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Production and downward flux of zooplankton fecal pellets in the anticyclonic gyre off Shikoku, Japan

Sediment trap
Fecal pellets
Production
Downward flux

Piège à sédiment
Pelote fécale
Production
Flux descendant

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ABSTRACT

Sediment trap experiments were conducted to assess the production, disintegration and downward flux of zooplankton fecal pellets in the upper 500 m water column of the anticyclonic gyre off Shikoku, Japan. The particulate organic carbon (POC) flux decreased from 53.7 mgC m^{-2} d^{-1} at 50 m to 23.7 mgC m^{-2} d^{-1} at 500 m. The POC flux at the bottom of the euphotic layer (100 m) was 37.9 mgC m^{-2} d^{-1}, which was equivalent to about 5 % of the daily primary production in the gyre. The estimated pellet carbon flux accounted for 0.4-1.7 % of the total POC flux. The pellet flux rapidly decreased in the upper 150 m layer, in parallel with the decrease in zooplankton abundance. A mid-depth peak of pellet flux, not associated with a noticeable population of zooplankton, was observed at 200-300 m. The pellet production rate of the copepod and euphausiid populations in the euphotic layer was estimated from zooplankton abundance data and shipboard measurements for pellet production rates. Comparison of pellet flux with the estimated pellet production rate showed that pellets produced by small copepods (< 1.5 mm) were disintegrated in the euphotic layer at an almost 100 % efficiency and pellets produced by large copepods (> 1.5 mm) and euphausiids at an 80 % efficiency.

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RÉSUMÉ

Production et sédimentation des pelotes fécales du zooplancton dans le tourbillon cyclonique au large de Shikoku, Japon

La production des pelotes zooplanctoniques et leur sédimentation dans les 500 premiers mètres de la colonne d'eau ont été étudiées à l'aide de pièges à sédiment au large de Shikoku, Japon. Le flux de carbone organique particulaire (POC) décroît de 53,7 à 23,7 mgC m^{-2} j^{-1} entre 50 et 500 m de profondeur ; au bas de la couche euphotique (100 m), il est de 37,9 mgC m^{-2} j^{-1}, soit environ 5 % de la production primaire journalière dans le tourbillon. Le flux de carbone dans les pelotes est estimé à 0,4-1,7 % du flux total POC. Le flux de pelotes décroît rapidement dans les 150 premiers mètres, comme l'abondance du zooplancton. A miprofondeur (200-300 m), il présente un pic, sans relation particulière avec une population zooplanctonique. Dans la couche euphotique, le taux de production de pelotes des populations de copépodes et d'euphausiacées a été estimé à partir des données d'abondance du zooplancton et des mesures de taux de production des pelotes. La comparaison du flux et du taux de production des pelotes montre que la proportion des pelotes dégradées dans la couche euphotique est de 100 % dans le cas des petits copépodes (< 1,5 mm) et de 80 % dans le cas des grands copépodes (> 1,5 mm) et des euphausiacées.

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INTRODUCTION

Particulate matter in seawater is broadly divided into two categories, comprising fine and large particles. The former constitutes the major medium in which the exchange of elements and compounds between dissolved and particulate phases takes place; the latter is responsible for the downward transport of elements and compounds (Bacon *et al.*, 1985). The study of particulate matter dynamics, therefore, is fundamental to elucidation of the behaviour and distribution of elements and compounds in the sea (Simpson, 1982; Fowler and Knauer, 1986).

Production of fecal pellets by zooplankton is one of the most important mechanisms whereby fine particles are integrated into large particles (McCave, 1975; 1984). The sinking rates of pellets produced by large zooplankton are high enough for them to reach the ocean floor within days to weeks (Small *et al.*, 1979; Komar *et al.*, 1981). Such a view is supported by the finding that pellets are among the most common components of the materials collected by sediment traps at depths (Wiebe *et al.*, 1976; Honjo, 1978). Under field conditions, however, pellets are subjected to different modes of disintegration, such as microbial degradation and coprorhexy (*cf.* Lampitt *et al.*, 1990). A rapid decrease in pellet flux in the upper water column has been shown by some studies with sediment traps (Urrere and Knauer, 1981; Sasaki and Nishizawa, 1989) or *in situ* filtration systems (Bishop *et al.*, 1980; 1986 *a*; *b*). A model predicts that most of the pellets produced by copepods are rapidly disintegrated and do not reach even the sea floor of a shallow continental shelf (Hofmann *et al.*, 1981). In some cases, pellets produced in the upper euphotic layer of oligotrophic oceans appear to be rapidly recycled *in situ* and contribute little to the particle flux out of the euphotic layer (Small *et al.*, 1987). Pellets collected in the bathypelagic zone do not always originate from the euphotic layer (Urrere and Knauer, 1981; Sasaki and Nishizawa, 1989).

