# Distribution and sedimentation of faecal pellets on the Nordvestbanken shelf, northern Norway, in 1994

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A close seasonal coherence between mesozooplankton and abundance of faecal pellets was encountered at Nordvestbanken, northern Norwegian shelf, in 1994. Mesozooplankton at Nordvestbanken influenced the vertical flux of organic matter by production, consumption, modification, and destruction of faecal pellets. On average, 11-37 % of particulate organic, vertical carbon flux was comprised by faecal pellets. The pelagic degradation of organic matter at Nordvestbanken appears to be reduced due to the low pelagic residence time in the upper 100 m of the water column of faecal pellets (1.3-8.3 d). The specific seasonal sinking rates of faecal pellets (12-77 m $d^{-1}$) fell well into the range of *in situ* and *in vitro* sinking rates reported in the literature for the dominating classes of faecal pellets at Nordvestbanken, i.e. from calanoid copepods and pteropods. The shape, colour, density, and degree of fragmentation of faecal pellets appears to reflect variations and changing preferences in the diet of mesozooplankton throughout the season. Although the vertical flux was dominated by detritus, faecal pellets comprised at any time significant fractions (up to 66 %) of the particulate vertical carbon flux. Minipellets were found throughout the water column and season, but comprised only a small amount of the total faecal pellet carbon due to their small volume:pellet ratio. Despite their size, minipellets may be important for the regulation of vertical export of organic matter.

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## INTRODUCTION

Vertical export of suspended particles is one of the fundamental carbon cycling processes in marine ecosystems. Sedimentation couples the dynamics of plankton with those of the benthos (e.g. Smetacek & al. 1984; Graf 1992). The seasonal dynamics of vertical flux, how much organic matter is sinking and to a certain extent also the composition of exported matter, has been investigated in a wide range of ecosystems. However, less is known about the regulatory mechanisms of vertical export of organic matter (Wassmann 1998). Two categories of large suspended particles, aggregates and faecal pellets, contribute the largest share of exported particulate matter (Fowler & Knauer 1986). For overviews on the significance of aggregates for vertical flux, see Alldredge & Silver (1988) and Kiørboe & al. (1994). An interest in zooplankton faecal pellets and their role in suspended and sinking biomass has emerged during the last two decades (e.g. Turner & Ferrante 1977; Honjo & Roman 1978; Smetacek 1980; Angel 1984; Noji 1991). The separation of the different types of faecal pellets (FP) and relating them to the respective zooplankton taxa who produced them is not based on widely accepted criteria (e.g. Moore 1931; Martens 1978). However, no clear-cut classification schemes or identification keys are as yet available.

How much organic matter is exported vertically and the extent of pelagic-benthic coupling depends on the predominant plankton species. If diatoms and large zooplankton species prevail, the export of carbon to deeper parts of the water column can be rapid due to the formation of aggregates and large faecal pellets. Small phytoplankton cells and faecal pellets generally contribute less to vertical export due to their smaller sinking rate and the heavy grazing. Both can be incorporated into rapidly sinking particles such as large faecal pellets and aggregates and, consequently, increase vertical export (Landry & al. 1994). However, zooplankton can also reduce the vertical flux due to feeding on phytoplankton blooms in the euphotic zone (Emerson & Roff 1987; Urrère & Knauer 1981.). Vertical flux mediation such as coprophagy, coprorhexy, and coprochaly adds to the reduction of the vertical flux (Lampitt & al. 1990;

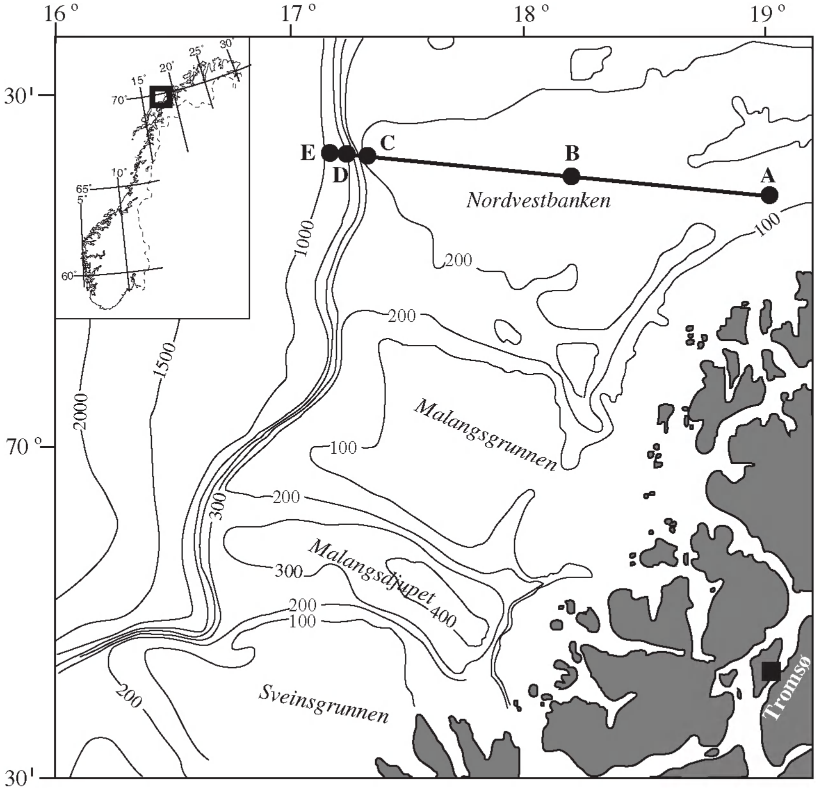

Fig. 1. Investigation area and the sampling stations A-E along the cross section over Nordvestbanken.

