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The origin of sedimenting detrital matter in a coastal system

Abstract—Total sedimentation and the fraction due to copepod fecal pellets were measured during the growth season (March–October 1989) in the southern Kattegat, Denmark. In this period the sedimentation of detritus made up 52 g C m^{-2}, equal to 82% of the sedimenting matter from the euphotic zone, but fecal pellets (11 g C m^{-2}) constituted only a minor fraction. The remaining detrital matter was produced by other heterotrophs than copepods. Published data on heterotrophic biomass and grazing obtained during the investigation in the Kattegat are reviewed in order to relate the sedimentation to processes in the pelagic system. Copepod defecation nearly equaled the sedimentation of fecal pellets, indicating that retention of this matter in the pelagic system was insignificant. A considerable fraction (10–24%) of the carbon flow processed by heterotrophic pico-, nano-, and microplankton was converted to detritus that was lost from the mixed system by sedimentation. The microbial food web is thus not an exclusively regenerating system.

Sedimentation of autochthonous matter from the pelagic system is quantitatively related to the input of nutrients that are available for primary production (Eppley and Peterson 1979). The connection is based on a mass balance consideration whereby new production in the euphotic pelagic system is matched by an equivalent output of sedimenting organic matter. Estimates of nutrient fluxes in oceans and in coastal waters accord with this mass balance (Eppley and Peterson 1979; Olesen and Lundsgaard 1995). However, the functional relationship between sedimentation and the pelagic structure and productivity is only partly understood. One major problem is the identification of material collected in sediment traps and the sources of this matter. The identification has been based mainly on microscopy or on analysis for chemical markers of characteristic components. This has provided information on the sedimentation especially of phytoplankton and fecal pellets that can be quantified by pigment analysis and by microscopy. Other recognizable components also contribute to the flux (e.g. molts from zooplankton, eggs, cysts, and dead organisms), but a large detrital fraction usually remains unidentified.

The seasonal sedimentation of phytoplankton and total organic matter from the euphotic zone was measured in the southern Kattegat, Denmark (Olesen and Lundsgaard 1995). In the present paper the fecal component of edimentation is estimated from both pigment data and by direct microscopy of material collected during this investigation. The sedimentation of fecal matter and other detritus is related to previously published independent estimates of the activity of the dominant heterotrophic components. The sampling station (56°17′30″N, 11°59′54″E) was visited 52 d during 1989. Water was sampled from the mixed zone (extending to a depth of 10–22 m) and sediment traps were deployed in the pycnocline as described in Olesen and Lundsgaard (1995).

The fecal pellets in the sediment trap material were quantified by microscopy on samples fixed in 1% glutaraldehyde. The peritrophic membrane was destroyed on most of the pellets and the content was swelling and disintegrating, but both intact and partly disintegrated pellets were counted. The average volumes of intact pellets were estimated using a semiautomatic image analysis system (MOP-Videoplan Kontron Bildanalyse) assuming a cylindrical shape with spherical ends. The number of pellets (intact and partly disintegrated) was multiplied by the average volume of intact

pellets and a measured carbon : volume ratio in order to calculate the sedimentation of fecal pellet carbon (FPC). The carbon : volume ratio of fecal pellets was determined on fixed samples from the sediment traps as well as on fresh and fixed material from cultured *Acartia tonsa* and from sediment trap samples from the northern Øresund, Denmark (Table 1). Both the exposure time of sediment traps and the incubation period of the copepod cultures were 24 h. Pellets were picked up individually from the samples by pipetting and were washed 3 times in 100 ml 0.2-μm filtered artificial seawater (NaCl solution). Fixed pellets were allowed to stay overnight in the artificial seawater. Subsamples of ~120 washed pellets were photographed and pellet volumes were measured on projections of the negatives using the image analysis system. Each subsample was transferred to a preignited 13-mm GFC filter, dried, and combusted in a tube furnace (Carbolite) at 700°C. The released CO_2 was quantified with an infrared gas analyzer (ADC 225 MK 3) calibrated with oxalate.

