

# Short-term sedimentation pattern of zooplankton, faeces and microplankton at a permanent station in the Bjørnafjorden (Norway) during April–May 1992

Humberto E. González<sup>1</sup>, Santiago R. González<sup>2</sup>, Geert-Jan A. Brummer<sup>2</sup>

<sup>1</sup>Alfred Wegener Institute for Polar and Marine Research, Postfach 120161, D-27570 Bremerhaven, Germany

<sup>2</sup>Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, The Netherlands

**ABSTRACT:** Sedimentation rates were determined daily over a 2 wk period (late April – early May 1992) under post spring bloom conditions at a permanent station in the Bjørnafjorden, Norway. Samples collected using floating sediment traps deployed at 50 and 100 m depth showed that sedimented seston, particulate organic matter, carbonate and lithogenic + opal fractions were, on average, twice as high at 100 m (221, 99, 51 and 76 mg m<sup>-2</sup> d<sup>-1</sup>, respectively) as at 50 m (119, 62, 27 and 34 mg m<sup>-2</sup> d<sup>-1</sup>, respectively). Faecal pellets made up the bulk of sedimenting matter, accounting for 87 and 92 % of the average total organic carbon recorded at 50 and 100 m, respectively. The remaining sedimented matter consisted mainly of tintinnids. Diatoms cells and resting spores, coccolithophorids and flagellates contributed a minor fraction. It is postulated that the vertical flux of faecal pellets was determined by a combination of 3 factors: (1) relatively high standing stock of actively grazing mesozooplankton dominated by calanoid copepods and appendicularians, which are known for their high faeces production rates; (2) a relatively high abundance of the cyclopoid copepod *Oithona similis*, which is reported to feed on faecal pellets produced by calanoid copepods, suggesting that coprophagy in the water column was high; (3) a phytoplankton community dominated by diatoms and coccolithophorids, whose mineral skeletons accelerate sinking rates of faecal pellets.

**KEY WORDS:** Norwegian fjord · Faecal pellets · Vertical flux · Plankton

## INTRODUCTION

Generally, the wide range of regional and seasonal variation in quantity and composition of sedimenting matter, as measured with sediment traps, is a function of the overlying pelagic system (Peinert et al. 1989), becoming more complex with increasing number of trophic links (Silver & Gowing 1991). Annual patterns of vertical particle flux from a number of sites in coastal, shelf and open ocean areas bordering the northern North Atlantic were recently compared and contrasted in reviews by Wassmann (1991) and Wassmann et al. (1991). These authors showed that there is considerable variation in seasonal patterns, presumably shaped by the combination of local or regional hydrography and the developmental dynamics of the pelagic system. Different scenarios for the relationship

between developmental stages of the pelagic system and the magnitude and composition of vertical flux were discussed by Peinert et al. (1989). They suggested that vertical flux is low in relation to surface primary production when mesozooplankton grazing pressure, in particular by copepods, attains characteristic summer levels. Mesozooplankton grazing leads to production of compact faeces known to have much higher sinking rates than food particles. Furthermore, at zooplankton biomass levels characteristic of the boreal summer [5 g particulate organic carbon (POC) m<sup>-2</sup> for the Norwegian Sea; Noji 1989] approximately 1 to 1.5 g POC m<sup>-2</sup> is defecated per day, assuming an assimilation efficiency in the range 70 to 80 % (Petipa et al. 1970, Corner et al. 1986). Why pellets do not sink has been speculated on by many authors. Ingestion (coprophagy), fragmentation (coprorhexy) and loosen-

ing (coprochaly) of faecal material by copepods have been suggested as the reasons for the efficient recycling of faecal pellets near surface layers in the Norwegian Current (Bathmann et al. 1987, Peinert et al. 1989, Lampitt et al. 1990, Noji et al. 1991).

In protected and semi-enclosed areas of western Norway, various sedimentation patterns have been reported, stressing the high variability in the particle flux in these areas. While gross sedimentation decreased with depth in land-locked fjords or polls (Wassmann 1991), it increased in open fjords in western Norway (Lutter et al. 1989, Wassmann 1991, Noji et al. 1993). Similar sedimentation patterns — with increasing amounts of sedimented matter with depth — have been described for other coastal (Smetacek et al. 1978, Landry et al. 1992) and oceanic environments (Small et al. 1987).

In order to unravel the mechanisms linking euphotic zone production and trophic structure to organic (and inorganic) sedimentation, more trap data are needed in conjunction with process-oriented studies in the water column. We conducted an intensive sampling program at a permanent station in the Bjørnafjorden. We analysed the distribution and abundance of micro- and mesozooplankton and faecal material both in the water column and sedimented in free-floating traps deployed at 50 and 100 m depths.

Shipboard experiments were carried out in order to estimate the role of copepods in the modification of the vertical flux of faecal pellets, i.e. faeces production and consumption in calanoid and cyclopoid copepods.

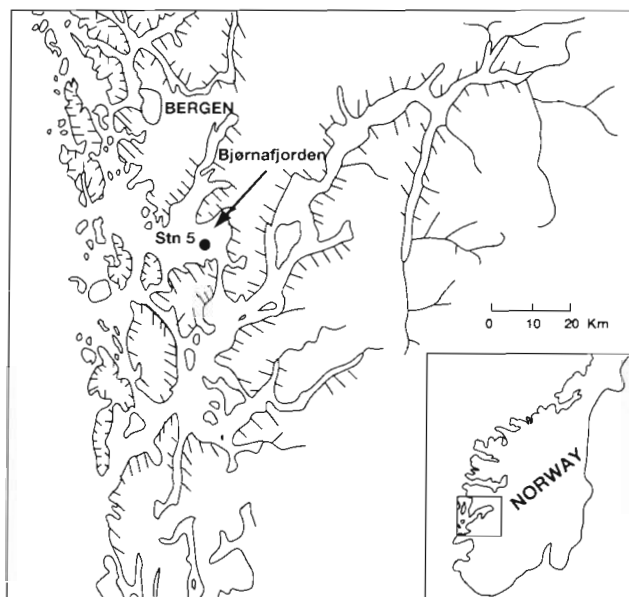


Fig. 1. The study area, showing the position of Stn 5 in the Bjørnafjorden

In addition, egg production rate was measured in calanoid copepods as an indirect measure of the suitability (as food) of the *in situ* phytoplankton assemblages.

## MATERIALS AND METHODS

Samples were collected on board the RV 'Pelagia' during the International Coccolithophorid Expedition (24 April to 7 May 1992), at a permanent station (Stn 5) in a 400 m water column in the Bjørnafjorden, Norway (Fig. 1).

The vertical flux of particulates was measured with paired funnel-shaped traps (Zeitzschel et al. 1978, Cadée 1986) deployed at 50 and 100 m depth for 24 h periods from 24 April to 2 May 1992. No poisons were used during the deployments. After recovery of the traps, the sedimented material was preserved with hexamine buffered formalin (final concentration 2%).

**Estimation of seston, organic matter, carbonate and lithogenic + opal fractions from sediment trap samples.** Preserved subsamples were taken and filtered on preweighed, precombusted GF/C filters, rinsed with distilled water, dried for 6 h at 60 °C and then weighed for estimate of total seston (Lenz 1971). The carbonate fraction was determined by reweighing the filters after decalcification with a few drops of HCl (1N), rinsed with distilled water and dried at 60 °C for 4 h. The total organic matter content fraction was estimated by reweighing the filters after combustion at 550 °C for 3 h. Thus, the reduction in weight after combustion was considered particulate organic matter, as ash-free dry weight, and the remaining material was considered lithogenic + opal fraction.

**Field estimation of zooplankton abundances and faecal matter.** Zooplankton and faecal pellets from the water column were collected from 0–50, 50–100 and 100–300 m depth strata using 2 opening/closing WP-2 nets (200 and 50 µm mesh size, respectively).

**Estimation of organic carbon from microplankton and faecal matter collected in sediment traps.** Preserved subsamples of the sedimented material were used for phytoplankton, microzooplankton and faecal material counting and sizing using standard microscopy methods (Utermöhl 1958). The carbon content of phytoplankton cells filled with cytoplasm was calculated from their cell volume (Smetacek 1975, Edler 1979).

