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ORIGINAL PAPER

Export or retention? Copepod abundance, faecal pellet production and vertical flux in the marginal ice zone through snap shots from the northern Barents Sea

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Abstract The balance between faecal pellet (FP) production and destruction that accelerates or diminishes vertical export has an effect on pelagic-benthic coupling, but is inadequately known. Production, export and retention of copepod FP were investigated in the marginal ice zone (MIZ) of the northern Barents Sea in July 2003. Older stages of *Calanus finmarchicus* and *C. glacialis* dominated the copepod biomass and FP production experiments revealed that more than 90% of the FP were produced in the upper 50 m where most of the copepods were located both day and night. Copepod pellets typically made up ~10% of the vertical particulate organic carbon flux, and significantly less than what was produced by the copepod community. This implies a variable but significant retention of pellets. We suggest that retention of FP is caused partly by the zooplankton themselves and that retention of FP is the rule rather than the exception in the Barents Sea, particularly during non-bloom scenarios.

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Introduction

Vertical flux of particulate organic carbon (POC) in the Barents Sea is temporally and spatially highly variable, ranging from 20 to 1,500 mg m^{-2} d^{-1} in the upper 200 m (Olli et al. 2002). Periods of high vertical fluxes are often related to the pronounced spring bloom frequently observed in the marginal ice zone (MIZ), which is initiated by ice melt stratification and sunlight. The retention capacity of the pelagic system determines how much of the spring bloom is exported. Only a minor fraction of the export production is injected into layers >200 m (Wassmann 1998; Noji et al. 1999; Turner 2002; Wassmann et al. 2003), and that the largest reduction in POC export from the euphotic zone takes place in the upper 100 m (Wassmann et al. 2003; and references therein). The composition of the settling biogenic matter is also known to differ, depending on species composition and structure of the food web (Bathmann et al. 1990; Olli et al. 2002). The POC flux may be dominated by diatoms and their debris which are generally associated with export systems (Wassmann et al. 2003), or auto- and heterotrophic flagellates, faecal pellets (FP) and/or detritus that are characteristic for recycling systems. Vertical flux regulation is thus of utmost significance for the biogeochemical cycling in the upper layer.

Zooplankton both accelerate and diminish the vertical flux of biogenic matter, depending on abundance and composition of key zooplankton species. While single cells of phytoplankton may have sinking rates of some few meters (Bienfang and Harrison 1984; Peperzak et al. 2003), the same cells packed into larger zooplankton FP may sink several 100 m per day (Komar et al. 1981; Cadée et al. 1992; Turner 2002).

The latter reduces the pelagic residence times of biogenic matter and exposure to physical, chemical and/or biological degradation in the upper layers. On the other hand, copepods may reduce vertical flux through grazing and/or destruction of organic matter which otherwise would have settled ungrazed toward bottom. Vertical flux mediation such as coprophagy, coprorhexy and coprochaly also adds to the reduction of particle flux through the water column (Sasaki and Nishizawa 1981; Noji et al. 1991; Gonzalez and Smetacek 1994; Sampei et al. 2004). Thus the balance between FP production and destruction that accelerates or diminishes vertical export and has an effect on pelagic-benthic coupling, is inadequately known.

We conducted several field experiments in the northern Barents Sea MIZ to study the impact of key zooplankton species on vertical flux regulation, with emphasis on the role of FP. The Barents Sea is particularly suitable for studying interactions at the copepod community level since relatively few copepod species make up a major component of biomass and abundance (Falk-Petersen et al. 1999; Arashkevich et al. 2002). Three *Calanus* species are found in the Barents Sea (*Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus*) and *C. finmarchicus* and *C. glacialis* often make up a major part of the mesozooplankton biomass. Other copepod genus of importance, in terms of biomass and/or abundance, includes *Metridia*, *Pseudocalanus, Microcalanus* and *Oithona*. Previously FP production experiments in the Barents Sea have been conducted with water from 10 m depth only, assuming that the copepods were feeding where food was more abundant (Wexels Riser et al. 2002). The resulting vertical flux profiles suggested an increased relative contribution of FPC to the POC export below 40–60 m depth. This suggests increased feeding and FP production activity at the 30–50 m depth interval. Therefore, in the present study we designed experiments that investigated more closely the vertical variability in FP production as related to vertical flux attenuation in the upper water layers. Improved vertical resolution in FP production, as well as zooplankton sampling, provided us with better total FP production estimates. Combined with vertical flux measurements the depth where the potential recycling of FP takes place can be detected.

We ask the following questions: (1) Does *Calanus* distribution and FP production vary with depth and with food availability? (2) Is the community FP production most sensitive to copepod abundance or individual FP production? (3) Is the vertical export of FP reflecting the production in the overlaying waters? and (4) Does *Calanus* FPC significantly add to the vertical export of POC?

Material and methods

Hydrography and pigments

Experiments were conducted and samples were collected at stations I–IV (Table 1) during a cruise with R/V *Jan Mayen* in July 2003 to the central northern Barents Sea (Fig. 1). Conductivity, temperature, depth (CTD) profiles were made at each station using a standard Sea-Bird SBE9 CTD-rosette system. Water from 1, 5, 10, 20, 30, 40, 50, 60, 90, 120, 150, 200 m and fluo-

Table 1 Sampling date, position, water depth, depth of maximum chlorophyll *a* and ice cover at station I–IV

Station	Date	Position	Water depth (m)	Chl *a* max (m)	Ice cover
I	10.07.03	75° 33.37N 30° 13.64E	361	37	4–7/10
II	13.07.03	78° 13.95N 27° 18.36E	317	24	4–7/10
III	15.07.03	79° 02.35N 25° 38.21E	212	28	4–7/10
IV	18.07.03	77° 03.39N 29° 09.67E	229	10	4–7/10

