Zooplankton feeding ecology: contents of fecal pellets of the appendicularian *Oikopleura vanhoeffeni*

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ABSTRACT: Using scanning electron microscopy, we examined the undigested contents of fecal pellets from hand-collected *Oikopleura vanhoeffeni* Lohmann. Our goals were to compare the size of food in fecal pellets to the pore size of the incurrent filters, and to compare the size and type of food in fecal pellets to the size and type of food available in the environment. We collected *O. vanhoeffeni* in coastal waters of Newfoundland in May 1983, during the spring diatom bloom, and in January 1984, when diatoms were rare. Because the pore size of the incurrent filters was large ($\bar{X} = 169 \times 88 \mu\text{m}$), *O. vanhoeffeni* was able to ingest the large, armored cells and diatom chains present during the spring bloom. The largest cells in fecal pellets were smaller than the mean pore width of the incurrent filters. The largest single cell in fecal pellets was the silicoflagellate *Distephanus speculum* (48 μm in diameter). Many tabular chains of pennate diatoms in fecal pellets were $>40 \mu\text{m}$ long. Spinous *Chaetoceros socialis* were ingested. In January, the fecal pellet contents were dominated by coccoliths along with common dinoflagellates and diatoms. Each fecal pellet was surrounded by a peritrophic membrane.

INTRODUCTION

Appendicularia are gelatinous, transparent zooplankters that use external and internal mucous nets to feed on a wide size range of suspended particles (Alldredge 1977, 1981). The complex apparatus containing the external mucous nets is known as the 'house'. Oikopleuridae is a group of appendicularians of cosmopolitan distribution that is abundant in neritic waters. Feeding mechanism and behavior of Oikopleuridae have been described in general and will not be reviewed here (Alldredge 1977, Alldredge & Madin 1982). Most oikopleurids draw water into the house through a pair of coarse, incurrent mucous filters (an exception is *Oikopleura longicauda* which has no incurrent filters: Alldredge 1977). The pore size of the incurrent filters determines the upper size limit of food particles available for ingestion (Alldredge 1975).

Since the pioneering work of Lohmann (1909), it has been accepted that the Oikopleuridae ingest primarily

ultraplankton $<3 \mu\text{m}$ in diameter and nanoplankton 3 to 20 μm in diameter. Reports of the diet of oikopleurids rarely include the description of net-phytoplankton $>20 \mu\text{m}$ in diameter. The few large cells that have been reported were found in lower proportion in fecal pellets than in the environment (Alldredge 1975, Jansa 1977). Chain-forming or spinous cells were excluded by the incurrent filters (Lohmann 1909, Alldredge 1977). However, these observations were of oikopleurids of small and medium body size from tropical and temperate waters. We know little of the diets of larger oikopleurids, and nothing of the diet of the large, abundant, cold ocean oikopleurid *Oikopleura vanhoeffeni*. Given the size of *O. vanhoeffeni* (adult trunk length 4 to 7 mm), and the pore size of its incurrent filters ($\bar{X} = 169 \times 88 \mu\text{m}$), it is likely that the size composition of its diet differs from that of the smaller, well-studied *O. dioica* (adult trunk length of 0.8 to 1.0 mm), with an incurrent filter pore width of 20 to 25 μm (Galt 1972).

Physiological information on *Oikopleura vanhoeffeni* is lacking even though it is one of the dominant

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zooplankters of coastal Newfoundland waters (Udvardy 1954). During the spring diatom bloom of 1983 (Apr–May), we discovered large, intact pennate diatoms in fecal pellets of hand-collected *O. vanhoeffeni*. We used the scanning electron microscope (SEM) to investigate the undigested contents of fecal pellets of *O. vanhoeffeni*, both during the spring diatom bloom and in mid-winter during flagellate dominance. Our goals were: (1) to compare the size of phytoplankton in fecal pellets to the pore width of the incurrent filters, and (2) to compare semi-quantitatively the size and species composition of phytoplankton in fecal pellets to phytoplankton available in the environment. This approach has been used successfully to observe the feeding habits of both gelatinous and crustacean zooplankton (Silver & Bruland 1981, Turner 1984a–c). There has been only one study of oikopleurid feeding that compared ingested phytoplankton to phytoplankton available in the environment (Alldredge 1975). There was no statistically significant difference in the size of the largest food particle on the feeding filter, in the gut, or in fecal pellets (Alldredge 1975). Therefore, we decided to examine the contents of fecal pellets.