It is often forgotten that pellet production occurs at any depth (Urrere and Knauer, 1981; Sasaki and Nishizawa, 1989) and that a pellet flux is the net balance between their production and disintegration in the water column (Fowler and Knauer, 1986). The disintegration rate of pellets, in turn, can be estimated from the pellet flux and the pellet production rate in the water column. However, few studies on pellet fluxes have included a detailed analysis of zooplankton distribution (Bishop *et al.*, 1986 *a*; *b*; Sasaki *et al.*, 1988). Although the pellet production rate of zooplankton has been investigated using cultured phytoplankton as food sources (Paffenhöfer and Knowles, 1979; Dagg and Walser, 1986), the data on pellet production rates of zooplankton feeding on natural particles are scarce (Small *et al.*, 1983; 1987; Ayukai 1987 *a*; 1991).

The present study was conducted as part of a multidisciplinary research programme on the structure and dynamics of the anticyclonic gyre off Shikoku. The hydrography and distributions of nutrients and chlorophyll have been described by Wada (1984), Takahashi *et al.* (1985) and Sugimoto *et al.* (1986), while the primary productivity has been reported by Hama *et al.* (1983). We report here the pellet flux in relation to the distribution of zooplankton in the upper water column. We also estimate the pellet production rate in the euphotic layer and compare it with the pellet flux at the bottom of the euphotic layer.

MATERIALS AND METHODS

All field measurements and experiments were carried out during the KH-82-3 cruise of R.V. *Hakuho-maru* of the Ocean Research Institute, University of Tokyo, to the gyre in June-July, 1982 (Fig. 1).

Sediment trap experiment

The basic design of the sediment trap used has been described elsewhere by Sasaki and Nishizawa (1981).

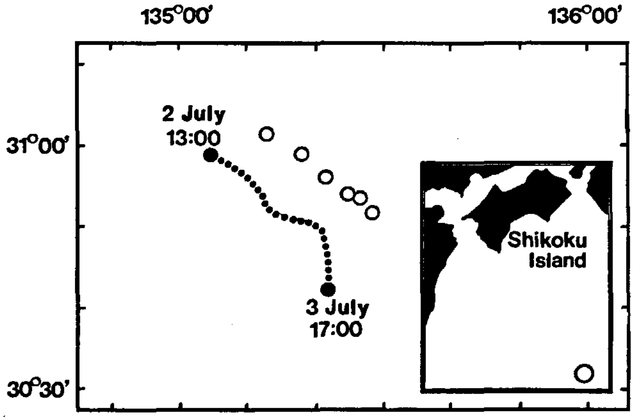

Figure 1

Study area off Shikoku and the path of the free-drifting sediment trap system. Open circles denote the Longhurst-Hardy Plankton Recorder stations.

Briefly, the trap is made of a PVC cylinder with an inner diameter of 13.5 cm and a height of 45 cm. A 0.8 µm Millipore filter (15 cm diameter) is fitted to the filter holder attached to the bottom of the trap. A honeycomb baffle (15 cm height, 8 mm grid size) with two tall sampling chambers (25 cm height, 4 cm inner diameter) is installed just above the filter. The baffles, although their effect on trap efficiency is dubious (US GOFS Planning Report No. 10, 1989), are essential to minimize aggregation of collected materials in sediment traps. The space between the filter holder and the bottom lid is filled with a 10 % buffered formalin solution to prevent degradation of collected materials.

A free-drifting system was deployed for 28 hours on 2 -3 July in the central part of the gyre. Paired traps were placed at depths of 50, 100, 150, 200, and 300 m and a single trap at depths of 400 and 500 m. One of each of the paired traps from 50 m to 200 m depths did not have sampling chambers. After retrieval, water above the baffles was first removed from a side drain and then the remaining water was filtered off. Materials collected on Millipore filters were desalted with graded NaCl solutions and frozen for later counting and sizing of pellets. Water in the sampling chambers was filtered through a pre-combusted Whatman GF/C glass fiber filter for later analysis of particulate organic carbon (POC).

Niskin-bottle casts were made at the site following deployment and retrieval. Water collected was analysed for chlorophyll, phaeopigments and POC. Chlorophyll and phaeopigments were determined by fluorometry and POC by the dry combustion method (Strickland and Parsons, 1972).

In the laboratory, Millipore filters with sedimented materials were dried at 40°C for 24 hours. Filters were cut into small pieces (about 5 cm^2), cleared and mounted on microscope slides using a mixture of the mounting solution (Eukitt, O. Kindler, Germany) and Xylene (3:1). Slides were scanned at x100 under an Olympus light microscope and the length and width of each pellet were measured using a micrometer at either x 100, x 200 or x 400. The whole filter area was examined, although sedimented materials were rather evenly distributed on filters.

Zooplankton distribution

Zooplankton were collected by oblique tows of a plankton net (45 cm mouth diameter, 180 cm length, 350 µm mesh size) mounted on the Longhurst-Hardy Plankton Recorder (LHPR, Benthos Inc., type 315). Each tow was made from about 500 m to the surface at 4 h intervals nearby the drifting system.

One-litre water samples for microzooplankton counting were also taken from the above-mentioned Niskin-bottle casts. The samples were preserved by a borax neutralized formalin solution at a final concentration of 1 %. The preserved samples were allowed to stand for 24 hours and concentrated 100-fold by slowly siphoning off the supernatant. Microzooplankton in concentrates were counted under an inverted microscope.

Table 1

Developmental stage and body length of copepods and euphausiids used for the fecal pellet production experiments.