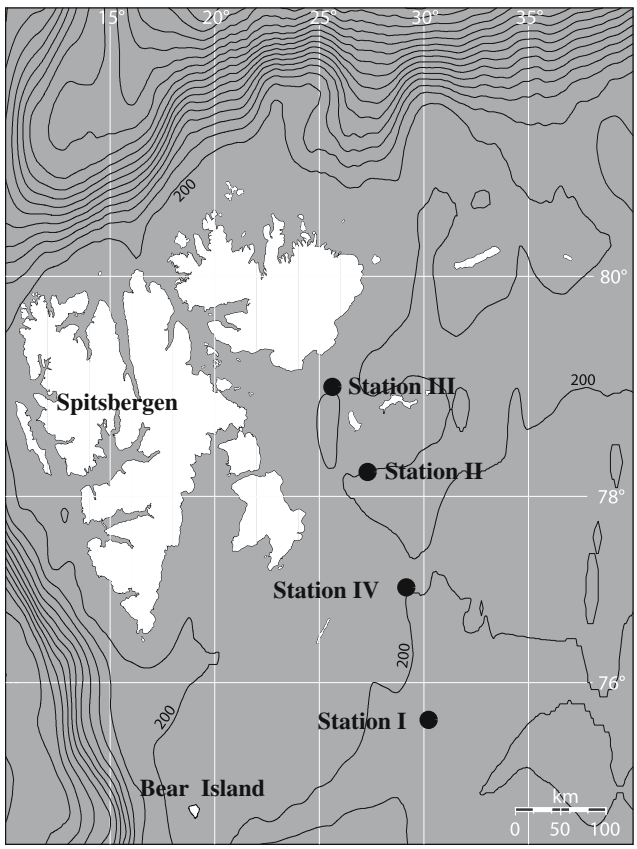

Fig. 1 Map of the north-western Barents Sea with sampling stations I, II, III and IV indicated

rescence maximum were sampled and subsamples (50–100 ml) for analysis of chlorophyll *a* (Chl *a*) were taken. After filtration on GF/F filters and overnight methanol extraction at room temperature (Holm-Hansen and Riemann 1978), Chl *a* concentrations were analysed onboard using a Turner Design AU-10 fluorometer, calibrated with pure Chl *a* (Sigma, C6144).

Copepod abundance and species composition

Vertical zooplankton net hauls for abundance and species composition were obtained by a multinet (180 μm, 0.25 m^2 mouth opening) equipped with five closing nets. Samples were obtained twice a day (about noon and midnight), from 0 to 20 m (upper layer, UL), 20–50 m (middle layer, ML) and 50–90 m (deeper layer, DL). In addition two deeper layers were sampled (100–150 and 150-bottom). The filtered volume was calculated from flow meter readings inside the net aperture. The samples were preserved in buffered formalin (4% final concentration).

All species and stages were quantified and their abundance was calculated. For the assessment of total biomass, dry weight was calculated using published individual dry weights and weight/length relationships, according to Hirche and Mumm (1992), Richter (1994) and Karnowsky et al. (2003).

Faecal pellet production experiments

Incubation water for FP production experiments was taken at three depths in each layer and pooled to represent the three different layers [5, 10 and 15 m (UL), 20, 30 and 40 m (ML) and 50, 60 and 90 m (DL)]. The water was mixed and carefully pre-screened through a 180-μm mesh to remove larger grazers. Subsamples were taken for Chl *a* measurements and analysed as described for suspended Chl *a*.

Calanus spp. (hereafter referred to as *Calanus*) for FP production experiments were collected with vertical net tows from UL, ML and DL, using a 0.5 m diameter WP-2 net (180 μm mesh size) with a non-filtering cod-end. Immediately after retrieval, copepods were gently transferred from the cod-end into 25 l of surface water to dilute the copepods. The dominating older stages of *Calanus* (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus* stage CIV–CVI) were picked out gently and active animals with no visible damage were incubated in chambers (0.9 l) containing a suspended insert with a false bottom (180 μm mesh size) to prevent copepod grazing on the produced FP. The proportion of each stage and species used in the experiments varied according to their relative abundances. Four replicates from each depth layer containing 3–5 animals were incubated for approximately 6 h and subsamples from the incubation water were taken to correct for suspended FP introduced via the incubation water. To ensure that no day/night differences in copepod grazing behaviour took place, experiments were conducted both at noon and midnight at Stn. II. The remaining experiments were conducted at night. The experiments were carried out in dim light in a temperature controlled room (0–2°C) close to in situ temperature. At the end of each incubation experiment, the contents from the experimental bottles were sieved through a 20 μm Nitex mesh and the FP were preserved with buffered formalin (2% final concentration) for subsequent quantification.

Laboratory treatment of FP and FP carbon measurements

All zooplankton FP were enumerated and sized (length and width) using dissecting or inverted microscopes with phase contrast and ocular micrometers (Zeiss IM 35). The volume of the FP was calculated using appropriate stereometrical configurations according to Edler (1979). Changes with time in FP volume due to fixation were investigated for fresh and stored samples. The FP produced during the experiments were categorised as entire pellets, end pieces or mid-parts. The total numbers of pellets were calculated by adding the sum of end pieces divided by 2 to the whole pellets. Mid-parts contributed to FP volume but not to the number of pellets. The FP from the sediment traps were classified according to their shape as cylindrical, filiform or ellipsoid. The cylindrical FP produced by copepods were separated from the filiform FP produced by krill based on different criteria. Krill FP can be separated from copepod pellets based on their general appearance – euphausiid pellets usually have a specific "striated" structure. Krill pellets also tend to be more fragile and are usually broken in several smaller fragments without elongated tips, characteristic for *Calanus* FP, and the diameter of krill pellets is usually significantly larger than that of the copepods.

To convert FP volume to FP carbon (FPC), conversion factors for different FP categories of freshly-produced FP were determined during fieldwork in the northern Barents Sea in July 2004 and May 2005. The pellets were rinsed three times in filtered seawater before filtration onto pre-combusted GF/F filters and analysed as described below for POC. *Calanus glacialis* FP were collected (n = 36–70) and measured from animals that were allowed to defecate for approximately 2 h after sampling. FP from *Oikopleura* were collected

and measured in each of five replicates. *Gammarus wilkitzkii* were collected by divers and allowed to defecate before FP were collected and then measured in each of six replicates. To convert krill (euphausiid) FP to carbon, a conversion factor established for the sub-Arctic Norwegian fjord, Balsfjord, in April 1997 was used. Krill FP were collected, from animals that were allowed to defecate for approximately 2 h after sampling, rinsed and sized before analysed as described for POC.