MATERIAL AND METHODS

We collected *Oikopleura vanhoeffeni* in 400 ml glass jars by hand using SCUBA. Appendicularians were collected in Logy Bay, Newfoundland, in water depths of 5 to 15 m. At the same time and depth, 10 l water samples were taken, from which duplicate subsamples (125 ml) were drawn to be fixed with Utermöhl's iodine for phytoplankton cell counts (Utermöhl 1958). Two collections were made during the spring diatom bloom (2 and 6 May, 1983), and one collection was made in mid-winter when diatoms were rare (24 January, 1984). Water temperature was 0.6 °C in May and –1.1 °C in January. Salinity was 31.5 ‰ in January, which is typical of Logy Bay throughout the year (Kendall 1980). Appendicularians and houses were not fixed in the field because we wished to first measure live individuals, and unfixed houses and fecal pellets.

Jars containing appendicularians were placed in a flow-through seawater bath in the laboratory within 30 min of collection. Water temperature in the bath was 1.0 to 2.0 °C higher than that at the depth of collection. Over the next 12 h appendicularians and houses were removed from each jar to collect fecal pellets. Many of the individuals were still feeding in the house in which they were collected. However, a few specimens had made as many as 3 houses since collection. Because the house of *Oikopleura vanhoeffeni* shrinks and becomes opaque quickly after being abandoned (1 to 2

h), it was possible to rank the houses in a jar in chronological order. Since fecal pellets remain trapped within the house, it was possible to determine the relative ages of fecal pellets in each jar. We found no qualitative difference in the contents of fecal pellets between the house in which the appendicularian was collected and houses produced in the laboratory for up to 12 h after collection.

Houses were teased apart with fine-tipped forceps, and fecal pellets collected individually with a Pasteur pipette. Each fecal pellet was either fixed immediately in 5 % borate buffered formaldehyde in filtered seawater (0.8 µm membrane), or was aged in filtered seawater at room temperature for 36 to 48 h before fixing so that bacteria could decompose the membrane surrounding the pellet. Using a stereomicroscope with ocular micrometer, fecal pellet length and width was measured to the nearest 12.5 µm, and trunk length, from mouth to the posterior margin of the stomach, and tail length was measured to the nearest 25 µm. The pore length and width of the incurrent filters was measured to the nearest 7.5 µm, using a compound microscope with phase contrast and ocular micrometer.

Fixed pellets for SEM examination were placed individually in filtered seawater, and were drawn onto Whatman GF/C glass fiber filters. Filters with attached fecal pellets were immersed in distilled water to eliminate salt, dehydrated in a graded ethanol series, critical-point dried, coated with gold:palladium, and examined with an ISI-30 SEM at 15 kV (Turner 1984a–c). Entire visible sides of fecal pellets were examined and recognizable contents were photographed. The 31 micrographs presented here (25 % of those taken) are representative of fecal pellet contents on all sampling dates.

Duplicate 50 ml subsamples of sea water were settled for a minimum of 24 h for inverted microscope counts of available food particles (phase contrast). Small cells (< 30 µm) were measured at 500 × magnification to the nearest 0.5 µm. Sufficient 1 cm transects were made until at least 30 individuals of the 3 dominant taxa were counted, resulting in a 95 % confidence interval of ±30 % of the count (Lund et al. 1958). Large cells were measured at 125 × magnification to the nearest 1.9 µm. One-half of the chamber was covered in counting large cells (subsample volume of 25 ml). Small cells (< 5 µm) that appeared featureless were classified as unidentified unicells, and all other small cells that appeared featureless but seemed to contain chloroplasts were classified as unidentified naked flagellates and monads. Dominant diatoms and dinoflagellates were identified to genus and species when possible. Cell volume was calculated by approximating cell shape to that of simple geometric solids (e.g. right cylinder, prolate spheroid, sphere).

