Title	Vertical Transport of Organic Carbon by Sinking Particles and the Role of Zoo- and Phytogenic Matters in Neritic Waters
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Citation	北海道大學水産學部研究彙報, 39(4), 265-274
Issue Date	1988-11
Doc URL	https://hdl.handle.net/2115/24009
Type	departmental bulletin paper
File Information	39(4)_P265-274.pdf

Bull. Fac. Fish. Hokkaido Univ.
39(4), 265-274. 1988.

Vertical Transport of Organic Carbon by Sinking Particles and the Role of Zoo- and Phytogenic Matters in Neritic Waters*

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Abstract

The origin of sinking particles was examined using a light microscope with samples collected from neritic waters of Funka Bay, Hokkaido. Organic carbon fluxes of the identified particles were estimated based on the calculated particle volume and the reported organic carbon content. Fecal pellet fluxes varied between 5 and 8 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$ in the stratified water column of the summer season, and 15 and 41 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$ in the mixed water column of the winter season. Their values corresponded to 2-4% and 5-25% of the total organic carbon fluxes, respectively. The size of fecal pellets in winter was larger than that in summer. This difference in the pellet size can be attributed to the size of dominant zooplankters. Observed pellet fluxes in summer were lower than the pellet production rate calculated from the zooplankton food requirement. It was considered that most of the slowly sinking small pellets produced by small zooplankton in summer were decomposed to some extent within the high temperature water column.

Introduction

It is thought that the zooplankton fecal pellet has an important role in the transportation of organic materials from the surface to the bottom (Honjo and Roman, 1978; Turner and Ferrante, 1979; Urrere and Knauer, 1981). There is, however, some evidence that the sedimentation of fecal pellets contributes little to material reaching the floor of the deep sea (Asper, 1987; Bathmann et al., 1987; Pace et al., 1984; Smetacek, 1980). While the larger and more compact pellets are transported to the sea floor before substantial degradation takes place (Emerson and Roff, 1987; Fowler and Small, 1972; Paffenhöfer and Knowles, 1979; Small et al., 1979), most of the very small pellets are being recycled in the upper waters (Komar et al., 1981; Lerenzen and Welschmeyer, 1983; Small et al., 1979; Smetacek, 1980). Since pellet size has been observed to be related to zooplankton size, that is larger organisms produce larger pellets (Paffenhöfer and Knowles, 1979), the zooplankton community can very well affect the vertical flux of organic material within the water column.

In Funka Bay, the cold Oyashio water flows into the bay in early spring. In summer, thermal stratification develops and a pycnocline is formed between the

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* *Contribution No. 199 from the Research Institute of North Pacific Fisheries, Faculty of Fisheries, Hokkaido University*
(北海道大学水産学部北洋水産研究施設業績第 199 号)

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surface and middle layers. Waters from the Tsugaru Warm Current, a branch of Kuroshio, come into the bay in late summer. Autumn wind gradually cools the surface water and, at the onset of winter, vertical mixing ensues (Ohtani and Akiba, 1970). These changes in prevailing water masses have been observed to influence the species composition of the zooplankton community in the bay (Hirakawa, 1983). It is also known that the mean volume of copepods is small in summer and large in winter and spring (Odate and Maita, in preparation). These changes may affect the vertical transport of organic matter in the water column.

The objectives of the present study were to estimate the flux of fecal pellets and to determine the biogenic sources of sinking particles within the vertically mixed water column and the thermally stratified one. In addition, the fecal pellet production rate in the upper water column was estimated according to Ikeda and Motoda's equation and compared with the observed pellet flux.

Materials and Methods

A sediment trap system [as described by Maita et al. (1986)] was moored at a depth of 74 m in the central part of Funka Bay (Station 30, 42°16.2′N, 140°36.0′E ; Fig. 1), for two week intervals, during the summer season (Aug. 21-Oct. 1) and winter season (Nov. 15-Dec. 3, Feb. 1-Mar. 15, and May 10-23). This system was composed of eight cylindrical traps, of which four were covered with screen while the remaining four were left open. Antiseptic treatment of 1.5 M NaCl with 1% formalin was applied to the screened traps and the open traps. In this study, subsamples from one of the treated open cylinders were examined using a light microscope fitted with an eyepiece micrometer.

