

## Spring Bloom Development in the Marginal Ice Zone and the Central Barents Sea

Paul Wassmann<sup>1\*</sup>, Tatjana Ratkova<sup>2</sup>, Inger Andreassen<sup>1</sup>,  
Maria Vernet<sup>3</sup>, Gunnar Pedersen<sup>2</sup> & Francisco Rey<sup>4</sup>

<sup>1</sup>Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway.

<sup>2</sup>Shirshov Institute of Oceanology, Academy of Sciences of Russia, 23, Nakhimovskiy avenue 36, 117541 Moscow, Russia.

<sup>3</sup>Marine Research Division, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093–0218, USA.

<sup>4</sup>Institute of Marine Research, PO Box 1870 Nordnes, N-5024 Bergen, Norway.

With 8 figures and 1 table

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**Abstract.** The knowledge of the relative contribution of algal groups and the environmental factors that control their abundance in the marginal ice zone of the Barents Sea is rather limited. Therefore, a field investigation to study the hydrography and the phytoplankton composition of the marginal ice zone (MIZ) in the central Barents Sea was carried out along a south–north transect in May 1993. The weakly stratified Atlantic sector of the transect appeared to be in a pre-bloom state and had intermittent intrusions from the meandering Polar Front and the Norwegian Coastal Current, introducing water of a more advanced bloom state. Pico- and nanoplankton flagellates and monads dominated, with a few diatoms and *Phaeocystis pouchetii* colonies. The average new production rate of  $26 \text{ g C} \cdot \text{m}^{-2}$  as reflected by  $\text{NO}_3$  depletion in the euphotic zone, however, indicated that the vernal bloom had been in progress for some time in the Atlantic sector without leaving specific signals in the suspended fraction. The ice-edge and Polar Front area was characterized by a dominance of centric colonial diatom genera *Chaetoceros* and *Thalassiosira* with some development of *P. pouchetii*. In the densely ice-covered and stratified Arctic zone the vernal bloom was at its maximum and dominated by the diatom genera *Fragilariopsis* and *Chaetoceros*. Diatoms were limited by silicate concentrations  $< 2 \mu\text{M}$  in 32% of all samples. New production, as revealed by the C equivalent of nitrate depletion in the upper layer, ranged between  $12 \text{ g C} \cdot \text{m}^{-2}$  in the north to  $45 \text{ g C} \cdot \text{m}^{-2}$  in the meandering Polar Front, with an average of about  $27 \pm 28\% \text{ g C} \cdot \text{m}^{-2}$ . The time development of the vernal bloom in the marginal ice zone and the central Barents Sea in late May 1993, with

\*To whom correspondence should be addressed. E-mail: paulw@nfh.vit.no

its complicated zonal structure, was not from south to north, but intermittently from north to south. Later during the year the general development of the vernal bloom was, as expected, from south to north.

## Problem

The Barents Sea is a productive high-latitude marine ecosystem characterized by a relatively shallow shelf and complex hydrography which has a zonal structure (Loeng, 1991; Loeng *et al.*, 1997). The Norwegian Coastal Current follows the Norwegian shelf break northwards to the Barents Sea and turns eastward in the vicinity of North Cape, creating a band of coastal water in the southern part of the Barents Sea. Further north, a broad tongue of the warmer Atlantic waters of the Norwegian Atlantic Current flows eastward into the Barents Sea. In the north, cold Arctic waters flow into the Barents Sea from the north-east and meet the warm Atlantic water flowing from the south-west, giving rise to a distinct front, the Polar Front. The northern, central and eastern Barents Sea is seasonally covered by ice (Vinje & Kvambekk, 1991). Marginal ice zones (MIZ) are unique frontal systems (Sakshaug & Skjoldal, 1989). Melt water formation during late spring and early summer gives rise to a strong vertical stability (Slagstad, 1985) which supports a conspicuous phytoplankton bloom that follows the receding ice cover (Rey & Loeng, 1985; Slagstad & Wassmann, 1997).

Nutrient concentrations in the Barents Sea vary considerably throughout the productive part of the year and in different localities (Skjoldal & Rey, 1989). At the end of the winter, nutrient concentrations are high (about 12, 6 and  $0.9 \mu\text{M}$  of  $\text{NO}_3$ ,  $\text{Si(OH)}_4$  and  $\text{PO}_4$ , respectively) and vary only minimally over the upper 200 m due to extensive vertical mixing (Skjoldal *et al.*, 1987; P. Wassmann, unpublished results). In spring and summer the water becomes stratified along the Polar Front and the ice-covered areas because of melting of sea ice, supporting a rapid phytoplankton bloom and followed by nutrient depletion (Sakshaug & Skjoldal, 1989). Stratification is mainly due to solar radiation in the Atlantic water south of the ice edge and the Polar Front. Consequently, the phytoplankton bloom develops more slowly, but the bloom is more consistent over time due to the steady supply of nutrients from below and vertical excursion of phytoplankton is significant (Rey & Loeng, 1985). The production regime of the MIZ and the Barents Sea is thus determined by the delicate balance between (a) Atlantic and Arctic water, (b) the general meteorological conditions as reflected in the wind field and (c) the ice conditions in the previous winter (Slagstad & Wassmann, 1997). The Barents Sea is thus not entirely a true part of the Arctic, but rather an area which balances between Norwegian coastal water and Atlantic dominance in the south, Arctic dominance in the north and an extensive, climatically variable intermediate area, *i.e.* the MIZ.

As in other polar seas, phytoplankton in the Barents Sea is exposed to strong seasonal variations of day length, solar radiation and sea ice coverage. Clouds and fog reduce photosynthetic active radiation (PAR) at the surface to about half of that of a cloudless day, but even less PAR is available in the water due to low solar angle (Sakshaug & Slagstad, 1991). Finally, sea ice coverage can play an important role in reducing PAR. Ice coverage varies greatly from year to year, reflecting the

interannual dynamics of inflowing Atlantic water (Ådlandsvik & Loeng, 1991; Loeng *et al.*, 1997). The dynamics of sea ice in the Barents Sea and its suppression of primary production during the short productive period at latitudes north of 70°N are therefore capable of influencing primary production and the carbon flux dynamics of the area, both seasonally (Wassmann & Slagstad, 1993) and interannually (Slagstad & Wassmann, 1997). Studies in the Barents Sea and other areas have shown that the ice edge is potentially one of the most productive environments in the Arctic, particularly during spring time (Smith *et al.*, 1987). This is due to high local primary production (several  $\text{g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) and the long time interval of the ice-edge bloom as the ice recedes northward (Slagstad & Wassmann, 1997). In these blooms, only a few species such as the diatoms *Chaetoceros* spp. and *Thalassiosira* spp. and the haptophyte *Phaeocystis pouchetii* dominate the phytoplankton assemblage (Rey *et al.*, 1987; Druzhkov & Makarevich, 1992; Evensen, 1994; Quillfeldt, 1996).

Particular emphasis has been given previously to a section ranging from 72°30' N to 80°N in the central Barents Sea (*e.g.*, Skjoldal *et al.*, 1987; Wassmann & Slagstad, 1993). The transect crosses the zonal structure of the Barents Sea with its main water masses: Atlantic water, the Polar Front, the ice edge and Arctic water (Fig. 1a). However, our knowledge of the relative contribution of algal groups and the environmental factors that control their abundance in the MIZ is more limited. Therefore, a field program to study the role of phytoplankton composition, specific phytoplankton-related processes and rates, as well as the vertical export of carbon from the upper layers was carried out. Although detailed results on primary production (Vernet *et al.*, 1998), grazing (Hansen *et al.*, 1995), faecal pellet production (Urban-Rich, 1997) and vertical flux (Andreassen & Wassmann, 1998) have been published previously, we present here information on the hydrography, nutrient concentrations and the phytoplankton community along the transect.

## Material and Methods

Phytoplankton was collected at 18 stations during a cruise in 1993 on R/V 'Jan Mayen' from May 17 at 08:00 h to May 18 at 20:00 h in the north-western and central part of the Barents Sea. The ship moved from south to north along the transect from 72°45.017' N, 30°21.014' E to 76°32.165' N, 32°55.526' E (Fig. 1). Standard hydrographic sampling was carried out with a Neil Brown Mk III CTD-profiler mounted with a General Oceanic Rosette Sampler equipped with 5-l Niskin bottles at 18 stations, Stn. 534–551 (see Figs 1b and 3,4,5,6,7). Sampling depths were chosen at the surface, 50, 30, 10, 1 and 0.1% of surface radiation. The depth of the 0.1% light level varied between an average of 58 m in the southern and central part and 32 m in the northern part of the transect. Additional samples were taken considering the physical and biological structure of the water column down to 80 m depth as revealed by profiles of temperature, salinity as well as *in vivo* fluorescence obtained with an *in situ* fluorometer.

Water samples for the analysis of nutrients and suspended pigments were taken at a maximum of 10 depths. Methods for the analysis of nutrients, chlorophyll *a* (Chl *a*) and phaeopigments (Phaeo) (fluorometric determination) are described in Wassmann *et al.* (1990) and Wassmann (1991). Assuming maximum concentrations of 12 and 6  $\mu\text{M}$  for  $\text{NO}_3$  and  $\text{Si}(\text{OH})_4$ , respectively, which are regularly recorded in the more than 200 m deep, homogeneously mixed water column in late winter (Skjoldal *et al.*, 1987; P. Wassmann, unpublished results), the total  $\text{NO}_3$  and  $\text{Si}(\text{OH})_2$  depletion in the euphotic zone was calculated. The C equivalent of the  $\text{NO}_3$  depletion (a measure for new production) was calculated by applying the Redfield ratio.

