at Stn IV (Fig. 7D) was dominated by *Chaetoceros* spp. both in numbers (2.0 to 2.5×10^5 cells l^{-1}) and biomass. The phytoplankton concentration was nearly uniform throughout the water column down to 60 m, and a decline in phytoplankton concentration was recorded between 60 and 100 m depth. Only a few *Phaeocystis* sp. colonies were found in the water column ($<4.0 \times 10^2$ colonies l^{-1}).

Vertical flux of particulate biogenic matter

For all stations, the vertical flux of POC, PON and chl *a* was highest in the upper water column; this vertical flux decreased with increasing depth in the upper water column (D & E of Figs. 3 to 6). The main decrease in the POC, PON and chl *a* vertical flux at Stn I was in the water column above 60 m and at Stns II and IV above 70 m. The vertical flux of POC, PON and chl *a* at Stn III decreased steadily from 20 to 140 m depth.

Below these depths there was no significant decrease or increase in the vertical flux of POC, PON and chl *a*.

The vertical flux of chl *a* was highest in the upper water column at Stns I and III (13.3 and 12 mg chl *a* $m^{-2} d^{-1}$, respectively, at 20 m; Figs. 3D & 5D). Stn II had slightly lower chl *a* vertical flux (8 mg chl *a* $m^{-2} d^{-1}$ at 20 m; Fig. 4D) and the lowest flux of chl *a* was found at Stn IV (2.1 mg chl *a* $m^{-2} d^{-1}$ at 20 m; Fig. 6D). Vertical flux of POC was 1090 and 880 mg C $m^{-2} d^{-1}$ at 20 m, respectively, at Stns I and III (Figs. 3E & 5E), 620 mg $m^{-2} d^{-1}$ at Stn II at 20 m (Fig. 4E) and 410 mg C $m^{-2} d^{-1}$ at Stn IV at 20 m (Fig. 6E).

The vertical flux of phaeo was shown to be different from the POC and chl *a* vertical flux. At Stn I the vertical flux of phaeo (Fig. 3D, E) at 20 m was high (11 mg $m^{-2} d^{-1}$), but decreased with depth to 2.5 mg $m^{-2} d^{-1}$ at 50 m. The vertical flux of phaeo was low in the upper water column at the other 3 stations (<3 mg $m^{-2} d^{-1}$ above 100 m; D of Figs. 3–5), but increased slightly with depth. Pigment composition of the exported matter changed from chl *a* $>$ phaeo in the upper water column to chl *a* $<$ phaeo below 60 m at Stns I and IV (Figs. 3D & 6D), below 70 m at Stn II (Fig. 4D) and below 100 m at Stn III (Fig. 5D).

Vertical flux of microplankton

The species composition of the sinking microplankton at 60 m was mainly similar to the species composition observed in the water column above the traps. Vertical flux of microplankton generally decreased with increasing depth, though some differences between groups were observed.

