# Seasonal variation in vertical flux of biogenic matter in the marginal ice zone and the central Barents Sea

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## Abstract

The spatial and seasonal variations in the vertical flux of particulate biogenic matter were investigated in the Barents Sea in winter and spring 1998 and summer 1999. Arrays of simple cylindrical sediment traps were moored for 24 h between 30 and 200 m along a transect from the ice-free Atlantic water to Arctic water with up to 80% ice cover. Large gradients in the quantity and composition of the sinking particles were observed in the south–north direction, and in relation to water column structure and stability, which depend on the processes of ice retreat. The magnitude of the vertical flux of particulate organic carbon (POC) out of the upper mixed layer ranged from background winter values ($30-70$ mg C m$^{-2}$ day$^{-1}$) to $150-300$ mg C m$^{-2}$ day$^{-1}$ in summer and $500-1500$ mg C m$^{-2}$ day$^{-1}$ in spring. Vertical flux of chlorophyll $a$ (CHL) was negligible in winter, generally $<1$ mg m$^{-2}$ day$^{-1}$ in summer, and up to 38 mg m$^{-2}$ day$^{-1}$ in spring. In spring, the proportion of phytoplankton carbon (dominated by *Phaeocystis pouchetii* in the Atlantic water and *Thalassiosira antarctica* in the Arctic water) in the sinking POC was up to 50%. Both colonial and single-celled forms of *P. pouchetii* were equally abundant in the water column and sediment traps. In contrast to the spring season, the vertical flux of phytoplankton during summer was dominated by a variety of flagellates (e.g. small unidentified flagellates, *Ochromonas crenata*, *Dinobryon balticum* and single-celled *P. pouchetii*). The magnitude of the vertical flux to the bottom in spring was comparable in the Arctic and Atlantic waters (ca. 200 mg C m$^{-2}$ day$^{-1}$), but the composition and C/N ratio of the particles were different.

The regulation of biogenic particle sedimentation took place in the upper layers and over very short vertical distances, and varied with season and water mass. The vertical flux was mainly shaped by the water column stratification (strong salinity stratification in the Arctic water; no stratification in the Atlantic water) and also by the activity of plankton organisms. Zooplankton faecal pellets were an important constituent of the vertical flux (up to 250 mg C m$^{-2}$ day$^{-1}$), but their significance varied widely between stations. The daily sedimentation loss rates of POC in spring exceeded the loss rates in summer on the average of 1.7 times. The complexity of the planktonic community during summer suggested the prevalence of a retention food chain with a higher capacity of resource recycling compared to spring.
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## 1. Introduction

The Barents Sea is a productive arctic marginal shelf sea of the eastern North Atlantic. The annual primary production is coupled to the spatial variation in ice cover, which is highly variable, both seasonally and interannually (Falk-Petersen et al., 2000). The extent of ice cover is influenced by two main water masses separated by the Polar Front, Arctic water entering from the northeast and Atlantic water entering from southwest. The Arctic water is periodically ice covered. Ice melts during spring and summer giving rise to a stratified and nutrient-rich euphotic zone, which supports a pronounced spring bloom in the marginal ice zone (MIZ) (Matrai and Vernet, 1997; Sakshaug and Skjoldal, 1989; Smith, 1987). Primary production rates up to 1460 mg C m$^{-2}$ day$^{-1}$ (Rey and Loeng, 1985) and new production rates up to 200–400 mg C m$^{-2}$ day$^{-1}$ (Luchetta et al., 2000) have been reported. At the MIZ, diatoms like *Thalassiosira antarctica*, *T. hyalina*, *Chaetoceros socialis*, *Fragilariopsis* spp. (von Quillfeldt, 2000) are believed to be the first algae to bloom, followed by the colonial form of the haptophyte *Phaeocystis pouchetii* (Rey and Skjoldal, 1987; Skjoldal and Rey, 1989). It is assumed that the MIZ-associated production sweeps across a large area of the northern Barents Sea into the Arctic Ocean and the result is a relatively large annual production between 50 and 150 g C m$^{-2}$ (Falk-Petersen et al., 1990; Slagstad and Wassmann, 1996; Wassmann and Slagstad, 1993). In areas dominated by Atlantic water, stratification develops slowly by solar radiation during spring and summer, and it is assumed that the resulting spring bloom is less distinct (Skjoldal and Rey, 1989).

Compared to other areas of the world's ocean, polar seas have a large influence on the atmosphere's $CO_2$ content (Anderson et al., 1990; Walsh, 1989), mainly due to deep-water formation. The Barents Sea, in particular, has recently been indicated (Olsson et al., 1999) as a major productivity site that transports the productivity signal to all water masses in the Eurasian Basin. This transport route is instrumental for long-term sequestration of carbon dioxide (Sarimento and Toggweiler, 1984). Sequestration of atmospheric $CO_2$ in polar seas takes place, in great part, through the action of the surface biota. A major loss of organic matter from the euphotic zone, and one way the

photosynthetically fixed carbon becomes inaccessible to the atmosphere, is the settling of phytoplankton cells, faecal pellets and phytoplankton-derived detritus (Wassmann, 1989). $CO_2$ sequestration has been often approached with studies where new production has been considered as the fraction of total primary production which can be exported below the euphotic zone (Jennings and Wallace, 1992; Platt et al., 1988, 1992). Usually the new production is estimated from the decrease of nitrate concentration in the water body during a given time interval and the nitrate consumption is converted to carbon production by using the Redfield ratio (e.g. Luchetta et al., 2000). However, relating the new production to the upper limit of export production assumes that the C/N ratio of the settling organic particles approximates the Redfield ratio, which may not be the case. Generally, nitrogen associated with particles is preferentially dissolved compared to carbon, resulting in POC/PON ratio of sinking particles above the Redfield ratio (Honjo et al., 1982; Olli et al., 2001; Smith et al., 1992; Wong et al., 1999). Consequently, in terms of carbon, the same amount of nitrate consumption can give rise to more carbon export than what corresponds to the Redfield ratio. The increase in export production is determined by the POC/PON ratio of the settling material. Therefore, for a better understanding of the carbon cycling in the ocean, we need an elementary understanding on the composition of settling particles and also how vertical export of biogenic matter into the ocean interior is regulated. The quantity and quality of sinking organic particles are strongly modified by the prevailing community of planktonic microorganisms (Heiskanen, 1998). The planktonic food web structure determines the physical properties of the sinking particles (e.g. intact phytoplankton cells, phytodetritus and faecal pellets) and the retention capacity of the pelagic community (Cho and Azam, 1998; Wassmann, 1998). Growing evidence for the significance of small cells and organisms in northern Norway and the Barents Sea (Hansen et al., 1995; Verity et al., 2002) suggests that in the northern waters, more carbon may be channelled through the microbial loop than previously assumed.

Quantification of sources and sinks of algal-derived organic carbon is instrumental to the basic understanding of marine ecosystems. This demands research on suspended matter, plankton dynamics,

vertical flux and its regulation. The aim of this study was to estimate the seasonal variability of the vertical flux in the central Barents Sea along a transect from Atlantic water in the south, through the main oceanographic and ecological boundary in the region—the Polar Front, to the Arctic water mass in the north. We expected the magnitude of the downward flux and composition of the sinking organic matter to reflect the variation in the phytoplankton bloom dynamics. Of particular interest were scenarios of vertical flux in diatom vs. *P. pouchetii*-dominated waters, the roles of plankton community structure and the mesozooplankton grazing activity in determining the quality and quantity of sinking particles. The eminent role of diatom blooms in channelling the surface production to the benthos is well known (Olesen, 1993; Waite et al., 1992), while the fate of *Phaeocystis* production in the high-latitude ocean is controversial (e.g. Riebesell et al., 1995; Smith et al., 1991; Wassmann et al., 1990). The cruises were scheduled to cover the maximum seasonal variation in the vertical flux. The winter cruise was scheduled to coincide with the maximum extent of ice cover (Falk-Petersen et al., 2000) and study the background condition before the start of the vernal production. The spring cruise aimed to observe the peak of the vernal production and sedimentation, and the summer cruise to follow a later stage of the temporal evolution of the plankton production.

