Abundance and biomass of pico-, nano-, and microplankton on a transect across Nordvestbanken, north Norwegian shelf, in 1994

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SARSIA

Ratkova TN, Wassmann P, Verity PG, Andreassen IJ. 1998. Abundance and biomass of pico-, nano-, and microplankton on a transect across Nordvestbanken, north Norwegian shelf, in 1994. *Sarsia* 84:213-225.

The seasonal variation of suspended microplankton on a transect across Nordvestbanken in 1994 revealed that pico- and nanoplankton flagellates and monads (< 2 µm and 2-20 µm, respectively) entirely determined total phytoplankton numbers and biomass. From March to May and from August to October nanoflagellates and monads comprised on average 90 % and up to 98 % of total phytoplankton biovolume. Only during the maximum diatom and dinoflagellate abundance in June and July, and during the appearance of *Halosphaera viridis* at selected stations on the mid shelf, did flagellates comprise less than 60-90 % of total biovolume. In general, the abundances of picoplankton, coccolithophorids and *Phaeocystis pouchetii* were low, never comprising more than a few percent of total biovolume. The estimated total biomass of pico-, nano- and microplankton (from biovolume), phytoplankton (from chlorophyll and epifluorescence estimates) and larger protozooplankton (from biovolume) in the upper layers were on average 3-16 g C m^{-2}, 1-5 g C m^{-2} and 15-400 mg C m^{-2}, respectively. The biomass of ciliates was low throughout the investigation and only one substantial peak in June/July was recorded over the entire shelf.

Despite significant consumption of nitrate and silicate, large cells such as diatoms and dinoflagellates were not abundant on the shelf. They must have been removed from the water column, and it is speculated that this was accomplished mainly by mesozooplankton grazing. The dynamics of flagellates, diatoms, and protozooplankton are interpreted as the result of variable grazing pressure by mesozooplankton on protozoa and diatoms, and by protozoa on flagellates.

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Keywords:Pico-, nano-, and microplankton; abundance; biomass; north Norwegian shelf.

INTRODUCTION

Knowledge regarding the seasonal abundance of phytoplankton and protozoa on the shelf of northern Norway is remarkably scattered (Gran 1930; Halldal 1953; Braarud & Nygaard 1978; Rey 1981; Evensen 1994; Hegseth & al. 1995; Quillfeldt 1996) while north Norwegian fjords have been more thoroughly investigated (e.g. Gaarder 1938; Heimdal 1974; Schei 1974; Throndsen & Heimdal 1976; Eilertsen & al. 1981; Riebesell & al. 1995). According to the latter studies, seasonal patterns of phytoplankton development in north Norwegian fjords includes a spring burst of diatoms and *Phaeocystis* in late March-April, followed by a late spring and summer flagellate-ciliate community. Dinoflagellates and coccolithophorids reach their maximum later in the summer (July-August), and in early autumn a moderate second bloom of diatoms or other taxa may develop. During winter, phytoplankton are sparse (Noji & al. 1993).

The present investigation is a segment of the Ocean Margin EXchange programme (OMEX), whose goal is the study of fluxes and processes occurring along the European shelf break facing the North Atlantic. The primary objective is to measure and model exchange processes at the ocean margin to improve the ability of global models to predict the impact of environmental changes on the oceanic system and more specifically on the coastal zone. A field campaign was carried out on Nordvestbanken, the north Norwegian shelf, in 1994 (Fig. 1). The investigation was part of the interdisciplinary research project "Comparative fluxes of biogenic matter and trophodynamic interactions across the shelf break of northern Norway", to identify the components involved and describe the seasonality of the exchange of particulate material between the epipelagic and

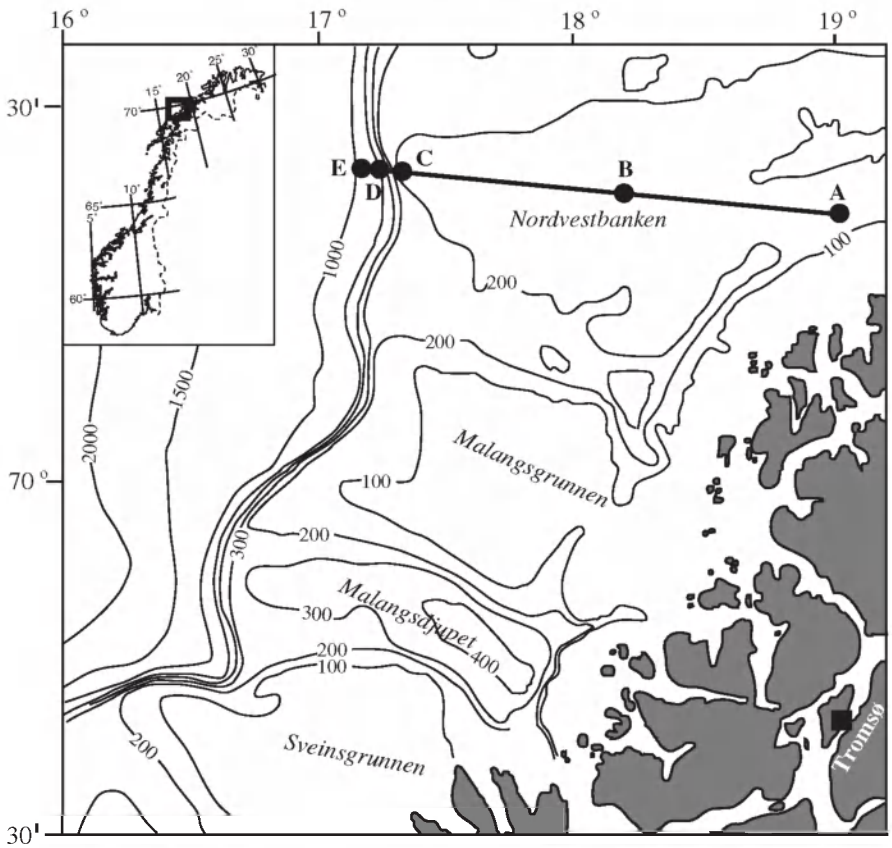

Fig. 1. Investigation area and the sampling stations A-E along the cross section over Nordvestbanken.

