

Seasonal variation in production, retention and export of zooplankton faecal pellets in the marginal ice zone and central Barents Sea

Christian Wexels Riser^{a,*}, Paul Wassmann^a, Kalle Olli^b,
Anna Pasternak^c, Elena Arashkevich^c

^aNorwegian College of Fishery Science, University of Tromsø, N-9037, Tromsø, Norway

^bInstitute of Botany and Ecology, University of Tartu, Lai 40, EE-51005, Tartu, Estonia

^cP.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovsky avenue 36, R-117581, Moscow, Russia

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Abstract

Vertical distribution and sedimentation of faecal pellets (FPs) as well as the production rates of FPs by larger copepods were studied during three cruises to the Barents Sea in March and May 1998, and July 1999. Three to five 24-h stations were selected during each cruise, where at least one main station was located in Arctic water (ArW), one in the polar front region (PF) and one in Atlantic water (AW). A winter scenario was encountered in March with very low concentrations of FPs in the water column, most of the time well below 0.1 mg faecal pellet carbon (FPC) per cubic meter, and with sedimentation rates below 3 mg FPC m⁻² day⁻¹ at all depths and stations. Increased concentrations of FPs were observed in May and the maximum biomass of FPs was found in ArW (4.8 mg FPC m⁻³). This was reflected in high vertical flux of FPs in the ArW, just below the chlorophyll maximum (~ 150 mg FPC m⁻² day⁻¹). FPC sedimentation explained ~ 40% of the total particulate organic carbon (POC) export at 90 m depth at this station. Copepod FP production was moderate to high in May, reflecting favourable feeding conditions. Large spatial variation in the estimated retention potential of FPs was observed, ranging from 96% in AW to ~ 40% in the PF region. The July scenario did not differ very much from that observed in May. The lowest suspended concentrations and vertical flux of FPs were again observed in AW, in spite of the high pellet-production rate. FPC explained 34% of the POC export out of the upper layer in ArW, 40% in the PF region, but only 8% in AW. The calculated retention potential of 70% of the produced copepod FPs in AW decreased to 60% and 47% in the PF region and ArW, respectively. Krill FPs comprised a significant fraction of both suspended and sedimented FPC throughout the central Barents Sea. The data show that spatial and temporal variations in the FP “retention filter” are extensive and evidently of importance for the patterns of vertical flux of organic matter and the regulation of pelagic–benthic coupling in the Barents Sea.

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1. Introduction

The Barents Sea is a relatively shallow continental sea in the northeastern Atlantic. The Norwegian

* Corresponding author.

E-mail address: chrisr@nfh.uit.no (C. Wexels Riser).

Atlantic Current (NAC) follows the Norwegian shelf break northwards and flows into the Barents Sea, where it divides into two main branches. One branch continues eastward parallel to the Norwegian Coastal Current system (NCC) while the other branch turns north along the Hopen Trench and divides there into smaller branches (Loeng, 1991). In the north, cold Arctic water (ArW) flows into the Barents Sea mainly through the opening between Spitsbergen, Frans Josef Land and Novaja Zemlja. When this cold ArW from the northeast meets the warm Atlantic water (AW) from southwest, a distinct front appears, the polar front (PF). The marginal ice zone (MIZ), the southern extension of which is regularly confined by the PFs in the western and central Barents Sea, is a unique frontal system (Sakshaug and Skjoldal, 1989). It is a highly dynamic area with large seasonal and interannual fluctuations in ice cover and ice transport (Falk-Petersen et al., 2000). The MIZ in the Barents Sea is ecologically important because it supports an extensive phytoplankton bloom in ArW north of the PF (Sakshaug and Skjoldal, 1989; Wassmann et al., 1999). Melt water formation during spring and summer gives rise to strongly stratified surface water that, in concert with light availability and winter-accumulated nutrients, creates conditions for a distinct phytoplankton bloom. The phytoplankton bloom follows the receding ice edge as it moves northwards.

The fate of the produced phytoplankton biomass depends on the intensity of various biological, physical and biogeochemical processes in concert with the composition and structure of the pelagic community (Wassmann, 1998). The phytoplankton biomass may be retained within the water column due to processes such as bacterial degradation, grazing, lysis, physical destruction etc. or may leave the euphotic zone ungrazed and be part of the export production. While the vertical flux of organic matter in the open ocean originally derives from primary production, much of the biogenic flux can be mediated by zooplankton (Smetacek, 1980; Bathmann et al., 1987; Carroll et al., 1998). Zooplankton may reduce the vertical flux of biogenic matter through grazing, but may also enhance it by producing large, fast-sinking, faecal pellets (FPs), which channels the otherwise slowly sinking phytoplankton carbon rapidly to great depths. Vertical flux mediation such as coprophagy, coprophexy and coprochaly adds to the reduction of vertical

particle flux through the water column (Lampitt et al., 1990; Noji et al., 1991). The Barents Sea is one of the most productive regions of the world ocean (Zenkevich, 1963; Sakshaug, 1997) and is well known for its rich but variable abundance of mesozooplankton (e.g. Skjoldal et al., 1987; Tande, 1991; Falk-Petersen et al., 1999) and krill (e.g. Dalpadado and Skjoldal, 1996). Zooplankton FP production and flux feeding (sensu Jackson, 1993) appear therefore to be significant in this arctic region.

The present investigation is part of the Arktisk Lys og Varme (ALV) programme and a continuation of research addressed during PRO MARE (Barents Sea), MARE NOR (subarctic fjords) and OMEX I (north Norwegian shelf). The project attempts to investigate the seasonal and climatic variability of vertical carbon export and its regulation in the Barents Sea, in particular in the MIZ where the greatest variability is predicted (Slagstad and Wassmann, 1996). Within the framework of this project, different aspects of the ecosystem were investigated, including phytoplankton and zooplankton distribution (Ratkova and Wassmann, 2002; Arashkevich et al., 2002, respectively) and the composition of suspended as well as sedimented biogenic matter (Olli et al., 2002). Since zooplankton pellets represent a potentially important transport pathway of surface derived organic matter to greater depths, the present study aims at quantifying the production, retention and export of faecal pellets produced by zooplankton over a variety of temporal and spatial scales. In particular, we endeavoured to quantify group-specific suspended faecal pellets, faecal pellet production and the fate of faecal pellets during vertical export.