## 2. Methods

### 2.1. Sampling

Data were collected during three R/V Jan Mayen cruises to the Barents Sea MIZ corresponding to winter (March 17–23, 1998), spring (May 18–28, 1998) and summer (June 30–July 9, 1999; see also Table 1). Each cruise started with a series of linearly spaced transect stations in the Atlantic water at south (72.5°N, 31.0°E) through the Polar Front and into the Arctic water at the MIZ. During the transect stations, CTD profiles (Seabird CTD profiler) were taken and based on salinity-temperature properties, the different water masses on the transect were identified (see Reigstad et al., 2002). Locations of the sediment trap stations (Fig. 1) were chosen to cover both the Arctic and Atlantic water masses.

The sediment trap station locations and identities of water masses are given in Table 1. At each station, a drifter with an array of sediment traps at eight depths (30, 40, 50, 60, 90, 120, 150 and 200 m), or as deep as the bottom topography allowed, was deployed and recovered ca. 24 h later. The sediment traps (KC maskiner og laboratorieudustyr, Denmark) were parallel cylinders mounted in a gimbaled frame equipped with a vane. At moderate current speeds, the cylinders remain vertical and perpendicular to the currents direction. The cylinders were 7.2 cm in diameter and

Table 1
Sediment trap deployment stations, times, locations, bottom depth of the station, the depth of the deepest sediment trap and the type of water mass

| Cruise | Station | Date | Location (°N, °E) | Bottom depth (m) | Deepest trap (m) | Water mass |
|--------|---------|------|-------------------|------------------|------------------|------------|
| ALV I | I | 23 March 1998 | 72.549, 30.981 | 300 | 200 | AT |
| | II | 21 March 1998 | 73.767, 31.876 | 350 | 200 | PF |
| | III | 19 March 1998 | 76.387, 33.209 | 256 | 200 | AR |
| ALV II | I | 28 May 1998 | 72.495, 30.947 | 301 | 200 | AT |
| | II | 26 May 1998 | 73.788, 31.643 | 340 | 200 | AT (PF) |
| | III | 24 May 1998 | 74.802, 32.458 | 168 | 150 | AR |
| | IV | 22 May 1998 | 75.612, 33.062 | 239 | 200 | AR |
| | V | 20 May 1998 | 76.020, 32.990 | 323 | 200 | AR |
| ALV III | I | 9 July 1999 | 73.799, 31.776 | 342 | 200 | AT |
| | II | 8 July 1999 | 75.122, 32.287 | 250 | 150 | AT |
| | III | 6 July 1999 | 77.082, 33.816 | 169 | 90 | AR |
| | IV | 4 July 1999 | 77.646, 34.211 | 190 | 150 | AR |
| | V | 2 July 1999 | 78.243, 34.230 | 194 | 150 | AR |

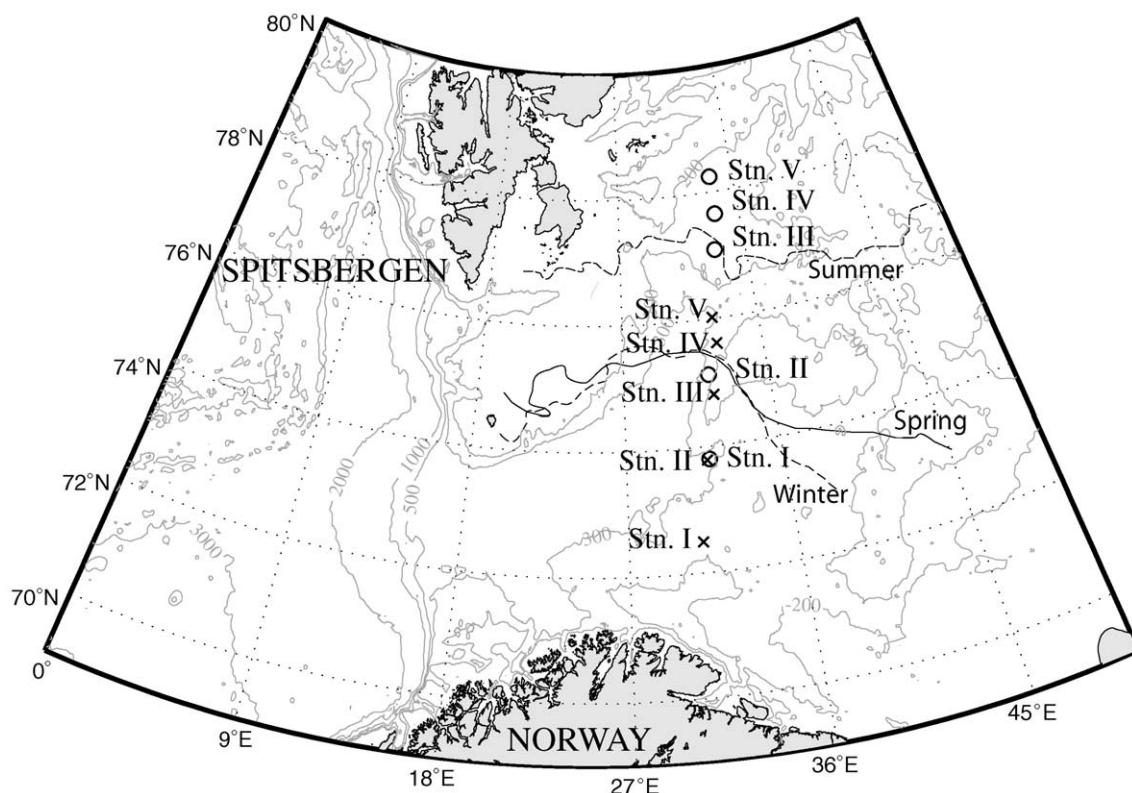AT—Atlantic water; AR—Arctic water; PF—Polar Front.

Fig. 1. Map of the Barents Sea with the Stns. I–V during the May cruise (×, notation on the left), July cruise (○, notation on the right), and the approximate location of ice edge.

45 cm high ($H/D$ ratio 6.25). No bafflers were used in the cylinder opening and no poison was applied during the deployment. Application of the $^{234}$Thorium method (Cochran et al., 1995) at selected depths during summer cruise revealed promising results with close to 100% trapping efficiency (Coppola, personal communication). At recovery, the sediment trap cylinders were pulled upwards and some surrounding water could have mixed into the trap cylinders. However, the concentration of particles in the water column was low compared to the amount of material in the trap and the potential error could not exceed a few percent. After recovery, the contents of the two replicate sediment trap cylinders were pooled into plastic bottles and kept cold and dark until processing ($< 0.5$ h). CTD profiles and water column samples during the sediment trap deployments were taken with a General Oceanic Rosette Sampler equipped with 5-l Niskin bottles from 11 fixed depths (0, 10, 20, 30, 40, 50, 75,

90, 120, 150 and 200 m) or as deep as the bottom topography allowed. Aliquots were taken to analyse the composition and abundance of planktonic microorganisms (PNMC), suspended chlorophyll $a$ (CHL), phaeopigments (PHAEO), particulate organic carbon (POC), nitrogen (PON) and transparent exopolymer particles (TEP).