mesopelagic zone. Here we investigate the seasonal dynamics of pico-, nano- and microplankton. In the study area, the Norwegian Coastal Current (NCC) flows northward along the shelf of northern Norway, creating a band of coastal water which is wide and shallow in summer, and narrow and deep in winter (Sætre & Mork 1981). Farther outside, a broad, meandering band of the warmer Atlantic water of the Norwegian Atlantic Current (NAC) is found. The NCC transfers Norwegian inshore waters, mixed with Atlantic water. Below the surface waters dominated by the NCC, waters of the NAC may penetrate deeper into the coastal zone over or between coastal banks (Wassmann & al. 1996). Due to the high temperature of the Atlantic water the NCC never freezes in winter and water column stability depends entirely upon solar heating and the limited freshwater input to this area (Wassmann & al. 1996). For details regarding the topography and hydrography of the investigation area in 1994, see Nordby & al. (1999).

In order to better understand the role of phytoplankton and protozoa in the food-web structure, and in particular to investigate their contribution and impact on suspended biogenic matter, an investigation was conducted of the seasonal composition, spatial distribution, and biomass of plankton. The investigation scrutinised for the first time the seasonal development of the plankton community on the north Norwegian shelf. While the dynamics of nutrients and pigments have been presented elsewhere (Wassmann & al. 1999a), the focus here is upon the numerical and biovolume variation of the plankton community, in particular phytoplankton and protozoa. More specific data regarding the autotrophic and heterotrophic components of the nano- and microplankton are presented by Verity & al. (1999) while mesozooplankton data are presented by Halvorsen & Tande (1999), in this same issue.

MATERIAL AND METHODS

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 from 0, 10, 30, 50 and 100 m horizons. For details of the sampling and analytical procedures, see Wassmann & al. (1999a). Suspended biomass samples were taken on the monthly base at 5 stations (Stns A, B, C, D, and E) from 23 March to 10 October in 1994 (Fig. 1). About 100 ml of seawater from each horizon were fixed with a glutaraldehyde-Lugol solution (Rousseau & al. 1990). This fixative was selected because it permits counting whole colonies of *Phaeocystis pouchetii* and flagellates, but it does not prevent the growth of fungi during storage. The latter problem overestimates nanoplankton biovolume.

Phytoplankton was counted with a standard light microscope furnished with a counting stage (Semina 1978). The whole sample was gently mixed with a large-bore pipette, which was slowly emptied in the bottle while progressively raised from bottle bottom to the opening, the lower end of pipette remaining barely immersed. Counting of pico- and the most abundant nanoplankton algae (< 2 µm and 2-20 µm, respectively) was carried out in the Fuchs-Rosenthal counting chamber with the magnification of 400 ×. Samples were allowed to settle for a week after the smaller phytoplankton was enumerated, and then slowly decanted through a glass tube covered with two layers fine-mesh nylon gauze. After gentle mixing the remaining sample was removed with a glass tube and placed into a 0.05 ml chamber. Cells were counted under magnification of 200 ×. In order to count rare (usually larger) forms in the whole sample, a special 1.0 ml chamber was used, but as it was rather thick and only a low-power objective (magnification of 100 ×) can be used. All the taxonomic identifications were carried out in fluid samples according to the shape of cells and colonies.

The biovolumes of individual cells were calculated from linear dimensions of measured cells applied to appropriate stereometric formulae (Smayda 1978). The carbon biomass of the pico-, nano- and microplankton (PNMC) was calculated from abundances and mean volumes and using a conversion factor of 0.11 pg C μm^{-3} (Edler 1979). Because photosynthetic and heterotrophic cells could not be reliably distinguished using light microscopy, PNMC includes contributions from both groups. However, Verity & al. (1999) distinguished between auto- and heterotrophs using fluorescence microscopy. In order to determine what fraction of PNMC represented only phytoplankton (PPC) the ratio of mean photosynthetic:heterotrophic (P:H) biomass from Verity & al. (1999) was multiplied with the mean PNMC for each station and date. Refer to Verity & al. (1999) for details of methods and discussion of P:H ratios.

The carbon biomass of (larger) protozooplankton (PZC) was calculated according to Garrison & Buck (1989). Because small heterotrophic flagellates were included in PNMC above, the biomass of PZC represents the contribution of larger protozoans, primarily ciliates. Verity & al. (1999) presents data on combined biomass of heterotrophic flagellates and dinoflagellates, plus mixo- and heterotrophic ciliates.

RESULTS

Phytoplankton species composition

In all, a total of 120 different phytoplankton species were identified: 73 diatom, 41 dinoflagellate, 3 chrysophyceae, 2 prymnesiophyceae and 1 prasinophyceae species. It should be noted that this is a minimum estimate because (a) some organisms were identified only to the genus level, (b) flagellates and coccolithophorids were identified only to higher taxa and (c) identifications were made with the light microscope only.

Flagellates and monads dominated phytoplankton abundance. Among the remaining cells the following predominant species were recorded: small dinoflagellates in May-August; large dinoflagellates such as *Ceratium horridum*, *Ceratium tripos* and *Peridinium* sp. in July-September; small centric diatoms *Chaetoceros socialis* and *Thalassiosira* spp. in March-June; large centric diatoms *Corethron criophilum*, *Coscinodiscus* spp., *Rhizosolenia styliformis* and small pennate diatom *Pseudo-nitzschia pseudodelicatissima* in July-August; large prasinophyceae such as *Halosphaera viridis* in August-October and the benthic diatom *Diploneis interrupta* in autumn. *Phaeocystis pouchetii* was not a dominant taxon and rarely recorded throughout the investigation. For taxonomic details and seasonal prevalence, see Table 1.

