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Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea

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Abstract

Seasonal and geographical variations of suspended single-celled organisms on a transect across the western part of the Barents Sea in March and May 1998 and in June–July 1999 revealed that pico- and nanoplankton flagellates and monads (<2 and 2–20 μm, respectively) entirely dominated total algae and protozoa numbers and biomass in March and in June–July, but in May, microplankton (>20 μm) prevailed in total biomass. In general, spring bloom progresses independently of the southern part of the Atlantic Water (AW) and follows the receding ice edge in the Arctic Water (ArW) to the north. The blooms started almost simultaneously and had similar composition (small diatom *Chaetoceros socialis* dominated total phytoplankton biomass) in both localities, so the share of resting spores, indicating the age of the bloom, differed markedly. As for underwater rise—the Sentralbanken (SBW) altered this pattern, and the spring bloom spreads from north to the south from the rise to the trench. The next stage of the bloom was dominated by the large diatoms *Thalassiosira antarctica* var. *borealis* above the Sentralbanken, in the Polar Front (PF) and in the ice-edge areas. In the southern part of transect, this stage of the spring bloom had a delay or was absent due to low stability of water column and/or due to grazing impact. The presence of ribbon-shaped forming species indicated the earlier stage of bloom in Marginal Ice Zone (MIZ). In May 1998 as well as in June/July 1999, at the ice-covered stations, early spring conditions—rather similar to the conditions in March 1998—were observed. Summer conditions at most of the stations in June–July 1999 were characterized by high species diversity of diatoms and dinoflagellates. High abundance of heterotrophic dinoflagellates and protozoans indicated the active functioning of the microbial loop in the nutritive chains.

Keywords: Arctic; Barents Sea; Picoplankton; Nanoplankton; Microplankton; Seasonal succession; Microbial loop; Top–down regulation

1. Introduction

The Barents Sea is a productive marine high-latitude ecosystem that is characterised by a shallow shelf and a complex hydrography that has a zonal structure (Loeng, 1991; Sakshaug, 1997). This marginal sea type ecosystem demonstrates a striking combination of large distances from the shores and shallowness, high latitude light conditions and substantial advection of heat, salt, nutrients and biomass by the Norwegian Atlantic Current (NAC) (e.g., Ådlandsvik and Loeng, 1991; Sakshaug et al., 1995). The ice can cover up to 90% of the sea surface in winter, but there is no multiyear ice (Vinje and

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Kvambekk, 1991). The ice-edge zone crosses most of the shelf during the spring bloom progress to the north (Sakshaug and Skjoldal, 1989). From a hydrographic point of view, the Barents Sea is a most heterogeneous region and the peculiarities of the phytoplankton distribution largely depend on the prevalent hydrography and hydrodynamics. Of outstanding importance is water column stability, which influences vertical mixing and thereby affects growth rates and the supply of nutrients from deeper layers to the euphotic zone (Backhaus et al., 1999; Wassmann et al., 1999b).

The history of phytoplankton studies in the Barents Sea ranges over more than a century. At first, emphasis was mainly given to the floristic description. More than 300 species of pelagic algae were described from the region (Makarevich and Larionov, 1992). The phytoplankton studies in 1960–1970s paid special attention to the functional characteristics of the plankton communities (e.g., Roukhiyainen, 1960). Most of these investigations were conducted in the coastal zone of the southern Barents Sea, but since the 1980s they were extended to the entire sea area (e.g., Druzhkov and Makarevich, 1992; Kristiansen et al., 1994; Hansen et al., 1996; Larionov, 1997; Hegseth, 1998; Wassmann et al., 1999b; Falk-Petersen et al., 2000; Luchetta et al., 2000; Owrid et al., 2000; von Quillfeldt, 2000; Pautova and Vinogradov, 2001). To obtain adequate seasonal coverage in the remote, extensive and ice-covered Barents Sea is difficult. Thus, the results from a multitude of campaigns at various seasons, years and regions, have been assembled to approximately describe the annual microplankton succession (Sakshaug and Skjoldal, 1989; Skjoldal and Rey, 1989; Druzhkov and Makarevich, 1992; Sakshaug et al., 1994). However, more uncompromising work has to be carried out to decipher the seasonal and spatial variation of phyto- and protozooplankton. In particular, the phytoplankton composition in the ice-covered northern part of the Barents Sea deserves increased attention.

The least investigated season in polar waters covers winter and early spring. Without ice-breaking capacity, sampling in winter in the inshore sites or in the open sea may be rather difficult or even impossible. Winter conditions are characterised by extensive ice cover, low irradiance and deep mixing. However, nutrient concentration is maximal late in winter and decreases rapidly when sufficiently light becomes available prior to the spring bloom (Lappalainen, 1960; Kristiansen and Farbrot, 1990). The start of the bloom has been defined as the time when 1 μM NO_3 (about 10% of the winter concentration) has been consumed, which corresponds to a production of about 0.5–1.0 mg Chl *a* l^{-1} (Skjoldal et al., 1987). The phytoplankton biomass does frequently not accumulate due to extensive grazing by zooplankton (Wassmann, 2001). As a result of the austere conditions, winter phytoplankton biomass is sparse in arctic seas. However, this low overwintering phytoplankton may serve as a seeding population for the early spring bloom development. One of the underlying assumptions is that the more abundant is the overwintering population, the more rapidly the spring bloom develops. Further, the composition of the overwintering population may determine the composition of the spring bloom and its hitherto unresolved interannual variability.

Earlier investigations on the north Norwegian shelf, which has a new production rates of >120 g C m^{-2} $year^{-1}$ (Slagstad et al., 1999), revealed that pico- and nanoplankton dominated throughout the productive season while protozooplankton was scarce despite of abundant food (Rat'kova et al., 1999; Verity et al., 1999). It was argued that overwintered and advected mesozooplankton was the cause (Bathmann et al., 1990) and the hypothesis of top–down regulation was offered (Verity et al., 1999; Wassmann et al., 1999a). However, significant accumulation of large-celled phytoplankton can only be encountered at a distance to the shelf break (e.g., the central Barents Sea) or areas restrained from regular, large-scale water exchange (e.g., fjords) (Wassmann, 2001). Stratification during spring (e.g., the Marginal Ice Zone—MIZ) promotes the vernal bloom development. A preliminary spring investigation along a south–north gradient in the Barents Sea revealed that large-celled phytoplankton indeed accumulated predominantly in the MIZ. However, the most prominent result was the ubiquitous presence of pico- and nanoplankton in the Atlantic water, the ice edge and the open and ice-covered Arctic water (Wassmann et al., 1999b). The question arises as to how widespread and important small (<20 μm) phyto- and zooplankton organisms are during the productive season in cold water systems.

This study attempts the following: (a) to describe the succession of phyto- and protozooplankton in the Barents Sea by investigating their abundance in the upper water column along a south–north transect; (b) to investigate the microplankton composition during late winter/early spring; (c) to study the phyto- and protozooplankton species and succession in the ice-covered northern Barents Sea; (d) to study the composition and seasonal changes of small phytoplankton (<20 μm in linear dimension), in particular, small flagellates and athecate dinoflagellates; and (e) to present a comprehensive list of species and convert abundance into biovolume and biomass. The latter estimates are of particular significance for concomitant system–ecological investigations of suspended biogenic matter and microbial cycling (e.g., Allen et al., 2002; Reigstad et al., 2002), zooplankton grazing (Arashkevich et al., 2002), vertical export of biogenic matter (Olli et al., 2002) and a dynamic, 3D carbon model (Slagstad and Wassmann, 1997).

2. Materials and methods

As part of the Norwegian research programme "Arktisk lys og varme" (ALV) phytoplankton was collected along Transect I (Wassmann et al., 1999b) during three cruises with R/V "Jan Mayen" in March (72°30′N, 30°59′E–76°23′N, 33°20′E) and May 1998 (72°30′N, 30°59′E–76°04′N, 32°51′E) and June–July 1999 (72°30′N, 30°59′E–78°12′N, 34°31′E) in the central Barents Sea (Fig. 1). The investigation crossed the zonal structure of the Barents Sea: the Polar Front (PF), the MIZ and the main water masses: Atlantic water (AW), and Arctic water (ArW) and a zone with mixed and modified AW above the Sentralbanken (SBW). For details, see Reigstad et al. (2002).

Each cruise started with transect stations. In these stations, CTD profiles and water samples for the analysis of nutrients, suspended pigments and phytoplankton were taken: at 0, (5), 10, 20, 30, 40, 50, 75 and 90 m depths. In March 17–23, 1998, 13 stations (Stns. 1–5 in AW; Stn. 6—PF; Stns. 7–9 in SBW; Stn. 10—PF; Stns. 11–13 in ArW; Stn. 13 was sampled in the same position ant time as Stn. III), in May 19–28, 1998, 12 stations (Stns. 1–6 in AW; Stn. 7—PF; Stns. 8–9 in SBW; between Stns. 9 and 10—PF; Stns. 10–12—in ArW) and in June 29–July 9, 1999, 19 stations (Stns. 1–7 and 10–14 in AW; Stns. 8–9 in SBW; Stn. 14—PF; Stns. 15–19 in ArW) were investigated (Fig. 1). The location for 24-h process stations were chosen on the return along the transect according to CTD and ice-coverage data to obtain representative scenarios for the AW, ArW and PF region. The data for the 24-h stations were obtained 1–7 days after the transect stations were collected. Samples for microplankton analysis were obtained at three stations (Stns. I–II in AW and Stn. III in ArW), five stations (Stns. I–II in AW; Stn. III in SBW; and Stns. IV–V in ArW) and five stations (Stns. I–II in AW; Stn. III in PF and Stns. IV–V in ArW) 24-h stations in March, May and July, respectively.

From each depth, 100-ml aliquots of sea water were preserved with a glutaraldehyde–Lugol solution (Rousseau et al., 1990). This fixative preserves flagellates and small dinoflagellates perfectly, but the disadvantages are low pH (possible dissolution of thin structures of diatoms and coccolithophorids) and poor preservation of yeast (which occasionally develop in the samples during storage).

In the laboratory, phytoplankton was counted with a standard (non-inverted) light microscope furnished with a mechanical counting stage (Guillard, 1978). The whole sample was gently mixed, and picoplankton (<2 μm) and the most abundant nanoplankton (2–20 μm) algae were counted in a Fuchs–Rosental (Guillard, 1978) counting chamber at 400× magnification. The samples were then allowed to settle for a week and slowly decanted through a glass tube covered with two layers fine-mesh nylon gauze. After gentle mixing, part of the remaining sample was removed with a glass tube (condensed sample had volume 1–4 ml) and placed into a 0.06-ml circular chamber with rulings. Microplankton, including protozoans (>20 μm), and less abundant species of nanoplankton were counted at 200× magnification. In order to count rare phytoplankton forms and protozoans in total sample volume, a special 1.0-ml circular chamber with rulings was used (Semina, 1978). Many algae, could only be identified to genus or to higher taxa. Picoplankton and the smallest flagellates were counted mainly in size groups (<2, 2–4, 4–6, and 6–10 μm). The total counts of the cells usually were more, than few hundreds and rather often more, than a

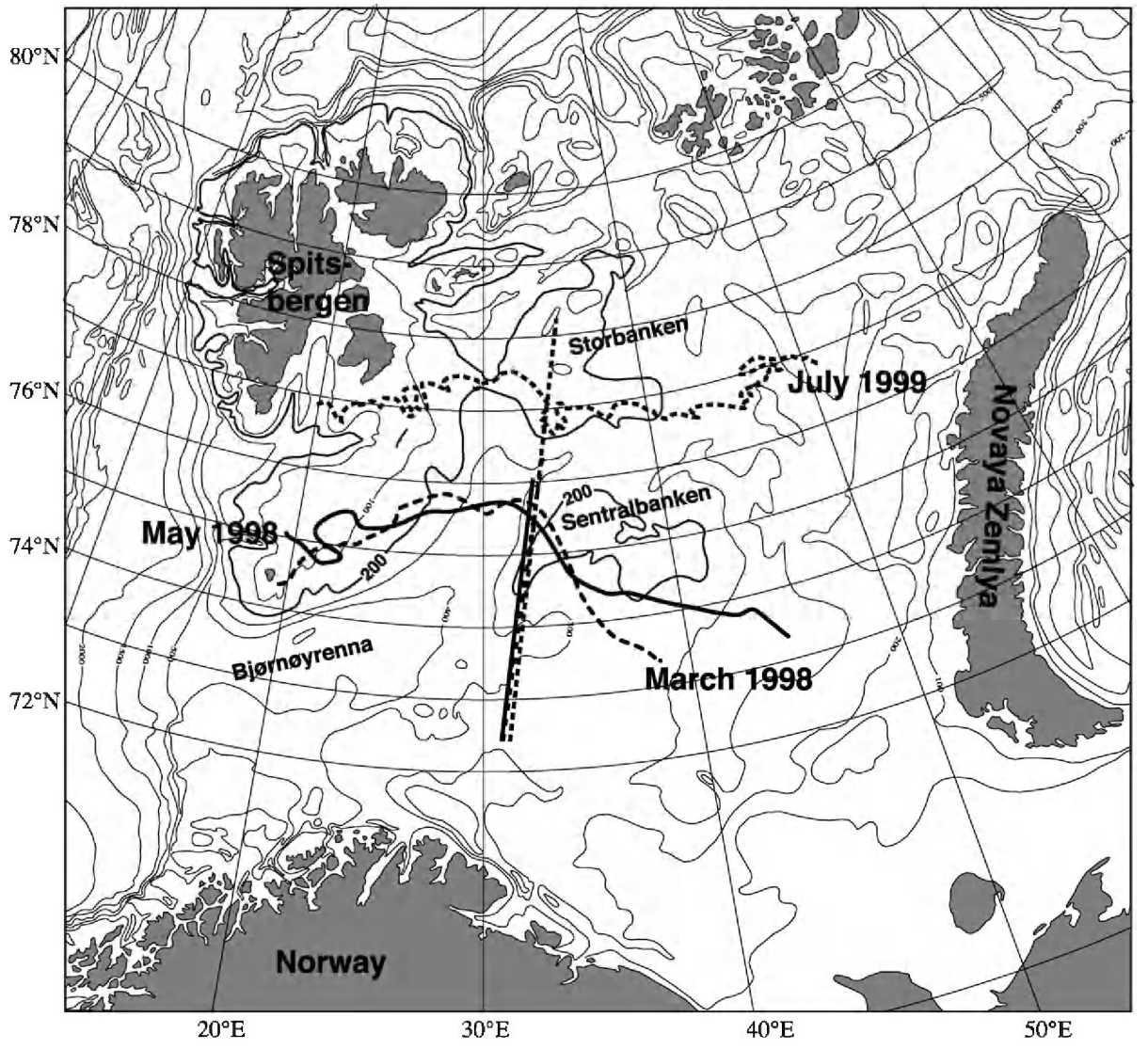


Fig. 1. The investigated area in the central Barents Sea, the transect and ice edge location during the three cruises in March 1998, May 1998 and July 1999.

thousand. For the most abundant single species, counts varied from 10 to 20 cells or colonies to few hundred cells or colonies. Rare species (cells counts less, than 10 cells or colonies) were included in the total and main groups biomass calculations, only.

The identification of diatoms was performed in the permanent mounts of Naphrax resin, as described by Hasle and Syvertsen (1997).

The applied method does not allow the distinction between auto- and heterotrophic flagellates, as well as to distinguish between alive and dead cells. Therefore, the term PNM (pico-, nano-, and microplankton), which includes autotrophic phytoplankton and heterotrophic flagellates in these size groups, is applied. This despite of that the choanoflagellates, some dinoflagellates and some chrysophytes are known as heterotrophic or mixotrophic. Picoplankton may, in part, include the largest bacteria as flagella were often not visible, especially in the smallest cells. For convenience, we grouped all undetermined coccoid and ovoid

cells into the categories "picoplankton" (<2 μm) and "undetermined flagellates" (2–4, 4–6 and 6–10 μm). Consequently, some of the cells may be yeast or cyanobacteria. Protozoa and small metazoa were not included in the PNM estimates.

