Journal of Marine Research, 47, 829–850, 1989

Composition and degradation of salp fecal pellets: Implications for vertical flux in oceanic environments

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ABSTRACT

Changes in the sinking rates, ash-free dry weights, particulate carbon and nitrogen content, and carbon:nitrogen ratios from the fecal pellets of several species of oceanic salps were examined in ten-day decomposition studies. Although bacteria and protozoa became abundant in the incubation vessels, most of the fecal pellets remained physically intact throughout the study. Bacterial activity in the pellets (measured by the rate of uptake of ^{3}H-thymidine) increased, but microbial degradation had little effect on the sinking speeds of most of the fecal pellets. The average losses of ash-free dry weight and carbon and nitrogen content, along with changes in carbon:nitrogen ratio, were small compared to their initial values. We conclude that microbial degradation of large salp fecal pellets would not prevent the vertical flux to the deep ocean of a significant fraction of the particulate organic material contained in the pellets. The fecal pellets of oceanic salps provide a rapid, and potentially important, mechanism for the consolidation and vertical transport of organic and lithogenic material associated with minute particles in the open ocean.

1. Introduction

Oceanic salps are uniquely suited among planktonic filter-feeders for effecting the vertical transport of microscopic particulate material to the deep ocean. These pelagic tunicates filter water at very high rates (relative to other planktonic organisms), removing minute particles and microorganisms (<5 μm) with high efficiency by means of a mucous feeding net (Madin, 1974; Harbison and Gilmer, 1976; Harbison and McAlister, 1979; Madin and Cetta, 1984; Alldredge and Madin, 1982). The daily defecation of these organisms constitutes a large percentage of their body weight, and they produce relatively large (>1 mm) fecal pellets which sink rapidly (Madin, 1982; Bruland and Silver, 1981; Small *et al.*, 1983). Because of these characteristics, grazing by salps can be an important mechanism for the rapid vertical flux of particles that would otherwise have negligible sinking rates.

A considerable amount of experimental work has been carried out on the microbial colonization and degradation of the fecal pellets of planktonic crustacea, primarily

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copepods (Honjo and Roman, 1978; Turner, 1979; Bathelt and Schelske, 1983; Gowing and Silver, 1983; Jacobsen and Azam, 1984). Copepod fecal pellets are rapidly colonized by bacterial and protozoan populations that degrade the peritrophic membrane enclosing the pellet, causing dispersal of the pellets in a relatively short time in warm water (a few hours at 20°C). Because of the rapid decomposition of these small pellets, it is probable that much of the fecal material produced by copepods in surface waters does not reach the deep ocean (Hofmann *et al.*, 1981).

Relatively little work has been done on the degradation of salp fecal pellets (Pomeroy and Deibel, 1980; Pomeroy *et al.*, 1984). These studies have demonstrated that fecal material of some salps is also degraded rapidly by microbial populations, and that these pellets contribute to the formation of suspended detrital aggregates (marine snow) in surface waters. However, these studies considered mainly small, coastal species of salps and doliolids. Larger species of salps that are more characteristic of oceanic environments produce larger and denser fecal pellets which may be less susceptible to microbial invasion and decomposition.

We examined the composition of salp fecal pellets, their microbial colonization, degradation and physical breakdown, and consequent changes in their sinking velocities. Filtration experiments with salps were run to ascertain the efficiency with which small particles were retained and incorporated into fecal pellets. From the results of these studies we conclude that fecal pellets of large salps remain largely intact during the time that they sink to the deep ocean. Bacterial production in or on the fecal pellets increased during incubations lasting up to thirteen days. However, the fecal pellets were not physically disrupted by microbial activity, the loss of particulate carbon and nitrogen was small (20–30%), and sinking rates remained high. Production of fecal pellets at several sites was estimated from new data on population densities of oceanic species, and compared with other data in the literature. In a variety of situations, salp fecal pellets appear to be an important mechanism for the vertical flux of material to the deep ocean.

2. Methods and materials

a. Collection of salps. Eight species of oceanic salps were collected on six cruises, four in the western North Atlantic in 1981, 1982, 1983 and 1984, one in the Tongue of the Ocean in 1985, and one at Station P in the eastern North Pacific in 1987. On all cruises, salps were hand-collected in quart jars by divers, and maintained at 21–22°C in large aquaria that were initially sterile. Ambient water temperatures during these cruises ranged from ≈19–28°C.

b. Filtration of small particles. The filtration rates and retention efficiencies of three species of salps (*Cyclosalpa affinis, Salpa maxima, Pegea confoederata*) were examined in 0.22 μm filtered seawater containing three species of cultured microorganisms. Clonal cultures of a small chrysophyte, *Isochrysis galbana* (nominal diameter ≈5.0 μm), a heterotrophic microflagellate *Bodo* sp. (diameter ≈2.0–2.5 μm), and a chroococcoid

cyanobacterium *Synechococcus* sp. (diameter ≈0.7–1.0 μm) were used as food. These species are representative of microorganisms in the nanoplankton (2–20 μm) and picoplankton (0.2–2.0 μm) size classes. Densities of the cells were determined by epifluorescence microscopy (Davis and Sieburth, 1982) when the salps were placed in the aquaria, and at regular intervals for a period of 360 minutes. Filtration rates (i.e., clearance rates) were calculated from the rate of decrease in the concentration of the prey using the method of Harbison and Gilmer (1976). Microbial densities were also counted in control aquaria without salps.

c. Elemental composition of salp fecal pellets. Fecal pellet samples for elemental analysis were frozen after collection. They were subsequently dried and subjected to neutron activation analysis according to the methods of Spencer *et al.* (1972, 1978). Fecal pellets were weighed onto a 37 mm Nuclepore membrane filter, and irradiated with a thermal neutron flux of 4×10^{12} n cm^{-2} sec^{-1} at the Rhode Island Nuclear Science Center, Narragansett, Rhode Island. Samples were irradiated 10 minutes, allowed to "cool" for 5 minutes to allow short lived activation products to decay away, and counted for 800 seconds with a Ge (Li) detector to identify and quantify the characteristic photopeaks. Samples were compared to standards prepared by drying standard solutions on Nuclepore membrane filters that were subsequently irradiated and counted.

d. Fecal pellet decomposition studies. Ten-day decomposition studies of salp fecal pellets were carried out. Salps that were used to produce fecal pellets for the decomposition study were held in 4 to 8 l of unfiltered seawater at 21–22°C. The seawater was replaced approximately every two hours to maintain near-ambient food concentration. Fecal pellets were collected over a period of four to twelve hours depending on the rate of pellet production. Pellets were removed as they were produced and placed in a flask containing 500 ml of unfiltered, natural seawater until enough were collected for the various analyses. In some cases, too few pellets were obtained to allow all analyses to be performed.