Vertical flux measurements

A sediment trap array was attached to a free drifting ice floe with traps sampling the upper 200 m for ~24 h at 20, 30, 40, 50, 60, 90, 120, 150 and 200 m depth. At station III, the deepest trap was located at 150 m. Sampling was carried out in a semi-Lagrangian manner following the drifting ice flow. All water column sampling was conducted in direct vicinity of the drifting sediment trap array. Vertical flux of FP and POC was determined for all depths, using transparent parallel plexiglas cylinders of 450 mm height and a inner diameter of 72 mm (aspect ratio = 6.2) mounted on a gimballed frame. The sediment traps used in this study (KC maskiner og laboratorieudstyr, Denmark), have previously been tested in the Barents Sea, and ^{234}Th data measured in suspended and trapped particles were used to estimate the catchment efficiency, confirming the accuracy of the sediment trap measurements (Coppola et al. 2002). No baffles were used in the cylinder opening and no fixatives were added to the traps prior to deployment. After recovery, the content of each plexiglas cylinder was collected and sub-sampled for different analyses.

Subsamples for analysis of POC were filtered onto pre-combusted Whatman GF/F filters and frozen at −20°C. Prior to analyses with a Leeman Lab 440 elemental analyser, the filters were exposed to concentrated HCl fumes for the removal of carbonates. Three replicate filters were analysed from each depth. For microscopic examination of FP, subsamples were fixed with buffered formaldehyde (2% final concentration) and analysed as described above. Vertical flux of FPC at each depth was calculated and related to the total production of similar-sized FPC above the trap (mg C m^{-2} d^{-1}). The FP retention was defined here as the discrepancy between the estimated daily FP production by older *Calanus* and the daily rates exported as measured by sediment traps.

Results

Water mass characteristics and phytoplankton bloom development

The southernmost station (Stn. I), located in the southern part of Hopen Deep, was clearly a part of the southern Barents Sea Atlantic domain. Sea ice and cold surface water of low salinity indicated that ice and Arctic Water (ArW) had drifted across the Polar Front and thus ice was melting on top of Atlantic Water (AW) (Fig. 2a, b). Vertical distribution of Chl *a* peaked at 37 m depth (2.4 µg Chl *a* l^{-1}) (Fig. 2c). Station IV located in the far north of the Hopen Deep had three distinct layers. The upper 10 m were characterised by cold, low-salinity water, followed by a pycnocline and a layer of ArW. Below 100 m a new pycnocline separated the ArW from deeper water of Atlantic origin (C. Kivimäe et al., submitted). The Chl *a* distribution at this station had maximum concentrations in the upper 20 m (~2 µg Chl *a* l^{-1}) decreasing rapidly with depth. Station II was located in the basin of Kong Karls

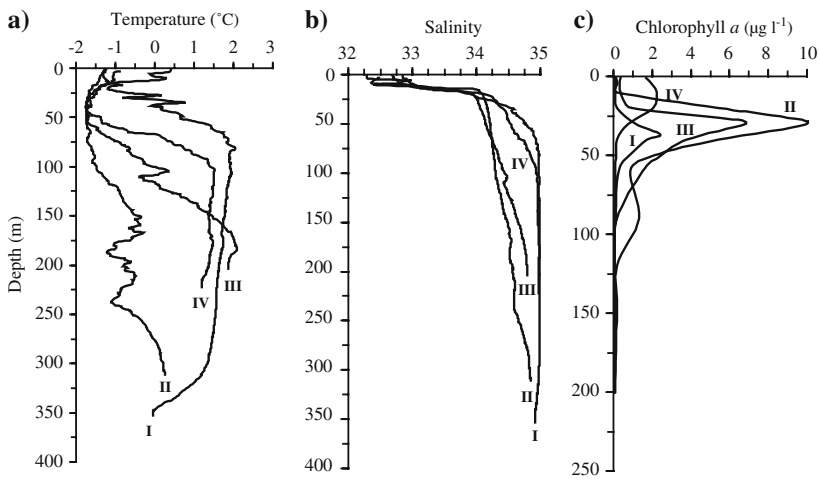

Fig. 2 Vertical distribution of **a** temperature, **b** salinity and **c** chlorophyll *a* at station I, II, III and IV

Land. This station was most heavily influenced by ArW, with three layers similar to that of Stn. IV, but water of Atlantic origin was found only at depths below 250 m (C. Kivimäe et al., submitted). Suspended Chl *a* concentrations of up to 10 μg Chl *a* l^{-1} were measured at 30 m depth (Fig. 2c). Station III in Erik Eriksen Strait was the northernmost station. The water column had four layers and the ArW was 30 m thick (at 20–50 m depth) and thus thinner than recorded further south. This suggests that there were several sources of ArW spreading over the northern part of the Barents Sea (C. Kivimäe et al., submitted). The vertical distribution of Chl *a* was similar to that of Stn. II, with a Chl *a* maximum at 30 m, but with slightly lower concentration (Fig. 2c). The ice coverage at the different stations ranged between 40 and 70% (Table 1) with 10–20% multiyear ice. For a more detailed physical description of the study area, see (C. Kivimäe et al., submitted).

Copepod composition and the vertical distribution of *Calanus*

The copepod biomass was dominated by three *Calanus* species, *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, making up 85–95% of the copepod biomass (Fig. 3). The older stages of *Calanus* (CIV–CVI) represented 82–94% of the total copepod biomass at the different stations. Other copepod species such as *Metridia longa*, and genera such as *Pseudocalanus*, *Microcalanus* and *Oithona*, constituted a minor fraction of the copepod biomass, but abundances, and hence biomass, of these species were likely underestimated because of the mesh size of the sampling gear employed.