Faecal pellets (distinguished as copepod, larvacean and euphausiid origin) were measured (length, width) and gently sorted by pipetting from natural net samples, sediment trap samples and from experimental flasks. These faeces were introduced into precombusted glass ampoules in groups of 50 to 200 units and

the carbon content was measured with a 0524B Total Carbon System of Oceanography International which uses a wet persulphate oxidation method (Cadée 1982). Average volume-to-carbon ratios for different types of faecal pellet were calculated and are included as a footnote in Table 2. Faeces collected in sediment traps (from metazoans and protists) were identified based on descriptions published elsewhere (González 1992a, b and references therein).

Total volume of faecal pellets collected in the sediment traps was calculated after counting and sizing (length and width) every intact and broken faecal pellet from a subsample using standard microscopy methods (Utermöhl 1958). It was assumed that copepod and euphausiid faeces have a cylindrical geometrical shape and appendicularian faeces an ellipsoidal shape. Faecal pellet carbon from sediment samples was calculated by using the estimated volume-to-carbon ratios (see Table 2).

**Experiments for assessing egg production rate and faecal pellet production and consumption.** Additional mesozooplankton samples were collected by short vertical tows using the WP-2 (200 µm mesh size) net in order to collect live copepods for experiments. Females of dominant calanoid and cyclopoid copepods were immediately sorted under a dissecting microscope and incubated at *in situ* temperature ( $6 \pm 1^\circ\text{C}$ ) in flasks filled with natural seawater collected from 10 m depth. In order to exclude large zooplankton already present in the seawater, this was prescreened through 300 µm gauze before starting the experiments.

**Egg production rate in *Temora longicornis*:** Six females were placed in 2 l flasks provided with a 400 µm screen located near the bottom. Only the eggs passed through the screen, avoiding potential ingestion of these eggs by the copepods. After 24 h the contents were filtered through a 20 µm mesh sieve and females and eggs were counted.

**Faecal pellet production and consumption rates in *Calanus finmarchicus* (CV) and *Oithona similis* (adults):** Experiments were conducted twice at 'low' and 'high' *in situ* chlorophyll *a* (chl *a*) concentrations:  $1.1 \mu\text{g l}^{-1}$  (26 April 1992) and  $2.2 \mu\text{g l}^{-1}$  (1 May 1992). Three treatments (with 9 replicates each) were used at the same temperature ( $6 \pm 1^\circ\text{C}$ ) and food level (natural phytoplankton assemblages). Undamaged copepods were allowed to defecate in the following 3 treatments:

**Treatment 1 (control):** Six females of *Calanus finmarchicus* were placed in 2 l flasks with a 400 µm mesh screen located near the bottom of the flask. Only the faeces passed through the screen.

**Treatment 2:** As Treatment 1, but without the screen. The copepods were allowed to reach the faeces they produced (enabling coprophagy and fragmentation of faeces).

**Treatment 3:** As Treatment 1, but including an additional 16 (26 April) or thirty (1 May) *Oithona similis* adults. Faeces produced by calanoid copepods and *O. similis* individuals were able to pass through the 400 µm net (enabling coprophagy and fragmentation of faeces by *O. similis*).

After 24 h the faeces produced by *Calanus finmarchicus* in each flask were collected on a 50 µm mesh sieve, counted, and sized using a dissecting microscope.

## RESULTS

### Hydrography

A 20 to 30 m thick, low salinity (<33‰, 6 to 7°C) surface layer was separated from underlying water (>34‰, >7°C) by a sharp thermocline between 25 and 50 m. From 24 April to the beginning of May, the thermocline descended to the 50–75 m depth stratum (Fig. 2A, B).

### Mesozooplankton vertical distribution and abundance

Almost all groups were most abundant in the 0–50 m depth stratum (Table 1). *Oithona similis* (cyclopoid copepod), *Calanus finmarchicus* and *Temora longicornis* (calanoid copepods), *Evadne nordmanni* (cladoceran), *Oikopleura* spp. and *Fritillaria borealis* (appendicularians) predominated in terms of abundance (Table 1). *O. similis* has been reported to be numerically dominant in Norwegian fjords (Magnesen 1989, Kaartvedt & Nordby 1992). Integrated abundances of mesozooplankton species showed relatively low variability with time, with the exception of 26 April (68 h), when a peak in the abundances in almost all taxa was recorded (Fig. 3).

### Types of faeces collected from the water column

The most common faecal pellets collected were: (1) larvacean pellets which had an ellipsoid shape, and an average volume and carbon content of  $8.02 \times 10^5 \mu\text{m}^3$  and  $0.032 \mu\text{g C}$  respectively; (2) cylindrical copepod pellets with an average volume and carbon content of  $5.6 \times 10^5 \mu\text{m}^3$  and  $0.032 \mu\text{g C}$  respectively; (3) cylindrical euphausiid pellets with an average volume and carbon content of  $9.3 \times 10^8 \mu\text{m}^3$  and  $14.46 \mu\text{g C}$  respectively; (4) semi-degraded and broken faecal pellets which precluded categorisation and are classed as unidentified faeces.

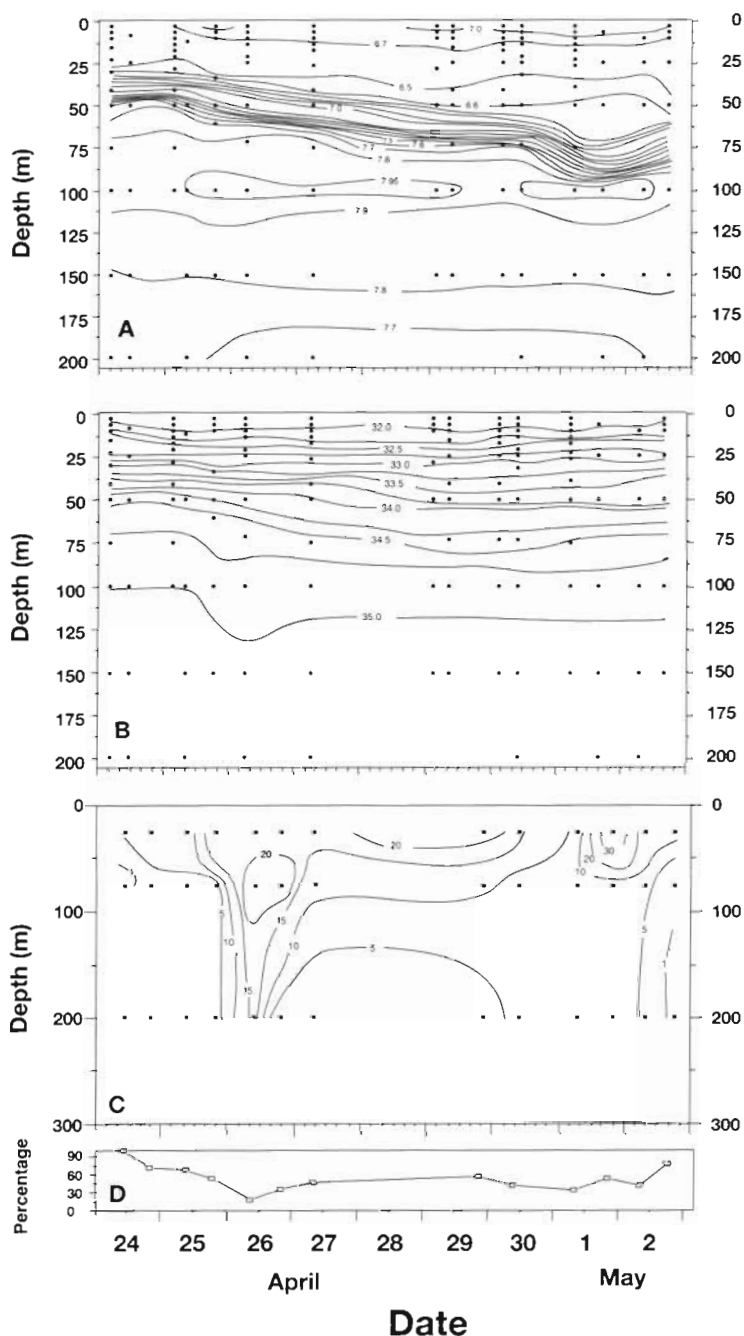


Fig. 2. Vertical distribution of: (A) temperature (°C), and (B) salinity (‰) in the upper 200 m water column. (C) Faecal material volume (mm<sup>3</sup> m<sup>-3</sup>) in the upper 300 m water column; dots represent the middle depth between the sampled strata (0–50, 50–100 and 100–300 m depth). (D) Percentage of total faecal pellet volume in the upper 50 m water column at Stn 5, between 24 April and 2 May 1992

#### Faecal pellet vertical distribution and abundance

Faeces concentration decreased with depth, and no statistical differences were found between samples collected at sunrise (approx. 07:00 to 08:00 h) and sun-

set (approx. 18:00 to 19:00 h) (Fig. 4). Faecal pellets in the water column during the investigation period (Fig. 2C) showed a patchy distribution (or high spatial variability) of faecal volume. A transient sedimentation of faeces below the thermocline was recorded on 26 April, but during this study, the bulk of the faecal material remained within the upper 50 m of the water column (Fig. 2D).