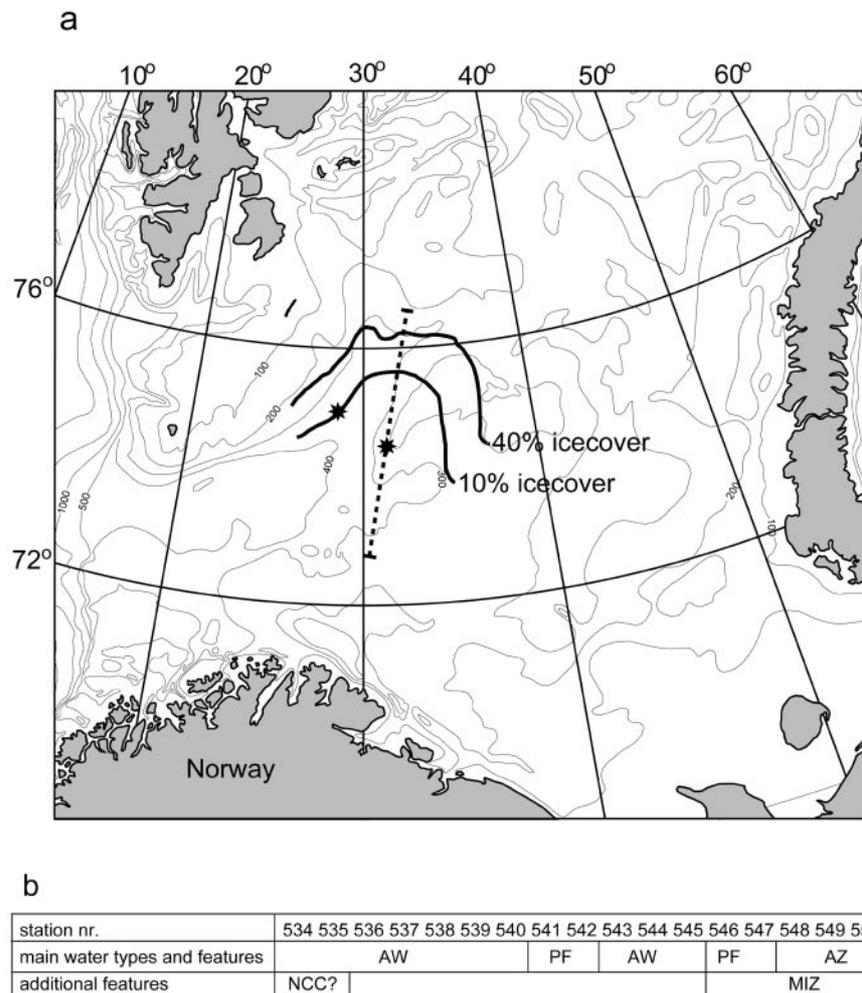


Fig. 1. a. The central Barents Sea and the investigated transect covering Atlantic water in the south, the marginal ice zone and the Polar Front in the central section and Arctic water in the north. The position of 10 and 40% ice coverage and the southernmost and northernmost sampling stations are indicated. Also shown are two stations (stars) investigated in 1987 by Wassmann *et al.* (1990). b. Position of stations 534–551 along the transect, identified water masses and the MIZ. AW, Atlantic water; PF, Polar Front; AZ, Arctic zone; NCC, Norwegian Coastal Current.

About 50 ml of sea water from three to four horizons of each station (0, 10, 25 and/or 50 m) were fixed with a glutaraldehyde-Lugol solution (Rousseau *et al.*, 1990). Phytoplankton was counted with a non-inverted light microscope furnished with a counting stage (Semina, 1978). The whole samples were gently mixed and counting of pico- and the most abundant nanoplankton algae was carried out in a Fuchs-Rosenthal counting chamber at a magnification of 400 $\times$ . Samples were allowed to settle for a week and then slowly decanted through a glass tube covered with two layers of fine-mesh nylon gauze. After gentle mixing the remaining sample was removed with a Pasteur pipette and placed into a 0.05 ml chamber. Cells were counted under a magnification of 200 $\times$ . The picoplankton fraction includes algae, cyanobacteria, heterotrophic flagellates and yeast (0.5–1.0–2.0  $\mu$ m). A comparison of picoplankton

abundance obtained with the present and an automatic epifluorescence technique revealed similar results (Ratkova *et al.*, 1999 and Verity *et al.*, 1999, respectively). Thus, the technique applied here suggests that picoplankton is adequately quantified although a underestimation of small cells during settling seems unavoidable. Epifluorescence microscopy was not available and thus we cannot distinguish between autotrophic and heterotrophic cells.

In order to count rare (usually larger) forms, a special 1.0 ml chamber was used, but as it is rather thick, only a low-power lens (magnification of  $10\times$ ) could be used. The biovolume of algae cells was calculated from the volume of appropriate stereometrical bodies (Smayda, 1978). All the taxonomic identifications were carried out in the wet samples according to the shape of cells and colonies only.

The glutaraldehyde-Lugol fixative permitted whole colonies of *Phaeocystis pouchetii* to be counted. The colonies are hollow and filled with water, and the carbon content of the colony matrix is low (Rijssel *et al.*, 1997); thus, only the cell content contributes significantly to the phytoplankton carbon. The correct quantification of the cells on the colony surface, however, is rather difficult, making biomass determination of *P. pouchetii* dubious. The *P. pouchetii* abundance is thus given as number of colonies per litre. In the case of senescent or damaged colonies the parts of the colonies were counted to reconstruct whole colonies.

## Results

### 1. Hydrography

The temperature distribution along the transect demonstrates the dominance of Atlantic water ( $2\text{--}4^\circ\text{C}$ ), which reached up to the MIZ at about  $75^\circ\text{N}$  (Stn. 547) (Fig. 2a). In the north a front was found between the Arctic and the Atlantic water as indicated by the sharp temperature gradient in the surface water. Thus, the Polar Front and the ice edge appear here at the same position. In the northern part of the transect, Arctic water with temperatures  $<1.5^\circ\text{C}$  was recorded in the upper 50 m. An additional front was recorded around  $74^\circ\text{N}$  (Stn. 541). This was part of the Polar Front east of the transect (Fig. 1a), which is situated approximately at the 200 m isobath; it sends a branch of low-temperature water westwards into the wide band of Atlantic water, which moves in a north-easterly direction. The warmest water ( $>4.0^\circ\text{C}$ ) was found in the southernmost part of the transect.

The salinity distribution indicates a similar hydrographic situation (Fig. 2b). Atlantic water that was characterized by salinities  $>35$  dominated the central and southern part of the transect. Less saline water from the meandering Polar Front and Norwegian Coastal Current east and south-west of the transect were visible at Stn. 541 and 536, respectively. Melting ice and the less saline Arctic water were clearly reflected in the decreased salinity of the MIZ and in the deeper parts of the section north of  $75^\circ30'\text{N}$ . The resulting density distribution (Fig. 2c) indicates little stratification in the Atlantic water up to about  $74^\circ\text{N}$ , while the meandering Polar Front and probably remains of melting sea ice gave rise to increased stratification between  $74$  and  $75^\circ\text{N}$ . The upper 50 to 75 m of the MIZ (Stn. 547–551) were strongly stratified. Water with increased salinity and weak stratification was recorded in the south-western part of the transect. This station might have been influenced by excursions of coastal water influenced by the Norwegian Coastal Current.

### 2. Nutrients

The distribution of nitrate, phosphate and silicate followed the hydrographic features described above (Fig. 3a–c). Compared to the winter nutrient con-