Calanus finmarchicus was the most abundant *Calanus* species at Stn. I, followed by *C. glacialis* (Fig. 4).

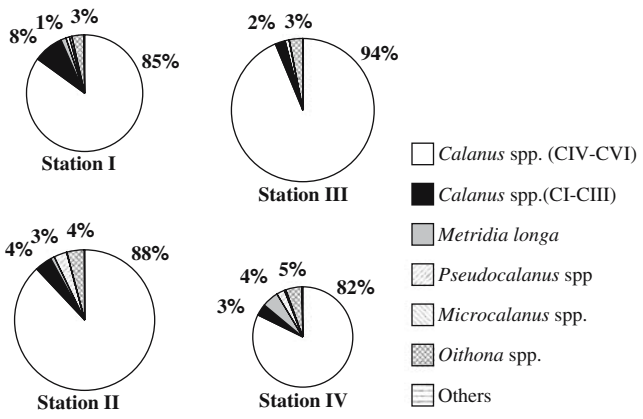

Fig. 3 Relative importance of different copepod groups for the total biomass of copepods, as average of the day and night sampling at each station (dry weight m^{-2}, 0–100 m depth). The different sizes of the pies indicate differences in total biomass

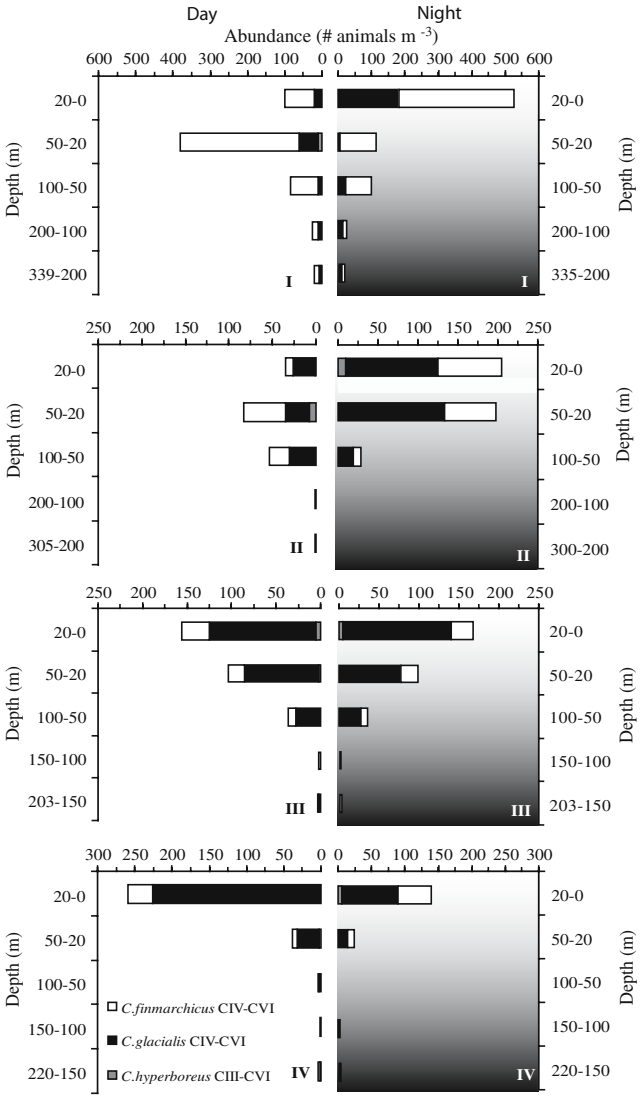

Fig. 4 Abundance (# m^{-3}) of older stages of *C. finmarchicus* (*white*), *C. glacialis* (*black*) and *C. hyperboreus* (*hatched*) at different depths and at day and night for stations I–IV

The dominance of *C. finmarchicus* reflects the AW prevailing at this station. *C. glacialis* was the most abundant *Calanus* species at Stns II–IV, suggesting major influence by ArW. *Calanus hyperboreus* made up a small proportion at all depths and stations. Most of the three *Calanus* species inhabited the upper 50 m both day and night. Relatively large variations in standing stock were observed, both between stations and different net tows at the same station.

CV and females were the dominating *C. glacialis* stages. *Calanus finmarchicus* was dominated by stage CIV and CV, but also with a significant proportion of females. *Calanus hyperboreus* was dominated by stage CIV and females with a noticeable contribution of CII at Stn. II only.

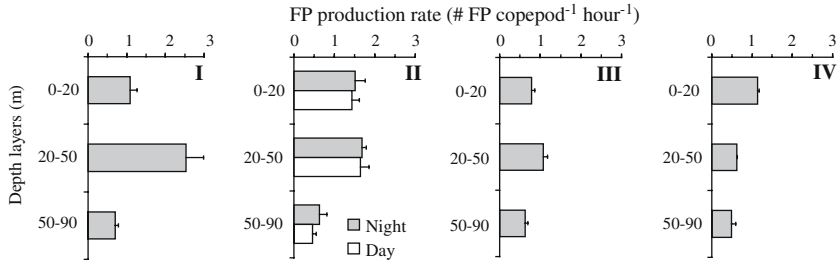

Fig. 5 Faecal pellet (FP) production rates by the predominating *Calanus* spp. stages at different depths (±SD). Presented as number of FP produced per copepod and hour

Faecal pellet conversion factors

Volumetric carbon conversion factors for *C. glacialis*, *G. wilkitzkii*, *Oikopleura* sp. and euphausiids ranged from 25 to 186 µg C mm^{-3}, with the lowest content for the appendicularian *Oikopleura* and the highest for the carnivorous *G. wilkitzkii* (Table 2). FP of *C. glacialis* and euphausiids contained 94 and 45 µg C mm^{-3}, respectively.