Pico- nano- and microplankton abundance, biovolume and carbon content

The microscopic investigation revealed that pico- and nanoplankton flagellates and monads entirely determined total microplankton numbers and biomass throughout the transect (Table 2). From March to May and from August to October, nanoflagellates and monads comprised ≥ 90 % of total microplankton biovolume. Flagellates had maxima in March, June and in August (Fig. 2). They were more abundant at Stns A-B, than at Stns D-E. The flagellates occurred less confined, but had often maxima near the surface. The concentration of flagellates below 25 m depth was greatly reduced from July to October at the shelf edge Stn E. Diatoms reached their highest estimated biovolume in June and near the surface (Fig. 3). Again, concentrations where highest at Stn A. Dinoflagellates were scarce during spring and summer, small dinoflagellates had the highest abundance in July (Fig. 4). A few large species became more numerous in late summer-autumn. The con-

centration was lowest at Stn E. On the middle shelf *Halosphaera viridis* became rather numerous in August-October, surpassing 20 % of total phytoplankton biovolume. *Phaeocystis* was not abundant and only during its maximum in July occurred at 10^4-10^6 μm^3 l^{-1}. The contribution of flagellates decreased to 60-90 % of total biovolume only in the period of the highest concentration of diatoms in June and of dinoflagellates in July. Picoplankton and coccolithophorids were of minor importance for total phytoplankton biovolume and never constituted more than a few percent of total biovolume.

At Stn A only one major maximum in flagellate biovolume was recorded in June (Fig. 2). On the middle shelf (Stn B) flagellates attained their main maximum in

Table 1. List of most prominent microplankton taxa and their seasonal prevalence from Stns A-E at Nordvestbanken, northern Norway, in 1994. Average concentrations from all stations and depths are shown. +, ++, +++, ++++ represents < 100, 100-1000, 1000-10 000 and > 10 000 cells l^{-1}; - : no observation. Taxonomic system according to Tomas (1997).

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
DIVISION CHROMOPHYTA								
Class Dinophyceae								
Amphidinium crassum Lohmann	-	-	+	+	++	+	-	-
Ceratium arcticum (Ehrenberg) Cleve	-	-	-	-	+	+	-	-
C. furca (Ehrenberg) Claparede & Lachmann	-	-	-	-	+	+	+	+
C. fusus (Ehrenberg) Dujardin	-	-	-	+	+	+	-	-
C. horridum (Cleve) Gran	-	-	+	+	++	+	+	+
C. longipes (Bailey) Gran	-	-	+	+	+	+	+	+
C. tripos (O. F. Muller) Nitzsch	-	-	-	+	+	+	+	+
Dinophysis acuminata Claparede & Lachmann	-	-	-	-	+	+	+	+
D. rotundata Claparede & Lachmann	-	+	+	+	+	+	+	+
Diplopsalis lenticula Bergh	-	-	-	-	+	+	+	-
Gonyaulax spinifera (Claparede & Lachmann) Diesing	+	+	+	-	+	+	-	-
Gymnodinium arcticum Wulff	+	+	-	++	++	++	+	-
G. wulffii Schiller	+	+	-	+++	-	++	++	+
G. sanguineum Hirasaka	+	+	-	-	+	+	+	-
Gyrodinium esturiale Hulburt	+	+	+++	++++	+++	+++	++	+
G. lachryma (Meunier) Kofoid & Swezy	-	-	-	-	+	-	+	-
G. pingue (Schutt) Kofoid & Swezy	+	+	-	+	++	+	+	+
G. sp.	-	-	-	-	++	-	-	-
Pronoctiluca acuta (Lohmann) Schiller	-	-	++	++	++	+	+	+
Protoperidinium breve (Paulsen) Balech	-	+	-	-	+	+	-	-
P. brevipes (Paulsen) Balech	+	+	-	+	+	+	-	-
P. bulla (Meunier) Balech	+	-	++	++	++	++	++	+
P. depressum (Bailey) Balech	+	-	+	+	+	+	+	-
P. pellucidum (Bergh) Balech	-	-	-	+	++	+	+	-
Prorocentrum balticum (Lohmann) Loeblich	+	+	++	-	++	++	-	-
P. micans Ehrenberg	+	-	+	+	-	-	-	+
P. minimum (Pavillard) Schiller	+	-	-	-	-	+	+	-
Scrippsiella trochoidea (Stein) Loeblich	+	+	+	+++	+	+	+	-
S. trochoidea cysts	-	+	+	+	+	-	-	-
Class Prymnesiophyceae								
Caliptrosphaera sphaeroidea var. *minor* Schiller	+++	++	+++	+++	+++	+++	++	-
Emiliania huxleyi (Lohmann) Hay & Mohler	+++	+	++	+	+++	++	++	-
Phaeocystis pouchetii (Hariot) Lagerheim	-	-	++	++++	++	+++	+++	+
Class Chrysophyceae								
Dictyocha speculum Ehrenberg	+	+	-	-	-	-	-	+
Class Bacillariophyceae								
Actinocyclus octonarius Ehrenberg	-	-	+	+	+	+	+	+
Chaetoceros borealis Bailey	-	-	+	+	+	+	-	-
C. concavicornis Mangin	-	+	++	++	++	+	-	-
C. curvisetus Cleve	-	+	-	+++	+	-	+	-
C. debilis Cleve	+		+	++	+++	+	+	-

August. Colonies of *Phaeocystis* were not recorded at all. In the frontal zone above the shelf break (Stn C), plankton distributions were similar to those of Stns A-B At the two stations beyond the frontal zone (Stns D-E) microplankton was less abundant, and its mass development began in May, earlier than at Stns A-B. Dinoflagellates were scarce in July-September (Fig. 3). Coccolithophorids were much more abundant than at Stns A-B and had maxima in March and in July-August.