Noji 1991) throughout the water column. The transport of particulate organic matter to depth, as a fraction or function of primary production, obviously depends on the structure and function of the prevailing planktonic food web (Peinert & al. 1989; Aksnes & Wassmann, 1993; Heiskanen & al. 1996).

The present investigation is based on the perspective that not only the seasonal vertical and horizontal flux dynamics of biogenic matter should be investigated, but also the impact of the most important zooplankton forms on the vertical flux and the recycling of biogenic matter in the water column. The investigation is part of the project "Comparative fluxes of biogenic matter and trophodynamic interactions across the shelf break of northern Norway", which, in turn is a segment of the Ocean Margin EXchange programme (OMEX) which takes into account the specific features of the European shelves. OMEX is concerned with the study of fluxes and processes occurring along European shelf breaks facing the North Atlantic Ocean. Its aim is to measure and model exchange processes at the ocean margin as a basis for the development of global models to predict the impact of environmental changes on the oceanic system and more specifically on the coastal zone. Here, we investigate the composition of suspended and sinking faecal pellets along a transect across Nordvestbanken and at the shelf break in 1994 (Fig. 1) with the objective to evaluate and quantify the role of zooplankton on the vertical flux of organic matter and to examine the significance of faecal pellets in suspended and sedimenting particulate organic carbon.

## MATERIAL AND METHODS

Water samples were obtained with a General Oceanic rosette using 5 litre Niskin bottles across the north Norwegian shelf at Nordvestbanken (Fig. 1). Samples for suspended FP were obtained from 5 stations (A-E) at monthly intervals from March to October 1994, usually at 5, 10, 20, 40, 75, and 100 m depth. Immediately after retrieval of the rosette, the water was drained from each Niskin bottle by attaching with tygon tubing a 1 litre PVC bottle with 28 µm Nitex screen on each side. The Niskin bottles were allowed to drain completely and then the remaining water trapped in the Niskin bottles below the spigot was collected and poured into the

1 l bottles. The retained FP were transferred to 250 ml plastic bottles and preserved with glutaraldehyde (2 % final concentration). Data from August and October are missing due to an accident with the rosette sampler and bad weather, respectively.

Vertical flux of FP was measured at the shelf break (Fig. 1, Stn E) using a drifting array for 24 hours at monthly intervals from April to September 1994. Double, gimballed sediment traps, 450 mm high and inner diameter of 72 mm, equipped with a vane were exposed at 14 depths ranging from 20 to 200 m depth (for details, see Andreassen & al. 1999). Samples for sedimenting FP were usually taken from 20, 60, 100, 160, and 200 m depth. The content of the cylinders (1.8 l) was poured into a glass bottle and a 250 ml aliquot of the suspension was preserved with (2 % glutaraldehyde, final concentration) for faecal pellet counts. Sediment traps were not deployed in March and October.

Both suspended and sedimented FP were enumerated using an inverted microscope with phase contrast and ocular micrometer (Zeiss IM 35). 100 ml of the suspended and 25 ml of the sedimented samples were settled for 24 hours in Utermöhl chambers (Utermöhl 1931, 1958). The FP were characterised according to their shape, colour, compactness (visual impression of light penetration), degree of fragmentation (percentage FPV compared to non-fragmented FP) and the presence or absence of a peritrophic membrane. The length and width of the pellets were measured and the faecal pellet volume (FPV) calculated using appropriate stereometrical configurations according to Edler (1979). The FP were classified according to their shape as cylindrical, spherical, and ellipsoid. Each of these categories was separated into size classes according to their width and degree of fragmentation. An attempt was made to quantify minipellets (*sensu* Gowing & Silver (1985); 40-60 µm), but their enumeration was insecure due to insufficient resolution of the light microscope. All FP from the various categories were counted in each sample.

To calculate the faecal pellet carbon content (FPC) of the total FPV, a factor of 0.061 mg C mm$^{-3}$ obtained for *Calanus finmarchicus* FP by González & Smetacek (1994) was applied. A daily loss rate of FPC at 100 m depth (L), the residence time of FPC in the 0-100 m interval (R) and the specific FPC sinking rate (S) out of the upper 100 m were calculated according to Hargrave & Taguchi (1978):

$$L = Sd/Sp \times 100 \qquad (1)$$

$$R = 100/L \qquad (2)$$

$$S = D/R \qquad (3)$$

where

L = loss rate of FPC ( % d$^{-1}$)
R = residence time of FPC (d$^{-1}$)
S = specific sinking rate of FPC (m d$^{-1}$)
Sd = sedimentation rate of FPC (mg C m$^{-2}$ d$^{-1}$, at 100 m)
Sp = suspended biomass of FPC (mg C m$^{-2}$; 0-100 m)
D = integrated depth (100m)

## RESULTS

### NUMERICAL ABUNDANCE OF FP

Table 1 shows the average numerical abundance of suspended FP for each station and month. The total number of suspended FP counted per sample ranged between 3 and 220, with a total average of 57. Among a total of 27 stations were FP were quantified, on average 8 stations had FP concentrations < 30 per sample, indicating that many samples were characterised by low abundance and consequently a low precision of the estimate. This was in particular the case in March and September. For these periods the volume sampled for the suspended FP samples was obviously too low in order to obtain a better precision. As a consequence, the various FP size categories, shapes, characteristics etc. cannot be presented properly in a quantitative manner. Thus we decided not to interpret the time and spatial variation of suspended FP concentrations in detail, although the FPV data are shown (Fig. 2). The suspended FP concentrations were rather pooled and interpreted as averages per station and month (Table 1). The total number of suspended FP counted per station ranged between 54 and 688 with an average of 221.