Faecal pellet production

No significant differences in FP production rates were detected between day and night at Stn. II (two-way ANOVA; $F = 0.50$, $P = 0.49$), but the FP production rate changed significantly with depth (Fig. 5). The highest FP production rate was measured in the upper and middle layer at Stn. II (~1.5 FP cop^{-1} h^{-1}) and decreased to ~0.5 FP cop^{-1} h^{-1} in the deeper layer. Similar trends were found at the other stations: both the highest FP production rate as well as individual FPC production rates were always observed in the upper and/or middle layers (Fig. 5 and Table 3) and these rates decreased with depth. On average 94 ± 4% (SD) of the community FPC was produced in the upper 50 m (Table 4).

A strong positive correlation was found between suspended Chl *a* concentration in the incubation water and FPC production ($r^2 = 0.83$) (Fig. 6a). A relatively weaker correlation was found between Chl *a* and the number of FP produced (Fig. 6b). These relationships suggest that Chl *a* seemed to be a good proxy for food availability. The copepods mainly fed on Chl *a*-containing food, or food that is closely related to autotrophic biomass. This also implies that increased Chl *a* concentration leads to production of larger FP rather than increased rates in terms of numbers. POC and Chl *a* in the incubation water were also highly positively correlated, indicating that phytoplankton cells made up a significant proportion of the POC.

The integrated *Calanus* community production of FP ranged from 20 to 60 mg FPC m^{-2} d^{-1} at the different stations (Table 4). The highest community production was measured at Stns. I and II (41 and 60 mg FPC m^{-2} d^{-1}, respectively). Station IV had the lowest community production (19 mg FPC m^{-2} d^{-1}) with slightly higher community production measured at the

Table 3 Chl *a* concentrations in the incubation water (µg l^{-1}), faecal pellet carbon (FPC) production rate (µg C cop^{-1} d^{-1}), proportion of intact FP recovered after experiments (intact FP as % of total number of FP produced) at station I–IV in different depth layers

Station (#)	Layer (m)	Chl *a* (µg l^{-1})	FPC prod (µg C cop^{-1} d^{-1})	Intact FP (% ± SD)
I	0–20	0.6	1.9	95 ± 1
I	20–50	1.8	5.9	98 ± 2
I	50–90	0.1	1.1	90 ± 6
II	0–20	1.6	9.3	94 ± 1
II	20–50	6.6	7.2	93 ± 3
II	50–90	0.4	1.8	80 ± 8
III	0–20	0.2	3.2	95 ± 2
III	20–50	3.8	5.0	93 ± 2
III	50–90	0.4	1.8	87 ± 3
IV	0–20	2.1	4.5	95 ± 2
IV	20–50	0.3	0.9	99 ± 2
IV	50–90	0.1	1.2	99 ± 2

Only the night experiment at station II were included

Table 2 Volumetric carbon conversion factors obtained for different faecal pellet (FP) categories

FP origin	FP category	FP width (µm)	Carbon content per FP (µg C)	FP carbon content per volume (µg C mm^{-3})	#FP per sample (*n* samples)
C. glacialis	Cylindrical	73 ± 16	0.285 ± 0.043	94.3	36–70 ($n = 3$)
Oikopleura	Ellipsoid	258 ± 46	0.866 ± 0.124	25.0	35 ($n = 5$)
Euphausiids	Filiform	133 ± 13	0.476	45.1	108–170 ($n = 2$)
G. wilkitzkii	Cylindrical	320 ± 59	39.54 ± 21.66	186.1	2–10 ($n = 6$)

FP width ± SD, carbon content per FP ± SD, FP carbon content per volume, number of FP per sample and number of measurements (*n*) are shown

Table 4 Integrated *Calanus* abundance (# CIV–CVI m^{-2}), faecal pellet carbon (FPC) produced by the *Calanus* community, integrated FPC production per *Calanus* and day, average daily FPC production weighted over the number of animals and FP production rates at different depths

Station (#)	Layer (m)	Calanus abundance (m^{-2})	FPC production (mg FPC m^{-2} d^{-1})	Av. FPC prod. (μg C $Calanus^{-1}$ d^{-1})	Vertical flux (mg FPC m^{-2} d^{-1})	Export (%)
I	0–20	6,260	12		9	77
I	20–50	7,256	43		3	6
I	50–90	3,641	4		1	2
I	0–90	17,157	58	3.4		
II	0–20	2,400	22		14[a]	64
II	20–50	4,779	34		30	53
II	50–90	1,637	3		16	27
II	0–90	8,815	60	6.8		
III	0–20	3,280	11		5	51
III	20–50	3,136	16		54	>100
III	50–90	1,445	3		53	>100
III	0–90	7,861	29	3.7		
IV	0–20	4,047	18		4	23
IV	20–50	960	1		8	41
IV	50–90	148	0		6	33
IV	0–90	5,155	19	3.7		

Vertical flux of *Calanus* FPC (mg FPC m^{-2} d^{-1}) was measured with sediment traps at 20, 50, 90 m depth at stations I–IV. Export production (%) is calculated as the above FPC community production sinking out at a specific depth

[a] Vertical flux was measured at 30 m due to lack of sediment trap at 20 m at station II

northernmost Stn. III (29 mg FPC m^{-2} d^{-1}). The highest integrated *Calanus* abundance was found at Stn. I, and the lowest at Stn. IV (Table 4).

Vertical carbon flux and the relative importance of FP

The vertical flux of POC was relatively low at the southernmost Stn. I, ranging from ~240 mg C m^{-2} d^{-1} at 20 m to ~110 mg C m^{-2} d^{-1} at 200 m depth (Fig. 7). Higher vertical fluxes were measured at Stns II–IV, further north, with a maximum in the upper 40 m, decreasing with depth. The highest vertical flux of POC was measured at 30 m depth at Stn. II with 760 mg C m^{-2} d^{-1}. The vertical flux of FPC was low at Stn. I (Fig. 8) with the highest rates in the upper 40 m (~10 mg C m^{-2} d^{-1}) decreasing with depth (<5 mg C m^{-2} d^{-1}). Vertical flux of FP at Stns II–IV was moderate, ranging from 10 to 80 mg FPC m^{-2} d^{-1}. The FPC flux was mainly made up by cylindrical FP produced by copepods, but also filiform FP produced by krill contributed to the vertical FP flux (Fig. 8). Oval FP, often observed in traps from ArW, did not contribute significantly to the flux during this investigation.

