Contribution by mesozooplankton fecal pellets to the carbon flux on Nordvestbanken, north Norwegian shelf in 1994

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Fecal pellet production rates for mesozooplankton (> 500 μm) were measured monthly at a shelf edge and inshore station in northern Norwegian coastal waters during March-September as part of the Ocean Margin Exchange (OMEX) study. The total potential fecal pellet carbon flux was higher at the inshore station except in May when *Calanus finmarchicus* (Gunnerus) was more abundant at the shelf edge. Mesozooplankton fecal pellets had the potential to contribute 2.5 % (April & September) to > 100 % (May-August) of the POC flux found in sediment traps. This compared with only 5-35 %, when fecal pellet carbon flux was measured from trap pellets suggests that a significant amount of fecal pellet remineralization or coprophagy was occurring in the surface waters. *Calanus finmarchicus* apparently plays a pivotal role in moderating pellet carbon flux on Nordvestbanken both through its potential fecal pellet production and possibly through coprophagy. Carbon ingestion by the large mesozooplankton at the shelf edge station was found to be 250 g C m^{-2} for the duration of the OMEX study (March-September). This is significantly higher than that estimated for new production during the course of this study suggesting that the large copepods were also feeding on detritus and/or microzooplankton. The high estimated carbon ingestion also indicates that the mesozooplankton were able to apply sufficient pressure to maintain the low chlorophyll standing stocks observed during this study.

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INTRODUCTION

Zooplankton fecal pellets play an important role in oceanic and coastal carbon cycles either through the sedimentation and removal of organic carbon or through the recycling and retention of carbon in the surface waters (Fowler & Small 1972; Angel 1984; Welschmeyer & Lorenzen 1985; Bathmann & al. 1987; Lampitt & al. 1990; Noji 1991; Marty & al. 1994). The contribution of fecal pellets to sediment traps has been found to range from < 1 % up to 100 % of the particulate organic carbon (POC) flux (Smetacek 1980; Urrère & Knauer 1981; von Bodungen & al. 1987; Fowler & al. 1991; Small & Ellis 1992; González & al. 1994; Lane & al. 1994). Many interacting biological and physical factors affect the export of particulate and dissolved organic carbon (DOC) by fecal pellets from the euphotic zone to deeper waters and the sediments. These factors include: fecal pellet production rates, the carbon content and settling velocity, as well as the zooplankton community composition, microbial activity, current velocities and physical mixing of the water column (Hofmann & al. 1981; Alldredge & al. 1987; Noji 1991; Lane & al. 1994; Urban-Rich 1997, 1999).

The quantity, quality and composition of the available seston influence production rates of copepod fecal pellets (Dagg & Walser 1986; Ayukai 1990). Typically, high concentrations of food result in faster fecal pellet production rates and greater concentrations of organic carbon in the fecal pellets due to superfluous feeding and selective grazing (Knauer & al. 1979; Cowles & al. 1988). Houde & Roman (1987) found that copepod ingestion increased with a decrease in the protein content of the food suggesting that the copepods try to maximize their intake of protein. Changes in the amount ingested could lead to variable defecation rates over the course of the year depending upon the quality and quantity of seston present. Changes in zooplankton grazing are also reflected in the C:N content of the fecal pellets. High C:N ratios are found in fecal pellets produced on a diet of phytoplankton in stationary growth with a high C:N ratio or on a diet of detritus (Checkley & Entzeroth 1985; Morales 1987; Butler & Dam 1994). Herbivory, carnivory and coprophagy can all result in fecal pellets with potentially different carbon concentrations. The seasonal aspect of the Ocean Margin Exchange (OMEX) study, prebloom conditions in spring to post-bloom conditions in the fall, allowed us to in-

vestigate how changes in the seston composition affected the pellet production rates, total potential fecal pellet flux, measured fecal pellet sedimentation and carbon content of pellets from copepods > 500 µm.

Zooplankton community composition can influence the total number of pellets produced in the water column and the number of pellets available for sedimentation (Hofmann & al. 1981; Corner & al. 1986; González & Smetacek 1994). Copepod fecal pellet production rates are negatively related to body size (Ayukai & Nishizawa 1986; Morales & al. 1993) while pellet volume is positively correlated with body size. Thus a community of small copepods will tend to produce many small pellets that are likely to be recycled within the water column while a community of large (> 500 µm) copepods will tend to promote carbon export by the formation of large, fast sinking fecal pellets. In contrast, gelatinous zooplankton have a defecation rate and pellet volume that corresponds proportionately with body size (Madin 1982). Salps, pteropods and pelagic tunicates frequently occur in swarms thereby producing large quantities of fast sinking fecal pellets that strongly influence local sedimentation (Bathmann 1988; Fortier & al. 1994 (references within)).

Both the zooplankton community structure and the seston composition changed over the course of the OMEX study period. The large calanoid copepod, *Calanus finmarchicus* (Gunnerus) dominated the community during the spring, while during the summer and fall, smaller, neritic species, larvaceans and pteropods were more prevalent (Halvorsen & Tande 1999). In terms of the seston, protozoans were more abundant in May-July while diatoms were more common earlier in the study, March-June (Ratkova & al. 1999). In a previous study in coastal Newfoundland waters, changes in the seston composition were reflected in the composition and density of *C. finmarchicus* and *Oikopleura vanhoeffeni* (Lohmann) fecal pellets (Urban & al. 1992; 1993). *Calanus finmarchicus* fecal pellet densities ranging from 1.07 g cm^{-3} in the spring to 1.20 g cm^{-3} in the fall with corresponding sinking velocities ranging from 20 m day^{-1} to > 100 m day^{-1} (Urban 1992; Urban & al. 1993). Sediment trap studies have found seasonal differences in the total particle flux and variations in the organic content of the particles presumably reflecting both the changes in the phytoplankton and zooplankton community biomass and composition (Honjo & al. 1988; Wassmann 1991; Wassmann & al. 1991; Wassmann & Slagstad 1993; Andreassen & al. 1996).

Norwegian coastal waters are dominated by *Calanus finmarchicus*, *Oithona* spp. and *Oncaea* spp., who have all demonstrated the ability for coprophagy (Noji & al. 1991; González & Smetacek 1994). Coprophagy, the consumption of fecal pellets, along with coprochaly and coprorhexy, the fragmenting of pellets by copepods, leads to a reduction in the total number of pellets and a reduction in the organic carbon content of the sedimenting fecal pellets. Previous studies in the Barents Sea, Norwegian Sea, North Sea and Norwegian fjords suggest that coprophagy, coprochaly and/or coprorhexy are common water-column processes that cause much of the potential fecal pellet flux to be recycled within the euphotic zone (Bathmann & al. 1987; Martens & Krause 1990; González & al. 1994; González & Smetacek 1994).

