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Minipellets: A new and abundant size class of marine fecal pellets

by Marcia M. Gowing[1] and Mary W. Silver[1]

ABSTRACT

Minipellets, fecal pellets from 3 to 50 μm in diameter, were found on detritus collected by a particle interceptor trap array in the upper 2000 m of the eastern tropical Pacific. The fluxes of minipellets reached 5×10^6 m^{-2} day^{-1}, and exceeded fluxes of larger (>50 μm diameter) fecal pellets by 3 orders of magnitude. Carbon flux of minipellets was 11–49% that of larger pellets; however, carbon flux of ultrastructurally intact cells (microalgae and bacteria) in minipellets was equal to that of intact cells in the larger pellets. Minipellets also occurred in water samples from similar depths, where they numbered up to 10^5 m^{-3}, and were usually not associated with particles. Minipellets appear ubiquitous; we have found them in all our samples of particulates from other cruises from surface waters to bathypelagic depths. Minipellet morphologies ranged from Type A, which contained intact, picoplankton-sized cells (cyanobacteria, nitrifying bacteria, morphologically non-descript, Gram-negative bacteria, *Chlorella*-like cells) in an amorphous matrix surrounded by a boundary, to Type D minipellets, which were identical to previously described olive-green "cells."

Minipellets are probably wastes of protozoans and small invertebrates that consume marine snow and larger fecal pellets throughout the water column, thereby maintaining the high numbers of minipellets from the surface to 2000 m. We found several sources of minipellets: two groups of sarcodine protozoans (phaeodarian and spumellarian radiolarians) and small hydromedusae. The minipellet producers reprocess a major portion of surface-derived detritus, and represent important biological intermediates that transform particulate matter settling through the ocean.

1. Introduction

Waste products of pelagic organisms provide an *in situ* record of the feeding habits and assimilation abilities of oceanic grazers. Unlike many of the organisms that produce them, the wastes do not actively elude sampling devices and therefore can give quantitative information about the relative abundance of consumers with different dietary habits. Fecal pellets also are primary agents in the vertical exchange of materials in the sea; their size distributions, contents, and the resulting sinking rates thus influence marine geochemical cycles.

Previous studies have focused primarily on the fecal pellets of invertebrate plankton and on the enigmatic olive green "cells" of the deep sea. Taken together, these wastes

1. Center for Marine Studies, University of California, Santa Cruz, California, 95064, U.S.A.

range in size from several millimeters in length (e.g. pellets of the swimming crab, *Pleuroncodes planipes* (Gowing and Silver, 1983a)) down to the 3–15 μm olive green "cells" (Hentschel, 1928, 1936; Schiller, 1931; Fournier, 1970, 1971, 1973; Hamilton *et al.*, 1968; Silver and Bruland, 1981; Silver and Alldredge, 1981). Fecal pellets larger than 50 μm in diameter have been examined for their contents (Honjo, 1978; Bienfang, 1980; Pomeroy and Deibel, 1980; Urrère and Knauer, 1981; Silver and Bruland, 1981; Turner, 1984), sinking rates (Smayda, 1969; Fowler and Small, 1972; Wiebe *et al.*, 1976, 1979; Turner, 1977; Small *et al.*, 1979; Bruland and Silver, 1981; Komar *et al.*, 1981; Lorenzen and Welschmeyer, 1983), distribution (Bishop *et al.*, 1977, 1980; Knauer *et al.*, 1979; Urrère and Knauer, 1981; Iseki, 1981), and decomposition (Honjo and Roman, 1978; Gowing and Silver, 1983a). Vertical distributions (Hasle, 1959; Hamilton *et al.*, 1968; Fournier, 1970, 1971; Fryxell *et al.*, pp. 203–239, 1979), contents (Fournier, 1970; Silver and Alldredge, 1981), and potential origins (Fournier, 1970; Anderson, 1975; Silver and Bruland, 1981; Silver and Alldredge, 1981) of olive green "cells" have also been examined. Only the larger pellets, however, have been recognized as major participants in the vertical flux of particulates, and Paffenhöfer and Knowles (1979) have suggested that small pellets are not significant in the vertical transport of organic matter.

We report here fluxes of what we call "minipellets," fecal pellets between 3 and 50 μm in diameter, collected in particle interceptor traps and water samples from mesotrophic waters (primary productivity was 470 mg C m^{-2} day^{-1}, G. Knauer, personal communication) of the eastern tropical Pacific Ocean. These abundant pellets have not been recognized previously in field samples, but they overlap in size with the olive green "cells" described previously, with larger naupliar pellets known from laboratory studies (Marshall and Orr, 1956; Paffenhöfer and Knowles, 1979), with some copepodid pellets (Paffenhöfer, personal communication), and with pellets of some adult copepods (Martens, 1972). Examination of the pellets with transmission electron microscopy has allowed us to describe four morphological types of minipellets, some of which contain intact picoplankton-sized cells surrounded by a boundary. We describe the distribution, production, and role of minipellets in carbon flux to the deep sea, discuss the implications of their abundance, and compare their importance to that of larger fecal pellets.

2. Methods

a. Collection of minipellets. Sinking particulates, including minipellets, were collected in "Multitrap" particle interceptors (Knauer *et al.*, 1979) during the VERTEX III (Vertical Transport and Exchange of Materials in the Upper Waters of the Ocean) cruise off Central Mexico (16N;107W). Traps were deployed from 9 to 30 November 1982 at 80, 120, 140, 200, 400, 700, 900, 1450, and 2000 m depth. Traps were filled with a preservative solution of 2% glutaraldehyde in borate-buffered sea water (pH 7.4) with 18% sucrose to provide a high density solution necessary to retain material in

the traps during recovery of the trap array (see Gowing and Silver, 1983a, for a discussion of the preservative solution). Water samples were collected in 10 L Niskin bottles near the trap depths, preserved with 0.5% buffered formaldehyde, and filtered onto 1.0 μm pore sized, 47 mm diameter, Nuclepore filters within 2 hr. of collection. The filters were placed in 20 ml of 2% glutaraldehyde in 80% sea water and 0.1 M cacodylate buffer (pH 7.4). Hereafter, we refer to particles in the water samples as "suspended" materials and particles from traps as "sinking" ones.

b. Microscopy. Minipellets were counted under the light microscope by three techniques. (1) Minipellets recognized by size (<50 μm and >3 μm in diameter) and appearance (usually spherical to ovoid and green to brown) were counted on 2 replicate aliquots of trap material filtered onto metricel (type GA-6) filters. The filters were rinsed with 2 ml of 0.2 μm filtered sea water and 2 ml of 0.2 μm filtered distilled water, cleared in a vacuum oven with w-15 immersion oil whose pH had been adjusted to 7.4 with 10N NaOH (M. Silver, unpubl.), covered with a coverslip, and examined at 500× by differential interference-contrast (Nomarski) optics. The minipellets in approximately 100 fields were counted and measured with an optical micrometer, and the concentration per trap calculated. (2) 2 aliquots of material from each trap were filtered onto 1 μm pore size Nuclepore filters and transferred to slides using the filter-transfer-freeze (FTF) technique (Hewes and Holm-Hansen, 1983). Counts and measurements were made as above. The counts from methods (1) and (2) were considered replicates for the final calculations. (3) At sea, five aliquots of material from each trap were filtered onto black 0.45 μm pore size Sartorius filters, the filters placed on slides with a few drops of 0.2 μm filtered sea water, and covered with a glass coverslip. The filters were then examined immediately with fluorescence microscopy. Minipellets (recognized by size and shape) containing autofluorescent algae (indicated by red chlorophyll *a* fluorescence) and cyanobacteria (recognized by yellow-orange phycoerythrin fluorescence) were counted and measured. The algae and cyanobacteria in the pellets were also counted and measured.