Particles were classified as phytogenic matter, zoogenic matter, or unidentified materials. The former two categories were further subdivided into intact organisms

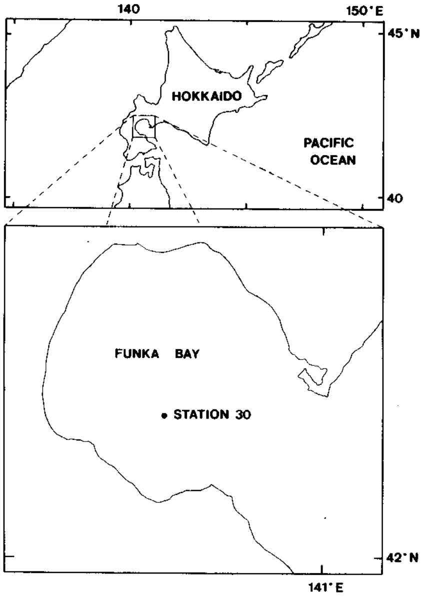

Fig. 1. Location of the experimental station in Funka Bay.

and fragments. Since fecal pellets are produced by the zooplankton, they were classified as zoogenic matter.

The volume of zoogenic matter was estimated based on the measurements of length and width. Phytoplankton volume was estimated by multiplying the total number of cells by 0.01×10^{-3} mm^3, the mean volume of *Thalassiosira* spp. (Odate, unpublished results). The volume of fragments was estimated by multiplying the surface area to an assumed thickness of 1.0 μm.

The fecal pellet volume was converted into the amount of organic carbon, by assuming a specific gravity of 1.22 (Wiebe et al., 1976), a dry : wet ratio of 0.11 and an organic carbon content of 20% (Johannes and Satomi, 1966). However, for the other components, a specific gravity of 1.0, a dry: wet ratio of 0.1 (Wiebe et al., 1975) and a organic carbon content of 0.4 (Ikeda, 1974) were applied.

Plankton samples were also collected at this station (Station 30, Fig. 1), monthly from April, 1984 to May, 1985. Phytoplankton organic carbon production and zooplankton food requirement during this period were reported elsewhere [Maita and Odate (in preparation) and Odate and Maita (in preparation), respectively].

The amount of fecal pellets excreted by zooplankton was estimated from the daily food requirement as determined during the same period (Odate and Maita, in preparation). For example, the biomass and individual number of nauplii in the water column (0-74 m) on August 21 was 118 mg dry weight•m^{-2} and $2{,}958 \times 10^3$ ind•m^{-2}, respectively. Under the water temperature conditions on that day, their total food requirement was calculated as 83.6 mgC•m^{-2}•d^{-1}, using Ikeda-Motoda's physiological method. Since the method includes the assumption of an assimilation efficiency of 70% (Ikeda and Motoda, 1978), 30% of required carbon ($83.6 \times 0.3 = 25.1$ mgC•m^{-2}•d^{-1} in Table 3) may be excreted as the fecal pellets.

Results

General description of sinking particles

Most of the sinking particles had irregular shape (Fig. 2-A) and were composed of fine grains (Fig. 2-B). These were classified as residual fraction, because of the difficulty of microscopic measurement. Aside from these unidentified particles, cylindrical fecal pellets (Fig. 2-C), intact bodies of zooplankton (Fig. 2-D), fragments of zooplankton (e.g. lorica of tintinnids; Fig. 2-E), and intact phytoplankton cells (Fig. 2-F) were observed. The examples shown in Fig. 2-C were typical small sized fecal pellets found in the stratified water column. Fecal pellets larger than 500 μm in length were rarely observed, but their contribution in terms of carbon amount was significant.