Faecal pellet carbon constituted a variable fraction of the total POC flux (Fig. 7). At Stn. I the contribution of FPC to vertical POC export was low, ranging from 1 to 7% with an average of 3%. FPC made up 2–24% of vertical POC export at Stn. II with an average of 11%. At Stn. III the average FPC contribution was found to be 16%, ranging from 3 to 37%. Station IV had an average FPC contribution to total POC flux of 9% (ranging from 3 to 14%). In general, the relative importance of FPC to total POC increased slightly with depth and the contribution of FPC to total POC was greater at depths below 50 m than above. This implies that the highest relative importance of FPC is encountered at greater depths than those where most of the FP are produced. The overall average FPC contribution to vertical POC flux was found to be 10%.

A comparison of the *Calanus* FP community production with the export of *Calanus* FP at different depths suggests a variable, but extensive FP retention at most depths and stations (Table 4). Highest FP retention was estimated for the southernmost station (Stn. I) where more than 90% of the pellets produced were removed at depths ≥20 m. A larger proportion of the FP produced appeared in the traps moving further north, which implies a less extensive retention. The results reveal that a larger proportion of the produced FP are retained rather than exported.

Discussion

Previous work conducted in the Barents Sea suggested that a significant fraction of the phytoplankton biomass is retained in the upper part of the water column (Olli et al. 2002; Wassmann et al. 2003, 2006). This can be deduced based on observations of reduction in

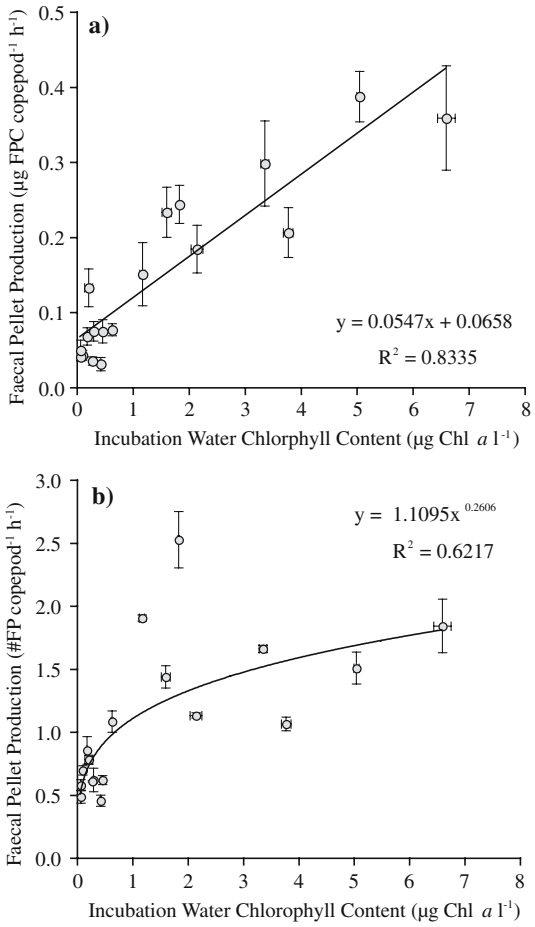

Fig. 6 Relationship between Chl *a* concentration in the incubation water (µg l^{-1}) and **a** FPC production per copepod per hour ± SE and **b** number of FP produced per copepod per hour ± SE

Chl *a*, phytoplankton biomass and POC export with depth, and is a consequence of retention processes such as copepod grazing. More than 50% of the produced FP never reach depths exceeding 50 m, and in the northern Barents Sea FP did not contribute more than 10% on average to the vertical POC flux, although the FPC production suggest a significantly higher potential vertical flux. The fate of FP produced after zooplankton grazing is thus a critical process that deserves attention.

Spatial complexity of the bloom development in the MIZ

The investigated stations highlighted the heterogeneity in physical as well as biological features characterising the Barents Sea (Falk-Petersen et al. 2000). Different water masses and ice cover, as well as three stages of the spring bloom were observed simultaneously over a limited spatial region. The southernmost station (Stn. I) was located in the Atlantic part of the Barents Sea. A subsurface Chl *a* maximum of 2.4 µg Chl *a* l^{-1} (37 m) and NO_3 concentrations below 0.3 µM in the upper 30 m (M. Sturluson et al., submitted) indicated that this area was in a late phase of the bloom. The stations further north were all influenced by ArW and with variable influence of AW at depth. High Chl *a* concentrations in the upper 30 m at Stns. II and III (6–10 µg Chl *a* l^{-1}) with NO_3 concentrations of ~1 µM (M. Sturluson et al., submitted) showed that these areas were in the middle of the spring bloom at the time of investigation. Station IV was covered by dense drift ice at the time when Stns I and II were sampled, but the drift ice opened at the end of the cruise period. The station was therefore in an earlier phase of the bloom with maximum Chl *a* concentrations in the upper 15 m (~2 µg Chl *a* l^{-1}) decreasing rapidly with depth, and nitrate was present throughout the water column (M. Sturluson et al., submitted).

This suggests a seasonal succession from station IV (early-bloom condition) to Stns. II and III (bloom condition) and finally Stn. I (post-bloom condition). It also clearly illustrates that the succession does not follow a simple south–north gradient, as previously suggested by Sakshaug and Skjoldal (1989). It is rather related to the atmospheric forcing determining the ice cover history, thickness and type of ice through local climate and wind-induced ice transport that controls the light regime for phytoplankton growth (Falk-Petersen et al. 2000).