2. Materials and methods

Three cruises were carried out with R/V *Jan Mayen* to the Barents Sea, in March and May 1998, and July 1999. Each cruise consisted of two parts. It started with a transect running from 72°30' N towards Kvitøya, with CTD stations every 20 nautical miles (see Fig. 1). The transect crossed the northern part of NCC, AW, PF and ArW. On the return, three to five 24-h stations were selected, where most of the rate measurements were carried out. During each cruise, at least one 24-h station was located in ArW, one in the PF region and at least

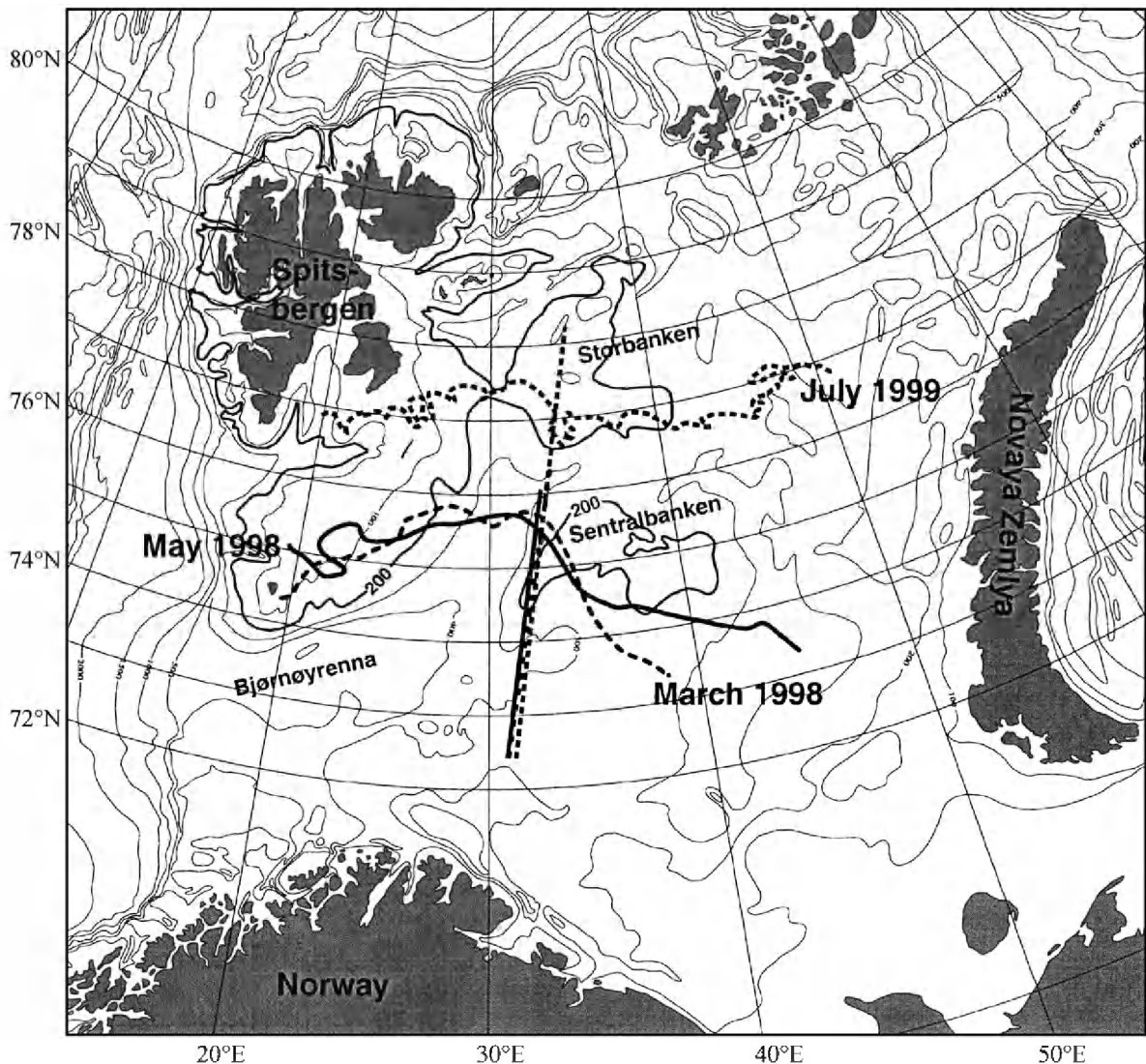


Fig. 1. The Barents Sea with bottom topography and the area of study. The inserted lines denote the trajectories from where the data were obtained. Also shown are the southern distributions of ice during the different cruises.

one station in AW. All data presented are obtained from these main stations (Fig. 2). In Figs. 4 and 6 and Tables 2 and 3, only three main stations per cruise are included. The selected stations were characterised by different water masses, from AW, PF region and ArW. For an overview of the hydrography of the transect, see Reigstad et al. (2002).

Suspended faecal pellets were collected at depths of 10, 30, 75 and 90 m in March 1998 and at 10, 30, 50, 100 and 150 m in May 1998 and July 1999.

Samples were taken twice a day (noon and midnight) with Niskin bottles, and concentrated from 10 l using 20 μ m sieves. The retained pellets were preserved with glutaraldehyde (2% final concentration) for later identification and enumeration.