The objective of the present study was to determine the contribution made by fecal pellets to particulate organic carbon flux at the shelf edge in northern Norwegian coastal waters during the growing season, March-September 1994. This study was conducted within the larger framework of the OMEX project, which examined the transport of particles along and across a northern Norwegian continental shelf and shelf break at Nordvestbanken. Since fecal pellets from mesozooplankton have a greater potential than pellets from microzooplankton to contribute to vertical export and transport off a continental shelf due to their larger size and higher sinking velocity, experiments were conducted with large (> 500 µm) sized copepods. A comparison of the potential fecal pellet flux and the amount of carbon ingested by large mesozooplankton was examined for an inshore and shelf edge station, in order to estimate the potential fecal pellet carbon export across and off the shelf.

MATERIAL AND METHODS

The study sites were located on a transect line running across the shelf at Nordvestbanken, off the coast of northern Norway (Fig. 1). For an overview of the topography, hydrography, nutrients, suspended biomass and phytoplankton abundance on Nordvestbanken in 1994, see Nordby & al. (1999). Experiments were conducted monthly, March-September at two stations (Fig. 1), an inshore Stn A (70°20'N, 18°57'E) and a shelf edge Stn D (70°24'N, 17°13'E), for fecal pellet production rates, POC and dry weight content of freshly egested fecal pellets for two size classes of copepods (500-1000 µm and > 1000 µm). Samples were also taken from a free-drifting sediment trap for the number and POC content of sedimented fecal pellets at the shelf break, for details on the sediment trap methods see Andreassen & al. (1999).

Fecal pellet production

Mesozooplankton were collected with vertical net tows from 30 m to the surface, using a 183 µm, 0.5 m diameter WP-2 net with a closed cod end. Immediately after

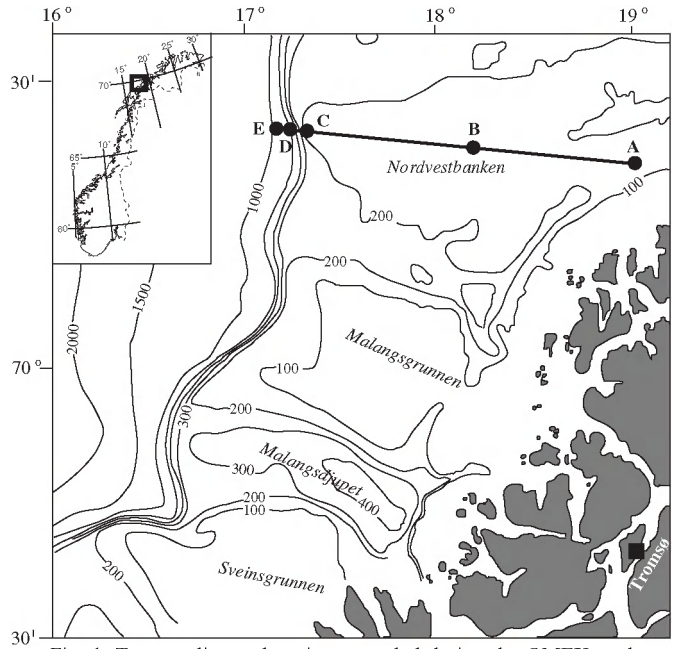

Fig. 1. Transect line and stations sampled during the OMEX study on Nordvestbanken in 1994. Station A (70°20'N, 18°57'E) was the inshore site while Station D (70°24'N, 17°13'E) was the shelf edge station.

retrieval of the net, the cod end was gently emptied into 10 l of surface water to dilute the copepods. The copepods were then gently size-fractioned into 500-1000 µm and > 1000 µm. Fecal pellet production rates for the two, copepod size-fractions were measured at 3 depths throughout the euphotic zone (100, 30 and 10 % surface irradiance (% I_o)). Surface irradiance levels were used so depth dependent, pellet production rates between months could be directly compared. For each depth and each size fraction, three experimental bottles (1.2 l) and one control bottle (1.2 l) were filled with water collected by Niskin bottles on a CTD rosette from 100, 30 and 10 % I_o. In each experimental bottle, 3-5 copepods were put into a suspended insert (900 ml) with 183 µm Nitex mesh on both ends, which allowed the pellets to fall through and prevented coprophagy. The bottles were covered with neutral density screening to obtain the correct % I_o and placed in a running seawater incubator for 3-5 h in both the morning and evening. At the end of the incubation, the copepods were removed and the contents from experimental and control bottles were sieved through a 20 µm Nitex mesh to collect the fecal pellets. Both the fecal pellets and copepods from each experimental and control bottle were preserved with 2 % glutaraldehyde for later counting.

The experiments were conducted once during each month from March to September 1994. The pellet production rate for both size fractions at each light percent was calculated after subtracting the fecal pellets found in the control from the experimental bottles and dividing the total number of pellets by the time of incubation. The average pellet production rate was calculated and then multiplied by the zooplankton abundance for each size fraction within the upper 20 m. Zooplankton abundance was determined by size fractioning samples collected with a MOCNESS (Multiple Opening Closing Net Environmental Sampling System.

Fecal pellet carbon production

The potential carbon flux due to fecal pellets from the community of copepods (> 500 µm) was measured by incubating 100-200 animals in 20 l of mixed (100, 30 and 10 % I_o) euphotic zone seawater for 6 h to collect fecal pellets for particulate organic carbon (POC) analysis. Incubations were kept short (6 h) to collect the freshest fecal pellets possible and to minimize microbial degradation, which would change the carbon content of the pellets. The community approach was used to obtain a large enough sample for analysis and to obtain a community average carbon content. However, by using this approach we were not able to determine carbon differences between calanoid or cyclopoid copepods or gelatinous zooplankters. One hundred to two hundred fecal pellets, containing a mixture of fecal pellet

types, were picked out from surrounding detritus and phytoplankton, rinsed with 0.2 µm filtered seawater and then filtered unto a 13 mm combusted glass fiber filter (Gelman A/E). The sample filter was placed on top of a second, blank backing filter (combusted Gelman A/E) during collection and rinsing of the pellets. This blank backing filter was treated the same as the sample filter and was used to correct for filter and machine error. Samples were analyzed on a Control Systems CHN analyzer in the Analytical Department of Horn Point Environmental Laboratory. To obtain the potential, daily pellet carbon flux produced in the euphotic zone, the average pellet carbon was multiplied by the estimated fecal pellet production.