#### Sedimented matter

Analysis of the vertical flux of particles showed that sedimented seston, organic matter, carbonate and lithogenic + opal fractions were, on average, twice as high at 100 m depth [mean (standard deviation)]: 221 (123), 99 (70), 51 (20) and 76 (40) mg m<sup>-2</sup> d<sup>-1</sup>, respectively, as at 50 m depth: 119 (52), 62 (21), 27 (20) and 34 (15) mg m<sup>-2</sup> d<sup>-1</sup>, respectively (n = 7) (Fig. 5).

Microscopical analysis of the sedimented matter showed that vertical flux was dominated by faecal pellets of different origins (copepods, larvaceans, euphausiids, protistan and unidentified) (Fig. 6, Table 2). Faecal pellets accounted, on the average, for 87% and 92% of the total organic carbon recorded at 50 and 100 m depth, respectively (Tables 2 & 3). The contribution of microzooplankton and phytoplankton accounted for 13% and 8% of total sedimented organic carbon at 50 and 100 m depth (Tables 2 & 3). Carbon content in phytoplankton and microzooplankton was calculated from estimates of the plasma volume or by using factors from the literature (Table 4). At both depths the microzooplankton carbon collected in the sediment trap consisted mainly of the tintinnids *Parafavella denticulata* and *Ptychocyclus arctica* (Table 3). Sedimented phytoplankton was composed predominantly of coccolithophorids (*Emiliania huxleyi*) and diatoms (*Skeletonema costatum*). Resting spores of *Chaetoceros* spp., and cells of *Dinobryon balticum* and *Phaeocystis pouchetii* were abundant.

#### Experiments

**Egg production rate in *Temora longicornis*.** The egg production rate correlated with *in situ* chl *a* concentration [Spearman rank correlation (r) = 0.964, n = 7,

Table 1. Average percentage of mesozooplankton taxa collected in 3 different strata in the Bjørnafjorden (Stn 5). Abundances (ind.  $m^{-2} \times 10^4$ , integrated over the upper 300 m water column) between 24 April and 5 May 1992, are also shown (standard deviations are given in parenthesis)

Taxa	Stratum (m)			Total (%)	Integrated abundance	N
	0–50	50–100	100–300			
<i>Calanus finmarchicus</i>	82.8	11.5	5.7	100	8.4 (10.0)	17
<i>Temora longicornis</i>	94.5	4.8	0.7	100	3.9 (5.2)	17
<i>Metridia lucens</i>	18.5	49.0	32.5	100	0.9 (0.8)	17
<i>Microcalanus</i> sp.	7.5	37.1	55.4	100	1.8 (1.6)	17
<i>Paracalanus parvus</i>	5.5	17.7	76.8	100	25.6 (21.0)	17
<i>Pseudocalanus elongatus</i>	57.4	30.8	11.8	100	2.8 (1.8)	17
<i>Oithona similis</i>	73.7	6.7	19.6	100	46.5 (21.9)	17
<i>Evadne nordmanni</i>	95.3	3.9	0.8	100	19.2 (30.6)	17
<i>Fritillaria borealis</i>	73.9	25.1	1.0	100	3.7 (2.5)	17
<i>Oikopleura</i> sp.	80.7	14.4	4.9	100	5.2 (3.6)	17
Lamellibranch larvae	80.7	14.2	5.1	100	2.2 (1.8)	17
Echinodermata larvae	92.1	7.1	0.8	100	5.3 (4.3)	17
Briozoa larvae	87.6	12.2	0.2	100	3.4 (2.7)	17
Polychaeta larvae	75.1	17.1	7.2	100	1.5 (1.3)	17

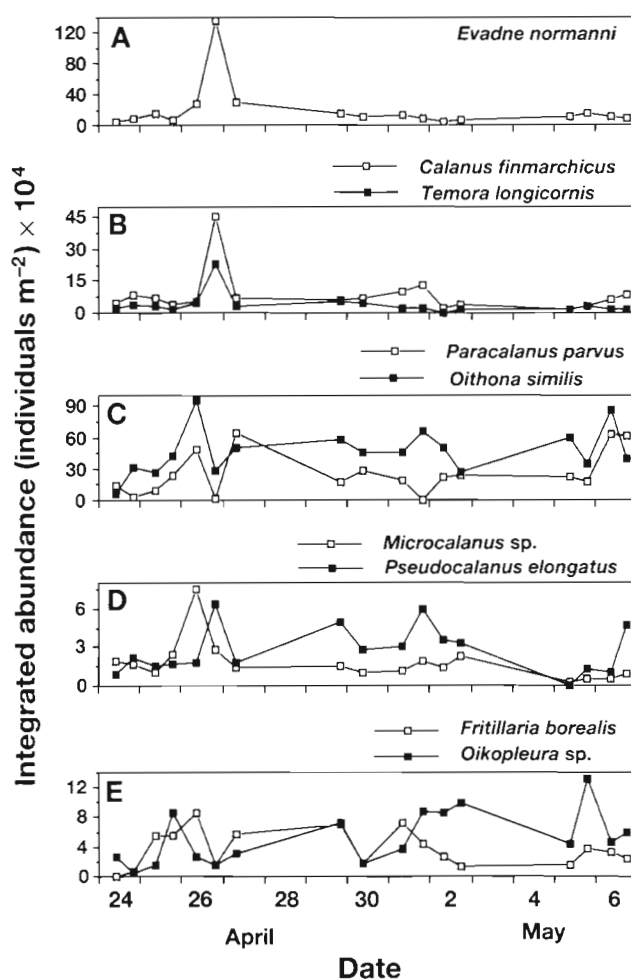


Fig. 3. Integrated abundance over the upper 300 m (ind.  $\times 10^4 m^{-2}$ ) of the predominant mesozooplankton species in the Bjørnafjorden (Stn 5), during 24 April to 6 May 1992. Note different scales of y-axis

$p = 0.018$ ], and ranged from 9.7 eggs female $^{-1} d^{-1}$ , when chl *a* concentration was 0.5  $\mu g l^{-1}$ , to 16.6 eggs female $^{-1} d^{-1}$ , when chl *a* concentration was 2.3  $\mu g l^{-1}$  (Fig. 7).