The suspended particles from the water samples were washed off the filters and aliquots for counting prepared using the cleared filter technique.

Minipellets within trap material were also counted and measured on a JEOL 100B transmission electron microscope on aliquots of trap material prepared for TEM as described by Silver and Alldredge (1981). Contents of the pellets were sized and counted. Ultrathin sections of material from six blocks from each depth were examined; numbers of pellets at each depth were variable in the sections. Therefore, results from different depths were pooled into the following depth zones: epipelagic, 80 m, mesopelagic, 120–700 m, and bathypelagic, 900–2000 m. The zones were selected on the basis of oxygen levels at the sampling site: 25 μM kg^{-1} at 80 m, 0–5 μM kg^{-1} between 120 and 700 m, and 8–43 μM kg^{-1} between 900 and 1500 m (Broenkow *et al.*, 1983).

Four potential sources of minipellets found in the trap material were examined with TEM. Spherical, pellet-like structures containing masses of minipellets (later identified as phaeodarian radiolarians by O. R. Anderson and J. and M. Cachon), spumellarian radiolarians, small (1.53 mm ± 0.26 S.D. long, $N = 8$), sexually mature Trachymedusae (Family Rhopalonematidae, C. Mills, pers. comm.) containing brown, minipellet-like particles in their stomachs, and crustacean nauplii were embedded using the same procedure as for the copepod and larvacean fecal pellets. These source organisms had entered the traps either on their own or in association with marine snow. The fixative in the traps prevented their feeding in the traps once they entered.

For comparison with minipellets, fecal pellets greater than 50 μm in one dimension were counted and measured under a dissecting microscope. Representative pellets of the predominant types (cylindrical pellets from the swimming crab *Pleuroncodes planipes,* ellipsoidal pellets from copepods and larvaceans, ribbon-shaped pellets from salps, and spherical pellets of unknown origin) were embedded for TEM and examined as described by Gowing and Silver (1983a).

We also examined selected additional samples of gut contents and fecal pellets from zooplankton embedded as described in Silver and Alldredge (1981) and Silver and Bruland (1981), and marine snow samples (embedded as described in Silver and Alldredge (1981)) from other collections for the presence of minipellets. These samples were from the California Current (Gowing and Silver, 1983a), a transect 600 km southwest of Monterey Bay, California (Alldredge and Silver, 1982), Southern California Basins (Silver and Alldredge, 1981), the Pacific Central Gyre (Gowing and Silver, 1983b), and DOS-1 off Woods Hole, Mass. (Wishner *et al.,* 1983).

c. Carbon conversions. Two carbon values, pellet carbon and "living" carbon, were calculated for large fecal pellets and minipellets. Pellet carbon was calculated as follows. The total volume flux (mean volume of a pellet × total number flux) of each pellet type was converted to dry weight flux by multiplying by 0.5. Dry weight flux was converted to carbon flux using the data of Small *et al.* (1983) for pellets from *Pleuroncodes planipes* (17.3% carbon), "mixed large and small zooplankton" (29.7% carbon), and from "small zooplankton" (27.1% carbon). We used these percentages, respectively, for pellets from *Pleuroncodes planipes,* pellets from large non-crab zooplankton, and minipellets.

"Living" carbon was carbon contained in ultrastructurally intact cells within fecal pellets. To calculate "living" carbon, total volume flux was first converted to cellular volume using factors from TEM and light microscopy. The proportions of fecal pellets occupied by bacteria and *Chlorella*-like cells were determined from TEM sections[2] (because autofluorescence of *Chlorella*-like cells faded rapidly and bacteria were too

2. The decimal fractions of fecal pellet volume that were bacteria were: 4.9×10^{-4} for pellets from *Pleuroncodes planipes,* 17.6×10^{-4} for pellets from non-crab zooplankton, and 2.3×10^{-3} for minipellets. Fractions that were *Chlorella*-like cells were: 6.2×10^{-4}, 28.1×10^{-4}, and 5.8×10^{-3}, respectively.

numerous to be counted accurately with light microscopy), and did not differ with depth zone. A correction factor for shrinkage during dehydration was made for the *Chlorella*-like cells and bacterial volumes calculated from cross-sectional areas measured with TEM. The correction factor (the diameter of embedded cells was 51% that of non-embedded cells) was determined by measuring diameters of cultured *Chlorella* cells preserved in the same fixative and *Chlorella* cells that had been fixed and embedded in resin on a microscope slide. It was assumed that the bacteria underwent the same degree of shrinkage as did *Chlorella*.

The proportions of fecal pellet volume that were cyanobacteria and 5–10 μm diameter algae were determined from light microscopy,[3] and these did not differ with depth zone. No correction for shrinkage was applied to these cell volumes because the cells were not embedded prior to determination of the proportion of fecal pellets that they occupied. The cellular volumes were then converted to carbon using the value 0.1 pg C μm^{-3} of Watson *et al.* (1977) for bacteria, cyanobacteria, and *Chlorella*-like cells. The value of 0.05 pg C μm^{-3} was used for diatoms and dinoflagellates (calculated from Mullin *et al.*, 1966).

d. Volume distribution of sinking minipellets. We estimated the mean volume ($\mu m^3\ m^{-3}$) of sinking minipellets of each size class in each zone using the formula:

$$\text{mean volume} = (\text{minipellet volume flux}) \times (\text{sinking rate})^{-1}$$

where minipellet volume flux ($\mu m^3\ m^{-2}\ day^{-1}$) was determined from our trap collections as follows. The volume of a pellet of each radius was calculated, multiplied by the frequency of pellets of that radius, divided by the collecting area of the traps, and divided by the number of days the trap was deployed. We estimated sinking rate ($m\ day^{-1}$) from minipellet size distributions, using the equation of Stokes (1901) and the assumptions of Paffenhöfer and Knowles (1979). The mean volume estimates could be converted to estimates of mass by multiplying by the density of minipellets.

3. Results

a. Morphology of minipellets. Four morphological types of minipellets were recognized with transmission electron microscopy. Type A (Fig. 1a) had a complete or nearly complete, thin (.0125 to .015 μm wide) boundary. Type B (Fig. 1b) had parts of a boundary, Type C (Fig. 1c) had no thin boundary but contained ultrastructurally intact contents, and Type D (Fig. 1d) had no boundary. Type D was identical to olive green cells of Group one described by Fournier (1970), and olive green and grey bodies lacking picoplankton-sized cells described by Silver and Alldredge (1981). These categories were used because all of the pellets examined fell easily into one of the

3. The decimal fractions of fecal pellet volume that were cyanobacteria were: 1.9×10^{-4} for *Pleuroncodes planipes*, 1.24×10^{-4} for non-crab zooplankton, and 1.5×10^{-3} for minipellets. Fractions that were 5–10 μm diameter algae were: 0.5×10^{-4}, 0, and 0, respectively.