The biovolume of algae and protozoans cells was calculated from the volumes of appropriate stereometrical bodies (Smayda, 1978). The PNM carbon content (PNMC) was estimated according to Strathmann (1967) and Menden-Deuer and Lessard (2000), who gave a universal equation ($\log C$ pg/cell = $\log V_{cell} \times 0.939 - 0.665$) for all kinds of phytoplankton and protozoans (excluding diatoms with cells volumes more than 3000 μm^3). Comparison between the two methods of estimates indicated some differences, especially for diatoms with cell volumes ranging from 1000 to 3000 μm^3 (PNMC calculated according to Menden–Deuer and Lessard was 20–30% higher) and small flagellates (PNMC calculated according to Menden–Deuer and Lessard was about 20% lower). The estimates of PNMC according to Strathmann were only 10% lower compared to those of Menden–Deuer and Lessard. To facilitate comparison with the previous investigations in the region (e.g., Rat'kova et al., 1999; Wassmann et al., 1999b) Strathmann's equations were applied. Carbon content for tintinnids was calculated as C pg/cell = $0.053 \times V_{cell} + 444.5$, according to Verity and Langdon (1984) and for other protozoans—according to Garrison and Buck (1989), as $\log C$ pg/cell = $0.941 \times \log V_{cell} - 0.6$.

3. Results

3.1. Phytoplankton composition

A total of 219 different phytoplankton species was observed. This is a minimum estimate, because some organisms were identified only to higher taxa or were accounted in size groups.

The lowest number of species was encountered in March (Table 1) and the highest number—in June/July. Species of the genera *Chaetoceros*, *Thalassiosira* (diatoms) and *Gyrodinium* and *Protoperidinium* (dinoflagellates), were very numerous in summer, but markedly less in spring. Species of the genus *Pseudo-nitzschia* (diatoms) were scarce in March, but were most abundant in May. In June/July, dinoflagellates were present with considerable more species than in March and May (Table 2). The waters above the Sentralbanken (SBW) and PF were inhabited with the mixture of Atlantic Water (AW) and Arctic Water (ArW) populations, so these waters were markedly depleted in comparison to the original

Table 1
Taxonomical composition of phytoplankton (mean number of the species, observed in the 0–90 m layer during the three ALV cruises

Season	March					May				June/July				Total
Water types	AW	PFs	SBW	PF	ArW	AW	PFs	SBW	ArW	AW	AWSB	PF	ArW	
Station no.	**7**	**1**	**3**	**1**	**3**	**8**	**1**	**3**	**5**	**13**	**2**	**2**	**7**	**56**
Taxa														
Bacillariophyceae	24	7	24	12	16	57	22	34	51	59	36	56	60	109
Dinophyceae	21	2	15	12	14	22	10	25	23	61	20	31	50	75
Dictyochophyceae	2	–	1	–	1	1	–	–	1	1	–	–	1	2
Primnesiophyceae	2	1	2	2	2	2	2	3	3	2	2	1	2	4
Chrysophyceae	2	4	3	4	4	6	3	4	4	6	5	6	8	8
Cryptophyceae	1	3	4	3	4	5	4	4	4	6	6	4	6	6
Chlorophyceae	1	–	–	1	–	1	–	–	1	1	–	1	1	1
Euglenophyceae	2	1	2	1	2	3	2	2	3	2	1	2	2	4
Prasinophyceae	2	–	1	1	–	2	–	–	1	4	2	1	4	4
Choanoflagellideae	2	1	1	2	1	3	2	3	2	3	1	3	4	4
Kinetoplastida	1	1	1	1	1	1	1	–	–	1	1	1	1	1
Ebridiida	–	–	1	–	–	–	1	1	1	1	1	–	1	1
Total	60	20	55	39	45	103	47	76	94	147	75	106	140	219

Water types: Atlantic water (AW), Sentralbanken Water (SBW), Atlantic water above the Sentralbanken (AWSB), south branch of the Polar Front (PFs), Polar Front (PF), and Arctic water (ArW). Data in bold—number of the stations.

Table 2
Average biomass of the most abundant species, observed in the 0–90 m layer (mg C m^{-2})

Season				March 1998					May 1998				June/July 1999			
Water types				AW	PFs	SBW	PF	ArW	AW	PFs	SBW	ArW	AW	AWSB	PF	ArW
Station no.				**7**	**1**	**3**	**1**	**3**	**8**	**1**	**3**	**5**	**13**	**2**	**2**	**7**
Taxa	V	E	GR													
Division chromophyta																
Class Bacillariophyceae																
Attheya septentrionalis (Østrup) Crawford	150	I-N	A–B	1	–	1	+	–	2	–	–	+	1	–	1	+
Bacterosira bathyomphala (Cleve) Syvertsen et Hasle	2200	N	A–B	–	–	–	–	1	10	220	50	60	20	6	180	10
Chaetoceros affinis Lauder	4600	N	A–B?	–	–	–	–	–	10	–	–	–	3	–	–	+
C. borealis Bailey	11250	M	A–B	–	–	–	–	–	6	–	–	+	1	5	1	–
C. brevis Schütt	1500	N	A–B	–	–	–	–	–	–	–	–	–	20	–	–	+
C. compressus Lauder	600	N	T–A–B	+	+	1	+	+	7	2	5	5	80	+	30	50
C. concavicornis Mangin	2200	M	A–B	–	–	–	–	–	10	–	+	+	9	4	20	9
C. curvisetus Cleve	900	N	C	–	–	–	–	–	–	80	4	–	1	3	–	–
C. debilis Cleve	600	N	T–A–B	+	+	+	+	+	80	450	350	130	5	+	4	3
C. decipiens Cleve	13,500	M	C	+	–	1	–	–	2	170	–	+	60	20	90	10
C. densus (Cleve) Cleve	18,000	M	T–A–B	–	–	–	–	–	+	–	–	–	10	–	30	20
C. diadema (Ehrenberg) Gran	3100	N	A–B	–	–	–	–	–	–	–	1	1	1	–	–	1
C. furcellatus Bailey	200	N	A–B	+	–	+	–	+	7	27	1	2	41	1	345	46
C. socialis Lauder	100	N	C	780	540	190	280	400	1360	1830	660	290	520	700	700	530
Cylindrotheca closterium (Ehrenberg) Lewin et Reimann	450	N	C	–	–	+	–	–	3	–	5	10	2	3	8	6
Dactyliosolen fragilissimus (Bergon) Hasle	5100	N	C	10	–	–	–	3	–	–	70	+	10	10	–	170
Entomoneis cf. *alata* (Ehrenberg) Poulin et Cardinal	3000	–	–	+	–	–	–	–	+	–	7	1	–	–	7	–
Eucampia groenlandica Cleve	1500	N	A–B	–	–	–	–	–	1	50	15	4	2	–	20	1
Fragilariopsis cylindrus (Grunow) Krieger in Helmcke et Kriger	100	I-N	BP	+	+	+	–	+	2	10	10	3	1	1	20	4
F. oceanica (Cleve) Hasle	400	I-N	A–B	+	–	+	–	+	10	70	60	30	1	–	50	2
Leptocylindrus danicus Cleve	1200	N	T–A–B	3	1	+	+	+	+	+	+	+	5	3	4	30
Navicula directa (W.Smith) Ralfs in Pritchard	9000	I-N	A–B	–	–	3	–	–	–	–	20	9	–	–	1	–
N. granii (Jørgensen) Gran	2700	N	A–B	70	–	–	–	–	20	–	+	–	–	–	–	–
N. pelagica Cleve	1100	N	A–B	–	–	–	–	–	3	10	10	10	–	–	–	–
N. vanhoeffenii Gran	2200	N	A–B	1	–	–	–	–	30	100	40	170	1	–	210	10
Pauliella taeniata (Grunow) Round et Basson	1000	M-N	A–B	–	–	–	–	+	+	–	20	6	1	–	180	30
Porosira glacialis (Grunow) Jørgensen	38,800	N	BP	1	–	–	–	–	1	10	90	40	3	190	9	2
Proboscia alata (Brightwell) Sundström	33,900	M	C	–	–	–	–	–	–	–	–	1	10	–	4	60
Pseudo-nitzschia cf. *austra lis* Frenguelli	3100	M	T–A–B	–	–	–	–	–	1	–	–	1	80	+	5	100
P. cf. *pseudodelicatissima* (Hasle) Hasle	100	M	A–B	+	–	1	+	–	2	4	3	3	1	–	+	3

Table 2 (*continued*)

Season				March 1998					May 1998				June/July 1999			
Water types				AW	PFs	SBW	PF	ArW	AW	PFs	SBW	ArW	AW	AWSB	PF	ArW
Station no.				**7**	**1**	**3**	**1**	**3**	**8**	**1**	**3**	**5**	**13**	**2**	**2**	**7**
Taxa	V	E	GR													
Rhizosolenia hebetata f. *semispina* (Hensen) Gran	37,500	M	C	–	–	–	–	–	–	–	–	–	10	–	40	20
Thalassiosira angulata (Gregory) Hasle	4300	N	A–B	1	2	+	2	1	30	–	330	40	1	19	5	1
T. anguste-lineata (A. Schmidt) Fryxell et Hasle	12,000	N	T–A–B	–	2	–	–	–	8	30	10	3	2	–	40	3
Thalassiosira cf. *antarctica* var. *borealis* Fryxell, Doucette et Hubbard	14,580	N	A–B	6	3	+	5	2	530	970	1300	720	9	3	1210	100
T. bulbosa Syvertsen	400	I-N?	A–B	–	–	–	–	–	+	–	+	+	–	–	1	–
T. constricta Gaarder	18,700	–	A–B?	–	–	–	–	–	4	–	20	9	–	–	30	3
Thalassiosira cf. *gravida* Cleve	9000	N	BP	–	–	–	–	–	+	–	1	+	+	–	1	1
T. hyalina (Grunow) Gran	6500	N	A–B	–	–	–	–	–	+	–	5	3	+	+	40	1
T. nordenskioeldii Cleve	2900	N	A–B	1	+	1	–	+	20	50	20	20	2	2	60	6
Class Dinophyceae																
Alexandrium tamarense (Lebour) Balech	19,000	N	T–A–B	–	–	–	–	–	6	60	4	10	10	+	20	50
Dinophysis acuta Ehrenberg	18,000	M-N	BP	–	–	–	–	–	–	–	–	–	1	–	–	–
Diplopelta parva (Abé) Matsuoka	5900	–	–	–	–	–	–	+	–	–	–	–	50	5	4	150
Diplopsalis lenticula Bergh	14,000	M	C	–	–	–	–	–	+	–	+	–	60	–	–	30
Entomosigma peridinioides Shiller	1200	N?	–	1	–	–	–	+	1	–	+	+	10	+	+	20
Gonyaulax alaskensis Kofoid	7800	–	A–B	–	–	–	–	–	–	–	–	–	7	–	–	4
G. digitale (Pouchet) Kofoid	40,000	M-N	T-B	3	–	–	–	–	–	10	–	–	20	–	–	80
G. grindleyi Reinecke	18,000	N	C	–	–	–	–	–	–	–	7	–	10	–	–	30
G. spinifera (Claparède et Lachmann) Diesing	9900	N	C	–	–	–	–	–	–	–	–	–	5	–	–	4
G. verior Sournia	7800	N	C	–	–	–	–	–	–	–	–	–	+	–	–	–
Gymnodinium frigidum Balech	4700	N	BP	–	–	–	–	–	–	3	2	–	–	–	–	–
G. simplex *(Lachmann)* Kofoid et Swezy	190	N	–	1	+	1	+	9	+	–	–	+	20	+	3	40
G. japonicum Hada	400	N	–	+	–	–	1	+	1	–	+	+	7	3	2	10
Gymnodinium cf. *blax* Harris	260	F	–	1	1	+	1	+	2	+	1	1	1	–	1	4
G. veneficum Ballantine	900	N	–	2	1	1	+	1	5	5	1	2	10	2	5	10
G. wulfii Schiller	1700	N	–	1	–	1	2	+	4	–	3	2	8	10	3	10
G. arcticum Wulff	4000	N	–	+	–	1	–	–	4	10	3	10	6	2	5	10
Gyrodinium cf. *aureolum* Hulburt	24,000	N	A–B	+	–	4	–	–	+	–	–	+	20	–	30	30
G. prunus (Wulff) Lebour	47,000	–	C	–	–	–	–	–	4	100	10	–	50	–	60	50
G. spirale (Berg) Kofoid et Swezy	17,000	N	C	–	–	–	–	1	–	–	4	5	9	–	+	20
Phalacroma.rotundatum (Claparède et Lachmann) Kofoid et Michener	12,000	M-N	C	–	–	–	–	–	–	–	–	6	4	20	5	–
Prorocentrum balticum (Lachmann) Loeblich III	400	N	C	+	–	–	–	–	1	1	+	–	10	1	+	20

(continued on next page)

Table 2 (*continued*)

Season				March 1998					May 1998				June/July 1999			
Water types				AW	PFs	SBW	PF	ArW	AW	PFs	SBW	ArW	AW	AWSB	PF	ArW
Station no.				**7**	**1**	**3**	**1**	**3**	**8**	**1**	**3**	**5**	**13**	**2**	**2**	**7**
Taxa	V	E	GR													
P. cordatum (Ostenfeld) Dodge	1600	N		–	–	–	–	+	–	–	–	–	20	+	1	4
Protoperidinium brevipes (Paulsen) Balech	10,100	N	A–B	–	–	–	–	–	+	–	6	–	6	–	4	6
P. islandicum (Paulsen) Balech	81,000	N	BP	–	–	–	–	–	–	–	–	–	20	–	–	–
P. nudum (Meunier) Balech	9400	N?	A–B	–	–	–	–	–	–	–	–	–	4	–	+	20
P. pellucidum Bergh	51,800	M-N	C	–	–	–	–	–	–	–	+	+	30	20	–	4
P. subinerme (Paulsen) Loeblich III	62,500	N?	C	–	–	–	–	–	–	–	–	–	–	–	10	–
Scrippsiella trochoidea (Stein) Loeblich III	5900	N	C	–	2	+	+	+	+	+	+	+	20	4	16	30
Warnowia schuetti (Kofoid et Swezy) Shiller	6000	–	–	6	–	–	–	–	2	30	11	–	7	–	6	10
Class Dictyochophyceae																
Dictyocha fibula Ehrenberg	5500	M	T–A–B	+	–	2	–	–	–	–	–	–	–	–	–	–
D. speculum Ehrenberg	6900	M	C	+	–	–	–	+	+	–	–	2	6	–	–	10
Class Prymnesiophyceae																
Emiliania huxleyi (Lochmann) Hay et Mohler	260	M	C	+	–	+	+	4	+	+	+	1	1	+	+	+
Phaeocystis pouchetii (Hariot) Lagerheim	200	M-N	BP?	610	220	560	210	1390	4910	4620	2260	1850	1610	1600	7380	1490
Class Chrysophyceae																
Calycomonas sp.	20			+	2	+	+	10	+	–	+	+	+	–	–	+
Dinobryon balticum (Schütt) Lemmermann	800	M-N	A–B	150	70	120	40	280	60	90	20	20	510	90	21,300	120
D. belgica Meunier	600	–	A–B	–	1	–	1	–	–	–	–	–	40	1	–	1
D. faculiferum (Willén) Willén	260	–	A–B?	–	–	–	–	–	2	–	–	–	9	+	7	5
Ochromonas crenata Klebs	900	–	A–B?	100	3	20	100	360	30	11	70	140	940	1140	200	140
Class Cryptophyceae																
Chroomonas marina (Büttner) Butcher	1100	–	–	2	+	1	2	1	3	2	1	2	6	1	30	11
Hillea fusiformis (Schiller) Shiller	64	–	–	10	–	+	1	60	6	110	110	4	30	7	8	5
Leucocryptos marina (Braarud) Butcher	480	–	–	–	–	–	–	–	+	–	–	–	+	1	–	2
Plagioselmis sp.	750			1	–	–	–	+	7	20	3	1	10	4	7	6
Teleaulax acuta (Butcher) Hill	340	–	–	10	3	9	5	7	20	8	7	9	30	20	8	50
Division chlorophyta																
Class Euglenophyceae																
Eutreptiella eupharyngea Moestrup et Norris	600	–	A–B	5	7	6	+	+	10	1	+	7	3	1	2	6
E. gymnastica Throndsen	2700	–	–	1	–	1	–	+	1	4	3	1	1	–	5	1

(continued on next page)

Table 2 (*continued*)

Season				March 1998					May 1998				June/July 1999			
Water types				AW	PFs	SBW	PF	ArW	AW	PFs	SBW	ArW	AW	AWSB	PF	ArW
Station no.				**7**	**1**	**3**	**1**	**3**	**8**	**1**	**3**	**5**	**13**	**2**	**2**	**7**
Taxa	V	E	GR													
Class Prasinophyceae																
Halosphaera viridis Schmitz	500	–	C	+	–	–	–	–	–	–	–	–	2	–	–	6
Pachysphaera pelagica Ostenfeld	100	–	–	–	–	–	–	–	–	–	–	–	+	+	+	1
Pyramimonas grossii Parke	320	–	C?	+	–	1	+	–	+	–	–	–	+	+	–	1
Phylum zoomastigophora																
Class Choanoflagellidea																
Desmarella moniliformis Kent	108	–	–	9	+	2	6	20	10	90	4	3	15	50	80	20
Parvicorbicula socialis (Meunier) Deflandre	2000	–	–	3	–	–	1	–	+	–	1	–	1	–	10	+

"+": <1 mg C m^{-2}.