## 2.2. Sample processing

Prior to subsampling, each bottle containing the sediment trap material was thoroughly mixed by gentle rotation and the content transferred into glass bottles equipped with Vogel type automatic pipette (Valderrama, 1995). Depending on the particle concentration, three 50–800 ml replicate aliquots from each sediment trap sample or 100–1000 ml aliquots from water column samples were filtered onto precombusted Whatman GF/F filters for analysis of POC,

PON, CHL and PHAEO. Five 50–100 ml replicate subsamples from sediment trap and water column samples were filtered with low pressure onto 0.45 μm pore size polycarbonate membrane filters and stained with Alcian blue for the analysis of TEP according to Passow and Alldredge (1995). For microscopic examination of pico-, nano- and microplanktons, 250 ml aliquots from sediment trap samples were fixed with ethanol–glutaraldehyde–Lugol solution (Rousseau et al., 1990), which preserves flagellates and mucilaginous matter more efficiently than formaldehyde.

CHL and PHAEO were extracted in 96% ethanol for 24 h at room temperature and analysed fluorometrically (Holm-Hansen et al., 1965) on a Turner Design AU-10 fluorometer. POC and PON samples were analysed on a Leeman Lab CEC 440 CHN analyser after removal of carbonate with fumes of concentrated HCl for 24 h (Fisher and Wefer, 1991). Pico-, nano- and microplanktons from the water column and sediment traps were counted with light microscope furnished with a counting stage (for details, see Ratkova et al., 2002). The organisms included diatoms, photo- and heterotrophic dinoflagellates, other photo- and heterotrophic flagellates, cyanobacteria, ciliates, radiolaria and foraminifera. No distinction was made between auto- and heterotrophic forms, and in the following, the combined biomass is termed pico-, nano- and microplankton carbon (PNMC). Zooplankton faecal pellet carbon in the sediment traps was estimated as described in Wexels Riser et al. (2002).

The vertical fluxes of sinking particles at each depth were calculated to mg m$^{-2}$ day$^{-1}$ and related to the standing stocks above the trap depth to calculate the loss rates (% day$^{-1}$). The standing stock of suspended biomass was calculated by vertically integrating the water column measurements of suspended POC, PON, PNMC and CHL to match the trap deployment depths.

## 3. Results

### 3.1. Hydrography

During winter, the warmer (1–3 °C) Atlantic water was separated by the cold (0–1 °C) Arctic water by a frontal region at approximately 73.76°N. Water column stratification was weak (Fig. 2) and only slight salinity stratification was evident at ca. 50 m depth close to the MIZ. Three trap stations were located in the Atlantic water (Stn. I), Polar Front region (Stn. II) and in the Arctic water (Stn. III). During the spring cruise, the Atlantic water in the southern part of the transect (2–4 °C) was separated from the cold Arctic water by a Polar Front at ca. 73.79°N. A strong stratification in the Arctic water was caused by ice melt. Although the ice edge was found as far north as ca. 75.5°N, spreading of melting water up to the Polar Front led to strong surface water stratification (Fig. 2). The maximum ice cover in this part of the Barents Sea is usually at the Polar Front. Thus, stratification is strong from the Polar Front and northward to the ice edge, forming a "functional marginal ice zone". Stratification weakened toward south and disappeared in the Atlantic water (Fig. 2). During the summer cruise, the spreading of fresh water was evident in all the stations, but the stratification was strongest in the Arctic side (Fig. 2).

### 3.2. Suspended biomass (POC, PON, CHL, TEP and phytoplankton)

The variation in the depth-integrated suspended biomass in the upper 50 m is summarized in Table 2. There was almost an order of magnitude difference between the background winter concentration (2.1–3.6 g POC m$^{-2}$; 0.3–0.6 g PON mg$^{-2}$) and the maximum spring values (14–34 g POC m$^{-2}$; 2.5–5.1 g PON mg$^{-2}$), while the summer concentrations were intermediate (7–16 g POC m$^{-2}$; 1.1–2.6 g PON mg$^{-2}$). The vertical distribution of the organic particles reflected the stratification of water column. In winter, POC and PON were relatively uniformly distributed in the weakly stratified water column. In spring, the bulk of the suspended particles in the strongly stratified Arctic water was in the upper 50 m water column, while in the deeply mixed Atlantic water, elevated particle concentrations reached 90–120 m depth. In summer, the vertical distribution pattern of the biomass concentration was similar to the spring situation, except that the deep mixing in the Atlantic water was less evident due to stronger salinity stratification. The POC/PON molar ratio of the suspended organic particles ranged from 6.5 to 9 (mean
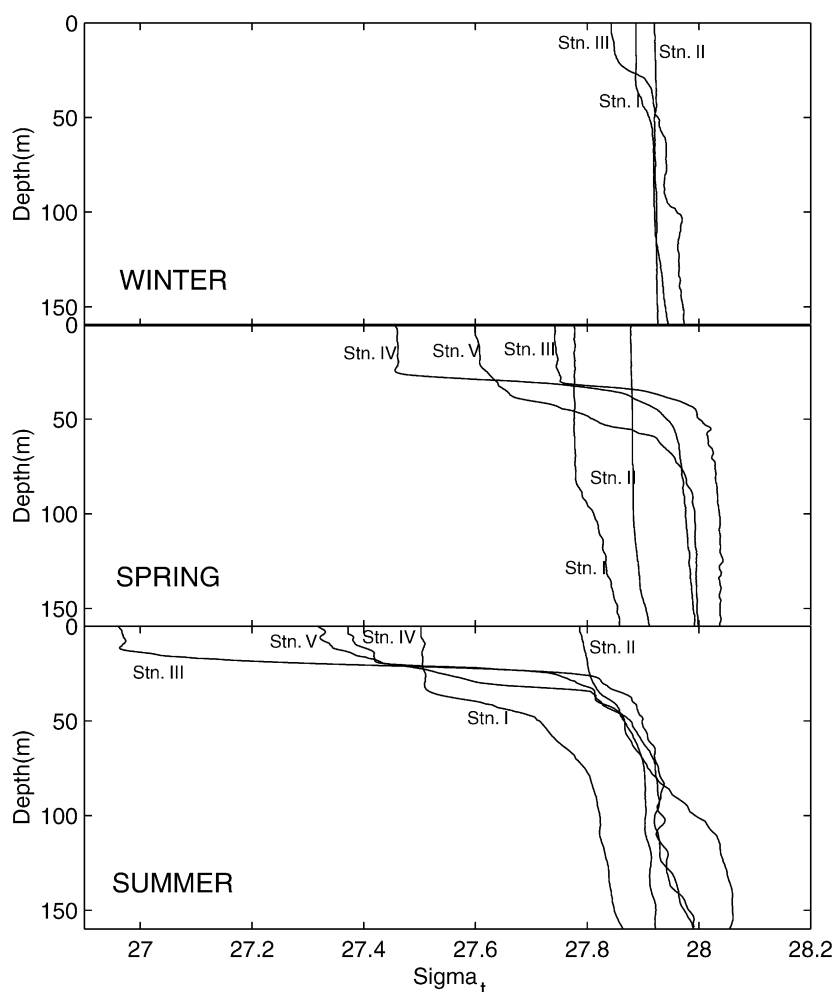
Fig. 2. The water density profiles (expressed as sigma$_t$) during the winter, spring and summer cruises at the sediment trap stations (station labels on curves).

7.6) during all the investigated periods (Table 2) and was relatively close to the Redfield ratio (6.6).

