SEASONAL CHANGES IN THE CHEMICAL AND PHYSICAL CHARACTERISTICS OF CALANUS FINMARCHICUS AND OIKOPLEURA VANHOEFFENI FECAL PELLETS

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SEASONAL CHANGES IN THE CHEMICAL AND PHYSICAL CHARACTERISTICS OF *CALANUS FINMARCHICUS* AND *OIKOPLEURA VANHOEFFENI* FECAL PELLETS

BY

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ABSTRACT

Fecal pellets from Oikopleura vanhoeffeni and Calanus finmarchicus were analyzed in the spring, summer, fall and winter to determine if there were changes in their physical (size, phytoplankton content & density) or chemical (particulate organic carbon & particulate silicate) characteristics. Changes in phytoplankton content due to seasonal succession were observed in both feces types which resulted from a change from a diatom based food chain in the spring to one based on the microbial loop in the fall. Changing phytoplankton content also resulted in seasonal changes in the dynamic density of the fecal pellets, due to the differential compactness of the component particles. Changes in the dynamic density resulted in changes in the potential of both fecal pellet types to exit the upper mixed layer and contribute to vertical nutrient and particle flux.

Current literature equations used for predicting the settling velocity of fecal pellets gave correct trends for my data but overestimated the actual rates by 2-100 times. Empirical settling velocity equations were developed for the two fecal types based on their physical characteristics. The resulting equations for both C. finmarchicus and O. vanhoeffeni were modified Stokes equations. For O. vanhoeffeni, the settling velocity (W_s) can be expressed as:

$$W_s = .002 \frac{1}{\mu} (\rho_s - \rho) g D_n^{2.0} \left(\frac{L}{D}\right)^{.331}$$

and for C. finmarchicus as:

$$W_s = .028 \frac{1}{\mu} (\rho_s - \rho) g L^{1.8} \left(\frac{L}{D}\right)^{-1.759}$$

where μ is the viscosity of the water, ρ_s is the density of the fecal pellet, ρ is the density of the water, g is gravity (981 cm s^{-1}, D_n is the diameter of an equivalent sphere, and L and D are the length and diameter of the fecal pellet. Using these equations, seasonal settling velocities were calculated for the copepod fecal pellets. Fall C. finmarchicus fecal pellets had the fastest settling velocities (25-95 m day^{-1}), indicating that these feces have a greater potential in contributing to the nutrient flux than do spring feces (7-35 m day^{-1}). The higher measured sinking velocities for O. vanhoeffeni fecal pellets suggests that they are more likely to leave the upper mixed layer and contribute to the nutrient flux than are copepod feces.

The decay rate for C. finmarchicus fecal pellets was the same in the spring, summer and fall in the field, suggesting that the seasonally dependent nutrient flux due to fecal pellets is determined not by how fast they decay, but by their ability to leave the upper mixed layer.

Decaying and fragmenting fecal pellets release dissolved free amino acids (DFAA) into the surrounding water. Changes in the physical characteristics of the fecal pellets resulted in the fall C. finmarchicus fecal pellets and the winter O. vanhoeffeni fecal pellets having the greatest potential to leave the upper mixed layer. This implies that, seasonally, the microbial loop can contribute to the nutrient and particle flux through copepod and tunicate feces.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 ROLE OF FECAL PELLETS

Fecal pellets are important in sedimentation processes and in the vertical transport of nutrients, pollutants and trace elements to the benthos, continental shelf and bathypelagic environments (Schrader, 1971; Fowler & Small, 1972; Honjo & Roman, 1978; Paffenhöfer & Knowles, 1979; Bruland & Silver, 1981; von Bodungen, et al. 1987). The contribution made by fecal pellets to nutrient flux can vary with season, the type of phytoplankton present and the zooplankton community structure (Paffenhöfer & Knowles, 1979; Bienfang, 1980; Angel, 1984; Skjoldal & Wassmann, 1986; Michaels & Silver, 1988; Wefer, et al., 1988). Swarms of salps and pteropods produce large numbers of fast-sinking fecal pellets which result in rapid transport of organic detritus to the benthos (Silver & Bruland, 1981; Matsueda, et al. 1986). During the time of the swarms, these fecal pellets may have a greater impact on geochemical fluxes than crustacean, copepod, feces since salp feces tend to be 100 times richer in organic carbon and nitrogen per unit dry weight (Honjo & Roman, 1978; Bruland & Silver, 1981; Smith unpubl. data). Gelatinous zooplankton are non-selective

filter feeders and can repackage small fecal pellets through coprophagy, accelerating their transport to depth (Silver & Bruland, 1981).