There was an obvious seasonal cycle in the numeri-

Table 1. Average number of suspended FP counted per sample at the sampling stations A-E. In parentheses the total numerical abundance of FP counted per station.

| Station | March | April | May | June | July | August | September |
|---|---|---|---|---|---|---|---|
| A | 15 (61) | 41 (124) | 116 (349) | 86 (345) | 172 (688) | ND | 21 (83) |
| B | 28 (190) | 28 (85) | 136 (409) | 40 (201) | 47 (236) | ND | ND |
| C | 28 (140) | 35 (140) | 119 (477) | 67 (201) | 98 (491) | ND | ND |
| D | 24 (122) | ND | 113 (450) | 37 (222) | 56 (56) | ND | 14 (54) |
| E | 35 (141) | 32 (126) | 45 (226) | 33 (198) | 63 (63) | ND | 21 (82) |
| Average | 26 | 34 | 106 | 53 | 87 | ND | 19 |

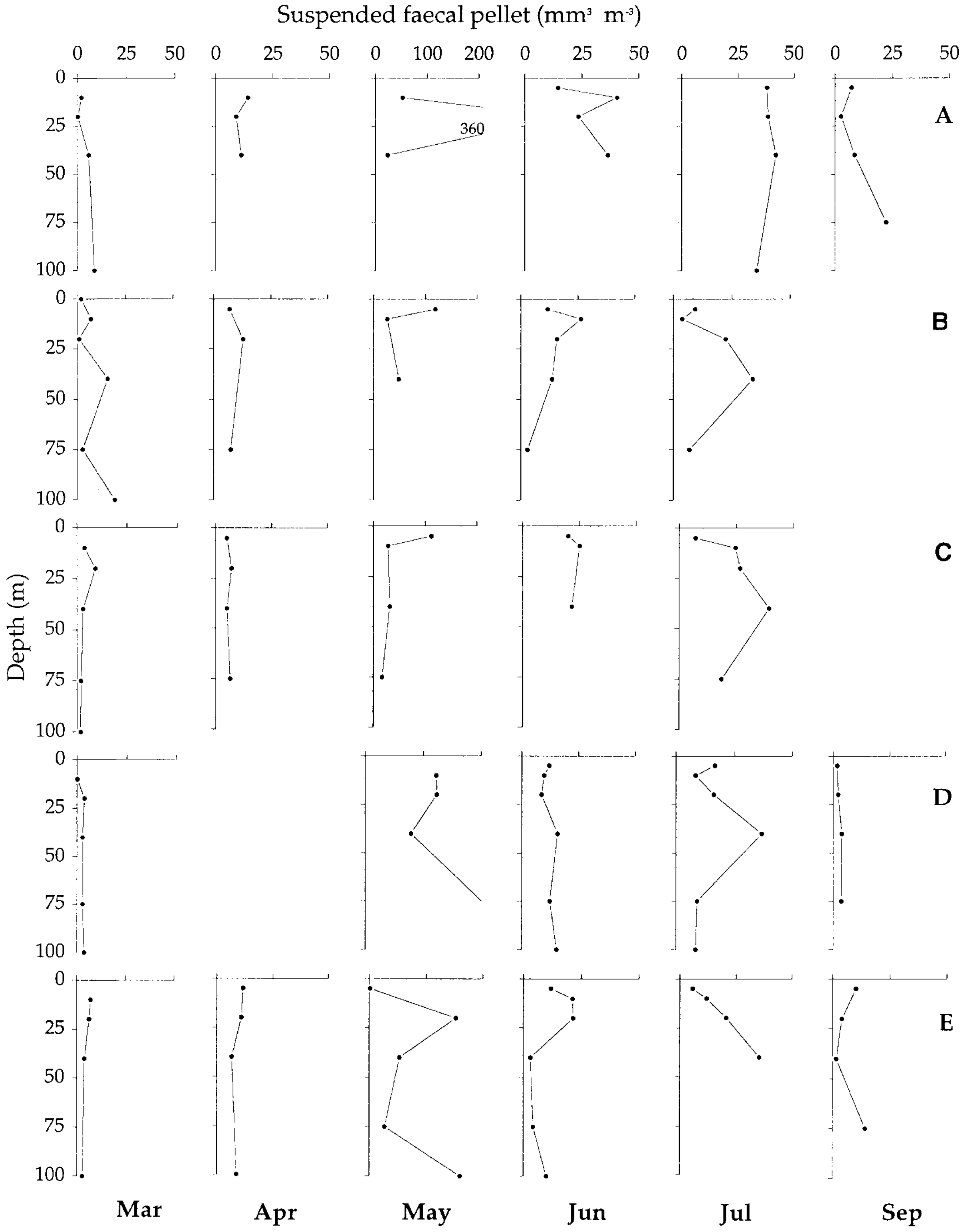

Fig. 2. Seasonal variation of suspended faecal pellet volume (FPV) at Stns A-E (mm$^3$ m$^{-3}$) at Nordvestbanken in 1994. Please notice the change in scales in May for Stns A-B.

cal abundance with low concentrations in March, April, and September and a distinct maximum in May. The numerical abundance was highest at Stn A and lowest off the shelf break at Stn E. The seasonal abundance of FP varied between 57 and 81 % at Stns A-D, but was distinctly lower off the shelf break at Stn E (average 38 %).

### Size, form and structure of FP

The dominating fraction in suspended and sedimented FP had peritrophic membranes. This was the case for both intact and broken pellets. Only a few FP lacked membranes. Ghost pellets (pellets with an intact membrane, but without any particulate content) were frequently observed in both suspended and sedimented fractions. From March to May FP were dominated by cylindrical pellets. The average size of these FP was 200 × 50 $\mu$m in March and 400 × 70 $\mu$m in April and May. In spring most of the FP were pale and almost transparent with less compactness compared to the summer and autumn period. From time to time compact FP with dense contents were recorded in spring. The pale and less compact FP were more often fragmented than the more compact ones.