The fecal pellets for each group of salps (usually aggregate individuals from the same chain) were pooled, and subsamples of 4 to 30 pellets were analyzed for initial (Time = 0) concentrations of particulate organic carbon, particulate organic nitrogen, and ash-free dry weight according to the procedures of Madin (1982). The remaining pellets were held in the dark in natural seawater at 22°C for 24 h. Another sample was taken after 24 h for each of the analyses mentioned above, and the pellets were then placed at 5°C in the dark for the remainder of the study period. This temperature regime was used because the rapid sinking rates of most of these pellets would remove them from the warm surface waters of the ocean within one day. No agitation of the incubation flasks was provided other than normal ship movement. Samples of pellets were taken again after nine days of incubation at 5°C (10 days total), and in some cases after three and six days as well. Enough pellets were obtained for two groups of salps

(*Pegea bicaudata* and *P. socia*) to allow incubations of replicate groups of pellets at 5°C (as described above) and at 22°C for the full ten day period to examine the effect of temperature on the rate of decomposition.

The rate of uptake of tritiated thymidine was measured over the course of the thirteen-day experiments in the fecal pellets of two species (*Pegea socia* and *Pegea bicaudata*) according to the procedure of Fuhrman and Azam (1982). Fecal pellets were incubated in the dark at either 5°C or 22°C for the entire thirteen-day period. The rate of uptake was determined in one hour incubations at a final concentration of 10 nM methyl ^{3}H-thymidine. Tritium uptake by pellets was separated from the uptake by suspended bacteria in the seawater surrounding the pellets by using controls of water from dishes containing pellets.

Fecal pellets were examined by light microscopy (transmitted and epifluorescence) and by scanning electron microscopy (SEM) to obtain information on the microbial populations present in the pellets. Unpreserved pellets were examined for the presence of protozoan populations, and pellets preserved with 1% glutaraldehyde were examined for bacteria using the DAPI epifluorescence microscopical technique (Porter and Feig, 1980) at a final stain concentration of 1–3 μg ml^{-1}. Fecal pellets of *Cyclosalpa bakeri* from Station P in the North Pacific were preserved with 2.5% glutaraldehyde in seawater, freeze dried on glass cover slips, and examined by SEM. Quantification of the microbial populations was not attempted because of the size and thickness of the pellets, and the large variability in their composition. We used direct microscopical observations only to determine gross qualitative composition of the pellets.

The sinking rates of a subset of fecal pellets from each group of salps were measured individually in a cylindrical chamber (≈50 cm high and 50 cm in diameter) by determining the time required to sink through a 30 cm column of natural seawater. Ten or twenty fecal pellets from each group of salps were removed at the beginning of the experiment and placed in a separate flask containing 500 ml of seawater. Because of the relatively high sinking velocities, it was possible to determine sinking rates at sea during calm weather. Each pellet was transferred to the chamber using a large bore pipette and released just below the surface of the water. Sinking was timed over a path that began ≈7 cm below the surface of the water and ended ≈7–10 cm above the bottom. The pellets were retrieved following the measurements and returned to the flasks containing 500 ml of seawater. Sinking rates were determined on the same ten or twenty pellets after 1, 3, 6 and 10 days of incubation for most groups of salps. Some of the groups were examined only initially and after 10 days. Incubation conditions were as described above.

e. Salp abundance. Populations of salps were sampled at stations in the western North Atlantic on three cruises made in 1982 and 1983. An open trawl net having a mouth area of 10 m^2 and a 4 mm mesh was fished off the side of the ship to a depth of 20 or 50 m. A TSK flowmeter was used to measure the distance traveled by the net. Salps collected were identified to species and generation, and their total lengths were

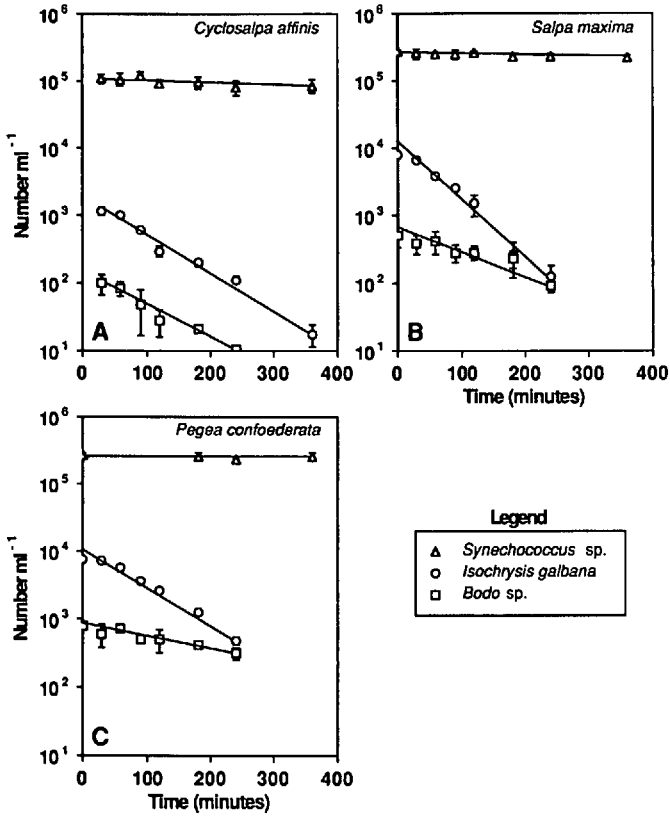

Figure 1. Removal of a small photosynthetic flagellate (*Isochrysis galbana*), a heterotrophic microflagellate (*Bodo* sp.), and a chroococcoid cyanobacterium (*Synechococcus* sp.) by three species of oceanic salps. Filtration rates of the salps for the three food species are indicated by the slopes of the regression lines, and are summarized in Table 1.

measured. Both day and night tows were made, but the salp species collected were not vertical migrators. Biomass of the salps was expressed as individuals per m^3; these values were converted to mg carbon per m^2 over the depth interval sampled, using the length to weight relationships of Madin *et al.* (1981). Estimates of fecal pellet production by these salp populations, expressed in mg fecal carbon per m^2 per day were made using the species-specific fecal production rates given by Madin (1982).

3. Results

a. Filtration efficiencies and fecal pellet composition. Salps are indiscriminate particle feeders, but the pore size of the filtering net determines the minimum size of particles that can be effectively removed from the water. The specimens of *C. affinis, S. maxima* and *P. confoederata* examined in this study were primarily consumers of planktonic organisms greater than or equal to 2 μm in size (Fig. 1, Table 1). Filtration

Table 1. Filtration rates, calculated from the regressions of Figure 1, of three species of salps for three food species. All salps used in these experiments were from the aggregate generation. Approximate body lengths of the individuals in the aggregates are given. Differences in the filtration rates for a particular species indicate differences in the retention efficiency of the salps for the food species. Numbers in parentheses are the filtration rates expressed as a percentage of the highest filtration rate for each species (the highest rate was observed for *I. galbana* in all cases).