Fecal pellet sedimentation

A drifting sediment trap was deployed for 24 h at the shelf break (methods described in Andreassen & al. 1999). From the 20, 50, 100, 150 and 200 m traps replicate, 200 ml aliquots were taken for fecal pellet counts and carbon analysis. One aliquot was preserved with 2 % glutaraldehyde for enumeration in the laboratory. The second aliquot, used for carbon analysis was sorted at sea by picking intact and fragmented fecal pellets. The pellets were rinsed with 0.2 µm filtered seawater and filtered onto combusted, 13 mm glass fiber filters and analyzed for POC as described above. To determine the number of pellets rinsed onto the filter, it was assumed that three pellet fragments equaled one whole pellet. This could be an over or under estimate depending upon the actual degree of pellet fragmentation.

Data analysis

In order to investigate differences between the two size fractions, stations and the measured pellet flux versus potential fecal pellet flux, paired t-tests were used with an alpha level of 0.05. Spearman rank correlation and t-test analysis were done to examine differences between the different sampling months and between depths in the water column. Linear regression analysis was used to examine the relationship between measured pellet flux (at each sediment trap depth) and potential flux. This was significant only at the 200 m depth, so for this depth multiple regression analysis was used to examine which variable that comprised the potential flux estimate (i.e. fecal pellet production rate, pellet carbon content, zooplankton abundance) most explained the correlation. Also the relationship between individual zooplankton species and measured pellet carbon flux was examined using a combination of multiple and lin-

Table 1. Fecal pellet production rates for two zooplankton community size classes (> 1000 µm and 500-1000 µm) through the euphotic zone and average pellet production rate values for the whole euphotic zone for day and night at the shelf edge station (70°24'N, 17°13'E) on Nordvestbanken, north Norwegian shelf in 1994. nd = no data

	Zooplankton fecal pellet production rates (# pellets copepod^{-1} hour^{-1})						
Light %	March	April	May	June	July	Aug	Sept
Day							
>1000 µm							
100	0.19	0.43	0.65	nd	2.01	0.37	0.45
30	0.17	0.49	0.57	nd	1.69	0.69	0.54
10	0.16	0.46	0.51	nd	1.05	0.35	0.29
Mean±SE	0.17±0.07	0.46±0.08	0.57±0.08	nd	1.58±0.20	0.47±0.22	0.42±0.19
500-1000 µm							
100	0.16	0.47	0.70	0.48	0.48	0.33	0.28
30	0.18	0.39	0.50	0.46	0.50	0.38	0.33
10	0.14	0.44	0.52	0.39	0.46	0.33	0.34
Mean±SE	0.16±0.09	0.43±0.16	0.57±0.13	0.44±0.17	0.48±0.17	0.34±0.20	0.31±0.09
Night							
>1000 µm							
100	0.19	0.17	0.64	nd	nd	0.27	0.65
30	0.16	0.13	0.68	nd	nd	0.34	0.66
10	0.17	0.15	0.56	nd	nd	0.32	0.58
Mean±SE	0.17±0.07	0.15±0.06	0.62±0.18	nd	nd	0.31±0.13	0.61±0.21
500-1000 µm							
100	0.16	0.16	0.80	nd	0.84	0.36	0.63
30	0.17	0.18	0.73	nd	0.96	0.52	0.71
10	0.15	0.14	0.92	nd	0.89	0.42	0.50
Mean±SE	0.17±0.05	0.16±0.06	0.81±0.28	nd	0.89±0.37	0.42±0.23	0.61±0.21

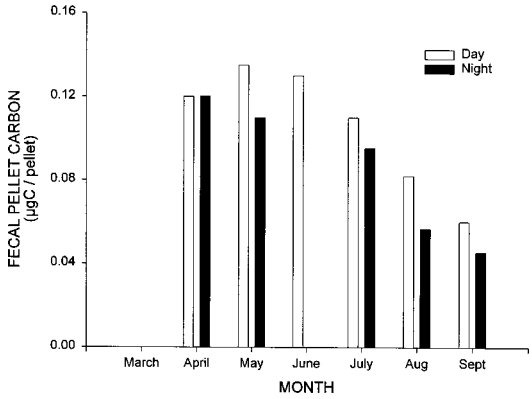

Fig. 2. Fecal pellet carbon content of freshly egested pellets, produced by > 500 µm mesozooplankton at the shelf edge station (70°24'N, 17°13'E). The copepods were fed natural seston from a mixture of seawater taken from 100, 30 & 10 % I_o.

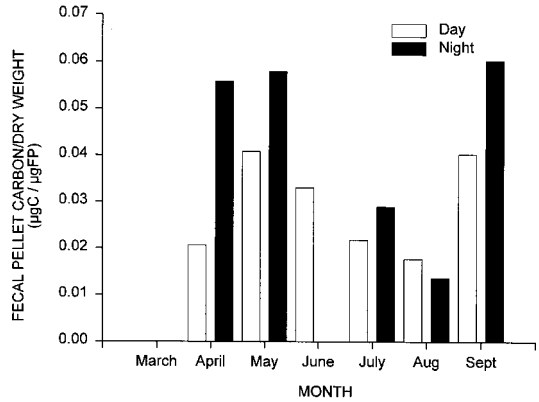

Fig. 3. Fecal pellet carbon : dry weight (FPC:DW) ratio for freshly egested pellets produced in shipboard experiments with > 500 µm mesozooplankton at the shelf edge station (70°24'N, 17°13'E) on Nordvestbanken in 1994.

ear regression. In order to examine the role of environmental variables (temperature, chlorophyll, POC and % I_o) on measured and estimated fecal pellet flux parameters, multiple regression analysis was applied to the data. All the statistical analyses were completed using Systat version 5.0.

RESULTS

Fecal pellet production rates and carbon content

The lack of significant diel variation in fecal pellet production rates within the euphotic zone (100-10 % I_o, Table 1) lead us to calculate an average monthly, day/night defecation rate for each size fraction. Defecation rates did not vary significantly between the two size classes (500-1000 and > 1000 µm) in any month except during the day in July (Table 1). However, there was a 2.5 to 9-fold variation in the average fecal pellet production rate over the course of the study. Maximum excretion rates occurred from May-September (Table 1). After the first months of investigation there was a slight tendency for higher pellet egestion rates at night. Results from multiple regression analysis showed that the only environmental variable (chlorophyll, POC, % I_o, water temperature) that pellet production rates were slightly correlated with was water temperature ($p < 0.05$, $r^2 = 0.10$). A comparison of the inshore and shelf edge stations revealed no significant differences in pellet production rates except in September when rates were lower at the inshore station (0.27 ± 0.09 vs 0.61 ± 0.21 pellets copepod^{-1} h^{-1}; data for the inshore station are not shown, shelf edge production rates are in Table 1).