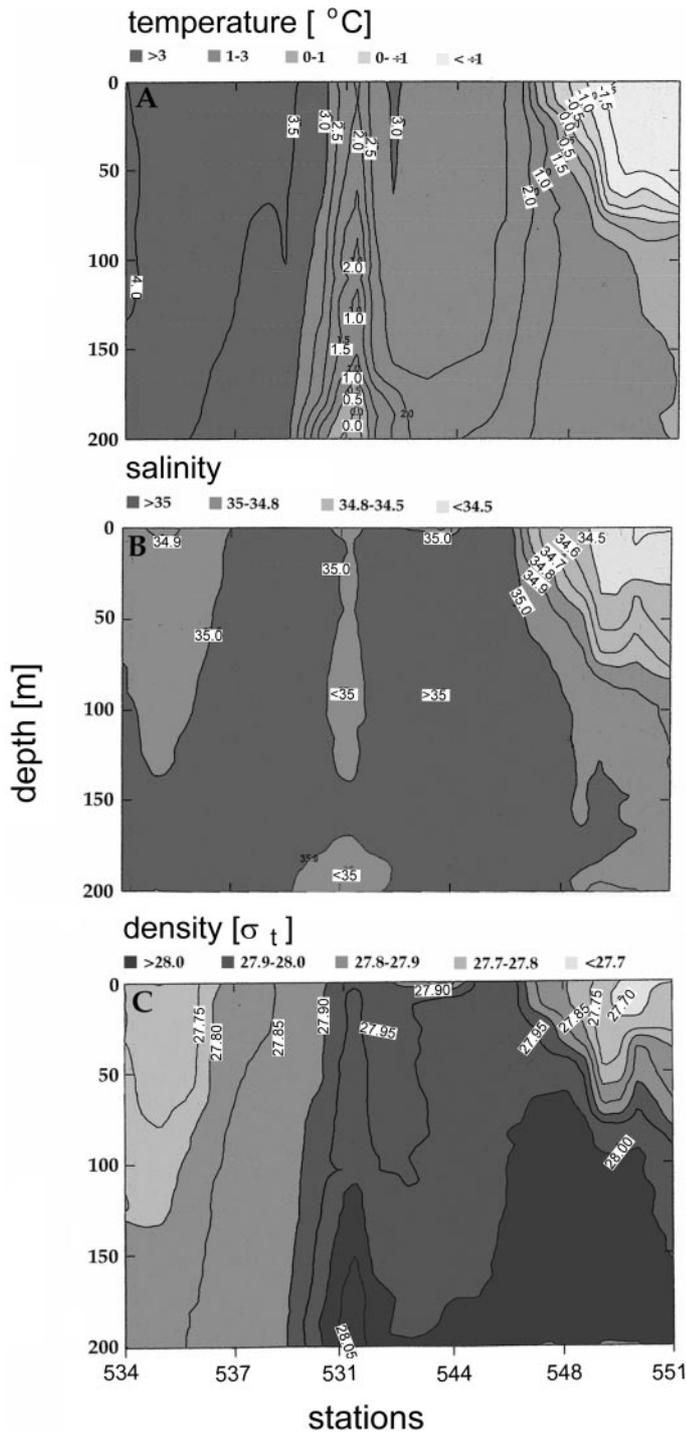


Fig. 2. Variation of temperature [°C], salinity [ $\sigma_t$ ] in the upper 200 m along the transect.

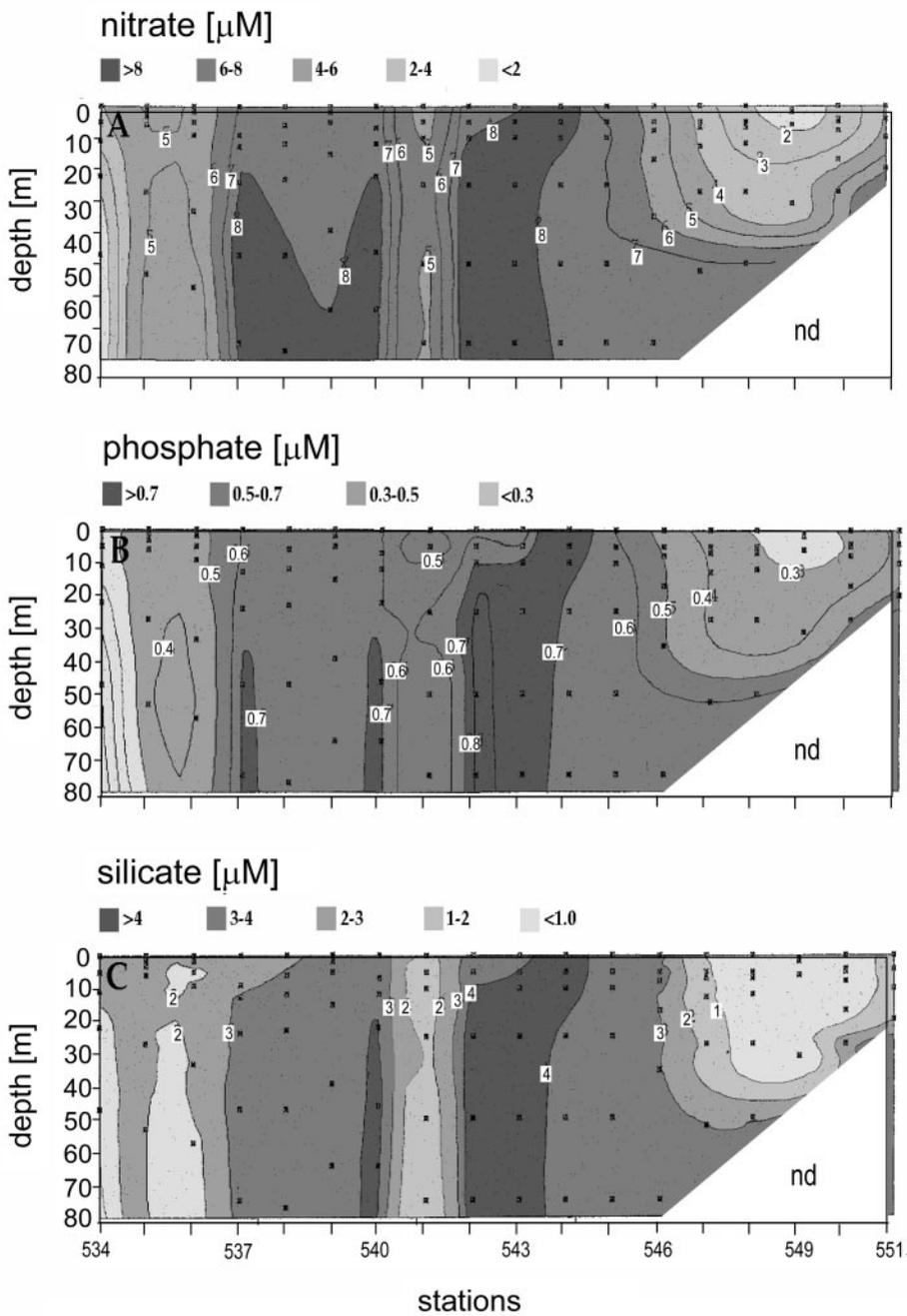


Fig. 3. Variation of nitrate [ $\mu\text{M}$ ], phosphate [ $\mu\text{M}$ ] and silicate [ $\mu\text{M}$ ] in the upper 80 m along the transect.

centrations some depletion was observed throughout the transect. The nutrient concentrations were highest in the Atlantic water and lowest in the southern part of the MIZ (around Stn. 549). The phytoplankton bloom in the MIZ left a distinct signature in the minimum in the upper 30 m, while nutrient concentrations were still high (*e.g.*, 3 to 4  $\mu\text{M}$   $\text{NO}_3$ ) in the upper layers of the northernmost part of the transect (Fig. 3a–c). The meandering Polar Front from the east (between Stn. 540 and 543) and the Polar Front (Stn. 546–548) were characterized by slightly decreased nutrient concentrations relative to the Atlantic water, implying that the spring bloom had started earlier. The relationships between  $\text{NO}_3$  and  $\text{Si}(\text{OH})_4$  concentrations (all depths) and depletion (based on integrated concentrations) were linear ( $r^2 = 0.96$  and  $0.90$ , respectively). Average new production estimates ranged between 12 and 45  $\text{g C} \cdot \text{m}^{-2}$ , with an average of about 27  $\text{g C} \cdot \text{m}^{-2}$ . The depletion of  $\text{NO}_3$  and  $\text{Si}(\text{OH})_4$  in the euphotic zone varied between 23 and 95% of the winter concentration, with an average of 52%, implying significant reduction of nutrients by mid-May.  $\text{Si}(\text{OH})_2$  concentrations ranged between 0.8 and 4.8  $\mu\text{M}$  (average 2.7  $\mu\text{M}$ ), indicating diatom proliferation and a tendency towards silicate limitation, in particular in the Polar Front and the Arctic sector. The average  $\text{Si}(\text{OH})_2$  concentration in the Arctic sector was 0.85  $\mu\text{M}$  and often close to detection limit.

### 3. Pigment concentration

The distribution of Chl *a* reflects the hydrography and the development of the phytoplankton community (Fig. 4a). The Chl *a* concentration in the Atlantic water of the southern part of the transect was generally  $< 1 \mu\text{g} \cdot \text{l}^{-1}$ . Concentrations up to 1 to 2  $\mu\text{g} \cdot \text{l}^{-1}$  were recorded at the meandering Polar Front around 74° N, probably caused by increased vertical stability. Higher Chl *a* concentrations (about 5  $\mu\text{g} \cdot \text{l}^{-1}$ ) were observed in the central part of the transect north of the meandering front. In the northern part of the transect (Stn. 547 and higher), they gradually increased, with a rapid increase in the MIZ and Polar Front area. The highest Chl *a* concentrations were found at 20 m depth at the northernmost stations, with maximum concentrations of about 14  $\mu\text{g} \cdot \text{l}^{-1}$ . An intense phytoplankton bloom was taking place in the densely ice-covered water at the time of the cruise.

Phaeopigments (Phaeo) concentrations were generally  $< 1 \mu\text{g} \cdot \text{l}^{-1}$  throughout the transect (Fig. 4b). The highest concentrations of 1.2  $\mu\text{g} \cdot \text{l}^{-1}$  were recorded in the upper layers of the MIZ at Stn. 549. Higher than average Phaeo concentrations were found in the meandering Polar Front (Stn. 541–543) and at all depths in the MIZ/Polar Front area. In the northernmost part of the transect, concentrations were low. Compared to the Phaeo concentrations a dominance of Chl *a* was recorded throughout the transect, indicating grazing activity.