RESULTS

Available phytoplankton cells

Unicells $<1.5 \mu\text{m}$ in diameter comprised 35 to 90 % of total cell number in all samples. Because of difficulty identifying these cells, and because of their small contribution to cell volume, they were not included in plots of frequency distribution of cell type and size (Fig. 1 & 2).

There was a marked difference in the composition and size frequency distribution of phytoplankton cells between May and January. On 2 May, the samples were dominated by small pennate diatoms which formed long tabular chains (Fig. 1). These pennate diatoms had a mean cell length of $19 \mu\text{m}$ (Table 1); they were primarily *Nitzschia grunowii* Hasle and *N. cylindrus* (Grunow) Hasle. On 6 May cell volume was dominated by the solitary pennate diatom *Nitzschia* sp. (Fig. 1) because of its larger mean size ($32 \times 7 \mu\text{m}$; Table 1). On both days the subdominant component of cell volume was the large centric diatom *Thalassiosira* sp. which was 25 to $29 \mu\text{m}$ in diameter (Fig. 1; Table 1). Total cell concentration and volume was similar on both sampling days in May (Table 1). In all samples collected in May diatoms made up 63 to 83 % of total cell number (excluding small unicells), and 81 to 98 % of total cell volume.

In January samples were numerically dominated (99 % of total number) by small monads and flagellates (Fig. 1) about $3 \mu\text{m}$ in diameter (Table 1). Cell volume

Fig. 2. Relative frequency of all phytoplankton taxa available for food of *Oikopleura vanhoeffeni* in 6 size classes from 0 to 5 to 80 to $160 \mu\text{m}$ least cell dimension (i.e. width or diameter). Vertical lines represent range of duplicate cell counts

Fig. 1. Relative frequency (% of total number and volume) of the dominant phytoplankton taxa available for food of *Oikopleura vanhoeffeni* on 3 sampling dates

was dominated (39 % of total volume) by larger flagellates and Chrysophyceae (Fig. 1), $5 \mu\text{m}$ in diameter (Table 1). Unarmored dinoflagellates made a codominant contribution to cell volume (Fig. 1). *Nitzschia grunowii* and *N. cylindrus* were rare, but the solitary *Nitzschia* sp. had a larger cell size than in May ($36 \mu\text{m}$ long; Table 1), and so diatoms made up 30 % of total cell volume (chains + solitary cells; Fig. 1). Total cell concentration was much higher than in May because of the dominance of flagellates, but total cell volume was an order of magnitude lower (Table 1).

Small, spinous *Chaetoceros* sp. were common on 2 and 6 May (Fig. 1), while the large pennate diatom *Rhizosolenia* sp. was found in concentrations of 2 to 3 ml^{-1} on both days, comprising 2 to 15 % of total cell volume. There were no coccolith plates or whole coccolithophores in any of the samples from May.

In January dinoflagellates were only slightly more concentrated than in May (4 to 11 ml^{-1}), but they comprised 29 % of total cell volume because of the paucity of diatoms (7 to 14 ml^{-1}). There were no *Rhizosolenia* sp. or *Chaetoceros* sp. present in January. However, there were some large pennate diatoms

Table 1. Dominant available food items for *Oikopleura vanhoeffeni* on 3 sampling dates