The seasonal differences were most pronounced in the concentration of suspended pigments. Compared to the CHL winter values ($<1$ mg CHL m$^{-2}$ in Arctic and 2.7 mg m$^{-2}$ in Atlantic water), the concentration increased by two orders of magnitude in spring (225–380 mg CHL m$^{-2}$) and one order of magnitude in summer (30–100 mg CHL m$^{-2}$). The relative proportion of phototrophic component in the total biomass was clearly highest during spring (CHL/POC ratio ca. $10-16 \times 10^{-3}$) and lowest during winter (CHL/POC $0.1-1.3 \times 10^{-3}$). The winter biomass of diatoms and

P. pouchetii (single-celled form) was $<1$ g C m$^{-2}$. A strong P. pouchetii bloom prevailed during the spring cruise, with highest intensity in the Atlantic waters (up to 8.5 g C m$^{-2}$) and decreasing towards northern stations (1.3–3.7 g C m$^{-2}$). Due to the weak stratification in the Atlantic water, substantial P. pouchetii biomass was mixed down to 90 m. Interestingly, single-celled form of P. pouchetii contributed considerably (on average 47%) to the total biomass of the species in spring. Diatoms were abundant all over the transect (1.8–2.4 g C m$^{-2}$, however, 0.4 g C m$^{-2}$ Stn. II), but their relative importance was higher in the stratified Arctic water. The summer plankton com-

Table 2
Standing stock of suspended biogenic matter in the upper 50 m water column at the sediment trap stations

| Cruise | ALV I | | | ALV II | | | | | ALV III | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Station/water mass | I/AT | II/PF | III/AR | I/AT | II/AT (PF) | III/AR | IV/AR | V/AR | I/AT | II/AT | III/AR | IV/AR | V/AR |
| POC (g C m$^{-2}$) | 2.14 | 3.59 | 3.11 | 34.37 | 18.63 | 25.38 | 26.03 | 14.54 | 13.28 | 15.52 | 8.82 | 10.9 | 7.5 |
| PON (g N m$^{-2}$) | 0.31 | 0.56 | 0.4 | 5.11 | 3.33 | 3.71 | 3.92 | 2.53 | 2.08 | 2.6 | 1.35 | 1.76 | 1.09 |
| PNMC (g C m$^{-2}$) | 2.05 | 2.61 | 2.46 | 18 | 12.13 | 10.17 | 8.94 | 7.67 | 8.31 | 9.62 | 8.55 | 8.26 | 5.57 |
| CHL (mg m$^{-2}$) | 2.7 | 0.3 | 0.7 | 378.1 | 277.4 | 364.4 | 250.5 | 224.8 | 33.3 | 80 | 98.8 | 80.3 | 35.5 |
| PHAEO (mg m$^{-2}$) | 1.1 | 1.1 | 1.2 | 76.1 | 58.5 | 109.1 | 70.9 | 54.5 | 6.9 | 10.6 | 53 | 100.7 | 24.8 |
| TEP (g xant. eq. m$^{-2}$) | 0.42 | 0.24 | 0.61 | 1.59 | 9.7 | 5.14 | 7.35 | 13.55 | 3.78 | 3.81 | 9.98 | 3.46 | 1.27 |
| POC/PON (molar) | 8.2 | 7.4 | 9.0 | 7.8 | 6.5 | 8.0 | 7.7 | 6.7 | 7.4 | 7.0 | 7.6 | 7.2 | 8.1 |
| CHL/POC ($\times 10^{-3}$) | 1.3 | 0.1 | 0.2 | 11 | 14.9 | 14.4 | 9.6 | 15.5 | 2.5 | 5.2 | 11.2 | 7.4 | 4.7 |
| Diatoms (g C m$^{-2}$) | 0.22 | 0.53 | 0.69 | 2.4 | 0.36 | 2.36 | 1.83 | 2.14 | 1.34 | 1.95 | 2.04 | 0.49 | 0.29 |
| *P. pouchetii* (g C m$^{-2}$) | 0.33 | 0.38 | 0.39 | 8.49 | 2.77 | 3.69 | 2.43 | 1.33 | 0.5 | 0.33 | 4.69 | 0.9 | 0.36 |

Water mass as in Table 1.

munity was diverse with no clear dominants. The most abundant organisms were unidentified flagellates (size 2–10 μm). Only at the ice edge (Stn. III) a single-celled *P. pouchetii* bloom (ca. 4.7 g C m$^{-2}$) and an elevated biomass of diatoms (ca. 2 g C m$^{-2}$) were encountered.

The concentration of suspended TEP was < 1 g xant. eq. m$^{-2}$ in winter, and 5–14 g xant. eq. m$^{-2}$ in spring, except in Stn. I (1.6 g xant. eq. m$^{-2}$) with intense *P. pouchetii* bloom. Apart from a weak correlation ($r = 0.3$) with suspended diatom biomass, there was no clear relationship between TEP concentration and any particulate group of plankton organisms. During the summer cruise, TEP concentration remained 3–4 g xant. eq. m$^{-2}$ (Table 2), except at the

ice edge (Stn. III; ca. 10 g xant. eq. m$^{-2}$) and in the northernmost Stn. V (1.3 g xant. eq. m$^{-2}$).

### 3.3. Vertical flux of particulate organic carbon, nitrogen, pigments and TEP

The vertical fluxes of POC in winter were 60–70 mg C m$^{-2}$ day$^{-1}$ in the Atlantic water and 20–50 mg C m$^{-2}$ day$^{-1}$ in the Arctic water (Fig. 3). The difference in the water masses was also reflected in the PON sedimentation (9 mg N m$^{-2}$ day$^{-1}$ in the Atlantic water and < 6 mg N m$^{-2}$ day$^{-1}$ in the Arctic water). There was almost no decrease of vertical flux with depth in the upper 200 m. Vertical fluxes of CHL (< 0.2 mg m$^{-2}$ day$^{-1}$) and PHAEO (< 0.4 mg m$^{-2}$
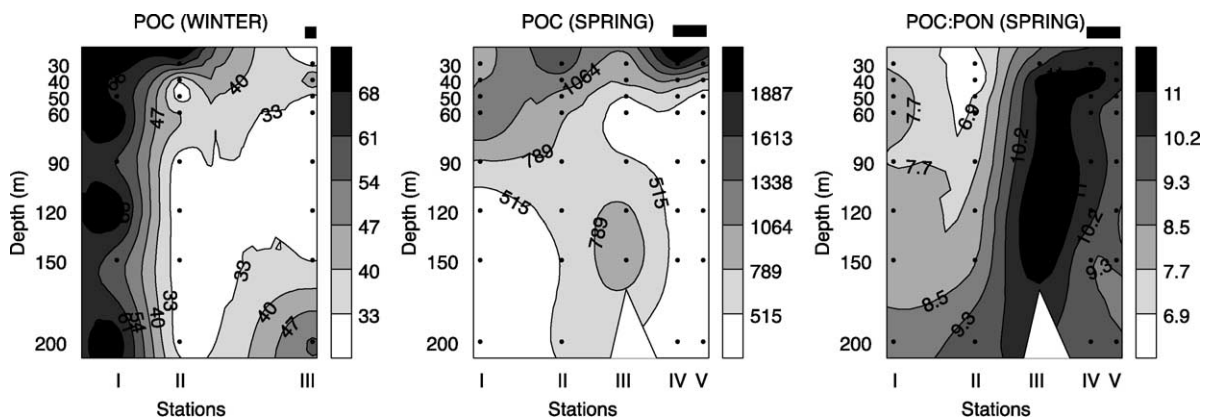


Fig. 3. The spatial variability in the vertical flux of POC during winter and spring cruises and POC/PON molar ratio of the settling material during spring. X-axis is proportional to the distance between the stations. The locations of the data points used for interpolation are shown with dots. The black bars on the right above the plots depict the 50–70% (winter) or 50–80% (spring) ice cover. Part of the bottom topography is shown with white overlay (spring only).

day$^{-1}$) were consistent with the negligible concentration of suspended pigments.