### 4. Phytoplankton species

In all, a total of 103 different phytoplankton species were observed (78 diatoms, 23 dinoflagellates and two silicoflagellate species). This is a minimum estimate because some organisms were identified only to the genus level and flagellates and

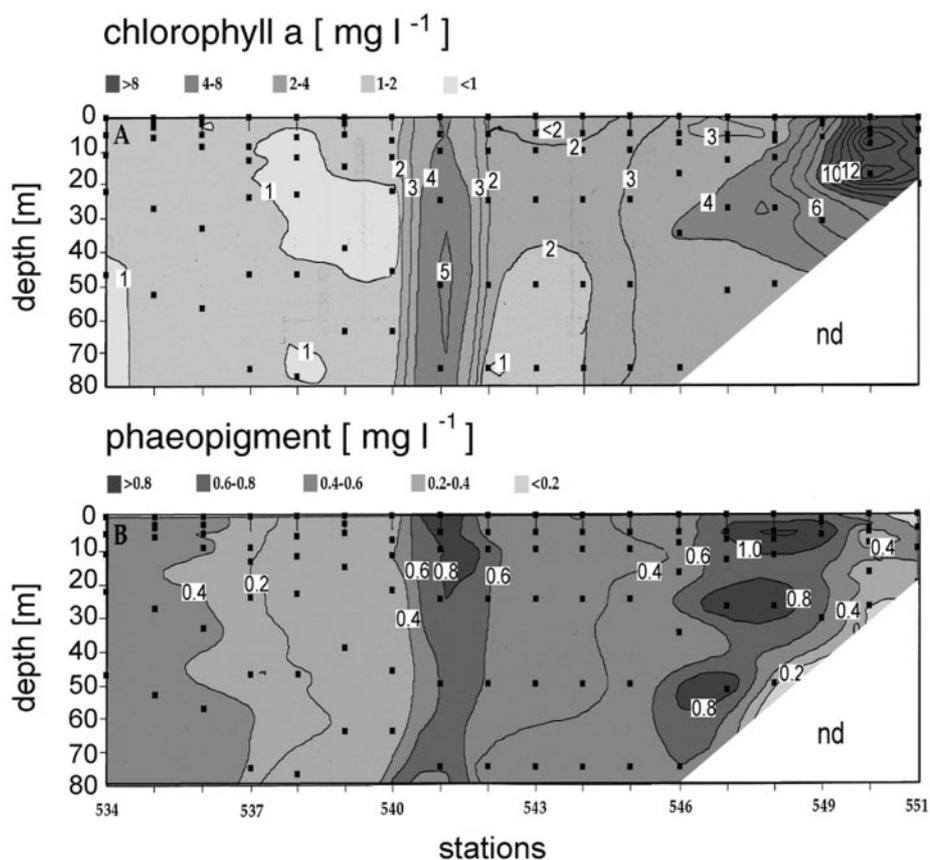


Fig. 4. Variation of chlorophyll *a* [ $\mu\text{g} \cdot \text{l}^{-1}$ ] and phaeopigments [ $\mu\text{g} \cdot \text{l}^{-1}$ ] in the upper 80 m along the transect.

coccolithophorids were identified only to higher taxa. Table 1 gives an overview over the most prominent phytoplankton species and their abundance.

Among the diatoms, *Pseudonitzschia* cf. *pseudodelicatissima* (Stn. 534–535) and *Chaetoceros socialis* (Stn. 536–545) numerically dominated the taxa identified to species level in the ice-free southern part of the transect, while *Chaetoceros decipiens*, *Porosira glacialis* (Stn. 534–535) and *Thalassiosira* cf. *antarctica* var. *borealis* (Stn. 536–545) dominated by biovolume. In the ice-covered part of the transect the southernmost stations 546 and 547 had the same dominant diatom species as Stn. 536–545. In Arctic waters north of the ice edge *Chaetoceros socialis* dominated by numbers and *Fragilariopsis oceanica* dominated by biovolume (Stn. 548–551).

*Phaeocystis pouchetii* colonies, which contained up to 600 cells per colony, were abundant in the frontal zone (Stn. 547), at the adjacent station (Stn. 548), the meandering Polar front and in the northern part of the Atlantic waters (Stn. 539–546), except at Stn. 544 where it was scarce. *Phaeocystis pouchetii* abundance was low at the southernmost stations 534–539 and in the Arctic water (Stn. 549–551).

Small flagellates and monads of pico- and nanoplankton size ( $< 2$  and 2 to 20  $\mu\text{m}$ ,

Table 1. Abundance of selected phytoplankton species in the 0–50 m layer along the transect between Stn. 534–551.

	534	535	536	537	538	539	540	541	542	543	544	545	546	547	548	549	550	551
Division Chromatophyta																		
Class Cryptophyceae																		
<i>Plagioselmis</i> sp.																		
Class Dinophyceae																		
<i>Amphidinium spenoides</i> Wulff	1	1	–	1	1	1	1	1	1	–	1	1	–	1	1	1	1	1
<i>Gonyaulax scrippsae</i> Kofoid	–	1	1	1	1	–	1	1	–	–	1	1	1	1	1	1	1	1
<i>Gymnodinium simplex</i> (Lochmann) Kofoid & Swezy	1	1	1	1	1	1	–	–	1	–	1	–	1	–	–	–	–	2
<i>Gymnodinium arcticum</i> Wulff	–	1	1	–	1	1	1	1	1	1	1	1	1	–	1	–	–	1
<i>Gyrodinium aureolum</i> (Hulburt)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gyrodinium spirale</i> (Bergh) Kofoid & Swezy	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Heterocapsa rotundatum</i> (Lochmann) Hansen	1	1	1	1	1	1	1	1	1	–	–	–	–	–	–	–	–	–
<i>Protoperidinium brevipes</i> (Paulsen) Balech	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Protoperidinium depressum</i> (Bailey) Balech	–	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Protoperidinium nudum</i> (Meunier) Balech	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Protoperidinium pellucidum</i> (Bergh) Balech	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Class Prymnesiophyceae																		
<i>Phaeocystis pouchetii</i> (Hariot) Lagerheim (colonies)	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2	1	1
<i>Emiliania huxleyi</i> (Lochmann) Hay & Mohler	2	1	–	1	–	–	–	–	2	–	1	2	2	1	1	–	–	–
Class Chrysophyceae																		
<i>Dictyocha speculum</i> Ehrenberg	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
Class Bacillariophyceae																		
<i>Bacterosira bathyomphala</i> (Gran) Syvertsen & Hasle	–	–	–	–	1	1	1	1	–	1	–	–	–	2	1	–	2	2
<i>Chaetoceros borealis</i> Bailey	1	1	2	1	1	1	1	1	–	1	–	–	–	1	–	–	–	–



respectively) had their maximal numbers and biovolume in the southernmost part of the transect (Stn. 534–537). A slightly higher abundance was recorded at stations 540–542 (meandering Polar Front), at the ice edge (Stn. 547) and at the northernmost station 551. Other groups of phytoplankton such as dinoflagellates, silicoflagellates and coccolithophorids were not abundant anywhere along the transect.

## 5. Phytoplankton abundance and biovolume

Four maxima of phytoplankton abundance (Stn. 535, 542, 547, 551) were found along the transect (Fig. 5). Picoplankton dominated cell numbers at all stations (80 to 90% of total). The highest cell numbers (up to  $10^8$  cells  $\cdot$  l $^{-1}$ ) developed in the southern part of Atlantic water (Stn. 535). Both pico- and nanoflagellates and monads in the picoplankton fraction had maximal abundance in this area (Fig. 5). Other maxima of picoplankton numerical abundance were encountered in the area of the two Polar Front areas and in the northernmost station in Arctic water (4 to  $5 \times 10^7$  cells  $\cdot$  l $^{-1}$ ). All phytoplankton groups increased by numbers in the area of the meandering Polar Front, but diatoms and *P. pouchetii* had their maxima at Stn. 541. In ice-covered stations and the Polar Front, diatom abundance increased up to  $1.2 \times 10^6$  cells  $\cdot$  l $^{-1}$ .

Five maxima of phytoplankton biovolume were recorded along the transect (Fig. 6). Three of them coincided with the maxima of numerical abundance (Stn. 535, 542 and 547), one was situated south of the Arctic water maximum of numerical abundance (Stn. 550) and one was found in the Atlantic water north of the meandering front (Stn. 544). Nanoplankton flagellates in the picoplankton fraction dominated total biovolume in the southern part of transect (Stn. 534–537) and the meandering Polar Front (Stn. 542–543). Diatoms dominated the biovolume in most other stations, in particular in the northern part of the transect (up to  $1.2$  mm $^3$   $\cdot$  l $^{-1}$ ). Pico- and nanoflagellates had similar distribution, but picoflagellate biovolume was much lower at most stations. Pico- and nanoplankton had the highest biovolume at Stn. 535 (about  $1.4$  mm $^3$   $\cdot$  l $^{-1}$ ). Most of the smaller flagellates may have been heterotrophic flagellates because Chl *a* concentrations in these waters were low (Fig. 4a).