The combined biomass of pico-, nano- and microplankton carbon (PNMC) and estimated phytoplankton carbon (PPC) are presented in Table 3. The seasonal PNMC in the upper 100 m on Nordvestbanken ranged between 1-28 g C m^{-2}. The maximum PNMC concentrations were recorded in March (average 16 g C m^{-2}) and the minimum in October (average 3 g C m^{-2}). The highest PNMC concentrations and largest variability were found at Stn A and the lowest concentrations and

Table 1. Continued.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
C. decipiens Cleve	-	-	++	++	++		+	-
C. densus (Cleve) Cleve	-	-	+	+	+	-	+	-
C. furcellatus Bailey	-	-	-	+	+++	++	-	-
C. diadema (Ehrenberg) Gran	-	-	-	-	+	+	-	-
C. furcellatus spores	+	-	+	-	-	+	-	-
C. socialis Lauder	++++	+	+++	+++	++	+	+	+
C. teres Cleve	-	-	+	+	+	-	-	-
C. wighamii Brightwell	-	-	-	-	+	+++	+	-
Corethron criophilum Castracane	-	+	+	+++	+	+	-	-
Coscinodiscus radiatus Ehrenberg	-	-	+	-	+	+	+	-
Cyclotella sp.	+	+	+	+	-	+	-	-
Cylindropyxis tremulans Hendey	+	+	++	++++	++	++	++	++
Cylindrotheca closterium (Ehrenberg) J. Lewin & Reimann	-	-	-	-	+	+	+	-
Fragilariopsis cylindrus (Grunow) Krieger	-	+	+	++	-	-	-	-
Gyrosigma tenuissimum var. *hyperborea*(Grunow) Cleve	+	+	-	-	-	-	-	-
Navicula avenaceae Brebisson & Grunow	+	+	+	+	+	+	-	+
Pleurosigma finmarchicum Cleve & Grunow	+	+	+	+	+	-	-	-
Proboscia alata (Brightwell) Sundstroem	-	-	-	-	+	+	+	-
Pseudo-nitzschia pseudodelicatissima (Hasle) Hasle	-	+	-	++	++	++++	+	+
P seriata (Cleve) H. Peragallo	+	+	-	+	-	-	-	-
Rhizosolenia hebetata f. *hemispina* (Hensen) Gran	-	-	-	-	+	+	+	-
R. setigera Brightwell	-	-	-	-	+	+	-	-
R. stylıformis Brightwell	-	-	-	-	+	+	+	-
Roperia tesselata (Roper) Grunow	-	-	-	-	-	+	-	-
Thalassionema nitzschioides (Grunow) Grunow & Hustedt	-	+	-	+	-	-	+	-
Thalassiosira angulata (Gregory) Hasle G. Frixell & Hasle	+	+	-	-	+	-	+	-
T anguste-lineata (A. Schmidt)	+	-	+	+	+	-	-	+
T antarctica var. *borealis* G. Frixell, Douchette & Q. Hubbard	+	+	+	+	+	+	-	+
T nordenskioeldii Cleve	+	+	-	-	-	-	-	-
DIVISION CHLOROPHYTA								
Class Prasinophyceae								
Halosphaera viridis Schmitz	-	-	-	+	-	++	++	+
PROTOZOA								
Myrionecta rubra	-	-	-	-	+	+	+	-
Strobilidium sp.	+	+	++	++	+	+	+	+
Strombidium spp.	+	+	+	++	+	+	+	-
Tontonia sp.	-	+	+	-	-	-	+	-
Acanthostomella norvegica	-	-	+	+	+	+	-	-
Tintinnopsis sp.	+	+	+	+	+	+	+	+
Parafavella gigantea	+	-	-	+	+	+	+	+

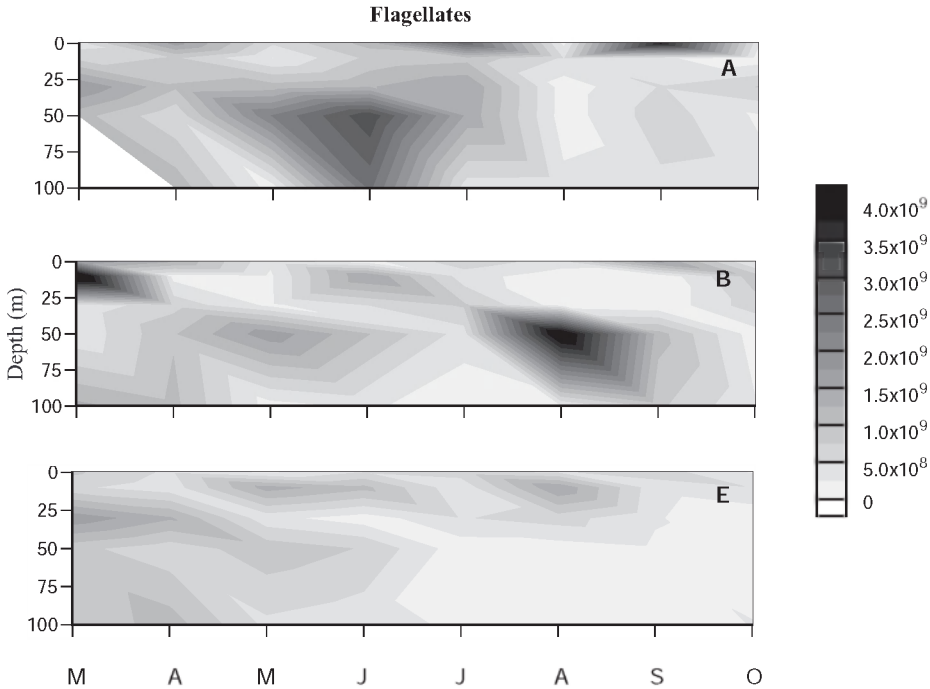

Fig. 2. Seasonal variation of flagellate biovolume ($\mu m^3 l^{-1}$) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994. The figure may give the impression of continuity in sampling over time, but each plot is based on only a 8 × 5 data set. Observe that the concentration of flagellates is one order of magnitude higher compared to that of diatoms, dinoflagellates and larger protozoa (see Figs 3-5).

smallest variability at offshore Stn E. The contribution of PNMC to the suspended particulate organic carbon (POC) was high. On average PNMC contributed approximately 50 % to the standing stock of suspended POC (Table 5). The contribution of PNMC was highest in spring (50-175 %) and decreased steadily from May to low levels in October (20 %). PNMC was probably overestimated, in particular in March, by fungi which were encountered in the samples, probably due to storage at room temperature.