Date	Dominant taxon	Cell length (µm)	Cell width (µm)	Cell diameter (µm)	Total cell concentration* (No. ml ⁻¹)	Total cell volume (µm ³ ml ⁻¹)
2 May 1983	<i>Nitzschia</i> sp. (chains)	19	7	–	1983	6.0 × 10 ⁶
	<i>Nitzschia</i> sp. (solitary)	27	7	–		
	<i>Thalassiosira</i> sp.	–	–	29		
	<i>Chaetoceros</i> sp.	–	–	7		
	Unid. flagellates and monads	–	–	3		
6 May 1983	<i>Nitzschia</i> sp. (chains)	19	7	–	1738	4.8 × 10 ⁶
	<i>Nitzschia</i> sp. (solitary)	32	7	–		
	<i>Thalassiosira</i> sp.	–	–	25		
	<i>Chaetoceros</i> sp.	–	–	7		
	Unid. flagellates and monads	–	–	4		
	Unid. large flagellates and Chrysophyceae	–	–	7		
24 Jan 1984	<i>Nitzschia</i> sp. (chains)	21	8	–	3506	2.3 × 10 ⁵
	<i>Nitzschia</i> sp. (solitary)	36	11	–		
	Unid. flagellates and monads	–	–	3		
	Unid. large flagellates and Chrysophyceae	–	–	5		
	<i>Gymnodinium</i> sp.	–	–	13		
	<i>Coccolithus pelagicus</i>	–	–	10		
* (Less small unicells <1.5 µm Ø)						

present (29 to 39 µm long) that were absent in May. Silicoflagellates 28 µm in diameter made up 2% of total cell volume, and coccoliths 4 µm in diameter were common (214 to 286 × ml⁻¹). No intact coccolithophores were found in any sample preserved with Utermöhl's iodine.

The size frequency distributions show that in May the most frequently occurring cells were in the 10 to 20 µm size class (Fig. 2). On 2 May the cell-volume frequency distribution was dominated by large cells in the 20 to 40 µm size class, while on 6 May cell volume dominance had shifted to a smaller size class, 10 to 20 µm long (Fig. 2). These distributions do not include the length of tabular chains of pennate diatoms. In January

the size frequency distribution showed the importance of small cells in the 0 to 5 µm size class (Fig. 2). The cell-volume frequency distribution was more even than in May, with relatively equal volume in size classes from 5 to 40 µm.

Contents of fecal pellets

The contents of fecal pellets reflected the type and size of available food particles. The fecal pellets collected during the spring diatom bloom were dominated by pennate and centric diatoms, while those collected in January were dominated by coccoliths and dinoflagellates and contained fewer diatoms.

Fecal pellets collected on 2 May contained a mixture of pennate and centric diatoms (Fig. 3). Predominant in the pellets were tabular chains of *Nitzschia grunowii*

and *N. cylindrus* (Fig. 3a, b). Also ingested was the centric diatom *Thalassiosira* sp. Although *Thalassiosira* sp. was often broken into fragments (Fig. 3c, d),

Fig. 3. *Oikopleura vanhoeffeni*. Contents of fecal pellets produced on 2 May 1983. Pellet contents reflect feeding in the field. (a) Pennate diatoms (PD), mostly *Nitzschia grunowii*; (b) pennate diatoms (PD), including *N. grunowii*, *N. cylindrus* and *Thalassiosira* sp. (T); (c) pennate diatom (PD) and a fragmented *Thalassiosira* sp. (T); (d) fragments of *Thalassiosira* sp. (T); (e) *Chaetoceros socialis* (Ch); (f) small centric diatom (SC). Note threads of pharyngeal mucus, particularly in (a) to (d)

intact cells in pellets were about 30 μm in diameter, similar to measurements made of available *Thalassiosira* sp. (Table 1). The unidentified centric diatoms were small, approximately 2 to 3 μm in diameter (Fig. 3f). Spinous cells (*Chaetoceros socialis* Lauder) passed through the incurrent filters of these large houses (Fig. 3e). *C. socialis* in fecal pellets were 6 to 7 μm wide, which agrees with measurements of available *Chaetoceros* sp. (Table 1). Few of the small pennate diatoms had crushed valves (Fig. 3b). There were small unicells in these fecal pellets (Fig. 3a, f). All cells were enmeshed in mucous fibers. These fibers were the remains of the pharyngeal mucous net.