	Developmental stage	Body length (mm)	No. of expts
Small copepods			
Clausocalanus spp.	CV, F,M	1.0-1.5	19
Oncaea sp.	CV,F	0.9-1.1	5
Paracalanus parvus	CV, F, M	0.9-1.3	6
Medium copepods			
Calanus tenuicornis	CV, F; M	1.7-2.2	13
Pleuromamma gracilis	CV	1.5-2.0	8
Scolecithrix danae	CV, F	1.8-2.0	3
Temora stylifera	CV, F, M	1.7-1.8	5
Large copepods			
Centropages bradyi	CV	2.2-2.5	2
Eucalanus attenuatus	CIV, CV	2.8-3.2	1
Eucalanus subcrassus	CIV	2.6-2.7	1
Pleuromamma robusta	CV	3.1-3.7	1
Rhincalanus nasutus	CIV	2.7-3.2	2
Euphausiids	Furcilia	3.6-5.1	6

Fecal pellet production experiment

Zooplankton for experiments were captured at six stations in the gyre by oblique tows of a plankton net (50 cm mouth diameter, 150 cm length, 105 µm mesh size and 1-litre cod-end volume) from 10, 30 or 75 m to the surface. A plankton net (45 cm mouth diameter, 180 cm length, 105 µm mesh size) with a calibrated flowmeter was also vertically towed from 100 m to the surface at each of 6 stations to check whether zooplankton used in pellet production experiments represented the zooplankton population in the gyre. In each experiment, sea water was collected with a Niskin bottle from the same depth as zooplankton (10, 30 or 75 m).

Female, male, CV and CVI copepods of twelve different species and juvenile euphausiids (Tab. 1) were sorted out from mixed zooplankton (< 1 h) and placed into beakers filled with Whatman GF/C filtered water. After 6 h acclimatization to laboratory conditions, 5 individuals of each copepod species or 2 juvenile euphausiids were introduced into each of 1.2 l glass bottles filled to the top with natural water, which had been passed through a 56 µm mesh screen to remove other pellet producers. Male copepods, because of their possible low metabolic activity, were separated from the rest of copepods. The bottles with and without animals were incubated at 20°C in the dark for 12 h. No mechanical stirring of water was done during incubation, but the contents were stirred at 2 h intervals by gently rotating bottles. At the end of incubation, samples were preserved by a borax neutralized formalin solution at a final concentration of 1 %. In the laboratory, these preserved samples were processed by the same procedure as microzooplankton samples. The number and size of pellets produced were measured under an inverted microscope.

RESULTS

Hydrography

Sugimoto *et al.* (1986) reported that the paths of drifting buoys with window-shade drogues at 100 m traced an anticyclonic circle at a speed of about 50 cm s^{-1}. The sediment trap system drifted in parallel with these buoys at a similar speed (about 45 cm s^{-1}; Fig. 1). The Subtropical Mode Water (Sugimoto *et al.*, 1986) was recognized between 100 and 500 m in the gyre (Fig. 2).

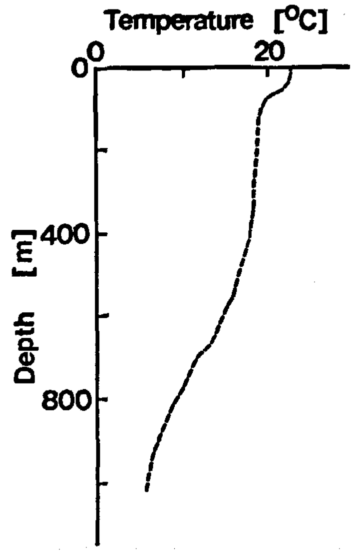

Figure 2

Typical temperature vertical profile at the sediment trap site in the anticyclonic gyre off Shikoku.

Distribution and flux of particulate matter

The subsurface chlorophyll maximum (SCM) was well developed in the gyre and the surrounding area (*see* also Takahashi *et al.*, 1985). At the sediment trap site, the SCM was observed at 90-100 m (Fig. 3). Although the POC concentration was high at the SCM, the vertical distribution of POC in the upper 100 m was more or less irregular, fluctuating from 17.8 to 37.6 µgC l^{-1}. The POC concentration decreased down to about 6 µgC l^{-1} at 300-500 m The POC flux had a maximum at 50 m and gradually decreased with depth.

The effect of zooplankton trapped in sediment traps on flux measurements has been recognized as a "swimmers" problem (Knauer *et al.*, 1979; 1984; Lee *et al.*, 1988; Karl and Knauer, 1989); trapped zooplankton not only become a source of contamination, but also actively alter collected materials. In this study, the microscopic analysis revealed that a large number of copepods were trapped in sediment traps (Tab. 2). During the drying and mounting processes, the somatic tissue of copepods was dissolved and part of the remaining molts were possibly broken. The numbers shown in Table 2 are molts, which were intact and/or contained undigested food materials inside. Most of trapped copepodites were less than 1 mm in total length and too small to remove from samples. In order to evaluate their effect on the POC flux value, therefore, their carbon weight was estimated by the equation describing the length-weight relationship for copepods (Uye, 1982). Trapped copepods accounted for 32 % of the POC flux at 50 m.

