

Sedimentation of copepod fecal material in the coastal northern Baltic Sea: Where did all the pellets go?

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Abstract

We investigated the sedimentation of copepod fecal pellets in three different sea areas representing a sheltered bay, an archipelago area, and the open sea on the southwestern coast of Finland in the northern Baltic Sea. Fecal carbon sedimentation was always <0.05% of the total sedimentation of particulate organic carbon, whereas the fecal carbon production (estimated from copepod abundance, assuming production rate of 10 pellets copepod⁻¹ d⁻¹) contributed to 4–17% of particulate organic carbon sedimentation. Thus, >99% of copepod fecal material was remineralized within the mixed water layer (0–20 m). However, in the area and season dominated by the large calanoid copepod *Limnocalanus macrurus* (bay station in spring), fecal carbon sedimentation was an order of magnitude higher than at the other two stations. From June onwards, when the bay station was dominated by cyclopoids, the situation changed: the fecal carbon sedimentation remained 30% lower in the bay than in the archipelago, although the fecal carbon production was estimated to be 2 times higher in the bay. Furthermore, pellet fragmentation (percentage of broken pellets of total fecal carbon sedimentation) was highest in spring and autumn at all areas and increased towards the open sea, being 27%, 45%, and 61% at the bay, archipelago, and open sea stations, respectively. This gradation was probably due to more intense turbulence and water column mixing in the open sea, resulting in more efficient loosening and breakup of pellets. The overall contribution of copepod feces to vertical carbon export in the northern Baltic Sea appears to be small, but seasonal and spatial variations in hydrography and mesozooplankton community structure significantly affect the fecal pellet sedimentation rates.

Many crustacean zooplankton taxa, such as copepods, mysid shrimps, euphausiids, and decapods, produce membrane-covered fecal pellets that have much higher sinking rates than do phytoplankton cells (Gauld 1957; Smayda 1969; Fowler and Small 1972). These pellets have been considered an important means by which particulate material leaves marine pelagic ecosystems (McCave 1975; Turner and Ferrante 1979; Angel 1984). There is, however, some

controversy surrounding the importance of this flux to pelagic carbon budgets. In certain areas, zooplankton fecal pellets do transport a significant fraction of primary production to the deep water (Emerson and Roff 1987; Fowler et al. 1991; Andreassen et al. 1996), whereas the majority of investigators have concluded that copepod fecal material is mostly recycled within the euphotic zone. This process has been demonstrated in the Kiel Bight (Smetacek 1980) and the North Sea (Martens and Krause 1990) and on the continental shelves off Norway (Bathmann et al. 1987), the USA (Lane et al. 1994), Canada (Sancetta 1989), Mexico (Small et al. 1987), and Japan (Ayukai and Hattori 1992).

One reason for the differing results is that a wealth of seasonally and spatially variable abiotic and biotic factors, such as water temperature (Honjo and Roman 1978), turbulence (Alldredge et al. 1987), stratification (Wassmann et al. 1996), and zooplankton community composition (Lampitt et al. 1990; Wassmann 1993; Lane et al. 1994) and food conditions (Voss 1991; Urban et al. 1993), have been shown to influence the sinking and decomposition rates of the fecal material. Therefore, the significance of zooplankton feces for

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Acknowledgments

We thank S. Degerholm, N. Harjamaa, M. Pokki, T. Sjölund, U. Sjölund, and A.-B. Åström for their skilful assistance in the laboratory and in the field. Tvärminne Zoological Station (University of Helsinki) is acknowledged for providing hydrographical and chlorophyll *a* data and excellent working facilities. We also gratefully acknowledge T. Kiørboe, H. Kuosa, I. Vuorinen, and two anonymous referees for their insightful comments on the manuscript. This study was supported by the Walter and Andrée de Nottbeck Foundation, the Maj and Tor Nessling Foundation, the Finnish Institute of Marine Research, and the Academy of Finland.

the vertical flux of organic matter in pelagic ecosystems needs to be studied with respect to spatial and temporal variations in these factors. However, few studies have made comparisons between areas or studied the sedimentation of zooplankton fecal pellets over an entire seasonal cycle.

In the northern Baltic Sea, the seasonal sedimentation dynamics have recently been investigated (Heiskanen and Leppänen 1995; Heiskanen et al. 1998; Heiskanen and Tallberg 1999), but the contribution of zooplankton feces to total sedimentation of organic matter has remained unknown. The northern Baltic has several features that should be considered when studying sedimentation rates of zooplankton fecal pellets. The Baltic Sea is shallow, brackish, strongly stratified, and characterized by a strong spring bloom during which >80% of the annual primary sedimentation takes place (Heiskanen and Leppänen 1995). The mesozooplankton community is a mixture of euryhaline marine, brackish, and limnetic taxa, including rotifers, cladocerans, and copepod genera with relatively small individuals, such as *Acartia*, *Eurytemora*, *Temora*, and *Pseudocalanus* (e.g., Viitasalo 1992); the only species comparable in size to oceanic copepods is *Limnocalanus macrurus* (*syn. L. grimaldii*), which mainly occurs in less saline and cooler waters (e.g., Kankaala 1987). Furthermore, because of the strong seasonal and spatial variation of abiotic and biotic environmental conditions, the mesozooplankton community varies markedly from area to area, from season to season, and from year to year (e.g., Vuorinen and Ranta 1987; Viitasalo 1992; Viitasalo et al. 1995b).

We investigated vertical fluxes of copepod fecal pellets at three stations on the southwestern coast of Finland in the northern Baltic Sea. Our objective was to obtain, for the first time in the Baltic Sea, quantitative information on sedimentation rates of zooplankton fecal material during different seasons and in different areas and to compare the magnitude of the fecal pellet flux with the total sedimentation of organic material. Furthermore, we analyzed the seasonal and spatial variations in pellet fragmentation and attempted to reveal factors that influence the sedimentation and degradation rates of fecal pellets in each study area.

Materials and methods

Study sites—The investigation took place at three locations situated east of the Hanko Peninsula (southwestern coast of Finland): a semienclosed bay area (Sällvik Deep in the Pojo Bay, depth = 42 m), an archipelago area (Storfjärden, depth = 32 m) and an open sea area (Storgadden, depth = 50 m) (Fig. 1). We hereinafter refer to these areas as the bay, archipelago, and open sea stations, respectively.