## 6. Vertical distribution of phytoplankton

The vertical distribution of total phytoplankton along the transect was more or less even in the Atlantic water, except some single deeper maxima (Fig. 7). In the frontal region (the Polar Front and the MIZ) phytoplankton abundance was higher in the surface layer (maximum at the surface of Stn. 547) and lower in the remaining part of water column. In the northernmost arctic part of the transect, sharp vertical gradients of phytoplankton distribution were encountered (Fig. 7). Near the surface, phytoplankton abundance was about one order of magnitude higher than at 40 m depth below the euphotic zone. This maximum could be explained by density gradients in the upper layers (Fig. 2c), the low irradiance below the ice cover (Figs 3, 4) and possibly intense grazing below the euphotic zone.

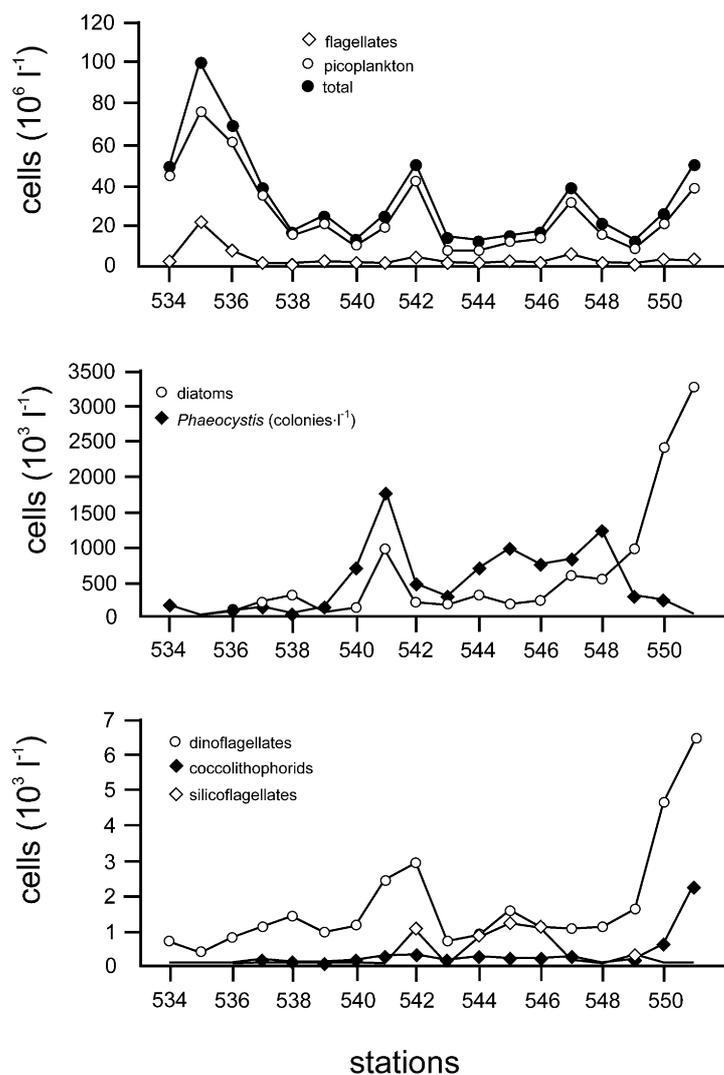


Fig. 5. Average phytoplankton cell concentration in the upper 50m along the transect. Upper panel: total cell concentration and those of flagellates and picoplankton ( $10^6 \cdot l^{-1}$ ); mid panel: numerical abundance of diatoms and *Phaeocystis* colonies ( $10^3 \cdot l^{-1}$ ); lower panel: cell concentration of dinoflagellates, coccolithophorids and silicoflagellates ( $10^3 \cdot l^{-1}$ ). Note the differences in scales.

Diatom biovolume increased from south to north, from less than  $0.1 \text{ mm}^3 \cdot l^{-1}$  in the southernmost part to 1 to  $2 \text{ mm}^3 \cdot l^{-1}$  in the upper 0 to 25m layer in the Arctic waters (Fig. 7a). In the Arctic water and in the frontal zones, diatom abundance was highest in the surface layer (0–40 m); in the rest of transect diatoms were distributed evenly throughout the water column. A single dinoflagellate maximum developed in the surface layer of the Polar Front region ( $>0.1 \text{ mm}^3 \cdot l^{-1}$ ) (Fig. 7b). Dinoflagellates were more abundant in the Arctic water than in the

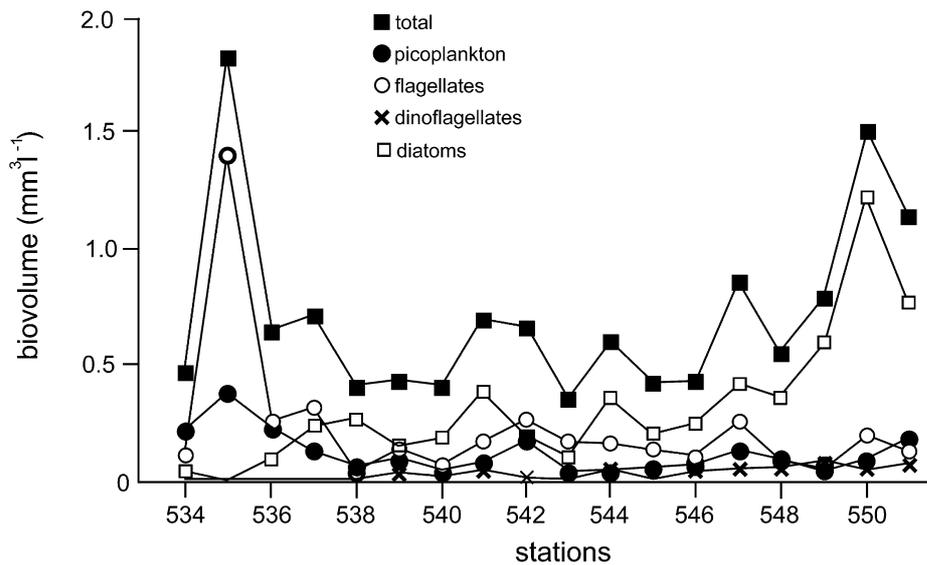


Fig. 6. Average phytoplankton biovolume [ $\text{mm}^3 \cdot \text{l}^{-1}$ ] in the upper 50 m along the transect.

Atlantic water. Generally, dinoflagellate abundance increased in the 20 to 30 m layer, but in the frontal zones the maximum was encountered in the surface layer.

The distribution of flagellates was similar to that of phytoplankton in general, except at the Polar Front meandering zone, where flagellates had no maxima (Fig. 7c). Picoplankton was distributed rather evenly throughout the transect (Fig. 7d). Weak maxima developed at the surface in frontal zones (Stn. 541, 546–547). In Arctic water, picoplankton had a lower abundance than in the Atlantic water, except at Stn. 551. A well-pronounced maximum was encountered at 50 m depth at station 535, but the monads which developed in this layer may have been heterotrophic because the Chl *a* content was low here.

*Phaeocystis pouchetii* was most abundant (up to  $2$  to  $4 \times 10^3$  colonies  $\cdot \text{l}^{-1}$ ) in the deeper parts of water column (25–50 m) of the meandering Polar Front and in the frontal zone (Polar Front + MIZ) (Fig. 7e). In the upper layer *P. pouchetii* abundance decreased. Similar vertical distribution patterns of *P. pouchetii* were observed in the remaining transect, but the abundance was much lower.

## Discussion

The spring bloom development in boreal, subarctic and arctic ecosystems usually starts with an early phase characterized by low concentrations and small forms such as monads, naked flagellates and picoplankton (Halldal, 1953; Sakshaug & Skjoldal, 1989; Kiørboe, 1993). The early phase continues into a second phase, the growth phase, which is often characterized by the proliferation of larger forms such as *Phaeocystis pouchetii* colonies and a few diatom genera (Druzhkov & Makarevich, 1992; Evensen, 1994). Flagellated forms are still present, but have a