Table 2

Number and carbon weight of copepods trapped in sediment traps (ST) and the measured and corrected particulate organic carbon (POC) fluxes in the anticyclonic gyre off Shikoku.

Depth (m)	Copepodites (No. ST^{-1})	Estimated carbon weight* (µgC ST^{-1})	Measured POC flux (mgC m^{-2} d^{-1})	Corrected POC flux (mgC m^{-2} d^{-1})
50	361.5	417.5	79.0	53.7
100	81.0	82.0	43.1	37.9
150	54.0	60.9	39.1	35.1
200	45.0	42.7	30.9	27.8
300	19.0	38.0	25.6	23.1
400	15.0	24.2	22.8	21.2
500	6.0	12.4	24.5	23.7

* *Estimated by the equation describing the length-weight relationship for copepods (Uye, 1982).*

Fecal pellet flux

Pellets were simply divided into two categories based on the ratio of length and diameter (L/D): *i. e.* elliptical (L/D < 2) and cylindrical (L/D > 2) pellets. Each category was further divided into four size classes. Elliptical pellets were far more abundant than cylindrical pellets. The flux of elliptical pellets was the highest at 100 m, while the maximum flux of

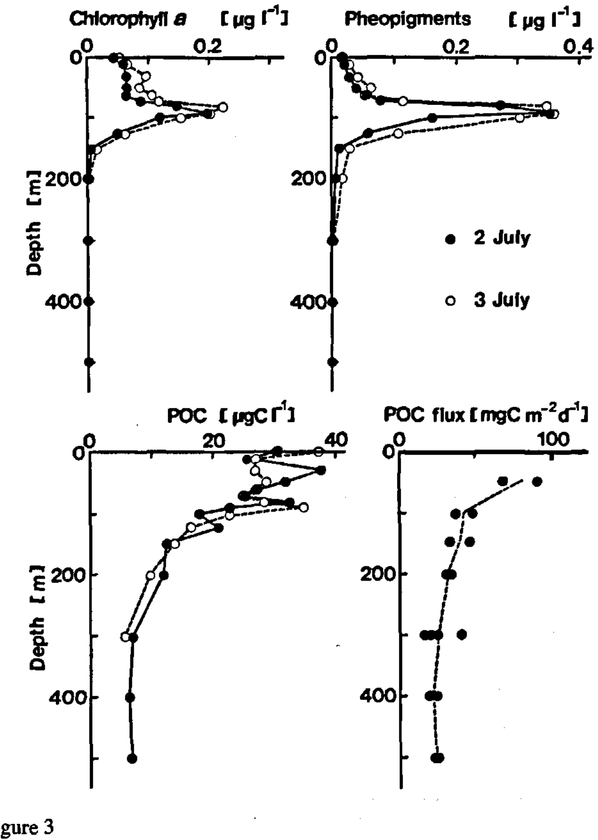

Figure 3

Vertical distributions of chlorophyll a, *phaeopigments and particulate organic carbon (POC) measured after deployment and retrieval of sediment traps in the anticyclonic gyre off Shikoku. The vertical profile of the POC flux is also shown.*

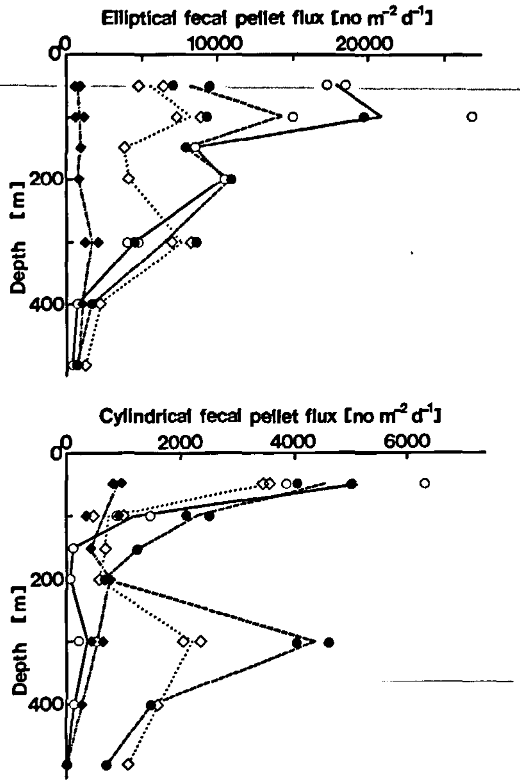

Figure 4

Vertical profile of the fecal pellet flux in the anticyclonic gyre off Shikoku. Elliptical pellets of < 50 µm (○), 50-100 µm (●), 100-200 µm (◇) and > 200 µm (◆). Cylindrical pellets of < 100 µm (○), 100-200 µm (●), 200-500 µm (◇) and > 500 µm (◆). Data from one of the paired traps at 150 and 200 m were discarded because of water leak.

cylindrical pellets was observed at 50 m (Fig. 4). Except for pellets in the largest size class, the fluxes of elliptical and cylindrical pellets sharply decreased in the 100-150 m layer. A second flux peak of elliptical and cylindrical pellets was observed in the 200-300 m layer.

Elliptical pellets in larger size classes made a large contribution to the total pellet volume flux (Tab. 3). The pellet carbon flux estimated after Knauer *et al.* (1979) accounted for only 0.4-1.7 % of the total POC flux.