Water types: Atlantic water (AW), Sentralbanken Water (SBW), Atlantic water above the Sentralbanken (AWSB), south branch of the Polar Front (PFs), Polar Front (PF) and Arctic water (ArW). Data in bold—number of the stations.

V—mean cells volume (μm^3), E—ecological characteristics (M—marine; N—neritic; I-N—ice-neritic; M-N—marine-neritic; F—freshwater; "–" unknown), GR—geographical ranges (A–B—arctic–boreal; C—cosmopolitan; BP—bipolar; T–A–B—tropic–arctic–boreal; T–B—tropic–boreal; "–" unknown).

water masses: many species, encountered from the AW and from the ArW, were absent in SBW and in PF. In all cruises the PF region exhibited the lowest number of phytoplankton species, except the June/July, when the lowest number was observed in the SBW area occupied with the AW in this time.

Most of the observed species, according to Semina and Sergeeva, 1983; Tomas, 1997; Konovalova, 1998; Okolodkov, 1998; Rat'kova, 2000, were arctic–boreal (54), followed by cosmopolitan species (41). Rather numerous were tropic–arctic–boreal species (22). A few bipolar and tropical species were also observed (nine and three species, respectively). The geographical ranges of the other species are uncertain. In March almost all species belonged to the arctic–boreal and tropic–arctic–boreal species. Cosmopolitans were presented by 12, bipolar by only four species (Table 2). In May, cosmopolitans and bipolar species became more numerous but most of them were observed in June/July.

Neritic and ocean-neritic species dominated total species numbers (67%), oceanic species were less numerous (23%) and ice-neritic were represented by 6% only. The remaining 4% were bottom and brackish water species. In March, oceanic and ocean-neritic species were rare and inhabited the AW exclusively. In ArW, neritic and a few ice-neritic species were observed. Some of the ice-neritic species inhabited AW in March also. In May the number of oceanic species increased, but they mainly inhabited the AW. Ice-neritic species were observed in the ArW, but a few were recorded also in the AW. In June/July, most of oceanic species were encountered in the AW, so some of them were observed in ArW, also. Most of the ice-neritic species were distributed along the entire transect (Table 2).

3.2. Phytoplankton abundance and biomass

3.2.1. March 1998

In March 1998, PNMC was low along the entire transect (<5 g C m^{-2} at most stations; all concentrations m^{-2} in 0–90 m depth interval). Unidentified small flagellates (diameter <6 μm) dominated PNM numbers and biomass (up to 3.7×10^9 cells l^{-1}; 2–4 g C m^{-2}), but we may suppose that they were predominantly heterotrophic, because low chlorophyll *a* concentration was observed in March 1998 (Reigstad et al., 2002). Flagellate biomass did not vary markedly along the transect and main variations in total biomass were

Table 3
Average biomass of the main taxonomical groups, observed in the 0–90 m layer (mg C m^{-2})

Season	March 1998					May 1998				June/July 1999			
Water types	AW	PFs	SBW	PF	ArW	AW	PFs	SBW	ArW	AW	AWSB	PF	ArW
Stations no.	**7**	**1**	**3**	**1**	**3**	**8**	**1**	**3**	**5**	**13**	**2**	**2**	**7**
Diatoms	900	500	200	300	410	2600	4100	4000	2800	1300	1700	8400	774
Dinoflagellates	20	8	30	10	15	70	220	150	140	790	150	520	524
Silicoflagellates	+	–	2	–	+	60	380	140	130	3	–	–	20
Coccolithophorides	4	+	+	20	4	1	+	2	10	8	10	3	20
Prymnesiophyta	490	220	560	210	260	6500	4600	2200	2800	900	1600	9000	2400
Chrysomonades	100	70	140	140	40	650	100	90	170	810	1200	1700	1300
Choanoflagellates	160	+	2	6	630	10	90	6	3	15	50	70	7
Prasinophytes	+	–	1	+	–	+	–	–	–	3	1	+	15
Cryptophytes	9	3	10	8	4	30	130	120	15	50	40	70	55
Chlorophytes	+	–	–	+	–	+	–	–	+	+	–	–	+
Euglenophytes	5	7	7	+	+	10	6	3	7	2	1	6	4
Zoomastigophores	1	+	2	+	1	+	1	–	–	25	2	1	14
Unidentified flagellates and monads	2300	2900	3400	3000	1600	5000	3700	2800	2900	3800	9500	2400	2700
Picophytoplankton	810	330	390	260	900	950	200	400	900	300	400	300	800
Cyanobacteria	–	–	–	–	–	140	–	140	80	40	30	50	95
PNMC	6300	4100	4800	4000	13,000	18,700	13,700	13,100	13,100	8100	14,700	26,800	33,400
Protozoa	8	+	10	120	1	40	20	50	100	550	120	170	490

"+": <1 mg C m^{-2}; "–": had not been found.
Water types: Atlantic water (AW), Sentralbanken Water (SBW), Atlantic water above the Sentralbanken (AWSB), south branch of the Polar Front (PFs), Polar Front (PF) and Arctic water (ArW). Data in bold—number of the stations.

due to diatoms, picoplankton and the prymnesiophyte *Phaeocystis pouchetii* (Table 3; Fig. 2). Diatoms were sparse at most stations and single cells and resting spores of *Chaetoceros socialis* dominated (Fig. 3). Two maxima of diatoms were observed: in the trench area (Stn. 5) and under the ice cover (Stn. 13). In the AW, *P. pouchetii* was most abundant in the vicinity of PF (1.8 g C m^{-2}), but the highest biomass of *P. pouchetii* (3.4 g C m^{-2}) and the chrysophytes *Dinobryon balticum* and *Ochromonas* spp. biomass (1.8 g C m^{-2}) was observed in the ArW at the ice-covered Stn. 13. Here, these three species dominated total phytoplankton biomass (Fig. 3). Dinoflagellates, dominated by small *Gymnodinium* spp. were sparse; cryptophytes were rather abundant at the ice-covered Stn. 13 (Fig. 4). Picoplankton was not abundant in March 1998, except at Stn. 5 in the northern AW and ice-covered Stn. 13 in the ArW.

In the AW, the highest PNMC concentration was observed close to the surface (Fig. 5a). A week later, at the 24-h stations, the PNMC maximum in AW was observed at 10 m depth (Fig 6). In ArW maximum of PNMC was situated deeper, than in AW, below the less saline upper water layer. In the PF zones and at the ice-covered Stn. 13 PNMC maximum occurred at the 30 m depth (Fig. 5a). Flagellates entirely determined vertical distribution of PNMC. *Paeocystis pouchetii* was present as single cells (both the flagellate and non-motile free living cells) along the entire transect. It had its highest biomass in the 0–20 m depth interval, but in the SBW, a *P. pouchetii* maximum was observed at 20–30 or 75 m depths.

3.2.2. May 1998

In May 1998, PNMC concentrations were very high at all transect stations (7–27 g C m^{-2}; Fig. 2). Four regions of highest PNMC biomass were observed: in the southern part of the AW (Stns. 2–3); in the trench area (Stn. 5); in the vicinity of PF zone (Stn. 9) and at the ice-covered Stn. 12. Biomass of flagellates did not changed too much in comparison to the March values, but diatoms and *P. pouchetii* increased their biomass markedly, and these taxa determined PNMC distribution in May. Diatoms and *P. pouchetii* dominated total phytoplankton biomass at most of the stations (Fig. 2). Diatoms had the highest

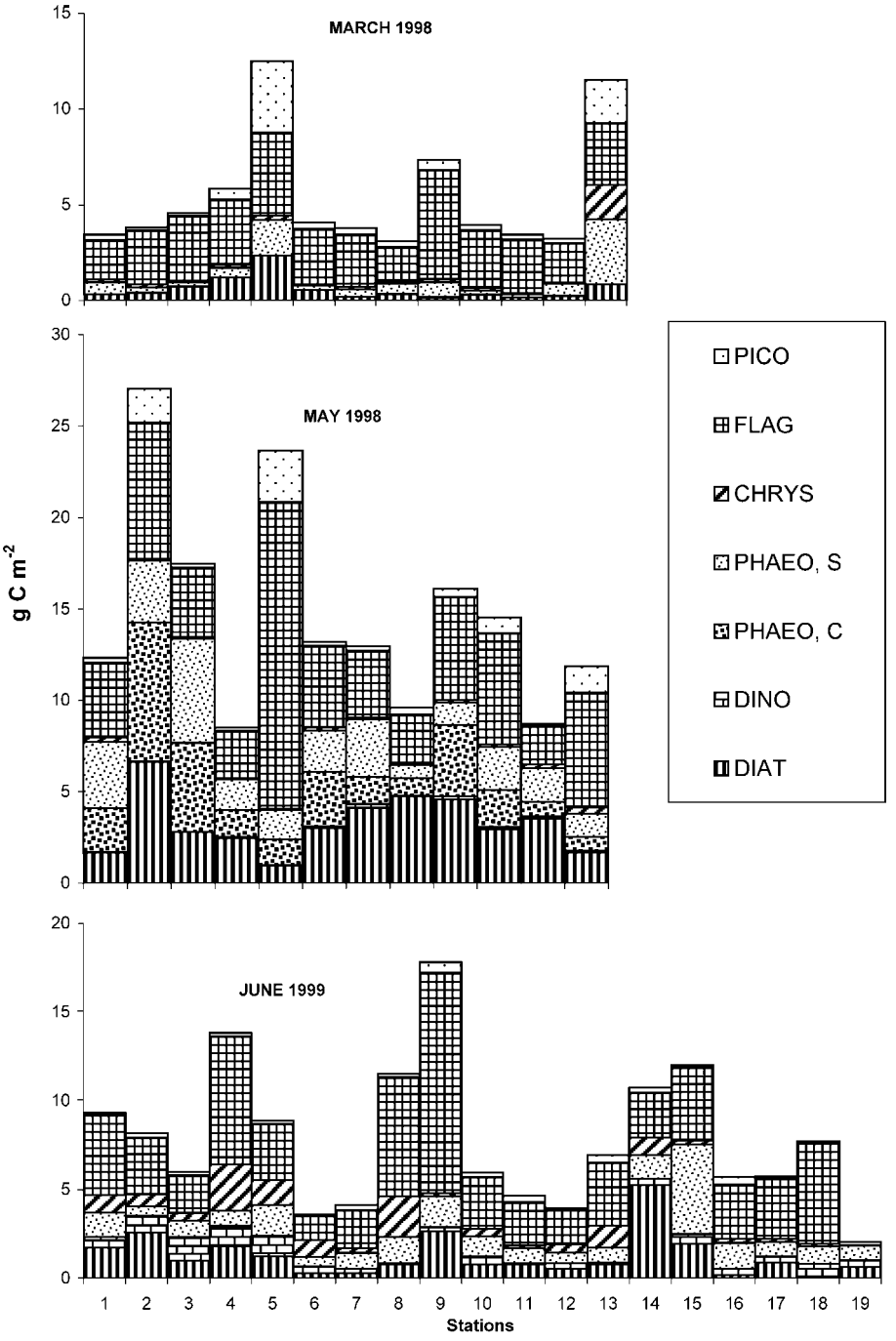


Fig. 2. Phytoplankton composition and distribution along the three ALV transects in the 0–90 m layer (g C m^{-2}). DIAT—diatoms; DINO—dinoflagellates; PHAEO, C—*Phaeocystis pouchetii*; cells in colonies; PHAEO, S—*P. pouchetii*; single cells; CHRYS—chrysophytes; FLAG—flagellates; PICO—picoplankton.