An independent estimate of fecal pellet sedimentation was based on concentrations of pheopigments (Pha) in the sediment traps, as these pigments are considered to be associated with sinking fecal pellets (Welschmeyer and Lorenzen 1985). Pigments were extracted in 96% ethanol and measured spectrophotometrically according to Lorenzen (1967) by using an absorption coefficient for Chl *a* in ethanol of 83.4 l g^{-1} cm^{-1} (Wintermans and DeMots 1965). To convert the sedimentation of pheopigments to fecal pellet carbon (FPC_{pha}), the C : Pha ratio was calculated according to

$$C:Pha = (C:Chl) \times (F:I) \times (Pha:Chl)^{-1},$$

where C : Chl is the phytoplankton carbon : chlorophyll ratio, F : I is the defecation : ingestion ratio with regard to carbon, and Pha : Chl is the ratio between pheopigment production and chlorophyll ingestion. The C : Chl ratio was determined by linear regression analysis between concentrations of POC and Chl in the suspended material during two intensive sampling periods (Olesen and Lundsgaard 1995). This ratio was 29 during the diatom spring bloom and 93 during the dinoflagellate-dominated period in the late summer. The average F : I ratio for copepods is ~0.33 (review by Conover 1978) and pigment decomposition ratios are typically ~0.66 (Shuman and Lorenzen 1975; Helling and Baars 1985; Kiørboe and Tiselius 1987). The theoretical C : Pha ratio is therefore (C : Chl) × 0.33/0.66, giving values of 15 and 47 using the actual C : Chl data.

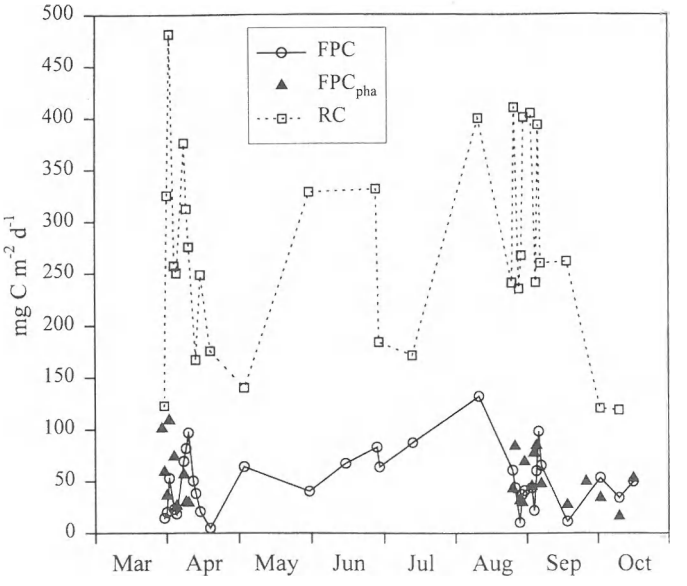

Fig. 1. Sedimentation of fecal pellet carbon estimated on the basis of microscopy (FPC) and pigment analysis (FPC_{pha}) as well as sedimentation of the remaining detritus fraction (RC).

The carbon : volume ratios of copepod fecal pellets were not significantly different when comparing sampling localities or absence/presence of fixation (*t*-test, $P = 0.05$ level). However, the food items influenced the carbon content of the pellets, but this could also be an indirect effect of different ingestion rates due to different prey size and concentration. The average carbon : volume ratio of pellets from the four different sources was 0.15 pg C μm^{-3} and this value was used for calculation of FPC (Fig. 1).

The results on FPC obtained by microscopical quantification were supported by the pheopigment-based estimates (Fig. 1). Differences between the two types of treatments were insignificant for both periods where C : Pha ratios could be calculated (paired and unpaired *t*-tests, $P = 0.05$ level).

Olesen and Lundsgaard (1995) presented data on the seasonal sedimentation of total particulate organic carbon (POC) and of phytoplankton carbon (PhytoC). PhytoC constituted 18% of the sedimenting matter integrated over the growth season. Detritus sedimentation was divided into two classes: FPC and the remaining detritus (RC; Fig. 1). FPC

Table 1. Carbon : volume ratios (C : vol; mean ± SD) of copepod fecal pellets collected from sediment traps and from cultures of *Acartia tonsa* feeding on *Rhodomonas baltica* or *Skeletonema costatum*. Samples fixed in 1% glutaraldehyde were used for some of the determinations as indicated.

Source of pellets	Fixation	C : vol (pg C μm^{-3})	No. of subsamples
Southern Kattegat, July–September, traps	+	0.18±0.07	3
Northern Øresund, May, traps	−	0.12±0.06	3
Cultures of *A. tonsa* feeding on *R. baltica*	−	0.18±0.07	5
	+	0.30±0.07	3
Cultures of *A. tonsa* feeding on *S. costatum*	−	0.078±0.032	7
	+	0.061±0.010	5

Table 2. Review of data on primary production, zooplankton ingestion, and bacterial uptake (mg C m^{-2} d^{-1}) in the mixed zone in the southern Kattegat 1989. Data were read from figures in the cited papers, recalculated as described in the text, and averaged for each of the four periods. The number of sampling days varied as indicated depending on the parameter.