Zooplankton distribution

The microzooplankton population in the gyre consisted mainly of naked ciliates, tintinnid ciliates, copepod nauplii and copepodites (Fig. 5). Copepodites collected by bottle casts were occupied by small individuals (< 0.5 mm), particularly by Cyclopoida at early developmental stages. These small copepodites were seemingly the most numerous component of the pellet producers in the gyre, but very rare in LHPR samples. Other microzooplankton, such as radiolarians and foraminifera, were rarely observed in the present samples. Naked ciliates, particularly the genus

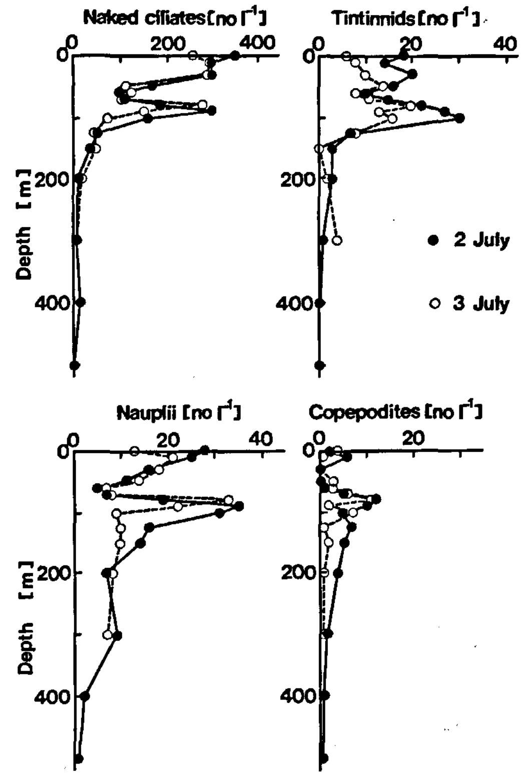

Figure 5

Vertical distributions of naked ciliates, tintinnids, copepod nauplii and copepodites measured by two Niskin-bottle casts after deployment and retrieval of sediment traps in the anticyclonic gyre off Shikoku.

Table 3

Estimated volume and carbon flux of fecal pellets in the anticyclonic gyre off Shikoku. Elliptical and cylindrical pellets were divided into four different classes based on their long axis. Values in parentheses are the percent contribution of pellets to the corrected particulate organic carbon flux shown in Table 2.

Depth (m)	Estimated pellet volume flux ($mm^3 m^{-2} d^{-1}$)									Estimated pellet carbon flux*
	Elliptical pellets (µm)				Cylindrical pellets (µm)					
	- 50	- 100	- 200	200 -	- 100	- 200	- 500	500 -	Total	($mg m^{-2} d^{-1}$)
50	0.29	1.42	5.44	1.45	0.18	0.76	1.85	1.63	13.02	0.349 (0.6)
100	0.31	2.85	8.77	1.71	0.04	0.34	0.33	1.86	16.21	0.434 (1.1)
150	0.12	1.31	3.80	1.75	< 0.01	0.18	0.27	1.32	8.75	0.235 (0.7)
200	0.17	1.80	4.73	1.59	< 0.01	0.09	0.24	2.11	10.73	0.288 (1.0)
300	0.06	1.12	7.91	2.77	0.01	0.61	1.06	1.38	14.92	0.400 (1.7)
400	0.01	0.28	2.79	1.93	0.01	0.21	0.60	0.86	6.69	0.179 (0.8)
500	< 0.01	0.08	1.55	1.21	0.00	0.10	0.47	0.00	3.41	0.091 (0.4)

* *Estimated from total pellet volume after Knauer* et al. *(1979).*

Table 4

Average abundance of the major zooplankton taxa collected by six LHPR tows in the anticyclonic gyre off Shikoku. Ap: appendicularia; ch: chaetognatha; cl: cladocera; Co: copepoda; Eu: euphausia; Me: medusa; Os: ostracoda.

Depth (m)	Zooplankton taxa (no m^{-3}) Ap	Ch	Cl	Co	Eu	Me	Os	Fish
0-50	15	8	8	65	2	2	2	2
50-100	+	4	1	54	2	2	4	+
100-150	+	2	+	20	+	1	4	+
150-200	+	+	+	11	+	+	3	+
200-300	+	+	+	7	+	+	2	+
300-400	+	+		6	+	+	1	+
400-500	+	+		9	+	+	+	+

+: < 1 animal m^{-3}.

Strombidium, were the most abundant of all the microzooplankton. An association of microzooplankton with the SCM was observed, although their abundance was also high at the surface.

Table 4 lists the major macrozooplankton taxa, which occurred at more than 1 ind. m^{-3} in at least one of the seven sediment trap layers from 0 m to 500 m. The abundance of macrozooplankton, except Ostracoda, had a maximum in the 0-50 m layer. Copepods were the most abundant and occurred at more than 1 ind. m^{-3} throughout the upper 500 m water column. There was no evidence to show the diel vertical migration of copepods, although the pattern of their vertical distribution varied among 6 LHPR tows (Fig. 6). This was the case for other major macrozooplankton listed in Table 4.