The vertical fluxes of POC and PON in spring were highest among the investigated seasons, 200–1500 mg C m$^{-2}$ day$^{-1}$ and 30–230 mg N m$^{-2}$ day$^{-1}$, respectively (Fig. 3). Much of the particulate vertical flux pattern correlated with the water column stratification. In the Arctic water and MIZ, the vertical flux was >500 mg C m$^{-2}$ day$^{-1}$, only above 50 m and decreased sharply thereafter. In the well-mixed Atlantic water, the vertical flux rates >500 mg C m$^{-2}$ day$^{-1}$ extended down to 90 m depth and below the vertical flux were similar or slightly higher (200–500 mg C m$^{-2}$ day$^{-1}$) than in the Arctic water. Closer to the Central Bank (Stn. III), the vertical flux did not decrease with depth, possibly because of the specific

hydrography and downward mixing associated with the specific bottom topography. The vertical flux of CHL in the upper mixed layer was 10–30 mg m$^{-2}$ day$^{-1}$ and the pattern generally paralleled that of POC (Fig. 4). In the Arctic water, the highest vertical flux of CHL was confined to the upper 50 m, and dropped to <5 mg m$^{-2}$ day$^{-1}$ below. In the weakly stratified Atlantic water, the elevated vertical flux of CHL (10–21 mg m$^{-2}$ day$^{-1}$) extended down to 90 m, and decreased to <5 mg m$^{-2}$ day$^{-1}$ thereafter. The vertical flux of PHAEO was 4–14 mg m$^{-2}$ day$^{-1}$, and the pattern was somewhat opposite to that of CHL (Fig. 4), i.e. the vertical flux of PHAEO in the Arctic water increased below the mixed layer (>12 mg m$^{-2}$ day$^{-1}$; Stn. IV) with little concomitant decrease with depth. However, in the Atlantic water,
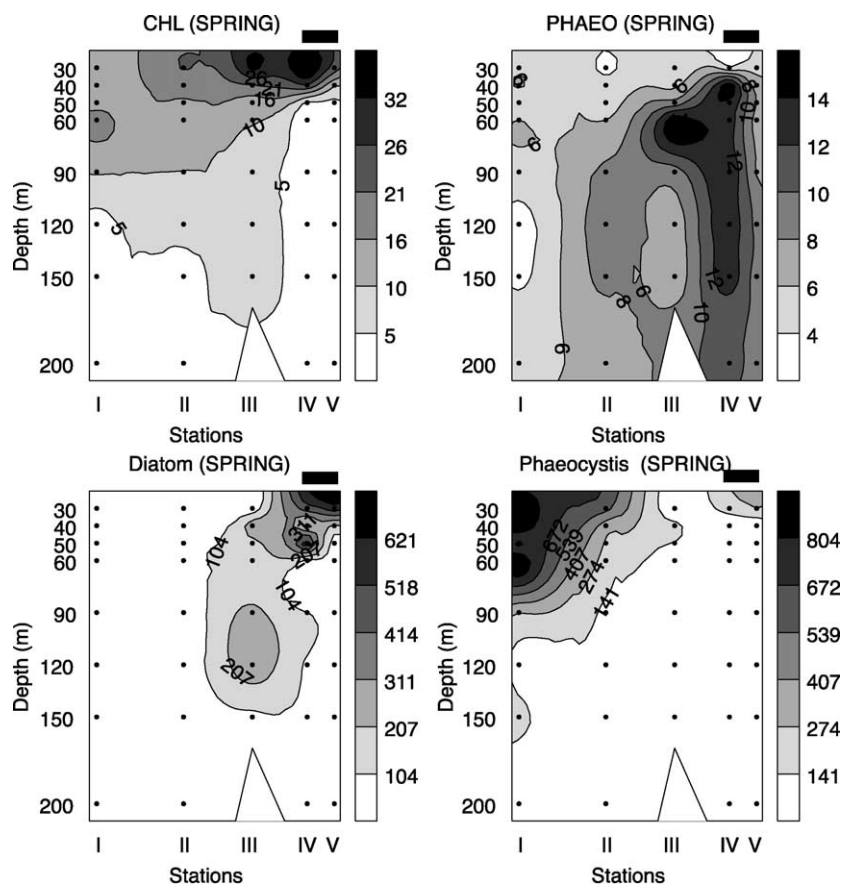


Fig. 4. The spatial variability in the vertical flux of CHL, PHAEO and the dominant groups of phytoplankton (diatoms and *P. pouchetii*) during spring.

the vertical flux of PHAEO was generally <6 mg $m^{-2}$ $day^{-1}$, but 6–10 mg $m^{-2}$ $day^{-1}$ at 60–200 m in Stn. II.

The vertical fluxes of POC and PON in summer were 100–400 mg C $m^{-2}$ $day^{-1}$ (Fig. 5) and 10–70 mg N $m^{-2}$ $day^{-1}$, respectively. The vertical flux was lower in the Arctic water and MIZ (generally <150 mg C $m^{-2}$ $day^{-1}$) compared to the Atlantic water. The vertical flux of CHL was generally <1.2 mg $m^{-2}$ $day^{-1}$, and only slightly elevated (0.8–2 mg $m^{-2}$ $day^{-1}$) in the upper layers (30–50 m) of Stns. II and III. The vertical flux of pigments continued in deeper layers (50–120 m) in the form of PHAEO (3–4.5 mg $m^{-2}$ $day^{-1}$). In the Arctic water, the vertical flux of PHAEO was generally <1 mg $m^{-2}$ $day^{-1}$ (Fig. 5).

### 3.4. Vertical fluxes of pico-, nano- and microplankton carbon and zooplankton faecal pellets

The vertical fluxes of PNMC in winter (ca. 10 mg C $m^{-2}$ $day^{-1}$ in the Atlantic water and 20–30 mg C $m^{-2}$ $day^{-1}$ in the Arctic water) were dominated by unidentified flagellates and were consistent with the low suspended biomass.

In spring, the vertical flux of PNMC was generally 150–900 mg C $m^{-2}$ $day^{-1}$ and corresponded to ca. half of the POC vertical flux. The spatial pattern of PNMC flux was generally similar to that of POC, although the species composition was drastically

different in the Atlantic and Arctic waters. At the ice edge (Stns. IV and V), the vertical flux of PNMC was dominated by diatoms (300–600 mg C $m^{-2}$ $day^{-1}$) and was mainly restricted to the upper 50 m (Fig. 4). The dominant species were *T. antarctica* (30–500 mg C $m^{-2}$ $day^{-1}$), in Stn. III also the resting spores of *T. antarctica* (50–150 mg C $m^{-2}$ $day^{-1}$), and to a lesser extent *Porosira glacialis* (ca. 30–40 mg C $m^{-2}$ $day^{-1}$). The role of diatoms in the vertical flux decreased along the north–south gradient. *P. pouchetii* dominated the vertical flux of PNMC (up to 900 mg C $m^{-2}$ $day^{-1}$) in the Atlantic water, and contributed significantly (200–270 mg C $m^{-2}$ $day^{-1}$; see also Fig. 4) at the 30 m depth in northernmost Arctic station. In the Atlantic water, the single-celled form of *P. pouchetii* prevailed in the sediment traps (about 80%), while in the Arctic water, almost equal shares of colonial and single-celled forms were observed. In the Atlantic water, the vertical flux of *P. pouchetii* was 60–150 mg C $m^{-2}$ $day^{-1}$ even at depths >90 m. Occasionally unidentified flagellates (6–10 μm size) were abundant in the sediment traps (about 40 mg C $m^{-2}$ $day^{-1}$), while other organisms did not contribute significantly to the vertical flux as recognizable cells.