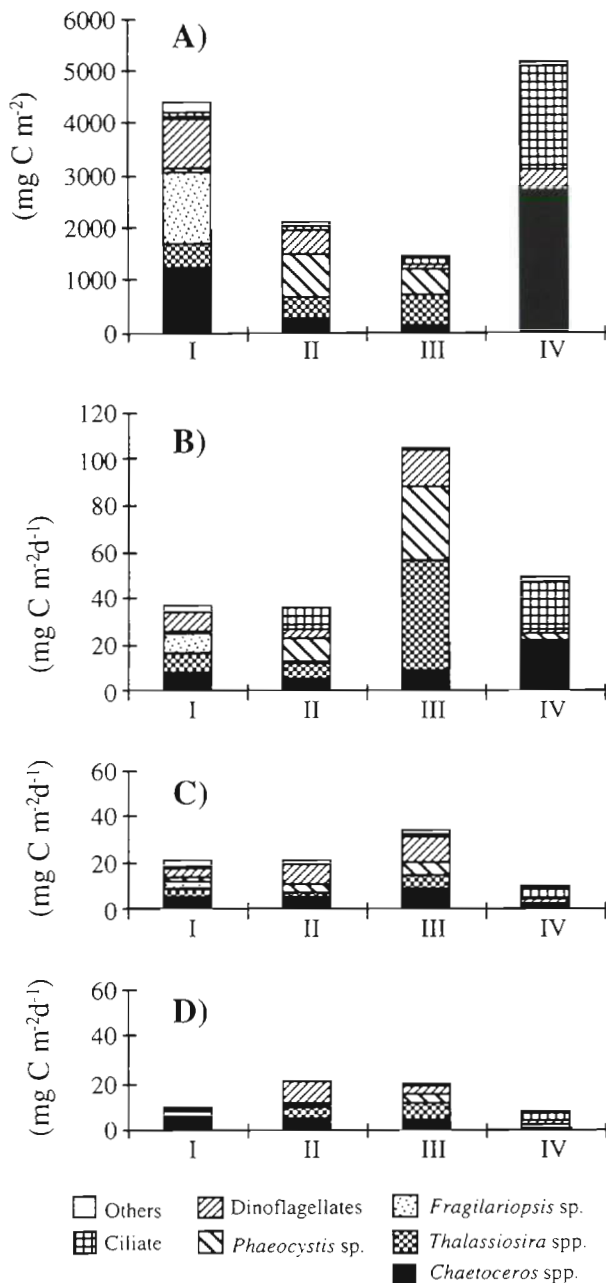


Fig. 8. (A) Integrated phytoplankton carbon from 0 to 40 m at Stn I and 0 to 60 m at Stns II, III, and IV. (B–D) Vertical flux of phytoplankton carbon at 60, 100 and 200 m, respectively

At Stn I the vertical flux of diatoms decreased with increasing depth from 26 to 9 $\text{mg C m}^{-2} \text{ d}^{-1}$ at 60 m and 200 m, respectively. While the vertical flux of *Thalassiosira* spp. decreased with increased depth throughout the water column, the vertical flux of *Chaetoceros* spp. and *Fragilariopsis* sp. was not significantly different at 100 and 200 m depth (Fig. 8C, D). The vertical flux of diatoms at 60 m depth was more than 4 times higher at Stn III than at Stn II (56 and 13 $\text{mg C m}^{-2} \text{ d}^{-1}$,

respectively). At Stn III the vertical flux of *Thalassiosira* spp. decreased substantially between 60 and 100 m depth, and at 200 m depth the vertical flux of diatoms was similar at Stns II and III (10 and 11 $\text{mg C m}^{-2} \text{ d}^{-1}$, respectively; Fig. 8D). The vertical flux of diatoms at 60 m at Stn IV was comparable to that at Stn I, but the rate decreased substantially from 60 to 100 m depth and diatoms were not important for the flux at 100 and 200 m depth.

Phaeocystis sp. colonies were not important for the vertical flux of PPC at Stns I and IV, but colonies were found in the traps at all depths. The highest vertical flux of *Phaeocystis* sp. colonies was observed at Stns II and III (2.67×10^6 and 1.75×10^6 colonies $\text{m}^{-2} \text{ d}^{-1}$ at 60 m, respectively). The vertical flux of *Phaeocystis* sp. carbon decreased between 60 and 100 m at both Stns II and III (Fig. 8), but the decrease was mainly due to smaller colony size and fewer cells in the colonies and not a decrease in number of sinking colonies. All *Phaeocystis* sp. colonies at 100 and 200 m depth at Stns II and III were senescent, and at 200 m *Phaeocystis* sp. colonies were difficult to recognise. Only a few *Phaeocystis* sp. cells were left in the colonial matrix, and phytodetritus, diatoms, ciliates and dinoflagellates were associated. In addition to the senescent colonies, aggregates of probable *Phaeocystis* sp. origin were found at 100 and 200 m depth. The number of sinking colonies/aggregates of *Phaeocystis* sp. was similar at 100 and 200 m. Fig. 8 includes only material that has been positively identified as *Phaeocystis* sp. due to remaining cells in the matrix.