Recent studies suggest that only large, rapidly sinking fecal pellets or those incorporated into larger aggregates reach depths greater than 1000 m (McCave, 1975; Urrère & Knauer, 1981; Lampitt, 1985; Alldredge & Gotschalk, 1988; Michaels & Silver, 1988). However, large size and high sinking velocity do not guarantee export out of the euphotic zone, as Alldredge, et al. (1987) found high concentrations of old euphausiid pellets in the surface waters off southern California. Over 90% of the euphotic zone organic production is recycled in the upper 400 m, mainly through degradation of fecal pellets and phytoplankton by microbes and coprophagy of fecal pellets by larger zooplankton (Bishop, et al., 1978; Small, et al., 1979; Hofmann, et al., 1981).

1.2 CONTROLS ON THE FLUX POTENTIAL OF FECAL PELLETS

Phytoplankton in temperate waters follow a seasonal progression from small, single-cell diatoms to large chain-forming diatoms to unarmored flagellates and back to single-cell diatoms (Marshall & Cohn, 1983; Marshall, 1984; Nielsen & Richardson, 1989). The kind of phytoplankton present will

influence the zooplankton community. Gelatinous filter feeders consume mainly micro- (20 -200 μm) and nano- (2-20 μm) plankters, whereas copepods ingest predominately larger, single-cell and chain forming diatoms (Turner, 1984; Deibel & Turner, 1985; Michaels & Silver, 1988). Thus, gelatinous zooplankters can feed on the primary members of the microbial loop, i.e. bacteria and heterotrophic nanoflagellates (Pomeroy, 1974; Michaels & Silver, 1988), whereas copepods are linked to the microbial loop through larger ciliates and protozoans (Berk, et al., 1977; Porter, et al., 1979; Klein Breteler, 1980).

The type of phytoplankton ingested affects the pellet's density, which in turn may effect its settling velocity. During the spring and fall phytoplankton blooms, the guts of copepods become saturated with food, resulting in rapid gut passage times (Penry & Jumars, 1986). Consequently, the feces are more dense and may be rich in organic matter, thereby sinking faster and contributing more to the organic flux than feces during the rest of the year (Dagg & Walser, 1986). This was demonstrated by Bienfang (1980), who found that fecal pellets composed primarily of flagellates were less dense (1.11 g cm^{-1}) and sank more slowly than feces composed primarily of diatoms (1.17 g cm^{-1}).

Sinking velocity is dependent in part on the difference between fecal pellet density and the density and viscosity

of the surrounding water (Komar, et al., 1981). As feces decay, they become less dense (Noji, et al., 1991) and should therefore sink more slowly. Previous studies suggest that the sinking velocity of a fecal pellet decreases with decreasing temperature due to increased water viscosity (Fowler & Knauer, 1986 and ref. within).

Water temperature can also affect the rate of fecal pellet decay (Honjo & Roman, 1978; Turner, 1979; Roy & Poulet, 1990). Most zooplankters produce fecal pellets with a peritrophic membrane. The breakdown of this membrane and the total decay of the pellet is a function of water temperature and its affect on microbial and protozoan activity. The peritrophic membrane is consumed by bacteria either from the water column or from within the feces. Alldredge, et al. (1987) found bacteria mainly within euphausiid fecal pellets, whereas Honjo & Roman (1978) found microbes attached to the outside of copepod pellets. These external bacteria may be an artifact of laboratory incubation or retrieval methods due to contact with the container's walls (Gowing & Silver, 1983), and may lead to an increased decay rate in the laboratory. More recent work suggests that zooplankton facilitate the decay process through coprochaly or coprohexy (Lampitt, et al., 1990; Noji, et al., 1991).