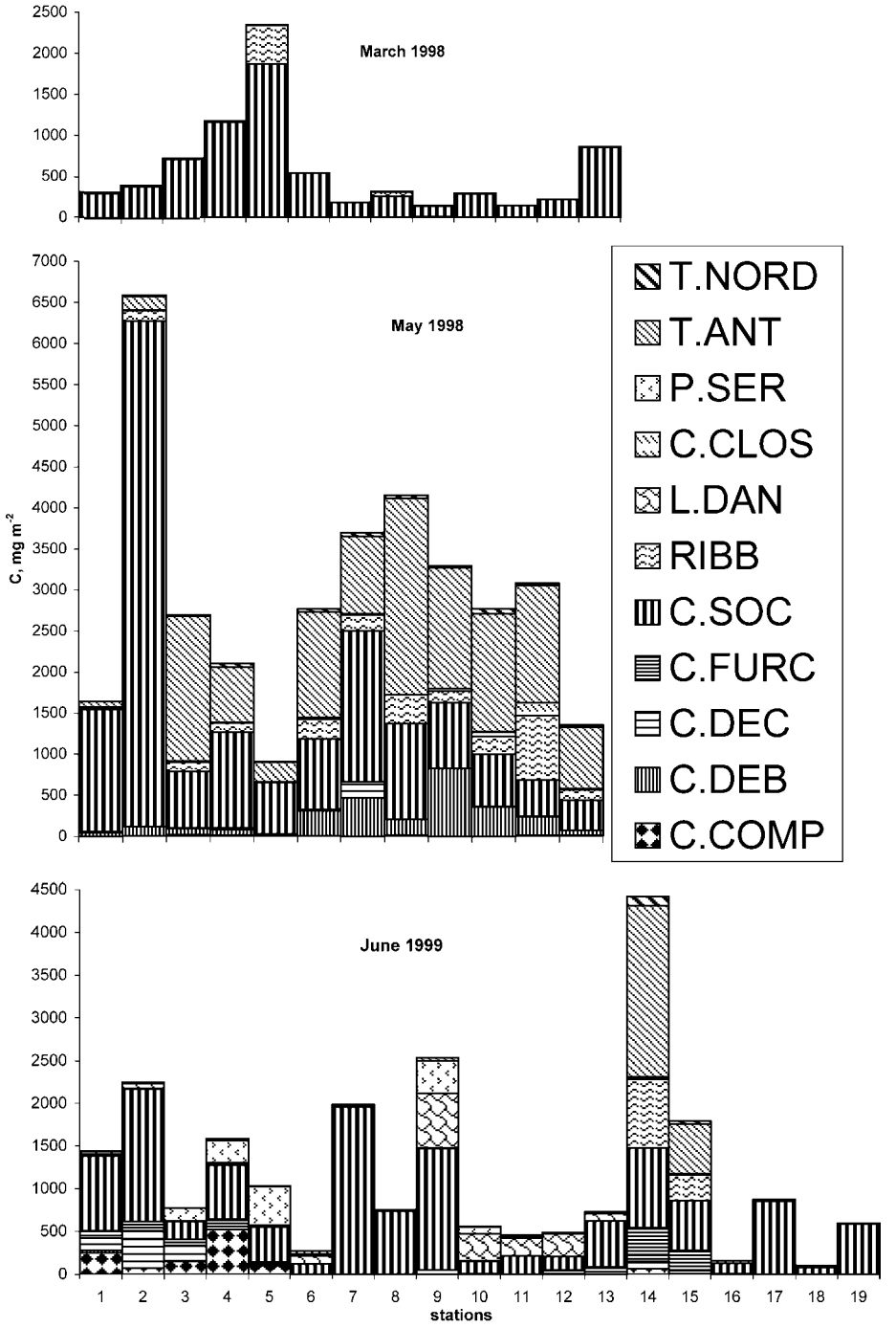


Fig. 3. Distribution of the most abundant diatom species along the three ALV transects in the 0–90 m layer (mg C m^{-2}). C. COMP—*Chaetoceros compressus*; C. DEB—*C. debilis*; C. DEC—*C. decipiens*; C. FURC—*C. furcellatus*; C. SOC—*C. socialis*; RIBB—pennates, forming ribbon-shaped colonies (mainly *Pauliella taeniata*; *Fragilariopsis cylindrus*; *F. oceanica*); L. DAN—*Leptocylindrus danicus*; C. CLOS—*Cylindrotheca closterium* and *Pseudo-nitzschia* spp. from the "Nitzschia delicatissima Complex"; P. SER—*Pseudo-nitzschia* spp. from the "Nitzschia seriata Complex"; T. ANT—*Thalassiosira* cf. *antarctica* var. *borealis*; T. NORD—*T. nordenskioeldii*.

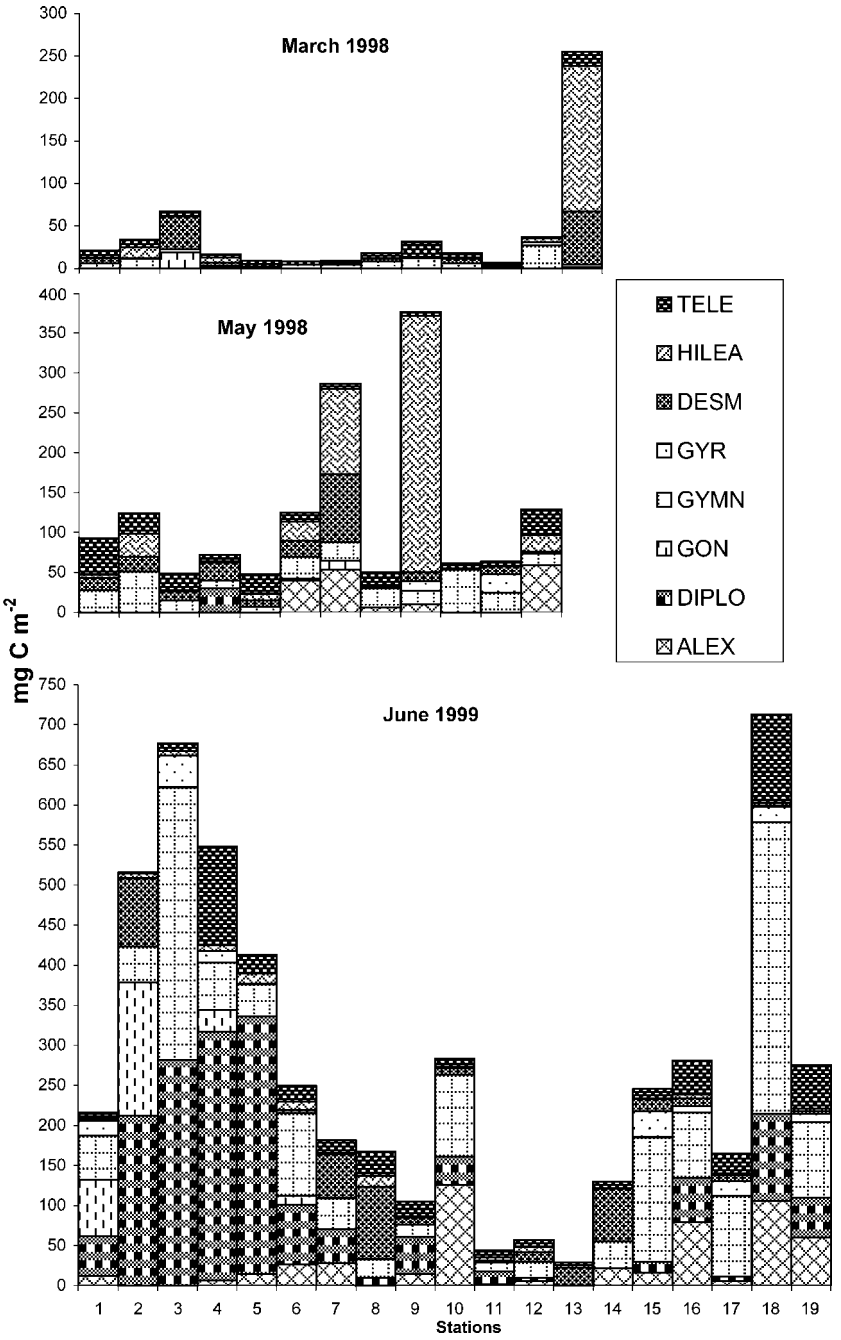


Fig. 4. Distribution of some flagellates species along the three ALV transects in the 0–90 m layer (mg C m^{-2}). ALEX—*Alexandrium* spp.; DIPLO—*Diplopelta* cf. *parva*, *Diplopsalis lenticula* and *D. minor*; GON—*Gonyaulax* spp.; GYMN—*Gymnodinium* spp.; GYR—*Gyrodinium* spp.; DESM—*Desmarella moniliformis*; HILEA—*Hilea fusiformis*; T. ACUT—*Teleaulax acuta*.

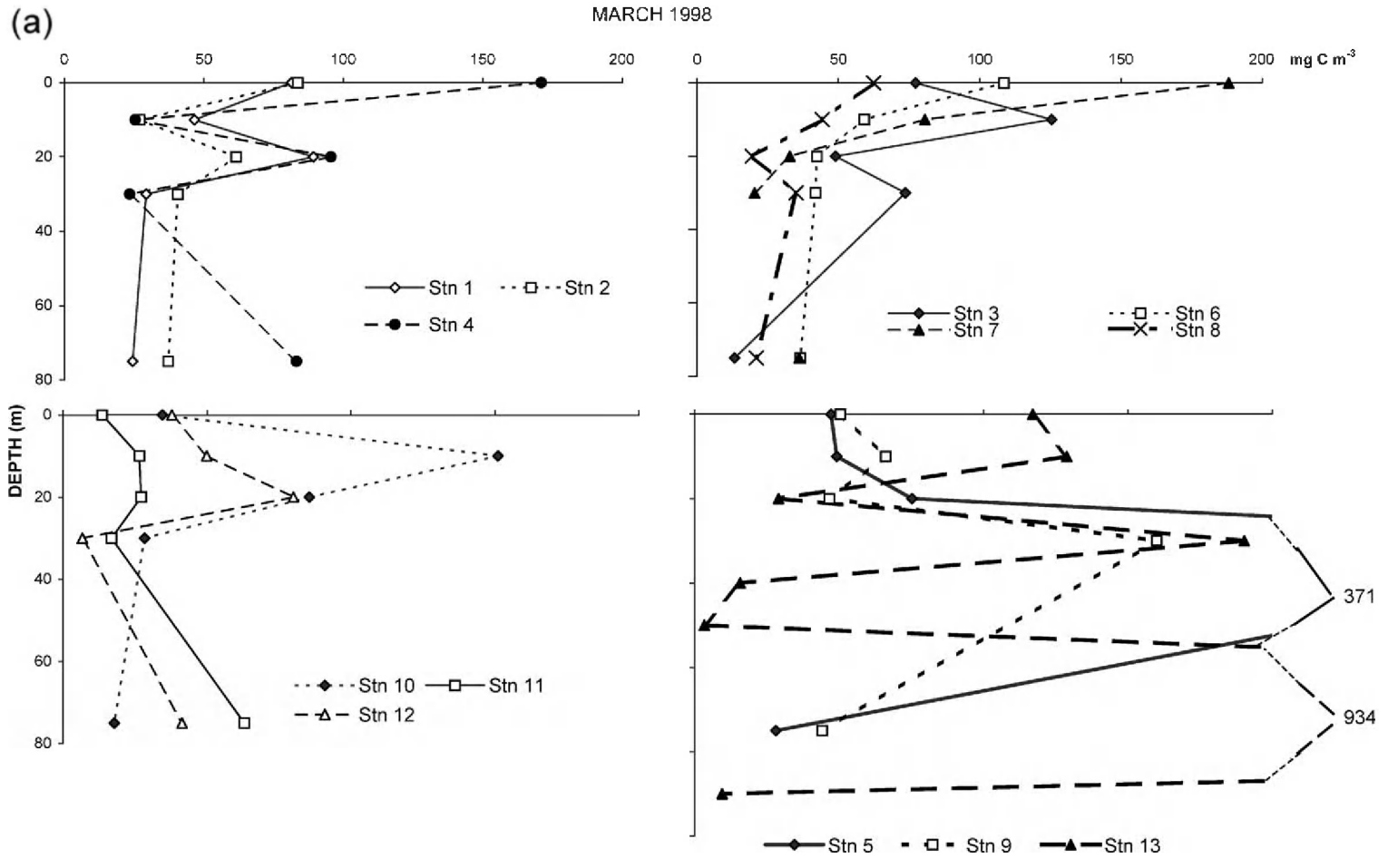


Fig. 5. (a) Vertical distribution of PNMC along the transect in March 1998. Stns. 1–5 in AW; Stns. 7–9 in SBW; Stns. 11–13 in ArW; Stn. 6—PFm (south branch of the PF); Stn. 10—PF (north branch of the PF); Stn. 11—MIZ; Stns. 12, 13—ice-covered. (b) Vertical distribution of PNMC along the transect in May 1998. Stns. 1–6 in AW; Stn. 8–9 in SBW; Stns. 10–12 in ArW; Stn. 7—PFm (south branch of the PF); Stn. 11—MIZ; Stn. 12—ice-covered. (c) Vertical distribution of PNMC along the transect in June/July 1999. Stns. 1–13 in AW; Stns. 15–19 in ArW; Stns. 8–9 in AW above the Sentralbanken; Stn. 14—PF; Stn. 15—MIZ; Stns. 16–19—ice-covered.

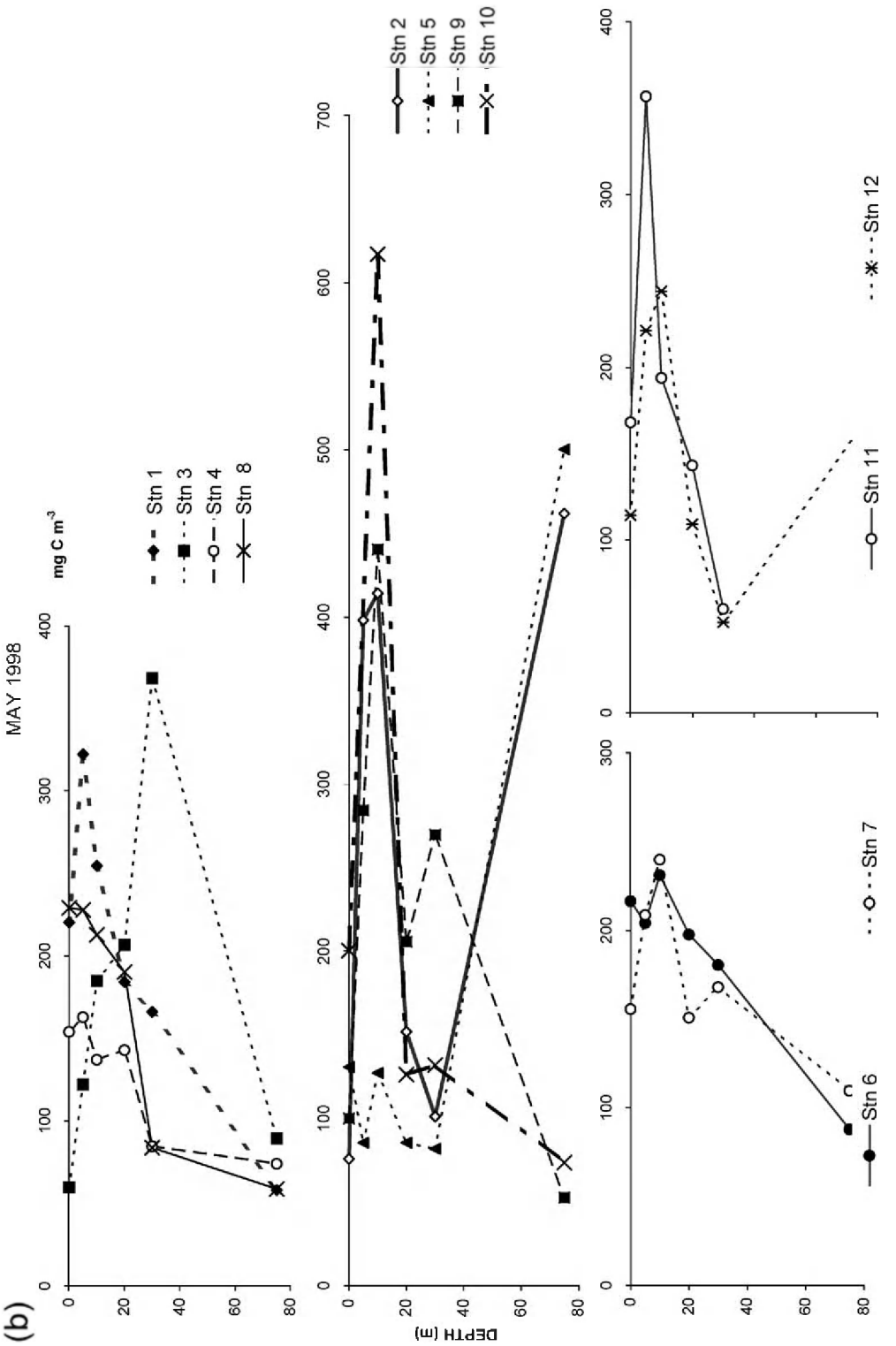
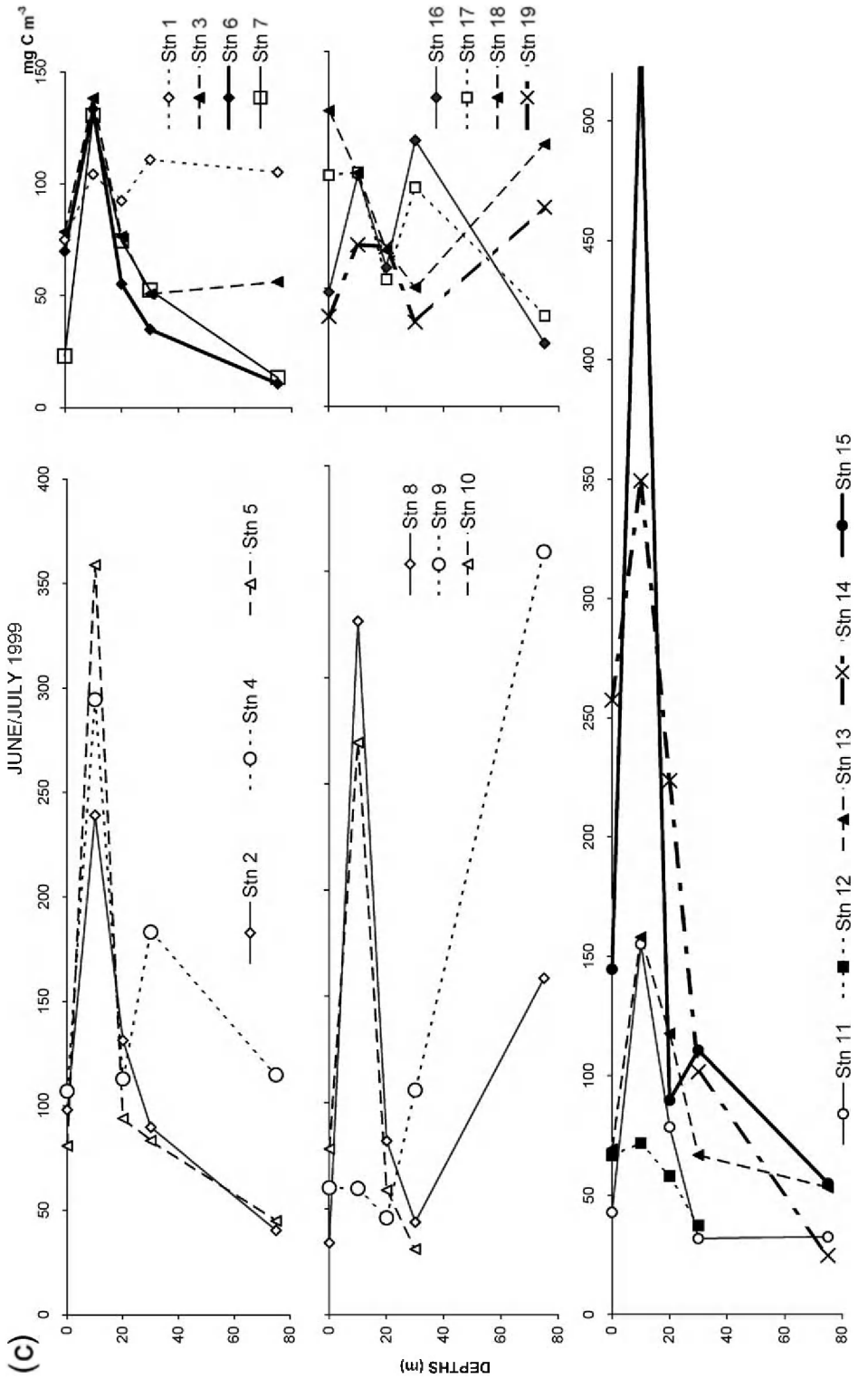