Fecal pellet production rate

Copepods listed in Table 1 comprised most of the common species in the gyre, but did not include some small genera, such as *Lucicutia*, *Oithona* and *Corycaeus*. Few broken pellets were observed after experiments and hardly affected the calculation of the pellet production rate. The POC concentration in seawater used for experiments ranged from 36 to 52 µgC l^{-1} with an average value of 44 µgC l^{-1}. No statistically significant correlation between POC concentration and pellet production rate was obtained for small, medium and large copepods and euphausiids, because of the large scatter of data points and the fairly narrow range of POC concentration. The overall average values of pellet production rates of small, medium and large copepods show that, at a given food condition, small copepods tend to produce more pellets than large copepods (Tab. 5). Pellets of large copepods and euphausiids appeared less compact than those of small copepods. The ratio of length to diameter of pellets was within a range of 3-6 for copepods and 7-13 for euphausiids.

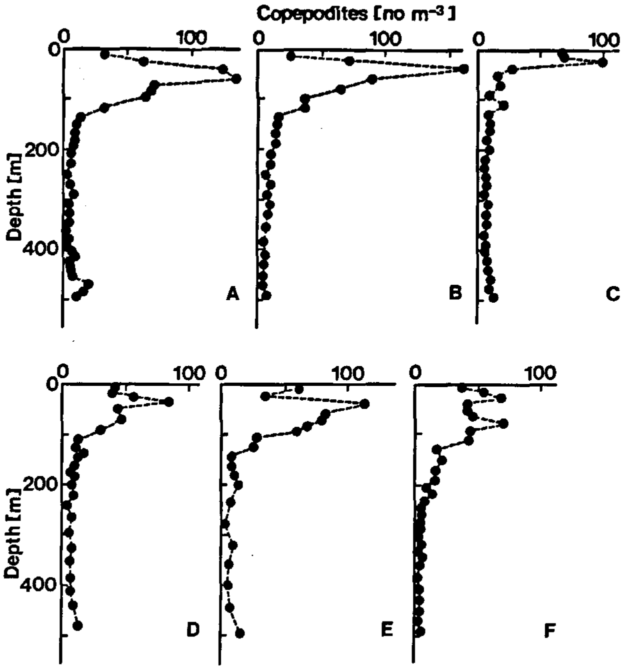

Figure 6

Vertical distribution of copepods in the upper 500 m of the anticyclonic gyre off Shikoku. Six Longhurst-Hardy Plankton Recorder tows were done at 0021-0135 (A), 0400-0513 (B), 0800-0927 (C), 1201-1325 (D), 1500-1606 (E) and 2008-2125 (F) on 3 July.

Table 5

Fecal pellet length and production rate of twelve species of copepods and euphausiids.

Species	Fecal pellet length (µm)	Fecal pellet production rate* (no ind^{-1} d^{-1})	Overall average* (no ind^{-1} d^{-1})
SMALL COPEPODS			13.3 ± 6.5
Clausocalanus spp.	118-155	15.6 ± 5.4	
Oncaea sp.	85-114	3.2 ± 1.1	
Paracalanus parvus	136-167	14.7 ± 4.1	
MEDIUM COPEPODS			10.4 ± 4.9
Calanus tenuicornis	150-262	7.5 ± 2.7	
Pleuromamma gracilis	151-208	12.0 ± 4.8	
Scolecithrix danae	295-340	18.0 ± 5.3	
Temora stylifera	228-242	10.7 ± 5.0	
LARGE COPEPODS			6.3 ± 5.1
Centropages bradyi	257-284	3.0	
Eucalanus attenuatus	298	16.0	
Eucalanus subcrassus	216	10.0	
Pleuromamma robusta	220	4.0	
Rhincalanus nasutus	275-292	4.0	
Euphausiids	381-629	9.0 ± 4.3	9.0 ± 4.3

** Data are X ± 1 SD.*

Fecal pellet production *vs.* flux

The abundance of copepods and euphausiids in the upper 100 m water columns was calculated from the data obtained by 6 LHPR tows (Tab. 6). However, the LHPR used was fitted with a 350 µm plankton net, so that small copepods were inadequately collected by the LHPR. The abundance of copepods of less than 0.5 mm in body length, therefore, was based on the data obtained by 2 Niskin-bottle casts (Fig. 4). Small copepods (< 1.5 mm) accounted for almost 100 % of the total copepods.

Table 6

Comparison of fecal pellet flux with fecal pellet production rate in the upper 100 m water column of the anticyclonic gyre off Shikoku. Values in parentheses are the percentage of fecal pellet flux to fecal pellet production rate.