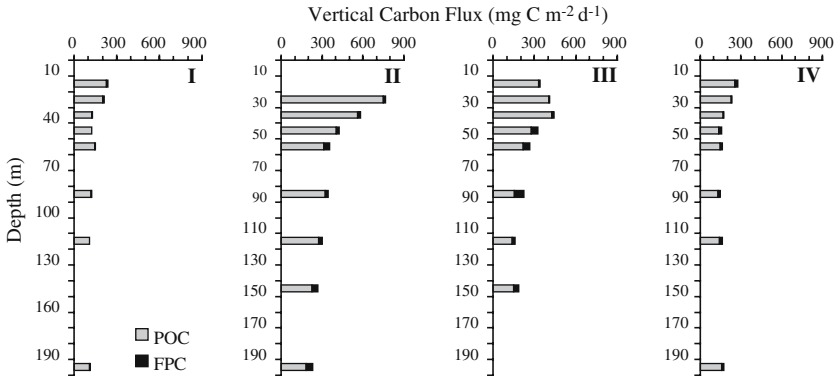

Fig. 7 Vertical flux of particulate organic carbon (POC, *whole bars*) and faecal pellet carbon (FPC, *black fraction* of the *bars*)

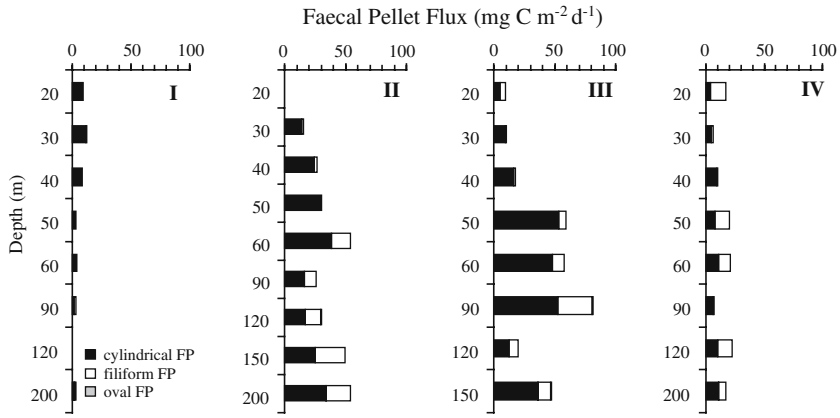

Fig. 8 Vertical flux of cylindrical-, filiform- and oval faecal pellets (FP) at Stns I–IV

Vertical variability in FP production

The highest number of *Calanus* FP produced per individual per day was found in the uppermost 50 m of the water column and the same was true for the daily FPC production, which showed that less than 10% of the FPC was produced below 50 m depth (in the 50–90 m interval). The close relationship between FPC production and Chl *a* concentration implies that *Calanus* did feed on Chl *a*-containing food. It might however be that they were also feeding on non-chlorophyll containing food in the proportion that the food types were present in the environment and that this proportion did not change with increasing chlorophyll concentrations. Higher Chl *a* concentrations not only gave higher number of pellets produced, but also resulted in larger FP, increasing the FP volume more than the number of produced FP. Determination of FP volume is therefore essential to estimate egestion rates by copepods.

The FP production rates obtained for the 0–20 and 20–50 m layer during the present study were similar to those previously measured by Wexels Riser et al. (2002) in the central Barents Sea during spring and summer, using incubation water from 10 m depth. The production rates typically ranged between 1 and 2 FP cop^{-1} h^{-1}. These are, however, significantly higher rates than what we measured for the deeper (50–90 m) layer during the present study (<1 FP cop^{-1} h^{-1}). *Calanus* distributions were closely related to the presence of available food, since copepod abundances were greatest in the upper water column where chlorophyll concentrations were highest. The FP production rate was not found to differ significantly between day and night, during the present study, suggesting that the older stages of *Calanus* were feeding as efficiently during the day as during the night. Lack of synchronised diel vertical migration (DVM) among *Calanus*, also supports the view that the grazing pressure from *Calanus* on the phytoplankton standing stock was similar during day and night. Several studies conducted in high latitude systems report reduced or total lack of DVM, assumed to be an anti-predator strategy, during the period of midnight sun (e.g. Båmstedt 1984; Falkenhaug et al. 1997; Arashkevich et al. 2002). This is probably related to the relatively constant light regime, and hence no cues for synchronised DVM. A recent study by Blachowiak-Samolyk et al. (2006) support this view and postulate that common zooplankton taxa in the MIZ of the Barents Sea do not perform DVM under the midnight sun. We can therefore state that most of the FP are produced in the upper 50 m, and active vertical zooplankton migration seems to be of minor importance during the Arctic summer or spring season.

Contribution of copepod FPC to vertical export

The average contribution of FPC to total POC flux was 10% (for all depths and stations), which was a bit lower than that encountered by Sampei et al. (2004) during a long-term study in the North Water Polynya of northern Baffin Bay. The highest biomass of copepods was found at Stns. II and III, i.e. the spring-bloom stations where the highest vertical fluxes of POC and FPC also were measured, although the highest copepod abundance was observed at Stn. I. This is explained by the species composition, with *C. finmarchicus* dominating at Stn. I, producing smaller, and thereby less carbon-rich FP. A lower POC export at this station may reflect suboptimal feeding condition seen as low Chl *a* concentrations, and stronger retention as the system goes from an export phase to a more retentive phase. The lower fluxes at Stn. IV reflect an earlier phase of the bloom in which phytoplankton stocks are building up.

The vertical flux of FP and POC is within the range found previously, during spring and summer in the central Barents Sea (Wexels Riser et al. 2002). The lower contribution of filiform FP to total FPC flux in

the present study, compared with that found by Wexels Riser et al. (2002), resulted from the use of a more accurate, and lower, volume-to-carbon conversion factor for krill FP (Table 2). The FPC contribution to total POC in the present study is, thus, more conservative than reported earlier from the Barents Sea. The vertical POC flux and decline with depth in the northern Barents Sea were within the range previously reported for the central Barents Sea during spring and summer (Olli et al. 2002). Also, the present study shows that the strongest vertical flux attenuation takes place in the upper 50 m. Changes below 50 m were less prominent, while FP slightly increased the contribution.