The bay station is sheltered and under a strong influence of freshwater runoff from the River Svartå at the northern head of the bay. High turbidity causes poor light conditions and a shallow productive layer, and primary and bacterial productions are consequently relatively low (Tallberg and Heiskanen 1998; Tuomi et al. 1999). At the archipelago station, the hydrography and mesozooplankton community composition are influenced by both riverine outflow and inflows of saline Baltic water, which both are ultimately con-

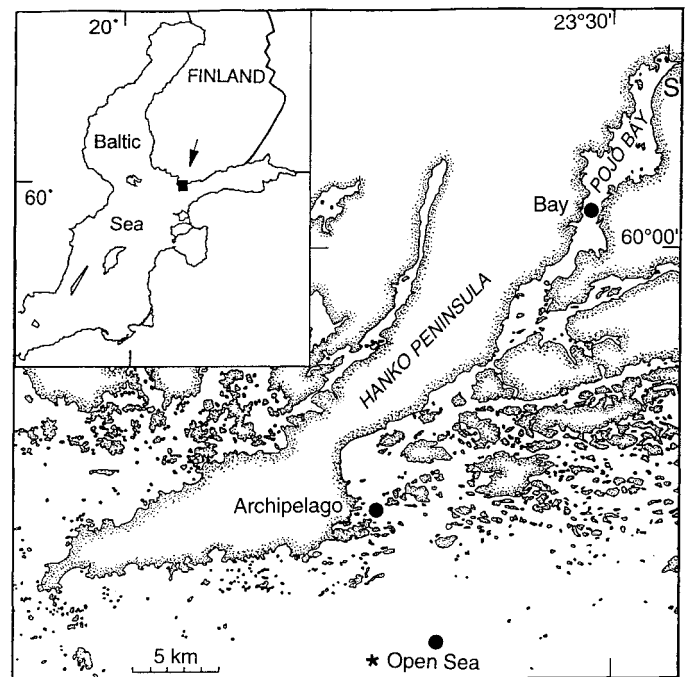


Fig. 1. Study area on the southwestern coast of Finland. ● = sediment trap and zooplankton sampling stations; in the open sea, * = zooplankton sampling station. S = mouth of the River Svartå.

trolled by weather conditions (precipitation and wind; Viitasalo et al. 1995b). At the open sea station, the hydrographical stratification and proportions of different water masses (freshwater, low-salinity surface water from the eastern Gulf of Finland, Baltic surface water, and upwelling deep water) vary rapidly, mainly in response to changes in air temperature and wind strength and direction (Haapala 1994). However, primary and mesozooplankton productions are higher here than at the bay and archipelago stations (Tallberg and Heiskanen 1998; Koski et al. 1999). At all stations, bacterial production is positively correlated with seasonal variations in water temperature (Tuomi et al. 1999).

Hydrography, chlorophyll *a*, and zooplankton—Vertical temperature and salinity profiles were obtained weekly with CTDplus 100 (SIS-Fieldsoft conductivity–temperature–depth probe). Chlorophyll *a* (Chl *a*) was determined from 0.5-liter water samples taken at 0-, 2.5-, 5-, 7.5-, and 10-m depths; the water samples were filtered on Whatman GF/F glass fiber filters, the filters were sonicated and extracted in 94% ethanol, and Chl *a* concentration was measured with a Shimadzu RF500 scanning spectrophotometer calibrated with pure Chl *a* (Sigma).

Zooplankton samples were taken with a Hensen-type plankton net (mesh size 100 μ m, diameter 0.6 m) with a single haul from near bottom to the surface, at 1–2-week intervals. At the bay and archipelago stations, zooplankton was sampled in the immediate vicinity of the sediment traps, whereas in the open sea, zooplankton data were obtained from a permanent zooplankton monitoring station affiliated with the University of Helsinki and the Finnish Institute of Marine Research (Längden, depth 60 m), which was situated

~4 km southwest of the sediment trap station (Fig. 1). The zooplankton samples were preserved in 4% buffered formalin and subsampled with a Folsom splitter before analyzing.

Sedimentation—Cylindrical sediment traps (diameter 0.1 m, aspect ratio 10:1) were moored below the seasonal thermocline depth (15 m at the bay station and 20 m at the other two stations). Thus, for most of the study period the traps were positioned below the mixed surface layer and the euphotic depth (Tallberg and Heiskanen 1998) and below the layer where the juvenile copepods dwell throughout the day and adult copepods reside during their main feeding period in the night (Burriss 1980). At the strongly stratified bay station, an additional trap was also placed at a depth of 30 m. Concentrated formaldehyde was added to the bottom of the cylinders through an external diffusion chamber, which resulted in a maximum formaldehyde concentration of 1.9% at the bottom of the cylinders. The traps were retrieved every week during spring and at 2-week intervals from the beginning of June. Water from the upper part of the cylinders was discarded, and the settled material was mixed with the remaining water (~4 liters), the volume of which was measured with an accuracy of 10 ml.

Subsamples for particulate organic carbon were filtered on precombusted (4 h at 450°C) Whatman GF/F glass fiber filters. Mesozooplankton swimmers were removed from the filters, and the filters were dried and stored at room temperature until analysis with a CHN analyzer (LECO and Lee-man Labs). Primary sedimentation of particulate organic carbon was estimated using the two-source mixing model of Gasith (1975), in which the highest organic carbon content of the settled material (as a percentage of total particulate material) was used as a label for primary settling material and the lowest as a label for resuspended material (Heiskanen and Tallberg 1999). Moreover, primary sedimentation values were corrected for the potential contamination by migrating phytoflagellates (*see* Heiskanen 1995) by subtracting the biomass of dinoflagellates and euglenoids (Tallberg and Heiskanen 1998) from the total sedimentation of particulate organic carbon.

Fecal pellets—Subsamples for fecal pellet analyses were taken from sediment trap samples and carefully rinsed onto a 20- μm mesh net. On average, 121 intact or broken pellets (range 3–1,104) were counted and measured from each sample with a Leica MZ12 binocular microscope at $\times 100$ magnification. Pellets were considered intact if their shape was clearly unchanged, whereas all pieces and irregularly shaped fragments were counted as broken pellets. In volume calculations, the intact pellets were assumed to be cylinders with spherical ends, whereas the broken pellets were assumed to be cylinders with flat ends. Carbon content of the pellets was estimated assuming a carbon:volume ratio of $0.057 \times 10^{-9} \text{ mgC } \mu\text{m}^{-3}$ (Gonzalez and Smetacek 1994). This value is valid for freshly produced fecal pellets and may thus overestimate the carbon content of pellets in the traps. Highly disintegrated fecal pellets and very small pieces could not be reliably quantified by microscopy, which in turn may slightly underestimate the fecal carbon production.

However, because the main objective of the study was to compare fecal pellet sedimentation rates in different seasons and study areas, these estimates were considered sufficiently accurate.

At the archipelago station, an exceptionally high pellet sedimentation rate was observed in late autumn. During this period, a large amount of detritus and other organic matter accumulated in the traps, and the fecal material could not be reliably quantified. Therefore, the late autumn values were discarded from the archipelago data.

A few very large pellet fragments (~500 \times 100 μm), possibly originating from mysid shrimps or fish larvae, were occasionally found in the samples; however, these fragments were not taken into account in the present study. Also, we were not able to identify cladoceran fecal pellets. Cladocerans produce looser fecal material than copepods (Sterner 1989), and their feces are therefore probably rapidly recycled in the mixed water layer.

Sediment traps moored at 15 or 20 m depth may not effectively collect pellets of vertically migrating copepods. If the copepods fed in the surface layer during the night but defecated mainly during or after the descent to deeper water, their fecal pellets would not enter the sediment traps. However, because only adult copepods display a strong diurnal migration in these study areas (Burriss 1980) and 65–89% of the copepods were younger copepodite stages, the majority of the pellets probably were produced above the 15 m depth.