During summer, the vertical flux of PNMC was on average 40–150 mg C $m^{-2}$ $day^{-1}$. The species composition was quite variable; diatoms contributed about 10–50 mg C $m^{-2}$ $day^{-1}$ (*Chaetoceros densus*, *C. socialis*), dinoflagellates 5–30 mg C $m^{-2}$
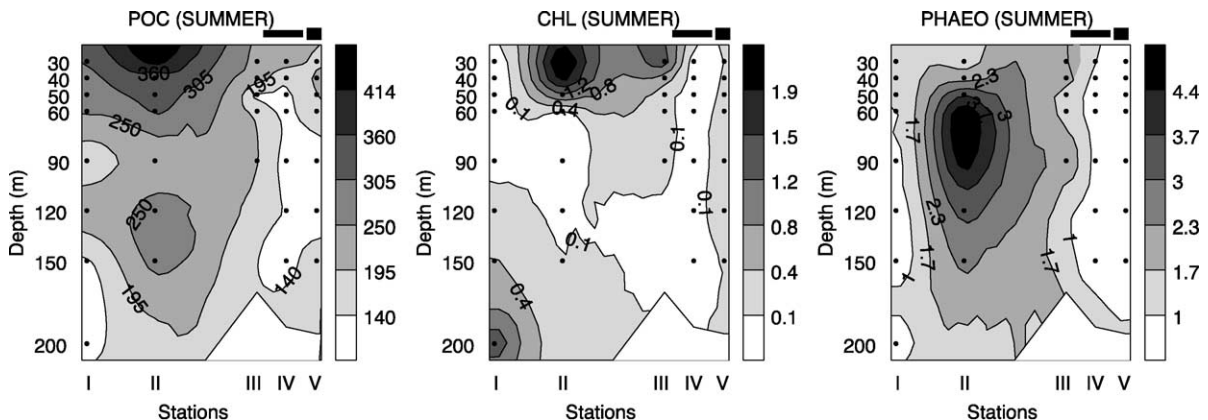


Fig. 5. The spatial variability in the vertical flux of POC, CHL and PHAEO during summer. The thin and thick bars on the right above the plots depict the 20–50% and 50–80% ice cover, respectively.

day $^{-1}$, other flagellates 30–70 mg C m $^{-2}$ day $^{-1}$ (*Ochromonas crenata*, *Dinobryon balticum* and unidentified flagellates). *P. pouchetii* contributed significantly to the vertical flux in Stn. III (20–80 mg C m $^{-2}$ day $^{-1}$; single-celled form only), which was consistent with the observed bloom in the water column at that station.

The vertical flux of zooplankton faecal pellet carbon (FPC) was generally <1 mg C m $^{-2}$ day $^{-1}$ (max 3.5 mg C m $^{-2}$ day $^{-1}$) in winter, and ranged from 2 to 260 mg C m $^{-2}$ day $^{-1}$ during spring and summer. In spring and summer, the FPC vertical flux varied with depth and between stations. At any given station, FPC vertical flux was generally relatively low at 30 m depth, increased at 40–90 m, and decreased again at deeper depths. In spring, the FPC vertical flux at 50 m increased from the *Phaeocystis*-dominated southern station (40 mg C m $^{-2}$ day $^{-1}$; Stn. I) to diatom-dominated northern stations (150 and 130 mg C m $^{-2}$ day $^{-1}$; Stns. IV and V, respectively). However, in the *Phaeocystis*-dominated and diatom-poor Stn. II (see Table 2), FPC vertical flux increased with depth from 19.3 mg C m $^{-2}$ day $^{-1}$ at 50 m to 100–130 mg C m $^{-2}$ day $^{-1}$ at 60–90 m. In summer, the FPC vertical flux was highest in the northernmost Stn. V (160 mg C m $^{-2}$ day $^{-1}$ at 50 m), but also in Stn. II (170 mg C m $^{-2}$ day $^{-1}$ at 50 m and 260 mg C m $^{-2}$ day $^{-1}$ at 60 m), and lower (<35 mg C m $^{-2}$ day $^{-1}$) elsewhere. For FPC production and retention during the cruises, see Wexels Riser et al. (2002).

### 3.5. Biochemical composition of sinking particles and loss rates

In winter, the POC/PON molar ratio of sinking particles was generally between 7 and 9, and without any consistent pattern along the latitudinal or depth gradients. The CHL/POC ratio (<2.5 × 10 $^{-3}$) of the sinking particles was consistent with the negligible concentrations of CHL in the water column and sediment traps. A clear pattern in the POC/PON ratio of the sinking particles along the north–south transect was evident in spring. The ratio was elevated (>10) in the diatom-dominated Arctic water, compared to the strongly *P. pouchetii*-dominated and deeply mixed Atlantic water (generally <8). In the Arctic water, the POC/PON ratio decreased with depth, while in the Atlantic water, a more usual increase with depth

was found. CHL/POC ratio was typically around 20 × 10 $^{-3}$ in the upper layers and generally <10 × 10 $^{-3}$ in deeper layers. The decrease was more pronounced in the stratified Arctic water (CHL/POC <3 × 10 $^{-3}$). In summer, the POC/PON ratio of the sinking particles was around 7–9. The CHL/POC ratio was generally <2.5 × 10 $^{-3}$ (often <0.5 × 10 $^{-3}$), indicating that the sinking particles were relatively CHL poor.

The daily sedimentation loss rates of POC remained in an order of a few percent. In winter, the loss rates were elevated in the Arctic water (3–5% day $^{-1}$ above 50 m; 1–3% day $^{-1}$ below), compared to the Atlantic water (1–1.6% day $^{-1}$ above 50 m; <1% day $^{-1}$ below). This reflects relatively higher suspended POC content and lower sedimentation rates in the Arctic water compared to the Atlantic water mass. In spring, the daily sedimentation loss rates of POC were up to 6% day $^{-1}$ above 50 m and 1–2% day $^{-1}$ below. During summer, the POC sedimentation loss rates remained <4% day $^{-1}$ above 50 m and <2% day $^{-1}$ below.

## 4. Discussion

### 4.1. Seasonality of the vertical flux

Our results revealed large differences in the vertical flux between the three seasons. Within each season, differences along the north–south transect, i.e. the Arctic water vs. Atlantic water, were apparent. Though, often the spatial differences were in the composition, rather than in the quantity of the sinking particles. An exception to this was the winter situation, when the vertical flux in the Atlantic water clearly exceeded the values in the Arctic water (60 vs. 30 mg C m $^{-2}$ day $^{-1}$). Interestingly, this difference between the water masses was inversely correlated with the concentration of suspended POC, which was higher in the Arctic water, and consequently translated into higher daily sedimentation loss rates of POC in the Atlantic water. This suggests a difference in the particle properties between the two water masses: in winter, the Arctic water being characterized by elevated concentration of slowly sinking particles and the Atlantic water by relatively fewer fast sinking particles. In the light of the C/N ratio of sinking particles (7–8) and lack of increase of the vertical

flux near the bottom, we consider resuspension an insignificant factor in fueling the particle sedimentation. Judged upon the consistent vertical profiles of major nutrients (nitrate, phosphate and silicate; see Reigstad et al., 2002) and negligible concentration of CHL in the water column and sediment traps, our vertical flux estimates are indicative to the true winter situation prior to the onset of the vernal primary production. To the best of our knowledge, this is the first time prebloom winter values of vertical flux have been estimated from the central Barents Sea.

The vertical flux of POC in the Barents Sea MIZ is known to be high during spring. Andreassen and Wassmann (1998) estimated $400-1100$ mg C m$^{-2}$ day$^{-1}$ in the upper $20-100$ m and $200-300$ mg C m$^{-2}$ day$^{-1}$ at 200 m in late May 1993, which is within the range of our estimates. In May/June 1984, Wassmann (1989) estimated a vertical export of POC below the euphotic zone ($40-60$ m) ca. 250 mg C m$^{-2}$ day$^{-1}$ in the central Barents Sea. In the present study, the vertical export of POC from the upper mixed layer (50 m) was approximately 500 mg C m$^{-2}$ day$^{-1}$ in the MIZ. At shallower depths (30 and 40 m), the vertical flux of POC was up to 2000 mg C m$^{-2}$ day$^{-1}$. This indicates that much of the regulation and attenuation of vertical flux takes place in the upper layers and over short vertical distances. The POC input of about 250 mg C m$^{-2}$ day$^{-1}$ into the deep layers (200 m) is comparable to upwelling areas (e.g. Pilskaln et al., 1996), but generally more than in coastal and shelf areas (Davies and Payne, 1984; Peña et al., 1996, 1999; Romero et al., 2000; Roy et al., 2000). In spring, relatively large proportion of the vertical flux was contributed by intact phytoplankton, which could also be seen from the elevated sedimentation rate of CHL.