At all stations large dinoflagellates and ciliates, probably heterotrophic, were important for the vertical flux of PPC at 60 m in terms of biomass, especially at Stn IV. Generally the vertical flux of protozoa decreased with increasing depth. Dinoflagellates and ciliates were often associated to aggregates in the deepest traps.

Daily loss rates of chl *a* and phytoplankton

Stns II and III had the highest daily loss rates of chl *a* standing stock recorded during this investigation. Loss rates at Stn III were 18% at 30 m and 8% at 60 m while at Stn II daily loss rates of chl *a* were 10% at 30 m and 4% at 60 m (Table 2). Daily loss rates of chl *a* at Stn IV were 1.6% at 30 m and decreased to 0.6% of standing stock at 60 m (Table 2). Daily loss rates of chl *a* at Stn I were 3.5% at 30 m and decreased to 0.4% of standing stock at 60 m.

Daily loss rates of microplankton at Stn I were in the range 0.4 to 1.7% at 60 m, with highest daily loss rates for *Phaeocystis* sp. and *Thalassiosira* spp. (Table 2). At Stn II ciliates experienced the highest daily loss rate

Table 2. Daily loss rates of chl *a* at 30 and 60 m and daily loss rates of 6 different microplankton groups at 60 m at the 4 stations

Daily loss rate ($\frac{\text{mg}}{\text{m}^3} \text{d}^{-1}$)	I	II	III	IV
Chl <i>a</i> (30 m)	3.5	10.2	18.4	1.6
Chl <i>a</i> (60 m)	0.4	4.0	7.7	0.6
Pennate chain-forming diatoms	0.6	–	–	–
<i>Phaeocystis</i> sp.	1.5	1.2	6.7	5.2
<i>Chaetoceros</i> spp.	0.6	1.9	7.4	0.8
<i>Thalassiosira</i> spp.	1.7	1.7	8.3	3.4
Dinoflagellates	0.8	1.1	13.0	0.4
Ciliates	0.4	8.7	–	1.1

with 8.7 %, the other microplankton groups had daily loss rates in the range 1.1 to 1.9 % (Table 2). The highest daily loss rates of microplankton during this investigation was observed at Stn III with 13 % of dinoflagellates and 6.7 to 8.3 % d^{-1} loss of *Phaeocystis* sp., *Chaetoceros* spp. and *Thalassiosira* spp. At Stn IV *Phaeocystis* sp. had the highest daily loss rates at 60 m with 5.2 % and *Thalassiosira* spp. also had a relatively high daily loss rate with 3.4 %. Daily loss rates for the remaining microplankton groups at Stn IV (Table 2) ranged between 0.4 and 1.1 %.

DISCUSSION

The vertical profiles of temperature and salinity (Fig. 2) show that the characteristics of the water column differed during the course of the drift period. Care should therefore be taken interpreting the results from the water column and vertical flux, as the sediment traps may have drifted through areas with patchy distribution of both phytoplankton and zooplankton. Except for those at Stn I, 1 to 3 of the upper traps were situated in the euphotic zone. This might have lead to some overestimation of vertical flux due to production inside the traps, but due to low production below 20 m (Vernet et al. 1998) we have reason to believe that overestimation due to production was insignificant.

Field results have shown that phytoplankton and phytodetritus may aggregate and sink rapidly out of the euphotic zone when living conditions deteriorate (Smetacek et al. 1978, Smetacek 1980, Wassmann et al. 1990). There is, however, no strict relationship between nutrient depletion and enhanced sinking rates (Bienfang et al. 1982, 1983) or nutrient depletion and aggregation potential on a species level (e.g. Kiørboe & Hansen 1993). Extensive sedimentation of phytoplankton might also take place during earlier stages of blooms due to aggregation (Kiørboe 1993, Kiørboe et

al. 1994) or deterioration of living conditions (i.e. light limitation; Waite & Thompson 1992).