Fig. 5 (*continued*).



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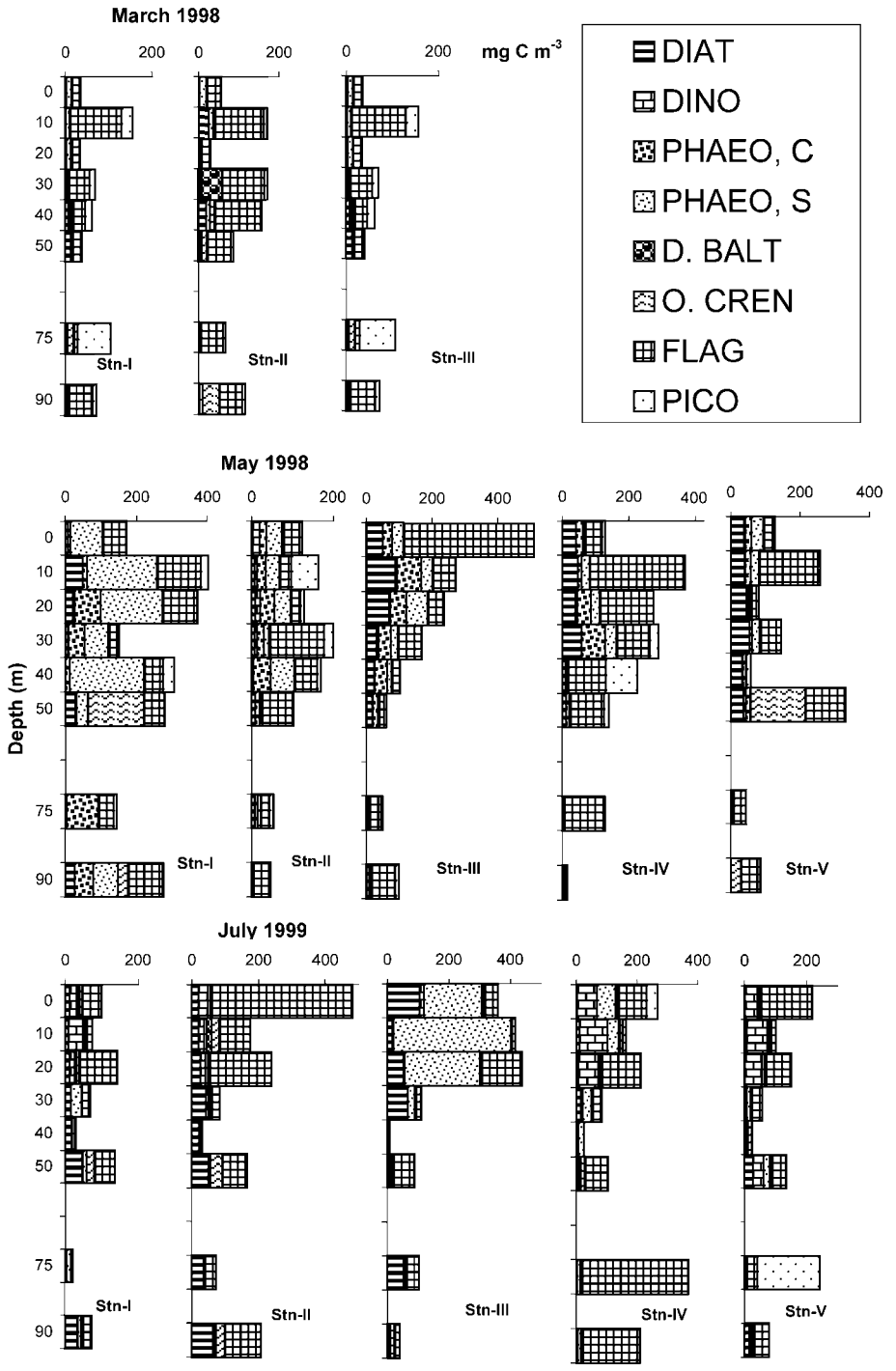

Fig. 6. Phytoplankton vertical distribution at the 24-h stations during the three ALV cruises (mg C m^{-3}). DIAT—diatoms; DINO—dinoflagellates; PHAEO, C—*Phaeocystis pouchetii*, cells in colonies; PHAEO, S—*P. pouchetii*; single cells; D. BALT—*Dinobryon balticum*; O. CREN—*Ochromonas crenata*; FLAG—flagellates; PICO—picoplankton.

biomass in the southern part of AW (dominated by *C. socialis*), in SBW (dominated by *Thalassiosira antarctica* var. *borealis*) and in the ice-edge zone (dominated by *T. antarctica* var. *borealis* and by diatoms, forming ribbon-shaped colonies; Fig 3). At the ice-covered stations, diatoms were least numerous and unidentified flagellates and single cells *P. pouchetii* dominated PNMC. Dinoflagellates had low biomass (<0.1 g C m^{-2}) in May. Choanoflagellates were sparse and cryptophytes were only abundant below the thermocline at the southernmost station of transect. Picoplankton was not abundant in May 1998 and its highest biomass was observed at Stn. 2 in AW and at the ice-covered Stn. 12 in ArW (1.5–2.0 g C m^{-2}).

Along the entire transect, the highest PNMC (200–400 mg C m^{-3}) concentration, dominated by unidentified flagellates and *P. pouchetii* was observed at 5–10 m horizons (Fig. 5b). A second maximum, dominated by the same groups in AW and by diatoms in ArW, occurred at 30–40 m depths. Total biomass of diatoms was distributed rather evenly in the upper 0–50 m along the entire transect (Fig. 6), but the vertical distribution of the different species varied. *C. socialis*, most abundant in AW, was dominated by spores and had the highest biomass in the lower horizons. *Chaetoceros debilis* that was represented mainly by vegetative cells, was most abundant in SBW and open ArW and was most abundant in the upper water. *T. antarctica* var. *borealis* had the highest biomass in SBW and ArW, its vegetative cells were more abundant below the 40 m depth in AW and were distributed rather evenly in 0–75 m depth interval in ArW. Its spores, which were especially abundant in the southern part of ArW, occurred mainly in the 40–90 m layer. Pennate diatoms, forming ribbon shaped colonies, occurred mainly at the ice edge (Stn. 11) and at the ice-covered Stn. V, where its biomass increased from the surface to 40 m depth. Below this depth it decreased rapidly. *P. pouchetii* had the highest biomass (up to 10 g C m^{-2}) in the southern part of AW (Stns. 1–3) and in PF and SBW (Stns. 6–7 and 9–10). Single cells dominated total *P. pouchetii* biomass at most of these stations, but cells joined in colonies were more abundant at Stns. 2 and 6 and in SBW.

3.2.3. June/July 1999

At the end of June–early July 1999, PNMC concentration was high along the entire transect (5–18 g C m^{-2}), but lower than in May 1998 (Table 3). Unidentified small flagellates dominated total biomass at most stations (Fig. 2) and 20–30% of them were heterotrophic (Verity et al., 2002). Three zones with PNMC maxima were observed along the transect: above the Bjørnøyrenna trench to the south of the Sentralbanken (Stn. 4), above the Sentralbanken (Stns. 8–9) and in PF/ice-edge region (Stns. 14–15). Together diatoms, chrysophytes and *P. pouchetii* comprised about 50% of PNMC at almost all stations. Diatoms were less abundant than in May 1998 and their maximum (20–50 mg C m^{-3}) was observed well below the pycnocline, except for Stn. III in the ice-edge zone, where the highest diatoms biomass occurred at the surface (Fig. 6). *C. socialis*, dominated by single vegetative cells, was the most abundant diatom at most stations, except the trench area and PF/ice-edge zone. In the southern AW, *Chaetoceros compressus*, *Chaetoceros decipiens* and *Pseudo-nitzschia* spp. (*P. seriata* Complex), and in the northern AW *Chaetoceros furcellatus* and *Leptocylindrus danicus* and *Pseudo-nitzschia* spp. were abundant, but only in the trench area *C. compressus* and *Pseudo-nitzschia* spp. together were more abundant, than *C. socialis*. *T. antarctica* var. *borealis* dominated the diatoms biomass in the PF and in the ice-edge area. Here, *C. furcellatus* and diatoms, forming ribbon-shaped colonies, were also abundant (Fig. 3). The biomass of *P. pouchetii* was relatively low (0.3–5.0 g C m^{-2}). Colonies were almost completely absent and single cells (mainly small motile ones) dominated *P. pouchetii* biomass. The highest *P. pouchetii* biomass (2.0–5.0 g C m^{-2}) was observed above the northern Sentralbanken (Stn. 9) and in the ice-edge zone (Stns. 15, III), where *P. pouchetii* dominated PNMC (Fig. 2).

In contrast to March and May 1998, dinoflagellates were very abundant along the southern transect and at the ice-covered stations (Fig. 2). Most of these dinoflagellates are known as heterotrophic species (*Dipplopelta* cf. *parva*, *Diplopsalis lenticula* and, in part *Gymnodinium* spp.). The autotrophic dinoflagellates *Gonyaulax digitale* and *Alexandrium tamarense* were most abundant above the Sentralbanken and at the ice-covered stations (Fig. 4). Chrysophytes *Ochromonas* spp. were abundant in the AW (0.1–3.0 g C m^{-2}). Picoplankton was scarce (<0.2 g C m^{-2}).

In June 1999, PNMC in AW, dominated by unidentified flagellates, had the highest concentrations at 10

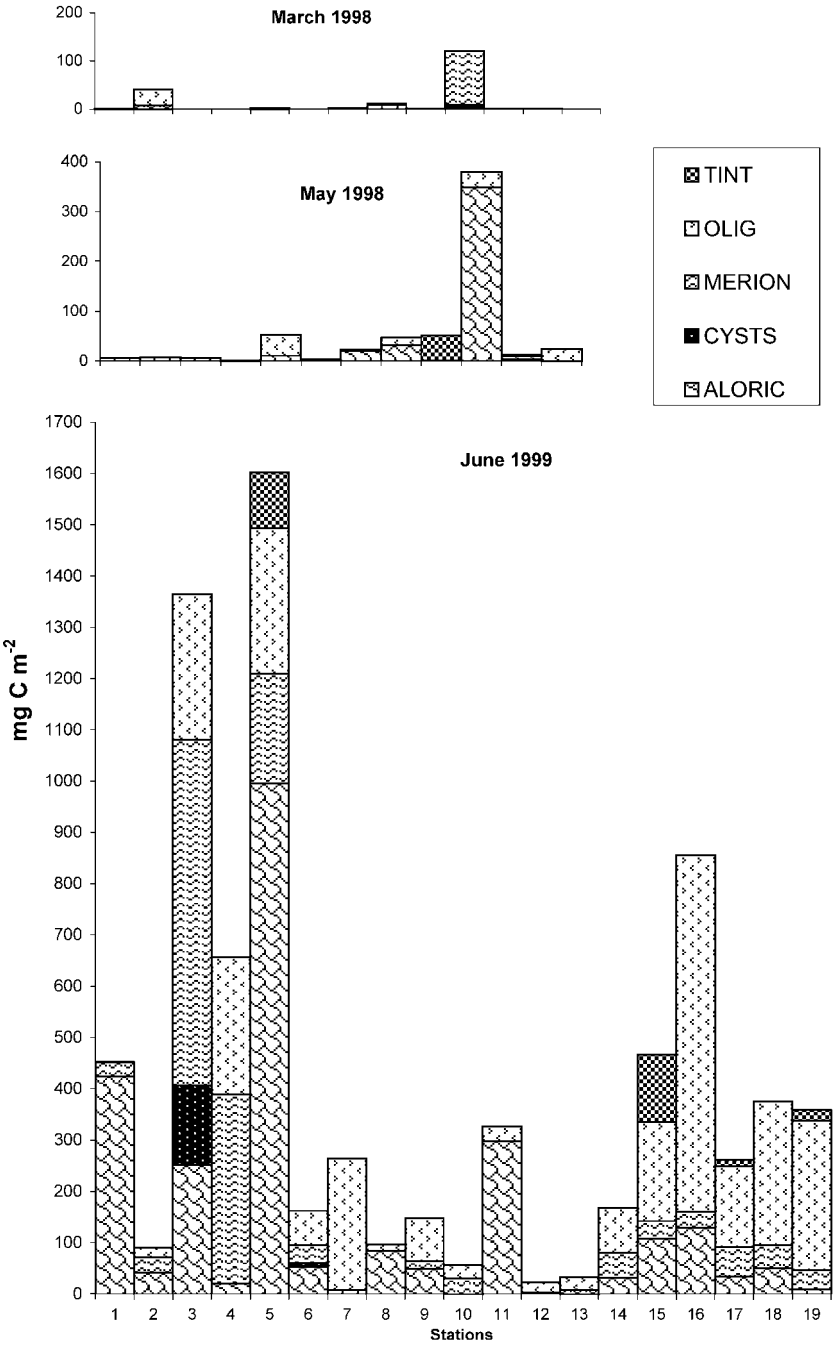

Fig. 7. Protozooplankton abundance along the three ALV transects in the 0–90 m layer (g C m^{-2}). ALORIC—unidentified aloricated ciliates; CYSTS—cysts; MERION—*Merionecta rubrum*; OLIG—Oligotrichina; TINT—tintinnids.