Fluxes in the stratified water column

The calculated biogenic fluxes from Aug. 21 to Oct. 1 are shown in Table 1. Daily carbon flux of the indentified components ranged from 22 to 55 mgC•m^{-2}, while the total organic carbon fluxes during the same period were 224 to 258 mgC•m^{-2}•d^{-1} (Maita et al., 1986). This shows that only 10 to 23% of the total organic carbon flux could be classified.

About 75 to 96% of the identified biogenic matter in the sinking particles

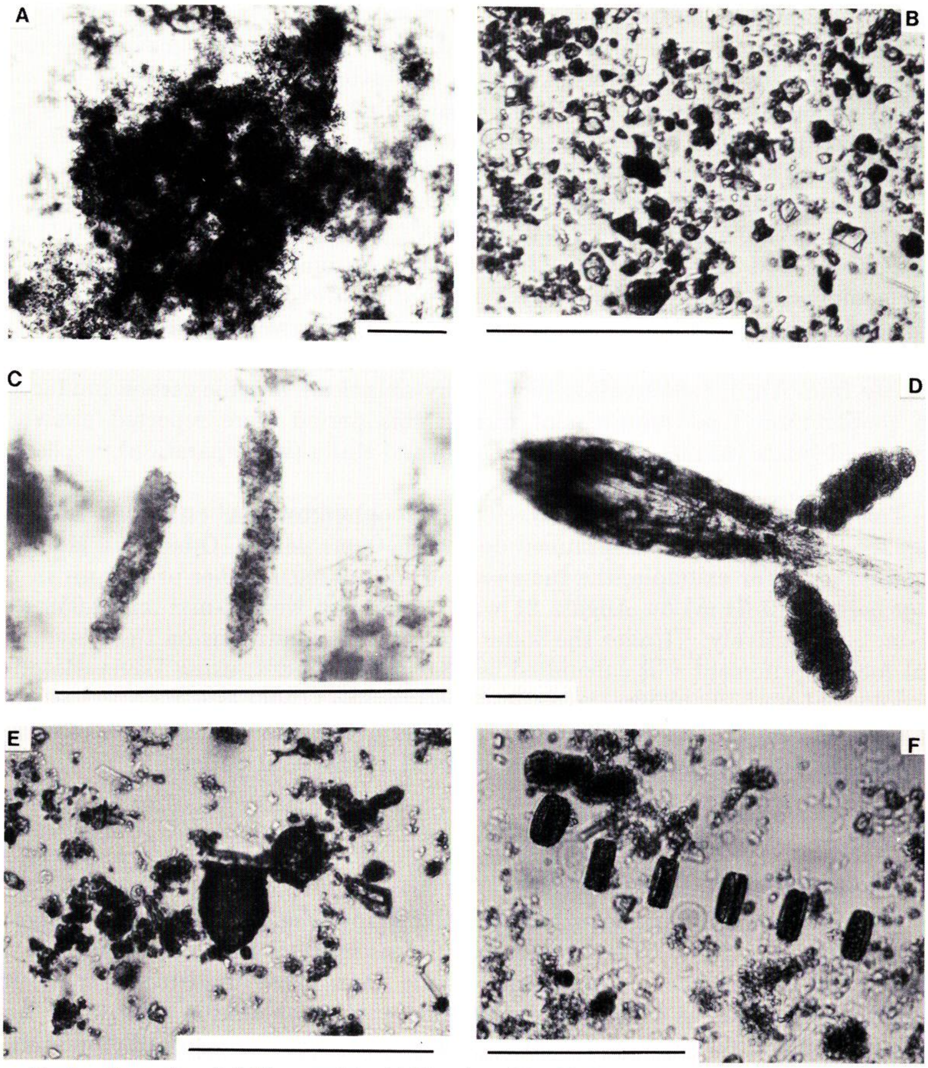

Fig. 2. Examples of sinking particles (A-F). A, unidentified amorphous, which were the most abundant in the trapped samples; B, very fine grain; C, fecal pellets; D, intact body of zooplankton; E, fragment of zooplankton; F, intact cell of phytoplankton. The volume of items A and B was not evaluated. Bars indicates 100 μm.