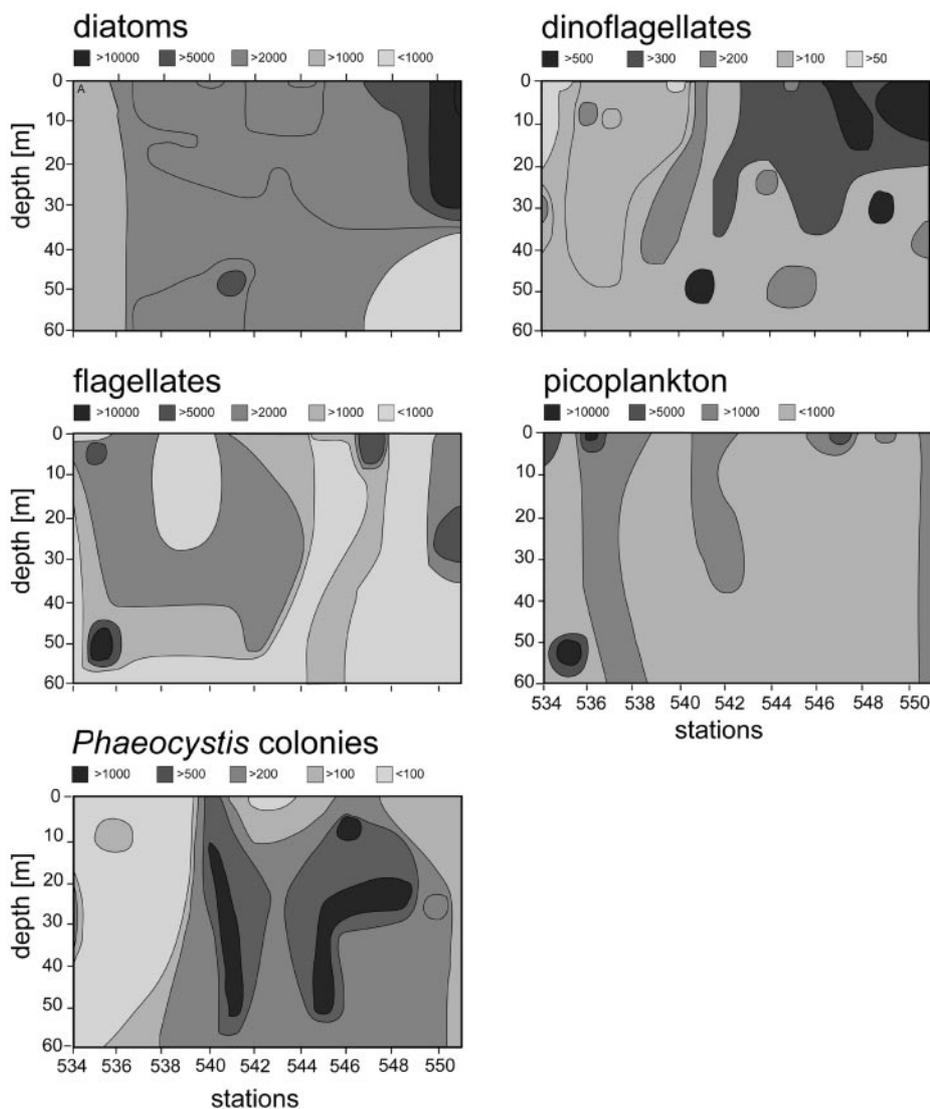


Fig. 7. Vertical distribution of diatoms, dinoflagellates, flagellates, picoplankton biovolume [ $\mu\text{m}^3 \cdot \text{l}^{-1}$ ] and *Phaeocystis* sp. [colony abundance  $\cdot \text{l}^{-1}$ ] along the transect.

limited impact on total biovolume as the Chl *a* concentrations are low (Slagstad & Wassmann, 1997). The maximum spring bloom following the growth phase is often characterized by a dominance of centric and chain-forming diatoms (*e.g.*, Evensen, 1994) or accumulations of *P. pouchetii* colonies (*e.g.*, Wassmann *et al.*, 1990), which can give rise to high phytoplankton biomass in the upper layers. After the vernal bloom an oligotrophic phase develops, again characterized by flagellated forms and low total biovolume (*e.g.*, Rey & Loeng, 1985; Sakshaug & Skjoldal, 1989). How is this general scheme reflected in the present transect crossing the central

Barents Sea and its different water masses? Before discussing phytoplankton succession, zonal structure along the transect and interannual variation of phytoplankton succession in greater detail, the various zones and phytoplankton assemblages along the transect will be summarized. The investigated transect can be divided into four principal zones: (a) the Atlantic zone (Stn. 534–540 and Stn. 543–545), (b) the Polar Front and ice edge zone (Stn. 546–547), (c) the Arctic zone (Stn. 548–551) and (d) the Polar Front meandering, which had similarities with the Polar Front and outer ice edge zone (Stn. 541–542), (see Fig. 1b).

## 1. Zones and phytoplankton assemblages

### Atlantic zone

The Atlantic zone was characterized by poor stratification (Fig. 2), decreased nutrient concentrations in winter (Fig. 3) and generally low chlorophyll concentrations (Fig. 4a). The phytoplankton biovolume was variable, but generally low. Pico- and nanoplankton flagellates and monads dominated the phytoplankton biovolume of the southernmost section (78%; Fig. 8a). Diatoms contributed up to 14% of the total biovolume, whereas dinoflagellates accounted for less than 3% and other groups were scarce in this zone. The contribution of diatom biovolume increased northwards (Stn. 539) and reached 38%, while picoplankton and flagellates decreased to 56% (Fig. 8b). In the Atlantic section north of the meandering Polar Front (Stn. 536–545) the phytoplankton composition was similar; however, in contrast to the dense pico- and nanoplankton population of southern stations, phytoplankton abundance in the mid transect was clearly lower. The situation at Stn. 541–542 in the meandering Polar Front was different (see below).

The Atlantic water part of the transect was characterized by low diatom and *Phaeocystis* abundance. Typical vernal bloom species such as *Chaetoceros socialis* and *Thalassiosira* cf. *antarctica* var. *borealis* dominated among diatoms. Previous investigations (Skjoldal & Rey, 1989) and modelling work (Slagstad & Wassmann, 1997) suggest that a substantial bloom does not take place in the Atlantic zone in April or May, but in June. This is caused by the slow development of vertical stability. Some larger phytoplankton cells were found, but flagellates and monad biovolume were prominent at most stations here. These taxa are characteristic for both summer and pre-bloom conditions. Thus, the Atlantic zone with its low chlorophyll and substantial nutrient concentrations apparently experienced a pre-bloom or early bloom rather than a post-bloom situation.

Despite the low pigment concentrations and the low numbers of individuals of typical vernal bloom species, the spring bloom had given rise to a major average new production of about  $26 \text{ g C} \cdot \text{m}^{-2}$ . Silicate depletion in the euphotic zone comprised 43% of the winter concentration, suggesting proliferation of diatoms. Major increases in diatoms or larger cell concentrations, however, were *not* recorded. Vertical mixing or grazing may have prevented accumulation of phytoplankton biomass in the upper layers (see below). The vernal bloom in the Atlantic sector had thus started ( $> 1/3$  of the annual new production; Wassmann & Slagstad, 1991), but was not reflected in major decreases in nutrient concentrations or typical vernal bloom phytoplankton species.

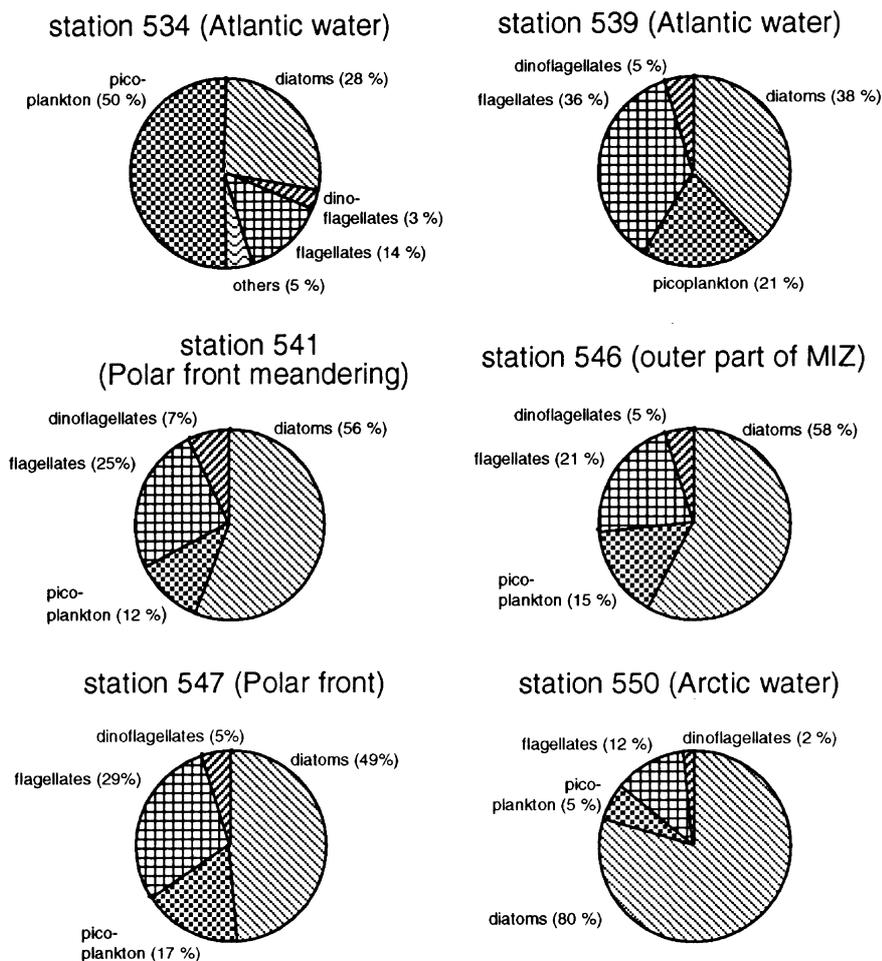


Fig. 8. The average biovolume composition (0–50 m) for picoplankton, flagellates, dinoflagellates, diatoms and colleagues at six selected stations along the transect (in percentage). Stn. 534 and 539 represent the Atlantic zone, 541 the Polar Front meandering, 546 the ice edge zone, 547 the slightly ice-covered Polar Front zone and 550 the heavily ice-covered Arctic zone.

### Polar Front and ice edge zone

The Polar Front and ice edge zone was characterized by increasing stratification (Fig. 2), moderate to high chlorophyll concentrations (Fig. 4a) and increasingly depleted nutrient concentrations towards the north (Fig. 3). The biovolume of diatoms became more important in the northern part of the Atlantic water, at the Polar Front and at the ice edge (48–58%; Stn. 546–547, Fig. 8d,e). *Phaeocystis* sp. developed mainly in the northern part (Stn. 541–548) (Fig. 5). Phytoplankton composition did not change considerably inside the frontal zones.