Long tabular chains of pennate diatoms and large centric diatoms also were contained in fecal pellets collected on 6 May (Fig. 4 & 5). *Nitzschia cylindrus* were small (6 to 10 μm long) and intact (Fig. 4a, 5a, b). There was a second type of tabular chain in these fecal pellets (Fig. 4b, c), with much larger cells (27 μm long) than those of 2 May (Fig. 3). Also, a large, singular,

pennate diatom was common on 6 May (*N. seriata*?, Fig. 5c, d). There were several centric diatoms of both small and medium size that were fragmented (Fig. 5c), and *Thalassiosira gravis* Cleve 30 μm in diameter that were intact (Fig. 5e). A few coccoliths were observed in May (Fig. 5d). There were no silico-flagellates or *Rhizosolenia* sp. in fecal pellets produced on 6 May.

Fecal pellets collected on 24 January were dominated by coccoliths and flagellates, reflecting the change in the composition of the phytoplankton community since the previous May (Fig. 6 & 7). Coccoliths, silicoflagellates, and dinoflagellates were relatively more important because of the decrease in the abundance of diatoms. *Coccolithus pelagicus* (Wallich) Schiller was about 8 to 10 μm in diameter (Fig. 6c), and the individual coccoliths were 4.5 μm in diameter (Fig. 6a, b). Large silicoflagellates – *Distephanus speculum* (Ehrenberg) Haeckel – passed through the incurrent filters (Fig. 6d). This specimen was 48 μm from spine

Fig. 4. *Oikopleura vanhoeffeni*. Contents of fecal pellets produced on 6 May 1983. Pellet contents reflect feeding in the field. (a) Chain of pennate diatoms (PD), probably *Nitzschia cylindrus*; (b) chain of unidentified pennate diatoms (PD); (c) chain of pennate diatoms (PD) and *Thalassiosira* sp. (T); (d) intact *Thalassiosira* sp. (T). Note threads of pharyngeal mucus, particularly in (d)

Fig. 5. *Oikopleura vanhoeffeni*. Contents of fecal pellets produced on 6 May 1983. Pellets were produced while the appendicularian was feeding in natural seawater in the laboratory within 12 h of collection. (a) Chain of pennate diatoms (PD) probably *Nitzschia cylindrus*; (b) pennate diatom (PD) (c) pennate diatom (PD) probably *N. seriata* and *Thalassiosira* sp. (T); (d) pennate diatom (PD) possibly *N. grunowii* and unidentified coccolith (Co); (e) and (f) *Thalassiosira* sp. (T)

tip to tip, and 24 µm in diameter. There were many dinoflagellates in these fecal pellets, most of which were intact (Fig. 6e, f). The *Prorocentrum* sp. in Fig. 6e was about 10 × 8 µm, and the *Peridinium* sp. in Fig. 6f was 35 × 30 µm.

The pennate and centric diatoms that were present in fecal pellets on 24 January were different from those present the previous May (Fig. 7). There were small pennate diatoms 6 to 7 µm long that formed short chains (*Achnanthes* sp.: Fig. 7a), and small, uniden-

Fig. 6. *Oikopleura vanhoeffeni*. Contents of fecal pellets produced on 24 January 1984. Some pellets were produced by this individual in the field, and some were produced after feeding in natural sea water in the laboratory. (a) and (b) Coccoliths; (c) semi-intact coccolithophore (arrow) with the cytoplasm and a portion of the outer covering of coccoliths missing (view is from the interior of the cell to the interior surface of interlocking coccoliths on the back side of the cell); (d) silicoflagellate (arrow); *Distephanus speculum* v. *regularis*; (e) *Prorocentrum* sp. (arrow); (f) *Peridinium* sp.

tified centric diatoms 3 to 4 μm in diameter (Fig. 7e, f). There was a large araphid diatom which was 35 μm long (Fig. 7b, d). Also, there were small, solitary pen-

nate diatoms that were about 8 μm long (*Nitzschia* sp.? Fig. 7c).