The average FP size during June and August decreased to about 200 × 50 $\mu$m. Again cylindrical FP with membranes dominated. The compactness of these FP varied, but dark and presumably more dense FP were more frequent compared to spring. Also during summer ghost pellets were sporadically encountered. A conspicuous amount of unidentified detrital particles was observed in the water column. Also some oval formed FP were observed, mainly in June to August.

While the FP composition varied less during summer compared to spring, differences in the FP composition were recorded in September. The suspended FP at Stn A in September were dominated by helical forms of 300 × 70 $\mu$m, with peritrophic membranes and marked compactness. At Stns D and E at the outer part of Nordvestbanken, cylindrical pellets sized 200 × 50 $\mu$m dominated as previously.

Fragmented suspended FP comprised between 30-86 % of the total biovolume (Table 2). They dominated at almost all sampling depths in March, May, June, and September throughout the transect. There were more fragmented suspended FP at the shelf break. The amount of fragmented FPV in the sediment traps was greater compared to the suspended FPV (Fig. 3). The largest flux of fragmented FP was observed in June. The fragmented fraction was always greater than the intact one, except for 60 m depth in August.

FP 40-60 $\mu$m in diameter were characterised as minipellets (*sensu* Gowing & Silver 1985). These pellets usually had a round shape and peritrophic membranes. Minipellets were observed at all stations, depths, and throughout the observation period, with a maximum in June. These data are not presented because there were considerable doubts if the quantification of these small pellets among other particles of this size fraction is indisputable.

### Suspended and sedimented FPV

The vertical distribution of FPV suggests minor variations, in particular in March, April, and September (Fig. 2). As a general rule, the vertical distribution of FPV was rather homogeneous, suggesting that FP were produced and recycled similarly throughout the water column. Only a few pronounced maxima occurred, for example in the upper layers in May and June. In July maxima occurred at middle depths. The vertical variability of suspended FPV concentration was lowest on the shelf break at Stns D and E and more pronounced on the shelf.

The minimum concentrations in suspended FPV observed in March, April, and September and ranged between 0.4 and 22.5 mm$^3$ m$^{-3}$ (Fig. 2). A distinct maximum in suspended FPV was recorded in May with about 360 mm$^3$ m$^{-3}$ at 20 m depth at Stn A. Also at Stns B and C suspended FPV concentrations were high in the uppermost layer in May (≈ 110 mm$^3$ m$^{-3}$), but at Stns D and E FPV concentrations were in general always far lower than 50 mm$^3$ m$^{-3}$.

The vertical flux of FPV in the upper 200 m at Stn E (Fig. 3) revealed greater seasonal variability compared to the suspended FPV (Fig. 2, Stn E). The highest vertical flux of FPV was recorded at 60 m depth in May (9000 mm$^3$ m$^{-2}$ d$^{-1}$), which represents an increase by a factor of 20 compared to the minimum rate in April at 200 m (390 mm$^3$ m$^{-2}$ d$^{-1}$). In June, the vertical FPV flux decreased by a factor of 44 (200 mm$^3$ m$^{-2}$ d$^{-1}$) between 60 and 200 m depth. This was the lowest FPV vertical flux observed during this investigation. A second, but smaller maximum in vertical FPV flux was recorded in July (1200 mm$^3$ m$^{-2}$ d$^{-1}$ at 160 m). In August the vertical flux decreased again to 340 mm$^3$ m$^{-2}$ d$^{-1}$ at 20 m, similar to the increase from June to July. In September the vertical flux of FPV increased in particular close to

Table 2. Seasonal average percentage of fragmented FP of total FPV at the sampling stations A-E.

| Station | Mar | Apr | May | Jun | Jul | Aug | Sep |
|---|---|---|---|---|---|---|---|
| A | 48 | 43 | 52 | 53 | 34 | ND | 75 |
| B | 56 | 35 | 85 | 59 | 30 | ND | ND |
| C | 78 | 61 | 60 | 80 | 41 | ND | ND |
| D | 81 | ND | 57 | 78 | 47 | ND | 66 |
| E | 86 | 32 | 52 | 62 | 37 | ND | 64 |
| Average | 70 | 43 | 62 | 66 | 38 | ND | 68 |

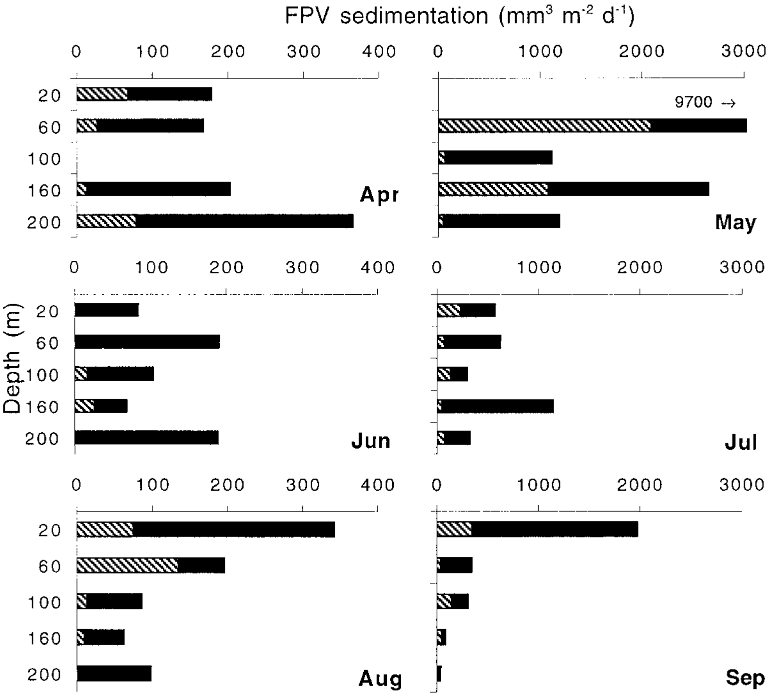

Fig. 3. The seasonal variation of vertical export of FPV of broken (black) and intact (hatched) faecal pellet at Stn E at Nordvestbanken (mm$^3$ m$^{-2}$ d$^{-1}$) in 1994. Note the differences in scales.

the surface (2000 mm$^3$ m$^{-2}$ d$^{-1}$ at 20 m). While vertical flux of FPV was more or less even throughout the water column in April to July, a decrease with increasing depth was recorded in August and September (Fig. 3).