Table 1. Fluxes of zoogenic and phytogenic matter ($\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$) and the percent contribution to the total organic carbon flux in the stratified water column in Funka Bay.

Period	Zoogenic matter			Phytogenic matter		sum (A)	Total* (B)	Unidentified (B)-(A)
	intact	fragments	fecal pellets	intact	fragments			
I	10	2	8	1	1	22	224	202
Aug. 21-Sep. 3	4%	1%	4%	ng	ng	10%	100%	90%
II	39	3	5	1	1	49	258	209
Sep. 3-Sep. 20	15%	1%	2%	ng	ng	19%	100%	81%
III	35	1	5	4	10	55	238	183
Sep. 20-Oct. 1	15%	ng	2%	2%	4%	23%	100%	77%

ng; negligible (less than 0.5%).

* Total orgaic carbon flux by Maita et al. (1986).

originated from the zoogenic matter. Intact organisms accounted for 45 to 80% of the calculated fluxes, whereas 2 to 7% was intact phytoplankton. Fecal pellet fluxes were 5 to 8 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$, which were equivalent to 2 to 4% of the total organic carbon flux.

Fluxes in the non-stratified water column

Table 2 shows the fluxes during the early mixing period (Nov. 15 to Dec. 3), late mixing period (Feb. 1 to Mar. 15), and after the mixing period (May 10 to May 23). During the early mixing period, the identified fraction of biogenic organic carbon

Table 2. Fluxes of zoogenic and phytogenic matter ($\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$) and the percent contribution to the total organic carbon flux in the mixed water column in Funka Bay.

Period	Zoogenic matter			Phytogenic matter		sum (A)	Total* (B)	Unidentified (B)-(A)
	intact	fragments	fecal pellets	intact	fragments			
IV	tr	tr	15	4	tr	19	189	170
Nov. 15-Dec. 3	ng	ng	8%	2%	ng	10%	100%	90%
V	65	tr	41	8	2	116	413	297
Feb. 1-Feb. 18	16%	ng	10%	2%	ng	28%	100%	72%
VI	78	tr	16	12	2	108	329	221
Feb. 18-Feb. 28	24%	ng	2%	4%	1%	33%	100%	67%
VII	63	1	40	20	1	125	157	32
Feb. 28-Mar. 15	40%	1%	25%	13%	1%	80%	100%	20%
VIII	507	tr	36	1	1	545	645	100
May 10-May. 23	79%	ng	6%	ng	ng	84%	100%	16%

tr; trace (less than 0.5 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$).

ng; negligible (less than 0.5%).

* Total organic carbon flux by Yanada (unpublished results).

(corresponding to 10% of the total carbon flux) was composed of fecal pellets (79%) and intact phytoplankton (21%).

In the late mixing period, a greater fraction of sinking particles could be identified. For example, the contribution of the identified matter to the total organic carbon flux increased to 28% in February and 70% in March. Intact organisms were the major component, comprising 50 to 72% of the identified matter or 63 to 78 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$. The contribution by phytogenic matter to the total carbon flux also increased. This increment corresponded to the spring bloom of phytoplankton, which was dominated by diatoms. The flux by the fecal pellets varied between 16 to 41 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$. Percent contribution of fecal pellets to the total organic carbon flux was 5 to 25%, which was higher than that in the stratified period.