The PNMC biomass includes contributions from both auto- and heterotrophic cells, which could not be distinguished via light microscopy. However, detailed investigations of aliquots of the same samples revealed that a majority of the pico- and nanoplankton (all stations) were not phototrophic but obligatory heterotrophic cells. Multiplying the PNMC biomass, at each station and date, with the ratio of phototrophic:heterotrophic (P:H) biomass, yields the particulate phytoplankton carbon (PPC). Table 3 indicates that the integrated PPC stock ranged from 1 g C m^{-2} in October to 6 g C m^{-2} in June, with a seasonal average of about 4 g C m^{-2}, implying that only about 40 % of PNMC was comprised by autotrophs. Despite the high nutrient consumption

Table 2. The percentage of pico- and nanoplankton of total microplankton biovolume.

Sampling site	Months								
	3	4	5	6	7	8	9	10	Average
A	99	99	94	79	91	79	96	94	91
B	99	99	91	79	82	88	95	95	91
C	99	93	96	67	77	75	93	98	87
D	99	99	99	74	72	96	94	ND	90
E	97	98	98	90	83	96	94	99	94
Average	99	98	95	78	81	87	94	97	91

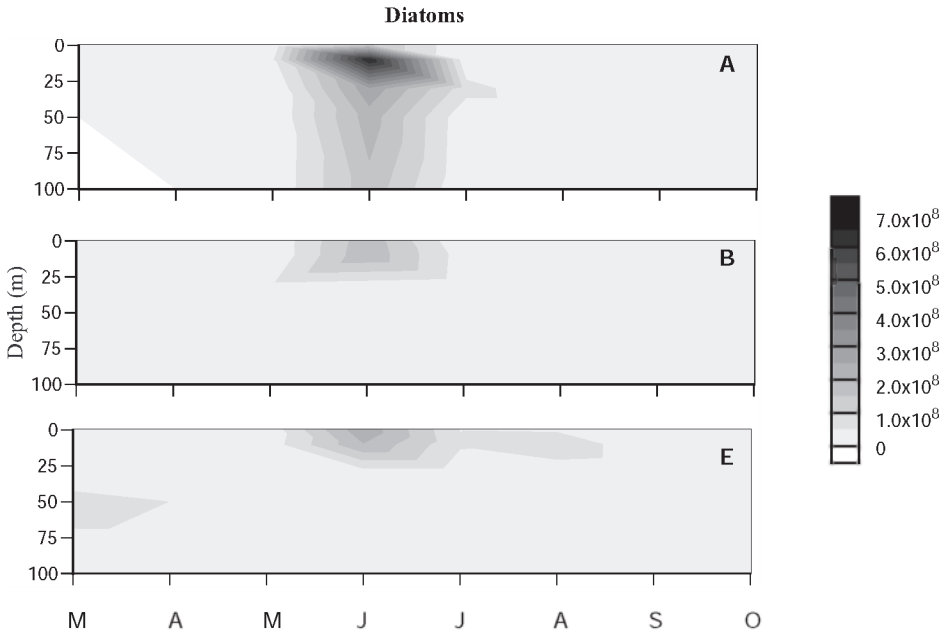

Fig. 3. Seasonal variation of diatom biovolume ($\mu m^3 l^{-1}$) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

rate, the average PPC contribution on Nordvestbanken in 1994 was thus only 22 % of the standing stock of POC. The latter percent contribution ranged from 26 % at Stn C in March and Stn E in October, to exceeding 60 % during July (data not shown).

Protozoa biovolume and abundance

The seasonal variation of protozoa, principally ciliates, is briefly summarised as follows: (a) protozoan cysts dominated protozoa in March, (b) in April-May, *Holotricha* became more important, (c) in June-July, blooms of *Oligotricha* (Family *Strobilididae*) took place, (d) in July, *Myrionecta rubra* displaced *Strobilididae* at Stn E, (e) in August and in September, *Myrionecta rubra* and *Strobilididae* still dominated protozoans, but their abundance decreased. The seasonal maximum of *Tintinnida* occurred in late summer-early autumn. In October, protozoan cysts again prevailed.

Mass development of protozoans began earlier at Stns A and B (June) and later (July) at other stations (Fig. 5). In August, numbers and biovolume of protozoa sharply decreased throughout the transect. The highest

Table 3. Integrated (0-100 m) seasonal carbon of pico-, nano- and microplankton (PNMC) (g C m^{-2}) at Stns A-E along the transect of Nordvestbanken in 1994. The biomass is based on the microscopical estimation of biovolume and 0.11 pg μm^{-3} (Edler 1979). The numbers in bold indicate integrals where 1 or 2 depths were missing. The numbers in italics indicate possible overestimation of PNMC. Also shown is the phytoplankton carbon (PPC). See text for details.

Sampling site	Months								
	3	4	5	6	7	8	9	10	Average
A	**12**	10	12	*28*	*14*	3	***12***	4	12
B	14	9	8	**12**	5	*18*	8	4	10
C	16	10	9	8	6	1	**4**	1	7
D	*27*	11	4	**5**	3	12	5	ND	7
E	11	9	8	7	**3**	5	3	2	6
Average PNMC	16	10	8	12	6	8	6	3	9
Average PPC	5	4	4	6	4	4	3	1	4