### CONTRIBUTION OF FP TO SUSPENDED AND SEDIMENTED PARTICULATE ORGANIC CARBON

Suspended FPC did not contribute significantly to the suspended POC. As an example the data from Stn E are presented (Table 3). Between 0.1 to 6.1 % of the suspended POC was comprised by FPC, with an average of 1.3 %. During March and April FPC comprised only about 0.4 % of the suspended POC until the maximum concentration in May. The seasonal variation of integrated suspended POC in the upper 100 m was lower compared to FPC and varied between 6 to 21 g C m$^{-2}$, with an average of about 15 g C m$^{-2}$. The maximum suspended POC was not encountered in May, but increased almost steadily until a maximum of 21 g m$^{-2}$ in the months of September (Wassmann & al. 1999).

In contrast to suspended FPC, vertical export of FPC did contribute significantly to POC export (Table 4). The seasonal variation of vertical POC and FPC flux followed each other more closely compared to suspended POC and FPC. The average vertical POC flux ranged between 140 to 280 mg m$^{-2}$ d$^{-1}$ and the percentage of FPC between 6 to 37 %. The maximum contribution of FPC to the vertical POC export was encountered in May with 66 % at 160 m depth. In April the contribution of FPC was low in the surface (7 % at 50 m), but increased to 17 % at 200 m. In May the contribution of FPC to vertical POC export was more variable and ranged between 23 and 66 %. Low FPC contribution to vertical POC export was recorded in June, on average 6 %, while the FPC percentage increased in July with a steady increase with depth from 12 to 38 %. August revealed again a decreased contribution of vertical FPC export, on average 6 %, while a clear increase with increasing depth was encountered in September.

Table 3. Seasonal variation in integrated (0-100 m) suspended particulate organic carbon (g POC m$^{-2}$) at Stn E (data from Wassmann & al. 1999). In parentheses the percentage of faecal pellet carbon (FPC).

| | Mar | Apr | May | Jun | Jul | Aug | Sep |
|---|---|---|---|---|---|---|---|
| POC (g m$^{-2}$) | 6.2 | 11.1 | 17.2 | 17.1 | 19.6 | 15.7 | 21.0 |
| FPC/POC ( %) | 0.4 | 0.4 | 6.1 | 0.3 | 0.2 | ND | 0.1 |

### RELATIONSHIP BETWEEN SUSPENDED AND SEDIMENTED FPC

The daily loss rates of sedimenting FPC at 100 m depth varied throughout the season from 12 to 77 % (Table 5). The lowest daily loss rates were recorded in April and June and the highest in May and September. This seasonal variation of suspended and exported FPC similarly reflected in the FPC residence time and specific sinking rates, a consequence of equations 2 and 3. The residence times in the upper 100 m were lowest in May and September and highest in June and April with 1.6 to 1.3 and 3.8 to 8.3 days, respectively. The specific sinking rates varied accordingly, ranging between 12 to 77 m $d^{-1}$.

## DISCUSSION

Spatial and temporal patterns in the flux of sinking organic matter are central to the understanding of elemental dynamics and food webs in the ocean (Smetacek & al. 1984; Legendre 1990; Wassmann & al. 1991; Lohrenz & al. 1992). Previously the general relation between primary production and suspended biomass has been scrutinised in order to comprehend the dynamics of pelagic-benthic coupling (e.g. Eppley & Peterson 1979; Berger & al. 1989; Wassmann 1990; von Bodungen & al. 1995). More attention is presently given to the processes that control vertical flux (e.g. Noji 1991; Kiørboe 1993; Passow & al. 1994; Wassmann 1998).

The export of phytoplankton from the euphotic zone in Norwegian waters is well documented during periods of limited mesozooplankton grazing, e.g. during the spring bloom in shallow coastal marine waters (Smetacek & al. 1984; Wassmann 1991) and marginal ice zones (Wassmann & al. 1991; Andreassen & Wassmann 1998). However, the processes regulating the export of organic matter under conditions of increased impact of planktonic heterotrophs are not as evident (Noji 1991; Aksnes & Wassmann 1993). Despite obvious limitations of our contemporary comprehension of zooplankton-induced regulation of vertical flux of particulate organic matter (Noji 1991; Silver & al. 1991), evidence from coastal northern Norway, the Norwegian Sea and the Barents Sea suggests that over-wintering and advection of mesozooplankton plays a vital role on shelves, in the open ocean (Skjoldal & Rey 1989; Tande 1991; Pedersen 1995) and even in fjords (Falkenhaug & al. 1995). Over-wintering zooplankton, e.g. CV stages of copepods, may ascend before the start of the spring bloom (e.g. Bathmann & al. 1990) and spawn and graze effectively on phyto- and microzooplankton. A numerical model for the Barents Sea indicated that vertical flux could vary between 38 and 61 g C $m^{-2}$ $year^{-1}$ due to variable concentrations of overwintering zooplankton (Wassmann & Slagstad 1993). This suggests that the supply of organic carbon to the aphotic zone in subarctic and arctic waters is only partly determined by the strength and duration of phytoplankton blooms, but strongly influenced by zooplankton dynamics. Zooplankton may therefore play a significant role for the export of organic matter in coastal and shelf environments (Wassmann & al. 1991; Pedersen 1995) as well as in all oceanic systems (Frost 1991).