In this part of the transect phytoplankton had typical spring features: the planktonic colonial centric diatoms *Chaetoceros socialis* and *Thalassiosira* cf. *ant-*

*arctica* var. *borealis* prevailed (Rey *et al.*, 1987; Quillfeldt, 1996). However, other forms such as flagellates, dinoflagellates and picoplankton comprised a substantial part of the biovolume here as well (41–50%). The nutrient concentrations and the increasing water stability supported growth of larger phytoplankton species and the start of a classical spring bloom. This is reflected in a higher average new production rate of  $34 \text{ g C} \cdot \text{m}^{-2}$ . Similar rates were recorded in the MIZ in June and July by Strass & Nöthig (1996). Silicate concentrations, however, were often  $< 2 \mu\text{M}$ . Diatoms are less likely to dominate at  $\text{Si}(\text{OH})_4$  concentrations  $< 2 \mu\text{M}$  (Doering, 1989; Egge, 1993). They aggregate, sink and leave the euphotic zone before phosphate and nitrate become depleted (Wassmann *et al.*, 1997). During sinking and in the upper part of the aphotic zone they continuously take up dissolved silicate (Rey & Skjoldal, 1986) and often form resting spores (*e.g.*, Pitcher, 1986). The remaining nutrients in the euphotic zone are then used by phytoplankton species which do not demand dissolved silicate, such as flagellates, *Phaeocystis* sp., dinoflagellates and coccolithophorids. Considering the low dissolved silicate concentrations in the Barents Sea, it can be assumed that diatoms play a less significant role during the vernal bloom as compared to the Norwegian Sea.

### Arctic zone

The Arctic zone was characterized by stronger stratification (Fig. 2) and significantly depleted nutrient concentrations (Fig. 3). Chlorophyll concentrations increased with increasing distance from the ice edge and reached rather high maximum concentrations of  $14 \mu\text{g} \cdot \text{l}^{-1}$  at Stn. 550 (Fig. 4a). A dense diatom population inhabited the waters below the ice cover (Stn. 549–551), accounting for 80% of total biovolume (Fig. 8f).

A conspicuous spring bloom took place under the ice in the northernmost Stn. 550–551, which also had the lowest temperature. These stations were characterized by a high biovolume of ribbon-shaped colonies of pennate, under-ice diatoms such as *Fragilariopsis oceanica* and the persistence of ice-associated algae such as *Nitzschia frigida*. The sub-ice phytoplankton assemblage may have been actively growing under low irradiance for as much as 2 months before the start of ice melt (Syvertsen, 1991). Pelagic diatoms such as *Chaetoceros socialis* became more important in the lower part of the euphotic zone. Despite a vernal bloom at its maximum and the low nutrient concentration in the euphotic zone, the new production was comparatively low, ranging from  $32 \text{ g C} \cdot \text{m}^{-2}$  in the south to only  $12 \text{ g C} \cdot \text{m}^{-2}$  in the north (average  $23 \text{ g C} \cdot \text{m}^{-2}$ ). This is due to the increasing stratification, which results in annual new production rates that decrease on average from 57 to  $13 \text{ g C} \cdot \text{m}^{-2}$  along a south-north gradient in the Barents Sea (Wassmann & Slagstad, 1991). The bloom appeared to be limited by silicate; on average, 83% of the winter-accumulated silicate in the euphotic zone had been consumed. Also, nitrate was probably close to limiting production.

### Polar Front meandering

The front was characterized by lower temperature ( $0\text{--}2^\circ\text{C}$ ) and lower salinity ( $< 35.0$ ). While little stratification was recorded in the Atlantic water up to about

74° N, the meandering Polar Front and probably remains of melting sea ice gave rise to shallow lenses of increased stratification between 74 and 75° N. Compared to the surrounding Atlantic water the nutrient concentration gradients were less prominent, but the front was nonetheless clearly discernible (Fig. 3) and suspended phytoplankton biovolume increased (Figs 4, 5, 6). Diatoms accounted for about half of biovolume at Stn. 541 in the middle of the meandering front (Fig. 8c). There were tendencies of silicate limitation inasmuch as on average 75% of the winter-accumulated silicate had been consumed at Stn. 541. The hydrography, nutrients, pigments, phytoplankton biovolume and species distribution clearly indicated that the water mass of the meandering Polar Front and the Polar Front water were more or less similar (compare Stn. 541 with 547; Fig. 8c,e). New production in this section was  $31 \text{ g C} \cdot \text{m}^{-2}$  on average, 20% higher than in the surrounding Atlantic section.

An analogous scenario was recorded in May/June 1987 when two stations at 75°00' N, 28°37' E and 74°29' N, 31°31' E were visited three times during 11- and 17-day intervals, respectively (Wassmann *et al.*, 1990). The western station was in an area dominated by Atlantic water, while the eastern one was in the vicinity of the Polar Front (Fig. 1a). The eastern station reflected the bloom dynamics of the meandering Polar Front area, with rapidly decreasing nutrient concentrations, the formation of a halocline and rapidly declining pigment concentrations. The station reflected the advection of increasingly 'mature' bodies of water from the Polar Front area (Wassmann *et al.*, 1990). The plankton ecology of the area around Stn. 540–543 seems to be affected by the position, meandering and time development of the Polar Front to the east of the transect. The meandering Polar Front therefore introduces water masses that are in a more mature bloom phase into the Atlantic water, which is in an early bloom phase.

West–east advection of water of different origin and bloom timing was possibly also found in the southern part of the Atlantic section. Here, an intrusion of less saline water with lower nutrient concentration and a high concentration of probably heterotrophic flagellates was recorded between Stn. 534 and 537 (Figs 3 and 6). As this water had salinities  $< 35$ , it may represent an excursion of the Norwegian Coastal Current intruding into Atlantic water of the North Cape Current. Species originating from coastal waters have been previously recorded as far off-shore as weather ship M in the Norwegian Sea, more than 800 km from the nearest coastline (Halldal, 1953).

## 2. Vernal bloom and phytoplankton succession

The general pattern of phytoplankton species succession during the vernal bloom presented here is similar to that recorded in the western Kara Sea (Makarevich & Druzhkov, 1994), the south-eastern Barents Sea (Druzhkov & Makarevich, 1992), the central Barents Sea (Rey *et al.*, 1987; Evensen, 1994) and the northern part of the North Atlantic (Vinogradova & Gruzov, 1990). According to these authors the growth phase of the spring bloom is characterized by a domination of ribbon-forming, pennate diatoms, followed by the main bloom maximum which coincides with mass development of centric diatoms. Another aspect of vernal blooms is the recurrent dominance of chlorophyll *a* over phaeopigments in the central Barents

Sea. However, the appearance of large phytoplankton species and Chl *a* dominance alone may be inadequate to assess whether a spring bloom has taken place or not. For example, selective grazing by zooplankton on large-celled forms could reduce the diatom biomass and chlorophyll concentrations. The grazing impact of advected and over-wintering mesozooplankton in the southern and central Barents Sea differs between years (Pedersen, 1995) and can be sufficient to prevent major blooms (Wassmann & Slagstad, 1993; Wassmann *et al.*, 1996b). Indeed, grazing experiments carried out during the present investigation along the transect revealed that grazing by micro- and mesozooplankton was significant along the entire transect (Hansen *et al.*, 1995). 19–86% of the total daily primary production (average  $43 \pm 60\%$ ) was grazed by zooplankton, mainly by ciliates and dinoflagellates. Another example for the lack of adequate, classical signals such as decreased nutrient concentration and the presence of discernible amounts of large phytoplankton species is that the vertical excursion of phytoplankton cells in weakly stratified waters could give rise to low concentrations (per volume), but appreciable integrated quantities (per  $m^2$ ). Already several decades ago it was claimed that vertical mixing and grazing were the most important processes for the low spring phytoplankton abundance at weather M in the Norwegian Sea (Halldal, 1953).

In the MIZ, water column stratification enhances phytoplankton development due to salinity and temperature gradients as predicted by Sverdrup (1953), Smetacek & Passow (1990) and Platt & Sathyendranath (1993). However, similar to the scenario in north Norwegian fjords (Eilertsen, 1993; Wassmann *et al.*, 1996a), the spring bloom in the Atlantic sector of the transect takes place in almost nonstratified waters. This has also been observed in other boreal shelf and open-ocean environments (Halldal, 1953; Townsend *et al.*, 1992), suggesting that the phenomenon is widespread and rather the rule than an exception in such environments. Deep penetration of light and the absence of wind-driven vertical mixing appear to support cell growth that overcomes the vertical excursion rates of the neutrally stable water column, giving rise to a bloom (Townsend *et al.*, 1992). Wind strength and direction during early spring, along with the light regime, appear thus to play a crucial role for the onset, development and fate of the spring bloom in arctic and subarctic areas (Sakshaug *et al.*, 1995; Slagstad & Wassmann, 1997).