Vertical flux of faecal pellets was determined for the upper 200 m (at depths of 30, 40, 50, 60, 90, 120, 150 and 200 m), using a Lagrangian approach with a drifting sediment trap rig. At four stations, the rig had to be restricted to 120 or 150 m because of the

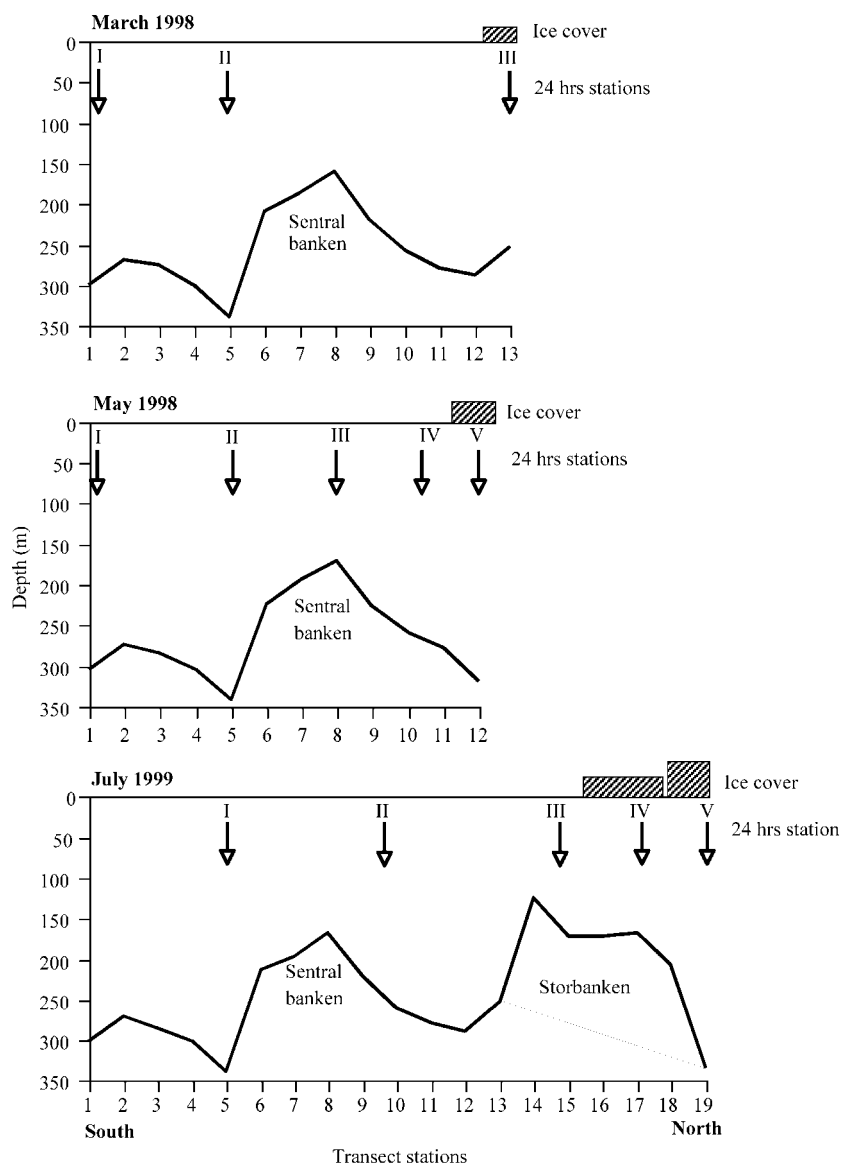


Fig. 2. Topography along the investigated gradient in the central Barents Sea in March and May 1998 and July 1999. Here we focus upon the 24-h stations (Roman numerals).

topography. The material was collected in Plexiglas cylinders of 450 mm length and a diameter of 72 mm (aspect ratio of 6.2). The sediment traps were unpreserved and deployed for ~ 24 h. During the July cruise the deeper sediment traps were calibrated against thorium and the sediment traps were found to have 90–110% sampling efficiency with respect to total particulate organic carbon (Coppola et al., in

press). After recovery, the content of each Plexiglas cylinder was collected and subsamples (100 ml) for microscopic examination were taken and fixed with glutaraldehyde (2% final concentration).

Subsamples from the sediment traps were taken for analysis of particulate organic carbon (POC). POC samples were filtered onto precombusted Whatman GF/F filters, exposed to concentrated HCl fumes for

Table 1

The different categories of faecal pellets identified, distinguished by form and size ((length) × (width))

Faecal pellet type	Size range (μm)	Likely producer
Large cylindrical pellets	(250–1000) × (50–90)	<i>Calanus hyperboreus</i> and older stages of <i>C. glacialis</i> and <i>C. finmarchicus</i>
Medium cylindrical pellets	(150–250) × (30–50)	<i>Metridia</i> spp. and younger stages of <i>Calanus</i> spp.
Small cylindrical pellets	(50–150) × (10–30)	Small copepods
Filiform pellets		Krill (euphausiids)
Oval (ellipsoid) pellets	(100–300) × (60–150)	Larvaceans

The likely producers are also indicated.

the removal of carbonates, and analysed with a Lee-man Lab 440 elemental analyser (Wassmann, 1991). Three replicate filters were analysed from each depth. Larger swimmers were removed from the filters if present, but were in general a minor problem (in average 1.8 copepod per sample including nauplii, based on microscopy counts).

Mesozooplankton for FP experiments were collected with vertical net tows (at low velocity) from 100 m to surface, using a 58 cm diameter WP-2 net (180-μm mesh size). Immediately after retrieval, zooplankton was gently transferred from the cod end into 10 l of surface water to dilute the zooplankton. The copepod fraction was then gently size-fractionated into 500–1000 μm (medium fraction) and >1000 μm (large fraction), using sieves. For each size fraction, three experimental bottles and one control bottle (0.9 l) were filled with water from 10 m depth. In each experimental bottle, three to five copepods were placed into a suspended insert with mesh on both ends, which allowed the pellets to fall through and prevented coprophagy and/or similar destruction of the pellets by the copepods (for details of the methods, see Urban-Rich et al., 1999). The experiments were carried out in dim light in an on-deck incubator for 3 h. At the end of the incubation experiment, the copepods were removed. The contents from the experimental bottles and the control bottles were sieved through a 20 μm Nitex mesh and preserved with glutaraldehyde (2% final concentration) for subsequent quantification.

Vertical zooplankton net hauls for abundance and species composition were obtained at noon and midnight from ca. 10 m above the bottom to the surface, using a WP-2 net (mesh size 180 μm). WP-2 nets have frequently been used for quantitatively collecting zooplankton, and a comparison of performance of WP-2 and MOCNESS shows that it is valid to use data from

WP-2 nets when calculating mean biomass and composition of copepods (Gjøsæter et al., 2000). WP-2 is less effective than other sampling gear (i.e. MOCNESS) in sampling large motile organism such as krill (Gjøsæter et al., 2000), so data on biomass and composition of krill and other macrozooplankton are not included. The mesozooplankton data used for calculating FP retention is presented in Arashkevich et al. (2002).