The rate at which fecal pellets are degraded controls

in part the rate at which nutrients are released to the surrounding water and the resultant supply of energy from fecal pellets to both the benthos and the bathypelagic environments. Jumars, et al. (1989) suggested that 90% of the DOC (dissolved organic carbon) in small fecal pellets (diameter < 100 μm) diffuses out within 2 s of egestion. Microbes also utilize many of the nutrients within feces (Pomeroy, et al., 1984). Amino acids and poly- and mono-unsaturated fatty acids in fecal pellets are utilized or degraded in the upper mixed layer (Wakeman, et al., 1984). However, wax esters and saturated fatty acids remain in feces collected from deep water, indicating that some feces can provide energy to the bathypelagic environment (Wakeman, et al., 1984; Matsueda, et al., 1986).

1.3 SITE DESCRIPTION

In Conception Bay, Newfoundland (47° 30'N, 53° 00'W), the surface water ranges from <-1° C to 12° C. The bay has a maximum depth of 270 m, and water below ca. 100 m is never above 0° C. The eastern coast of Newfoundland is dominated by the Labrador Current, which enters Conception Bay as a tongue of cold water at a sill depth of 170 m (Leggett, et al., 1984; Taggart & Leggett, 1987). The spring diatom bloom occurs when the surface water is still < 0° C, and is

dominated by chain-forming Chaetoceros spp., Thalassiosira spp. and Skeletonema costatum (Greville) Cleve (McKenzie, unpubl. obs.). Bacterial numbers and activity at this time are suppressed due to low temperatures and substrate levels (Pomeroy & Deibel, 1986; Pomeroy, et al., 1991), and much of the phytoplankton sinks intact to the sediment (Thompson, et al, 1986). Zooplankton abundance lags behind the peak of the diatom bloom due to the effect of temperature on copepod development rate (Redden & Deibel, unpubl. obs.).

Calanus finmarchicus, a raptorial suspension feeder, is one of the most abundant large copepods in the bay. Copepod fecal pellets have been found in sediment traps in Conception Bay at the end of May and in June, near the end of the spring bloom, and they peak in September and October (McKenzie, unpubl. obs.). This suggests that at certain times the fecal pellets from C. finmarchicus could be contributors to the vertical particle flux.

Oikopleura vanhoeffeni is a pelagic tunicate that produces a mucous house and filter feeds with a mucous net. It is most prevalent in the fall through early spring (October to March) (Davis, 1982). When phytoflagellates predominate it is an important grazer and contributes both houses and feces to the organic flux (Redden, et al., 1988). Fecal pellets from O. vanhoeffeni have been found in

sediment traps in all months, but with a maximum in December (McKenzie, unpubl. obs.).

1.4 PURPOSE AND OBJECTIVE

The objective of my research is to determine seasonal changes in physical (size, phytoplankton content, density and decay rate) and chemical (particulate organic carbon, particulate silicate) characteristics of Calanus finmarchicus and Oikopleura vanhoeffeni fecal pellets. Measured settling velocities will be compared to predicted values obtained from current literature equations to determine the accuracy of these equations for predicting seasonal settling velocities. The dependence of fecal pellet settling velocity with physical characteristics of the feces will be examined. This seasonal data will then be analyzed to determine if any variations in the physical or chemical characteristics of the fecal pellets will affect the potential particle and nutrient flux due to these feces in coastal Newfoundland waters. Could the potential of these fecal pellets to leave the upper mixed layer and contribute to the vertical nutrient flux be seasonally dependent?

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 ANIMAL AND PELLET COLLECTION

Oikopleura vanhoeffeni was collected in 400 ml glass jars by SCUBA divers in March, June and November 1990, and January and February 1991, from Logy Bay, Newfoundland, Canada (47° 37'N, 52° 39'W). Immediately after collection the jars containing animals were placed in a flow-through seawater bath in the laboratory. After 1 h and no longer than 12 h later, any jars containing houses (> 90% of the jars) had the houses shaken by hand to release pellets trapped inside. The house and animal were then removed and the remaining water was poured through a 20 μm nitex filter to collect pellets. Fresh, intact pellets were removed from the filter and pipetted into a beaker or vial, or onto a filter for further analysis.