**Faecal pellet consumption (coprophagy) in *Calanus finmarchicus* and *Oithona similis*.** Experiments demonstrated that only *O. similis* ingested a significant volume of faecal material. An average consumption rate of approximately  $3 \times 10^6 \mu m^3 ind.^{-1} d^{-1}$  was measured when *O. similis* was allowed to feed on faecal material produced by *C. finmarchicus* (Fig. 8). No significant differences between Treatments 1 (control) and 2 were found, indicating that *C. finmarchicus* did not feed on its own faecal pellets. However, the size frequency distribution of faecal pellets shifted to-

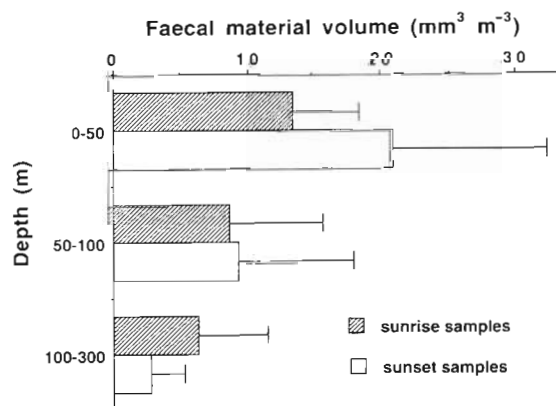


Fig. 4. Time-averaged vertical distribution of faecal material volume ( $mm^3 m^{-3}$ ) in 3 strata of the upper 300 m water column, at sunrise (between 07:00 and 08:00 h) and sunset (between 18:00 and 19:00 h) at Stn 5. Horizontal lines represent standard deviation,  $n = 9$

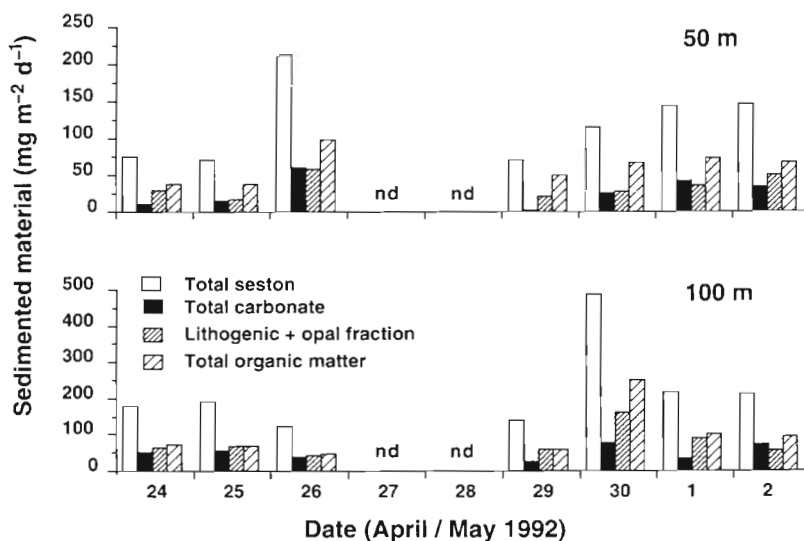


Fig. 5. Sedimented material (mg m<sup>-2</sup> d<sup>-1</sup>), divided into total seston, carbonate, lithogenic + opal and organic matter, as measured by sediment traps deployed at 2 depths (50 and 100 m) at Stn 5, during 24 April to 2 May 1992. Note different scales of y-axis. nd = no data

ward smaller sizes (unpubl. data), suggesting that pellets were broken due to copepod activity (coprorhexy and coprochaly, sensu Lampitt et al. 1990 and Noji et al. 1991).

Faecal pellet production rate in *C. finmarchicus* increased from a faeces volume of  $7.5 \times 10^6 \mu\text{m}^3 \text{ ind.}^{-1} \text{ d}^{-1}$  (Fig. 8A), to  $33.4 \times 10^6 \mu\text{m}^3 \text{ ind.}^{-1} \text{ d}^{-1}$  (Fig. 8B), when *in situ* chl *a* increased from  $1.1 \mu\text{g l}^{-1}$  (26 April) to  $2.2 \mu\text{g l}^{-1}$  (1 May) respectively.

## DISCUSSION

### Hydrography

Temperature and salinity data at Stn 5 indicate that in general intrusion of other water masses did not take place during the study period (Fig. 2A, B). Therefore, the variability in the abundance and distribution of zooplankton and faecal material may be interpreted as

Table 2. Faecal pellet sedimentation rate (mg C m<sup>-2</sup> d<sup>-1</sup>) measured at Stn 5 during 7 deployments at 50 and 100 m depth. Faecal material is distinguished by 5 different origins

Sediment trap no.: Date:	1 24 April	2 25 April	3 26 April	4 29 April	5 30 April	6 1 May	7 2 May	Mean (SD)
<b>Pellet origin</b>								
<b>Depth 50 m</b>								
Larvacean <sup>a</sup>	0.14	0.09	0.26	1.23	0.56	1.90	7.55	
Copepods <sup>b</sup>	0.38	1.79	5.11	1.64	3.00	4.27	2.11	
Euphausiids <sup>c</sup>	0.02	0.13	3.24	0.29	–	–	9.02	
Protistan <sup>d</sup>	0.34	0.14	0.10	0.05	0.67	0.42	1.06	
Unidentified <sup>e</sup>	3.82	9.54	43.58	17.58	15.84	31.24	23.28	
Total	4.70	11.69	52.29	20.79	20.07	37.83	43.02	27.2 (17.5)
<b>Depth 100 m</b>								
Larvacean	7.87	5.29	2.75	4.65	55.86	14.09	2.89	
Copepods	3.16	4.36	3.94	2.51	34.85	5.57	3.99	
Euphausiids	2.64	0.09	10.21	7.02	7.33	10.88	6.59	
Protistan	1.69	2.90	0.85	0.48	2.12	1.83	1.49	
Unidentified	41.35	32.12	25.74	22.12	131.98	70.98	28.54	
Total	56.71	44.76	43.49	36.78	232.14	103.35	43.50	80.1 (70.7)

<sup>a</sup> A mean value of 0.042 mg C per mm<sup>3</sup> faecal pellet was used (present study)  
<sup>b</sup> A mean value of 0.057 mg C per mm<sup>3</sup> faecal pellet was used (present study)  
<sup>c</sup> A mean value of 0.016 mg C per mm<sup>3</sup> faecal pellet was used (present study)  
<sup>d</sup> Pellet volume was multiplied by 0.11 (Bathmann et al. 1987)  
<sup>e</sup> An average value (from Footnotes a, b & c) of 0.038 mg C per mm<sup>3</sup> faecal pellet was used

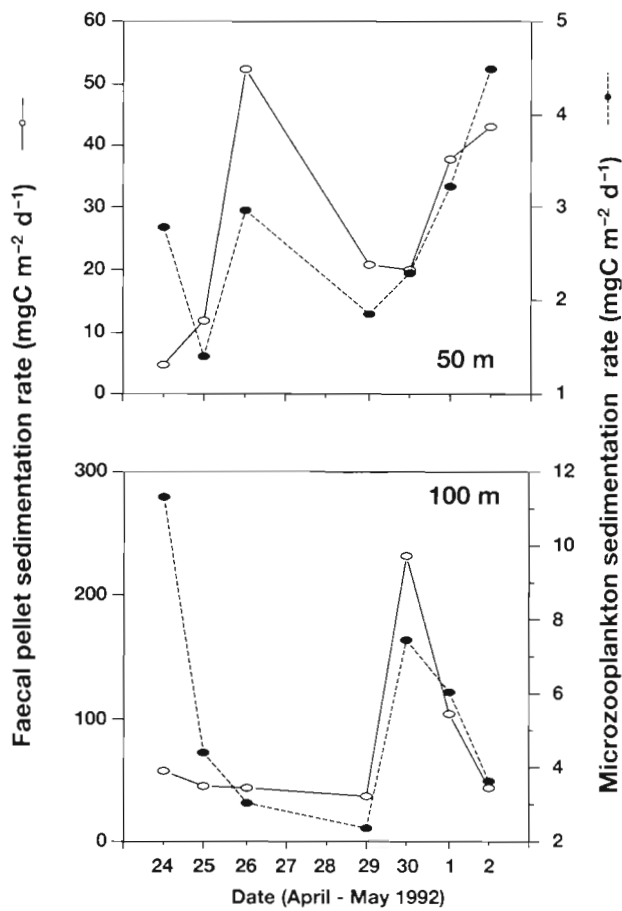


Fig. 6. Faecal material (○) and microzooplankton (●) sedimentation rate ( $\text{mg m}^{-2} \text{d}^{-1}$ ), collected by the 50 m and 100 m deep traps at Stn 5. Note different scales of y-axis

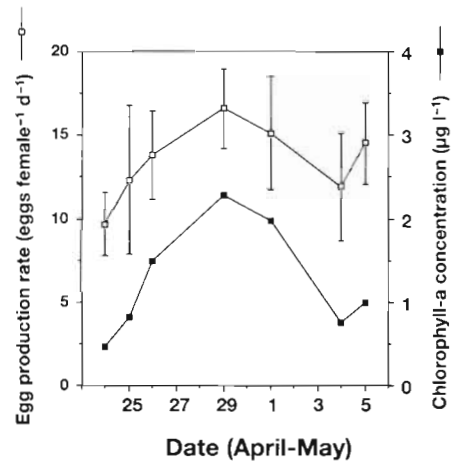


Fig. 7. Egg production rate (egg female<sup>-1</sup> d<sup>-1</sup>) in *Temora longicornis* (□), and chl a concentration ( $\mu\text{g l}^{-1}$ ) (■), during 24 April to 5 May 1992 at Stn 5. Vertical lines represent standard deviation of 9 replicates

developments in the water mass under observation and not due to advection. No evidence for diel vertical migration in any zooplanktonic groups was found from the net samples.