	Filtration Rates (ml salp^{-1} min^{-1})		
Food Species and Nominal Diameter (μm)	*Cyclosalpa affinis* (size ≈17 mm)	*Salpa maxima* (size ≈17 mm)	*Pegea confoederata* (size ≈19mm)
Synechococcus sp. (0.7–1.0 μm)	0.08 (9%)	0.06 (3%)	<0.05 (<3%)
Bodo sp. (2.0–2.5 μm)	0.75 (83%)	0.75 (43%)	0.65 (33%)
Isochrysis galbana (5.0 μm)	0.90 (100%)	1.73 (100%)	2.00 (100%)

rates (and therefore retention efficiencies) for *Isochrysis galbana* were somewhat greater than the values for the slightly smaller *Bodo* sp., and rates for both were much greater than rates calculated for the removal of *Synechococcus* sp. from the water (Table 1). Filtration rates of the salps for *I. galbana* ranged from 1.7× to >40× the rates calculated for the removal of the cyanobacterium at the same time and from the same aquaria. The small changes in the density of particles ≤1.0 μm in size are within the microscopical counting error. Densities of the microbial populations in the controls (without salps) also did not change significantly during the incubations.

Qualitatively, the results of the filtration experiments described above were confirmed by direct microscopical observation of fecal pellets produced by salps held in natural seawater (Fig. 2). Bacteria, chroococcoid cyanobacteria and nanoplankton observed using epifluorescence microscopy were present in these pellets primarily as clumped cells (e.g. Fig. 2C), while nanoplankton were present both as single cells and in clumps (Fig. 2D–F). In general, the identifiable material composing the fecal pellets was dominated by the structures of nanoplankton and microplankton species (Fig. 2E, F). The contents of newly produced fecal pellets were, of course, influenced by prey availability in each environment, and perhaps by selective digestion in the salps. It is probable that these factors also affected the density of bacteria and cyanobacteria in the fecal material.

Elemental analysis of the fecal pellets of three species of salps revealed that, of the elements analyzed, calcium was most abundant in all three species (Table 2) making up more than 10% of the mean dry weight of the fecal pellets. Three other elements (Mg, Sr, Al) were present in quantities >1 μg^{-1} dry weight. The concentrations of six of the ten elements was highly variable between the species examined. Coefficients of variation for concentration among the samples were lowest for calcium, magnesium, iodine and aluminum, and ranged to nearly 50% for the other elements.

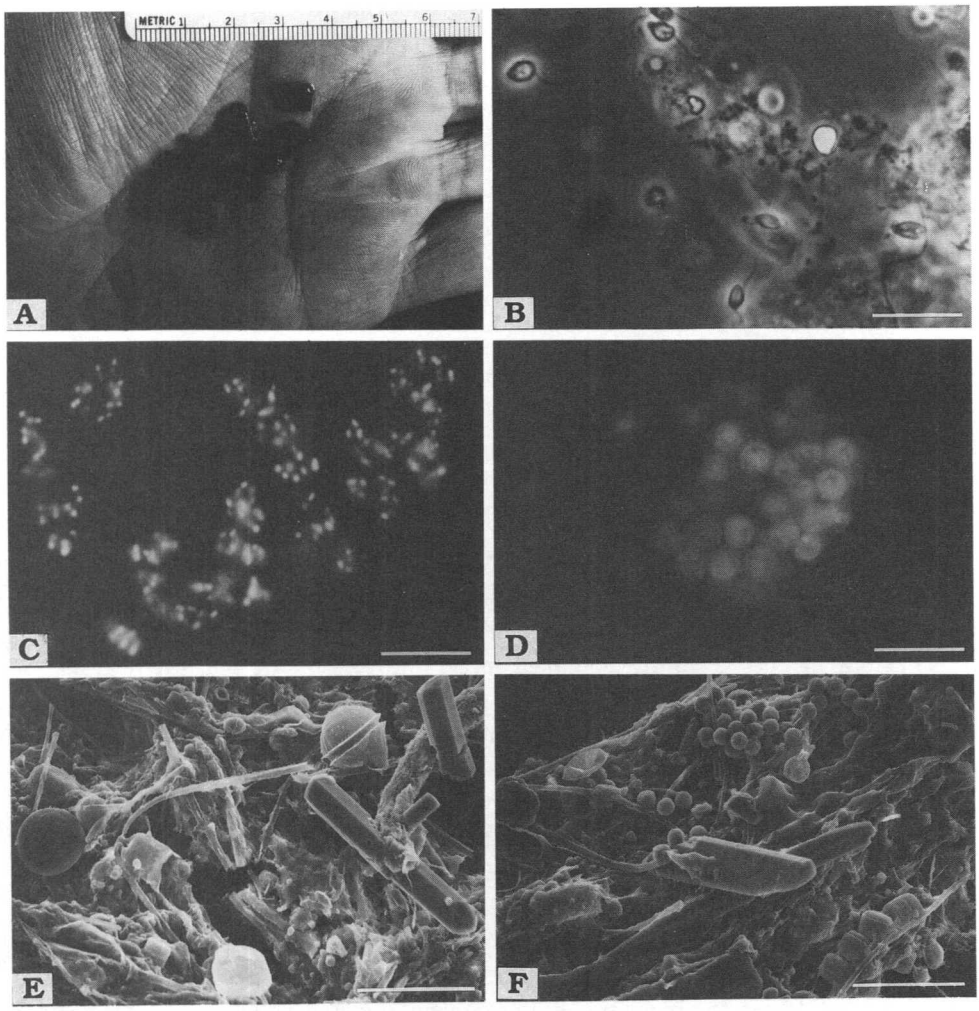

Figure 2. Fecal pellets of *Salpa maxima* (A) illustrating their size and cohesiveness. Phase contrast photomicrograph (B) of heterotrophic microflagellates associated with the "fraying" end of a fecal pellet after 6 days of incubation. Epifluorescence photomicrographs of autofluorescent chroococcoid cyanobacteria (C) and eukaryotic algae (D) in a freshly collected fecal pellet. (E,F) Scanning electron micrographs of freshly collected fecal pellets of *Cyclosalpa bakeri*. Visible objects include *Chaetoceros* sp., dinoflagellates, small centric diatoms, unidentified small cells and debris. Marker bars are 15 μm (B-D) and 50 μm (E,F).

b. Fecal pellet degradation studies. Microbial degradation studies were conducted on fecal pellets collected from a total of 18 groups of salps from eight species (Table 3). Fecal pellets produced by these species were not discrete entities, but were produced as flat ribbons that broke at random to form pellets of varying length. For the species

Table 2. Elemental composition of salp fecal pellets. All values are expressed in $\mu g\ g^{-1}$ dry weight. *Pegea bicaudata* data are from one sample. *Cyclosalpa affinis* and *Salpa maxima* data are the means of three samples.