Statistical methods—Prior to the statistical analyses, different sizes of pellets were grouped according to their seasonal variations. Groups were established by calculating Pearson correlations between different sizes of pellets (i.e., time series of sedimentation rates of pellets with widths of 20, 30, 40 μm , etc.). The analysis showed that at all stations pellets with widths of 20, 30, and 40 μm covaried (Pearson correlation coefficients, $r = 0.46\text{--}0.92$, $P < 0.01$), and at the bay station, pellets with widths of 50 and 60 μm formed another covarying group ($r = 0.39$ and 0.36 for the pellets in the 15- and 30-m traps, respectively; $P < 0.05$). We hereafter refer to the 20–40- μm -wide pellets as small pellets, whereas all other pellets are called large pellets. At the bay station, the 70–90- μm pellets also formed their own groups, but because they were very scarce, they were added to the group of large pellets.

The connections between pellet fluxes and various external variables were investigated with correlation and multiple regression analyses (using the statistical package SYSTAT 5.0). The analyses were made for weekly data; the missing weeks were estimated using linear interpolation. First, Spearman rank correlations were calculated between the time series of pellet sedimentation rates and water temperature, Chl *a* concentration, and abundances of various copepod taxa. Second, a multiple regression analysis (with interactive forward stepping method) was made to identify the relative importance of the different copepod taxa to pellet sedimentation rates. In this analysis, pellet fluxes were used as dependent variables and abundances of various copepod counting units (copepodite stages 1–3, 4–5; total copepodites; females; males; and adults) as independent variables. The 0 to 2-week lags between zooplankton and pellet time series

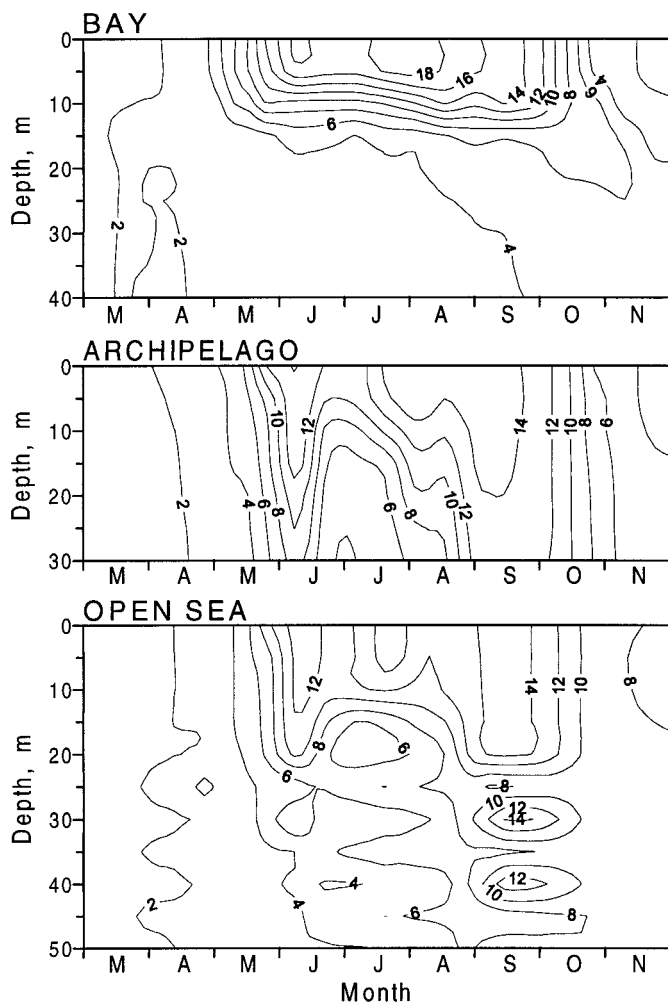


Fig. 2. Water temperature development at the three sampling stations in March–November 1992.

were taken into account. Time lags may arise because of turbulence that keeps pellets suspended in water and because the sediment traps collected pellets during 5–21 d, whereas zooplankton net hauls reflected instantaneous population densities.

Results

Hydrography and Chl *a*—At the bay station, a high fresh-water outflow created a strong pycnocline, which separated the top 10 m from the deeper water layers. In June–September, the temperature in the 0–10-m layer varied from ~10°C to 19°C (Fig. 2, upper panel) and salinity ranged from 0 to 4 permilles practical salinity units (psu; data not shown). Below the top 15 m, the water was almost uniform, with temperature mostly varying from 3°C to 6°C and salinity varying from 4 to 5 permilles psu throughout the year. At the archipelago and open sea stations, the seasonal development of hydrography and stratification was relatively similar (Fig. 2). The location of the thermocline varied between ~10 and 20 m, according to weather conditions, and salinity was 5–6.5 permilles psu in the whole water column. The

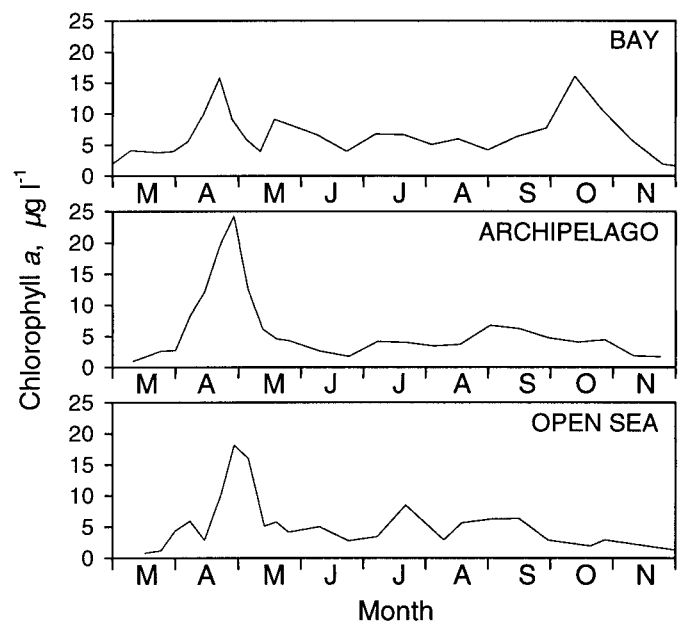


Fig. 3. Seasonal development of the mean Chl *a* concentration in the 0–10-m water layer at the three sampling stations in March–November 1992.

development of the average Chl *a* concentration in the 0–10-m water layer at the three stations is shown in Fig. 3. Highest values occurred in late April, except at the bay station, where a distinct peak was also observed in October.

Copepod abundances and fecal pellet sedimentation rates—At all stations, copepod abundances were low in spring (Fig. 4A); at the bay station, the mesozooplankton biomass (not shown) was dominated by the large calanoid copepod *Limnocalanus macrurus*, whereas in the archipelago and the open sea *Acartia* spp. was (in March–May) the only important copepod taxon. At all stations, copepod abundances started to increase in June. At the bay station, cyclopoids dominated the summer copepod community by >90%, whereas in September–November calanoids (*Acartia* spp., *Eurytemora affinis*, and *Centropages hamatus*) were also relatively important. At the archipelago station in summer and autumn, *Acartia* spp. and *E. affinis* were the dominant copepods. In the open sea, the copepod community resembled that in the archipelago, except that the highest abundances occurred later (in September).