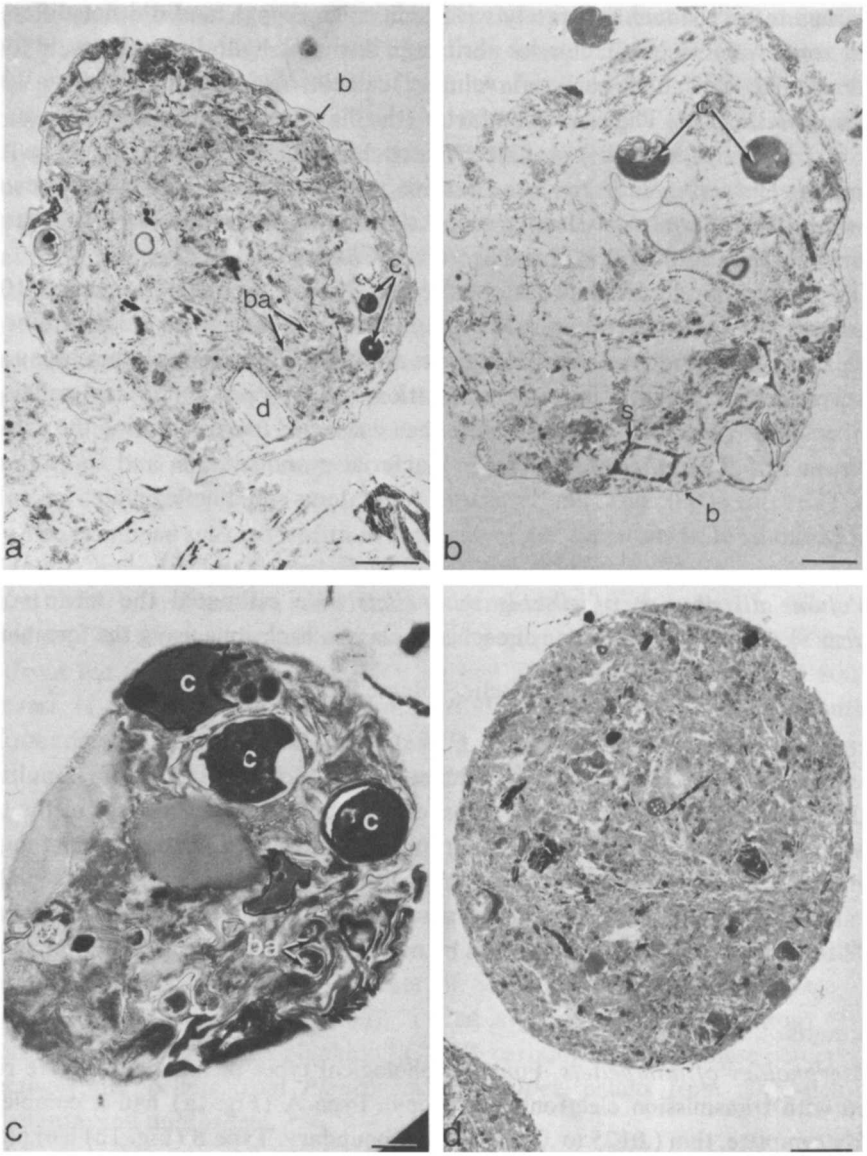

Figure 1. Transmission electron micrographs of sections of minipellets from particulate material in the eastern tropical Pacific Ocean. a. Type A minipellet from 80 m with a boundary (b), intact *Chlorella*-like cells (c), bacteria (ba), and an empty diatom frustule (d). Scale bar = 4 μm. b. Type B minipellet from 140 m with a boundary (b) around part of the pellet, intact *Chlorella*-like cells (c), and a fragment of silica (s). Scale bar = 2 μm. c. Type C minipellet from 2000 m, lacking a boundary. Intact cells include *Chlorella*-like cells (c) and bacteria (ba). Scale bar = 1 μm. d. Type D minipellet from 400 m, identical to previously described olive green "cells." Note the lack of both a boundary and intact cells. Scale bar = 4 μm.

Table 1. Contents of minipellets shown as mean percentages ± standard error of cross-sectional areas of minipellets examined with TEM. N = number of pellets examined. Mean diameter = mean diameter of cross-section of pellets examined. There was no significant difference (see text) between the percentages of bacteria, cyanobacteria, and *Chlorella*-like cells within minipellets of Types A, B, and C within a zone. Percentages of bacteria and *Chlorella*-like cells did not differ significantly among zones in pellets of Types A, B or C. There were significantly more cyanobacteria in minipellets of Type A, B and C in the epipelagic than in the mesopelagic, but percentages of cyanobacteria did not differ between the mesopelagic and bathypelagic or between the epipelagic and bathypelagic.

Zone	Type	N	Mean diameter (μm)	Percentage of Bacteria	*Chlorella*	Cyanobacteria
Epipelagic	A	13	19.8	.39 ± .13	.28 ± .17	.09 ± .06
(80 m)	B	9	18.4	.06 ± .03	.87 ± .17	.14 ± .09
	C	17	11.9	.11 ± .06	.47 ± .36	.03 ± .02
	D	18	8.7	0	0	0
Mesopelagic	A	9	13.0	.31 ± .17	.94 ± .82	.01 ± .001
(120–700 m)	B	9	10.9	.04 ± .03	.25 ± .25	0
	C	31	8.3	.29 ± .08	.23 ± .19	.01 ± .01
	D	198	8.8	.01 ± .004	0	0
Bathypelagic	A	0		0	0	0
(900–2000 m)	B	7	13.8	.24 ± .15	1.58 ± 1.50	0
	C	6	9.6	.37 ± .26	0	0
	D	76	7.8	.002 ± .002	0	0

categories. Types A, B, and C may well be decomposition stages of the same type of pellet, whereas Type D could be a very late decomposition stage or, alternatively, a different type of waste product. Contents recognizable with TEM included ultrastructurally intact bacteria (nondescript Gram-negative bacteria, cyanobacteria,[4] and nitrifying bacteria) and *Chlorella*-like cells (also called *Nannochloris:* see Sarokin and Carpenter, 1982; Johnson and Sieburth, 1982), and silica fragments from diatoms and radiolarians, all commonly in an amorphous matrix. Intact diatoms and dinoflagellates were rarely seen in minipellets examined with the fluorescence microscope, and none were encountered in TEM sections. Types A, B, and C contained similar contents, whereas Type D only rarely contained intact cells, and then only bacteria (Table 1). Among Types A, B, and C, there was no significant difference in the percentages of bacteria, cyanobacteria, and *Chlorella*-like cells within minipellets in each zone, as assessed with Kruskall-Wallis nonparametric one way analyses of variance. Thus the three types were pooled and the contents compared among zones with a Kruskall-Wallis analysis. The percentage of cyanobacteria differed significantly with zone ($p = 0.05$), whereas the percentages of *Chlorella*-like cells and bacteria did not differ

4. The majority of cells counted as cyanobacteria were Type 1 cells of Johnson and Sieburth (1979) and cells like those shown in Figure 3a and b of Silver and Alldredge (1981). It is possible, however, that a few nitrifiers and methane oxidizers, which possess intracellular membrane systems rather like those of cyanobacteria, were included in the cyanobacteria counts (P. Johnson and J. McN. Sieburth, personal communication).

Table 2. Mean proportion of cross-sectional area of minipellets and large fecal pellets that was ultrastructurally intact cells (±S.E.). N = sample size.

	Type of fecal pellet			
	Large		Minipellet	
Zone	Mean	N	Mean	N
Epipelagic	.004 ± .003	8	.009 ± .003	45
Mesopelagic	.002 ± .001	18	.007 ± .002	55
Bathypelagic	.007 ± .002	13	.012 ± .009	13

with zone ($p > 0.05$). The percentage of cyanobacteria in the epipelagic zone was significantly higher than in the mesopelagic (Mann-Whitney U test, $p < 0.05$), but there was no difference between the epipelagic and bathypelagic or the mesopelagic and bathypelagic. A comparison of the percentage of minipellets that were of Type A, B or C of the total minipellets [(A+B+C/A+B+C+D) × 100] in TEM sections showed no significant difference among the depth zones (Kruskall-Wallis analysis, $p > 0.05$).