Element	*Pegea bicaudata*	*Cyclosalpa affinis*	*Salpa maxima*	Mean of three Species (CV as %)	Mean % of Dry Weight
Calcium	126,000	125,000	103,000	118,000 (9)	11.8
Magnesium	13,600	8,970	9,770	10,800 (19)	1.08
Strontium	6,020	13,000	9,600	9,550 (30)	0.95
Aluminum	3,280	3,260	2,370	2,970 (14)	0.30
Barium	211	800	628	546 (45)	0.05
Copper	744	474	217	478 (45)	0.05
Titanium	456	239	308	334 (27)	0.03
Iodine	153	200	196	183 (11)	0.02
Manganese	207	93	69	123 (49)	0.01
Vanadium	7	13	9	10 (30)	0.00

examined in this study, pellets ranged in size from approximately 0.3 × 1.0 mm (for small *Pegea bicaudata*) to 3 × 4.0 mm (for large *Salpa maxima*).

The fecal pellets generally remained intact throughout the ten day degradation study (Fig. 3), with only minor "fraying" apparent along the edges where the pellets were broken from the fecal ribbon. In general, the pellets were physically quite durable (Fig. 2A). The exceptions to this generality were fecal pellets produced by large (55–70 mm in length) *Pegea socia* (Fig. 3I); large portions of which "unraveled" during the incubation. The resulting strands of fecal material apparently were the remains of the mucous feeding web that had been compressed to produce the fecal ribbon. This "unraveling" was not seen in pellets of smaller *P. socia* or the other species.

Although the fecal pellets remained relatively intact, organic material was undoubtedly released during the incubations. Large populations of bacteria developed in the flasks by the first day, and a protozoan assemblage developed during the following days. Heterotrophic microflagellates dominated most of the protozoan assemblages in the flasks, but small bacterivorous ciliates became abundant in some containers. The protozoa were abundant on the surface of the fecal pellets, particularly at the "fraying" edges (Fig. 2B), but their activities did not significantly affect the physical integrity of the pellets. In no instances were protozoa observed inside pellets that had not first been physically disrupted (e.g. the large *P. socia* pellets that became unraveled).

Maintenance of the physical integrity of the fecal pellets over the ten days resulted in relatively small losses of ash-free dry weight (Table 3). In four of the nine groups of pellets examined, there was virtually no decrease in AFDW. The largest decrease among the groups (42%) was observed for the fecal pellets of large *P. socia* that unraveled during the study. Losses of particulate organic carbon (POC) and particu-

Table 3. Changes in ash free dry weight, carbon:nitrogen ratios and sinking rates of salp fecal pellets that were freshly collected (Initial) or incubated at 22°C for 1 day and then at 5°C for 9 days (Final). The *Salpa cylindrica* were the solitary generation. All other salps were from the aggregate generation. An asterisk (*) indicates fecal pellets that were incubated at 22°C for the entire 10-day period. Errors on the sinking rates are ± 1 standard deviation.

Species	Salp body length (mm)	Ash free dry weight (μg^{-1} fecal pellet)			Carbon:nitrogen ratio (by weight)		Sinking rate (m day^{-1})		
		Initial	Final	% of Initial	Initial	Final	Initial	Final	% of Initial
Salpa maxima	22–24	—	—	—	18.1	29.3	950 ± 180	800 ± 130	84
Salpa maxima	35–55	407	268	66	12.8	12.4	2470 ± 990	2150 ± 900	87
Salpa maxima	75–85	—	—	—	—	13.8	2170 ± 150	1820 ± 380	84
Salpa cylindrica	30–40	69	74	>100	8.9	8.9	490 ± 90	380 ± 70	78
Pegea socia	17–19	19	17	89	24.1	—	460 ± 200	270 ± 20	59
*Pegea socia**	17–19	19	18	95	24.1	—	460 ± 200	250 ± 100	54
Pegea socia	47–52	170	170	100	17.9	15.4	980 ± 110	810 ± 70	83
Pegea socia	55–70	530	310	58	17.1	23.6	1670 ± 270	1240 ± 270	74
Pegea bicaudata	17–19	—	—	—	22.8	29.4	650 ± 80	570 ± 50	88
Pegea bicaudata	43–47	183	133	73	12.8	14.3	1410 ± 150	1490 ± 150	100
*Pegea bicaudata**	43–47	183	150	82	12.8	11.5	1500 ± 180	1340 ± 120	89
Pegea confoederata	12–14	—	—	—	11.5	17.5	300 ± 40	260 ± 30	87
Pegea confoederata	30–36	—	—	—	10.0	11.6	1040 ± 110	860 ± 90	83
Cyclosalpa affinis	22–28	—	—	—	20.6	23.9	650 ± 70	440 ± 80	68
Cyclosalpa affinis	33–37	69	74	>100	7.3	16.1	570 ± 100	530 ± 130	93
Cyclosalpa affinis	45–55	—	—	—	17.2	20.5	1290 ± 200	940 ± 160	73
Brooksia rostrata	47–53	—	—	—	14.5	15.4	1040 ± 60	860 ± 60	83
Ihlea punctata	20–25	—	—	—	10.2	14.5	530 ± 40	340 ± 60	64