The fluxes of copepod fecal pellets varied both seasonally and between stations. Pellet carbon fluxes at the bay station were highest in May (0.1–0.6 mgC m⁻² d⁻¹; see Fig. 4B, shaded bars in the upper panel), despite a relatively low sedimentation rate of intact pellets (4–10,000 pellets m⁻² d⁻¹; the continuous line). This finding indicates a high contribution of large fecal pellets. At the archipelago station, pellet sedimentation rates peaked later than at the bay station: the highest carbon fluxes occurred in August and September (~0.15–0.25 mgC m⁻² d⁻¹). This flux mainly consisted of small pellets, as indicated by the high sedimentation rate of intact pellets (10–40,000 pellets m⁻² d⁻¹). At the open sea

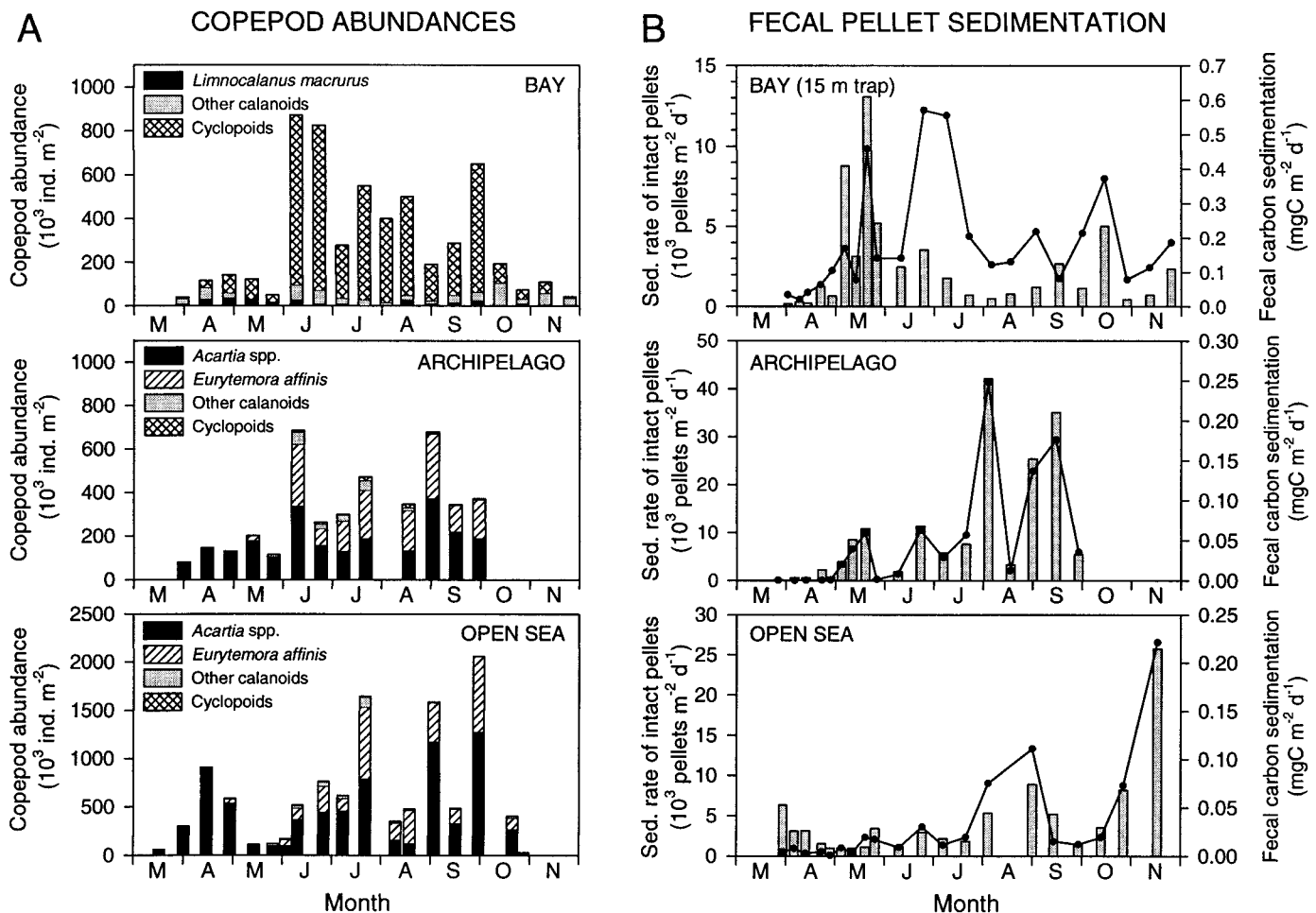


Fig. 4. Copepod abundances (A) and sedimentation rates of fecal pellets (B) at the three sampling stations in March–November 1992. In B, the solid lines denote sedimentation rates of intact pellets ($\text{pellets m}^{-2} \text{d}^{-1}$) and the vertical bars denote total sedimentation of fecal carbon (both intact and broken pellets, $\text{mgC m}^{-2} \text{d}^{-1}$). Note the different scales on y-axes.

station, the pellet flux was lower than at the archipelago station, mostly remaining below $0.1 \text{ mgC m}^{-2} \text{d}^{-1}$ (Fig. 4B).

Fecal pellet carbon flux compared with primary and total sedimentation—To compare fecal pellet sedimentation rates with primary and total sedimentation of particulate organic carbon ($\text{POCS}_{\text{prim}}$ and POCS_{tot} , respectively) in different seasons and areas, we calculated spring, summer, and autumn averages for these variables. Table 1 shows these results, along with fecal pellet production rates, which we estimated assuming a (conservative) pellet production rate of 10 pellets copepod $^{-1} \text{d}^{-1}$ (see table 24 in Mauchline 1998). Table 2 presents the estimated fecal carbon production and observed fecal carbon sedimentation in relation to POCS_{tot} and $\text{POCS}_{\text{prim}}$. At all stations, fecal carbon sedimentation was always $<0.05\%$ of POCS_{tot} and $<0.5\%$ of $\text{POCS}_{\text{prim}}$. The estimated fecal carbon production, in contrast, contributed to much larger percentages of POCS_{tot} , varying from $\sim 4\%$ to 17% in different seasons and areas (Table 2). The 100–1,000-fold difference between fecal pellet production and sedimentation rates (Table 1) implies that $>99\%$ of the fecal pellets produced were remineralized before entering the sediment traps.

There were notable differences between the stations, however. At the bay station in spring, the observed fecal carbon sedimentation was an order of magnitude higher than that at the other two stations, despite the similar range of copepod abundances (Table 1). In summer, when cycloids dominated at the bay station, the situation changed: fecal carbon production was estimated to be 2 times higher in the bay than in the archipelago, but the observed fecal carbon sedimentation however remained 30% lower in the bay (Table 1). The open sea station differed from the other two stations in summer by having the highest copepod abundances and the lowest fecal carbon sedimentation rates.