Period (No. of sampling days)	28 March–9 April (7–10)	10 April–8 August (9–13)	21 August–8 September (10–15)	9 September–12 October (2–3)	Source of primary data
Copepod ingestion	200	100	190	120	Kiørboe and Nielsen 1994
Ciliate ingestion	170	440	430	230	Nielsen and Kiørboe 1994
Dinoflagellate ingestion	520	480	840	510	Hansen 1991, 1992
Bacterial uptake	960	160	60	30	C. Lundsgaard, M. Olesen, and P. K. Bjørnsen (unpubl.)
Sum	1,850	1,180	1,520	890	
Primary production	2,480	1,240	No data	300	Richardson and Christoffersen 1991

and RC constituted 17 and 65%, respectively, of the POC sedimentation integrated over the growth season. Variability of the carbon : volume ratios of fecal pellets and the potential loss of material from pellets following the disintegration of the peritrophic membrane may affect the accuracy of the FPC estimate. In case of an error of −50%/+100% in this estimate the RC fraction would still have been the largest, i.e. 42–74%.

Sedimentation from the euphotic zone at the study site was likely dominated by autochthonous matter because of (1) the relatively short residence time of particulate matter in the pelagic system compared to the current patterns and the distance from land, (2) the relatively low C : N ratio (average 8.6 by weight) for the sedimenting matter, and (3) the agreement between the estimates of new production based on nutrient inputs and the sedimentation (Olesen and Lundsgaard 1995). Consequently, biological processes in the pelagic system were the source of the sedimenting detritus. Independent estimates of carbon flow processed by the dominant pelagic organism groups were obtained by reviewing published results from studies conducted at the same station and during the same period (Table 2). The data were averaged for each of four periods corresponding to the peak and the decline of the diatom spring bloom (28 March–9 April), the summer period with low phytoplankton biomass (10 April–8 August), a late summer situation where dinoflagellates dominated (21 August–8 September), and the early autumn (9 September–12 October). Copepod and ciliate ingestion were calculated from production estimates assuming growth efficiencies of 0.33 and 0.40, respectively (Kiørboe and Nielsen 1994; Nielsen and Kiørboe 1994). The biomass of heterotrophic dinoflagellates in the upper mixed layer (Hansen 1991) averaged 470, 170, 300, and 190 mg C m^{-2} in the four periods, and these estimates were converted to ingestion using maximum specific ingestion rates of 1.1, 2.8, 2.8, and 2.7 d^{-1}, respectively. These ingestion rates were calculated using the average cell volume of heterotrophic dinoflagellates in each period (6,600, 2,100, 9,400, and 4,800 μm^3, respectively; P. J. Hansen pers. comm.), the scaling of maximum growth rate vs. cell volume (Hansen 1992), a Q_{10} of 2.5 for growth rates (Fenchel and Finlay 1983), and a growth efficiency of 0.20. Bacterial production was estimated by C. Lundsgaard, M. Olesen, and P. K. Bjørnsen (unpubl. results) from measures of tritiated thymidine incorporation and volume estimation by epifluorescence microscopy. Bacterial carbon uptake was calculated using a cell yield constant of 1,100 cells per fmol thymidine (Riemann et al. 1987), a carbon content of 0.35 pg C μm^{-3} (Bjørnsen 1986), and a growth efficiency of 0.40. Primary production was determined by ^{14}C incorporation (Richardson and Christoffersen 1991).

A part of the heterotrophic carbon demand was probably met by ingestion of heterotrophic biomass instead of phytoplankton. Nevertheless, the direct estimates of primary production (Richardson and Christoffersen 1991) were higher than the summarized zooplankton ingestion and bacterial carbon demand (Table 2) except for September–October where a low average primary production was based on only two determinations. Sedimentation of phytoplankton cells only accounts for a limited part of the excess primary pro-

Table 3. Sedimentation of fecal pellet carbon (FPC) and the remaining detritus fraction (RC) in absolute numbers and relative to estimates of heterotrophic activity in the mixed zone. See text for definition of C_{micro} and $PP_{diff.}$.

Period	28 March–9 April	10 April–8 August	21 August–8 September	9 September–12 October
FPC (mg C m^{-2} d^{-1})	51	59	48	37
FPC/copepod ingestion (%)	26	59	26	30
RC (mg C m^{-2} d^{-1})	258	218	301	181
RC/C_{micro} (%)	16	20	23	24
RC/PP_{diff} (%)	10	20	No data	(140)