Depth (m)	**Zooplankton group**	**Abundance (ind m^{-2})**	**Fecal pellet production rate (no ind d^{-1})**	**Water column fecal pellet production rate (no m^{-2} d^{-1})**	**Fecal pellet flux (no m^{-2} d^{-1})**
0-100	Small copepods (< 1.5 mm)	412 000	13.3	548 000	3 510* (< 0.1)
	Medium copepods (1.5-2.5 mm)	470	10.4	4 890	
	Large copepods (> 2.5 mm)	162	6.3	1 020	
	Euphausiids	178	9.0	1 600	
				7 510	1 350** (18.0)

* *Flux of cylindrical fecal pellets of < 200 µm.*
** *Flux of cylindrical fecal pellets of > 200 µm.*

As mentioned above, both copepods and euphausiids produced only cylindrical pellets (L/D > 2). For convenience, pellets of less than 200 µm were assumed to be produced by small copepods (< 1.5 mm) and pellets of more than 200 µm by medium and large copepods (> 1.5 mm) and euphausiids (*see* Tab. 5). The estimate in Table 6 suggests that only a fraction of pellets produced by small copepods sink below the euphotic layer. On the other hand, about 20 % of pellets produced by medium and large copepods and euphausiids settled down below 100 m.

DISCUSSION

A small contribution of fecal pellets to the total carbon flux can reflect either low pellet production or rapid pellet turnover in the gyre. In the latter case, a sizable proportion of pellets is recycled at the depth of production and the remainder can be transported downwards in forms of other large sinking particles. Evaluation of the role of fecal pellets on the transport and recycling of elements and compounds requires not only pellet flux measurements, but also attempts to quantify their production and disintegration (*cf.* Fowler and Knauer, 1986).

Validity of measured flux

We carried out this study before the problems in sediment trap experiments were identified by the US GOFS working group (US GOFS Planning Report No. 10, 1989). Although the basic designs of our sediment traps and the drifting system are along their recommendations, the high flow condition in the gyre may give rise to some uncertainty over the efficiency of our sediment traps (aspect ratio = 3.3). As mentioned above, however, the buoy systems with a drogue at 100 m (Sugimoto *et al.*, 1986) drifted at a similar speed to our system. Although their current meter at 45 m recorded a flow speed of > 50 cm s^{-1}, the flow relative to sediment traps below 100 m appears to be insignificant. In addition, the geostrophic current velocity estimated by them does not show the presence of strong current shears between 100-500 m at the sediment trap site. Thus the flux values below 100 m seem unbiased.

Zooplankton distribution *vs.* fecal pellet flux

The pellet flux, except for elliptical pellets in the largest size class, was high in the euphotic layer and rapidly decreased in the 100-150 m layer. Such a vertical profile is analogous with that of zooplankton abundance and suggests a close coupling of production and disintegration processes of pellets in this layer.

The high pellet flux at 200 or 300 m, on the other hand, was not associated with a noticeable population of zooplankton. The lateral advection of water towards the centre of the gyre (Olson, 1986), if it exists, may be responsible for this contentious result. Otherwise, it may reflect the dynamic physical characteristics of the gyre. The uplifts of the thermocline, nutricline and SCM in the centre of the gyre indicate the presence of upwelling (Takahashi *et al.*, 1985; Sugimoto *et al.*, 1986). They have also reported that upwelling is intermittent, resulting in a 4-fold variation in phytoplankton biomass at the SCM. Such a non-steady food supply may cause a fluctuation in zooplankton populations and a subsequent imbalance between production and disintegration processes of pellets in the euphotic layer.

There have been several reports on a bimodal distribution of pellet flux (Bishop *et al.*, 1980; 1986 *a*; Urrere and Knauer, 1981; Sasaki *et al.*, 1988). In their cases, the pellet flux peak at the mid-depth can be explained either by *in situ* particle production via microbial organisms (Karl *et al.*, 1984; Karl and Knauer, 1984) or by the presence of mesopelagic zooplankton populations, and undoubtedly consists of pellets in limited size classes or categories. In this study, however, the increase in pellet flux is seen in both categories, elliptical and cylindrical, in all size classes. In the gyre, only the zooplankton population in the euphotic layer is likely to produce such a wide range of fecal pellets. It is probable that pellets collected at 200-300 m originate in the euphotic layer.

Unfortunately, we cannot identify the actual cause of the bimodal distribution of pellet flux in the gyre. Future studies require flux measurements at fine depth intervals. It is also necessary to resolve the temporal and spatial variabilities of plankton production and biomass. Such approaches will reveal the response of the downward transport processes of particulate matter to varying physical conditions in the gyre and provide useful information on the performance of the so-called biological pump (*cf.* US GOFS Planning Report No. 11, 1990) under non-steady state conditions.

Fecal pellet production rate *vs.* flux

We applied what is probably the most gentle way of dealing with pellet samples, so that the measured pellet flux at 100 m seems reliable. On the other hand, there is a possibility that the pellet production rate in the upper 100 m water column (Tab. 6) is seriously underestimated, as mentioned below. If so, it becomes more obvious that only a fraction of pellets produced in this layer are transported to the underlying water column.

There are at least three reasons why the water column pellet production rate seems underestimated:

1) The abundance of small copepods (< 1.5 mm) based on the Niskin-bottle samples was slightly lower than the average abundance based on the vertical plankton net tows (105 µm in mesh size) at six different stations in the gyre, *i. e.*: 542 000 ± 30 000 ind. m^{-2} (X ± SE).

2) We assumed that copepods and euphausiids were the only producers of cylindrical pellets (*cf.* Fowler and Knauer, 1986).