Fecal pellet carbon content of freshly, egested pellets was maximum in the spring and decreased through the summer and early fall (Fig. 2). There was no significant day/night difference in the total carbon content of the fecal pellets. The dry weight of freshly egested fecal pellets remained relatively constant throughout the year until September when there was a 3 to 4-fold decrease in dry weight. Both fecal pellet carbon and dry weight tended to be higher in the day yet the carbon: dry weight ratio was significantly higher at night in 4 out of 6 months (Fig. 3).

Potential fecal pellet flux

The potential *in situ* fecal pellet flux was calculated by multiplying the zooplankton abundance per size class in the upper 20 m by the average fecal pellet production rate and the pellet carbon concentration. Results from paired t-tests showed significant seasonal differences in the potential pellet flux, with maximums occurring in May through July at both sites (Figs 4 & 5). The potential fecal pellet flux was higher at the inshore station for all months except May when the *in situ* pellet production was 6-fold higher at the shelf edge. Plotting the estimated, potential fecal pellet production against zooplankton abundance, fecal pellet production rates and pellet carbon content suggests that zooplankton abundance had the greatest influence on the flux potential (data not shown). Neither the potential *in situ* fecal pellet production, fecal pellet production rates nor zooplankton abundance was correlated with suspended POC or with suspended chlorophyll stocks.

Carbon ingestion by mesozooplankton > 500 µm was calculated by assuming a 70 % assimilation efficiency. The highest estimated carbon ingestion occurred in May, 40.4 g C m^{-2} month^{-1} and 237.4 g C m^{-2} month^{-1} at the

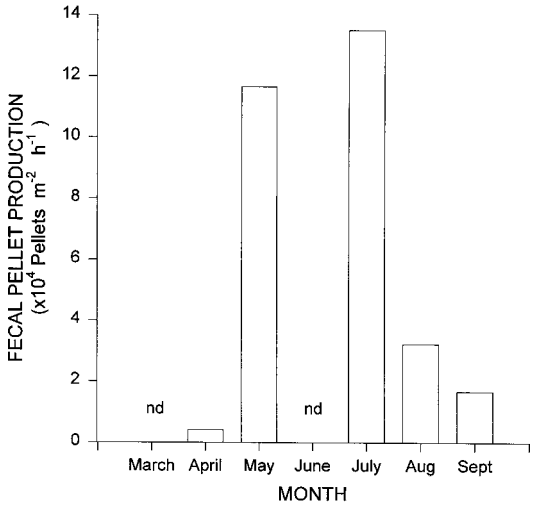

Fig. 4. Fecal pellet production throughout the euphotic zone (0-20 m) by > 500 µm copepods at the inshore station (70°20'N, 18°57'E) on Nordvestbanken, north Norwegian shelf in 1994.

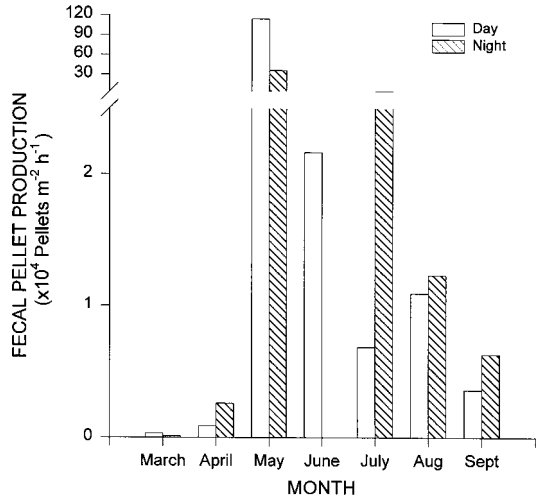

Fig. 5. Fecal pellet production throughout the euphotic zone (0-20 m) by > 500 µm copepods at the shelf edge station (70°24'N, 17°13'E) on Nordvestbanken, north Norwegian shelf in 1994.

inshore and shelf edge stations respectively (Table 2). However, at the inshore site the amount of carbon ingested in July (33.5 g C m ^{2} month ^{1}) was only slightly lower than that ingested in May. A comparison between the two sites reveals that significantly more carbon was ingested over the course of the whole OMEX study at the shelf edge than at the inshore site, due to the high amount ingested during May (Table 2). For the duration of the OMEX study (March-September), 250 g C m ^{2} was ingested within the euphotic zone at the shelf edge station.

Sedimented fecal pellet flux

A minimum of 5-35 % of the total POC flux in the sediment traps at 20 and 200 m could be attributed to identifiable fecal pellet material (Table 3). The maximum pellet carbon contribution occurred in the spring during April and May when *C. finmarchicus* was most abundant. Linear regression analysis showed that the measured fecal pellet carbon flux was positively correlated with the estimated, potential fecal pellet flux only at 200 m ($p < 0.05$, $r^2 = 0.93$). The potential flux was calculated from fecal pellet production rates, mesozooplankton abundance and pellet carbon content. Taking the variables that comprise the potential flux estimate and using multiple regression showed that the measured pellet carbon flux in the sediment traps was correlated only with mesozooplankton abundance ($p < 0.001$, $r^2 = 0.97$).

Table 2. Macrozooplankton (> 500 µm) carbon ingestion at the shelf edge station (70°24'N, 17°13'E) and inshore station (70°20'N, 18°57'E) on Nordvestbanken, north Norwegian shelf in 1994, assuming a 70 % assimilation efficiency. nd = no data

Month	Shelf edge station (g C m^{-2} month^{-1})	Inshore station (g C m^{-2} month^{-1})
March	0.1	nd
April	0.4	1.6
May	237.4	40.4
June	3.4	nd
July	6.1	33.5
August	2.0	4.7
September	0.6	2.0

The estimated, potential *in situ* fecal pellet carbon flux created by large mesozooplankton in the euphotic zone could contribute from 2 % to >100 % of the measured fecal pellet carbon flux in the sediment trap at 20 m. More fecal pellet carbon was found in the 20 m sediment trap then was estimated to be produced by the > 500 µm copepods in April and September. In contrast, during the remainder of the study, May-August, < 50 % of the estimated, potential *in situ* fecal pellet flux was found in the 20 m trap. However summing the integrated trap material from 0-200 m, indicates that more fecal pellet carbon was measured in the traps than was potentially, produced in the overlying euphotic zone by the > 500 µm copepods, in every month except May. In May, only 11 % of the estimated *in situ* fecal pellet flux (3464 mg C m^{-2} d^{-1}) was found as recognizable fecal pellet carbon in all the sediment traps (382 mg C m^{-2} d^{-1}) and only 3 % was collected in the 200 m trap (105 mg C m^{-2} d^{-1}).