The vertical flux in summer was generally $200-400$ mg C m$^{-2}$ day$^{-1}$ in the upper layers, with the higher end of the range in the Atlantic water. The attenuation of the POC vertical flux with depth was relatively weak and the vertical flux at $150-200$ m remained $120-260$ mg C m$^{-2}$ day$^{-1}$. These estimates generally exceed earlier reports (ca. $80-118$ mg C m$^{-2}$ day$^{-1}$) during summer in the central Barents Sea (Wassmann, 1989; Wassmann et al., 1994). In contrast to the spring season, the vertical flux of CHL in summer was only $<2$ mg m$^{-2}$ day$^{-1}$. This is in accord with the tight coupling between phytoplankton

growth and grazing by microzooplankton during the summer cruise (Verity et al., 2002). Verity et al. (2002) estimated that $64-97\%$ of the daily CHL production in the surface layer was lost by grazing, mainly by microzooplankton, leaving little for sedimentation. The highest vertical flux of pigments was found in Stn. II, with up to 2 mg m$^{-2}$ day$^{-1}$. CHL flux at 30 and 40 m depth continued as elevated vertical flux of PHAEO ($1-5$ mg m$^{-2}$ day$^{-1}$) below. This coincided with the elevated vertical flux of zooplankton faecal pellets ($100-260$ mg C m$^{-2}$ day$^{-1}$) in Stn. II. However, elevated vertical flux of faecal pellets was also observed in Stn. V (up to 160 mg C m$^{-2}$ day$^{-1}$) with no signal of elevated PHAEO sedimentation. The settling faecal pellets in Stn. V might have originated form carnivorous or detritovorous zooplankton as opposed to herbivorous zooplankton in Stn. II. It is more difficult to formulate conceptual scenarios about the vertical flux regulation during the summer cruise. Apparently, a major part of the phytoplankton production was channelled into the microbial food web (Verity et al., 2002). The vertical flux of organic particles in the Atlantic water exceeded the corresponding values in the MIZ. In contrast to the spring cruise, this elevated flux in the Atlantic water cannot be easily ascribed to physical downward mixing, which was probably limited due to the salinity stratification. The vertical flux pattern of CHL does not correlate well with any of the phytoplankton groups, suggesting that no single group dominated the sedimentation of phototrophic cells. Indeed, the species composition of the planktonic organisms found in the sediment traps during summer was much more diverse compared to the strong dominance of only a few species in spring (see below).

The interannual variation of vertical flux in the Barents Sea is determined by the dynamics of the inflowing warm, nutrient-rich Atlantic Water, which determines the extent of ice cover and imports variable amounts of overwintering zooplankton (Slagstad and Wassmann, 1991, 1996). Slagstad and Wassmann (1996) used a 3-D numerical model to estimate that the average annual vertical export of POC in the Barents Sea can vary from about 17 g C m$^{-2}$ during cold years (e.g. 1981) to 39 g C m$^{-2}$ during warm years (e.g. 1984). Based on the above calculation, we can expect approximately 2.3 times difference in the vertical export during warm and cold years. Thus, the

interannual variability in the vertical flux of POC is less than our estimated ca. four times difference during spring and summer at respective depths, and earlier reported seasonal variability in the Barents Sea (Andreassen and Wassmann, 1998; Wassmann, 1989; Wassmann and Slagstad, 1993; Wassmann et al., 1994).

### 4.2. Diatom vs. Phaeocystis scenarios of the vertical flux during spring

The spring cruise provided a good example of the vertical flux in water masses with contrasting planktonic community and stratification regime. Although *P. pouchetii* was a major phytoplankton species all over the transect, the relative proportion of diatoms increased from the mixed Atlantic water to the stratified Arctic water. This agrees with the hypothesis that *P. pouchetii* is a better competitor when vertical mixing is deep and not too rapid, while diatoms tend to dominate in stratified waters with shallow mixed depth (Goffart et al., 2000; Palmisano et al., 1986). In the Arctic water, we could expect a strong vertical flux pulse dominated by fast sinking diatoms. Alternatively, in the presence of an abundant herbivorous community, we could expect a decrease, but faecal pellet-dominated vertical flux. Clearly, the later scenario prevailed. Nevertheless, a substantial amount of organic particles ($250-400$ mg C m$^{-2}$ day$^{-1}$) was introduced to $150-200$ m depth in the Arctic water.

In the Atlantic water, the suspended and settling phytoplankton was dominated by *P. pouchetii*. The role of *P. pouchetii* in the carbon cycle is far from clear, and scenarios from aggregate formation (Passow and Wassmann, 1994) and substantial sedimentation (Wassmann et al., 1990) to grazing by zooplankton (Hansen et al., 1994) have been reported. During the spring cruise, we found substantial sedimentation of *P. pouchetii* cells in the Atlantic part of the transect ($>270$ mg m$^{-2}$ day$^{-1}$ down to 90 m in Stn. I). The vertical flux of *P. pouchetii* was less in Stn. II, possibly because of increased herbivorous grazing as indicated by the elevated vertical flux of faecal pellets between 60 and 90 m ($30-40$ mg m$^{-2}$ day$^{-1}$ in Stn. I vs. $100-130$ mg m$^{-2}$ day$^{-1}$ in Stn. II). At 150 and 200 m depth, the vertical flux of *P. pouchetii* had decreased to ca. 10% of the maximum rates. Differences in the mesozooplankton grazing activity, as judged upon the faecal

pellet production and sedimentation (Wexels Riser et al., 2002), suggest that the decrease of POC vertical flux was relatively more due to herbivorous grazing at Stn. II and more due to other processes, e.g. microbial decomposition, at Stn. I. The presence and dietary preferences of mesozooplankton in *P. pouchetii*-dominated systems can have a significant effect on the vertical flux pattern. Because of the controversy and uncertainty in the fate of *P. pouchetii* and trophic links to zooplankton, it is difficult to outline general scenarios. The vertical flux of *Phaeocystis* in the nonstratified Atlantic water cannot be unambiguously attributed to gravitational sinking alone. It is likely that vertical mixing transported substantial quantities of *Phaeocystis* cells down to mid-water depths. The production and fate of *P. pouchetii* seem to be controlled by deep mixing, which gives a competitive advantage over diatoms (Goffart et al., 2000), but also transports significant amounts of carbon to the deeper layers, and zooplankton activity.

Comparing the vertical flux of POC at 200 m reveals that it was even somewhat lower in the diatom-dominated Arctic water (Stns. IV and V; ca. 250 mg C m$^{-2}$ day$^{-1}$) compared to the *P. pouchetii*-dominated Atlantic water ($325-550$ mg C m$^{-2}$ day$^{-1}$). According to Reigstad et al. (2002), the new production, estimated from nitrate depletion since winter, was twice as high in the Atlantic water than in the MIZ, probably because more new nutrients become available in the southern part of the transect due to deeper mixing. If we assume that export production is proportional to new production, then over a longer time scale, the potential for export production in the Atlantic water is expected to be higher. However, the export production potential is further modified by the C/N ratio of the settling or downward mixed particles, which was close to the Redfield ratio in the Atlantic water but $>10$ in the MIZ. The mean C/N ratio of sinking particles at 40 m depth in Stns. I–III was 11.2, as compared to 6.9 in Stns. IV–V. Thus, the carbon export per unit new production can vary by a factor of 1.6 (i.e. 11.2/6.9), or by a factor 1.7 if the sinking particles are assumed to have a Redfield C/N ratio. This calculation shows the uncertainty in export production assessments by using the new production estimates based on nitrate depletion and ignoring the C/N ratio of sinking particles.