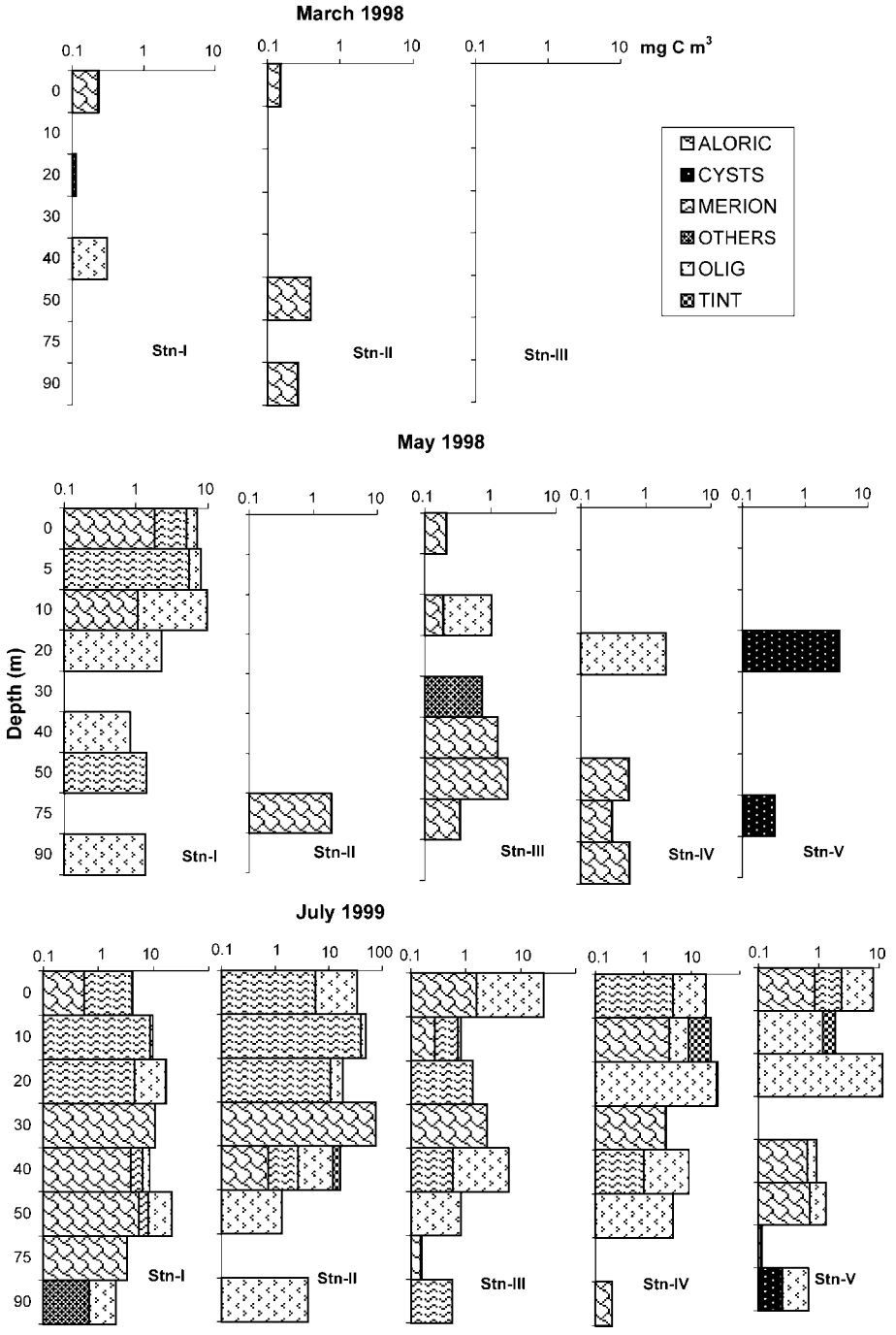

Fig. 8. Vertical distribution of protozooplankton at the 24-h stations during the three ALV cruises (mg C m^{-3}). ALORIC—unidentified aloricated ciliates; CYSTS—cysts; MERION—*Merionecta rubrum*; OTHERS—Foraminifera and Radiolaria; OLIG—Oligotrichina; TINT—tintinnids (logarithmic scale).

m depth along the transect and at the surface and at 20 m depth at 24-h stations (150–450 mg C m^{-3}). A marked minimum of PNMC was observed at 30–40 m depth. Below this layer, PNMC increased at some of the stations at 40–50 m depth because of increasing diatom biomass (Figs. 5c and 6). In the ice-edge zone, PNMC was dominated by the single-celled stage of *P. pouchetii* (400 mg C m^{-3}) and was highest at the 10–20 m depths. In this region, diatoms had their highest biomass at the surface (100 mg C m^{-3}) and unidentified flagellates—at the 20 m depth (150 mg C m^{-3}). Dinoflagellates were especially abundant in the upper 0–20 m, with maximum biomass at 10 m depth (10–100 mg C m^{-3}) in AW and in the ice-covered part (Fig. 6). The vertical distribution of PNMC in the upper 0–50 m layer at the ArW stations was similar to vertical distribution of PNMC in AW, but in contrast to AW, dinoflagellates were responsible for the increase of PNMC at 50 m depth in the ice-covered area.

3.3. Protozoa composition and biomass

Protozoa were scarce in March 1998 (Table 3) and were almost absent below the ice (Fig. 7). Protozoans were distributed rather evenly in the water column. The autotrophic ciliate *Merionecta rubrum* was rather abundant at Stn. 10 in the southern border of the melt water (up to 4 mg C m^{-3} at 30 m depth).

In May 1998, protozoans were almost absent in AW, except at Stns. 5 and 1, where oligotrich ciliates were rather abundant. In ArW protozoans were more abundant, especially in the ice edge (Stn. 10). Unidentified aloricated ciliates dominated protozoan biomass at most stations. Tintinnids were abundant at Stn. 9. Oligotrich ciliates dominated protozoan biomass in the trench area (Stn. 5) and at the ice edge (Stn. 12).

Unidentified aloricated ciliates and the *M. rubrum* dominated total protozoa biomass in the upper 0–10 m layer. Below this layer, oligotrich ciliates became the most abundant protozoans at the southernmost Stn. I. Oligotrich ciliates (10–20 m depths) and unidentified aloricated ciliates below this layer dominated protozoa biomass above the Sentralbanken and in the ice-edge zone. In the ice-covered region, protozoa were scarce and represented by cysts. The highest biomass of these cysts occurred at 20 m depth (Fig. 8).

In June 1999, protozoa were very abundant in the southern part of the AW, except at Stn. 2. Unidentified aloricated ciliates and especially *M. rubrum* dominated total protozoan biomass, but also oligotrich ciliates were abundant. Tintinnids were rare. Protozoa biomass decreased rapidly to the north of Stn. 5 and was low up to the PF region. In ArW protozoans were more abundant than in the northern part of the AW and oligotrich ciliates dominated total protozoans biomass. Unidentified aloricated ciliates were much less abundant in the ArW than in the southern AW. *M. rubrum* and unidentified aloricated ciliates biomass decreased in the ice-edge zone and under the ice, but oligotrich ciliates biomass increased from north to south. Tintinnids were the second abundant group at the ice-covered Stn. 19 and at Stn. 15 to the north of PF.

In AW, protozoa were rather evenly distributed in the upper 0–40 m. *M. rubrum* was the most abundant in the upper 0–30 m and unidentified aloricate ciliates below this depth. Oligotrich ciliates had the highest biomass at 20 m depth at Stn. I, at the surface at Stns. II and III and at 20 m depths at the ice-covered Stns. IV and V (Fig. 8).

4. Discussion

4.1. Biomass: spatial variations

Strong spatial variations in PNMC with the amplitude up to a factor of 4 were observed during the all studied seasons: 3–13, 8–27, and 4–18 g C m^{-2} in March, May and June–July, respectively. This estimates were in rather good agreement with the POC and PON values obtained at the 24-h stations (Olli et al., 2002). The closest results were obtained along this very same transect in MIZ in May 1993: phytoplankton biomass varied from 4 to 13 g C m^{-2}. It had the least value in the ice-edge zone, and was the highest under the ice cover (Hansen et al., 1996). As high phytoplankton biomass, as 78 μg C l^{-1} were observed at the surface at the ice-edge station in late June 1991 (Luchetta et al., 2000). More often, phytoplankton abundance are evaluated as biovolume and/or as chlorophyll concentration (Skjoldal et al., 1987; Savinov, 1997; Larionov, 1997; Wassmann et al., 1999a,b; Owrid et al., 2000; Pautova and Vinogradov,

2001), but simplified recalculation had shown that, in general, the scale of the data were the same.

Flagellates, dominated PNMC in March 1998 and in June/July 1999, had the least biomass variations in time and in space: 3–9 g C m^{-2} on average for the each zone in each season (Table 3). The main source of the PNMC variations were attributed to diatoms and *P. pouchetii* biomass. On average, integrated in the 0–90 m layer PNMC was the highest in March and in June/July in ArW and in AW in May. The ice-edge zone had low phytoplankton biomass in March and in May, but in June/July marked increase of diatoms and *P. pouchetii* biomass was observed in the ice edge. This finding is in apparent contradiction with the previous data (Skjoldal et al., 1987; Wassmann et al., 1999b). In March, it may be explained with the winter conditions of the plankton: the phytoplankton development had not started by this time. In May, strong grazing may have reduced PNMC biomass, because zooplankton biomass was very high in the ice-edge zone in May and only in July, when the grazing became lower (Arashkevich et al., this volume), the high biomass of phytoplankton may be accumulated in MIZ.

The waters above the Sentralbanken represented with the special SBW water type in March and May and with Atlantic water in June/July (Reigstad et al., 2002) differs from the other AW by the increased diatoms biomass during the all seasons studied. In March, the reason for enriched phytoplankton populations may be the resuspension of resting spores from the bottom, and in May and in July, it may be the favourable nutritive conditions due to the less stable water column in the anticyclonic gyre in May and because of lateral transgression of AW from the Bjørnøyrenna in June/July (Reigstad et al., 2002). PNMC was lowest in the PF area in March, probably because of exclusively unstable water column (Reigstad et al., 2002) but was rather high in May and in June/July, which may probably be due to the same factor. If it is so, it may be an evidence of seasonal variability of the impact of similar conditions: what may be unfavourable in nutrients—reach, unstable early spring conditions, may support the higher phytoplankton biomass during the nutrient-depleted, stratified water column conditions in late spring–early summer, because the PF zone is enriched with nutrients due to mixing process (Reigstad et al., 2002).

4.2. Late winter phytoplankton composition and the spring bloom inoculum

The winter conditions may be defined as the time of deep mixing, high and uniform nutrients content, high and uniform salinity and low and uniform temperature distribution in the water column. The low nutrient consumption, low chlorophyll *a* concentration revealed the winter conditions of phytoplankton to the south of the ice-edge zone in March 1998 (Reigstad et al., 2002). PNMC was low at most of the stations (< 5 g C m^{-2}) and represented mainly by small flagellates. Diatoms were rare and dominated by the resting spores and single, may be, dormant cells of *C. socialis*. Species that usually develop colonies in spring (*Chaetoceros* spp., *Fragilariopsis* spp., *Navicula* spp.) were presented as single cells or as very short chains. These winter phytoplankton may serve as a seeding population for the spring bloom development.

However, the low vegetative cell numbers, inhabiting the water column, in winter/early spring are probably not sufficient to act as inoculum (Hansen and Eilertsen, 1995). In ice-covered areas, sea-ice algae may serve as the seeding population for spring bloom onset (Syvertsen, 1991; Gradinger et al., 1999). In the shallow-water areas (< 150 m), the upper layer of bottom sediments may content overwintering resting spores and resting cells (Savinov, 1997), and their resuspension into the water column may be a factor of earlier onset of the spring bloom. Experiments have revealed photoperiodic germination dependence and showed that most spores germinated when daylength exceeded 12 h (Eilertsen et al., 1995). So the bottom sediments may serve as the cause of dormant stages of phytoplankton inoculum to the water column (Kashkin, 1964; Hegseth et al., 1995). That is probably why the spring bloom starts in the inshore shallow waters, above the banks and under the sea-ice first because of the seeding with populations from the bottom and from the ice. Species composition revealed this suggestion: in the ice-covered zones, the first spring bloom species are the ribbon-shaped colonies forming ice-neritic species (Mikhailovsky and Zhitina, 1989; Wassmann et al., 1999b; von Quillfeldt, 2000; Pautova and Vinogradov, 2001). Somewhat later in the season, the species, forming resting spores and perhaps originated from the sediments, replace these ice-neritic

species (Savinov, 1997; Wassmann et al., 1999b; von Quillfeldt, 2000). In shallow coastal waters, favourable light conditions down to the bottom and reduced mixing under the ice allowed algae to start growth earlier, than in deep water open sea areas at the same latitude (Roukhiyainen, 1960; Druzhkov et al., 1997; Pautova and Vinogradov, 2001). The higher is overwintering population, the more rapid may be onset of the spring bloom development.

In March 1998, the pronounced increase of diatoms was observed south of the Sentralbanken. *C. socialis*, dominated by single cells, became rather abundant at 30 and 40 m depths. An observed weak increase in salinity in this area may indicate the water movement from the Sentralbanken slope to the trench (Reigstad et al., 2002). This water may be enriched with diatoms from bottom sediments. The composition of algae supports this suggestion: resting spores and single cells of *C. socialis* had the highest biomass rates at these stations (Fig. 4). Waters below the ice were not enriched with the sea-ice diatoms in March. It seems likely that melting had not yet begun because salinity was rather high below the ice (34.6 ‰). Sea-ice algae were not released from the ice. Species composition of diatoms supported this suggestion: derived mainly from the melting ice, diatoms species, forming ribbon-shaped colonies, were very sparse (Fig. 3). Without this inoculum at the ice-covered Station 13, phytoplankton was in the pre-bloom conditions: marked increase of *C. socialis* vegetative cells, high *P. pouchetii* single cells and chrysophytes biomass, the moderate nutrient consumption indicated by a decrease in nitrate concentration by 0.8 μmol NO_3 l^{-1} in the upper 20–100 m depths, in comparison to the 100 m–bottom layer, and the prominent salinity gradient observed in the upper 0–50 m (Reigstad et al., 2002) may indicate the onset of phytoplankton development.

4.3. Development and succession of phytoplankton

In March, the late winter/early spring conditions were characterised by low species diversity. Almost all of the species were neritic while ice-neritic species are few and mainly observed in the SBW. A few oceanic and ocean-neritic species were observed in the AW and the SBW, and were almost absent at the ArW. Most of the observed species were arctic–boreal ones. This winter stage of the phytoplankton development was dominated by small unidentified flagellates, chlorophyll content was low, and it may be supposed that heterotrophic processes dominated in the community. Protozoa were very sparse. Under the ice, phytoplankton was in pre-bloom conditions: biomass of single-celled *C. socialis*, *P. pouchetii* and cryptophytes flagellates increased, but was still low, and unidentified small flagellates dominated total PNMC. Protozoa abundance was low but autotrophic *M. rubrum* was observed in the ice-edge zone.