Connections between copepod abundances and pellet sedimentation rates—The correlation analysis (Table 3) showed that the sedimentation rate of small pellets correlated positively with surface layer temperature at all stations ($P < 0.01$), whereas there was no significant correlation with Chl *a*. At the bay station, the flux of small pellets also correlated with the abundances of cycloids and *E. affinis* adults, whereas at the other two stations highest correlations occurred with *E. affinis* and, at the archipelago station, with

Table 1. Seasonal averages for copepod abundance, fecal pellet production, average pellet volume, pellet sedimentation, total sedimentation of particulate organic carbon (POCS_{tot}), and primary sedimentation of particulate organic carbon (POCS_{prim}) at the three sampling stations in March–November 1992.

Station	Trap depth (m)	Season (period)	Copepod abundance (m ⁻²)	Pellet volume (10 ⁵ μm ³)	Fecal production		Fecal sedimentation		POCS _{tot} § (mgC m ⁻² d ⁻¹)	POCS _{prim} (mgC m ⁻² d ⁻¹)
					Pellet* (pellets m ⁻² d ⁻¹)	Carbon† (mgC m ⁻² d ⁻¹)	Pellet‡ (pellets m ⁻² d ⁻¹)	Carbon (mgC m ⁻² d ⁻¹)		
Bay	15	Spring (26 Mar–11 June)	203,000	4.59	2.03 10 ⁶	53.2	7,272	0.164	413	32
		Summer (12 June–3 Sep)	486,000	1.29	4.86 10 ⁶	35.6	7,608	0.067	434	37
		Autumn (4 Sep–25 Nov)	233,000	3.81	2.33 10 ⁶	50.5	7,155	0.096	449	32
Archipelago	20	Spring (27 Mar–9 June)	198,000	1.72	1.98 10 ⁶	19.4	1,781	0.017	513	224
		Summer (10 June–1 Sep)	410,000	0.76	4.10 10 ⁶	17.7	22,108	0.095	506	110
		Autumn (2 Sep–24 Nov)	397,000	0.65	3.97 10 ⁶	14.8	32,674	—	799	105
Open sea	20	Spring (24 Mar–10 June)	366,000	0.82	3.66 10 ⁶	17.0	3,750	0.017	337	189
		Summer (11 June–1 Sep)	911,000	0.71	9.11 10 ⁶	36.7	8,557	0.034	212	112
		Autumn (2 Sep–17 Nov)	884,000	0.68	8.84 10 ⁶	34.0	22,316	0.086	835	150

* Estimated by assuming 10 pellets produced per individual per day (see table 24 in Mauchline 1998).

† Calculated by multiplying the fecal pellet production (pellets m⁻² d⁻¹) in each season by the mean pellet volume and carbon:volume ratio of 0.057 × 10⁻⁹ mgC μm⁻³ (Gonzalez and Smetacek 1994).

‡ Sum of sedimentation of intact and broken fecal pellets; the sedimentation rate of intact pellets was obtained from trap data, and the sedimentation rate of broken pellets was back-calculated to intact pellets by dividing the sedimentation rate (μm³ m⁻² d⁻¹) of broken pellets with mean pellet volume in each season and adding this number to the observed sedimentation rate of intact pellets.

§ Source: Heiskanen and Tallberg (1999).

|| Estimated from POCS_{tot} using the two-source mixing model of Gasith (1975) and by correcting for the contamination by migrating phytoflagellates.

Acartia spp. adults. Sedimentation of large pellets, which were abundant only in the bay, covaried with abundance variations of *L. macrurus* adults.

Table 4 shows the parameters of the multiple regressions that produced the highest percentages of explained variation. At the bay station, 94% of the variation in fluxes of small intact pellets (at 15 m depth) was explained by abundances of cyclopoid copepodites, *E. affinis* adults, and *Acartia* spp. adults as positive variables and abundance of *E. affinis* copepodites as a negative variable (suggesting pellet breakup by *E. affinis* copepodites). At the archipelago station, the flux of small pellets was best explained ($r^2 = 0.74$) by abundance variations of *E. affinis* adults and *Acartia* spp. females as positive variables and *Temora longicornis* adults as a negative variable. The sedimentation rate of the largest pellets, in turn (here 60–90-μm-wide pellets at 30 m depth) was best explained ($r^2 = 0.55$) by abundance variations of *L. macrurus* copepodites and females. Figure 5 shows the copepod

data and the good match between the predicted and observed sedimentation rates of small pellets at the bay and archipelago stations. At the open sea station, in contrast, several different combinations of zooplankton variables explained a relatively high percentage of the variation, but the solution was unstable: removing or adding variables in the regression equation yielded equally high r^2 values. Thus, pellet fluxes at the open sea station could not be reliably predicted by copepod abundances.

Size variation and fragmentation of fecal pellets—Plotting widths of intact pellets against their length (Fig. 6) shows that at the archipelago and open sea stations there was one basic pellet type, with widths of 20–40 μm and with lengths mainly varying between 60 and 160 μm. At the bay station, there were many of the larger pellets, with widths of 50–90 μm and lengths of 100–440 μm.

At the bay and archipelago stations, pellets were generally largest in April–May, whereas at the bay station, very large pellets also occurred in mid-September (Fig. 7). Further, pellet lengths decreased toward the open sea: the means (of the daily averages) were 187 μm (SE = 12, $n = 22$), 139 μm (SE = 9, $n = 18$) and 108 μm (SE = 4, $n = 18$) for the bay, archipelago, and open sea, respectively.

The degree of pellet fragmentation also varied between stations (Fig. 8). Notably, the proportion of total fecal carbon sedimentation accounted for by broken pellets increased towards the open sea: the mean values for the whole study period were 27%, 45%, and 61% at the bay, archipelago, and open sea stations, respectively. At all stations, the proportion of broken pellets was highest in spring, lowest in summer, and again higher in the autumn (Fig. 8). The proportion of broken pellets in the archipelago correlated positively with that in the open sea (Pearson $r = 0.621$, $P < 0.01$, $n = 18$), whereas the breakup percentage at the bay station

Table 2. Percentage contribution of fecal carbon production (FCP) and sedimentation (FCS) of total and primary sedimentation of particulate organic carbon (POCS_{tot} and POCS_{prim}) in different seasons and study areas.

Station	Season	FCP:		FCS:	
		POCS _{tot} (%)	POCS _{prim} (%)	POCS _{tot} (%)	POCS _{prim} (%)
Bay	Spring	12.9	166.1	0.040	0.514
	Summer	8.2	96.3	0.015	0.180
	Autumn	11.3	157.9	0.021	0.301
Archipelago	Spring	3.8	8.7	0.003	0.008
	Summer	3.5	16.1	0.019	0.087
Open sea	Spring	5.0	9.0	0.005	0.009
	Summer	17.3	32.8	0.016	0.031
	Autumn	4.1	22.7	0.010	0.057

Table 3. Spearman rank correlation analysis between the time series of sedimentation rates of small (width 20–40 μm) and large (width 50–90 μm) intact fecal pellets and temperature, Chl *a* concentration, and abundances of various copepod taxa at the three sampling stations in March–November 1992. Correlations with the percentage of broken pellets (see Fig. 8) also shown. Correlation coefficients are multiplied by 100. Number of observations: bay = 35, archipelago = 27, open sea = 29, C = copepodites, A = adults.