The flux of identified particles after the mixing period (545 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$) comprised 84% of the total organic carbon flux (645 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$; Yanada, unpublished results). Ninety three percent of that was composed from the intact zooplankton, mostly copepods (*Calanus plumchrus*). The flux of phytogenic matter was only 2 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$, being comparable to the rate during the summer period. The flux of fecal pellets in the period after mixing was nearly the same as the late mixing period, 36 $\mathrm{mgC \cdot m^{-2} \cdot d^{-1}}$. The contribution of fecal pellets to the total organic

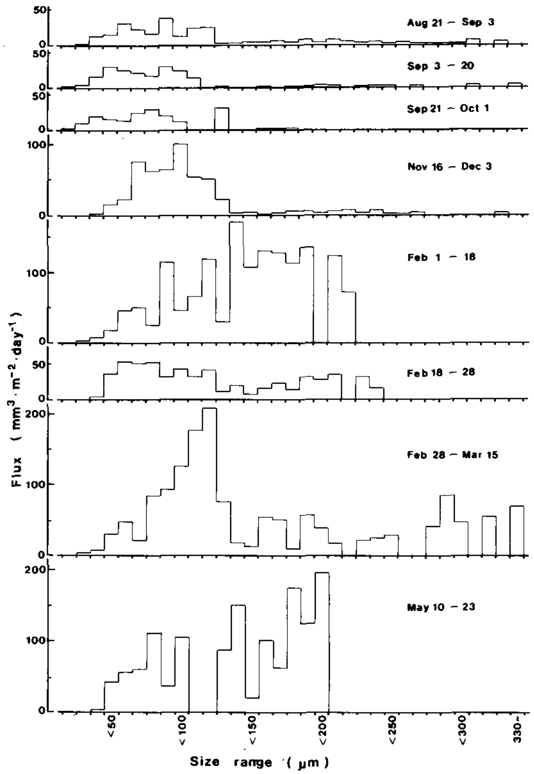

Fig. 3. Fecal pellet flux in each size class.

Table 3. Estimated fecal pellet production by copepods and observed fecal pellet flux (mgC•m^{-2}•d^{-1}).

Date	nauplii	Fecal pellet production copepodites (large)*1	(small)*2	sum	mean	observed flux
Aug. 21	25.1*3	8.8	49.9	83.8		
					158.8	7.8
Sep. 3	85.2	nd	148.5	233.7		
					153.2	5.4
Sep. 21	30.5	2.8	39.4	72.7		
					62.1	5.0
Oct. 1	21.7	7.6	22.2	51.5		
Nov. 15	6.5	4.0	9.5	19.9		
					26.0	14.5
Dec. 3	9.0	20.7	2.4	32.1		
Feb. 1	1.5	1.6	0.3	3.4		
					3.3	40.7
Feb. 18	1.0	0.6	1.5	3.1		
					5.7	15.6
Feb. 28	2.3	4.7	1.2	8.2		
					11.7	40.0
Mar. 15	7.0	4.8	3.3	15.1		
May. 10	nd	88.6	nd	88.6		
					69.9	35.5
May. 23	12.5	25.9	12.8	51.2		

*1 ; larger than 200 μm in width, collected by a Norpac net.

*2 ; smaller than 200 μm in width, collected by van Dorn sampler.

*3 ; fecal pellet production rate was estimated based on the food requirement calculated by the Ikeda-Motoda's equation. An example of this calculation is given in Materials and Methods in this text.

nd ; not determined.

carbon flux was only 6%.

Size distribution of fecal pellet flux

The size range of fecal pellets converted to spherical diameter is shown in Fig. 3. In summer, the predominant size range of pellets was between 30 and 130 μm. In winter, however, the range shifted to larger sizes, increasing the flux and the contribution by pellets to the total flux.

Estimated production of fecal pellets and observed pellet flux are shown in Table 3. During the stratified period, the observed pellets in the trap accounted for only 3 to 7% of the estimated fecal pellet production. In the early mixing period, the observed pellet flux increased, while the pellet production rate decreased. The observed pellet flux surpassed the pellet production rate during the late mixing period. After the mixing period, the pellet production rate increased.