In May many oceanic species enriched the neritic flora, observed in March in AW, and more ice-neritic species were observed in the SBW and in the ArW. Cosmopolitan species became numerous. Species diversity was still low but it was higher compared to March. Species, which were most abundant in March, in May became the main species of the bloom: *P. pouchetii* and *C. socialis*—in AW; *P. pouchetii* and *T. antarctica* var. *borealis*—in the SBW; *T. antarctica* var. *borealis* and the ice-neritic pennate diatoms—in the ArW. *C. socialis* and *P. pouchetii* presented with single cells in March, developed large colonies (up to 100 and up to 200–600 cells in each colony, respectively). The maximum rate of diatoms and *P. pouchetii* development was observed at the southern part of AW and the second maximum was observed in the southern part of ArW. These two peaks of spring species biomass revealed the independent development of the spring bloom in AW and in ArW. Species composition and succession also differ markedly between these two blooms peaks (Pautova and Vinogradov, 2001) in the eastern Barents Sea. The spring bloom of phytoplankton is really a bloom of a few species of diatoms and *P. pouchetii* (usually dominated by the ribbon-shaped colonies forming ice-neritic diatoms at the ice-covered and MIZ stations and *P. pouchetii* and neritic *Thalassiosira* spp. in MIZ and in open water of the ArW and neritic *C. socialis* and *P. pouchetii* in AW).

In the SBW area, *C. socialis* was present mainly as resting spores, *T. antarctica* var. *borealis* was not abundant in the upper layer and was mainly observed below the 40 m depth. Single cells dominated *P. pouchetii* biomass. Species composition clearly shows that the bloom started in SBW earlier, consistent with the mixture in the two communities, and culminated during the last 10 days of May. A week later, at the 24-h stations, similar conditions were observed along the

entire AW. To the north of PF at the transect stations, single cells likewise dominated the *P. pouchetii* biomass but in contrast to the AW, the colonies became more abundant a few days later at the 24-h stations, and we may suppose that in ArW, spring bloom was already in progress at the end of May. In the ice-covered station, phytoplankton conditions were almost the same as in March but the higher biomass of ice-neritic diatoms may indicate active ice melting. The biomass of protozoa increased, aloricated ciliates were the most abundant, and Tintinnids were observed in SBW.

New production—nitrate uptake—is high during the pre-bloom and bloom periods (Kristiansen et al., 1994). The decay of spring bloom may be described as the time when mineral nutrients are exhausted from the upper mixed water, thermocline is well developed, and mixing is reduced. Phytoplankton biomass decreased markedly. Spring bloom species are replaced by summer species. Most of this species are able to consume the regenerated nutrients and/or are motile and are able to migrate from the nutrient-depleted layer to the pycnocline where nutrients are available. Diatoms sank below the thermocline where the nutrients are available but the illumination may be too low for the rapid growth of phytoplankton. Grazing may be of great importance. The ratio between chlorophyll and its degradation product, phaeophytin, may be as high as 50% (Hansen et al., 1990). Species diversity reaches its highest rate as well vertical distribution—the most complicated, because many factors such as nutrients availability, illumination, grazing impact and vertical day–night migrations of the motile species influence its pattern.

In June/July, species diversity reaches its highest peak. Many oceanic species were observed in the AW. Some of them (diatom *Chaetoceros brevis*, chrysophyte *Dinobryon faculifer*), encountered only in AW in May, developed in the PF and ArW by in June/July. In turn, some of the ice-neritic species spread (may be with the subsurface flow of the ArW) to the south of PF. In AW, a few tropic–boreal species were observed, indicating the inflow of waters originating from the Atlantic Ocean. The biomass of spring bloom species decreased, and they were observed as mainly single cells. Dinoflagellates and chrysophytes became abundant in the AW. Diatoms *Cylindrotheca closterium* and summer species of genera *Chaetoceros* and *Pseudo-nitzschia* were encountered in the AW and SBW. The only area where the spring species *C. socialis*, *C. furcellatus*, *T. antarctica* var. *borealis* and *P. pouchetii* were still abundant was the PF. In the ice-covered zone, diatoms were not abundant and were dominated by *C. socialis*. Biomass of dinoflagellates (*Alexandrium* spp., *Dinophysis* spp., which are known as autotrophic; *Gyrodinium* spp., the species of *Diplopelta–Diplopsalis* group, which are known, as heterotrophic, and *Gymnodinium* spp. which may be heterotrophic, autotrophic or/and mixotrophic) was high in the upper 0–20 m water layer below the ice. The reseeding of the algae from the ice seems to be low because ice-neritic species were not abundant in June–July below the ice (ice cover from 20–50% in the southern part of MIZ to 50–80% in the northern). In contrast to the spring conditions when sea-ice algae may be very abundant below the ice (Wassmann et al., 1999b), in summer these algae are sparse—probably because algae development in ice was inhibited due to nutrients exhaustion (Gradinger et al., 1999) or because the algae was released from the ice due to melt water input and physical disturbance of the sea-ice–water interface (Risgaard et al., 2001). Protozoa biomass at its highest, indicating the activity of the microbial loop. Aloricated ciliates, including *M. rubrum*, dominated in AW and Oligotrichina ciliates dominated in ArW. Tintinnids were observed in MIZ.

The general pattern of phytoplankton species succession before, during and after the spring bloom in the central Barents Sea in 1998–1999 were very similar to that described by other researchers in the Barents Sea (Roukhiyainen, 1960; Rey et al., 1987; Druzhkov and Makarevich, 1992; Evensen, 1994; Larionov, 1997; Wassmann et al., 1999b), Kara Sea (Makarevich and Druzkov, 1994); White Sea (Mikhailovskyi and Zhitina, 1989), the Northern Atlantic (Vinogradova and Gruzov, 1990) and Canadian Arctic (Bursa, 1963). Taxonomic composition of the standing crops varies according to local initial composition of the phytoplankton (Braarud et al., 1953), and selective grazing (Bathmann et al., 1990).

4.4. Impact of grazing

Many factors contribute to the variability of composition and magnitude of spring bloom. Vertical

mixing will hinder phytoplankton accumulation in the euphotic zone, so spring bloom may start in the waters with neutral stability (Hegseth et al., 1995). Further, if the upward migration of the bulk of overwintering copepods from deep water occurs shortly before or concomitant with increased diatoms spring growth, bloom formation could be obstructed. The timing and duration of the biomass increase in phytoplankton stock and grazing potential of herbivores, already present in surface waters in late winter/early spring, are vital factors that affect the biological conditions in spring. The success of overwintering diapausal copepods, the timing of their mass migration to the surface, and the size of wintering stocks of surface herbivores may be responsible for the occurrence of flagellates rather than diatoms in the phytoplankton species composition (Bathmann et al., 1990).

Zooplankton abundance also varies seasonally and follows the same trend as primary production with a 2- to 3-week lag period (Skjoldal et al., 1987). Grazing of large calanoid copepods consumes 5–20% of primary production in spring and up to 65–90% in summer (Eilertsen et al., 1989). Grazing of Protozoa and copepods nauplii and small copepodites may be of great importance, too (Hansen et al., 1996; Arashkevich et al., 2002; Verity et al., 2002). The classical model for cold water ecosystems based on large phytoplankton as food for large copepods and krill was gradually replaced by data, showing the importance of the microbial food loop (Azam et al., 1991). It was shown that seasonal decrease in primary production could result from decrease in standing stock rather than changes in instantaneous growth rates of the phytoplankton (Kristiansen et al., 1994). Comparison of the spring bloom development in the cold 1979 and 1981 and in warm 1980, 1982–1983 years (Skjoldal et al., 1987) had shown that, in the cold years when sea-ice extended far south, melting may start earlier due to higher temperature of the surrounding water. Early blooms in cold years might be advantageous for the maturation and spawning and possibly also for the development of nauplii but copepodites may not reach a size that allow them to utilise the bloom prior to its culmination. In contrast, slower bloom development in warmer years may be favourable for copepodite development. The longer the spring bloom endures, the higher is the annual primary production and more favourable timing of the bloom in warm years may be supposed to be the more advantageous for copepods *Calanus finmarchicus*. The fate of the large fraction of daily primary production was to be channeled through microzooplankton (Hansen et al., 1996; Verity et al., 2002). In March and in May 1998, ciliates Protozoa were scarce. Heterotrophic flagellates and small dinoflagellates were the most important grazers because copepods were in deep hibernation in March. In May, copepods that were in their youngest developmental stage became very abundant (up to 50% of the total copepod biomass) and they may become the most important grazers. In June/July, ciliates were very abundant and mesozooplankton started to decrease (Arashkevich et al., 2002). The main grazers for the area in June/July were protozoa (nanoplankton flagellates, ciliates and dinoflagellates) and small copepods (Arashkevich et al., 2002; Verity et al., 2002). It may be concluded that grazing activity and composition of the grazers changed as the season progresses in the investigated area. In winter, small heterotrophic flagellates are the main important grazers, feeding on the pico- and nanoplanktonic flagellates. During the spring, bloom copepods consumed the greatest part of the algal biomass, and high grazing impact on the microheterotrophs may be expected, too. In summer, the microbial loop accounted for the major portion of algae production consumption.

4.5. Significance of small-sized plankton

Till the mid-1980s, the autotrophic nanoplankton (<20 μm) was not studied quantitatively in the Barents Sea. The first investigation of the seasonal dynamics of nanophytoplankton (Druzhkov et al., 1992), which was carried out by using the methods of epifluorescent microscopy, had shown the significant role played by the group in the East Merman coastal zone. Nanoplanktonic algae accounted for up to 98% of the total phytoplankton biomass during summer 1987. Two major types of the temporal dynamics can be discerned for autotrophic flagellates: (a) "background" pattern—when nanophytoplankton is observed in significant amounts throughout the year; and (b) "maximum" pattern—when increased biomass of nanophytoplankton is observed for at least at one stage of the phytoplankton growth season. The

different patterns may be observed in different years at the same locality with the range of less than 1 μg WW l^{-1} in winter to 750 μg WW l^{-1} in summer (Druzhkov et al., 1992).

Pico- and nanoplankton biomass did not change markedly in the course of seasons covered by the investigation in the central Barents Sea. However, the share of small-sized plankton in PNMC varied from 80% to 90% in late winter to less than 30% during the spring bloom. The dominant phytoplankton species during the spring bloom in the Barents Sea are usually diatoms and prymnesiophyte *P. pouchetii* while flagellates species usually dominated in the nutrient-poor surface water in summer (Rey and Loeng, 1985; Owrid et al., 2000; Hegseth, 1998). Taxonomic studies confirm this shift. A significant fraction of total nitrogen uptake can be attributed to small algae. Nanoplankton flagellates are able to consume regenerated nitrogen in summer when the supply of nitrate nitrogen became exhausted (Kristiansen et al., 1994). They may be consumed by large zooplankton but in this case, flagellate concentration should be very high (Arashkevich and Drits, 1984). Microzooplankton may consume flagellates more effectively than large zooplankton (Verity et al., 2002). Regarding microzooplankton, three main groups are usually mentioned: heterotrophic nanoflagellates, dinoflagellates and ciliates (Verity et al., 2002), but became evident that small copepods (small species and nauplii and copepodites of large species) should be included in this group, too (Arashkevich et al., 2002). Microzooplankton actively grazed on the nanophytoplankton community. The fraction of daily Chl *a* production ingested by microzooplankton exhibited a wide range—from 64% to 97% in July 1999, when higher grazing losses were observed in smaller size classes (Verity et al., 2002). The same results were obtained in May 1993 (Hansen et al., 1996). The role of the "microbial loop" (Azam et al., 1991) may be to channel production of the small phytoplankton. It may be that, except for the peak of the vernal bloom, microzooplankton are a major food source for mesozooplankton in the Barents Sea (Wassmann et al., 1999b; Verity et al., 2002) and the importance of top–down influences on community structure and ecosystem function may be a general feature of these waters (Verity et al., 1999; Wassmann et al., 1999a; Wassmann, 2001).

5. Conclusion and outlook

The dominant phytoplankton species in the AW and MIZ/ArW are similar, but the timing of the spring bloom and seasonal development are rather different. In AW, due to deep mixing and rather even vertical distribution of PNMC, the integrated PNMC is high, and so moderate per cubic meter. Significant blooms take place in the Polar Front area and in MIZ, particularly in May, but integrated PNMC in MIZ was lower due to PNMC accumulation in the shallow layer above the halocline and lower biomass below it. The ice-edge bloom in summer is moderate. Summer blooms in the ArW take place in surface waters and over extensive spatial domains.

Plankton during late winter/early spring along the entire transect was dominated by nanoplankton and picoplankton flagellates and monads (including the single-celled *P. pouchetii*). Diatoms and dinoflagellates were represented by the nanoplankton species, too. Large diatoms and *P. pouchetii* colonies were very sparse. It is speculated that the biomass of large-celled phytoplankton may be too small to give rise to a bloom and that additional inoculum is supplied by vertical mixing (in particular from shallow regions) in AW and sea ice in the ArW. Phytoplankton blooms are mainly due to diatoms and *P. pouchetii* colonies, which were very abundant in May and that of dinoflagellates in June/July. These blooms occur on the base of a less variable, but substantial flagellate community.

It is suggested that the share of small cells increased by overwintered mesozooplankton grazing on large phytoplankton and protozoans.

Our investigation supports the concept that small-sized phyto- and zooplankton organisms are widespread and important even in cold water systems. Top–down regulation (Wassmann, 2001; Verity et al., 1999) of the community structure and ecosystem function appears to be a general feature along the North Atlantic continuum, which extends into the central and northern Barents Sea. Only shortly, the excellent match between primary producers and consumers is interrupted in the ice-edge zone in May, favouring extensive proliferation of large-celled phytoplankton. This mismatch is frequently described as the ice-edge bloom and has given rise to the notion that the MIZ is highly productive. Small-celled phytoplankton plays a far more significant role for eco-

system functioning and carbon flux over the entire Barents Sea (and at all seasons) than previously assumed. As shown previously, climate change and global warming will expose the present southern seasonal ice zone for increased radiation and vertical mixing (Slagstad and Wassmann, 1997). Consequently, the influence of AW may expand northwards in the future. The concurrent "atlantification" of the seasonal ice-cover zone will result in an expansion of Atlantic species northwards and significant changes in biomass, seasonal variation and spatial distribution of phytoplankton. In the southern region of the seasonal ice zone, relative biomass of small-celled phytoplankton species and *P. pouchetii* will increase. These changes in variation and spatial distribution of phytoplankton will result in distinct changes in biogeochemical cycling because of lower sedimentation and higher recycling rates, usually observed in the waters dominated by small-celled phytoplankton.

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References

Ådlandsvik, B., Loeng, H., 1991. A study of the climatic system in the Barents Sea. Polar Res. 10, 45–49.

Allen, A.E., Howard-Jones, M.H., Booth, M.G., Frischer, M.E., Verity, P.G., Bronk, D.A., Sanderson, M.P., 2002. Importance of heterotrophic bacterial assimilation of ammonium and nitrate in the Barents Sea during summer. J. Mar. Syst., this issue.

Arashkevich, E.G., Drits, A.V., 1984. The influence of food sizes and food concentration on consumption rate in herbivores copepods of the genus Calanus. Oceanologia 24, 677–683 (In Russian with English summary).

Arashkevich, E., Wassmann, P., Pasternak, A., Wexels Riser, C., 2002. Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. J. Mar. Syst., this issue.