The contents of minipellets were similar to those of large fecal pellets of herbivores, with the exception that the larger fecal pellets contained coccolithophorids and more diatoms and dinoflagellates. Minipellets contained twice as much intact cellular material in a cross-sectional area as the larger pellets (Table 2).

b. Number of sinking minipellets. Fluxes of total numbers of minipellets ranged from 1.24×10^6 m^{-2} day^{-1} at 2000 m to 5.22×10^6 m^{-2} day^{-1} at 400 m (Fig. 2), with no significant difference in flux with depth (Kruskall-Wallis test, $p = 0.11$). Fluxes of total numbers of minipellets in each depth zone were significantly different (Kruskall-Wallis test, $p = 0.04$), with no significant difference between the epipelagic and mesopelagic or the epipelagic and bathypelagic, but a significantly higher flux in the mesopelagic than the bathypelagic (Mann-Whitney U test, $p = 0.02$). Most of the minipellets from the trap samples were associated with flocculent marine snow, although the marine snow could have scavenged individual minipellets after they entered the trap.

c. Volumes of sinking minipellets. Total volume flux of minipellets (Fig. 3) ranged from 1.88×10^9 μm^3 m^{-2} day^{-1} at 2000 m to 1.27×10^{10} μm^3 m^{-2} day^{-1} at 80 m. There was no significant difference in volume flux among depth zones (Kruskall-Wallis test, $p > 0.05$).

Mean volume of individual minipellets (Fig. 4) ranged from 1.02×10^3 μm^3 at 400 m to 3.3×10^3 μm^3 at 140 m. There was no significant difference in mean pellet volume among depth zones (Kruskall-Wallis test, $p > 0.05$).

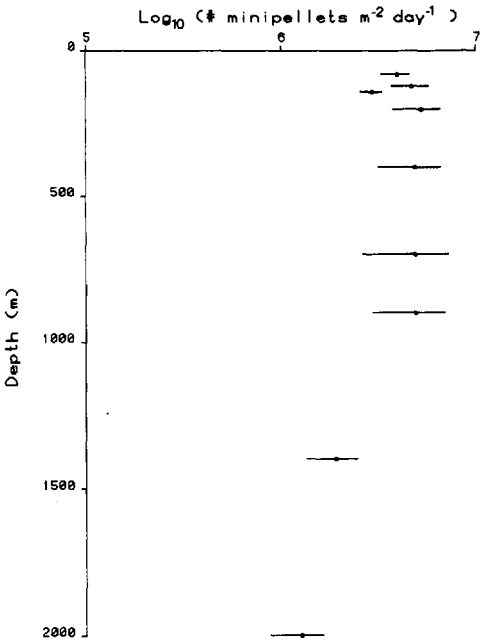

Figure 2. Mean flux of minipellets. Bars = S.E.

d. Comparison of sinking minipellets and large pellets. A comparison of large fecal pellets and sinking minipellets (Table 3) showed approximately 1000 times as many minipellets m^{-2} day^{-1} as large fecal pellets in the three zones. The volume flux of large fecal pellets exceeded that of minipellets but only by a factor of 2 to 9 at the most. The "living" carbon flux, or carbon contained in ultrastructurally intact cells, was not significantly different between large fecal pellets and minipellets, although the total carbon flux in large pellets was 10 times that of minipellets. Total fecal pellet carbon flux made up 8% of the epipelagic carbon flux, 53% of the mesopelagic, and 18% of the bathypelagic carbon flux. Minipellet carbon flux made up 2% of the epipelagic carbon flux, 5% of the mesopelagic carbon flux, and 6% of the bathypelagic carbon flux.

e. Volume distribution of sinking minipellets. The distribution of volume of minipellets in the three zones (Fig. 5) was similar, with the largest volume in each zone contributed by minipellets of 6 μm radius. Pellets larger than 12 μm radius contributed little to the volume of pellet material.

f. Producers. Three types of organisms contained Types, A, B, C and D minipellets. Phaeodarian radiolaria, which occurred in traps from all depths, contained many minipellets (Fig. 6). Nineteen individuals were examined ultrastructurally for this

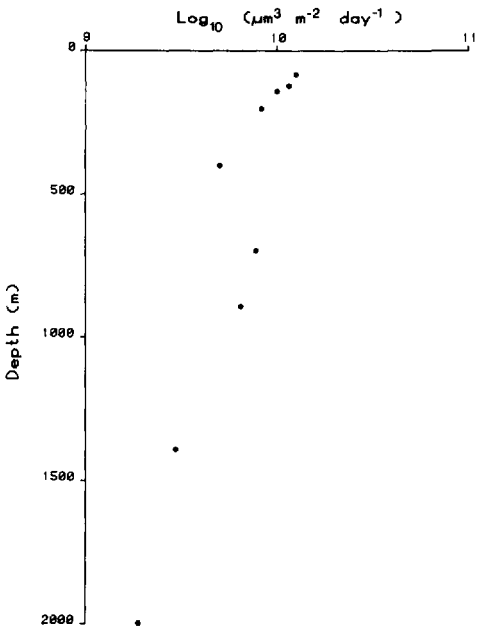

Figure 3. Mean volume flux of minipellets. The values were calculated from the data in Figure 4.

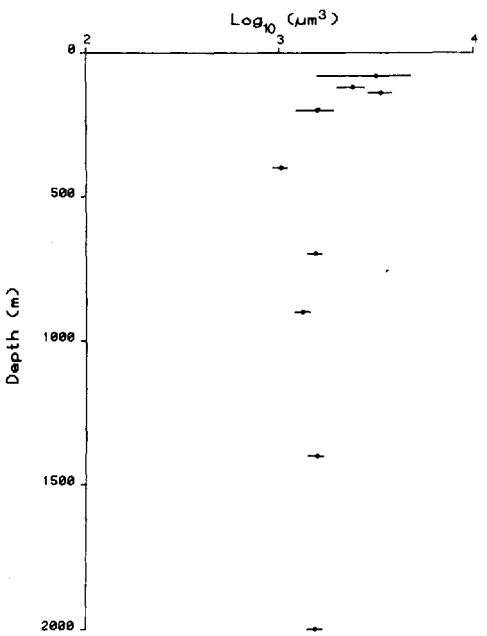

Figure 4. Mean volume of minipellets. Bars = S.E.

Table 3. Contributions of minipellets and large pellets to carbon flux. Pellet carbon flux was calculated from pellet volumes using the measurements of carbon in fecal pellets (Small *et al.*, 1983). All fecal pellets were assumed to be 50% water. "Living" carbon is carbon in ultrastructurally intact cells. See text for an explanation of the "living" carbon calculation. Trap carbon flux was determined by G. Knauer and corrected for salts.

Zone	Number flux # m^{-2} day^{-1}	Volume flux μm^3 m^{-2} day^{-1}	"living" C flux	Pellet C flux gC m^{-2} day^{-1}	Trap C flux
Epipelagic					8.99×10^{-2}
Large	3.50×10^{3}	6.26×10^{10}	2.02×10^{-5}	5.92×10^{-3}	
Mini	3.98×10^{6}	1.27×10^{10}	2.20×10^{-5}	1.72×10^{-3}	
Mesopelagic					2.21×10^{-2}
Large	2.7×10^{3}	6.64×10^{10}	7.27×10^{-5}	1.05×10^{-2}	
Mini	4.6×10^{6}	8.46×10^{9}	1.47×10^{-5}	1.15×10^{-3}	
Bathypelagic					8.36×10^{-3}
Large	2.8×10^{3}	2.93×10^{10}	2.50×10^{-5}	1.04×10^{-3}	
Mini	2.6×10^{6}	3.74×10^{9}	6.50×10^{-6}	5.08×10^{-4}	