High POC and chl *a* vertical flux and chl *a*/phaeo ratios >1 at the 3 northernmost stations (I, II, III) indicate sinking of phytoplankton or phytodetritus in the upper water column, while at Stn IV the vertical flux of both POC and chl *a* was low, indicating sinking of less phytoplankton and more decomposed material. Environmental and biological factors that might have been important for the vertical flux of phytoplankton at the 4 stations in the Barents Sea in May 1993 will be evaluated in the following discussion. The importance of loss of phytoplankton due to sinking compared to loss due to grazing will also be discussed.

Bloom development, nutrient and light conditions and vertical flux of microplankton

Reduced nutrient concentrations and high concentrations of chl *a* and diatoms at Stn I indicated a well-developed ice edge bloom. The species composition with *Fragilariopsis* sp. and *Thalassiosira* spp. and *Chaetoceros* spp. is typical of marginal ice zones (Horner 1989, Kang & Fryxell 1992) and later stages of arctic spring blooms (Quillfeldt 1996). Diatoms are less likely to dominate at $\text{Si}(\text{OH})_4$ concentrations <2 μM (Doering et al. 1989, Egge 1993) and may aggregate, sink and leave the euphotic zone before phosphate and nitrate become depleted (Wassmann et al. 1997). Considering nutrient conditions and species composition, high loss of phytoplankton through sinking could be expected at Stn I. The high vertical flux of POC and chl *a* in the upper water column seems to support this assumption.

The euphotic zone (down to 0.1 % light depth) at Stn I only extended to 25 m depth (Vernet et al. 1997), and the daily loss rate of chl *a* at 30 m (3.5 % of standing stock d^{-1}) indicates increased sinking out of the euphotic zone. The uniform distribution of nutrients and biomass in the upper 50 m though indicates mixing of the water above the pycnocline. The total upper water column down to the pycnocline must therefore be considered periodically part of the euphotic zone. The vertical flux rates at Stn I were reduced below the pycnocline and chl *a* loss rate at 60 m was only 0.4 % of standing stock d^{-1} . Although there was a considerable amount of phytoplankton sinking in the euphotic zone, little material escaped from the mixed layer, either due to mixing or due to other forms of loss (i.e. grazing). The low daily loss rates through sinking imply that no extensive sedimentation of phytoplankton took place, despite high vertical chl *a* flux at Stn I. This conclusion finds support in that Stn I did not have significantly different daily loss rates of phytoplankton and chl *a* com-

pared to Stn IV, and both Stns II and III had higher daily loss rates. Stns II, III and IV all experienced high nutrient concentrations.

The phytoplankton community at both Stns II and III was dominated by species (*Phaeocystis* sp. colonies, *Chaetoceros* spp. and *Thalassiosira* spp.), often observed during spring bloom in the Barents Sea (Rey et al. 1987, Sakshaug & Skjoldal 1989, Druzhkov & Makarevich 1992). Despite differences in vertical stability and water column characteristics, Stns II and III had similarities with regard to phytoplankton composition, suspended biomass and vertical flux. Insignificant differences in biomass and species composition above and below the pycnocline, however, indicate that the upper layer of melt water at Stn II had recently formed or arrived at this site and had not yet influenced the general biomass and species composition. Low biomass and reduced, but still high, nutrient concentrations indicate that the blooms at Stns II and III were in an early phase of bloom development, when high loss rates should not be expected. A comparison of chl *a* daily loss rates from Stns II and III and previous observations made in the same area during conditions of nutrient depletion (Wassmann et al. 1990) show that the loss rates were 3 to 4 times higher in 1993. This indicates that loss of phytoplankton at Stns II and III through sinking was extensive during the period of investigation.

Reduced light due to increased ice cover or mixing of the water column are factors that may induce less favourable growth conditions and thus induce sinking of phytoplankton. The ice cover at Stn II was less than that at Stn I and it decreased during the drift. Therefore light limitation by increased ice-cover is not a satisfactory explanation for the increased loss of phytoplankton at Stn II. High primary production (Vernet et al. 1998) and reduction in nutrient concentrations during drift confirm this conclusion.