An increasing number of publications indicates that the larger FP comprise a substantial fraction of exported biogenic matter (periodically > 80 %) not only in coastal areas (Gonzáles & al. 1994; Riebesell & al. 1995; Wexels Riser 1998), but even in off shore areas (Bathmann & al. 1987; Bodungen & al. 1995; Carroll & al. 1998). The presence of meso- and macrozooplankton obviously promotes vertical export by FP production. Processes such as FP incorporation or FP break-down in these ecosystems were not efficient enough to significantly reduce the FP export signal. There was a clear match between phyto- and mesozooplankton at Nordvestbanken in 1994 with substantial concentrations of mesozooplankton and low microplankton biomass throughout the season (Ratkova & al. 1999; Verity & al. 1999). The high new production (Wassmann & al. 1999) and strong grazing pressure on pico-, nano- and microplankton at Nordvestbanken (Verity & al. 1999) suggests that FP production must have been substantial. By implication FP may play a vital role for the export of organic matter. The high vertical phaeopigment export rates (Andreassen & al. 1999) also support the

Table 4. Seasonal sedimentation rates of particulate organic carbon (mg POC $m^{-2}$ $d^{-1}$) at 50, 160, and 200 m depth at Stn E (data from Andreassen & al. 1999). In parentheses the percentage of faecal pellet carbon (FPC).

| Depth | April | May | June | July | August | September |
|---|---|---|---|---|---|---|
| 50 m | 150 (7) | 290 (23) | 160 (7) | 320 (12) | 170 (8) | 170 (40) |
| 160 m | 130 (9) | 250 (66) | 160 (3) | 240 (29) | 130 (4) | 150 (5) |
| 200 m | 130 (17) | 310 (23) | 160 (7) | 190 (38) | 130 (6) | 130 (10) |
| Average | 135 (11) | 280 (37) | 160 (6) | 250 (26) | 140 (6) | 150 (18) |

interpretation that FP and FP-derived material were the main fraction of vertical POC export at Nordvestbanken. Thus suspended and sinking FP and FP-derived matter were expected to be of significance at Nordvestbanken. How significant were they?

### SIGNIFICANCE OF FP FOR SUSPENDED AND SINKING POC

The suspended FPC concentrations varied relatively little throughout the season at Nordvestbanken, except for single high concentrations in the upper 50 m in May (Fig. 2). Except for the FPC maximum in May less then 1 % of the average standing POC stock of 16 C $m^{-2}$ was contributed by FP (Table 3). For comparison, the average seasonal contribution of phytoplankton carbon (PPC) was about 4 g C $m^{-2}$ (Ratkova & al. 1999) while that of FPC was 2 orders of magnitude lower, about 50 mg C $m^{-2}$ (Table 5). Thus the detritus fraction comprised by far the greatest share of the suspended POC in the upper layers. It appears that only during episodes of substantial mesozooplankton concentration, adequate food and high grazing rates, FP could contribute significantly to the suspended POC stock at Nordvestbanken. The large suspended detritus and small FP fraction suggests also that FP were either sinking fast out of the water column or are recycled by coprophagy/rhexy/chaly (e.g. Noji 1991) or microbial degradation (e.g. Jacobsen & Azam 1984).

FP are reported to comprise a variable, but often high proportion of the total vertical POC flux (e.g. Bathmann & al. 1987; Carroll & al. 1998). At Nordvestbanken, however, their contribution to vertical biogenic export was moderate. In April and May, when mesozooplankton was found mainly in the upper 100 m (Halvorsen & Tande 1999), the contribution of FPC to the vertical POC flux was on average 24 %, but varied widely (7-66 %; Table 4). During July to September, the FPC fraction of the vertical POC export decreased on average to 13 and 18 %, respectively. High mesozooplankton standing stock, new production and intensive grazing were clearly reflected in substantial vertical export of FP, but particulate carbon retention by zooplankton must have been moderate to effective during this period, both with regard to the suspended and sinking FP. Otherwise far higher suspended concentrations and sinking rates would had been encountered. Also previous investigations in north Norwegian fjords (Riebesell & al. 1995; Wexels Riser 1998) have shown that vertical POC flux can be dominated by FP, but in contradiction to Nordvestbanken a substantial sinking FP fraction was here produced by krill which were rarely observed in the present study. In June, FPC contribution to vertical POC export was minimal (3-7 %), suggesting that coprophagy/rhexy/chaly was most efficient during this period. This is reflected in an increased residence time of FP-derived matter in the upper layers, about 8 times compared to spring (Table 5).

In summary, generally high sinking rates and low residence times at Nordvestbanken imply that FP contributed substantially to vertical export of POC, reflecting the significant grazing impact and top-down regulation of carbon fluxes. However, considering the high mesozooplankton biomass (generally > 2 g C $m^{-2}$; E. Nordby & K.S. Tande, pers. commn) and its strong grazing impact on phyto- and protozooplankton (e.g. Wassmann & al. 1999; Verity & al. 1999) at Nordvestbanken in 1994, the contribution of FP to the suspended and sinking POC fraction was lower than expected. Mechanisms which degrade FP to slowly sinking detritus must have been prominent. Advected zooplankton, probably short in food supply, presumably took care of most of the larger particles (e.g. diatoms, ciliates, FP, aggregates), promoting the retention of biomass and nutrients on the shelf.