All fecal pellets from May and January were sur-

Fig. 7. *Oikopleura vanhoeffeni*. Contents of fecal pellets produced by the same individual as in Fig. 6. (a) Pennate diatoms (PD), probably *Achnanthes* sp., and a small centric diatom (SC); (b) pennate diatom (PD); (c) small pennate diatom; (d) pennate diatoms (PD); (e) small intact centric diatom <4 µm in diameter; (f) small centric diatoms (SC), <6 µm in diameter

rounded by a membrane (Fig. 8). After 24 to 36 h at room temperature parts of the membrane were broken and its surface was populated by rod-shaped bacteria forming colonies 6 to 10 µm long (Fig. 8a).

DISCUSSION

Appendicularians seem to be true suspension feeders, collecting food particles by pumping water

Fig. 8. *Oikopleura vanhoeffeni*. Contents of fecal pellets produced by the same individual as in Fig. 6 & 7. Note peritrophic membrane (PM) partially covering pellet contents composed primarily of coccoliths, threads of pharyngeal mucus, and diatoms

through a series of mucous filters. They do not positively select particles from a specific size range, but do exclude particles larger than the pore size of their incurrent filters (Alldredge 1975, 1977). Little is known of the physiology or ecology of the cold ocean appendicularian *Oikopleura vanhoeffeni*. We have

examined the undigested contents of fecal pellets of *O. vanhoeffeni* to compare to the pore size of its incurrent filters, and to compare to available food particles.

The mean pore size of the incurrent filters of a subsample of juvenile and adult *Oikopleura vanhoeffeni* collected in May and January was $169 \pm 21 \times 88 \pm 9 \mu\text{m}$ ($\pm 95\%$ CI; $n = 20$; range = 112 to 292×50 to $123 \mu\text{m}$). The sizes of appendicularians and fecal pellets shown in Fig. 3 to 8 are summarized in Table 2. Although larger specimens had filters with larger pore widths, there was no statistically significant relation between pore width and trunk length or maturity stage. This is the largest incurrent filter pore width yet reported for any oikopleurid. In a study of 6 oikopleurid species, Alldredge (1977) found the incurrent filter pore width to vary from 13 ± 5 to $54 \pm 9 \mu\text{m}$ ($\pm$ SD). There was no statistically significant relationship between pore width and trunk length (Alldredge 1977).

The contents of fecal pellets of *Oikopleura vanhoeffeni* reflect the type and size frequency of available food particles. Alldredge (1975) found that the fecal pellets of 6 species of tropical oikopleurids contained predominantly bacteria, small unidentified particles, and naked flagellates, with secondary importance of dinoflagellates of moderate size and coccolithophores. Large dinoflagellates and diatoms occurred in much lower proportion than their occurrence in the environment, and particles $>6 \mu\text{m}$ in size were excluded by all species to some extent. We found that the largest particles in the fecal pellets of *O. vanhoeffeni* were smaller than the mean pore size of the incurrent filters. We also established that fecal pellet contents were dominated by medium sized diatoms and intact tabular chains of small pennate diatoms. Extremely long pennate diatoms, such as *Rhizosolenia* sp. (300 to 400 μm long), were ingested infrequently.

Irregularly shaped or spinous cells have been reported not to be consumed by oikopleurids (Lohmann 1909, Alldredge 1975). Lohmann (1909) found the gut contents of *Oikopleura albicans* to be colorless and $<3 \mu\text{m}$ in diameter, and to include skeletal parts of Peridineae, Diatomeae, and Coccolithophoridae. The largest particle Lohmann found in the gut was 20 μm in diameter, while the largest particle found by Zaika (1972) in the gut of *O. dioica* was 40 μm in diameter. Lohmann (1909) did not find the remains of the large and/or chain-forming diatoms, *Chaetoceros* sp., *Skeletonema* sp., *Bacteriastrium* sp., and *Rhizosolenia* sp. in fecal pellets. However, Zaika (1972) found various dinoflagellates and diatoms in the gut of *O. dioica*, including *Peridinium* sp., *Thalassiosira* sp., and *Distephanus* sp. We observed *Chaetoceros socialis* with spines attached, and long tabular chains of pennate diatoms in the fecal pellets of *O. vanhoef-*