Numbers of sedimenting fecal pellets decreased with depth yet the flux of organic carbon due to fecal pellets

increased with depth in May, June and August (Table 4). This resulted in a doubling of the carbon/pellet ratio suggesting more recently egested fecal pellets with depth. Visual examination of the trap contents revealed many large calanoid and euphausiid type pellets. July and September sediment trap data showed a mid-water depth increase in the carbon/pellet ratio. During all the months except September, the 20 and 60 m sediment trap carbon/pellet values resembled that measured in the freshly egested fecal pellets from mesozooplankton. September pellet trap measurements were 5-fold higher than that measured in the freshly egested fecal pellets.

DISCUSSION

Estimated potential fecal pellet carbon flux

In coastal regions where a diverse population of grazers exists that range in size from < 1 µm to > 10 mm, it is difficult to characterize and predict fecal pellet carbon flux. An increasing number of studies show that the zooplankton community composition strongly affects the amount and type of carbon available for export (Hofmann & al. 1981; Krause 1981 Welschmeyer & Lorenzen 1985; Emerson & Roff 1987; González & Smetacek 1994; Lane & al. 1994, Wassmann 1998). On Nordvestbanken, the zooplankton community structure shifted both seasonally and along an in-shore to off-shore gradient. In the spring, *Calanus finmarchicus* dominated the zooplankton community, especially in May when it made up numerically ≥ 70 % of the zooplankton community. During the summer the community shifted to smaller, neritic species and in late summer to early autumn, the pteropod *Limacina* sp. comprised a significant fraction of the zooplankton community (Halvorsen & Tande 1999). This change in zooplankton community structure could be expected to result in different potential fecal pellet flux estimates and in the actual pellet flux measured in sediment traps. Large fecal pellets produced by *C. finmarchicus* would presumably contribute significantly to the vertical flux of carbon to the sediments while smaller pellets produced by *Acartia longiremis, Temora longicornis* and *Oithonia* spp. would likely be recycled in the water column. Generally, results from this investigation support this simplistic view, as fecal pellet carbon contribution to POC flux at 200 m was highest in April and May when *C. finmarchicus* was most abundant (Table 3).

Besides zooplankton species composition, environmental variables such as food concentration and water temperature could be expected to influence the potential fecal pellet carbon production in the euphotic zone. Generally, fecal pellet production rates increases with food supply (Dagg & Walser 1986; Ayukai 1990) so during a phytoplankton bloom it could be assumed that fecal pellet production rates would be higher than during other seasons. Zooplankton grazing rates and thus fecal pellet production rates increase with water temperature (Huntley & Lopez 1992) and with a decrease in body size (Ayukai & Nishizawa 1986; Morales & al. 1993). In coastal Norwegian waters there is a temporal lag between these environmental variables (food supply and water temperature) that along with changes in zooplankton size structure could possibly balance each other such that no seasonal changes in a community average fecal pellet production rate would be measurable. However, changes in pellet production rates did occur between months and were positively correlated with water temperature but only a small percent (r^2 = 0.10) of the variance could be explained by temperature. At the shelf edge station maximum pellet production rates occurred either during May when zooplankton abundance was the highest and dominated by *C. finmarchicus* or July when *Oithona* spp. were dominant. These monthly changes in pellet production rates most likely reflect changes in both seston composition and quality along with changes in zooplankton species, i.e. high food supply rate in May and smaller copepods with warmer water in July.

Phytoplankton growth rates and chemical composition can change with depth in the water column so presumably fecal pellet production rates by mesozooplankton could also change with depth. The lack of a significant change in fecal pellet production rates within the euphotic zone (Table 1) suggests that either the seston or zooplankton community structure was homogeneously mixed or that the methods employed in this study were not adequate to determine small significant changes in pellet production rates. The

Table 3. Particulate organic carbon (POC) sedimentation (mg C m^{-2} day^{-1}) from 20 m and 200 m from a drifting sediment trap and the percent composition of fecal pellet carbon to total carbon during the OMEX study on Nordvestbanken, north Norwegian shelf in 1994. [1]Data from Andreassen & al. (1999)

	[1]POC Flux mg C m^{-2} day^{-1} (% Fecal pellet carbon)					
Depth	April	May	June	July	August	September
20 m	200 (11 %)	300 (21 %)	230 (5 %)	300 (5 %)	200 (5 %)	230 (23 %)
200 m	120 (29 %)	300 (35 %)	130 (18 %)	185 (7 %)	130 (13 %)	130 (7 %)

high degree of variability in individual copepod feeding behavior (Paffenhöfer 1994) may have obscured any depth dependant variability in production rates.

Typically in coastal north Norwegian waters a spring bloom occurs in May-June while water temperatures are still fairly cold (Rey 1981; Hegseth & al. 1995). During this study in 1994, no spring bloom was observed via a build up of chlorophyll stocks. However nutrient levels during the investigation suggest this was an area of high primary production (Wassmann & al. 1999a). The high, build up of *C. finmarchicus* biomass in May (Halvorsen & Tande 1999), must reflect a high grazing pressure and suggests that the zooplankton community on Nordvestbanken was able to maintain the phytoplankton biomass. Examining the fecal pellet production rates from March-May, presuming they reflect *C. finmarchicus* pellet production rates (as they made up the numerically dominant component of the zooplankton community at this time), indicates a 2 to 5-fold increase in production rates (Table 1). This increase in pellet production rates most likely reflects an increase in the rate of food supply. However, with the current data set it is not possible to tease out the effects of changing temperature, food supply and zooplankton species on the community average fecal pellet production rate.

Chlorophyll levels remained low and constant throughout the year (data shown in Wassmann & al. 1999a). Based on the estimated carbon ingestion, mesozooplankton grazing could have maintained these low chlorophyll stocks. The high carbon ingestion value, 250 g C m^{-2} for the duration of the OMEX study is substantially higher than the new production values (70 g C m^{-2}) calculated by Wassmann & al. (1999a) through nutrient depletion. Even if allowance is made for all the potential errors associated in assuming a constant assimilation value, obtaining an average fecal pellet production value and in calculating new production based on nutrient depletion, the estimated carbon ingested by mesozooplankton was significantly above that being produced through new production. It seems logical to conclude that the mesozooplankton were also consuming detritus and/or microzooplankton, especially since flagellates comprised a dominant component of the phytoplankton biomass during this study (Ratkova & al. 1999). This conclusion would suggest that there was an active microbial food web on Nordvestbanken in 1994, the same as concluded by Ratkova & al. (1999) based on the abundance and biomass of pico-, nano- and microplankton. While it was traditionally thought that polar waters and Norwegian coastal waters were dominated by short food chain, several recent studies have shown that much of the carbon in polar waters is channeled through a microbial food web (Nielsen & Hansen 1995; Hansen & al. 1996; Verity & al. 1999).