Variables†	Pellet sedimentation rate of small pellets			Large pellets, Bay	% broken pellets		
	Bay	Archipelago	Open sea		Bay	Archipelago	Open sea
Temperature (0–10 m)	61**	78**	63*	–33	–42	–21	–44
Chl <i>a</i> (0–10 m)	–27	–17	4	27	18	47	1
<i>Acartia</i> spp. C	–20	10	–4	11	15	4	26
<i>Acartia</i> spp. A	12	62*	24	–3	10	–43	–60*
<i>Eurytemora affinis</i> C	17	64**	60*	10	–9	–30	–50*
<i>Eurytemora affinis</i> A	65**	65**	67**	–23	–9	–35	–55*
<i>Temora longicornis</i> C		31	43			–63*	–55*
<i>Temora longicornis</i> A		14	–7			–49	6
<i>Centropages hamatus</i> C	10			–2	15		
<i>Centropages hamatus</i> A	–8			–3	34		
<i>Pseudocalanus elongatus</i> C		37	–9			–37	–5
<i>Limnocalanus macrurus</i> C	–10	18	–21	–7	–35	–63*	–5
<i>Limnocalanus macrurus</i> A	–18			51*	50*		
Cyclopoida spp. C	61**	45	48	–22	–30	–36	–62**
Cyclopoida spp. A	68**	–17		–26	–19	–49	

* $P < 0.01$; ** $P < 0.001$.

did not correlate significantly with those at the other two stations ($P > 0.79$). Furthermore, the correlation analysis (Table 3) showed that the proportion of broken pellets mostly correlated negatively (or indifferently) with copepod abundances; only at the bay station was there a positive correlation between the percentage of broken pellets and the abundance of *L. macrurus* adults.

Discussion

The sinking speed of a zooplankton fecal pellet depends on its size and density; larger and denser pellets sink faster than smaller and looser ones (Smayda 1969; Emerson and Roff 1987; Urban et al. 1993). Generally, pellet size corre-

lates positively with the body size of the animal (Paffenhöfer and Knowles 1979; Uye and Kaname 1994), although food concentration may also have an influence within species (Dagg and Walser 1986). The density of a pellet, in turn, depends on its contents, i.e., on the diet of the zooplankton (Voss 1991; Butler and Dam 1994). Zooplankton species may also themselves break down and consume pellets in the water column (e.g., Lampitt et al. 1990; Gonzalez and Smetacek 1994), but the remineralization rate of the feces essentially depends on their sinking speed relative to the amount and activity of microbes in the water (Hansen et al. 1996) and inside the pellets (Gowing and Silver 1983). The vertical carbon export due to fecal pellets thus depends on the structure of the zooplankton community, food species available

Table 4. Multiple regression analysis with time series of sedimentation rates (pellets $\text{m}^{-2} \text{d}^{-1}$) of intact fecal pellets as dependent variables and abundances of various copepod groups as independent variables. Lag periods indicated in brackets imply that the copepod parameter in question occurred earlier than fecal pellet sedimentation rates. Standardized coefficients show the relative effect of each parameter in the equation. All copepod parameters chosen in the equations were significant ($P < 0.05$). C = copepodite stages 1–5; A = adults; CL = copepodite stages 4–5; F = females.

Pellet size (width)	Station	Trap depth (m)	r^2	Parameter	Coefficient	Standardized coefficient
Small (20–40 μm)	Bay	15	0.94	Cyclopoida C (2-week lag)	0.40	0.50
				<i>Eurytemora affinis</i> A	8.04	0.43
				<i>Acartia</i> spp. A (2-week lag)	9.30	0.24
				<i>Eurytemora affinis</i> C	–4.85	–0.52
				Constant	–946.90	0.00
Small (20–40 μm)	Archipelago	20	0.74	<i>Eurytemora affinis</i> A (2-week lag)	8.71	0.62
				<i>Acartia</i> spp. F	10.31	0.58
				<i>Temora longicornis</i> A (1-week lag)	–48.51	–0.74
				Constant	–1198.06	0.00
Large (60–90 μm)	Bay	30	0.55	<i>Limnocalanus macrurus</i> CL (2-week lag)	3.45	0.59
				<i>L. macrurus</i> F (1-week lag)	2.19	0.31
				Constant	–122.43	0.00

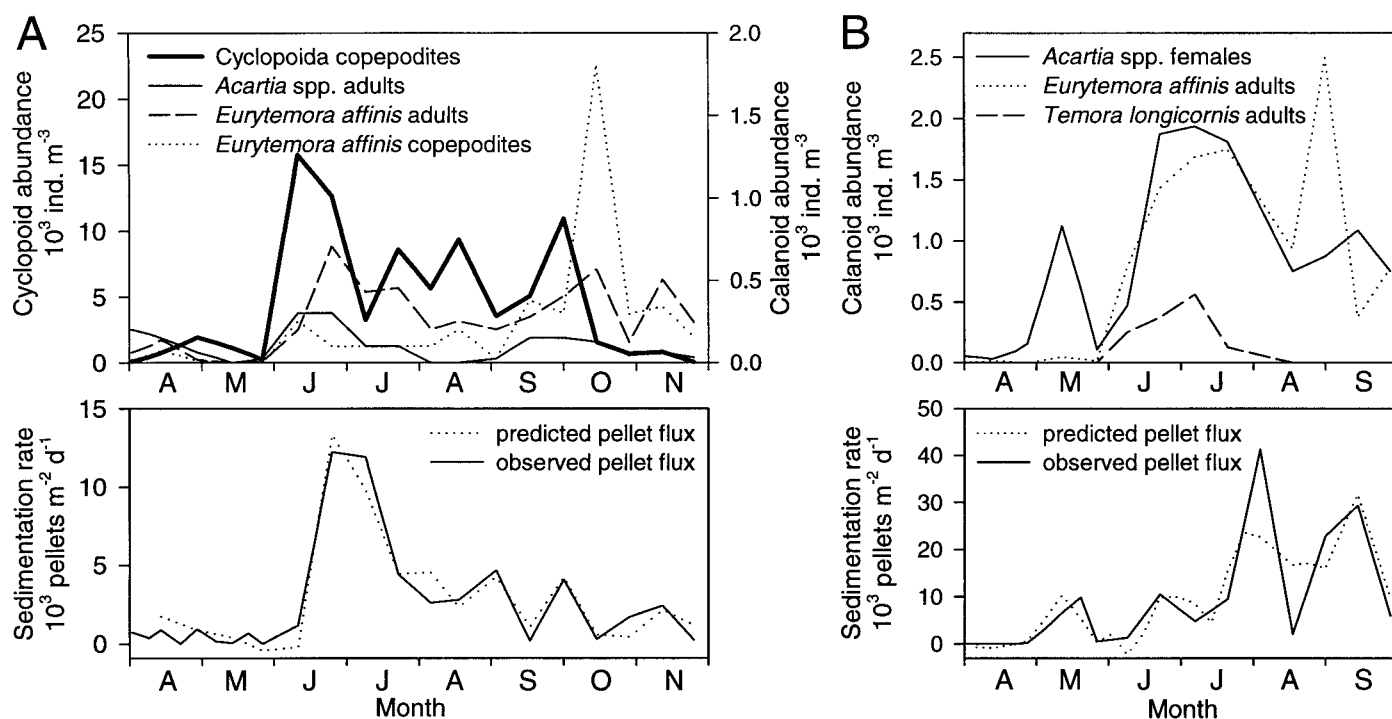


Fig. 5. Parameters of the multiple regression equations shown in Table 4 for the bay station (A) and archipelago station (B). The upper panels show the abundances of the copepod taxa used in the regressions; the lower panels show the predicted and observed sedimentation rates of small pellets (width 20–40 μm).

to zooplankton, and the hydrographic and microbiological conditions of the water.