Stn III was lacking a strong stratification and unstratified water is sensitive to mixing by wind (Sakshaug et al. 1994), which may induce light limitation. Observations of spring bloom development in weakly stratified waters are not rare (Eilertsen 1993, Townsend et al. 1993, Wassmann et al. 1996) and have frequently been made in the Atlantic sector of the Barents Sea (e.g. Skjoldal & Rey 1989, Wassmann et al. 1998). Wind conditions were calm both before and during drift and CTD and fluorescence profiles (data not shown) taken during the drift did not indicate enhanced mixing. This conclusion is further supported by the results from Stn IV. Temperature, salinity, stability and biomass (in terms of chl *a*) were similar at Stns IV and III, but Stn IV had low vertical flux of organic matter and low daily loss rates. Hydrographical conditions seem therefore not to give any satisfactory explanation for the increased loss of phytoplankton at Stns II and III.

Species-specific sinking

Different species or groups of species dominated the phytoplankton biomass at the 4 stations, but generally the same species were found at all stations. Species-specific differences in sinking behaviour have been found in other ecosystems (e.g. Passow 1991) as well as in the Barents Sea (P. Wassmann & F. Rey unpubl.). Species-specific loss rates were therefore calculated to see if the species composition and species-specific loss rates could explain the differences in loss rates between the stations.

A comparison of the composition of suspended phytoplankton in the mixed layer and sinking cells at 60 m (Fig. 8, Table 2) revealed no major differences between groups at each station. There were increased daily loss rates of ciliates at Stn II and dinoflagellates at Stn III, but this conclusion may not be significant due to the low cell numbers in the samples. The same may be valid for *Phaeocystis* sp. and *Thalassiosira* spp. at Stn IV. The dominance of certain groups of phytoplankton in the sinking material at 60 m was thus not due to higher sinking rates of specific species. The high loss rates of phytoplankton at Stns II and III included the entire phytoplankton community.

Extracellular carbon and aggregation — a probable explanation for increased loss rates?

The production of extracellular carbon (high-molecular-weight carbohydrates) by phytoplankton may influence the fate of the particulate primary production. Mucilage and particulate matter which is sticky [e.g. transparent exopolymer particles (TEP); Alldredge et al. 1993, Riebesell et al. 1995] may increase coagulation (Jackson 1990) and thus increase the vertical flux of particles. During the investigation in 1993, Vernet et al. (1998) found an increasing proportion of primary production as extracellular carbon (39 to 55% of primary production) from Stn I to Stn III. Stn IV, however, had the lowest production of extracellular carbon with only 18% of primary production. Extracellular carbon includes both mucilage and dissolved organic carbon (DOC) and probably consist of polysaccharides (Vernet et al. 1998). Although production of extracellular carbon was also high at Stn I, production of extracellular carbon compared to standing stock of phytoplankton was highest at Stns II and III. Based on the species composition, diatoms are believed to have dominated the production of extracellular carbon at Stn I, while both *Phaeocystis* sp. and diatoms contributed to the production of extracellular carbon at Stns II and III (Vernet et al. 1998). Production of extracellular carbon may have increased the aggregation potential of sus-

pended particles and consequently have caused the high daily loss rates at Stns II and III. Direct observations of the aggregation potential of the natural community were unfortunately not carried out. Therefore, we only have circumstantial evidence that aggregation was the main reason for the observed differences in vertical export of phytoplankton among the 4 stations.

Dissolution of sinking *Phaeocystis* sp. colonies below 60 m

Sedimentation of *Phaeocystis* sp. colonies has been observed in the Barents Sea and in northern Norwegian fjords, but vertical flux has been shown to decrease below 40 to 60 m depths (Wassmann et al. 1990, Riebesell et al. 1995). A dissolution of *Phaeocystis* sp. colonies in the upper aphotic zone and at mid-water depth has been suggested (Passow & Wassmann 1994, Wassmann 1994).