Table 4. Zooplankton fecal pellet flux measured in terms of fecal pellet numbers and fecal pellet carbon from a drifting sediment trap during the OMEX study on Nordvestbanken, north Norwegian shelf in 1994.

Depth (m)	Apr	May	Jun	Jul	Aug	Sep
Fecal pellet flux ($\times 10^3$ pellets m^{-2} day^{-1})						
20	243	470	74	206	139	270
60	235	548	106	298	114	146
100	471	580	91	120	79	97
160	317	449	75	218	45	75
200	436	399	131	142	63	70
Fecal pellet flux (mg C m^{-2} day^{-1})						
20	22.2	62.0	11.2	15.3	9.5	53.7
60	32.5	61.8	9.9	32.3	19.6	43.9
100	35.0	52.9	12.6	36.6	11.0	30.4
160	15.6	100.2	26.6	19.3	15.7	18.1
200	34.5	104.7	22.8	13.3	16.5	9.5

The changes in fecal pellet carbon (FPC) and dry weight (DW) content over the course of this study suggest both changes in diet and changes in zooplankton producers. The total carbon content of the pellets decreased over the study, however the carbon to volume ratio remained fairly constant all months (data not shown). Thus, the smaller copepods that were present in the summer and fall made smaller pellets with less carbon per pellet. However, since the DW of the pellets in the summer was similar to that in the spring it would suggest that these pellets are densely packed with small, easily compressed food items with a low initial carbon content (Urban & al. 1993). The low carbon content of the fall pellets with the corresponding high FPC/DW ratio suggests that these pellets were produced either by grazers with low assimilation efficiency or there was a change in the available seston. Flagellates were abundant in the fall (Ratkova & al. 1999) which could possibly explain the results found here. The differences observed between the day and night FPC/DW ratio for April, May and September are not easily explained. Besides investigator error, it could possibly be due to an inherent diel change in assimilation efficiency in the copepods or in the chemical composition of the phytoplankton. For both April and September the day/night FPC/DW differences were significant at $p \leq 0.001$. While the percent of total carbon due to amino acid carbon was 2 times higher at night in the pellets but the percent of total carbon due to amino acids in the seston remained similar (Urban-Rich 1997) suggesting changes in the assimilation of various organic compounds by the copepods. More work would be needed to determine if an inherent, diel metabolism exists in polar copepods. However, it appears that the time of fecal pellet production can influence the amount and type of organic carbon available for export.

Potential fecal pellet flux vs measured pellet flux

If we assume that the discrepancy in the estimated *in situ* pellet carbon production and that measured in the 20 m, sediment traps is accurate then coprophagy, coprorhexy, coprochally and/or microbial degradation would be important water column processes on Nordvestbanken. This is especially true for May when only 11 % of the estimated, *in situ* fecal pellet carbon production was recovered in the traps from 20 to 200 m. *Calanus finmarchicus* was the dominant mesozooplankter during that sampling period (Halvorsen & Tande 1999). These results indicate that *C. finmarchicus* plays an important role in mediating the vertical flux of organic carbon in the spring both through the production of fecal pellets and potentially through coprophagy, coprorhexy and/or coprochaly (Noji & al. 1991). While little is known about the activity and role of the microbial food web in this area, several previous studies have indicated that copepods play an important role in modifying the vertical organic carbon flux (Bathmann & al. 1987; Lampitt & al. 1990; Martens & Krause 1990; González & al. 1994; González & Smetacek 1994).

The significant differences in May-August, 1994 in the estimated fecal pellet production (Fig. 5) and the actual amount of fecal pellet carbon found in the sediment traps (Table 4) illustrates the importance of fecal pellets in the recycling of nutrients in the euphotic zone through degradation or coprophagy. Only, April and September had a lower estimated fecal pellet carbon production then was actually measured in the sediment traps. This suggests that for these two months some source other then large copepods was contributing ≥ 96 % of the fecal pellet carbon flux. Possible explanations for this variation could be due to investigator errors with estimates of pellet carbon flux or sediment trap collection. Alternatively, zooplankton other than large copepods were important in pellet carbon flux in these months. The latter possibility seems to be likely for September. The measured fecal pellet carbon content from the 20 and 60 m sediment traps in September was 5-fold higher than that measured from freshly egested fecal pellets (0.20-0.30 µg C pellet^{-1} vs 0.04-0.06 µg C pellet^{-1}). The pteropod, *Limacina* sp. was abundant during this sampling period (Halvorsen & Tande 1999). While no attempt was made to quantify the different fecal pellet types, pteropod pellets were observed in the sediment trap samples in August and September. It is unlikely that the pteropods fed during the shipboard incubations thus the community average fecal pellet carbon value would not contain these pellets. The surface traps in September probably reflect the input of pteropod pellets that was not estimated based on the shipboard experiments.

Sedimenting fecal pellets decreased with depth yet the organic carbon content of the pellets doubled in May, June and August (Table 4), suggesting more recently egested fecal pellets from vertically migrating zooplankton. However, MOCNESS and ADCP data did not indicate any vertical migration at any of the stations across Nordvestbanken (E. Nordby & K.S. Tande, pers. commn). Yet, large calanoid and euphausiid pellets were observed in the trap samples. Euphausiids frequently occur in localized patches. It is entirely possible that a swarm of euphausiids passed over our study site shortly before we began sampling and thus were not detected. Alternatively the calanoid or euphausiid pellets could have been advected into the study site from a population of vertically migration zooplankton in the slope waters by the strong coastal currents present at the shelf edge (Moseidjord & al. 1999). The strong current patterns along the coast of northern Norway suggest that horizontal advection can play a major role in transporting particles from their origins. July and September trap data showed a mid-water depth increase in the carbon/pellet ratio indicating a short vertical migration or the presence of a mid-water column community of zooplankton. The latter scenario is supported by the zooplankton samples (Halvorsen & Tande 1999) which showed a mid-water population of *Metridia* spp. and *Microcalanus pusillus*. There was no significant correlation between individual zooplankton species and the measured pellet carbon flux so it was not possible to determine the role of individual species on pellet flux.