The only exception to the hydrographic conditions described above occurred on 26 April, a rainy and windy day on which a lateral advection of water from other fjords or from the coast probably took place. On this day, the 35‰ isohaline (Fig. 2B) and the faecal pellet volume isopleths (Fig. 2C) dipped. In addition, the highest abundances of some copepods (*Calanus finmarchicus* and *Temora longicornis*) and cladocerans (*Evadne normanni*) were recorded on this day (Fig. 3A, B).

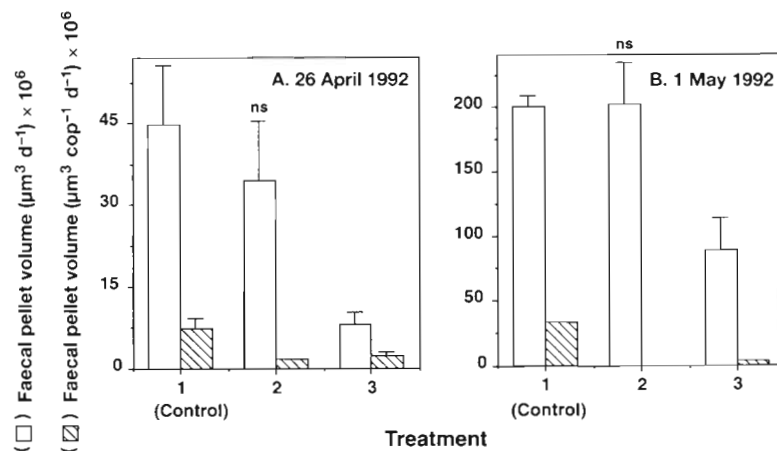


Fig. 8. Total average faecal material standing stock (expressed in volume,  $\mu\text{m}^3 \times 10^6 \text{d}^{-1}$ ) (open bars) collected per treatment, and faecal pellet production (Treatment 1) or consumption (Treatments 2 & 3) rates ( $\mu\text{m}^3 \times 10^6 \text{cop}^{-1} \text{d}^{-1}$ ) (hatched bars). Treatment 1 represents faecal pellet production in 6 individuals of *Calanus finmarchicus*. Treatment 2 represents faecal pellet consumption by 6 individuals of *C. finmarchicus*. Treatment 3 represents faecal pellet consumption by 16 (26 April) or 30 (1 May) individuals of *Oithona similis*. Experiments were conducted at  $6 \pm 1^\circ\text{C}$ , and natural assemblages of phytoplankton of 1.1 (26 April) and 2.2 (1 May)  $\mu\text{g chl a l}^{-1}$  were used as a food. For further explanations see 'Materials and methods'. ns = not significantly different from the control. Vertical lines represent standard deviation of 9 replicates. Note different scales of y-axis

Table 3. Carbon sedimentation rates ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) calculated for phytoplankton and microzooplankton at Stn 5 during 7 deployments at 50 and 100 m depth

Sediment trap no. Date: Depth (m):	1 24 April		2 25 April		3 26 April		4 29 April		5 30 April		6 1 May		7 2 May	
	50	100	50	100	50	100	50	100	50	100	50	100	50	100
<b>Ciliates (Tintinnids)</b>														
<i>Parafavella denticulata</i>	1.41	6.73	0.59	2.24	2.12	2.10	0.43	1.32	0.94	4.87	1.09	3.32	2.15	1.36
<i>Ptychocylis arctica</i>	0.20	0.94	0.08	0.20	0.05	0.10	0.04	0.15	0.10	0.69	0.17	0.65	0.23	0.21
<i>Acanthostomella norvegica</i>	0.002	0.01	0.003	—	0.005	0.005	0.006	0.01	0.02	0.03	0.01	0.05	0.05	0.03
Aloricate ciliates (50 µm)	0.02	—	—	0.06	0.03	—	0.06	0.05	0.02	—	—	—	0.53	0.02
<b>Diatoms</b>														
<i>Nitzschia 'seriata'</i>	0.005	—	0.01	0.02	—	—	0.0002	0.003	0.03	0.008	0.02	0.06	0.07	0.08
<i>Chaetoceros</i> spp.	0.04	0.28	0.04	—	0.008	0.02	0.005	0.07	0.03	—	0.007	—	—	—
<i>Chaetoceros</i> (resting spores)	0.003	0.25	—	0.04	—	0.005	—	0.007	—	0.03	0.001	0.02	0.006	—
<i>Rhizosolenia delicatula</i>	0.02	0.11	—	0.13	—	—	0.008	0.02	0.03	—	0.03	0.06	—	0.07
<i>Thalassiosira nordenskiöldii</i>	—	0.45	—	0.005	—	—	0.004	—	—	0.05	—	—	—	—
<i>Thalassiosira</i> spp.	—	—	—	—	—	—	0.003	—	—	—	—	0.23	—	—
<i>Skeletonema costatum</i>	0.03	0.12	0.003	0.17	0.02	0.02	0.0004	0.02	0.009	0.01	0.002	0.01	0.01	—
<i>Coscinodiscus</i> sp.	0.28	—	—	—	0.22	—	0.08	0.12	0.33	—	0.22	0.14	0.15	0.46
<i>Eucampia groenlandica</i>	0.06	—	0.38	—	0.02	0.27	0.03	0.10	—	0.51	0.07	0.08	—	0.47
<b>Dinoflagellates</b>														
<i>Protoperidinium depressum</i>	0.01	—	—	—	—	—	0.19	0.05	0.05	0.03	0.14	—	—	—
<i>Ceratium</i> spp.	—	—	—	—	—	—	0.01	—	0.02	—	—	—	—	—
<i>Dinophysis</i> spp.	0.009	—	—	—	—	0.006	0.009	0.006	—	0.009	—	—	—	—
Dinoflagellate cysts	0.43	1.86	0.07	0.28	0.17	0.14	0.07	0.21	0.08	0.48	0.13	0.47	0.17	0.13
Naked dinoflag. (< 20 µm)	0.01	—	0.0002	—	0.0003	—	—	0.0003	0.0002	0.006	0.009	—	—	—
<b>Other groups and species</b>														
<i>Emiliania huxleyi</i>	0.007	0.06	0.004	0.02	0.01	0.004	0.003	0.007	0.01	0.04	0.01	0.04	0.04	0.05
<i>Dinobryon balticum</i>	0.001	—	0.01	0.01	—	—	0.001	0.008	0.005	0.007	0.003	0.01	0.01	0.02
<i>Phaeocystis pouchetii</i>	—	0.03	0.003	—	—	—	—	0.001	—	—	—	—	—	—
Radiolarians	0.06	0.47	—	0.97	0.25	0.25	—	—	—	0.37	—	0.30	0.33	—
Bivalve larvae	0.02	—	—	0.26	0.07	—	0.05	—	—	0.07	0.06	—	0.09	0.36
Polychaeta larvae	0.02	—	0.09	—	—	—	—	—	0.26	—	—	0.11	—	0.06
Pteropods ( <i>Limacina</i> sp.)	—	—	—	—	—	—	—	—	—	—	0.31	0.20	—	0.22
Cyclopoid copepods	—	—	—	—	—	—	0.37	—	—	—	0.46	—	0.64	—
Nauplii of crustaceans	0.06	—	0.13	—	—	0.13	0.19	—	0.37	0.26	0.49	0.31	—	0.09
Copepod eggs	0.09	—	—	—	—	—	0.29	0.20	—	—	—	—	—	—
Total	2.79	11.31	1.41	4.41	2.97	3.05	1.85	2.35	2.30	7.47	3.23	6.06	4.48	3.63