All the zooplankton faecal pellets were enumerated using a dissecting microscope or inverted microscope with phase contrast and ocular micrometer (Zeiss IM 35). The length and width (equally to the diameter) of the pellets were measured and the faecal pellet volume (FPV) calculated using appropriate stereometrical configurations according to Edler (1979). The pellets were classified according to their shape as cylindrical, filiform or ellipsoid. The cylindrical pellets were separated into different size classes according to the length and width of the pellets (Table 1). The cylindrical FPs were separated from the filiform FPs on the basis of following features: (1) The cylindrical FPs from copepods have a well-developed peritrophic membrane that forms either rounded or elongated end of the pellets; (2) the size (total length and width) and the width/length ratio; (3) general appearance—euphausiid pellets usually have a specific “striated” structure. A volumetric carbon conversion factor of 69.4 μg C mm⁻³ (Riebesell et al., 1995) was applied to estimate the faecal pellet carbon (FPC).

Standing stock of FPC was calculated according to Eq. (1):

Integrated suspended FPC (FPC m⁻²)

$$= \sum_{i=1}^5 (((pd_{i+1}) - pd_i)(FPC_i + (FPC_{i+1}))/2) \times 1000 \quad (1)$$

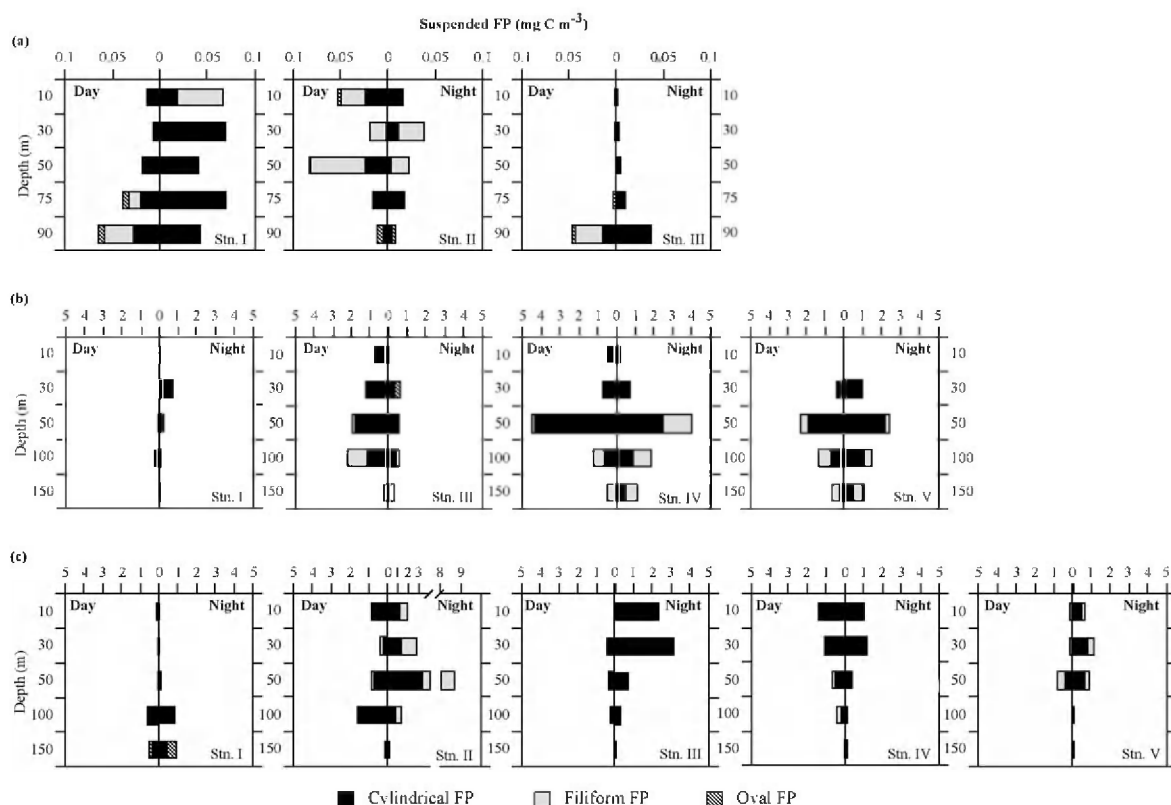


Fig. 3. Spatial and day/night variation in biomass and composition of FPs at the 24-h stations in (a) March 1998, (b) May 1998 and (c) July 1999.

where pd_i is the depth of sampling (1 = 10 m, 2 = 30, 3 = 50...) and FPC_i is the faecal pellet carbon (FPC l^{-1}) at depth i .

Vertical flux of FPC was calculated according to Eq. (2):

$$\text{Vertical flux of FPC (mg C m}^{-2} \text{ day}^{-1}) = pc \times fv \times fa/d \quad (2)$$

where pc is the total FPC in the analysed sediment trap volume, fv is a volume factor (total volume of the sample/the analysed volume), fa is an area factor ($1/\text{sampling area of the sediment trap}$) and d is the exposure time (days).

Retention rates of FPs were calculated according to Eq. (3):

$$\text{FPC retention (\%)} = (A - B) \times 100/A \quad (3)$$

where A is the total FPC production (FPC production copepod $^{-1}$ day $^{-1}$ multiplied by the abundance of copepods m^{-2} (0–90 m) and B is the FPC sedimentation rate (mg C m^{-2} day $^{-1}$) at 90 m depth.