Table 2. *Oikopleura vanhoeffeni*. Body size and fecal-pellet size in Fig. 3 to 8

Figure	Trunk length (μm)	Tail length (μm)	Pellet length (μm) [*]		Pellet width (μm) [*]
3	1969	7438	581 $\pm$ 24	(n = 4)	153 $\pm$ 16
4	2100	8500	544 $\pm$ 27	(n = 4)	169 $\pm$ 44
5	—	—	438 $\pm$ 14	(n = 4)	103 $\pm$ 17
6–8	3300	12875	900	(n = 1)	275

^{*} Mean $\pm$ 95% confidence interval
 — Data not available

feni (Fig. 3 to 7). Thus, *O. vanhoeffeni* could have a major impact on large, armored cells during the spring diatom bloom in cold ocean waters. The largest single particle we observed in fecal pellets of *O. vanhoeffeni* was the silicoflagellate *Distephanus speculum*, which was 48 μm from spine tip to tip. The longest tabular chains of pennate diatoms in fecal pellets were >40 μm long.

The nutritional value of diatoms and thecate dinoflagellates to pelagic tunicates has not been investigated. The frequency of intact cells in the fecal pellets of *Oikopleura vanhoeffeni* was remarkable (Fig. 3 to 8), but was not surprising, since oikopleurids have no chewing or grinding mouthparts. As Alldredge (1975) found, coccolith plates appeared to be intact and to have undergone no solution. Examination of fecal pellets from salps using transmission electron microscopy have shown many intact diatoms with no cytoplasm, indicating a high frequency of digestion and leaching of cell contents (Silver & Bruland 1981). Because of similarity in feeding mechanism and in the type of food consumed by salps and appendicularians, we suspect that *O. vanhoeffeni* also extracts diatom cytoplasm from intact cells. However, the digestive enzymes of appendicularians have not been investigated.

The fecal pellets of *Oikopleura vanhoeffeni* were surrounded by a 'membrane' (Fig. 8), which we assume is analogous in function to the peritrophic membrane which surrounds the fecal pellets of planktonic copepods (Honjo & Roman 1978, Turner & Ferrante 1979). This membrane was continuous in freshly produced fecal pellets, but was rapidly decomposed by bacteria when the pellets were incubated at room temperature (Fig. 8). Apparently the fecal pellets of other pelagic tunicates are surrounded by a membrane (Silver & Alldredge 1981, Madin 1982), although these membranes have not been described.

In January, the fecal pellets of *Oikopleura vanhoeffeni* contained many coccoliths (*Coccolithus pelagicus*; Fig. 6 & 7). Because of the high clearance rates of *O. vanhoeffeni* (up to 15 l d⁻¹; Deibel unpubl.), and the high fecal pellet production rates (3 to 4 h⁻¹ at 2 °C:

Deibel unpubl.), a single *O. vanhoeffeni* can capture and package great numbers of coccolithophores into fecal pellets each day. Since *O. vanhoeffeni* is usually present and is often dominant in Newfoundland waters (up to 450 m⁻³; Davis 1982), its populations may have a significant impact on the transport of calcite to the benthos. This role has been proposed for other pelagic tunicates (Gowing & Silver 1983).

It is likely that the incurrent filters of *Oikopleura vanhoeffeni* will exclude few of the common phytoplankton of Newfoundland coastal waters. The pore width of the incurrent filters was greater than the minimum dimension (i.e. diameter or width) of all of the available phytoplankton we identified (Table 1). However, the spatial orientation of the largest cells or tabular chains is probably important if they are to pass through the incurrent filters. We have investigated the undigested contents of fecal pellets that were detected by SEM. It is likely that unarmored cells not detected by SEM comprise a large portion of fecal pellet contents. Our results indicate that because of the large pore size of the incurrent filters of *O. vanhoeffeni*, both large armored cells and small unarmored cells should be included in future considerations of the diet.

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