Mechanisms that may affect FPC retention

The differences between the measured FP production by larger *Calanus* and the actual vertical FP fluxes measured suggest significant biological, chemical and/or physical removal and destruction of FP. If all the produced FP had been exported out of the upper 90 m of the water column the POC flux would have increased by 10–25% at the different stations. Instead, only ~10% of POC sank as recognisable FP. Several investigations have suggested that the fate of sinking particles, especially FP may be strongly influenced by retention processes, which promote re-utilisation and recycling (Viitasalo et al. 1999; Wexels Riser et al. 2001; Sampei et al. 2004). Therefore, FP retention may be one of the more important processes regulating the flux of biogenic matter in the northern Barents Sea. There may be several possible reasons for the loss of FP: microbial degradation, horizontal transport, physical destruction through turbulence or zooplankton-induced breakdown. The latter could be due to coprophagy (feeding on FP), coprorhexy (FP fragmented but not ingested) or coprochaly (loosening of the FP) as described by Noji et al. (1991). The robustness of FP may also depend on the food types available and concentrations (personal observation).

Microbial activity leads to a rapid leakage/release of carbon from the FP, mainly in form of dissolved organic carbon (DOC) (Urban-Rich 1999; Thor et al. 2003). Microbial breakdown of pellet membranes and POC is a much slower process which takes several days at low temperatures (Jacobsen and Azam 1984; Roy and Poulet 1990; Thor et al. 2003). Thus, it is unlikely to affect FP removal/retention due to the high sinking speed of large FP, and consequently low residence time in the upper layers (Komar et al. 1981). Advection in the upper and middle layers could horizontally export surface-derived material, including FP, away from the sampling area, but FP, with an assumed sinking speed of >100 m per day (e.g. Smayda 1969), still should have a local origin. Hence, removal of FP by zooplankton themselves remains the most likely fate of FP in the upper layer.

Zooplankton induced retention of FPC in the water column

Earlier investigations have shown that by far the largest proportions of the FP recovered from sediment traps are fragmented or partly-broken pellets (own observations). Thus, the daily sedimentation of FP, as numbers, is difficult to calculate and FP export is usually presented as flux of FP volume or carbon. How does this fragmentation happen? The FP production chambers used in this study had false bottoms to prevent copepod grazing on, or destruction of the produced FP. Thus, a very high proportion of the FP recovered after the incubation experiments appeared intact (92 ± 5%) (Table 3). The lack of a positive relationship between the Chl *a* concentrations in the incubation water and FP fragmentation indicates that the strength of the pheritrophic membrane surrounding the FP was not affected by the food availability, production rate or the size of FP. The low fragmentation rate of fresh experimentally produced FP even after handling (similar to FP in sediment traps), suggests that freshly-produced FP are robust. Aging of FP can make them more fragile, but due to low residence times in the upper layers this cannot explain the high rate of FP fragmentation often found in shallow traps. Thus, we believe that zooplankton active in the water column can be responsible for the high rate of fragmentation found in even shallow sediment traps.

Coprophagy has been suggested as an important factor, and the cyclopoid *Oithona* spp. is the most frequently cited coprophagous copepod, being cosmopolitan and highly abundant (Gonzalez et al. 1994; Gonzalez and Smetacek 1994). *Oithona* spp. is a key genus, in terms of abundance in the northern Barents Sea (Falk-Petersen et al. 1999). However, its presence cannot be used as an explanatory factor for coprophagy alone, as *Oithona* spp. does not necessarily feed on or increase fragmentation of FP (Reigstad et al. 2005). Retention of FP can also result from mechanical destruction/fragmentation when copepods encounter FP during filter feeding or swimming activities, or more likely a combined effect of the two as described for *Acartia tonsa* and *Temora longicornis* (Poulsen and Kiørboe 2005).

Our results suggest that a significant proportion of the FP are retained within the upper layer. This was revealed for instance at Stn. I where 90% of the FP

produced was retained in the upper 50 m. The results indicating larger export of FP than what can be explained by the community production in the lower strata of Stn. III, however, challenge this interpretation (Table 4). The retention estimates rely on the assumption that the experiments are truly Lagrangian, which is not necessarily true. The high sedimentation rates of FP at medium depth at Stn. III must have been produced by a substantial *Calanus* population, and suggest that sampling took place in a transient zooplankton patch not captured by the two samplings that formed the basis for the FP community production. The significantly lower sedimentation rates of FP in the upper layer (20–40 m depth), where most of the copepods were located support the view that the experiments have been quasi-Lagrangian. Among a number similar experiments carried out so far (Wexels Riser et al. 2001, 2002) Stn. III is the only one that has given rise to a clearly unrealistic result. The interpretation of this type of experiment that aims to shed light on the processes of pelagic-benthic coupling is always based on assumptions such as a Lagrangian drift and that sampling is adequate and accurate when conclusions are drawn. However, the main conclusion remains that the fate of copepod FP is primarily retention in the upper layers of the water column rather than export to depth.

We believe that enhanced concentrations of copepods and associated activity at certain depths, often just below the Chl *a* maximum, may cause the high degree of FP fragmentation seen in sediment traps. Fragmentation of FP is probably the first step in FP recycling and obviously an important factor reducing the vertical flux of FP. Mechanisms causing fragmentation and the fate of fragmented versus intact FP should therefore be focused to advance our understanding of FP retention and vertical flux regulation.

Conclusions

Depth specific measurements of FP production revealed that >90% of the FPC was produced in the upper 50 m depth as a result of high *Calanus* biomass as well as higher individual FP production rates in the upper layer. The close relationship between FPC production and Chl *a* concentrations, implies that chlorophyll was a good proxy for food availability during the different bloom scenarios encountered. The FPC production was more than twice as high during the bloom compared to the post-bloom scenario. The average contribution of FPC to total POC flux was only 10%. If all the produced FP had been exported out of the upper 90 m of the water column, the POC flux would have increased by 10–25%. This implies that a substantial proportion of the FP produced in the upper layers is retained there due to processes that are still not fully understood.

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