A comparison of Figs 2, 3, 4, 5, 6, 7 reveals the zonal structure which characterizes the central Barents Sea during spring. The physical oceanography, the nutrient distribution, as well as the abundance of pigments and phytoplankton species indicate that the conditions for and the timing of the spring bloom are quite variable along the transect. The different water masses, their transport along or across the transect and the resulting variability in timing of the vernal bloom give rise to a 'sandwich-like' structure along the transect where contrasting vernal bloom stages follow each other. A general model of phytoplankton development of the Barents Sea as presented by Sakshaug & Skjoldal (1989), where the bloom consecutively follows the ice edge and where the time succession can be followed by proceeding along a south-north gradient, is simplistic. It may be representative for the Barents Sea MIZ only, lacks meso-scale features and presumes continuous ice-melting. The results presented here show that the differences in timing, phytoplankton biomass and depth of the layer containing proliferating phytoplankton cells along the gradient can be significant. The general bloom development in the

central Barents Sea during late May in 1993 was north–south, with possible intrusions of more biologically mature bodies of water.

### 3. Interannual variation of phytoplankton succession

The timing and phytoplankton species composition in the transect area of the Barents Sea is supposedly variable in different years. Wassmann *et al.* (1990) described a massive, almost mono-specific bloom of *P. pouchetii* at its maximum in the Atlantic water close to the transect at 75°00' N, 28°37' E in late May/early June 1987 (Fig. 1a). Evensen (1994) recorded significant phytoplankton biomass accumulation of the vernal bloom and the phytoplankton species composition during 1988 and 1989 in the northern part of the central Barents Sea. This is in contrast to the present investigation, where the suspended biomass was much lower and none of the stations were dominated by *P. pouchetii* in mid-May. The scarcity of *P. pouchetii* in 1993 was rather surprising as this species is one of the dominant and regular spring bloom components in the central Barents Sea (Rey *et al.*, 1987; Evensen, 1994). *Phaeocystis pouchetii* clearly undergoes substantial interannual variability in the Barents Sea, analogous to the variable *Phaeocystis*/diatom ratio during the spring bloom in the subarctic coastal waters of northern Norway (Eilertsen *et al.*, 1981; Lutter *et al.*, 1989; Riebesell *et al.*, 1995). Halldal (1953) does not comment upon *Phaeocystis*, probably due to dissolution of the colonies during preservation and storage.

Although explanations for the differences in timing are found in processes such as ice coverage, wind direction and water temperature (*e.g.*, Slagstad & Wassmann, 1997), the reasons for the variation in phytoplankton species composition are less well known. Variable amounts of Atlantic or Arctic water with their accompanying phytoplankton cells, winter stages (Fryxell, 1994), variable resuspension of cysts caused by deep vertical mixing (Itakura *et al.*, 1997) and variable interspecific competition caused by changes in light availability (Eilertsen *et al.*, 1995) and stratification may increase interannual variation in phytoplankton proliferation. The regulation of the vernal phytoplankton species composition is thus a matter of debate. In this context it is interesting to note that the *P. pouchetii* colonies in 1993 were frequently covered by dense populations of *Pseudonitzschia cf. pseudodelicatissima* and the flagellate *Plagioselmis* sp., imparting a hedgehog-like appearance. This was not observed in 1987 (Wassmann *et al.*, 1990) and no such comments were made by Evensen (1994). It is speculated that the impact of epiphytic organisms such as *Pseudonitzschia cf. pseudodelicatissima* and *Plagioselmis* sp. limited the success of *P. pouchetii* during the 1993 vernal bloom.

The culmination of the spring bloom in this area has been observed to vary within a period of about three weeks (Rey & Loeng, 1985; Rey *et al.*, 1987; Wassmann *et al.*, 1990; Evensen, 1994). Climatic variation play probably an important role in these differences. Modelling of the carbon flux during cold and warm years revealed that during cold years with an extensive ice cover, the spring bloom started several weeks earlier in the central part of the transect compared to warmer years (Slagstad & Wassmann, 1997). The annual extent of ice coverage varies and is determined by the combined effects of (a) the heat capacity of the underlying water, (b) the extent of the ice cover the previous year and (c) the dominating wind

direction during the following winter. Obviously, spring bloom development is effected by the dynamic conditions in the Barents Sea.

## Conclusion

The vernal bloom in the central Barents Sea in mid May 1993 had clearly started several weeks earlier as reflected by average estimated new production of  $26 \text{ g C} \cdot \text{m}^{-2}$  in the Atlantic sector, 31 and  $34 \text{ g C} \cdot \text{m}^{-2}$  in the Polar Fronts and  $23 \text{ g C} \cdot \text{m}^{-2}$  in the Arctic sector. On average about 52% of the winter-accumulated nutrients in the euphotic zone along the transect had been consumed by late May. The sequence of events characterising the spring bloom development (Fig. 8) included:

- (a) a scenario dominated by ribbon-shaped, colony-forming diatoms such as *Fragilariopsis oceanica* and the colonial centric diatom *Chaetoceros socialis* in the densely ice-covered Arctic zone (vernal bloom at its maximum);
- (b) a scenario dominated by the centric colonial diatoms *Chaetoceros socialis* and *Thalassiosira cf. antarctica* var. *borealis*, with some development of *P. pouchetii* in the Polar Front and ice-edge zone (vernal bloom);
- (c) a scenario dominated by pico- and nanoplankton, flagellates, monads, a few diatoms and *P. pouchetii* in the weakly stratified Atlantic zone (early bloom state);
- (d) a scenario dominated also by pico- and nanoplankton flagellates, monads, but increased numbers of diatoms and *P. pouchetii* in an intermittent intrusion from the meandering Polar Front in the middle of the Atlantic sector (vernal bloom);
- and
- (e) a scenario strongly dominated by (heterotrophic?) pico- and nanoplankton flagellates in an intermittent intrusion of water from the Norwegian Coastal Current into the southern part of the Atlantic sector.

The central Barents Sea and its marginal ice zone thus has a complicated zonal structure in which the vernal bloom starts in the southern part of the MIZ. In a wave-like motion the vernal bloom proceeds *both* north and south, as reflected in two- and three-dimensional, biological-physical coupled models (Wassmann & Slagstad, 1993; Slagstad & Wassmann, 1997, respectively). The over-all time variation of phytoplankton development at the start of the vernal bloom in May 1993 was north to south. This vernal bloom wave propagates from the southern MIZ into the Atlantic water and is regulated by slowly decreasing vertical mixing. The bloom is wide and abundant as it covers the entire southern part of the central Barents Sea. The other wave propagates as a more or less narrow band from late May onwards along with the receding ice-edge steadily to the north (combined effect of light penetration and stratification), as described by Sakshaug & Skjoldal (1989), until light limitation in September/October brings the ice-edge bloom to an end (Hegseth, 1997).

The vernal bloom in the Atlantic water ceases in late June and oligotrophic conditions prevail for the remaining year in surface waters. Between these two waves a band of nutrient- and phytoplankton-poor surface water stretches all over the central Barents Sea in June (Slagstad & Wassmann, 1997). This is the signature of the start of the vernal bloom in the southernmost part of the MIZ. This band widens over time and covers the entire ice-free Barents Sea from late June onwards.

This general picture can be obscured over the short-term by east–west excursions of different water masses such as the Polar Front, eddies, meso-scale features and meanders of the Norwegian Coastal Current into the south which introduce less or more mature vernal bloom sequences in the central Barents Sea. Little is known about these variations. Andreassen & Wassmann (1998) describe noteworthy short-term variations in the thermo- and halocline over periods of 36 h in the MIZ close to Stn. 551 and 548 several days after the samples for the present investigation were taken, suggesting hydrographic meso-scale features of unknown diameter. Similar short-term changes in the Atlantic water and the meandering Polar Front close to Stn. 554 and 524, respectively, were minor (Andreassen & Wassmann, 1998). However, some features encountered in the present investigation seem more or less permanent. For example, the meandering of the Polar Front around Stn. 541 was found at the same position in March and May 1998 (P. Wassmann, unpublished results). Due to the various east–west excursions of different water masses, phytoplankton spring blooms may vary over brief periods, in particular in the MIZ. At a larger scale, vernal blooms may be found simultaneously and develop independently at different latitudes and sites in the Barents Sea. The general picture elucidated above can also be camouflaged by interannual variations of zooplankton grazing (elimination of large cells) and extensive vertical excursions of suspended particles in the weakly stratified waters in the Atlantic sector (decrease of concentration) during low pressure passage (Sakshaug *et al.*, 1995).

While classical signals such as high nutrient concentration, low phytoplankton biomass and few large-sized cells suggest pre-bloom conditions, a vernal bloom in the Atlantic sector can already have developed for several weeks. In the present study, the new production until mid-May already comprised about 45% of the annual new production, as calculated by modelling (Wassmann & Slagstad, 1993), despite of high nutrient concentrations, low phytoplankton biomass and few large-sized cells. Care must therefore be taken when interpreting bloom sequences based on nutrient concentrations and prevailing phytoplankton species alone. Vernal blooms are clearly not necessarily reflected in large-celled phytoplankton biomass. In comparison with previous investigations (for summaries, see Loeng, 1987; Skjoldal & Rey, 1989; Sakshaug *et al.*, 1991) and models (Wassmann & Slagstad, 1993; Slagstad & Wassmann, 1997), the present investigation underlines, in great detail and with emphasis on phytoplankton species biovolume, the general knowledge of the spring bloom development in the Barents Sea.

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