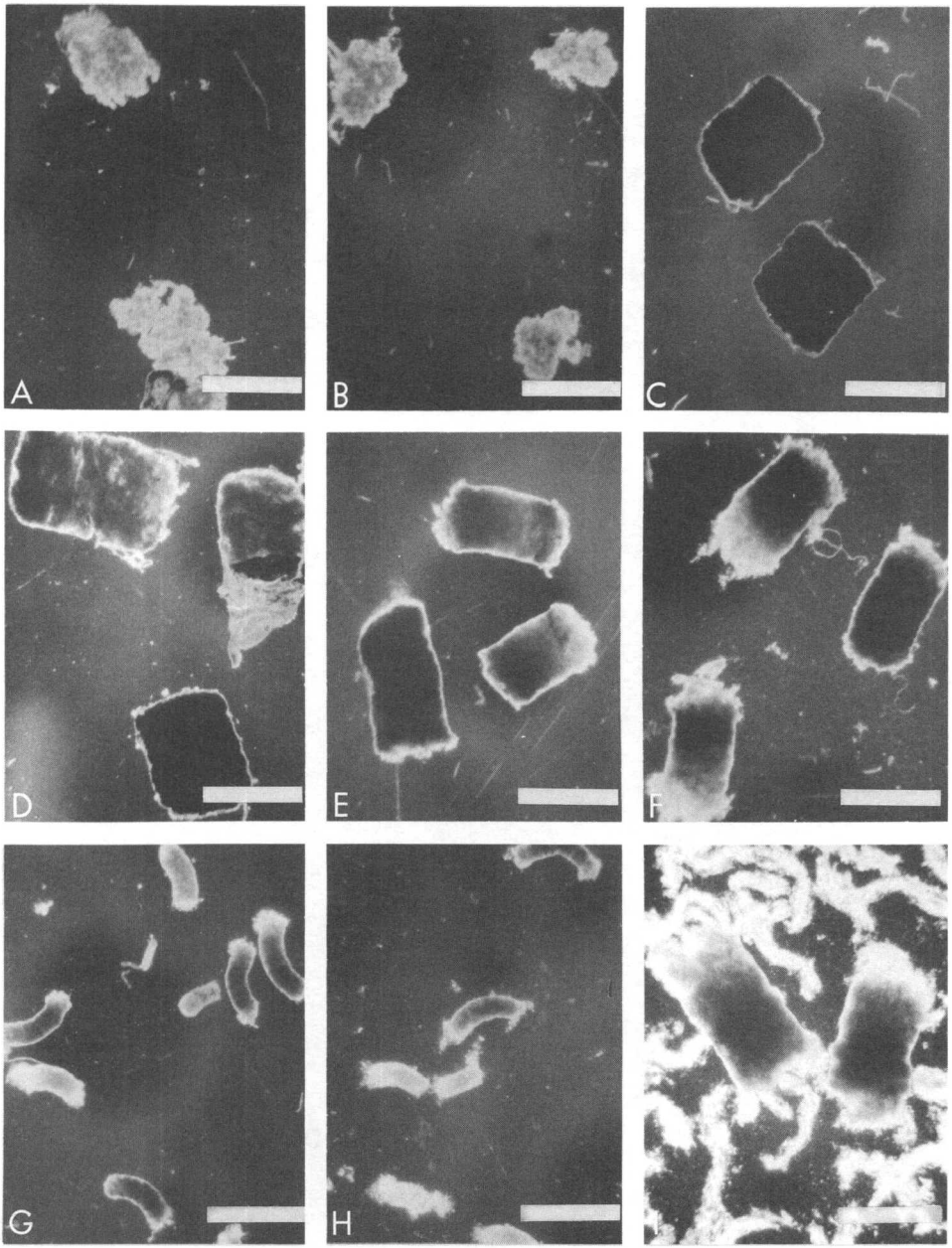

Figure 3. Fecal pellets of solitary individuals of *Salpa cylindrica* (A,B), or aggregates of *Salpa maxima* (C,D), *Pegea bicaudata* (E,F), and *Pegea socia* (G,H,I). The pellets were produced over a six-hour period by a single batch of each species, split into two aliquots and photographed immediately (A,C,E,G), or after six days (B,D) or ten days (F,H,I) of incubation at 22°C. *Pegea socia* fecal pellets were formed by salps that were 17–19 mm in length (G,H) or 55–70 mm in length (I). "Unraveling" of the mucous strand is apparent for the large *P. socia* pellets (I). All marker bars = 3.0 mm.

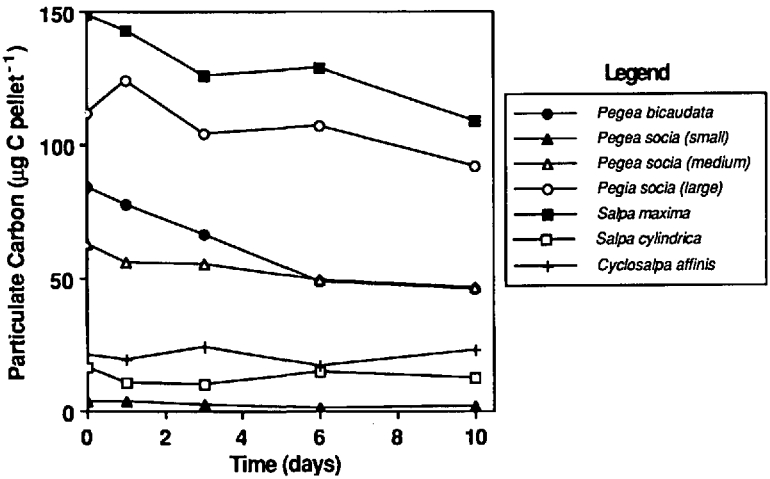

Figure 4. Time course of the loss of particulate carbon from seven groups of salp fecal pellets during a ten day decomposition experiment.

late organic nitrogen (PON), determined for all groups, were also small. On average, the fecal pellets retained 78% (CV = 25) of their initial POC concentration and 69% (CV = 19) of their initial PON concentration after ten days. These losses correspond to decay rates of 0.025 d^{-1} and 0.037 d^{-1}, respectively. The time course of POC loss during the ten day incubations for seven groups of salp fecal pellets indicated a relatively gradual loss of POC (Fig. 4).

Carbon:nitrogen ratios for the salp fecal material were quite variable for the organisms sampled in this study (Table 3). Initial C:N ratios ranged from 7.3 to 24.1, and there were no observable trends in this ratio with species or the size of the salps. There also was no consistent pattern between the initial and final C:N ratios. Out of the 15 groups of fecal pellets for which initial and final ratios were determined, the C:N ratios of 8 groups increased by more than two units over the course of the ten day incubation, while the C:N ratios of 7 groups showed little or no increase, or a decrease. Presumably, the C:N ratio of the fecal material was highly dependent on the particulate material present in each environment.

Incubation temperature had a significant effect on the rate of uptake of ^{3}H-thymidine and on the rate of loss of particulate carbon during the degradation experiment (Fig. 5). Thymidine uptake was 1.4× to 7.6× greater at 22°C than at 5°C for pellets collected from two species of salps (Fig. 5A, B). In addition, this rate generally increased at both temperatures over the course of the experiment, indicating a dramatic increase of the growth rate of the bacterial assemblage on the fecal material and/or an increase in the bacterial biomass of the pellets. Greater bacterial abundance in the fecal pellets at the end of the degradation study was confirmed with DAPI-stained preparations, but the large size and thickness of the pellets made quantification of these differences impossible.

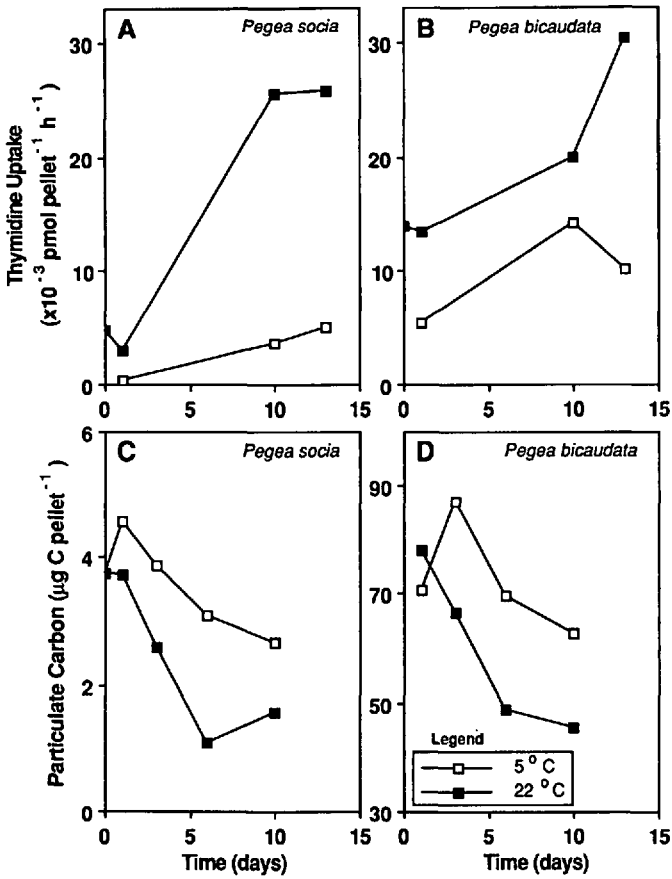

Figure 5. Uptake of tritiated thymidine (A,B) and loss of particulate carbon (C,D) by the microbial populations present in and on the fecal pellets of *Pegea socia* (A,C) and *Pegea bicaudata* (B,D) incubated at 5°C or 22°C.