3. Results

3.1. Suspended faecal pellets

The biomass of FPs was low in March and most of the time well below 0.1 mg C m^{-3} (Fig. 3). No clear differences in vertical distribution of FPs were observed between day and night sampling. Low concentrations were found both in ArW north of the PF region and in AW. Up to five times higher FP concentrations were observed in May compared to March, but no difference in composition or total FPC were found

between day and night sampling (Fig. 3). The maximum concentration of FPs in May (4.8 mg C m^{-3}) was found in ArW just below the chlorophyll maximum. The FP fraction was dominated by large cylindrical pellets, produced by larger calanoid copepods. Minor standing stocks of FPs were observed moving towards the PF region and into AW (Fig. 4). The maximum biomass of FPs in July (9 mg FPC m^{-3}) was found in the PF region at 50 m depth. Again, no principal differences in FP biomass were observed between day and night sampling except for one single maximum in the PF at night, caused by filiform FPs produced by krill. In AW a deep maximum in biomass of FPs was observed, probably caused by ontogenetic migration of copepods and a significant fraction of oval FPs, produced by appendicularians. The lowest standing stock of FPs was again observed in AW. The highest seasonal variations in standing stock of FPs was observed in the PF region, while the seasonal variation in AW was relatively low (Fig. 4).

3.2. Vertical flux of faecal pellets

The vertical flux of FPs was very low in March ($<5 \text{ mg C m}^{-2} \text{ day}^{-1}$). The highest FP flux was found south of the PF region at depths between 50 and 100 m. Below 100 m depth the FP flux was close to zero (Fig. 5). In May, high vertical fluxes of FPs were

measured in the northern part of the transect (100–150 $\text{mg FPC m}^{-2} \text{ day}^{-1}$), with a maximum just below the chlorophyll maximum. Filiform pellets produced by krill dominated the vertical FP flux in ArW, but also large cylindrical FPs produced by *Calanus* spp. were of significance (Fig. 5). High sedimentation rates of FPs were also found in the PF, dominated by krill pellets. Relatively low FP flux was measured in AW in May ($<50 \text{ mg FPC m}^{-2} \text{ day}^{-1}$). In July the flux of FPs in ArW (northernmost station) was high, but the maximum sedimentation rates were measured in the PF region ($\sim 250 \text{ mg FPC m}^{-2} \text{ day}^{-1}$ at 60 m). Low FP fluxes were recorded in AW, but at 150 m depth an increase caused by oval FPs, produced by appendicularians was encountered.

3.3. Faecal pellet production by copepods

In March the pellet production rate by copepods, larger than $500 \mu\text{m}$, was very low at all stations ($<7 \text{ FP copepod}^{-1} \text{ day}^{-1}$). The experimental design used, was inadequate at such low production rates. Thus, the results are not shown and will not be discussed in detail.

In May, the FP production rates by copepods ranged from 20 to 55 pellets $\text{copepod}^{-1} \text{ day}^{-1}$. There were no clear differences in the number of pellets produced by the medium ($500\text{--}1000 \mu\text{m}$) and the large ($>1000 \mu\text{m}$)

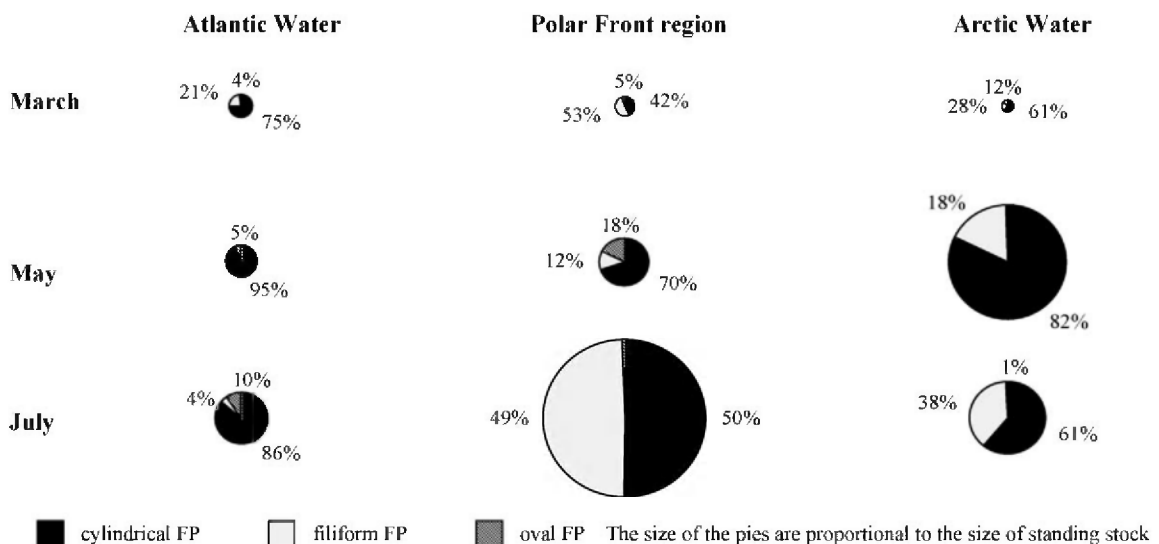


Fig. 4. Seasonal and spatial variation in biomass and composition of FPs (integrated from surface to 100 m depth).