In the Barents Sea in 1993 vertical flux of diatoms showed minor variations or a small decrease with depth, while the vertical flux of *Phaeocystis* sp. in terms of carbon showed a sharp decline below 60 m at all stations. These observations are consistent with earlier observations, but the matrix from *Phaeocystis* sp. colonies was found in the traps at 100 and 200 m in comparable numbers to the vertical flux of colonies at 60 m. We may therefore conclude that the matrix of *Phaeocystis* sp. may reach the deep water of the Barents Sea, but that the cells may escape from the matrix during sinking. Geographical differences in sinking and dissolution of *Phaeocystis* sp. cannot be excluded, but use of preservatives that do not preserve colonial matrix may be a reason for lacking observations of sinking *Phaeocystis* sp. matrix in other areas. In terms of vertical flux of carbon, the matrix of *Phaeocystis* sp. colonies may be less important, but if they act as scavengers for other particles, creating aggregates with high sinking speed, the matrix may be of significance for vertical carbon export.

Meso- and macrozooplankton influence on vertical flux

The vertical flux of both chl *a* and POC decreased with depth in the upper water column at all stations and only a small fraction of intact phytoplankton reached deeper waters. PPC at the 4 stations comprised 5 to 9% of the vertical POC flux at 100 and 200 m (data not shown), indicating that identifiable phytoplankton cells represented a small portion of the vertical flux at these depths. The decrease in vertical POC and chl *a* flux was accompanied by a change in pigment composition to a dominance by phaeo at

depth, indicating that sinking matter in the deeper water column consisted of degraded matter. This indicates that the sinking material was dominated by faecal material, which was confirmed by data from J. Urban-Rich (unpubl. data on total faecal pellets carbon). The vertical flux data thus indicate both retention of phytoplankton biomass due to grazing and a considerable contribution of faecal matter to vertical flux.

Calanoid copepods are regarded as the main herbivorous species during spring in the Barents Sea (Båmstedt et al. 1991, Tande 1991), but experiments carried out by Hansen et al. (1996) during the cruise in 1993 indicated low copepod grazing rates (0.2 to 1% of daily primary production, or 1.5 to 15 mg C m⁻² d⁻¹) in the euphotic zone due to low biomass of the most important herbivorous copepods. Faecal pellet production by calanoid copepods was also too small to contribute significantly to vertical flux (Urban-Rich 1997). Mesozooplankton grazing activity can thus explain neither the observed retention of phytoplankton nor the vertical flux of faecal matter.

This points to a possible underestimation of zooplankton grazing. Mesozooplankton grazing potential was estimated only for the most dominant copepod species, and macrozooplankton species such as euphausiids, pteropods, and amphipods from the water column and under-ice fauna were not evaluated (Hansen et al. 1996). However, euphausiids, for example, are important contributors to zooplankton biomass in the Barents Sea (Dalpadado & Skjoldal 1991). Krill and other macrozooplankton species may thus have been important consumers of phytoplankton and contributors to the vertical flux of matter, as shown in other geographical areas (von Bodungen et al. 1987, Bathmann et al. 1991, Riebesell et al. 1995). Therefore, copepod grazing per se might not have been underestimated, but the total grazing pressure from large zooplankton might have been underestimated due to incomplete sampling. This is further confirmed by the observation of krill pellets in the sedimented material (J. Urban-Rich pers. comm.).

Microzooplankton influence on vertical flux

Protozoan grazing was shown to be much higher than that of copepods during this study (Hansen et al. 1996; Table 3: 125 to 720 mg C m⁻² d⁻¹). Microzooplankton distribution followed, in general, that of phytoplankton and was dominated by heterotrophic dinoflagellates (Hansen et al. 1996). Heterotrophic dinoflagellates are known to be able to prey on phytoplankton similar to their own size, particularly the large forms that feed using feeding appendages (Jacobson & Anderson 1986). Due to high grazing rates

Table 3. Grazing rates of meso- and microzooplankton integrated from 0 to 50 m (from Hansen et al. 1996)

Stn	Grazing potential of mesozooplankton (mg C m ⁻² d ⁻¹)	Grazing potential of microzooplankton (mg C m ⁻² d ⁻¹)
I	5	720
II	2.0	280
III	1.5	125
IV	15	425

and absence of faecal pellet formation, or production of small and slow-sinking pellets, microzooplankton may contribute to the retention of biomass and nutrients in the euphotic zone (Antia 1991). Although pellets from microzooplankton may be important components of the vertical flux (Nöthig & von Bodungen 1989), microzooplankton acting as the main consumers of phytoplankton may reduce the export of carbon or phaeo compared to scenarios where mesozooplankton are the main herbivores (Buck & Newton 1995).