Calculating accurate bacterial production rates is tenuous because it depends on an accurate factor for converting moles of thymidine incorporated to bacterial cells produced. In addition, thymidine uptake rates determined in this study must be taken as lower limit estimates of the actual rates because diffusion of the label into the pellet may be significantly decreased by the density of this material. Nonetheless, crude estimates of bacterial productivity can be calculated using the conversion factor of Fuhrman and Azam (1982). Based on this factor we estimate that the range of production values in the fecal pellets was 0.96–73.2 $\times$ 10^3 bacteria produced pellet^{-1} h^{-1}, but these absolute values must be considered suspect because of the complications mentioned above.

Losses of particulate organic carbon from the fecal material complemented increases in the rate of uptake of thymidine (Fig. 5C, D). Decreases in particulate

organic carbon concentration were greater for fecal pellets incubated at the higher temperature. These results are consistent with a more active bacterial assemblage in the fecal material incubated at 22°C. However, even after incubation for ten days at 22°C, the pellets remained physically intact and retained most of their particulate organic carbon and nitrogen and ash-free dry weight.

In contrast to the bacterial assemblage, abundances of autofluorescent (chlorophyll-containing) cells generally decreased during the ten-day incubation. All pellets had fewer autofluorescent cells at the end of the study relative to freshly produced pellets, and autofluorescence was noticeably less in pellets incubated at 22°C.

The large fecal pellets of these oceanic salps sank rapidly (range of initial rates = 300–2,470 m day^{-1}). Mean sinking velocities for the groups of pellets at the beginning and end of the ten-day incubation are given in Table 3. The average variance about the mean for all the measurements was high (CV = 18% of the rate), because of the variation in size and compactness of the pellets in each group. Overall, the sinking rates for all groups after ten days of degradation averaged 80% of the initial rates (CV = 12%). The largest decreases in the sinking rates were observed for the smallest fecal pellets (small *P. socia*). In general, all fecal pellets were so durable that repeated gentle handling of the pellets with a wide bore pipette for the measurement of their sinking rates did not cause any perceptible physical disruption of the pellets during the ten-day study.

c. Salp abundance and fecal pellet flux. Data on salp biomass were collected at stations in the western North Atlantic (Table 4). These stations were mostly in the Gulf Stream and transitional waters between the Gulf Stream and the Slope water. The densities of the salp populations were a typical range for these subtropical species, not nearly as high as in the "swarm" populations of some other species. The three species listed, *S. cylindrica, S. maxima* and *P. confoederata,* are commonly found in surface waters, and do not make diel migrations. For the estimates of fecal pellet flux in Table 4 we assumed continuous feeding and defecation at constant rates over 24 hours. For comparison, data from other studies on denser populations of salps are summarized in Table 5.

4. Discussion

a. Filtration efficiencies and fecal pellet composition. The filtration rates determined for oceanic salps in this study are within the range of rates determined for some of these species in previous investigations (Harbison and Gilmer, 1976; Harbison and McAlister, 1979; Madin and Cetta, 1984). Retention efficiencies of oceanic salps that have been examined previously decreased dramatically for particles <2.0 μm in size (Harbison and McAlister, 1979). The three microorganisms used in this study spanned this critical size range (Fig. 1, Table 1), and in our experiments also, retention of particles <2.0 μm in size was much less efficient than for larger particles. Retention

Table 4. Biomass and estimated fecal carbon production of salp populations collected in oblique tows to indicated depths with a 10 m^2 trawl net. Salp biomass is expressed as the average density of salps per 1000 m^3 (*) over the depth interval sampled (0–25 or 0–50 m), and as the number of salps per m^2 (**) for this same depth interval.

Sampling date	Station location	Depth (m)	Salp species present	Salp biomass Number $10^3 m^{-3}$*	Number m^{-2}**	mgC m^{-2}	Fecal flux mg C $m^{-2} d^{-1}$
5/30/82	30° 06′ N 73° 18′ W	25	*Salpa cylindrica*	8.5	0.21	0.02	0.01
5/31/82	36° 22′ W 73° 13′ W	25	*S. cylindrica*	88.4	2.21	0.14	0.04
5/31/82	30° 24′ W 73° 14′ W	25	*S. cylindrica*	35.2	0.88	0.14	0.04
2/25/83	26° 37′ W 73° 41′ W	50	*S. maxima*	1.2	0.06	0.05	0.01
2/26/83	26° 29′ W 73° 25′ W	50	*S. maxima, Pegea confoederata*	2.8	0.14	0.12	0.07
3/2/83	27° 04′ W 78° 02′ W	50	*S. cylindrica, P. confoederata, S. maxima*	1.2	0.06	0.15	0.05

Table 5. Estimates of salp fecal production based on population sampling or sediment trap collections. Depth is the sampling depth for population data, or trap depth for sediment trap data.

Location	Depth (m)	Salp species present	Salp biomass Number m^{-2}	Salp biomass mg C m^{-2}	Fecal flux mg C $m^{-2}d^{-1}$	Reference
Estimates from salp population data						
40° 12′ N 33° 00′ N	25	*Cyclosalpa pinnata*	0.2	1.6	0.14	Madin, 1982
ca 38° N 70° W	100	*Salpa aspera*	6500	909	8.5–137	Wiebe *et al.*, 1979
Estimates from sediment trap data						
Ligurian Sea	100	*Salpa fusiformis*	750	n.d	576	Morris *et al.*, 1988
	100	*Salpa fusiformis*	12.5	n.d.	18	Morris *et al.*, 1988
ca 45 N 165 W	200	*Salpa* spp.	n.d.	n.d.	10.5	Iseki, 1981
	900	*Salpa* spp.	n.d.	n.d.	6.7	Iseki, 1981
36–58 N 127–32 W	740	unknown	n.d.	n.d.	23	Matsueda *et al.*, 1986
	1440	unknown	n.d.	n.d.	6.7	Matsueda *et al.*, 1986
	4240	unknown	n.d.	n.d.	8.7	Matsueda *et al.*, 1986

efficiency for planktonic bacteria would, presumably, be even lower than for *Synechococcus* sp. because bacteria are, on average, considerably smaller (Ferguson and Rublee, 1976; Watson *et al.*, 1977). Nevertheless, salp fecal pellets did include bacteria and cyanobacteria (Fig. 2C). Previous investigations of salp feces have also shown that bacteria are present, usually in low numbers (Silver and Bruland, 1981; Pomeroy *et al.*, 1984).