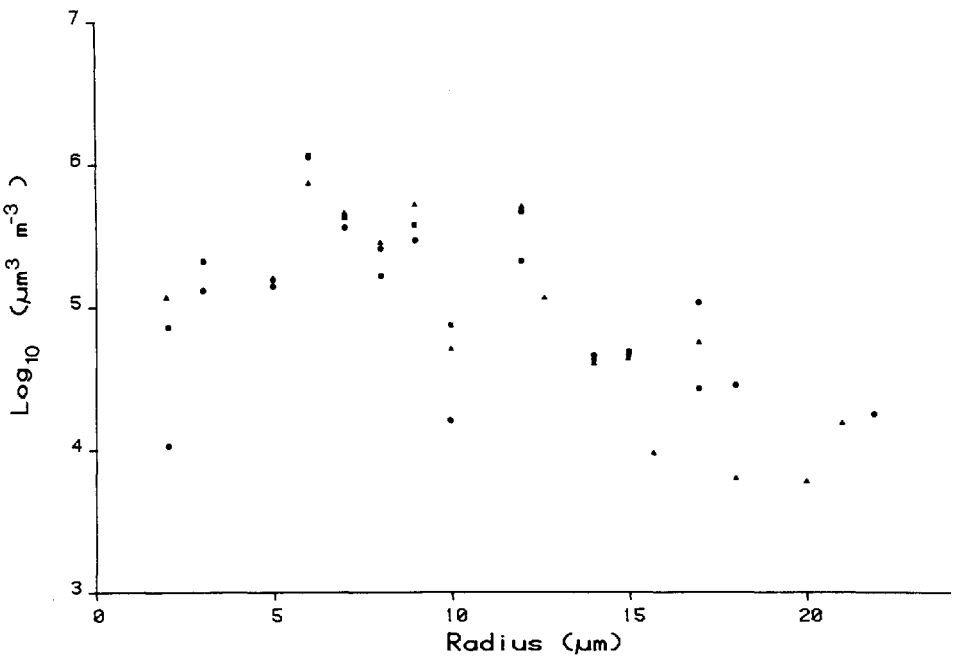

Figure 5. Volume distribution of minipellets (flux × sinking $rate^{-1}$) of various radii. (●) = epipelagic zone (80 m), (▲) = mesopelagic zone (120–700 m), (■) = bathypelagic zone (900–2000 m).

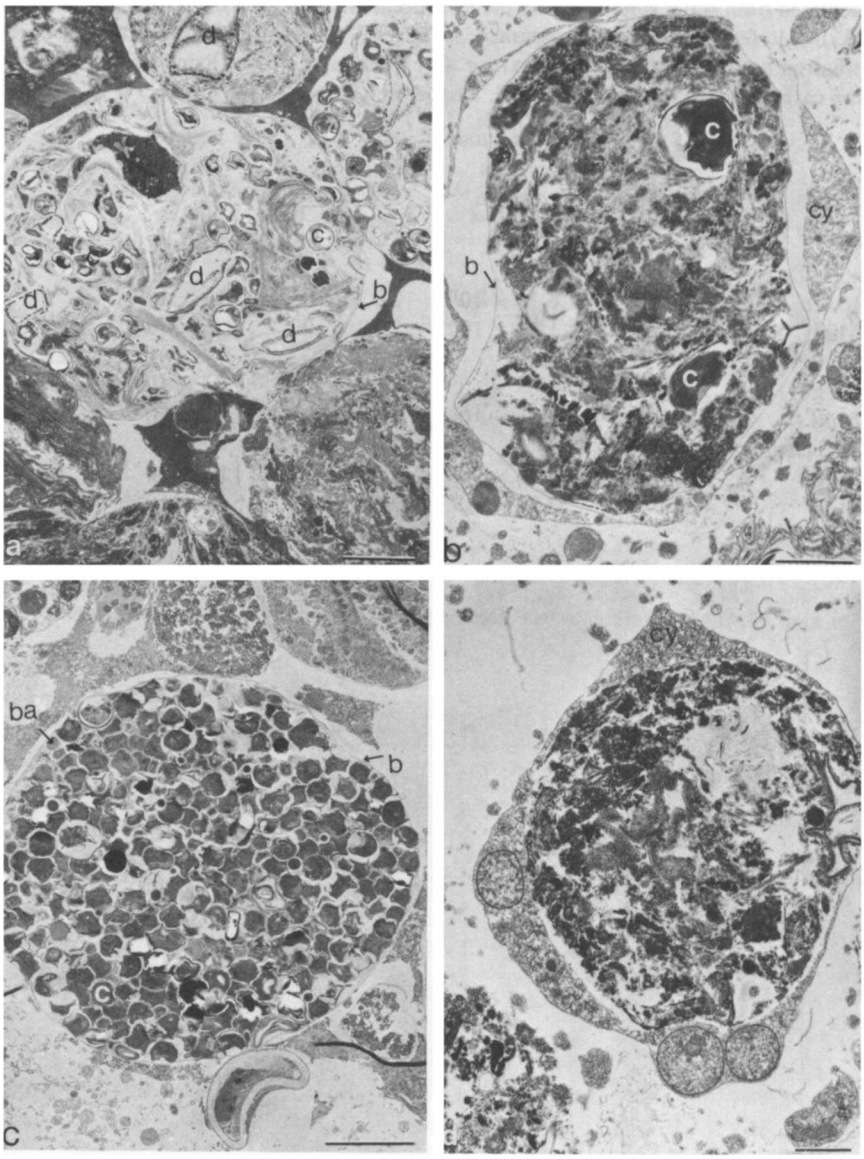

Figure 6. Transmission electron micrographs of sections of minipellets within phaeodarian radiolarians. The abbreviations are the same as in Figure 1. a. Region of specimen from 400 m showing several minipellets or vacuoles within the central capsule. Scale bar = 4 μm. b. Type A minipellet surrounded by radiolarian cytoplasm (cy). The specimen was from 80 m. Scale bar = 2 μm. c. Type A minipellet from a radiolarian from 80 m. Scale bar = 4 μm. d. Type D minipellet from radiolarian from 400 m. Scale bar = 1 μm.

study; since then we have examined 50 individuals from the Central Pacific Gyre and all contained minipellets. Individual Phaeodaria from VERTEX III contained an average of 1141 ± 1472 S.D. minipellets (range 38 to 4054 pellets, calculated from the area of minipellets in 1 μm thick cross sections of 17 Phaeodaria). Spumellarian radiolaria were also examined (Fig. 7). These organisms contained fewer minipellets per individual (552 ± 457 S.D., range 0 to 1139, $N = 6$) than the Phaeodaria. The same types of ultrastructurally intact cells found in the trap minipellets were found in the radiolarian minipellets, and some of the Phaeodaria contained minipellets, or perhaps more correctly vacuolar material with a boundary, with very high densities of ultrastructurally intact cells within the central capsule (Fig. 6c). Small hydromedusae, found only in the 80 m trap, contained approximately 2400 minipellets per organism ($N = 7$). Representative minipellets from sections of the hydromedusae are shown in Figure 8.

None of the ten nauplii examined in TEM sections contained minipellets or recognizable gut contents.

None of the producers were found in water samples taken during the trap deployment, so it was not possible to determine their density in the water column. Their absence from the water samples could have been due to low abundance and our examination of material from relatively small volumes of water, a patchy distribution in time or space, or to the association of the producers with rapidly sinking detritus, which is poorly sampled with water bottles.

g. Minipellets suspended in the water. The number of minipellets per liter of water (Fig. 9) differed significantly with depth zone. There were significantly more minipellets in the mesopelagic than in either the epipelagic (Mann-Whitney U Test, $p = .01$) or the bathypelagic (Mann-Whitney U Test, $p = .04$) zones. The number of minipellets per liter of water did not differ between the epipelagic and the bathypelagic zones (Mann-Whitney U Test, $p = .06$) and most of these on our filters were not obviously associated with larger detrital aggregates.

4. Discussion

a. Input throughout the water column. The distribution of sinking minipellets with depth suggests that they are produced throughout the water column; alternatively, minipellets may be produced at one or a few depths and settle without loss, a possibility we find less likely. We hypothesize that small consumers, most likely detritivores reprocessing sinking detritus, occur in significant numbers to 2000 m and continually produce minipellets. Our argument is based on the abundance profile of the pellets with depth, the predicted sinking rate of the minipellets, and the cell content of the pellets.