Table 4. Average sedimentation rate ( $\text{ind. m}^{-2} \text{d}^{-1}$ ) at 50 and 100 m depth during the 7 deployments at Stn 5 (SD in parenthesis). Plasma volume (PV) and carbon (C) values assigned to plankton taxa are also given. For carbon estimation, when no source is mentioned,  $C = PV \times 0.13$  was used for armoured dinoflagellates and  $C = PV \times 0.11$  for all other phytoplankton (Smetacek 1975)

	Mean no. (50 m depth) ( $\text{ind. m}^{-2} \text{d}^{-1}$ )	Mean no. (100 m depth) ( $\text{ind. m}^{-2} \text{d}^{-1}$ )	Mean PV ( $\mu\text{m}^3 \text{cell}^{-1}$ )	Mean C ( $\text{pg C ind.}^{-1}$ )	Carbon estimation (source)
<b>Ciliates (Tintinnids)</b>					
<i>Parafavella denticulata</i>	$88.3 \times 10^3$ ( $48.4 \times 10^3$ )	$221.4 \times 10^3$ ( $142.2 \times 10^3$ )	258 773	14 159	Boltovskoy et al. (1991)
<i>Ptychocylis arctica</i>	$10.3 \times 10^3$ ( $6.3 \times 10^3$ )	$35.2 \times 10^3$ ( $28.0 \times 10^3$ )	216 261	11 906	Boltovskoy et al. (1991)
<i>Acanthostomella norvegica</i>	$11.2 \times 10^3$ ( $13.2 \times 10^3$ )	$15.6 \times 10^3$ ( $13.4 \times 10^3$ )	14 913	1 235	Boltovskoy et al. (1991)
Aloricate ciliates (50 $\mu\text{m}$ )	$13.0 \times 10^3$ ( $27.2 \times 10^3$ )	$2.5 \times 10^3$ ( $3.5 \times 10^3$ )	65 450	7 199	
<b>Diatoms</b>					
<i>Nitzschia 'senata'</i>	$750.5 \times 10^3$ ( $986.7 \times 10^3$ )	$942.6 \times 10^3$ ( $1.3 \times 10^6$ )	232	26	
<i>Chaetoceros</i> spp.	$148.0 \times 10^3$ ( $141.9 \times 10^3$ )	$433.6 \times 10^3$ ( $848.6 \times 10^3$ )	1 090	120	
<i>Chaetoceros</i> (resting spores)	$123.7 \times 10^3$ ( $197.7 \times 10^3$ )	$4.2 \times 10^6$ ( $7.5 \times 10^6$ )	109	12	
<i>Rhizosolenia delicatula</i>	$47.9 \times 10^3$ ( $53.1 \times 10^3$ )	$184.0 \times 10^3$ ( $173.3 \times 10^3$ )	2 636	290	
<i>Thalassiosira nordenskiöldii</i>	$3.5 \times 10^3$ ( $9.1 \times 10^3$ )	$432.3 \times 10^3$ ( $1.0 \times 10^6$ )	1 500	165	
<i>Thalassiosira</i> spp.	$0.9 \times 10^3$ ( $2.4 \times 10^3$ )	$78.9 \times 10^3$ ( $208.7 \times 10^3$ )	3 754	413	
<i>Skeletonema costatum</i>	$409.8 \times 10^3$ ( $389.8 \times 10^3$ )	$2.0 \times 10^6$ ( $2.6 \times 10^6$ )	236	26	
<i>Coscinodiscus</i> sp.	$3.5 \times 10^3$ ( $2.1 \times 10^3$ )	$1.9 \times 10^3$ ( $3.2 \times 10^3$ )	482 085	53 029	
<i>Eucampia groenlandica</i>	$69.5 \times 10^3$ ( $115.7 \times 10^3$ )	$174.7 \times 10^3$ ( $183.4 \times 10^3$ )	10 673	1 174	
<b>Dinoflagellates</b>					
<i>Protoperidinium depressum</i>	$2.4 \times 10^3$ ( $3.3 \times 10^3$ )	$0.5 \times 10^3$ ( $0.9 \times 10^3$ )	177 273	23 045	
<i>Ceratium</i> spp.	$0.5 \times 10^3$ ( $0.9 \times 10^3$ )	0.0 (0.0)	70 909	9 218	
<i>Dinophysis</i> spp.	$0.9 \times 10^3$ ( $1.6 \times 10^3$ )	$1.1 \times 10^3$ ( $1.4 \times 10^3$ )	21 273	2 765	
Dinoflagellate cysts	$46.7 \times 10^3$ ( $36.8 \times 10^3$ )	$148.8 \times 10^3$ ( $179.2 \times 10^3$ )	26 364	3 427	
Naked dinoflag. (< 20 $\mu\text{m}$ )	$37.0 \times 10^3$ ( $60.5 \times 10^3$ )	$10.9 \times 10^3$ ( $27.1 \times 10^3$ )	736	81	
<b>Other groups and species</b>					
<i>Emiliania huxleyi</i>	$1.7 \times 10^6$ ( $1.6 \times 10^6$ )	$4.7 \times 10^6$ ( $3.1 \times 10^6$ )	65	7	
<i>Dinobryon balticum</i>	$263.1 \times 10^3$ ( $264.3 \times 10^3$ )	$506.9 \times 10^3$ ( $427.1 \times 10^3$ )	150	17	Smetacek (1975)
<i>Phaeocystis pouchetii</i>	$90.2 \times 10^3$ ( $238.7 \times 10^3$ )	$1.2 \times 10^6$ ( $3.1 \times 10^6$ )	36	4	
Radiolarians	$0.8 \times 10^3$ ( $1.2 \times 10^3$ )	$2.9 \times 10^3$ ( $2.8 \times 10^3$ )		116 700	Anderson (1983)
Bivalve larvae	$1.3 \times 10^3$ ( $1.1 \times 10^3$ )	$3.1 \times 10^3$ ( $4.8 \times 10^3$ )	281 818	31 000	
Polychaeta larvae	$1.3 \times 10^3$ ( $2.3 \times 10^3$ )	$0.6 \times 10^3$ ( $1.0 \times 10^3$ )	380 133	41 815	
Pteropods ( <i>Limacina</i> sp.)	$0.6 \times 10^3$ ( $1.5 \times 10^3$ )	$0.8 \times 10^3$ ( $1.3 \times 10^3$ )		75 000	Conover & Lalli (1974)
Cyclopoid copepods	$0.9 \times 10^3$ ( $1.2 \times 10^3$ )	0.0 (0.0)		230 000	G. Franz (pers. comm.)
Nauplii of crustaceans	$3.0 \times 10^3$ ( $3.1 \times 10^3$ )	$1.9 \times 10^3$ ( $2.1 \times 10^3$ )		59 920	G. Franz (pers. comm.)
Copepod eggs	$0.6 \times 10^3$ ( $1.2 \times 10^3$ )	$0.3 \times 10^3$ ( $0.8 \times 10^3$ )		90 000	H. González (unpubl.)

### Sedimentation of faecal pellets versus phytoplankton

The great variation in vertical fluxes on a time scale of 24 h indicates that sinking particles are formed/destroyed by many different types of biological processes in the overlying water column (Peinert et al. 1989). Aggregate formation (Alldredge & Silver 1988) and faecal pellet production are the main processes in the formation of the larger particles which make up most of the flux in the world's oceans (Wefer 1989). In the Bjørnafjorden, grazing probably constitutes the most important biological process contributing particles to the vertical flux during the study period, since faecal pellets make up the bulk of the organic matter collected in sediment traps.