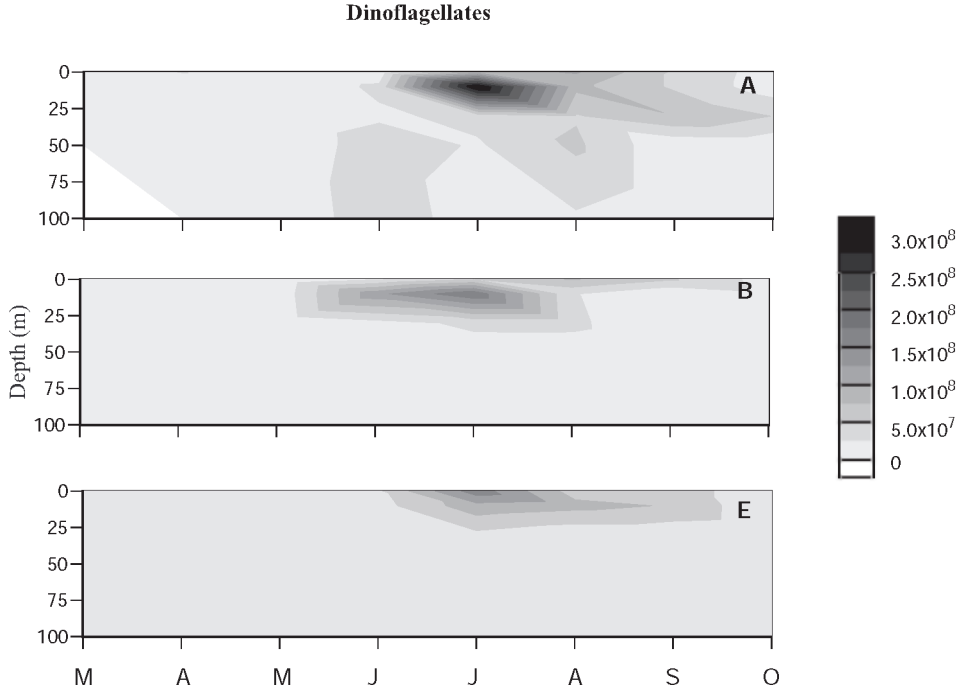

Fig. 4. Seasonal variation of dinoflagellate biovolume ($\mu m^3 l^{-1}$) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

abundance of protozoa was encountered at Stn A (2.2×10^4 cells l^{-1} and 1.8×10^8 μm^3 l^{-1}) and at Stn B (3.5×10^3 cells l^{-1} and 2.7×10^7 μm^3 l^{-1}) in June. At Stns C, D and E ($1.5\text{-}3.5 \times 10^3$ cells l^{-1} and $2.8\text{-}9.0 \times 10^7$ μm^3 l^{-1}) maximal abundance of protozoa were observed in July. The protozoan biovolume maxima in June-July developed mainly in upper 0-30 m layer. The seasonal variation in protozoa biomass and the differences between Stn A-E is presented in Table 4. On average the protozooplankton carbon (PZC) ranged between about 70 mg C m^{-2} in March to 15 mg C m^{-2} in October, with a maximum of 400 mg C m^{-2} in June. The maximum in 30 m depth at Stn A in June is mainly due to *Strobilididae* and that in 10 m depth at Stn E in July due to *Myrionecta*. These maxima influenced the total biovolume.

The seasonal trend was similar at all stations. The highest abundance of protozoa occurred earlier at Stn A and B compared to the offshore stations C, D and E. The smallest variation was encountered at the shelf break at Stn D. The contribution of PZC to the suspended POC was low, on average about 0.6 %. The contribution of PZC was higher in March (0.8) and was maximal in June-July (1.7-1.9 %), decreasing steadily from July to low levels in October (0.1%).

Table 4. Integrated (0-100 m) seasonal protozooplankton carbon (PZC) (mg C m^{-2}) at Stn A-E along the transect of Nordvestbanken in 1994. The carbon biomass of (larger) protozooplankton (PZC) was calculated according to Garrison & Buck (1989).

Sampling site	Months								
	3	4	5	6	7	8	9	10	Average
A	92	64	196	1470	175	60	59	28	268
B	33	83	51	244	165	15	20	5	77
C	42	33	18	131	330	165	39	27	98
D	132	48	137	97	251	117	46	ND	103
E	63	58	62	81	751	90	43	13	159
Average	72	57	93	405	334	89	41	15	99

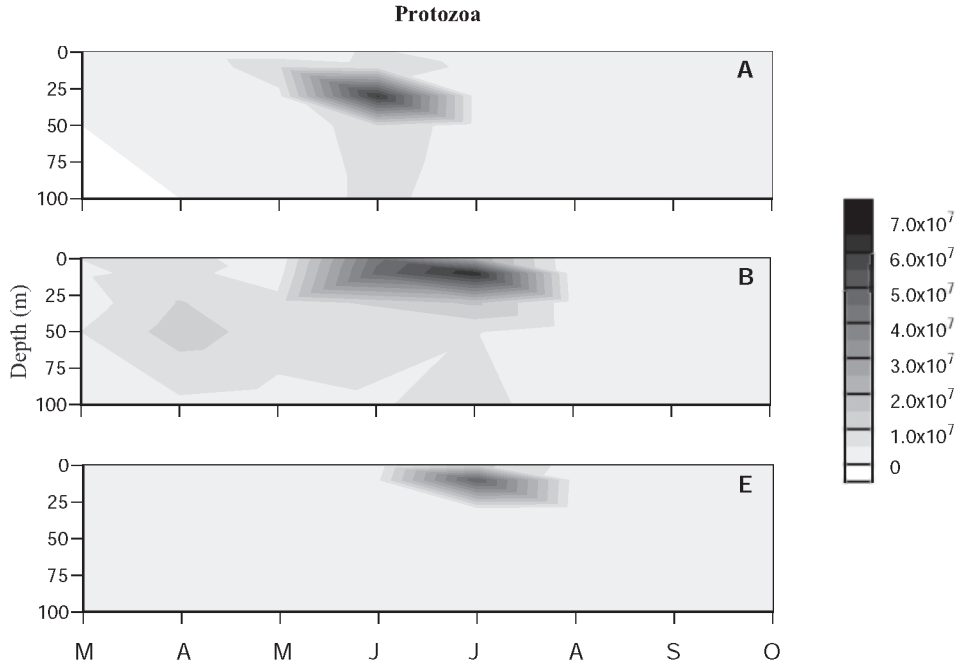

Fig. 5. Seasonal variation of biovolume of larger protozoa ($\mu m^3 l^{-1}$) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

DISCUSSION

Conceptual models of the trophodynamic functioning of planktonic ecosystems (Legendre & Le Fèvre 1989, 1994) have proposed that hydrodynamic singularities, such as fronts, eddies, upwelling, play a major role in favouring export production over *in situ* recycling and, as a result, the prevalence of short food webs over the microbial loop. According to these models, physical forces act upon the biological system in a series of bifurcations by setting the conditions leading to the dominance of a given microplankton assemblage and by controlling the processes involved in the fate of produced matter. For example, frontal structures and vertical mixing, across shelf-breaks and in slope waters are crucial in controlling phytoplankton primary production, activity of grazers and distribution of larvae of fishes, and ultimately in determining the structure of the pelagic food web in that area (Holligan & al. 1984; Kahru & al. 1984; Kiørboe & al. 1988; Fernandez & al. 1993). Physical forcing is thus of utmost significance for shelf ecosystems and bottom-up regulation is supposed to play an important role for pelagic cycling.