Minipellets occurred at all depths in both water and trap samples, with high and nearly constant concentrations to 2000 m. The likelihood of pellet loss through

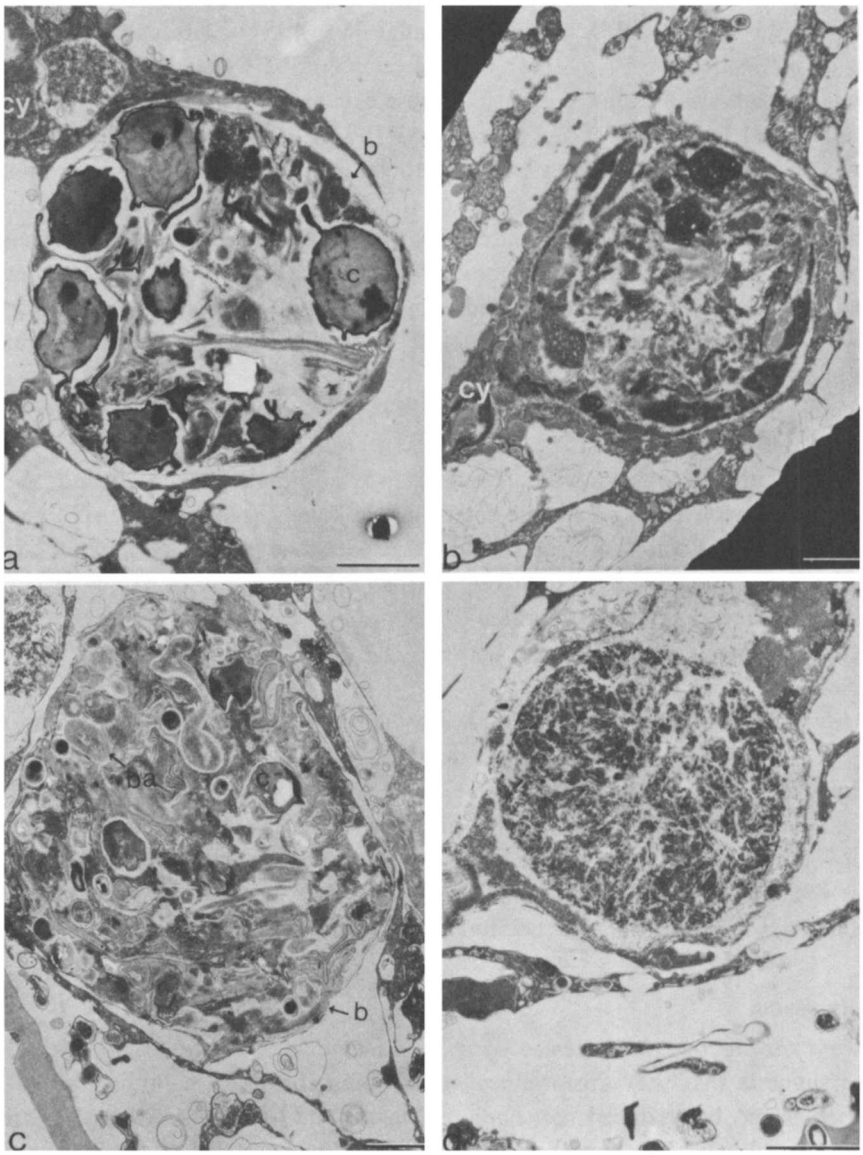

Figure 7. Transmission electron micrographs of sections of minipellets from within spumellarian radiolarians. All scale bars = 1 μm. Abbreviations are the same as in Figure 1. a. Type A minipellet from specimen from 400 m. cy = cytoplasm of radiolarian. b. Type D minipellet from radiolarian from 200 m. c. Type A minipellet from specimen from 400 m. d. Type D minipellet from specimen from 400 m.

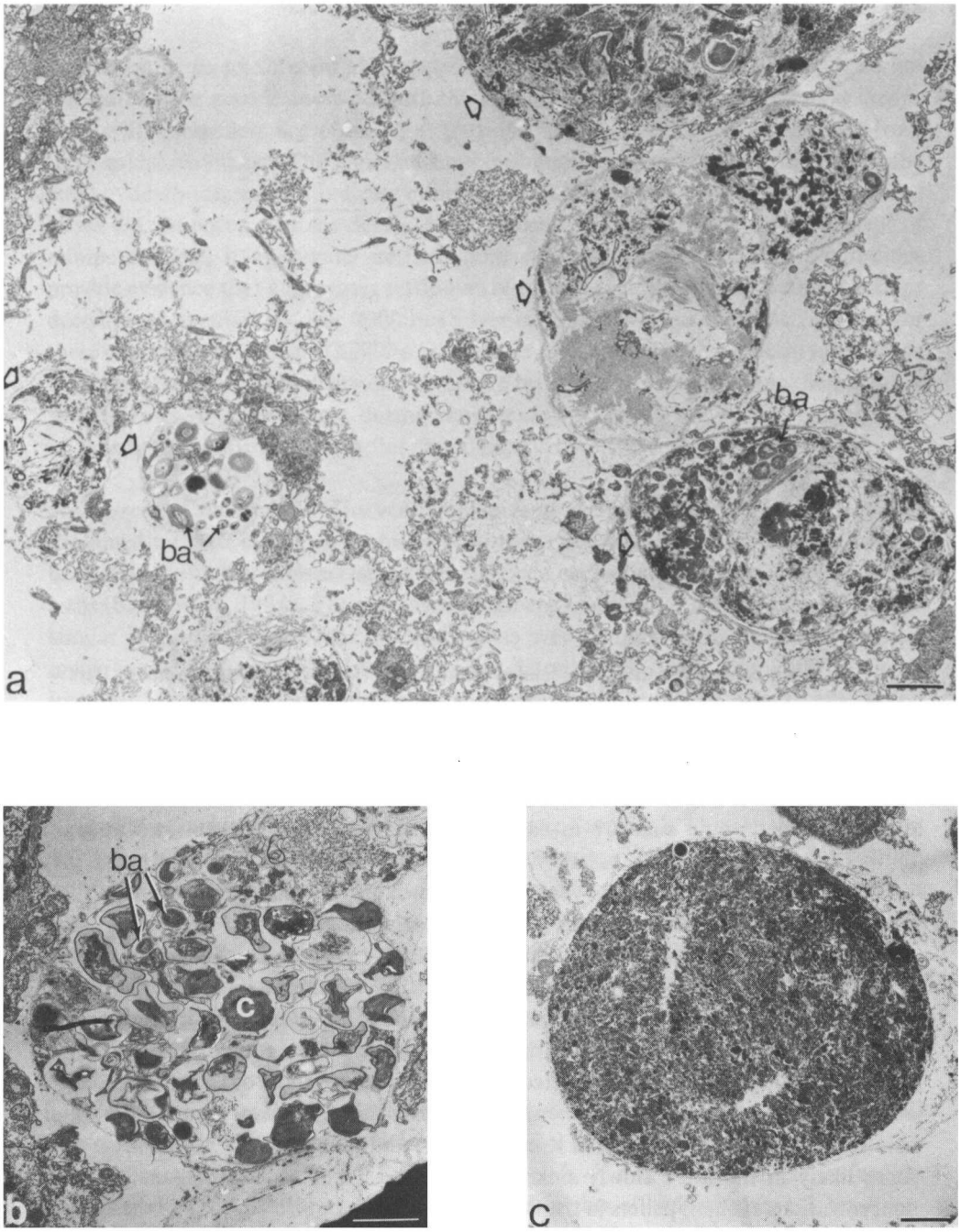

Figure 8. Transmission electron micrographs of sections of minipellets from within hydromedusae from 80 m. All scale bars = 2 μm. Abbreviations as in previous figures. a. Section showing several minipellets (open arrows) surrounded by hydromedusan tissue. The large bacteria in the small minipellet are cyanobacteria. b. Type A minipellet. c. Type D minipellet.