During reported spring diatom blooms in Kiel Bight (Smetacek 1980a, 1985) and the Kattegat (Olesen 1993), sedimenting matter consisted almost entirely of phytoplankton, probably due to the uncoupling with the beginning of the copepod grazing on these blooms. In the Norwegian Current a close coupling of phytoplankton and copepods during spring resulted in low sedimentation rates, where faecal pellets comprised the bulk of settled matter (Peinert et al. 1987). High numbers of faecal pellets were collected on 26 April in the 50 m trap (Fig. 6), coinciding with peak numbers of almost all zooplankters (Fig. 3). Faeces distribution in the water column also showed a high volume of faecal material near the surface on 26 April. A relatively high volume of faecal material ( $15 \text{ mm}^3 \text{ m}^{-3}$ ) in deeper layers (100 to 300 m depth) was recorded only during the sunset sampling that day (Fig. 2C, D), suggesting that a sedimentation of a small patch of faecal pellets took place in the vicinity of the trap. However, no signal was recorded in the sedimented faecal material collected at 100 m depth (Fig. 6). Without large-scale changes in the hydrographic conditions in the study area, variability in the particle flux of faecal pellets may be due to: (1) patchy distribution of zooplankton and phytoplankton, (2) characteristics of the zoo- and phytoplankton, e.g. species composition, abundance, size and developmental stage of populations, (3) characteristics of the faecal pellets (size, compaction, with or without peritrophic membrane, shape, etc.). In addition, the extent of small-scale spatial variability (centimetres to metres) in vertical particle fluxes due to lateral advection is uncertain.

### Egg production rate

There was a remarkable correlation between the egg production rate in *Temora longicornis* and the *in situ* chl *a* concentration (Fig. 7). This result and the comparatively low (see below) egg production rates

generally recorded suggest that the copepods were food-limited and/or that the grazing rate was high enough to keep chl *a* at rather low concentrations, typically  $1.4$  to  $0.3 \mu\text{g chl } a \text{ l}^{-1}$  at the surface and bottom of the euphotic zone (which ranged from 25 to 50 m depth; M. Veldhuis unpubl. data). Egg production in small copepod species closely followed the variation in food intake during the preceding 24 h (Kjørboe et al. 1985, Fransch & González 1991). In *T. longicornis*, low egg production rates (between 3 to 25 eggs female<sup>-1</sup> d<sup>-1</sup>) were found at the end of the spring bloom related to limiting food conditions at concentrations of  $\leq 2 \mu\text{g chl } a \text{ l}^{-1}$  (Van Rijswijk et al. 1989). Furthermore, egg production rates of up to 70 eggs female<sup>-1</sup> d<sup>-1</sup> were measured when chl *a* concentration rose to  $20 \mu\text{g l}^{-1}$  in the Marsdiep (Fransch & González 1991).

### Sedimented matter

Sedimentation of POC ranged between 3 and 15% (mean = 8%, SD = 4,  $n = 6$ ) of primary production at 50 m depth, and between 13 and 51% (mean = 27%, SD = 15,  $n = 6$ ) at 100 m depth in the Bjørnafjorden. Average values of total sedimented matter recorded during this study ( $119$  and  $221 \text{ mg m}^{-2} \text{ d}^{-1}$  at 50 and 100 m depth, respectively) are in the lower range ( $100$  to  $8000 \text{ mg m}^{-2} \text{ d}^{-1}$ ) of sedimentation rates recorded in other fjords and polls of western Norway (Wassmann 1991, Noji et al. 1993). In some of these shallow fjords, sedimentation increases with depth due to resuspension of sediments with a high silt-clay content (Lutter et al. 1989, Wassmann 1991, Noji et al. 1993). In our study area, low seston-to-organic matter ratios were found in sedimented matter: average values of 1.9 (SD = 0.3,  $n = 7$ ) and 2.4 (SD = 0.3,  $n = 7$ ) at 50 and 100 m respectively. This result is one indication that fairly fresh organic matter was caught in our traps, and that resuspension was not important. Microscopic analysis of the sediment trap samples demonstrated a dominance of faecal material, especially at 100 m depth, and a modest contribution of silt-clay particles and fine-grained rock-forming minerals probably transported from local rivers. These results are in agreement with other estimates for coastal and oceanic areas where increases of flux in deeper compared to shallower traps have been reported (Smetacek et al. 1978, Urrere & Knauer 1981, Karl & Knauer 1984, Karl et al. 1984, Small et al. 1987, Wassmann 1991, Noji et al. 1993). These authors put forward several reasons for these atypical values: (1) lateral influx of organic matter at depth; (2) repackaging of slowly settling particles by intermediate- and deep-living zooplankton; (3) shallow-water grazing and mid-water defecation by vertically migrating animals (bypassing); (4) resuspen-

sion. However, it has been shown that traps located well below the mixed layer collected more phytoplankton than those located in the mixed layer (Smetacek et al. 1978). The latter authors argue that this anomalous finding is a result of differences in catch efficiency of sediment traps suspended in turbulent and quiescent layers, i.e. efficiency increases with depth. As our traps were identical to those used by Smetacek et al. (1978) this explanation probably applies here as well. Subsequent studies confirmed the potential bias in particle flux due to differences in fluid dynamics (Gardner 1980, Butman 1986, Baker et al. 1988, Buesseler 1991).

### Sedimented microplankton

High numbers of *Chaetoceros* spp. resting spores and increasingly high numbers of *Emiliania huxleyi* were collected in sediment traps as time proceeded. Concurrent studies of phytoplankton abundance and species composition in the water column showed the presence of high numbers of diatoms (many of them with resting spores), coccolithophorids and armoured dinoflagellates (M. Veldhuis unpubl.). Along the Norwegian coast coccolithophorid blooms recur annually and their blooming period is fairly predictable. Low values of silicate (<2 µM) and CO<sub>2</sub> (10 to 13 µM) concentrations predominated in the upper 50 m of the Bjørnafjorden (M. Veldhuis unpubl.). These factors have been suggested to be conducive to growth of coccolithophorids as compared to diatoms (see Egge &

Aksnes 1992 for [Si] and Riebesell et al. 1993 for [CO<sub>2</sub>]).

Average values of sedimented POC in the Bjørnafjorden (approx. 58 mg C m<sup>-2</sup> d<sup>-1</sup>) are lower than those reported for the Baltic Sea during a similar period (April–May) (approx. 99 mg C m<sup>-2</sup> d<sup>-1</sup>) where mainly phytoplankton sedimented (Smetacek et al. 1978). High numbers of diatom resting spores and low nutrient concentrations suggest that we covered the period of phytoplankton spring bloom decline (Rey & Loeng 1985, Smetacek 1985). Also, the high abundance of zooplankton in late spring has been shown to be concomitant with a decline in sedimentation rates, particularly in April–June, when herbivore stocks reach their first maximum (Smetacek 1975). The *Calanus finmarchicus* population was almost entirely composed of copepodite V. These copepods probably correspond to those which migrated upward during spring (April–May) after overwintering in deep layers (Østvedt 1955). Faecal pellet standing stocks in the water column (Fig. 2C) and collected in sediment traps indicate that zooplankton grazing and subsequent production of faecal pellets does not necessarily enhance sedimentation rates. A comparison of faecal pellet flux with integrated faecal pellet production rate in 2 layers (0–50 and 0–100 m) of the water column shows that a minor proportion of the daily production in the upper 50 m of the water column (1.6 to 10%) is collected in the 50 m trap, when compared with the 100 m depth (6 to 22%), where low numbers of copepods were recorded in the 50–100 m stratum (Table 5). On the

Table 5. Comparison of faecal pellet flux (as measured with sediment traps) with integrated faecal pellet production rate in 2 layers (0–50 and 0–100 m) of the water column at Stn 5. Values in parentheses are the percentage of faecal pellet flux to faecal pellet production rate. TFP and C+A denote the total and the copepod plus appendicularian faecal pellet flux, respectively. All values are averages for the study period