In summary, during spring, we found a completely different ecological setting along the south–north gradient, with respect to (i) dominant plankton organisms (*Phaeocystis* vs. diatoms), (ii) physical forcing (vertical mixing vs. strong stratification), and (iii) magnitude of new production (Reigstad et al., 2002). Yet, the final outcome with respect to vertical flux of POC at 200 m was relatively similar, but composition of the exported material was very different.

### 4.3. The role of the planktonic community in vertical flux regulation

Herbivorous grazing was probably responsible for a large part of the disappearance of sinking diatoms in the Arctic water during spring. The vertical fluxes of CHL ($11-38$ mg m$^{-2}$ day$^{-1}$) and diatoms (up to 600 mg C m$^{-2}$ day$^{-1}$) ceased abruptly between 40 and 50 m, and transformed into a vertical flux of PHAEO ($7-13$ mg m$^{-2}$ day$^{-1}$). Faecal pellet carbon sedimentation was increased up to 150 mg C m$^{-2}$ day$^{-1}$ below the mixed layer in the Arctic waters (Stns. IV and V), but also in the Atlantic water (Stn. II), and contributed up to 40% of the POC vertical flux. The relative proportions of herbivory vs. carnivory and aggregate feeding in the faecal pellet production remain uncertain. Although faecal pellets are not the only source of phaeopigments, the relationship between the vertical fluxes of FPC and PHAEO suggest a tight coupling and indicate that algae were an important food source for mesozooplankton. However, data from the spring cruise suggest that at highest vertical flux rates of faecal pellets, the phaeo-

pigment vertical flux levels off (Fig. 6), possibly because the relative proportion of algae in the diet of mesozooplankton decreased. We hypothesize that mesozooplankton grazed upon the abundant sinking diatoms at the MIZ. When the algal diet becomes insufficient, mesozooplankton gradually switched to omnivory and the vertical fluxes of PHAEO and PFC became uncoupled.

During the spring cruise, only a relatively small number of phytoplankton species was found in high numbers in the sediment traps, particularly in the Atlantic water where single-celled form of *P. pouchetii* dominated. In the Arctic water, diatoms dominated by *T. antarctica* (including resting spores) were most abundant. This is in contrast to the summer cruise, when the taxonomic composition of the most abundant planktonic organisms in the sediment traps was quite broad. Unidentified flagellates with size ranges from 2 to 10 μm, *O. crenata* (Chrysophyceae), *D. balticum* (Chrysophyceae), *P. pouchetii* (single cells; in Stn. III only), were most common organisms. Diatoms were only important occasionally (*C. densus*, *C. socialis*, *T. antarctica*). To assess the species diversity in the sediment traps and water column, we used Shannon's entropy index, with *e* as a basis of logarithms, and carbon biomass of a species as abundance descriptor (Margalef, 1958). We calculated the index for every water column and sediment trap sample including all the identified species or groups of planktonic protists (including both producers and consumers) and cyanobacteria. Fig. 7 shows a box and whisker plot for every station. Although there was some variability in the species diversity between different depths, some gen-
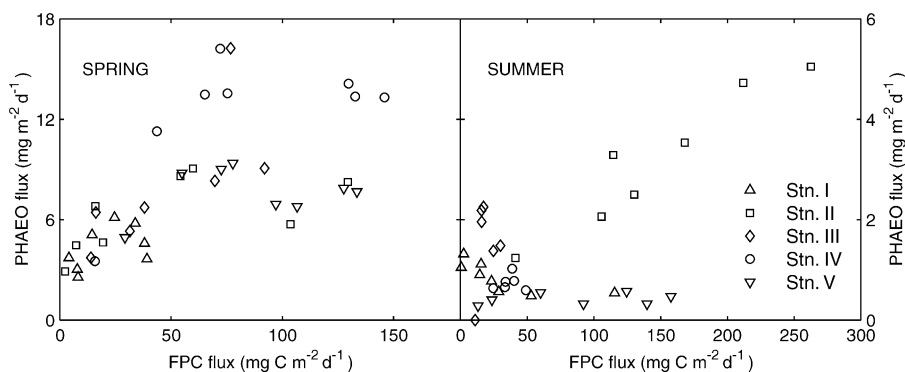


Fig. 6. The vertical flux of zooplankton faecal pellets vs. phaeopigments during spring and summer.
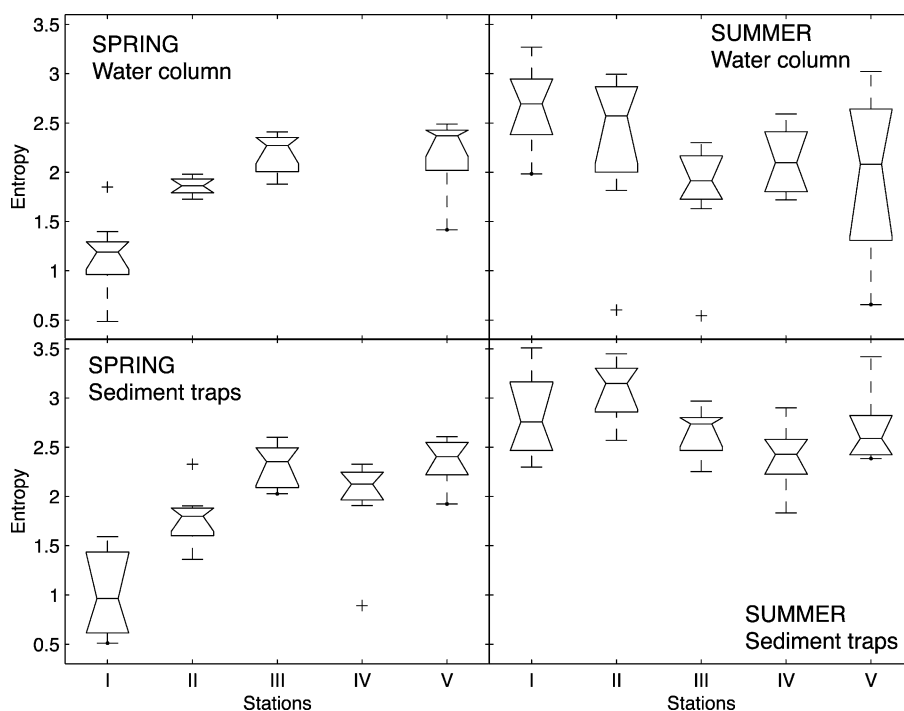
Fig. 7. Box and whisker plots of Shannon's species diversity indices from the water column and sediment traps for each station during spring and summer cruises. The boxes have lines at the lower quartile, median and upper quartile values. The whiskers are lines extending from each end of the box to show the extent of the rest of the data. Outliers are data with values beyond the ends of the whiskers.

eral trends become apparent. Firstly, the diversity indexes within the sediment traps and water column covary. Secondly, during spring, the diversity was notably lower in the Atlantic water, which was due to the strong dominance of *P. pouchetii*, increased toward north (Stns. I–III) and remained high in the Arctic water (Stns. IV–V). This spatial trend was not the case during summer, when the species diversity tended to be higher in the Atlantic water. Comparing the two seasons, the diversity was higher during summer. This suggests that compared to the spring period, the planktonic community in summer was more structured and complex. This difference in community complexity was reflected in difference in daily loss rates. On the average, the daily loss rates of POC and PON were respectively 1.7 and 1.5 times higher during spring than in summer season. Thus, our findings support the general concept that a more diverse, mature and complex planktonic community is more of a retention food web type and has a higher potential to minimize sedimentation losses from the productive layer.

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