### ORIGIN OF SUSPENDED AND SEDIMENTED FP

Faecal pellet production at Nordvestbanken in 1994 revealed that both the type and quantity varied seasonally in concert with the mesozooplankton community

Table 5. Sedimented (at 100 m depth) and suspended (0-100 m) faecal pellets carbon (FPC) at Stn E. Also shown are the daily loss rates ( %), the residence time (d) and the specific sinking rates (m $d^{-1}$) of FPC in the upper 100 m.

| Months | Sedimentation at 100 m (mg C $m^{-2}$ $d^{-1}$) | Suspended 0-100 m (mg C $m^{-2}$) | Daily loss rate (%) | Residence time (d) | Specific sinking rate (m $d^{-1}$) |
|---|---|---|---|---|---|
| March | ND | 24.5 | - | - | - |
| April | 12.0 | 45.7 | 26 | 3.8 | 26 |
| May | 67.0 | 105.3 | 64 | 1.6 | 64 |
| June | 6.2 | 53.8 | 12 | 8.3 | 12 |
| July | 18.4 | 42.3 | 44 | 2.3 | 44 |
| August | 6.1 | ND | - | - | - |
| September | 18.9 | 24.4 | 77 | 1.3 | 77 |
| Average | 21.4 ± 91 % | 49.3 ± 55 % | 44.6 ± 53 % | 3.5 ± 74 % | 44.6 ± 53 % |

composition (Urban-Rich & al. 1999). During the first months of the investigation period FP were dominated by elongated, cylindrical pellets 400 × 70 µm in size. These light-brown FP were most likely produced by *Calanus finmarchicus*, the dominating mesozooplankton species during spring and early summer. The light-brown colour probably derives from a diatom diet (Hansen & al. 1996). For details of the mesozooplankton community, see Halvorsen & Tande (1999).

There was a change in the mesozooplankton community at Nordvestbanken during June when *C. finmarchicus* started on its ontogenetic vertical migration to deeper waters and smaller species such as *Oithona similis* dominated the zooplankton community. The dominating FP during this period were cylindrical of the size of 200 × 50 µm. The impact of *O. similis* may be reflected in the large number of fragmented FP (Table 2, Fig. 3) and the high residence times (Table 5). *O. similis* is known to participate in coprorhexy, the breaking of pellets (Noji & al. 1991; Gonzáles & Smetacek 1994). However, also a high abundance of *Bolinopsis* sp. was recorded in June. The feeding behaviour of *Bolinopsis* sp. could also have added to the large number of fragmented FP during June. Compared to spring the FP in June had a darker brown colour. Together with the decreased size, the darker colour points at a shift in diet, probably from diatoms to flagellates.

In July and August, dark, cylindrical FP, 200 × 50 µm in size dominated. In contradiction to June, suspended FP were dominated by intact pellets, in particular in July. The mesozooplankton community was still dominated by *O. similis*, but the species appeared to graze to a lesser extent on FP during this period. *O. similis* is omnivorous and prefers presumably food with a higher energy content than FP, for example ciliates and phytoplankton, if available. The increased concentrations of large-celled phytoplankton (diatoms, dinoflagellates) and larger protozooplankton in July supports this interpretation (Ratkova & al. 1999).

*Limacina retroversa* became more frequent from August and onwards, in particular at the innermost station. In September *L. retroversa* became the dominant species at Nordvestbanken. *L. retroversa* is known for its production of helical FP about 300 × 70 µm in size (Silver & Bruland 1981) and investigations in north Norwegian fjords and the Norwegian Sea have indicated that *L. retroversa* is a dominant zooplankton form at the end of the productive season (Bathmann & al. 1991; Keck & Wassmann 1996). It has been suggested that increased vertical export of pteropod aggregates partially may have been the result of faeces production (Noji & al. 1997).

### ARE MINIPELLETS SIGNIFICANT FOR THE REGULATION OF VERTICAL EXPORT?

Minipellets are most probably produced by protozoa, heterotroph flagellates, nauplia, larger ciliates, and other microzooplankton forms (Gowing & Silver 1985). An increasing number of investigations indicate that these organisms play an important role for recycling of organic matter and energy flow as they represent a link between pico- and nanoplankton to higher trophic levels (Gowing & Silver 1983; Gonzáles 1992; Mostajir & al. 1995). Heterotroph flagellates and ciliates can compete with mesozooplankton for phytoplankton and ciliates while being grazed upon by mesozooplankton and are even known to graze on diatoms (Gonzáles 1992; Nejstgaard 1997). Microzooplankton can also ingest fragmented FP of mesozooplankton origin and repack these into minipellets. This coprophagic process can thus increase the vertical export of FP to depth (Gonzáles 1992), and minipellets have been observed down to 4500 m depth (J.C. Miquel pers. commn).

Similarly to other investigations (e.g. Gowing & Silver 1985; Nöthig & von Bodungen 1989), minipellets where the most abundant type of FP in both the suspended and the sedimented fractions. However, they comprised only negligible amounts of the total suspended and sinking FPC due to their small volume:pellet ratio. Their small size implies that exact identification of minipellets under the light microscope among detritus and the predominant pico- and nanoplankton is difficult. Staining samples with the photochrome DAPI may represent a possibility to distinguish minipellets from possible faeces-like producers such as unarmored dinoflagellates, large ciliates etc. (Mostajir & al. 1995). Improvements in the identification are necessary in order to obtain more reliable results. The abundance of suspended and sedimented minipellets did not decrease with increasing depth which could be expected due to their comparatively low sinking rate and degradation/ingestion. This suggests that they were produced throughout the water column (Gowing & Silver 1985). Being numerically so dominant the question arises how *significant* minipellets are *for the regulation of vertical export* on the north Norwegian shelf?