3) Most of the copepods used in pellet production experiments appeared to be omnivorous or carnivorous. Thus the prescreening of experimental water with a 56 µm mesh screen could certainly remove the significant proportion of their major food and reduce their pellet production rate. It could also affect the size, shape, density and therefore the sinking rates of pellets (Dagg and Walser, 1986).

The flux of cylindrical pellets of less than 200 µm at 100 m was 0.38 mm^3 m^{-2} d^{-1} and accounted for only 2.3 % of the total pellet volume flux. However, this does not mean that small copepods, the most likely producers of small cylindrical pellets, are of trivial importance as pellet producers in the euphotic layer. That is, if one assumes that 99.9 % of small cylindrical pellets is disintegrated in the euphotic layer, the total amount of small cylindrical pellets produced in the euphotic layer is estimated as 380 mm^3 or 10.2 mgC. In addition, if the assimilation efficiency of 70 % is assumed (*cf.* Parsons *et al.*, 1984), the ingestion rate of the small copepod population in the euphotic layer is estimated as 34 mgC m^{-2} d^{-1}, which is equivalent to some 5 % of the daily primary production rate (about 700 mgC m^{-2} d^{-1}) (Hama *et al.*, 1983). In contrast, medium and large copepods and euphausiids are less important as pellet producers than small copepods, but can exercise an important influence on the downward material transfer in the gyre, by virtue of their large pellets.

In this study, copepods were arbitrarily divided into small, medium and large copepods. Even so, it may be surprising that pellets produced by small copepods are disintegrated in the euphotic layer at an almost 100 % efficiency. The rest of the results, however, do not seem extraordinary in comparison with the previous results. For instance, the contribution of intact pellets to the total carbon flux ranged from 0.4 to 1.7 %. These values are not unusual for oligotrophic oceanic waters (Knauer *et al.*, 1979).

The measured POC flux at 100 m was 43.1 mgC m^{-2} d^{-1}. Betzer *et al.* (1984) carried out primary production and flux measurements at four stations in the equatorial Pacific. Their equation describing the relationship between primary production, carbon flux and depth predicts a POC flux of 55 mgC m^{-2} d^{-1} at 100 m, assuming an annual primary production rate of 250 gC m^{-2} yr^{-1} (*see* Hama *et al.*, 1983). The measured POC flux value is lower, but of the same magnitude as the predicted one.

Pellet disintegration does not always mean recycling of whole pellets. Rather, it is more likely that a sizable fraction of pellets enter the pool of fecal matter, which is a subset of amorphous aggregates collectively described as marine snow (*cf.* Bishop *et al.*, 1986 *a*). It is worth noting that the isotopic ratio of particulate matter collected by sediment traps is similar to that of pellets and dissimilar to phytoplankton and other suspended particles (Altabet and Small, 1990). They have suggested that fecal pellets are the important precursors of large sinking particles like marine snow. Even if identifiable, intact pellets are rare in sediment trap samples, zooplankton are no doubt important in integrating small particles into large ones and still have a strong influence on the flux and biochemical property of sinking particles.

The processes responsible for rapid disintegration are beyond the scope of the present study. However, a large number of copepods in the sediment traps at 50 m, while they certainly affect the POC flux value, may imply their involvement in the disintegration process of pellets. If so, it is interesting to note that the trapped copepods were dominated by *Oncaea* spp. and *Microsetella norvegica*, accounting for about one third of the total number. Alldredge (1972) has reported the association of these copepods with discarded larvacean houses, which are one of the most important sources of marine snow. Although the trend of coprophagy (or coprorhexy) is more or less common among copepods (Paffenhöfer and Strickland, 1970; Paffenhöfer and Knowles, 1979; Ayukai, 1987 *b*; Lampitt *et al.*, 1990), there is a possibility that certain species of copepods are particularly responsible for pellet disintegration in the field.

Rapid disintegration of pellets is obviously an important mechanism by which primary production is retained in the euphotic layer. The processes affecting the fate of pellets have been studied and identified, but little is known about the rates at which the processes operate under natural conditions (Lampitt *et al.*, 1990). Uncertainty as to pellet production and disintegration rates in the field has been an obstacle to construction of models for the downward transport and recycling of elements and compounds. For instance, all fecal pellets from macrozooplankton were assumed to sink below the euphotic layer without disintegration in the study on the carbon and nitrogen cycles in the tropical Pacific (Small *et al.*, 1983). A similar assumption was made in the model to predict the production and fate of phytoplankton pigments in a temperate fjord and in the oligotrophic Pacific (Welschmeyer and Lorenzen, 1985). Such an oversimplification was not always favoured (Dagg and Walser, 1986). Further attempts to compare pellet flux with water column pellet production rate in different areas, although time-consuming, may lead to a major breakthrough in this issue.

Biological productivity in warm-core rings on the poleward side of western boundary currents is higher than that in the parent water masses, because of convective overturn in winter-spring and localized upwelling in the ring core (*cf.* Wiebe and McDougall, 1986). Intermittent upwelling in the central area of the gyre probably explains its relatively high productivity to that in the Kuroshio water (Wada 1984; Takahashi *et al.*, 1985; Sugimoto *et al.*, 1986). The high productivity in the gyre can be sustained through the high retention and recycling of pellets in the euphotic layer, although whether this is a persistent feature awaits further investigations.

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