Protozoan grazing was largest at Stns I and IV (Hansen et al. 1996). Both stations had high phytoplankton biomass and high primary production (Vermet et al. 1998), but low daily loss rates. The reduction in vertical chl *a* flux and change of pigment composition mainly took place above 60 m at Stns I and IV, where microzooplankton also dominated. The low daily loss rates of biogenic matter to deeper waters at these stations may therefore partly be explained by retention due to microzooplankton grazing. The distribution of microzooplankton and the large grazing potential gave the microzooplankton the possibility not only of further controlling phytoplankton production, but also of retaining biogenic matter and nutrients in the upper water column at these stations.

Stns II and III experienced lower protozoan grazing pressure between 0 and 50 m compared to Stns I and IV (Hansen et al. 1996). This coincided with larger vertical flux of phytoplankton to deeper water. It is uncertain to what extent protozoans are able to graze on *Phaeocystis* sp. colonies, but ciliates and heterotrophic dinoflagellates are probably capable of grazing on single cells liberated from colonies (Lancelot et al. 1991).

CONCLUSION

The interpretation of the present material is complicated by the limited investigation time and the complexity of the pelagic community along the gradient. Careful analysis of the results, however, indicates that hydrography, nutrient status and light did not have a profound influence on the vertical flux of phytoplank-

ton during this investigation. The results show that high vertical flux is not necessarily connected to high daily loss rates, but may be due to low or moderate daily loss rates of a large suspended biomass. It may be relevant to question the use of the term mass sedimentation as used by e.g. Wassmann et al. (1990). High vertical flux of phytoplankton (or other particles), especially during conditions with low nutrient concentrations, is often referred to as mass sedimentation. The use of this term under such conditions may be misleading, and should be reserved for scenarios of high daily loss rates.

High daily loss rates of phytoplankton from the euphotic zone was observed at the 2 stations (II and III) with high nutrient concentrations. The high loss rates were possibly due to production of extracellular carbon, which may have increased the aggregation potential of the phytoplankton community. This indicates that phytoplankton in the Barents Sea during spring may be subjected to aggregation and sinking before the termination of the spring bloom by nutrient or light limitation.

Evidence of incomplete dissolution of *Phaeocystis* sp. colonies was observed to a depth of 200 m. The results show that the matrix of *Phaeocystis* sp. may reach the deep water of the Barents Sea, but that the cells probably escape the matrix during sinking. The importance of sinking *Phaeocystis* sp. for the carbon flux in the Barents Sea is, however, still uncertain.

Only a small fraction of intact phytoplankton reached deeper waters due to retention by grazers, and the vertical flux of biogenic matter to deeper water masses was dominated by faecal matter. Earlier hypotheses (Eilertsen et al. 1989, Wassmann et al. 1990, Wassmann & Slagstad 1993) based on the assumption that mesozooplankton grazers (i.e. calanoid copepods) are important regulators of the vertical flux during spring in the Barents Sea were shown to be inadequate in explaining the retention of phytoplankton matter in the upper water column. Mesozooplankton probably did not play an important role in retaining matter in the upper water column. Protozoan grazing was more important in terms of retaining organic matter and nutrients in the upper water. There are indications that macrozooplankton (i.e. euphausiids), as mediator of vertical flux through production of fast-sinking pellets, were important in structuring the carbon flow in the pelagic system.

These conclusions imply that not only the physical environment but also biological processes are important factors in the regulation of the vertical flux of biogenic matter in the northern and central Barents Sea during the spring period. In future studies phytoplankton-related processes such as production of extracellular carbon and aggregation should be studied, and the

entire size spectra of phytoplankton consumers and their role in structuring the carbon flow in the pelagic system should be considered.

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