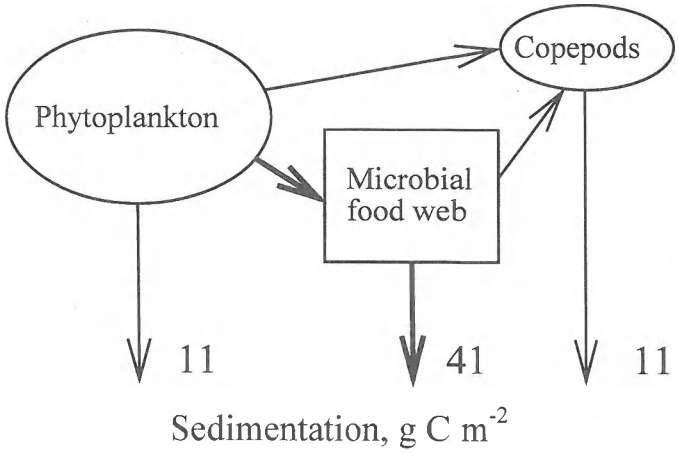

Fig. 2. Summarized presentation of the contribution of major pelagic groups to the sedimentation integrated over the growth season.

duction and the remaining discrepancy may be due to methodological errors or undersampling of specific organisms.

Sedimentation of FPC constituted 26–59% of the copepod ingestion (Table 3), and these fractions were in the upper range of defecation : ingestion ratios reported for copepods (Conover 1978). The results thus indicate that most of the fecal pellets escaped the mixed zone in spite of some disintegration. This is in contrast to other studies where disintegration due to microbial decomposition (Jacobsen and Azam 1984) or mesoplanktonic grazing activity (Lampitt et al. 1990) is considered as important for retention of the fecal matter in the pelagic system.

The sedimenting RC is assumed to consist of products from heterotrophic processes in the water column other than copepod grazing. These processes can be quantified in two ways: by summing up the ingestion by dinoflagellates and ciliates and the bacterial carbon demand (C_{micro}), and by subtracting the copepod grazing, the sedimentation of phytoplankton and the increase in phytoplankton biomass from the primary production (PP_{diff}).

The sedimentation loss of RC relative to the carbon flow through the pico-, nano-, and microzooplankton was ≥20% except during the decline of the spring bloom where a high fraction of the carbon flow was processed by bacteria (Table 3). Thus, the fractional sedimentation loss was in some periods at the same level for microzooplankton as for copepod grazing. The detritus loss from the microbial food web is possibly derived from several trophic levels and not only from grazers on phytoplankton. The relative detritus loss from each level is therefore smaller than from the total microbial compartment as whole.

Several mechanisms for the formation of detritus can be suggested to account for the sedimentation loss, i.e. defecation, secretion of particulate matter (e.g. transparent exopolymeric particles; Alldredge et al. 1993), and death of living biomass by virus infection or grazer feeding inefficiencies (sloppy feeding). The significance of copepod defecation in the formation of the sedimenting detritus has gained much attention, while assimilation efficiency, fecal production, and fate of fecal debris are poorly understood with regard to nano- and microzooplankton. A few studies have shown net assimilation efficiencies of 60–80% for nanoflagellates and ciliates (e.g. Fenchel 1982; Stoecker 1984; Caron et al. 1985), and these efficiencies accord with the relative detritus loss from microbial activity in this study. Additionally, it is known that ciliates and dinoflagellates produce distinct fecal particles (Elbrächter 1991; Stoecker 1984). However, these particles are much smaller than copepod fecal pellets and their sinking velocity is therefore lower.

Average sedimentation velocities of RC were calculated by dividing the sedimentation rates by the suspended concentrations. An estimate of the RC fraction in the water was obtained by subtracting the biomass of phytoplankton (Olesen and Lundsgaard 1995), copepods (Kiørboe and Nielsen 1994), ciliates (Nielsen and Kiørboe 1994), and dinoflagellates (Hansen 1991) from the concentration of suspended POC. The average sinking velocity of RC was 1.5 m d^{-1} (range 0.7–4.0 m d^{-1}), equivalent to an average daily sedimentation loss from the euphotic zone of 12%. This is a minimum estimate because the suspended concentration was neither corrected for the biomass of, for example, bacteria and nanoflagellates (except dinoflagellates) nor for the suspended copepod fecal pellets. Aggregation of detritus particles produced in the microbial food web may explain why these small particles are sedimenting with velocities of >1.5 m d^{-1}. The dominance of fluffy aggregates in the sedimented matter supports this assumption.

We conclude that the detritus production from the pico-, nano-, and microzooplankton is significant for the total sedimentation of matter from the pelagic system as summarized in Fig. 2. Copepods have been ascribed a major role for sedimentation due to production of fast sinking fecal pellets and in this study probably most of the defecated pellets left the mixed euphotic zone. Nevertheless, the copepod fecal pellets were of minor significance for the total sedimentation because a limited fraction of the carbon flow was processed by the copepods. Estimates of between 10 and 24% of the primary production processed by pico-, nano-, and microzooplankton was lost from the system by sedimentation, indicating that the microbial food web is not exclusively a regenerating compartment.

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