Pico- and nanoplankton species were dominant at Nordvestbanken, comprising on average 91 % of the total biovolume of pico-, nano- and microplankton (Ratkova & al. 1999). However, heterotrophic plankton forms predominated among the biomass of pico-, nano- and microzooplankton at Nordvestbanken (Verity & al. 1999). The large proportion of small heterotrophic plankton forms at Nordvestbanken could explain why minipellets were found throughout the season. Indeed, protozooplankton and in particular larger ciliates had a maximum abundance in June/July when the largest concentration of minipellets was encountered. If mesozooplankton would not impede the growth of larger ciliates (Verity & al. 1999), the contribution by minipellets could have been far greater, in particular due to the high abundance of their food. Despite their size, minipellets may be important for the continuous vertical export of organic matter repeatedly ingested by the smallest fraction of grazers. In particular because they seem to be produced throughout the water column. The lack of knowledge regarding dynamics of autotrophic and heterotrophic microplankton communities on the north Norwegian shelf and improved minipellet identification techniques prevent a more thorough investigation of what role these FP play for the carbon flux in general and the vertical export in particular.

### SINKING SPEED OF FP

The sinking rate of FP under laboratory conditions under the exclusion of turbulence has been thoroughly investigated and ranges from 30 to 3000 m $d^{-1}$ (Smayda 1969; Bienfang 1980; Bruland & Silver 1981; Cadée & al. 1992). To the best of our knowledge, only Lorentzen & Welschmeyer (1983) measured FP sinking rates *in situ*. Simultaneous short-term investigations of suspended and sinking FP and the assumption that homogenous distribution along the trajectories of suspended and sinking FP permits the calculation of specific sinking rates (Table 5). The sinking rates at Nordvestbanken fall well within the range of sinking rates presented in the literature for large calanoid copepods and pteropods. The specific sinking rate at Nordvestbanken, i.e. the average sinking rate of the quantified size classes of FP in the 0-100 depth interval varied greatly throughout the season, reflecting the changes in composition of the zooplankton community. In June when fragmentation was most significant and *O. similis* prevailed, specific sinking rate of FP was clearly reduced to 12 m $d^{-1}$. In May when *C. finmarchicus* dominated and zooplankton flux mediation was reduced, specific sinking rates of about 64 m $d^{-1}$ were calculated. The maximum specific sinking rate of FP in September (77 m $d^{-1}$) was found when *Limacina retroversa* produced large and compact FP.

Based on the current understanding of the physical oceanography of the area (Sætre & Mork 1981; Sundby 1984) profound effects on the dynamics of plankton over the shelf and the shelf break of northern Norway have been observed during selected months (Rey 1981; Hegseth & al. 1995; Ratkova & al. 1999; Wassmann & al. 1999). Thus, a straight-forward comparison of short-term observations of suspended and sinking FP are obscured by differences of current speed along the shelf edge and over the shelf (Moseidjord & al. 1999) as well as zooplankton patchiness. The difference between horizontal and vertical flux of FP is three orders of magnitude. The areas where FP are produced and where they sediment are thus different. Assuming a sediment trap depth of 100 m, the calculated sinking FP rates (Table 5) and an average horizontal current speed at the shelf break of ≈ 55 cm $sec^{-1}$ (Sundby 1976), sinking trajectories of FP between the place of production and deposition at the 100 m isobath varied between 60-400 km. Particles in the sediment trap and suspended particles are only directly related to each other when they derive from an adequately large, homogenous water body. This assumption may hardly be valid over distances of 60-400 km along the north Norwegian shelf.

As current speed and direction are neither constant on spatial nor on temporal scales, the trajectories will be curved and variable. Slow and rapidly sinking, inert particles which drifted from a mid-shelf position in northern Norway in a model simulation were deposited in strikingly different areas (Wassmann & Slagstad 1995). The slowly sinking particles followed a current pattern which was clearly dominated by the topography and settled on the shelf. The rapidly sinking particles, such as FP, were transported along and deposited in waters off the shelf break or caught into eddies. Suspended particles on the shelf will therefore sediment in different areas depending on their sinking rate and topography. *Vice versa*, different size classes of particles from a sediment trap at a certain depth will comprise a mixture of particles which can be derived from very different geographic areas.

### INTERPRETATION AND IDENTIFICATION PROBLEMS

The present investigation of FP in north Norwegian waters was the first of its kind and is characterised by some obvious shortcomings. For example, the volume of water sampled for suspended FP was evidently too small to achieve adequate precision during periods of low suspended FP biomass (Table 1) and for the few, large FP per sample. Because of this inadequacy, no differentiation between the miscellaneous FP types was made and the results were expressed in total FPV and FPC. Due to problems of identification, small broken or destroyed faeces may not have been taken into account. The volume of faecal pellets (FPV) is therefore probably underestimated. The irregularities of the suspended FP sampling (see Fig. 2) also contributes to that the interpretation of these results in constrained. Another caveat in the interpretation of the sediment trap results is the fact that vertically migrating zooplankton could have grazed on phytoplankton/detritus and defecated inside the trap or removed material caught inside the trap. Swimmers were never observed in any larger numbers inside the traps, but poisoned traps usually show the presence of swimmers. It is, however, not evident if the presence of swimmers in poisoned traps is the result of a process taking place in traps in general (implying potential grazing and defecation) or an artefact induced by coma during vertical migration. The question of the potential and compromising role of zooplankton in unpoisoned traps cannot be solved at present.

Also the assumption of a fixed volume:POC ratio of FP introduces questions regarding the accuracy of our calculations as it is known that these ratios may vary as function of food supply, feeding mode and species (Dagg & Walser 1986; Paffenhöfer & Knowles 1979; Butler & Dam 1994; Hansen & al. 1996). Estimations of the volume:POC ratio for the larger faecal pellets at Nordvestbanken gave a lower maximum contribution of 35 % (Urban-Rich & al. 1999). FPV/POC ratios for FP of *C. finmarchicus*, *Thyssanoessa* sp. and appendicularians in spring in north Norwegian fjords revealed an average of 0.0691 mg C $\text{mm}^{-3}$ (E. Arashkevich, pers. commn). The uncertainty regarding the FPV/POC ratio results in a noteworthy uncertainty estimating the contribution of FP to the vertical export of POC.

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