The presence of digestion-resistant eukaryotic algae in the pellets is also consistent with previously published reports on the contents of salp feces (Silver and Bruland, 1981). The packaging of small algae into salp feces may contribute to the large number of nanoplankton-sized autofluorescent cells in rapidly sedimenting particles in the deep ocean (Silver and Alldredge, 1981; Silver and Bruland, 1981). The results of the incubations at 5°C and 22°C in the present study indicate that low temperature would act to preserve the autofluorescence of these cells during their descent. We have no evidence, however, that these cells are viable or growing in the pellets. The gradual decrease in autofluorescence during our ten-day incubations does not support the hypothesis of growth of phototrophic microorganisms in the pellets, but it also does not negate the possibility that algae were able to grow heterotrophically in the dark without producing chlorophyll. We did not incubate fecal pellets in the light, and have no results pertinent to the suggestion that phototrophs may benefit from being in a fecal pellet environment (Porter, 1973, 1976; Silver and Alldredge, 1981). The rapid sinking rates of salp pellets would presumably remove them from surface waters in a relatively short time, however, minimizing the potential benefits for algae.

Salp fecal pellets are composed predominantly of organic compounds related directly to the material that they ingest (Madin, 1982; Matsueda *et al.*, 1986). However, other elements were present in significant quantities in the fecal pellets of three species of salps (Table 2). The presence of calcium and strontium in fecal material presumably reflects the presence of skeletal structures of coccolithophorids and planktonic sarcodines (foraminifera, acantharia) in the diet of these organisms, while some of the magnesium may derive from chlorophyll in ingested phytoplankton. The presence of significant amounts of aluminum apparently reflects the filtration and defecation of suspended lithogenic particles (Wallace *et al.*, 1981) and aluminum adsorbed to particles and microorganisms.

b. Fecal pellet degradation. The succession of microbial populations that we observed in the incubation vessels containing fecal pellets was qualitatively similar to patterns described for fecal material of other zooplankton (Honjo and Roman, 1978; Pomeroy and Deibel, 1980; Jacobsen and Azam, 1984; Pomeroy *et al.*, 1984). The release of significant amounts of organic material from the pellets was evident from the growth of dense populations of bacteria and protozoa in the water of the incubation vessels. The surface of the pellets also supported luxuriant bacterial growth. However, the resulting breakdown of the fecal pellets in this study, and concomitant changes in their sinking rates, were strikingly different from results obtained by other investigators for neritic

species of salps and doliolids (Pomeroy and Deibel, 1980; Pomeroy *et al.*, 1984). Specifically, the fecal pellets of the species that we examined were much more resistant to physical and biological degradation than the feces of neritic species. Protozoa were shown to be important for the physical disruption of the less cohesive feces of neritic tunicates (Pomeroy and Deibel, 1980; Pomeroy *et al.*, 1984). It is probable that their activities were also instrumental for enhancing further bacterial degradation. But, for the most part, protozoa could not penetrate the dense pellets produced by the oceanic species in this study. The slow rates of decomposition that we observed may have been due, in part, to the exclusion of protozoa from the pellets.

Differences in pellet decomposition between neritic and oceanic species may also result from the different sizes of the salps and their fecal pellets. We found that the largest decrease in sinking rates occurred in fecal pellets produced by the smallest salps. The species studied by Pomeroy and his coworkers (*Thalia democratica, Dolioletta gegenbauri, Salpa cylindrica*) are smaller (except the solitary form of *S. cylindrica*) than any used in our investigation, and make much smaller fecal pellets. It is likely that microbial decomposition may be more important for small pellets. In addition to size differences, the consistency of the fecal material produced by salps in neritic and oceanic environments may differ as a result of the nature of the particulate food available. Pomeroy and Deibel (1980) described the feces produced by *Salpa cylindrica* as microscopically similar to flocculent detrital aggregates that were easily disaggregated by microbial activity. They did not specify whether the aggregate (8–12 mm length) or solitary (30–60 mm length) generation of *S. cylindrica* was studied; the two produce fecal pellets of different size. Fecal pellets produced by *S. cylindrica* in oceanic environments were amorphous in shape but were considerably more cohesive than marine snow particles from these environments (Caron *et al.*, 1982, 1986). These pellets remained intact throughout the ten-day degradation study (Fig. 3A, B).

The salp fecal pellets we examined did not appear to have a true, peritrophic membrane. However, the remnants of the mucous feeding net that passed through the gut produce a membranous matrix that appears very durable and resistant to microbial invasion and disaggregation, unless first physically disrupted. It is possible that oceanic species of salps produced fecal pellets containing a larger percentage of this material (relative to the food particles), resulting in a pellet that is initially more resistant to physical stress and microbial decomposition. This mucous matrix may be what Matsueda *et al.* (1986) interpreted as a peritrophic membrane around pellets found in their traps.

Extrapolation of the results of our laboratory-based studies on the degradation of salp fecal pellets to field situations is complicated by possible artifacts of incubations in small containers (Pomeroy *et al.*, 1984). It has been proposed that confinement in small volumes of water may enhance microbial degradation of feces. If this were the case, then the microbial degradation of salp feces *in-situ* might be even slower than the rates that we measured (decomposition rates ≈ 0.02–$0.04\ d^{-1} = 2.3$–$4.6 \times 10^{-7}\ s^{-1}$ of the

particulate organic carbon were calculated based on changes in the POC during the incubations). These rates are consistent, even conservative in some cases, when compared with the few field data that are available (Iseki, 1981; Cole *et al.*, 1987; Martin *et al.*, 1987; Matsueda *et al.*, 1986). For example, Iseki (1981) noted a decrease in the flux of organic carbon of salp fecal pellets in the North Pacific between 200 m and 900 m of 36%, and Matsueda *et al.* (1986) found a 71% decrease in flux from 740 to 1400 m (Table 5). Based on the sinking rates reported here and elsewhere (Bruland and Silver, 1981, Madin, 1982), salp pellets would take between 0.28 and 2.8 days to sink the 700 m between the traps set by Iseki or Matsueda *et al.*, losing, on average, from 0.56 to 5.6% of their carbon content to microbial degradation while sinking. Other mechanisms such as horizontal advection, midwater coprophagy or interception by other particles must account for the losses between sediment trap depths (Silver and Gowing, in prep.).