Pelagic community structure and pellet sinking rates—The copepod community in the study area was dominated by relatively small neritic and estuarine species, such as *Acartia* spp., *E. affinis*, *T. longicornis*, and *Pseudocalanus elongatus*, and cyclopoids (with adult prosome lengths of ~0.6–0.8 mm; Viitasalo et al. 1995a). Only at the bay station was a larger species, *L. macrurus* (prosome length ~1.5 mm) important in spring. As shown by the correlation and regression analyses, the largest fecal pellets (widths of 60–90 μm) most probably belonged to *L. macrurus*, whereas the small pellets (widths of 20–40 μm) were mainly produced by cyclopoids and *E. affinis* at the bay station and by *Acartia* spp. and *E. affinis* at the other two stations. These findings are supported by the prosome length–pellet volume regression of Uye and Kaname (1994), which predicts pellet volumes of $6.52 \times 10^5 \mu\text{m}^3$ for 1.5 mm long copepods, and $0.91 \times 10^5 \mu\text{m}^3$ for 0.7-mm-long copepods. These values are close to the volumes observed in the present study: $6.22 \times 10^5 \mu\text{m}^3$ and $0.78 \times 10^5 \mu\text{m}^3$ for the abundant (see Fig. 2) 60- \times 240- μm and 30- \times 120- μm pellets, respectively. A crude estimation of the sinking velocities (w_s) of these two pellet size classes at different temperatures was made using the equation of Komar et al. (1981),

$$w_s = 0.079\mu^{-1}(\rho_s - \rho)gL^2(L/D)^{-1.664},$$

where μ is the viscosity of water (~0.017 $\text{g cm}^{-1} \text{ s}^{-1}$ at 2°C and ~0.011 $\text{g cm}^{-1} \text{ s}^{-1}$ at 16°C), ρ_s is the density of the

pellet (1.22 g cm^{-3} ; Komar et al. 1981), ρ is the density of the water (~1.006 g cm^{-3} for 6 psu seawater), g is the acceleration of gravity (981 cm s^{-2}), and L and D are pellet length and width (in centimeters), respectively. For the small pellets (30 \times 120 μm), a sinking velocity of 12–19 m d^{-1} is predicted (at temperatures of 2°C and 16°C, respectively), whereas the large pellets (60 \times 240 μm) would sink 48–75 m d^{-1} . This 4-fold difference between the sinking speeds of the large (i.e., *L. macrurus*) pellets and the small pellets may explain the high fecal carbon flux at the bay station in spring.

The summer fecal carbon sedimentation in the bay was 30% lower than that in the archipelago, although the fecal carbon production was estimated to be two times higher in the bay (Table 1). Possibly the strong pycnocline at the bay station slowed down the sinking of small fecal pellets (i.e., those of cyclopoids and *E. affinis*), and most of the feces were consequently recycled within the shallow surface layer.

Another factor that may influence sinking and degradation rates of fecal pellets is the food species eaten by copepods (Bienfang 1980). In the study area in summer, diatoms are scarce, and copepods mostly feed on athecate flagellates and ciliates (Kivi et al. 1993). According to Voss (1991), pellets produced after feeding on athecate flagellates sink slower than those produced after feeding on diatoms or dinoflagellates, and flagellate-based pellets are also more rapidly colonized by bacteria than are diatom-based pellets (Hansen et al. 1996). In this way, a food web based on the microbial loop may enhance recycling of copepod fecal pellets during the stratified periods in summer.

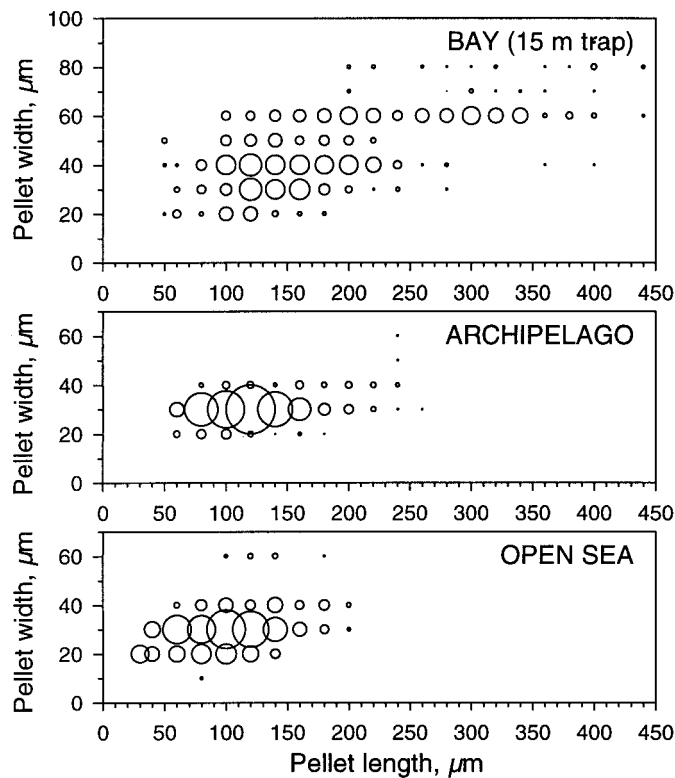


Fig. 6. Size categories of copepod fecal pellets at the three sampling stations in March–November 1992. Pellet widths plotted against pellet lengths; the area of the circles corresponds to the percentage proportion of each length–width class of the total number of pellets in the samples; the number of pellets in each sample was weighted by sample-specific pellet sedimentation rates in order to display the annual contribution of each size class in the whole material.

Coprophagy and fragmentation of fecal pellets—Zooplankton may feed on fecal material and contribute to the fragmentation and loosening of fecal pellets by coprorhexy and coprochaly (Noji et al. 1991). Cyclopoids have been suggested to function as a coprophagous filter that actively consumes sinking fecal pellets in oceanic ecosystems (Gonzalez and Smetacek 1994). In the present study, fecal pellet sedimentation rate was low in the area and season dominated by cyclopoids, i.e., the bay station in summer. This finding might imply that cyclopoids consume their own feces in the bay. However, the cyclopoids in the study area belong to the genera *Thermocyclops* and *Mesocyclops*, which are probably more predatory (see Kerfoot 1978) than their sluggish oceanic relatives *Oithona* spp., to which the coprophagous filter refers (Gonzalez and Smetacek 1994). Thus, the role of Baltic cyclopoids in pellet recycling remains to be determined.