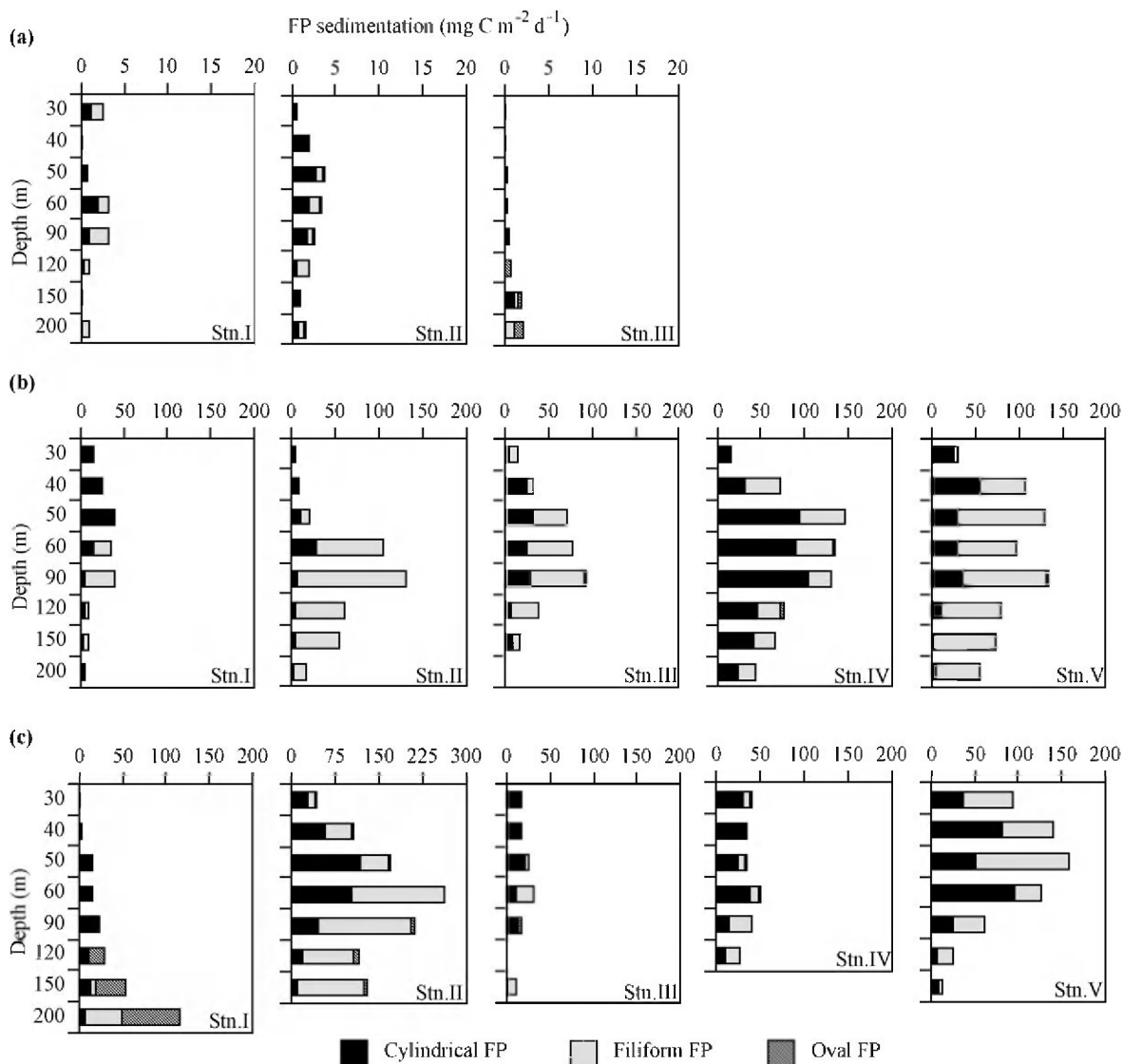


Fig. 5. Spatial variation in FP sedimentation ($\text{mg C m}^{-2} \text{day}^{-1}$) at different depths in (a) March 1998, (b) May 1998 and (c) July 1999. The different pellet categories are also shown.

copepod fraction (Fig. 6). The differences between the locations were also small, although the production rates tended to be highest in AW. The average production rate was ~ 35 pellets copepod $^{-1} \text{day}^{-1}$.

The maximum FP production rate in July was measured in AW, with $\sim 80 \pm 16$ pellets copepod $^{-1} \text{day}^{-1}$ (large copepods). The pellet production rate decreased northwards and in ArW production was only $\sim 30 \pm 7$ pellets copepod $^{-1} \text{day}^{-1}$. The spatial

variation in pellet production was less pronounced among the medium-sized copepods and pellet production ranged between 40 and 50 pellets copepod $^{-1} \text{day}^{-1}$ (Fig. 6).

3.4. Faecal pellets and vertical flux of organic carbon

In March, FPs played a minor role for the vertical flux of total POC out of the euphotic zone. FPC

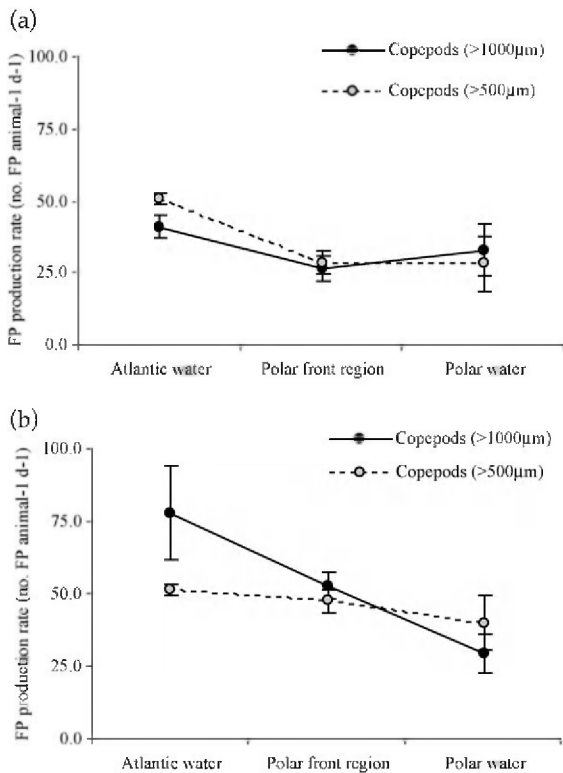


Fig. 6. Faecal pellet production rates (FP copepod⁻¹ day⁻¹) by large (>1000 μ m) and medium-sized copepods (500–1000 μ m) in (a) May and (b) July.

explained only 2–8% of total POC export at 90 m depth (Table 2), with the highest contribution of FPs in the PF region. In the same period the average contribution of FPC to total POC flux was \sim 3% at 150 m depth. In May the FPC fraction of total POC at 90 m depth was 40% in ArW, but decreased southwards to 17% in the PF region and 4% in AW. In July the FPC/POC fraction was still high and ranged from 30% in the PF region to 40% in ArW, but remained low in AW with \sim 8%.