Table 5. Suspended POC in the upper 100 m (g C m^{-2}) along the transect (sampling sites A (inner shelf), B and C (mid shelf) and D and E (shelf break) from March to October 1994 (data from Wassmann & al. 1999a).

Sampling site	Months								
	3	4	5	6	7	8	9	10	Average
A	9.1	16.9	17.6	29.9	21.5	23.7	28.4	18.4	20.7
B	11.2	13.9	17.2	22.9	17.5	24.2	27.9	12.2	18.4
C	9.2	12.2	13.7	22.3	24.0	20.4	31.9	17.8	18.7
D	9.9	10.2	15.9	16.8	17.1	24.0	22.0	ND	16.7
E	6.2	11.1	17.2	17.1	19.6	15.7	21.1	12.7	15.4
Average	9.1	12.9	16.3	21.8	19.9	21.6	23.9	15.1	18.0

The lack of large phytoplankton

The physical environment determines nutrient availability, influences new production, the prevalence of large cells, the aggregation of sticky particles and hence the particles potentially available for sedimentation. Thus we would expect a strong impact of bottom-up regulation on plankton on Nordvestbanken with a dominance of large phytoplankton cells such as diatoms during periods of high nutrient concentration (e.g. the vernal bloom based on winter-accumulated nutrients) or increased nutrient supply (e.g. during episodic upwelling). Only during calm periods in late summer and early August would small cells and a well developed microbial food web be expected.

Several provocative and instructive conclusions derive from the present study: (1) the lack of a spring phytoplankton outburst (Wassmann & al. 1999a); (2) that microplankton biomass was continuously dominated by flagellates and other small cells (Table 2); and (3) that the ratio of biomass of photosynthetic:heterotrophic plankton in near-shore waters exceeded 2.0 only during mid-May to mid-August (Verity & al. 1999). If the investigation of the pico-, nano- and microplankton samples from Nordvestbanken would have been conducted without knowledge about the environment from which they were acquired, inappropriate conclusions could have been obtained. One could have reached the conclusion that the samples were obtained from an area characterised by oligotrophic conditions, limited seasonal amplitude in physical forcing, a prevalence of the microbial food web and extensive recycling of nutrients. An interpretation of the Nordvestbanken plankton based on classical indications from the light microscope would obviously fail to characterise the basic environmental conditions on the north Norwegian shelf.

Earlier investigations in the Norwegian Current (Halldal 1953) revealed a delay of the vernal bloom maximum and prolonged phytoplankton growth compared to the inner shelf (Rey 1981) and fjord environments (Heimdal 1974). This has been attributed to the physically less stable environment on the mid shelf and the shelf break, compared to the less exposed fjords, giving rise to delayed stratification and thus a later start of the spring bloom. It is, however, unlikely that stratification alone is the cause for the slow build-up of phytoplankton biomass on the shelf, because the spring bloom develops in water masses with no or very low stratification, usually peaking during April (Hegseth & al. 1995). Although similar with regard to stratification, the vernal bloom developed earlier and stronger in the Barents Sea compared to the north Norwegian shelf (Evensen 1994). Kiørboe (1993) shows that high levels of turbulence and light limiting growth conditions may result in a community dominated by flagellates. This seems to be the case at Nordvestbanken in March. Contrary to nitrate, no major decline in silicate concentrations was found during March-April (Wassmann & al. 1999a), implying that phytoplankton species which do not require silicate (e.g. flagellates) dominated growth during the early spring bloom.

Despite significant consumption of silicate on Nordvestbanken in May-August, 1994, implying that about 1/3 of the new production (> 75 g C m^{-2} y^{-1}) was due to diatoms (Wassmann & al. 1999a), diatoms were not numerous even during their seasonal maximum in June (< 25 % of total microplankton biovolume). Other large cells such as dinoflagellates and colonies of *P. pouchetii* were also scarce. Very similar conditions were described for the Norwegian Current in 1986 (Peinert & al. 1987). Despite high nutrient reserves and favourable hydrographic conditions, a spring bloom did not developed in this year, and phytoplankton was dominated by flagellates. Previous investigations have not reported such an apparent lack of large phytoplankton cells. Rey (1981) describes a *P. pouchetii* bloom in the upper layers at the shelf break off Hekkingen lighthouse in mid-April 1978 and comments that the spring outburst is mainly composed of diatoms in this area. Hegseth & al. (1995) reports that typical spring phytoplankton species were dominant in north Norwegian shelf ecosystems, i.e. diatoms and *P. pouchetii*. It is not obvious if the lack of large phytoplankton cells at Nordvestbanken in 1994 was temporally/geographically exceptional or it may be rather usual event for the NCC and NAC region.