However, calanoid copepods may also consume fecal material (Paffenhöfer and Knowles 1979; Green et al. 1992). For instance, *E. affinis* and *T. longicornis* are omnivorous, predominantly suspension feeding copepods (Schnack 1982; Tiselius and Jonsson 1990) that may feed on fecal pellets among other particles. The multiple regression analysis also identified a negative relationship between pellet sedimenta-

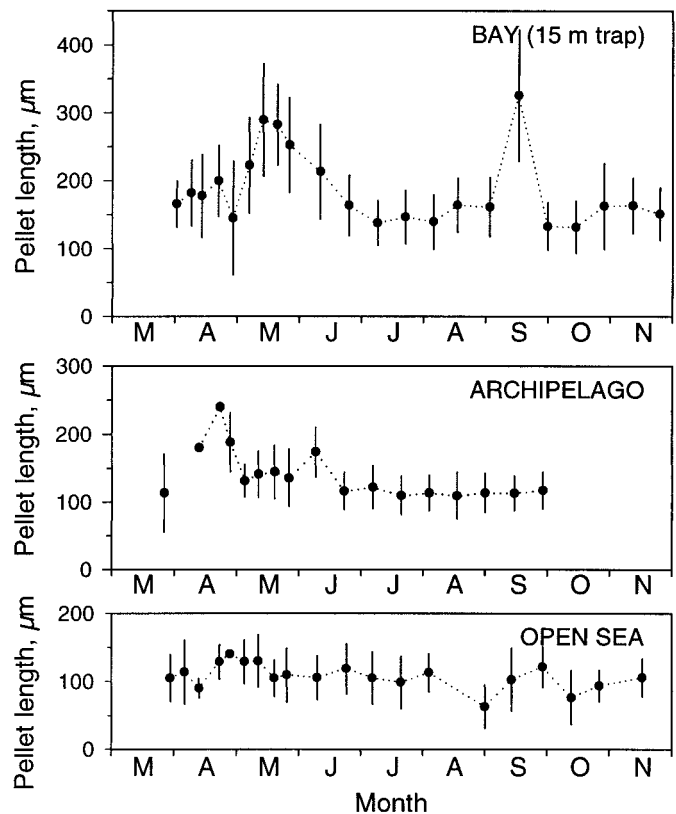


Fig. 7. Seasonal variations in fecal pellet length at the three sampling stations in March–November 1992. ● = mean; bars = standard deviations.

tion rates and *E. affinis* copepodites and *T. longicornis* adults (Table 4), which suggests coprophagy by these species. However, the regression analysis cannot confirm coprophagy or coprochaly by species that themselves produce many pellets. Alternatively, we may assess the coprorhexous effect by analyzing the relationship between copepod abundances and pellet breakup during different seasons. The correlation

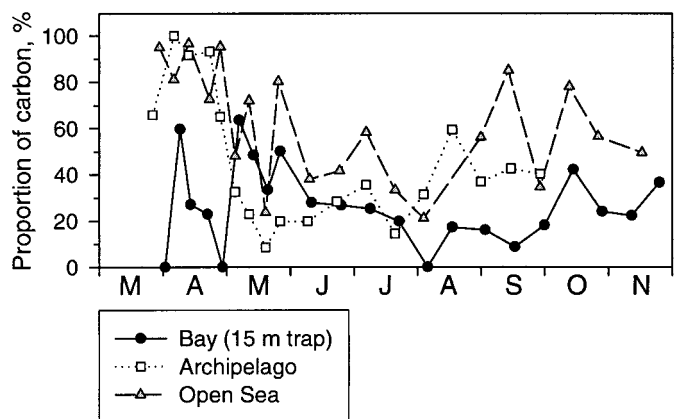


Fig. 8. Percentage contribution of broken fecal pellets of total fecal carbon sedimentation at the three sampling stations in March–November 1992.

analysis (Table 3) however indicated that a high copepod abundance usually coincided with a high sedimentation rate of intact pellets. Only *L. macrurus* adults at the bay station had a positive correlation with the proportion of broken pellets, suggesting coprophagy by this species.

Water stratification and pellet degradation rates—In the present study areas, bacterial production was positively correlated with water temperature (Tuomi et al. 1999), which should result in a faster decomposition of pellets during periods of warm water (see Honjo and Roman 1978). However, the pellets were the least fragmented during summer (June–August; Fig. 8), which suggests that the effect of microbial activity on pellet degradation rates was balanced by other simultaneous factors. Because the analysis did not confirm coprophagous or coprorhexous processes, we assume that abiotic processes played a role.

The most important abiotic factors that may directly or indirectly affect the sedimentation and remineralization of zooplankton feces are water temperature, turbulence, and hydrographical stratification. In cooler and more saline water, where the density difference between a pellet and the surrounding water is the smallest, pellets will sink more slowly than in warm and less saline water. The negative relationship between water viscosity and temperature will further strengthen this effect. We estimated that pellet sinking speeds increase by 56–58% when water temperature increases from 2°C to 16°C. Rapid sinking will lead to a low degree of pellet remineralization in the euphotic layer, which could explain the relatively small amount of broken pellets entering the traps in summer. However, water turbulence may increase the residence time of fecal pellets in the water column, thus allowing more time for the feces to be remineralized by microbial activity (Alldredge et al. 1987). In the present study areas, the wind-induced turbulence is obviously more intense in the archipelago and the open sea than in the sheltered bay area. Also, winds are usually stronger during the autumn than during the warm periods in summer (which is also reflected as a deepening of the thermocline in September–October; see Fig. 2). Because the proportion of broken pellets was lowest during the stratified period and increased toward the open sea (Fig. 8), we conclude that our data support the hypothesis of wind-induced turbulence enhancing the degradation of copepod feces in the water column.

Conclusions

Our results showed that mesozooplankton fecal pellets are a minor if not insignificant factor in the vertical transport of organic carbon in the coastal northern Baltic Sea. We thus agree with the wealth of studies suggesting that in areas and seasons dominated by small zooplankton species, most of the fecal material is degraded and remineralized within the euphotic zone (e.g., Smetacek 1980; Hofmann et al. 1981; Bathmann et al. 1987; Small et al. 1987; Lampitt et al. 1990; Lane et al. 1994). In the present study areas, the fecal carbon flux was always <0.05% of the total particulate organic carbon sedimentation. This is the lowest value reported. By comparison, in the Kattegat (Lundsgaard and Olesen 1997),

in the Norwegian Sea (Bathmann et al. 1987), and on the Japanese coast (Sasaki et al. 1988), fecal pellets contributed to 4–20% of particulate organic carbon sedimentation. Apparently, the special characteristics of the coastal northern Baltic Sea, i.e., steep hydrographical stratification, potential dominance of athecate flagellates and protozoans in the diet of copepods, and especially the dominance of small copepods, all make this area an extreme case in this respect. However, the magnitude of the fecal carbon sedimentation was highly dependent on the structure of the copepod community, i.e., on the relative proportions of cyclopoids, *L. macrurus*, and other calanoids. This effect seemed to balance or override other potentially important factors, such as seasonal and spatial variations in microbial activity or food concentration (Chl *a*). Therefore, significant changes in sedimentation rates of copepod fecal material may occur along with long-term changes in zooplankton community composition, which commonly occur in the northern Baltic Sea (e.g., Viitasalo et al. 1995b; Flinkman et al. 1998; Vuorinen et al. 1998).

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Received: 22 October 1998

Accepted: 15 April 1999

Amended: 28 April 1999