Discussion

Many kinds of particles were observed in the trap samples (e.g. Fig. 2-A to F). Most of these had irregular forms and could not be identified in terms of origion. Among them, large amorphous matter may have been discarded larvacean houses.

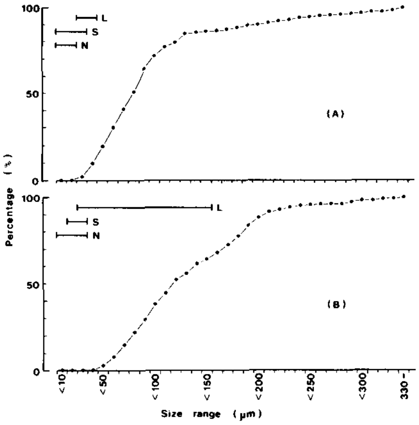

Fig. 4. Accumulated percent contribution of fecal pellet size to total pellets flux. Horizontal bars denote the calculated size range of pellet following the equation of Paffenhöfer and Knowles (1979). A, stratified water column; B, non-stratified water column. L, large copepodites; S, small copepodites; N, nauplii.

This material is an important source of marine snow, i.e. large flocculent particles (>0.5 mm), the distribution of which is particularly abundant in coastal waters (Alldredge and Madin, 1982). Larvaceans were observed commonly in the water column during summer. Large amounts of unidentified flux in summer (Table 1) may be explained by these discarded larvacean houses.

Furthermore, the intact bodies of zooplankton also consitituted a large portion of the samples during all periods. Knauer et al. (1979) have noted that the majority of animals actively swam into the trap, so that they were settled by the antiseptic before feeding on the trapped organic matter. In that case, the intact bodies of zooplankton should not be included in the vertical flux.

After intact animals, fecal pellets comprised the next largest share. The flux of the pellets was low in the stratified period and high in the mixed period (Fig. 2). This trend is consistent with the results of Knauer et al. (1979).

Figure 4 summarizes the accumulated contribution of size range to the total pellet flux. In summer, most of the pellets (>80%) were smaller than 130 μm (Fig. 4A). In winter and spring, however, about 40% of the pellets were larger than 130 μm (Fig. 4B). This difference in pellet size can be attributed to the size of dominant organisms during the period (Paffenhöfer and Knowles, 1979; Odate and Maita, in preparation). Horizontal bars in Fig. 4 denote the size range of the pellet calculated by the equation of Paffenhöer and Knowles (1979), using zooplankton size in the upper water column from the surface to 74 m in depth (Odate and Maita, in preparation). Observed pellets in trap samples were larger than calculated pellet size in summer. This implies that most of the pellets produced by small copepodites and nauplii, which were the major pellet producers during that period (Table 3), did not reach the depth of 74 m, directly. It is supposed that small pellets are being decomposed at a significant rate while slowly sinking, since the decomposition rate of particulate organic matter increases under high temperature regimes (Maita and Yanada, 1978; Yoshida et al., 1983). In addition, fecal pellets are a potentially large food source for particle-grazing animals (Johannes and Satomi, 1966). Coprophagy may contribute to the significant loss of small pellets in the water column (Paffenhöfer and Knowles, 1979; Lerenzen et al., 1983; Emerson and Roff, 1987). The great discrepancy between the expected and observed pellet flux can be accounted for by these processes. Moreover, some part of the unidentified aggregated matter might be derived from destroyed small pellets.

On the other hand, in the early mixing period and the period after mixing, the discrepancy was smaller than that in summer. This may result from a decline in decomposition rate in the water column and/or the fact that large-sized pellets (Fig. 3) sink more rapidly (Small et al., 1979). In the late mixing period, however, a larger amount of pellets than was expected were caught by the trap. This suggests a significant contribution by larger zooplankton and micronecton other than copepods (e.g. euphausiids, amphipods, fish larvae).

Acknowledgments

We thank the officers and crew members of the T/S Ushio Maru, Hokkaido University, for their assistance in mooring and recovering of the sediment trap system.

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