Azam, F., Smith, D.C., Hollibaugh, J.T., 1991. The role of the microbial loop in Antarctic pelagic ecosystems. Polar Res. 10 (1), 239–243.

Backhaus, J.O., Wehde, H., Nøst Hegseth, E., Kämpf, J., 1999. Phyto-convection: the role of oceanic convection in primary production. Mar. Ecol. Prog. Ser. 189, 77–92.

Bathmann, U.V., Noji, T.T., Bodungen, v.B., 1990. Copepod grazing potential in late winter in the Norwegian Sea—a factor in the control of spring phytoplankton growth? Mar. Ecol. Prog. Ser. 60 (2), 225–233.

Braarud, T., Gaarder, R.K., Grøntved, J., 1953. The phytoplankton of the North Sea and adjacent waters in May, 1948. Rapp. Proc.-Verb. 133, 1–187.

Bursa, A.S., 1963. Phytoplankton successions in the Canadian Arctic. In: Oppenheimer, C.H. (Ed.), Symposium on Marine Microbiology. Charles C. Thomas Publisher, USA, pp. 625–628.

Druzhkov, N.V., Makarevich, P.R., 1992. Structural characteristic of the microphytoplankton seasonal development in the coastal ecosystem. Phytoplankton of the Barents Sea. KNC RAN, Apatity, pp. 83–96.

Druzhkov, N.V., Larionov, V.V., Makarevich, P.R., 1992. Role of Autotrophic Nanoplankton in the Coastal Phytoplankton Community. KNC RAN, Apatity, pp. 97–103.

Druzhkov, N.V., Kuznetsov, L.L., Baitaz, O.N., Druzhkova, E.I., 1997. The seasonal cycling processes in the coastal pelagic ecosystems of North Europe (on the example of Central Murman, Barents Sea). In: Volkova, L.P., Timofeeva, S.V. (Eds.), Plankton of the Seas of the Western Arctic. Kola Scientific Centre RAS, Apatity, pp. 145–178 (in Russian).

Eilertsen, H.C., Tande, K.S., Taasen, J.P., 1989. Vertical distribution of primary production and grazing by *Calanus glacialis* Jashnov and *C. hyperboreus* Krøyer in Arctic waters (Barents Sea). Polar Biol. 9, 253–260.

Evensen, A., 1994. Planteplankton i Barentshavet: Artssammensetning og suksesjon. Regionale variasjoner i varoppblomstringen relatert til miljø. Cand. Scient. Thesis, University of Tromsø, p. 137.

Falk-Petersen, S., Hop, H., Budgell, W.P., Hegseth, E., Korsnes, R., Løyning, T.B., Ørbaek, J.B., Kawamura, T., Shirasava, K., 2000. Physical and ecological processes in the marginal ice zone of the northern Barents Sea during the summer melt period. J. Mar. Syst. 27, 131–159.

Garrison, D.L., Buck, K.R., 1989. Protozooplankton in the Weddell Sea, Antarctica: abundance and distribution in the ice-edge zone. Polar Biol. 9, 341–351.

Gradinger, R., Friedrich, C., Spindler, M., 1999. Abundance, biomass and composition of the ice sea biota of the Greenland Sea pack ice. Deep-Sea Res. II 46, 1457–1472.

Guillard, R.R.L., 1978. Counting slides. In: Sournia, A. (Ed.), Phytoplankton Manual. UNESCO, Paris, pp. 182–189.

Hansen, G.A., Eilertsen, H.C., 1995. Modelling the onset of phytoplankton bloom: a new approach. In: Skjoldal, H.R., Hopkins, C.C.E., Erikstad, K.E., Leinaas, H.P. (Eds.), Ecology of Fjords and Coastal Waters. Elsevier, Amsterdam, pp. 73–83.

Hansen, B., Berggreen, U.C., Tande, K.S., Eilertsen, H.C., 1990.

Post-bloom grazing by *Calanus glacialis*, *C. finmarchicus* and *C. hyperboreus* in the region of the Polar Front, Barents Sea. Mar. Biol. 104 (5), 5–14.

Hansen, B., Christiansen, S., Pedersen, G., 1996. Plankton dynamics in the marginal ice zone of the central Barents Sea during spring: carbon flow and structure of the grazer food chain. Polar Biol. 16, 115–128.

Hasle, G.R., Syvertsen, E.E., 1997. Marine diatoms: preparation for light microscopy. In: Tomas, C.R. (Ed.), Identifying Marine Phytoplankton. Academic Press, p. 334.

Hegseth, E.N., 1998. Primary production of the northern Barents Sea. Polar Res. 17 (2), 113–123.

Hegseth, E.N., Svendsen, H., Quillfeldt, v.C., 1995. Phytoplankton in fjords and coastal waters of northern Norway: environmental conditions and dynamics of the spring bloom. In: Skjoldal, H.R., Hopkins, C.C.E., Erikstad, K.E., Leinaas, H.P. (Eds.), Ecology of Fjords and Coastal Waters. Elsevier, Amsterdam, pp. 45–71.

Kashkin, N.I., 1964. On the winter stock of planktonic algae in the sublitoral sediments. Trudy Inst. Tokeanol. Akad. Nauk USSR (IOAN SSSR), vol. 65, pp. 49–57 (in Russian).

Konovalova, G.V., 1998. Dinoflagellatae (Dinophyta) of the Far Eastern Seas of Russia and Adjacent Waters of the Pacific Ocean. Dal'auka, Vladivostok, 300 pp. (in Russian).

Kristiansen, S., Farbrot, T., 1990. Nitrogen uptake rates in phytoplankton and ice algae in the Barents Sea. Polar Res. 10 (1), 187–192.

Kristiansen, S., Farbrot, T., Wheeler, P.A., 1994. Nitrogen cycling in the Barents Sea—seasonal dynamics of new and regenerated production in the marginal ice zone. Limnol. Oceanogr. 39 (7), 1630–1642.

Lappalainen, T.N., 1960. Some peculiarities of the hydrochemical conditions in the southern Barents Sea. Trudy MMBI 2 (6), 41–58 (in Russian).

Larionov, V.V., 1997. General patterns of the space–time variability of phytoplankton in the Barents Sea. In: Volkova, L.P., Timofeeva, S.V. (Eds.), Plankton of the Seas of the Western Arctic. Kola Scientific Centre RAS, Apatity, pp. 65–92 (in Russian).

Loeng, H., 1991. Features of the physical oceanographic conditions of the Barents Sea. In: Sakshaug, E., Hopkins, C.C.E., Øritsland, N.A. (Eds.), Proceedings of the PRO MARE Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. Polar Res., vol. 10 (1), pp. 5–18.

Luchetta, A., Lipizer, M., Socal, G., 2000. Temporal evolution of primary production in the central Barents Sea. J. Mar. Syst. 27, 177–193.

Makarevich, P.R., Druzhkov, N.V., 1994. Comparative characteristic of the microphytoplankton of the South-west Kara Sea and South-east Barents Sea. Algologia 1, 113–125 (in Russian).

Makarevich, P.R., Larionov, V.V., 1992. Taxonomical composition of phytoplankton and history of the phytoplankton studies in the Barents Sea. Phytoplankton of the Barents Sea. Kola Scientific Centre, Apatity, pp. 17–51.

Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationship for dinoflagellates, diatoms and other protists plankton. Limnol. Oceanogr. 45 (3), 569–579.

Mikhailovskyi, G.E., Zhitina, L.S., 1989. Ice planktonic flora of the White Sea and its seasonal dynamics revealed by correlation analysis methods. Okeanologia 29 (5), 796–803 (in Russian).

Okolodkov, Y.B., 1998. A checklist of dinoflagellates recorded from the Russian Arctic Seas. Sarsia 83, 267–292.

Olli, K., Wexels Riser, C., Wassmann, P., Ratkova, T., Arashkevich, E., Pasternak, A., 2002. Seasonal variation in vertical flux of biogenic matter in the marginal ice zone and the central Barents Sea. J. Mar. Syst., this issue.

Owrid, G., Socal, G., Civitarese, G., Luchetta, A., Wiktor, J., Nöthig, E.-M., Andreassen, I., Schauer, U., Strass, V., 2000. Spatial variability of phytoplankton, nutrients and new production estimates in the waters around Svalbard. Polar Res. 19 (2), 155–171.

Pautova, L.A., Vinogradov, G.M., 2001. South-eastern Barents Sea phytoplankton in April 2000. Okeanologia 41 (2), 224–230 (in Russian).

Rat'kova, T.N.Phytoplankton composition in the White Sea Basin in summer–autumn 1998 and 1999. In: Rachor, E. (Ed.), Scientific Co-Operation in the Russian Arctic: Ecology of the White Sea with the Emphasis on its Deep Basin. Ber. Polarforsch., vol. 359, pp. 97–109.

Rat'kova, T.N., Wassmann, P., Verity, P.G., Andreassen, I.J., 1999. Abundance and biomass of pico-, nano-, and microplankton on a transect across Nordvestbanken, north Norwegian shelf, in 1994. Sarsia 84 (3–4), 213–226.

Reigstad, M., Wassmann, P., Wexels Riser, C., Øygarden, S., Rey. F., 2002. Variation in hydrography, nutrients and chlorophyll *a* in the marginal ice-zone and the central Barents Sea. J. Mar. Syst., this issue.

Rey, F., Loeng, H., 1985. The influence of the ice and hydrographic conditions on the development of stress on marine organisms. In: Gray, J.S., Christiansen, M.E. (Eds.), Marine Biology of Polar Regions and Effect of Stress on Marine Organisms. Wiley, Chichester, pp. 49–63.

Rey, F., Skjoldal, H.R., Slagstad, D., 1987. Primary production in relation to climatic changes in the Barents Sea. In: Loeng, H. (Ed.), The Effect of Oceanographic Conditions on Distribution and Population Dynamics of Commercial Fish Stocks in the Barents Sea. Proc. 3rd. Sov. Norw. Symp., pp. 29–46.

Risgaard, S., Kuhl, M., Glud, R.N., Hansen, J.W., 2001. Biomass, production and horizontal patchiness of the sea ice algae in a high-Arctic fjord (Young Sound, NE Greenland). Mar. Ecol. Prog. Ser. 223, 15–26.

Roukhiyainen, M.I., 1960. Development pattern of the phytoplankton community during May–June 1958 in the southern Barents Sea. Trudy MMBI 2 (6), 59–67 (in Russian).

Rousseau, V., Mathot, S., Lancelot, C., 1990. Calculating carbon biovolume of *Phaeocystis* sp. from microscopic observations. Mar. Biol. 107 (2), 305–314.

Sakshaug, E., 1997. Biomass and productivity distributions and their variability in the Barents Sea. ICES J. Mar. Sci. 54, 341–350.

Sakshaug, E., Skjoldal, H.R., 1989. Life at the ice edge. Ambio 18, 60–67.

Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H., Mehlum, F., 1994. Structure, biomass distribution, and energetics of the pelagic ecosystem in the Barents Sea: a synopsis. Polar Biol. 14, 405–411.

Sakshaug, E., Rey, F., Slagstad, D., 1995. Wind forcing of marine primary production in the northern atmospheric low-pressure belt. In: Skjoldal, H.R., Hopkins, C.C.E., Erikstad, K.E., Leinaas, H.P. (Eds.), Ecology of Fjords and Coastal Waters. Elsevier, Amsterdam, pp. 15–25.

Savinov, V.M., 1997. Photosynthetic pigments and primary production in the Barents Sea: the spatial distribution. In: Volkova, L.P., Timofeeva, S.V. (Eds.), Plankton of the Seas of the Western Arctic. Kola Scientific Centre RAS, Apatity, pp. 93–126 (in Russian).

Semina, H.J., 1978. Treatment of an aliquot sample. In: Sournia, A. (Ed.), Phytoplankton Manual. UNESCO, Paris, p. 181.

Semina, H.I., Sergeeva, O.M., 1983. Plankton flora and biogeographical description of phytoplankton of the White Sea. Trudy Belomorskoy Biolog. Stanzii MGU, vol. 6, pp. 3–17 (in Russian).

Skjoldal, H.R., Rey, F., 1989. Pelagic production and variability of the Barents Sea ecosystem. In: Sherman, K., Alexander, L.M. (Eds.), Biomass and Geography of Large Marine Ecosystems. Westview Press, Boulder, CO, pp. 243–283.

Skjoldal, H.R., Hassel, A., Rey, F., Loeng, H., 1987. Spring phytoplankton development and zooplankton reproduction in the central Barents Sea in the period 1979–1984. In: Loeng, H. (Ed.), The Effect of Oceanographic Conditions on Distribution and Population Dynamics of Commercial Fish Stocks in the Barents Sea. Proc. 3rd Sov.–Norw. Symp. Inst. Mar. Res., Bergen, pp. 59–89.

Slagstad, D., Wassmann, P., 1997. Climate change and carbon flux in the Barents Sea: 3-D simulations of ice-distribution, primary production and vertical export of particulate organic matter. Mem. Natl. Inst. Polar Res. Spec. Issue 51, 119–141.

Slagstad, D., Tande, K., Wassmann, P., 1999. Modelled carbon fluxes as validated by field data on the north Norwegian shelf during the productive period in 1994. Sarsia 84, 303–317.

Smayda, T.J., 1978. From phytoplankters to biovolume. In: Sournia, A. (Ed.), Phytoplankton Manual. UNESCO, Paris, pp. 273–279.

Strathmann, R.R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12 (3), 411–418.

Syvertsen, E.E., 1991. Ice algae in the Barents Sea: types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. In: Sakshaug, E., Hopkins, C.C.E., Øritsland, N.A. (Eds.), Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. Polar Res., vol. 10 (1), pp. 277–287.

Tomas, C.R. (Ed.), 1997. Identifying Marine Phytoplankton. Academic Press, 858 pp.

Verity, P.G., Langdon, C., 1984. Relationships between lorica volume, carbon, nitrogen and ATP content of tintinnids in Narragansett Bay. J. Plankton Res. 6, 859–868.

Verity, P.G., Wassmann, P., Ratkova, T.N., Andreassen, I., Nordby, E., 1999. Seasonal pattern in composition and biomass of autotrophic and heterotrophic nano- and microplankton communities on the north Norwegian shelf. Sarsia 84 (3–4), 265–278.

Verity, P.G., Wassmann, P., Frischer, M.E., Howard-Jones, M.N., Allen, A.E., 2002. Grazing of phytoplankton by microzooplankton in the Barents Sea during early summer. J. Mar. Syst., this issue.

Vinje, T., Kvambekk, A.S., 1991. Barents Sea drift ice characteristics. Polar Res. 10 (1), 59–68.

Vinogradova, L.A., Gruzov, L.N., 1990. On the distribution of phytoplankton communities in the upper layer of waters in North Atlantic and adjacent areas. Proceedings of State Oceanographical Institute (GOIN), vol. 182, pp. 112–133 (in Russian).

von Quillfeldt, C.H., 2000. Common diatom species in the arctic spring bloom: their distribution and abundance. Bot. Mar. 43, 499–516.

Wassmann, P., 2001. Vernal export and retention of biogenic matter in the north-eastern North Atlantic and adjacent Arctic Ocean: the role of the Norwegian Atlantic Current and topography. Mem. Natl. Inst. Polar Res., Spec. Vol. 54, 377–392.

Wassmann, P., Andreassen, I., Rey, F., 1999a. Seasonal variation of nutrients and suspended biomass along a transect on Nordvestbanken, north Norwegian shelf, in 1994. Sarsia 84, 199–212.

Wassmann, P., Ratkova, T.N., Andreassen, I.J., Vernet, M., Pedersen, G., Rey, F., 1999b. Spring bloom development in the marginal ice zone and the central Barents Sea. P.S.Z.N. I. Mar. Ecol. 20 (3/4), 321–346.