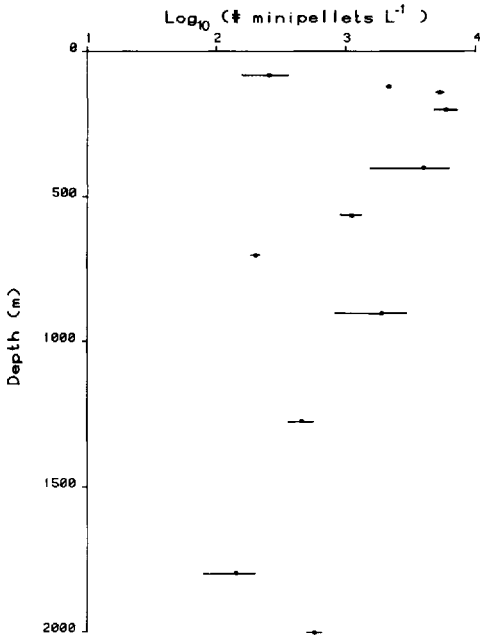

Figure 9. Mean concentration of "suspended" minipellets from water bottle samples. Bars = S.E.

consumption or decomposition increases as pellets age. Using Stokes' (1901) equation, we estimate that a 50 μm diameter minipellet would sink 21 m day^{-1}, and a 3 μm diameter pellet would sink .07 m day^{-1} at 25° C (with even slower rates at lower temperatures). If these pellets settle singly (not in association with other detritus), they would require many months or years to sink through the 2000 m depth interval we studied. Since minipellets contain more microorganisms per unit area than larger pellets, and decomposition from within minipellets is probably mediated by some of these microorganisms (Gowing and Silver, 1983a), the little pellets should not remain intact longer than larger pellets. Dissolution of the minipellets should also be faster than that of larger pellets because of the higher surface:volume ratio of the minipellets, if decomposition is also surface-related. There is evidence of loss of larger fecal pellets and repackaging of contents into new pellet classes during descent through the water column (Honjo, 1978; Urrère and Knauer, 1981) and such processes would seem even more likely in the more slowly sinking minipellets. Thus the maintenance of high concentrations of small pellets in the flux would seem to require inputs over the 2000 m interval.

Minipellets may also be produced on sinking detritus or trapped by it, especially by the complex aggregates of marine snow. Silver and Alldredge (1981) found small fecal pellets within individually collected aggregates of marine snow. In the present study, it

was not possible to differentiate between minipellets on marine snow and those not associated with marine snow because the marine snow, once in a trap, can scavenge pellets. If minipellets are often on aggregates, sinking rates may be different from those calculated above. The high and similar abundance of minipellets throughout the 2000 m depth range could indicate either rapid sinking rates of the aggregates so that losses did not occur over the depth range, or could suggest continual replacement of minipellets lost, if aggregates settled more slowly. Data from ciliate populations provide evidence that aggregates settle slowly enough to allow radical changes in their decomposer populations over 2000 m (Silver *et al.*, 1984), but the time required for these changes is unknown. Thus, we presently cannot exclude the possibility that large numbers of minipellets are carried down more rapidly than expected from their solitary sinking rates, but any losses during their transit to depth are nearly balanced by replacement to maintain minipellet abundance.

b. Sources of minipellets. The very small size of the minipellets we describe is best explained by their origin as wastes of protozoans or small, possibly juvenile, invertebrates. Such small organisms have generally been neglected in studies of deep sea food webs (Silver *et al.*, 1984). The presence of high and similar numbers of minipellets, and similar proportions of the four types of pellets over depth, indicate continual replacement by detritivores with similar trophic characteristics over the 2000 m depth interval. Furthermore, the general ultrastructural similarity of intact cells within minipellets to those on marine snow and in fecal pellets in traps (Gowing and Silver, 1983a) suggests the latter two could be food sources for the consumers that produce the minipellets. That hypothesis could also account for the higher concentration of cells in minipellets than in the two sources. That is, the "useable" fraction of the sinking detritus is assimilated and the minipellets are repositories of compacted, indigestible materials, including refractory cells. The classes of intact cells (*Chlorella*-like green algae and cyanobacteria) found in minipellets are those we and others have found to be abundant in fecal material of various epipelagic grazers (Silver and Bruland, 1981; Johnson *et al.* 1982; Gowing and Silver, 1983a), and these cells and their accompanying detritus are probably re-eaten and repackaged as the detrital rain settles. Such repackaging for larger pellet classes has already been mentioned above (Honjo, 1978; Urrère and Knauer, 1981).

Minipellets are probably produced by many different organisms, since any small detritivore consuming oceanic detritus could be expected to produce pellets with similar contents and sizes. We found Types A, B, C and D minipellets in feeding vacuoles and waste products of radiolarians and in guts of hydromedusae. Ultrastructurally intact radiolarians (including Spumellaria and Phaeodaria) were found in traps throughout the depths sampled. Solitary Spumellaria contained fewer minipellets per individual than Phaeodaria, and the minipellets were always located outside the central capsule. The rate of production of minipellets by Spumellaria is unknown. The

concentration of Spumellaria at our study site is unknown, but investigators have found living Spumellaria at most depths in the Pacific Ocean (Petrushevskaya, pp. 319–329, 1971: 0–5000 m; Casey, 1966: 0–1000 m; Gowing and Silver, 1983b: 0–2000 m).

Phaeodarian radiolarians in our samples contained minipellets inside the central capsule and in the phaeodium (a waste repository outside the central capsule), or just in the phaeodium. The rate of release of the minipellets is unknown, as is whether they are released singly, in groups, or as a phaeodium. Phaeodarian distributions have been less well-studied than spumellarian distributions (Anderson, 1983), but Haeckel (1887, cited in Anderson, 1983) found living Phaeodaria down to 5600 m, Kling (1976) reported living Phaeodaria in the upper 400 m of the Pacific, Reshetnyak (1955) found Phaeodaria between 4000 and 8000 m in the Kurile-Kamchatka Trench, and Gowing and Silver (1983b) found living Phaeodaria in traps to 2000 m (the deepest depth sampled). Phaeodaria are potentially more important than Spumellaria as a source of minipellets below 500 m because their flux at depth is greater than that of Spumellaria (Gowing, unpubl. data).

The hydromedusae were found only in the euphotic zone, and the minipellets within their stomachs could have been formed by the hydromedusae or could have been obtained by eating prey containing them. Different hydromedusae release their waste as pellets or as loose aggregations (C. Mills, personal communication), but waste production rates are not yet known. We were unable to estimate the field abundance of hydromedusae because they swam into the trap but were not caught in any quantitative net tows. Distributions of oceanic hydromedusae can be patchy (C. Mills, personal communication), so they could be important in producing local high densities of minipellets.

Copepod nauplii produce fecal pellets within the size range of minipellets (Marshall and Orr, 1956; Paffenhöfer and Knowles, 1979), but we did not find minipellets in the ten specimens that we examined with TEM. This may be a sampling artifact, from either a small sample size, rapid and infrequent pellet formation by the nauplii, or defecation as they encounter the fixative in the trap. It is difficult to screen the nauplii for presence of gut contents with the light microscope, and it is possible that some of the embedded specimens were not feeding nauplii. Marshall and Orr (1956) have reported that *Calanus finmarchicus* does not feed until the Nauplius III stage, and nauplii of *Euchaeta* do not feed (G.-A. Paffenhöfer, personal communication). Peaks of density of nauplii were found between 35 and 85 m (15113 m^{-3}) in the epipelagic, between 762 and 859 m (154 m^{-3}) in the mesopelagic, and between 1083 and 1186 m (67 m^{-3}) in the bathypelagic zone in quantitative opening/closing tows (M. Tuel, pers. comm.) at the sampling site, but no corresponding peaks were found in minipellet numbers in trap material or in water samples near those depths. Marshall and Orr (1956) found that the size of fecal pellets produced by copepod nauplii in the laboratory varied greatly, depending on the food organism. Thus until minipellets are found within field collected and preserved nauplii, the role of nauplii in minipellet production cannot be determined.