Table 2
FPC contribution to total POC sedimentation (%) at 90 and 120 (numbers inside parenthesis) m depth

	Atlantic water	Polar front region	Arctic water
March	5 (1)	8 (7)	2 (2)
May	5 (2)	18 (5)	42 (27)
July	8 (13)	40 (41)	34 (18)

Table 3

Daily FPC production, sedimentation, export and retention by the copepod community (medium and large-sized copepod)

	FPC production (mg m ⁻² day ⁻¹)	FPC sedimentation (mg m ⁻² day ⁻¹)	FP export (%)	FP retention (%)
<i>May</i>				
Atlantic water	104	4	4	96
Polar front region	43	27	63	37
Arctic water	62	32	52	48
<i>July</i>				
Atlantic water	60	18	30	70
Polar front region	104	42	40	60
Arctic water	20	12	60	40

FPC export and FPC retention (as percentage of total production) in May and July at different locations.

3.5. Faecal pellet retention potential

In May the calculated retention potential of copepod FPs in the upper 90 m ranged from 96% in AW to 37% in the PF region (Table 3). The retention potential in the northernmost part of the transect was \sim 49%. These calculations imply that <5% of the FPs produced in AW sank to 90 m depth. In contrast, \sim 50% of the FPs produced north of the PF reached the same depth. In July the scenario was similar to that in May the previous year, but with higher FP export in AW. The highest pellet retention was again found in the southernmost part of the transect (70%) and decreased towards north to 60% in the PF region and 37% in the ice edge zone (Table 3).

4. Discussion

The patterns of phytoplankton production and sedimentation in the Barents Sea are strongly influenced by the seasonal and interannual dynamics of sea ice (Rey and Loeng, 1985). The spring bloom in the southern Barents Sea only results in moderate phytoplankton accumulation due to extensive vertical mixing (Sakshaug, 1997; Wassmann et al., 1999). The bloom takes place in May/June and is usually dominated by diatoms (e.g. *Chaetoceros socialis*) and *Phaeocystis pouchetii* colonies (Wassmann et al., 1999; Ratkova and Wassmann, 2002). Phytoplankton growth starts already in late March, but stabilisation of

surface water by solar radiation is a slow process in these areas and the increase in phytoplankton biomass is hence slow. North of the PF the stabilisation of surface water is much stronger and develops faster due to sea-ice melting. This implies that the spring bloom may appear earlier north of the PF than in AW, that biomass accumulation in the upper layers is substantial and that most of the annual primary production occurs within a time window of only a few months (Sakshaug, 1997; Hegseth, 1998). High zooplankton abundance will strongly mediate the biogenic flux deriving from primary production (Wassmann, 1998). The seasonal and interannual variation in zooplankton abundance in the Barents Sea is closely linked to physical and biological processes typical for high latitude ecosystems (Skjoldal et al., 1987; Pedersen et al., 1995). The seasonal variation in composition, abundance and feeding activity of zooplankton strongly influences the pelagic–benthic coupling by determining the quality and quantity of the sinking organic matter at a certain depths.

4.1. Suspended faecal pellets: seasonal and spatial variation

During the March cruise, the nutrient concentrations clearly indicated a prebloom situation. Nutrients and chlorophyll were uniformly distributed and temperature and salinity showed low stratification (Reigstad et al., 2002). The low food abundance and the fact that most of the mesozooplankton occupied the layers below 100 m in March (Arashkevich et al., 2002) explains the low suspended biomass of FPs (Fig. 3a). Prominent species in this region such as *Metridia longa*, *Calanus finmarchicus* and *Calanus glacialis* are usually not found in surface water before April/May (Pedersen et al., 1995). The zooplankton was presumably still in the overwintering mode and large-celled phytoplankton was scarce (Ratkova and Wassmann, 2002).

The standing stock of FPs was much higher in May compared to March (Fig. 3b) matching the increased food availability. The highest biomass was observed north of the PF, just below the chlorophyll maximum. The absence of day/night variations in vertical distribution of FPs suggests that the zooplankton stayed day and night in the upper 100 m to graze and produce FPs. The diurnal vertical distribution of mesozoo-

plankton clearly shows that this was actually the case (Arashkevich et al., 2002). The biomass of pellets was totally dominated by large cylindrical pellets, produced by copepods such as *Calanus* spp. The standing stock of FPs in the upper 100 m decreased significantly south of the PF (Fig. 4), this in spite of higher mesozooplankton abundance and biomass and the fact that the faecal pellet production was high in AW (Fig. 6). This low standing stock of FPs in AW must have been caused by physical, biological or chemical processes that effectively removed or destroyed FPs soon after they were produced.

Nutrients were strongly depleted in the surface water during the cruise in July, suggesting a post-bloom situation with pronounced stratification in the upper 30 m along most of the transect (Reigstad et al., 2002). The highest suspended FP concentrations were located in the upper 50 m of the transect corresponding to the mixing depth (30–50 m) where food availability were highest. The only exception was the southernmost station where the highest concentration of FPC was found below 100 m both day and night. This deep maximum of FPs could be due to ontogenetic migration of *C. finmarchicus* to greater depth (Arashkevich et al., 2002). A significant fraction was oval FPs, probably produced by appendicularians.

4.2. Vertical flux of faecal pellets: seasonal and spatial variation

Previous investigations in ArW have shown that low herbivore biomass at the end of the winter period and the rapid increase in food supply during the spring bloom may cause extensive vertical export of ungrazed phytoplankton cells (e.g. Wassmann et al., 1991; Wassmann and Slagstad, 1993). This period is frequently followed by reduced losses due to the advent of a more complex zooplankton community, resulting in higher grazing pressure. The low FP sedimentation rates in March reflect very low FP production rates and concomitant low concentrations of suspended FPs (Fig. 4). The low suspended chl-*a* and POC concentrations (Olli et al., 2002) suggests that low FP production was caused by shortage of food and that the copepods probably relied on stored energy resources (Falk-Petersen et al., 1999; Paster-nak et al., 2002).

The high vertical export of FPs in May, especially in the northernmost part of the transect, was mainly due to large vertical flux of large filiform pellets produced by krill. In addition, the vertical export of copepod FPC increased strongly in May, in particular at the ice edge. This increase in vertical FPC export resulted from increased FPC production (Fig. 6) and FPC standing stock (Figs. 3b and 4), and reflects the accumulation of phytoplankton carbon (Ratkova and Wassmann, 2002) and POC (Olli et al., 2002) in the upper layer in May. Vertical FPC export from the upper layers in the MIZ (up to $150 \text{ mg C m}^{-2} \text{ day}^{-1}$) suggest extensive grazing in the seasonally ice-covered region.