A minimum of 5-35 % of the total POC that was collected in the sediment traps came from fecal pellet carbon. The measured carbon flux is likely to be an underestimate of the total pellet flux due to the fact that many pellets could be broken or degraded beyond recognition or to enhanced total POC flux due to swimmers (Michaels & al. 1990). However, estimates of fecal pellet carbon flux to POC flux based on suspended fecal pellet concentrations give an average range of 6 to 37 % (Wassmann & al. 1999b) which is very similar to that measured in this study. Using all potential data, *in situ* fecal pellet production, measured pellet flux, suspended fecal pellet concentration and estimated pellet flux indicate that fecal pellets could be a significant fraction of the export POC flux during most months (Table 3).

CONCLUSIONS

Results from this study show that mesozooplankton fecal pellets can contribute a large percent (35 %) of the carbon flux at the shelf edge in northern Norwegian waters. Fecal pellet contribution to POC flux depended primarily on zooplankton abundance. Maximum estimated potential fecal pellet flux along with the measured pellet carbon flux was found in May when *C. finmarchicus* was the dominant species. However, only

11 % of the estimated potential pellet flux was recovered in the sediment traps from 20 to 200 m. Also only 3 % of the potential pellet carbon flux was recovered in the trap at 200 m, indicating that there was a rapid and large recycling of pellet material occurring in the water column either through coprophagy and/or microbial degradation. These results indicate that *C. finmarchicus* is an important mediator of POC flux in northern Norwegian waters both through its *in situ* fecal pellet production and possibly through coprophagy.

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REFERENCES

Alldredge AL, Gotschalk CC, MacIntyre S. 1987. Evidence for sustained residence of macrocrustacen fecal pellets in surface waters off Southern California. *Deep-Sea Research* 34:1641-1652.

Andreassen I, Nöthig EM, Wassmann P. 1996. Vertical particle flux on the shelf off northern Spitsbergen, Norway. *Marine Ecology Progress Series* 137:215-228.

Andreassen IJ, Wassmann P, Ratkova TN. 1999. Seasonal variation of vertical flux of phytoplankton and biogenic matter at Nordvestbanken, north Norwegian shelf in 1994. *Sarsia* 84:227-238.

Angel MV. 1984. Detrital organic fluxes through pelagic ecosystems. In: Fasham MJR, editor. *Flows in energy and material in marine ecosystems theory and practice*. New York: Plenum Press. p 475-516.

Ayukai T. 1990. Fecal pellet production by two species of planktonic calanoid copepods fed on naturally occurring particles. *Bulletin Plankton Society Japan* 37:167-169.

Ayukai T, Nishizawa S. 1986. Defecation rate as a possible measure of ingestion rate of *Calanus pacificus pacificus* (Copepoda: Calanoida). *Bulletin Plankton Society Japan* 33:3-10.

Bathmann UV. 1988. Mass occurrence of *Salpa fusiformis* in the spring of 1984 off Ireland: implications for sedimentation processes. *Marine Biology* 97:127-135.

Bathmann UV, Noji TT, Voss M, Peinert R. 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. *Marine Ecology Progress Series* 38:45-51.

Bodungen B von, Fischer G, Nöthig E-M, Wefer G. 1987. Sedimentation of krill faeces during spring development of phytoplankton in Bransfield Strait, Antarctica. *SCOPE/UNEP Sonderband* 62:243-257.

Butler M, Dam HG. 1994. Production rates and characteristics of fecal pellets of the copepod *Acartia tonsa* under simulated phytoplankton bloom conditions: implications for vertical flux. *Marine Ecology Progress Series* 114:81-91.

Checkley DM, Entzeroth LC. 1985. Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. *Journal of Plankton Research* 7:553-568.

Corner EDS, O'Hara SCM, Neal AC, Eglinton G. 1986. Copepod faecal pellets and the vertical flux of biolipids. In: Corner EDS, O'Hara SCM, editors. *The biological chemistry of marine copepods*. Oxford: Clarendon Press. p 260-321.

Cowles TJ, Olson RJ, Chisholm SW. 1988. Food selection by copepods: discrimination on the basis of food quality. *Marine Biology* 100:41-49.

Dagg MJ, Walser WE Jr. 1986. The effect of food concentration on fecal pellet size in marine copepods. *Limnology & Oceanography* 31:1066-1071.

Emerson CW, Roff JC. 1987. Implications of fecal pellet size and zooplankton behaviour to estimates of pelagic-benthic carbon flux. *Marine Ecology Progress Series* 35:251-257.

Fortier L, Le Fèvre J, Legendre L. 1994. Export of biogenic carbon to fish and to the deep ocean: the role of large planktonic microphages. *Journal of Plankton Research* 16:809-839.

Fowler SW, Small LF. 1972. Sinking rates of Euphausiid fecal pellets. *Limnology & Oceanography* 17:293-296.

Fowler SW, Small LF, La Rosa J. 1991. Seasonal particulate carbon flux in the coastal northwestern Mediterranean Sea, and the role of zooplankton fecal matter. *Oceanologica Acta* 14:77-85.

González HE, González SR, & Brummer G-JA. 1994. Short-term sedimentation pattern of zooplankton, faeces and microplankton at a permanent station in the Bjørnafjorden (Norway) during April-May 1992. *Marine Ecology Progress Series* 105:31-45.

González HE, Smetacek V. 1994. The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. *Marine Ecology Progress Series* 113:233-246.

Halvorsen E, Tande KS. 1999. Physical and biological factors influencing the seasonal variation in distribution of zooplankton across the shelf at Nordvestbanken, northern Norway, 1994. *Sarsia* 84:279-292.

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

Hegseth EN, Svendsen H, Quillfeldt CH von. 1995. Phytoplankton in fjords and coastal waters of northern Norway: environmental conditions and dynamics of the spring bloom. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP, editors. *Ecology of Fjords and Coastal Waters*. Elsevier Science. p 45-72.

Hofmann EE, Klink JM, Paffenhöfer G-A. 1981. Concentrations and vertical fluxes of zooplankton fecal pellets on a continental shelf. *Marine Biology* 61:327-335.

Honjo S, Manganini SJ, Wefer G. 1988. Annual particle flux and a winter outburst of sedimentation in the northern Norwegian Sea. *Deep-Sea Research* 35:1223-1234.

Houde SEL, Roman MR. 1987. Effects of food quality on the functional ingestion response of the copepod *Acartia tonsa*. *Marine Ecology Progress Series* 40:69-77.

Huntley ME, Lopez MDG. 1992. Temperature-dependent production of marine copepods: a global synthesis. *American Naturalist* 140:201-242.

Knauer GA, Martin JH, Bruland KW. 1979. Fluxes of particulate carbon, nitrogen and phosphorus in the upper water column of the Northeast pacific. *Deep-Sea Research* 26:97-108.