Other organisms that have recently been shown to produce wastes within the size range of minipellets include copepodid stages (G.-A. Paffenhöfer, personal communication), *Oithona* adults (Martens, 1972), heterotrophic dinoflagellates (Sieburth and Davis, 1982), and loricate and non-loricate ciliates (Stoecker, 1984).

c. Minipellets and olive green "cells." Although Types A, B, C, and D minipellets were all found inside radiolarians and hydromedusae, there are probably other sources of minipellets, especially of Type D. Type D minipellets looked most like olive green "cells" previously reported (Fournier, 1970; Silver and Alldredge, 1981). Thus these minipellets could have come from hypothesized sources of olive green "cells": autolyzed cells, single cells, including algae, that went through metazoan guts, wastes of small metazoans, protozoan vacuolar contents (Silver and Alldredge, 1981; Silver and Bruland, 1981), or from senescent diatoms (Anderson, 1975). We also think that Type D could also have come from degradation of Types A, B, and C because of the few pellets of Type D that contained bacteria.

Minipellets occurred throughout the 2000 m water column examined, and have been present in all sizable samples of detritus and suspended particulates that we have examined (listed in 2b above). Thus minipellets appear ubiquitous, occurring abundantly in the aphotic depths that harbor olive-green "cells" as well in the euphotic zone, where the olive-greens are rare or absent. Our minipellet density data from water samples are not directly comparable to data from previous studies of olive green "cells" because the size range of minipellets (3–50 μm diameter) is greater than that of olive green "cells" (1–15 μm, Fournier, 1970; Hamilton *et al.*, 1968). The general depth distribution pattern of minipellets in the water column does, however, have the mesopelagic peak found for olive green "cells" noted by other investigators (Fournier, 1971; Hamilton *et al.*, 1968).

d. Role in flux and food chains. Although the numbers of minipellets were generally three orders of magnitude greater than those of larger pellets, their overall role in mass and carbon transport would appear relatively minor, due to their small size. However, the minipellets are equal in importance to larger pellets in transporting intact cells to depth. The cell richness of minipellets implicates producers of minipellets as major reprocessors of detritus in the deep sea.

The producers of minipellets alter the characteristics of detritus and thus the food quality of the detrital rain; their activities constitute some of the biological transformations occurring as particulates settle through the ocean. We hypothesized above that the minipellet producers consume the larger and more rapidly sinking particles such as marine snow and larger pellets. The numbers of refractory algae in the minipellets are evidence that the materials incorporated in these small pellets are reworked detritus derived ultimately from the euphotic zone. The equal quantities of refractory algae in the flux of minipellets and large fecal pellets indicate that equivalent amounts of detrital materials may be represented by both. This hypothesis depends on the

non-growth of algae in pellets after leaving the euphotic zone; we presently have no direct or persuasive indirect evidence for growth of these refractory algae in the aphotic zone.

Minipellets in the water column are available to filter feeders at all depths, and minipellets on marine snow (probably the predominant source in our traps) are available to browsers on marine snow or to large particle feeders. Previous studies have shown one class of minipellets, the olive green "cells," to occur in a number of different types of grazers. These "cells" have been found in guts of copepods (Wheeler, 1970; Harding, 1974), colonial tunicates (Fournier, 1973), a salp (Fournier, 1973), and a benthic ascidian (Fournier, 1973). We have found Type D minipellets in salp, copepod, polychaete, and holothurian guts. Olive green "cells" have also been found in fecal pellets examined with light microscopy (Urrère and Knauer, 1981). We have found Types A, B, C and D minipellets in fecal pellets produced by salps and pteropods (Silver and Bruland, 1981), larvaceans, and the swimming crab *Pleuroncodes planipes* (Gowing and Silver, 1983a), and Type D minipellets in doliolid feces. The minipellets of Types A and B found in fecal pellets represent carbon that has passed through two digestive processes, indicating that at least some of the bacterial carbon in minipellets, in addition to the refractory algae, escapes digestion.

The minipellet producers must be abundant, but their biomass or that of their minipellet wastes cannot be readily calculated from our sediment trap data. Traps capture sinking materials in direct proportion to their sinking rates and thus are biased samplers of mass. (Traps sample mass flux, which is the product of mass and sinking rate.) If minipellets and large pellets sank into the traps individually, the difference in sinking rates of the two dominant classes of pellets (i.e. 12 μm vs. 100 μm diameter) would suggest that the traps "undercollect" the minipellet mass by a factor of 69 (based on Stokes' (1901) equation and an assumption of equal pellet density) as compared with the larger pellets. If minipellets mostly entered the trap with marine snow and other materials, then the mass of minipellets is misrepresented in the trap by the difference in the sinking rates between those aggregates and the large fecal pellets. We presently cannot estimate the field concentrations of minipellets from trap samples because we do not know the extent of their association with other sinking detritus, but traps most probably underestimate the mass of wastes produced by small organisms as opposed to the wastes produced by large organisms.

5. Conclusions

1. Compact waste bodies between 3–50 μm, called "minipellets" in this paper, occurred abundantly in a profile from the eastern tropical Pacific (VERTEX III site) and in other samples we have examined from the North Pacific and North Atlantic. In the VERTEX material, the minipellets numbered 10^5–10^7 m^{-3} in water samples and 10^6–10^7 m^{-2} day^{-1} in trap collections of sinking detritus.

2. Four types of minipellets were recognizable, ranging from ones that appeared newly produced and bore intact boundaries to ones that had no boundaries, usually

lacked recognizable internal contents, and were identical to wastes previously described as "olive green cells."

3. As seen by transmission electron microscopy, minipellets of Types A, B, and C contained occasional intact bacterial cells (including nondistinctive, Gram-negative forms, nitrifiers, and cyanobacteria) and very small algae (*Chlorella*-like eukaryotes). Type D minipellets only rarely contained intact cells, and then only bacteria. Minipellets contained about twice as many intact cells (by volume) as larger pellets, and these cells appeared to be the same digestion-resistant forms that typify those found in pelagic detritus.

4. Proportions of Types A + B + C of the total minipellets did not differ with depth, and slightly higher numbers (about 2×) of minipellets occurred in the mesopelagic than in the bathypelagic zone. In the "suspended" fraction obtained by water bottles, minipellet numbers also peaked in the mesopelagic zone.

5. Minipellets were about 10^3 times more abundant that larger (>50 μm diameter) fecal pellets in trap samples, but their volume flux was about ½–⅙ that of the larger pellets because of their small size (dominant size category was 12 μm diameter). Because of their cell richness, however, the sinking minipellets carried about as many intact cells to depth as did the large pellets.

6. In our VERTEX samples, we found three types of organisms to contain very large numbers of minipellets (i.e. 10^2–10^3 minipellets per individual): phaeodarian radiolarians, spumellarian radiolarians, and small hydromedusae. We suggest that these, and probably other protozoa and small invertebrate zooplankton, may produce minipellets at depth.

7. We hypothesize that minipellets are produced by organisms that consume surface-derived detritus and that these organisms are sufficiently abundant and active over the 2000 m depth interval to maintain the high concentrations of pellets found here. The high algal content of the minipellets implicates the minipellet producers as major reworkers of euphotic zone detritus and indicates that these organisms are involved substantively with the biological transformations that occur in the decomposition of organic matter in the deep sea.

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