Also in July, copepod and krill FPs comprised the vast majority of the vertical FPC flux (Fig. 5). In the south, FPC export was more confined to waters below 50 m while in the north vertical FPC export was encountered in the upper layers down to 60 m depth. This reflects both the vertical distribution of small-celled plankton (Ratkova and Wassmann, 2002) and zooplankton (Arashkevich et al., 2002). While phytoplankton biomass in July, as reflected by chl-*a*, was only 10–50% of that recorded in May, the total biomass of pico, nano- and microplankton was similar (Ratkova and Wassmann, 2002). A substantial fraction of the smaller cells was probably heterotrophic (Verity et al., 2002). The similar access to pico, nano- (through protozooplankton?) and microplankton cells and larger protozooplankton is reflected by similar vertical FPC export in May and July, despite of the differences in the plankton community structure. This implies that zooplankton had adequate access to small plankton cells, but a smaller fraction of phytoplankton, suggesting that zooplankton was not strictly herbivorous in summer.

4.3. The unresolved role of krill for vertical flux regulation in the Barents Sea

The patchy distribution of krill and the scarcity of their rapidly sinking FPs (several hundred meters per day; e.g. Fowler and Small, 1972; Cadée et al., 1992) results in difficulties to sample their suspended FPs adequately, in particular when clogging of screens (by *P. pouchetii* colonies) prevents the sampling of large water volumes. Consequently, the standing stocks of filiform krill pellets in the present investigation are

probably underestimated. Sediment traps, on the contrary, integrate vertical export in time (24 h) and space (Lagrangian-type movement of rig and advection of water), which results in more reliable estimates.

Based upon earlier reports on the distribution of krill species such as *Thysanoessa inermis* and *Thysanoessa longicaudata* in the Barents Sea, it was assumed that krill would only be of significance in the southern region of the transect, in particular the southwestern shelf break (e.g. Dalpadado and Skjoldal, 1991, 1996). Thus, a WP-2 net, suitable for adequate sampling of copepods, was applied during the present investigation, and FP production experiments for krill were not planned. This was obviously a misconception as the filiform FPs from krill contributed significantly to the suspended biomass and vertical carbon export at all seasons and throughout the central and northern Barents Sea (Fig. 5). As WP-2 nets do not sample krill quantitatively, no reliable standing stock estimates of krill exist (Arashkevich et al., 2002). The lack of quantitative abundance data of krill results in the dilemma that we are unable to assess the role of krill for vertical flux regulation in the Barents Sea. Thus, the strength of the retention or coprophagous filter (sensu González and Smetacek, 1994) for krill FPs cannot be approximated. It has been suggested that highly effective retention filters can be short-circuited by krill (Wexels Riser et al., 2001; Wassmann et al., 2002). Krill can thus deplete surface water for biomass and nutrients and cause an instantaneous pelagic–benthic coupling. We suggest that this is partly the case during the productive season and throughout the Barents Sea.

4.4. The fate of faecal pellets

Although some FPs produced in the surface layer reach the deep ocean intact, recent studies indicate that the likely fate of copepod faecal pellet is rather consumption, fragmentation and destruction than vertical export (González et al., 2000; Wexels Riser et al., 2001), as hypothesised by Smetacek (1980) two decades ago.

The present combined analysis of concomitant FP production of the medium- and large-sized copepods and vertical export rates of their respective FPs enables the direct calculation of seasonal and spatial differences in FP retention. It is obvious that powerful

mechanisms for FP retention exist: 37–96% of the produced copepod FPs were retained in the upper 100 m (Table 3).

Medium- and large-sized copepods produce FPs which usually have a residence time in the upper 100 m of less than 2 days (Smayda, 1969; Komar et al., 1981). This makes significant disintegration of FPs due to microbial degradation unlikely (Turner and Ferrante, 1979; Gowing and Silver, 1983). The fact that a peritrophic membrane surrounds freshly produced copepod FPs also makes it less likely that the massive retention is caused by physical destruction or microbial degradation. This suggests that flux feeding may be one of the dominating retention mechanism and the most likely candidates are coprophagy, coprorhexy and coprochaly (Smetacek, 1980; Lampitt et al., 1990; Noji et al., 1991). Flux feeding implies efficient detection and rapid response by animals encountering relatively infrequent particles, which sink with a high velocity (e.g. Kiørboe and Visser, 1999; Svensen and Kiørboe, 2000). Most of the zooplankton was found in the 50–100 m layer, and the vertical flux profiles clearly indicate that a large fraction of the produced FPs were removed at depths <100 m (Fig. 5).

The fate of FPs in the Barents Sea appears to be manifold. Copepod FPs are predominantly recycled within the upper 100 m when phytoplankton concentrations are low. Increased FP export takes place during phytoplankton blooms, but even during blooms approximately 40% of the FPs were retained.

5. Conclusion

The pelagic community in the Barents Sea has obviously developed functional modes to reduce the loss of “potential food” to a minimum. This concept implies that the fraction of the produced biomass, which is exported out of the upper layer, can be regarded as a leakage of the retention filter. The efficiency of the retention filter is not uniform throughout the Barents Sea, between seasons or years, but probably depending on food availability, the zooplankton community structure, patchiness and feeding efficiency. The high sinking velocity of krill FPs most likely gives rise to low FP retention. The retention filter was extraordinarily efficient in AW in May 1998

where it removed 96% of the produced copepod FPs (in the upper 90 m), but its efficiency decreased northwards to about 50% in ArW. The retention of medium- and large-sized FPs in July was lower and decreased also northwards from 70% in AW to 40% in ArW. The present investigation clearly suggest spatial as well as temporal variation in FP production and retention, which is of importance for the patterns of vertical flux of biogenic matter. Zooplankton has thus a significant role in vertical flux regulation in the Barents Sea by grazing or destroying fast-sinking particles such as large phytoplankton cells, FP aggregates and FPs.

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