Krause M. 1981. Vertical distribution of faecal pellets during flex '76. *Helgoländer Meeresuntersuchungen* 34:313-327.

Lampitt RS, Noji T, Bodungen B von. 1990. What happens to zooplankton faecal pellets? Implications for material flux. *Marine Biology* 104:15-23.

Lane PVZ, Smith SL, Urban JL, Biscaye PE. 1994. Carbon flux and recycling associated with zooplanktonic fecal pellets on the shelf of the Middle Atlantic Bight. *Deep-Sea Research* 41:437-457.

Madin LP. 1982. Production, composition and sedimentation of salp fecal pellets in oceanic waters. *Marine Biology* 67:39-45.

Martens P, Krause M. 1990. The fate of faecal pellets in the North Sea. *Helgoländer Meeresuntersuchungen* 44:9-19.

Marty JC, Nicolas E, Miquel JC, Fowler SW. 1994. Particulate fluxes of organic compounds and their relationship to zooplankton fecal pellets in the northwestern Mediterranean Sea. *Marine Chemistry* 46:387-405.

Michaels AF, Silver M, Gowing MM, Knauer GA. 1990. Cryptic zooplankton "swimmers" in upper ocean sediment traps. *Deep-Sea Research* 37:1285-1296.

Morales CE. 1987. Carbon and nitrogen content of copepod faecal pellets: effect of food concentration and feeding behavior. *Marine Ecology Progress Series* 36:107-114.

Morales CE, Harris RP, Head RN, Tranter PRG. 1993. Copepod grazing in the oceanic northeast Atlantic during a 6 week drifting station: the contribution of size classes and vertical migrants. *Journal Plankton Research* 15:185-211.

Moseidjord H, Svendsen H, Slagstad D. 1999. Sensitivity studies of circulation and ocean-shelf exchange off northern Norway. *Sarsia* 84:191-198.

Nielsen TG, Hansen B. 1995. Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. *Marine Ecology Progress Series* 125:239-257.

Noji TT. 1991. The influence of macrozooplankton on vertical particulate flux. *Sarsia* 76:1-9.

Noji TT, Estep KW, Macintyre F, Norrbin F. 1991. Image analysis of faecal material grazed upon by three species of copepods: evidence for coprorhexy, coprophagy and coprochaly. *Journal of Marine Biological Association UK* 71:465-480.

Nordby E, Tande KS, Svendsen H, Slagstad D. 1999. Oceanography and fluorescence at the shelf break off the north Norwegian coast (69°20'N-70°30'N) during the main productive period in 1994. *Sarsia* 84:175-189.

Paffenhöfer G-A. 1994. Variability due to feeding activity of individual copepods. *Journal of Plankton Research* 16:617-626.

Ratkova TN, Wassmann P, Verity PG, Andreassen IJ. 1999. Abundance and biomass of pico-, nano-, and microplankton on a transect across Nordvestbanken, north Norwegian shelf, in 1994. *Sarsia* 84:213-225.

Rey F. 1981. The development of the spring phytoplankton outburst at selected sites off the Norwegian coast. In: Sætre R, Mork M, editors. *The Norwegian Coastal Current*. Proceedings from the Norwegian coastal current symposium; 1980 Sep 9-12; Geilo, Norway. p 649-680.

Small LF, Ellis SG. 1992. Fecal carbon production by zooplankton in Santa Monica Basin: the effects of body size and carnivorous feeding. *Progress in Oceanography* 30:197-221.

Smetacek VS. 1980. Zooplankton standing stock, copepod faecal pellets and particulate detritus in Kiel Bight. *Estuary and Coastal Marine Science* 11:477-490.

Urban JL. 1992. Seasonal chemical and physical characteristics of *Oikopleura vanhoeffeni* and *Calanus finmarchicus* fecal pellets. Memorial University of St. John's. Newfoundland, Canada.

Urban JL, Deibel D, Schwinghamer P. 1993. Seasonal variations in the densities of fecal pellets produced by the pelagic tunicate *Oikoplura vanhoeffeni* and the copepod *Calanus finmarchicus*. *Marine Biology* 117:607-613.

Urban JL, McKenzie CH, Deibel D. 1992. Seasonal changes in the chemical and physical characteristics of *Oikopleura vanhoeffeni* and *Calanus finmarchicus* faecal pellets: illustrations of zooplankton food web shifts in coastal Newfoundland waters. *Marine Ecology Progress Series* 84:255-264.

Urban-Rich JL. 1997. *Latitudinal variations in the contribution by copepod fecal pellets to organic carbon and amino acid flux* [PhD dissertation]. University of Maryland, USA.

Urban-Rich J. 1999. Release of dissolved organic carbon from copepod fecal pellets in the Greenland Sea. *Journal of Experimental Marine Biology and Ecology* 231:107-124.

Urrère MA, Knauer GA. 1981. Zooplankton fecal pellet fluxes and vertical transport of particulate organic material in the pelagic environment. *Journal of Plankton Research* 3:369-387.

Verity PG, Wassmann P, Ratkova TN, Andreassen IJ, Nordby E. 1999. Seasonal patterns in composition and biomass of autotrophic and heterotrophic nano- and microplankton communities on the north Norwegian shelf. *Sarsia* 84:265-277.

Wassmann P. 1991. Dynamics of primary production and sedimentation in shallow fjords and polls of western Norway. *Oceanography and Marine Biology Annual Review* 29:87-154.

Wassmann P. 1998. Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. *Hydrobiologia* 363:29-57.

Wassmann P, Andreassen IJ, Rey F. 1999a. Seasonal variation of nutrients and suspended biomass on a transect across Nordvestbanken, north Norwegian shelf, in 1994. *Sarsia* 84:199-212.

Wassmann P, Hansen L, Andreassen IJ, Wexels Riser C, Urban-Rich J. 1999b. Distribution and sedimentation of faecal pellets on the Nordvestbanken shelf, northern Norway, in 1994. *Sarsia* 84:239-252.

Wassmann P, Peinert R, Smetacek V. 1991. Patterns of production and sedimentation in the boreal and polar Northeast Atlantic. In: Sakshaug E, Hopkins CCE, Øritsland NA, editors. *Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12-16 May 1990*. Polar Research 10(1). p 209-228.

Wassmann P, Slagstad D. 1993. Seasonal and annual dynamics of particulate carbon flux in the Barents Sea. *Polar Biology* 13:363-372.

Welschmeyer NA, Lorenzen CJ. 1985. Chlorophyll budgets: Zooplankton grazing and phytoplankton growth in a temperate fjord and the Central Pacific Gyres. *Limnology and Oceanography* 30:1-21.

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