Zooplankton, microplankton size spectrum and phytoplankton carbon

The significant decrease in nitrate and silicate concentrations implies that large phytoplankton cells such as diatoms are produced at Nordvestbanken, but they do not accumulate in greater numbers except for minor "blooms" in June/July (Figs 3 & 4). In western Norway nitrate and silicate concentrations can decrease to 1.0-1.5 µM and 0.6-1.0 µM, respectively, as early as by the end of March in fjords with sharp salinity gradients (Erga 1989). During the present study nutrients concentration were rather high until June even in surface waters (Wassmann & al. 1999a). The characteristic low vertical stability of north Norwegian waters during spring (Eilertsen 1993) dispersed algae throughout the water column well below the euphotic zone (see also Nordby & al. 1999). In May/June vertical stability increased a little and some diatoms accumulated in the upper 10 m layer. However, in particular at the shelf break nutrients became never limiting throughout the season (Wassmann & al. 1999a) and growth conditions for phytoplankton

prevailed. Therefore, an effective mechanism which removes large cells from the water column must exist. It is hypothesised that this mechanism is grazing. Already in March a mesozooplankton biomass of 0.3 g C m^{-2} was recorded along the transect (E. Nordby & K.S. Tande pers. commn). In April 1994, mesozooplankton biomass equalled the normal maximum biomass (≈ 1.3 C m^{-2}) of north Norwegian fjords which is usually reached in May-June (Tande 1991). Mesozooplankton biomass attained maxima up to 20 g C m^{-2} in May and high average biomass (2.3-3.4 g C m^{-2}) prevailed throughout summer and autumn (E. Nordby & K.S. Tande pers. commn).

Kiørboe (1993) argues that even though turbulence is a prerequisite for diatoms to prevail, the success of diatoms is dependent on an escape from grazing pressure. Due to different timing of diatom production and mesozooplankton grazing in relatively shallow coastal environments, and the grazing control of nano- and picoplankton by protozoa, diatoms tend to dominate production and biomass during spring. It is hypothesised that advection of overwintering mesozooplankton onto or transport along the north Norwegian shelf prior to, or in concert with, the vernal bloom resulted in diatoms and large protozoa being controlled by mesozooplankton grazing. The delay of the vernal bloom maximum and prolonged phytoplankton growth, lower biomass yields and a significant contribution by flagellates in the NAC (Halldal 1953) has been interpreted as a result of selective grazing from copepods (Peinert & al. 1987; Bathmann & al. 1990).

Already in March a well developed mesozooplankton community dominated by adult *Calanus finmarchicus* was recorded on the shelf (Halvorsen & Tande 1999). They were presumably grazing upon large phytoplankton cells as well as larger protozoa. Thus the abundance of e.g. diatoms and protozoa was low, but that of flagellates high (because significant removal of flagellates was limited by the low abundance of protozoa; compare Figs 2 and 5). This situation continued until June/July when *C. finmarchicus* started on its ontogenetic migration to deeper water layers in the Norwegian Sea. This change in the zooplankton community coincided with increased abundance of large-celled phytoplankton and protozoa (Figs 3-5), while the abundance of flagellates experienced minima at depths where protozoa accumulated, but not below these depths (Fig. 2). The mesozooplankton biomass on Nordvestbanken in late summer and autumn was characterised by smaller calanoid copepods such as *Oithona* sp., and *Limacina retroversa* (Halvorsen & Tande 1999). Their impact on the abundance of microplankton is thought to be similar to that of *C. finmarchicus*: large cells of phyto- and protozooplankton were grazed while the grazing pressure on autotrophic and heterotrophic flagellates weakened. As a consequence the abundance of diatoms, dinoflagellates and protozoa decreased sharply (Figs 3-5) while that of flagellates increased at Stns B and E and in surface waters at Stn A (Fig. 2). The advent of winter conditions in October, reflected in decreased radiation and increased vertical mixing due to storms, resulted in declining abundance of all types of plankton.

The most prominent features of the seasonal development of phyto- and protozooplankton on Nordvestbanken in 1994 were (a) the lack of accumulation of larger cells which would have been expected for the high new production rate, and (b) the lack of signs of the vernal bloom which is a most prominent feature in the inner part of the north Norwegian coastal zone (e.g. Hegseth & al. 1995; Riebesell & al. 1995) and the Barents Sea shelf (e.g. Wassmann & al. 1990; Slagstad & Wassmann 1997). Further, the seasonal contribution of PNMC and PZC to the suspended standing stock of POC along the transect A-E (on average 50 % and 1 %, respectively; Tables 3-5) implies that a significant fraction of the suspended POC standing stock was comprised by other carbon fractions such as faecal pellet carbon and detritus (Wassmann & al. 1999b). However, comparing PNMC to suspended POC (Tables 3-5) suggest that PNMC was overestimated, in particular in March and perhaps also in April at all stations when fungi developed in samples during storage. From May to October, the average percentage of PNMC contained within POC ranged between 50 and 20 %, respectively (Tables 3-5).

Concluding remarks

The microscopic investigation and their interpretation points at significant top-down regulation of the pelagial by mesozooplankton *and* the presence of a rich community of small planktonic forms. The traditional concept of plankton dynamics in subarctic environments emphasising short food-chains involving large organisms seems inadequate to understand pelagic cycling of biogenic matter at Nordvestbanken in 1994. The proposed prevalence of short food webs over the microbial loop under the influence of hydrodynamic singularities such as fronts, eddies and upwelling, is not necessarily accurate on shelves as proposed by Legendre & Le Fèvre (1989) because advection and overwintering of mesozooplankton may be of significance for pelagic carbon cycling. The hydrodynamic conditions on shelves do play a major role in favouring export of organic matter (see Andreassen & al. 1999), but this export is strongly influenced by both mesozooplankton grazing and *in situ* recycling. Joint regulation by resource availability and predation as suggested by Verity & Smetacek (1996) offers a new conceptual framework in which the apparent regulation of the pelagic trophic structure on the north Norwegian shelf can be resolved.

ACKNOWLEDGEMENTS

The assistance of the crew of R/V *Jan Mayen* is gratefully acknowledged. Chrisje van Ek, Lena Hansen and Fride Tonning helped during the cruises. The skilful and dedicated expertise of Sigrid Øygarden in the laboratory contributed to the success of this investigation. Thanks to Cecilie von Quillfeldt for commenting the phytoplankton taxonomy. This work was supported by the Research Council of Norway (project no. 101323/410 and 108085/122) the European Union in the framework of the MAST programme, contract no. MAS2-CT93-0069 and MAS3-CT96-0056 (Ocean Margin EXchange – OMEX), by the Russian Foundation of Basic Research, grant 95-05-15443 and by the U.S. National Science Foundation grant OCE-95-21086.

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Accepted 15 January 1999 – Printed 15 November 1999
Editorial responsibility: Ulf Båmstedt