Depth (m)	Zooplankton group	Abundance (ind. m <sup>-2</sup> )	Faecal pellet production rate (µm <sup>3</sup> ind. <sup>-1</sup> d <sup>-1</sup> )	Water column faecal pellet production rate <sup>a</sup>		Faecal pellet flux (mg C m <sup>-2</sup> d <sup>-1</sup> )
				mm <sup>3</sup> m <sup>-2</sup> d <sup>-1</sup>	mg C m <sup>-2</sup> d <sup>-1</sup>	
0–50	Small copepods	128 450 <sup>b</sup>	9.84 × 10 <sup>6</sup> d	1 264	72	27.2 (10.0 %) TFP
	<i>Calanus finmarchicus</i>	69 552	20.45 × 10 <sup>6</sup>	1 422	81	
	Appendicularians	68 797 <sup>c</sup>	38.51 × 10 <sup>6</sup> e	2 649	111	4.3 (1.6 %) C+A
					264	
0–100	Small copepods	227 500	9.84 × 10 <sup>6</sup>	2 239	128	80.1 (22.2 %) TFP
	<i>Calanus finmarchicus</i>	79 212	20.45 × 10 <sup>6</sup>	1 620	92	
	Appendicularians	86 419	38.51 × 10 <sup>6</sup>	3 328	140	21.7 (6.0 %) C+A
					360	

<sup>a</sup>Volume to carbon conversion factors as in Table 2

<sup>b</sup>Pooled abundances of *Pseudocalanus elongatus*, *Paracalanus parvus*, *Microcalanus* sp., *Metridia lucens* and *Temora longicornis*

<sup>c</sup>Pooled abundances of *Oikopleura* sp. and *Fritillaria borealis*

<sup>d</sup>Measured for *T. longicornis* fed on natural phytoplankton from Stn 5 (H. González unpubl.)

<sup>e</sup>Assuming a production rate of 2 pellets ind.<sup>-1</sup> h<sup>-1</sup> (D. Deibel pers. comm.) and an average volume of 8.02 × 10<sup>5</sup> µm<sup>3</sup> pellet<sup>-1</sup>, n = 563 (present study)

Norwegian shelf, late spring trap collections (after the phytoplankton spring bloom) contained relatively little intact phytoplankton, and the bulk of the trap collections consisted of faeces, sometimes loaded with tintinnid loricae (Peinert 1986, Wassmann et al. 1991).

The vertical flux of organisms often represents a more sensitive record of upper ocean processes than bulk measurements of total mass (Taylor & Karl 1991), and may provide information on planktonic processes which otherwise might be undetectable (Passow & Peinert 1993).

### Sedimented faecal matter

Faecal pellets may constitute a fast-sinking vehicle for the export of organic matter towards deeper layers (Fowler & Knauer 1986, Small et al. 1987), or may largely be recycled in near-surface layers (Smetacek 1980b, Bathmann et al. 1987). Recent evidence supports the idea that 3 of the most important factors governing the fate of faecal material are: (1) the role of meso- and macrozooplankton in the consumption and/or fragmentation of faecal pellets (Lampitt et al. 1990, Noji 1991); (2) faecal pellet content, where the ingestion of food with mineral skeletons results in high compaction and sinking rates (Bienfang 1980, Voss 1991, Cadée et al. 1992); (3) the shape of the faecal material, where round or elliptical shapes result in higher sinking rates than cylindrical ones of similar volume (Cadée et al. 1992).

In general, slightly higher numbers of faecal pellets were collected in the 0–50 m than in the 50–100 m depth stratum of the water column (Fig. 4). In contrast, more faecal pellets were collected in the deeper than in the shallower sediment trap. Probably, this is due to higher catch efficiency of settling particles by the 100 m traps (Smetacek et al. 1978, Gardner 1980).

Surprisingly, copepod faecal pellets made up a relatively minor contribution to the total faecal material (Table 2), although copepods constituted the most important group of the zooplankton. It is unknown whether copepods selectively ingested or fragmented mainly their own faeces. It is also possible that other types of faeces settled out faster due to their shape (ellipsoid faeces produced by larvaceans) or size (large strings produced by euphausiids), and are hence exposed for a much shorter period to copepod activity within the euphotic zone. Underestimation of copepod faecal pellets may also be due to more rapid break-down of these faeces. The bulk of the unidentified faecal pellets (Table 2) was similar in some characteristics (e.g. color, texture, content) to the faecal material of copepod origin, but because the peritrophic membranes were partially or totally de-

graded, it was not possible to identify this material with certainty.

Another factor is repacking of faecal detritus into other types of faeces below the thermocline, which modifies the signal originating from the euphotic zone. In addition to copepods (Fig. 8; Sasaki et al. 1988), several groups of detritivores and omnivores have been reported to consume the faecal pellets of other zooplankton, e.g. pteropods (Gilmer & Harbison 1991), radiolarians (Gowing 1989) and ciliates (Meunier 1910). All of these groups were collected in the sediment traps (Tables 3 & 4). Production and consumption of faecal material by protistan and metazoans within the sediment trap may be possible, e.g. radiolarians may produce minipellets (M. M. Gowing pers. comm.).

### Faecal pellet contents

The contents of both copepod and larvacean faeces consisted of densely packed coccoliths of *Emiliana huxleyi*, diatoms *Thalassiosira* spp. and *Chaetoceros* spp. (vegetative cells and spores), and dinoflagellates *Prorocentrum* spp. and *Dinophysis* spp. Similar food remains have been recently found in faeces of the dominant copepod and appendicularian species (*Calanus finmarchicus* and *Oikopleura vanhoefeni*), collected in spring from coastal Newfoundland waters (Urban et al. 1992). The predominance of thecate food items has been reported to enhance faecal pellet export (Voss 1991), which contrasts with high retention times of *C. finmarchicus* faecal pellets filled with fluffy, amorphous material, probably remains of microflagellates (Bathmann et al. 1987).

Urban et al. (1992) suggested that, in waters off Newfoundland, a seasonal change occurs from the flux of opal due to diatoms in appendicularian faeces in the spring, to calcite (from coccolithophorids) in the autumn and winter faeces. In Norwegian Fjords, late April to early May constitutes the period in which coccolithophorid (*Emiliana huxleyi*) blooms started. Concurrent experiments carried out in mesocosms filled with natural water from the Bjørnafjorden demonstrated that copepod and larvacean faecal material was packed with the coccoliths of *E. huxleyi* (González & van der Wal unpubl.). The Norwegian Abyssal Plain and the West Norwegian Sea are dominated by carbonate flux, where the most important contributors are coccolithophorids and foraminifers during spring-summer (Honjo et al. 1988, Wefer 1989), and pteropods in autumn (Bathmann et al. 1991). *E. huxleyi*, which can form large blooms in Norwegian fjords (Berge 1962), may influence pCO<sub>2</sub> through growth and coccolith formation (Flynn 1990) and subsequent sedimentation in faecal pellets without dissolving (Honjo 1976, Holligan et al. 1983).

## CONCLUSIONS

In protected fjords of western Norway, half of the total sedimented seston corresponded to organic matter during the April–May transition. Carbonate and lithogenic + opal fractions each accounted for approximately one-fourth of the seston.

Vertical flux was dominated by faecal pellets with a rather modest contribution by microzoo- and phytoplankton. Whereas the carbonate fraction consisted mainly of coccoliths of *Emiliania huxleyi*, diatom frustules (opal) included in faecal pellets or aggregates may be the main contributor to the lithogenic + opal fraction, since rather low numbers of mineral grains and clay were found in sediment trap samples.

Average values of mass flux here recorded (119 to 221 mg m<sup>-2</sup> d<sup>-1</sup>) are in the lower range of sedimentation rates recorded in other fjords and coastal areas of Norway. Although high numbers of faecal pellets were found in the water column, only a small percentage of them (2 to 6% for copepod plus appendicularian faeces) sedimented out of the photic zone. The contribution of faecal pellets to sedimented matter is postulated to result from a combination of 3 factors: (1) high standing stock of actively grazing mesozooplankton dominated by calanoid copepods and appendicularians with high faeces production rate; (2) a relatively high number of the cyclopoid copepod *Oithona similis*, a species which feeds on faecal pellets produced by calanoid copepods; (3) a phytoplankton community dominated by diatoms and coccolithophorids, both groups having mineral skeletons which accelerate sinking rate of faecal pellets when predominant in the faecal content.

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