It has been demonstrated that the uptake of ^{3}H-thymidine is relatively specific for the bacterial assemblage, and its rate of incorporation is now employed routinely as an index of bacterial productivity (Fuhrman and Azam, 1982). However, the appropriate factor for converting moles of thymidine taken up by bacterial cells to the production of bacterial cells has been increasingly questioned in recent years (Moriarty, 1984). For this reason, and because of the previously mentioned problem of diffusion of the label into the fecal pellets, our conclusions concerning bacterial productivity are based on relative differences in the rate of uptake of ^{3}H-thymidine between bacteria in the fecal pellets and surrounding seawater, or between fecal pellets incubated at different temperatures.

The rate of uptake of the label by salp fecal pellets generally increased during the ten-day incubation period (Fig. 5), indicating an increase in the growth rate of the bacterial population present in and on the pellets, and/or an increase in bacterial biomass. Microscopical observations of DAPI-stained preparations confirmed that more bacteria were indeed present in and on the fecal pellets at the end of the incubation. These results differ from some other decomposition studies in which bacterial abundance increased during the first 24 hrs but then decreased (Jacobsen and Azam, 1984; Pomeroy and Deibel, 1984). These differences were presumably a result of the inability of bacterivorous protozoa to penetrate the salp pellets and consume the bacteria. Our results are, however, consistent with the theory that much of the decomposition of fecal pellets is mediated by bacteria that are passed through the gut alive and are contained within the pellet, rather than from the outside by colonizing bacteria (Gowing and Silver, 1983).

A significant depression of microbial decomposition of fecal pellets at low temperature has been noted previously (Honjo and Roman, 1978). Thymidine uptake in our study was greater at 22°C than at 5°C, perhaps indicating a more active bacterial community in pellets at the warmer temperature. This conclusion was supported by a more rapid decrease in particulate carbon from fecal pellets incubated at 22°C (Fig. 5C, D). However, bacterial activity was not reflected in a consistent pattern in the

C:N ratio. Bacterial C:N ratios are low (≈5; Nagata, 1986; Lee and Fuhrman, 1987), and the C:N ratios of the fecal pellets should have decreased during the study if bacterial biomass constituted a significant fraction of the total carbon and nitrogen, as has been suggested with some copepod fecal pellets (Turner, 1979). This was not the case with the salp feces, because approximately ½ of the groups of fecal pellets showed increases in their C:N ratios over the ten-day study.

c. Removal of organic carbon and lithogenic material. The production of a salp fecal pellet in the open ocean must, on average, be a rare event (Table 4). However, a relatively large amount of organic material is contained in a single pellet; even the smallest pellets produced by oceanic salps are quite large compared to fecal pellets of copepods. Because of their size, salp fecal pellets sink rapidly compared to the pellets of most other grazers. A rapid mechanism for the vertical flux of particulate material to the deep ocean has been hypothesized, based on the presence of short half-lived radionuclides in the deep ocean (Osterberg *et al.*, 1963), and on observations of the seasonality of sedimentation in the deep ocean (Deuser and Ross, 1980; Honjo, 1982). It is likely that salp fecal pellets play a role in this process. However, the extent to which these pellets are intercepted and repackaged in the water column is presently unknown. One point is exceedingly clear from the results of our study however—if sinking salp fecal pellets are not slowed by organisms or other particles, microbial decomposition alone will not result in significant loss of the organic material in these pellets during the time they take to reach the deep ocean.

Several instances have been cited in which the flux of salp fecal pellets was the major mechanism for the transport of organic material to the deep ocean (Table 5; also Wiebe *et al.*, 1979; Dunbar and Berger, 1981; Iseki, 1981; Matsueda *et al.*, 1986; Bathmann, 1988; Morris *et al.*, 1988). These situations involved sporadic "blooms" of salps. A determination of the importance of the much lower "background" abundances of salps in the open ocean will require much more work. Our estimates of salp fecal pellet carbon flux (Table 4) are similar to some recent estimates of the flux of particulate carbon to the deep oligotrophic North Atlantic (Deuser and Ross, 1980; Honjo, 1980). Recent modeling studies also have demonstrated the potential importance of oceanic salps for the vertical flux of biogenic material (Andersen and Nival, 1988; Michaels and Silver, 1988). It is not certain, however, that sediment traps will quantitatively detect these rare events, or that salp fecal pellets would not be intercepted before reaching a trap. Although these studies indicate a potentially important contribution of salps to the flux of material in the deep ocean, their importance in truly oligotrophic environments remains largely conjectural.

Similarly, the relative contribution of salp fecal pellets and the fecal pellets of other organisms to total flux and to the flux of specific elements in the ocean remains unclear. Copepod fecal pellets and the fecal material of other organisms undoubtedly contribute to the flux of material to the deep ocean (Honjo and Roman, 1978; Dunbar and Berger, 1981; Urrere and Knauer, 1981). However, the ability of salps to filter extremely small

particles from seawater indicates that they may be the major mechanism for the packaging and sinking of particles less than 5 μm in size. Significant correlations have been observed between the flux of biogenic material (organic carbon) and lithogenic material (e.g. aluminum) associated with the smallest particles in the ocean (Honjo, 1982; Deuser *et al.*, 1983; Wallace *et al.*, 1981). Our data on the aluminum content of salp fecal pellets (Table 2) support the hypothesis that these organisms can contribute to the flux of small particles to the deep ocean. Sinking of these pellets may help explain the relatively high ratio of aluminum flux to organic carbon flux in the deep North Atlantic (Al:C $\approx$0.28, from Fig. 1 in Deuser *et al.*, 1983).

Salps combine the unique features of high filtration rates, efficient grazing on nearly the entire size spectrum of suspended particles in the ocean, and the production of dense, rapidly sinking fecal pellets. From our results, it appears that little microbial degradation of these fecal pellets occurs while they are sinking to the deep ocean. This result is due not so much to a slow decomposition rate for these pellets, but to the cohesive nature of the pellets and their rapid sinking rates. We hypothesize that grazing and defecation by salps plays an important role in the vertical transport of organic material and inorganic elements to deep water in both coastal and oceanic regions.

Acknowledgments. The authors gratefully acknowledge the assistance of Catherine Cetta, Gregg Dietzmann and Jennifer Purcell in the collection of specimens, and Anthony F. Michaels for helpful comments on the manuscript. G. Deitzmann counted the trawl samples and Bonnie Woodward performed the CHN analysis for the determination of particulate carbon and nitrogen. We also thank Michael Bacon and Alan P. Fleer of WHOI, and A. Francis DiMeglio, Director, and the staff of Rhode Island Nuclear Science for the elemental analysis on salp fecal pellets supplied by LPM. This work was supported by NSF Grants OCE-8024441, OCE-8112991 and OCE-860776, Ocean Industry Program Grant 4473 and the Woods Hole Oceanographic Education Program. Contribution number 7013 of the Woods Hole Oceanographic Institution.

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Received: *9 February, 1989;* revised: *18 July, 1989.*