Calanus finmarchicus was collected from Conception Bay, Newfoundland, in April, July and September 1990 and April 1991, from oblique net hauls with a 0.5 m plankton net fitted with 350 μm nylon mesh (Nitex) and a closed cod end cup. The net was lowered to 200 m, towed for 1 minute, and then retrieved at a rate of 13 m min^{-1}. Cod end contents were emptied into a bucket containing water from the

subsurface chlorophyll maximum (SCM). Within 3 h, adult C. finmarchicus females were removed from the bucket and placed in a large (24 x 24 x 15 cm) PVC cup with a bottom of 505 μm nitex mesh. The cup was suspended in a bucket containing water from the SCM and incubated in the laboratory at ambient seawater temperature (-1° to 10° C) for 1-12 h. During the 1-12 h incubation period, the PVC cup was removed from the bucket and the water was passed through a 20 μm nitex mesh to collect all fecal pellets. Pellets were removed from the filter by pipette and placed in a beaker or vial, or onto a filter for further analysis.

CHAPTER 3

SEASONAL DIFFERENCES IN THE FECAL PELLET CONTENTS: IMPLICATIONS FOR FOOD WEB DYNAMICS IN COASTAL NEWFOUNDLAND WATERS

3.1 ABSTRACT

The contents of fecal pellets from Oikopleura vanhoeffeni and Calanus finmarchicus were examined in the spring, summer, fall and winter. The content of the fecal pellets varied seasonally, resembling available particles in the water column. This indicated a temporal succession from a diatom-based food chain in the winter and spring to one based on the microbial loop in the summer and fall. Bacteria, cyanobacteria, choanoflagellates, ciliates, and heterotrophic dinoflagellates were found in the feces, suggesting a direct link between the microbial loop and both crustaceans and pelagic tunicates.

3.2 INTRODUCTION

Primary production by phytoplankton and bacteria forms the basis of all aquatic food webs. The composition of the phytoplankton community in coastal, temperate waters varies seasonally, from a predominance of large, chain-forming diatoms in the winter and spring to dinoflagellates, protozoans and nanoplankton in the summer and early fall (Marshall & Cohn, 1983; Marshall, 1984). This results in a succession from a predominately diatom-based food chain in the winter and spring to one based on the microbial loop in the summer and fall. However, interactions among phytoplankton, bacteria, protozoans and zooplankton are not well understood. How and to what extent are microbial food webs linked to metazoans? Do small plankton act as energy links (i.e. prey) or as sinks (i.e. decomposers)? How does the nature of this linkage vary seasonally in coastal Newfoundland waters that are dominated by the sub-arctic Labrador current?

Primary production in many oceanic and coastal areas is dominated annually by nanoplankton (2-20 μm) and picoplankton (< 2 μm) (Booth, et al., 1982; Murphy & Haugen, 1985; Hoepffner & Haas, 1990). It is known that copepods and euphausiids are not able to feed efficiently on particles < 10 μm in diameter (Marshall & Orr, 1955; Nival &

Nival, 1976; Fenchel, 1988), and that protozoans, such as ciliates and choanoflagellates, may consume 4-70% of the annual phytoplankton production (Burkill, et al., 1987 and ref within). These observations suggest that at certain times most of the primary production is recycled in the upper mixed layer (i.e. through the microbial loop), and that only large phytoplankton > 20 μm in size contribute to the nutrient flux out of the euphotic zone. However, mucous-net feeders that occur in brief swarms, such as salps, doliolids and appendicularians, ingest nanoplankters and picoplankters efficiently (Harbison and McAlister, 1979; Mullin, 1983; Deibel and Lee, unpubl. obs.). Thus, small (< 20 μm) plankters can be transported to depth through the feces of mucous-net feeders (Michaels & Silver, 1988).

The purpose of my study was to examine how the phytoplankton content of the feces from Calanus finmarchicus, a raptorial, suspension-feeding copepod, and Oikopleura vanhoeffeni, a pelagic tunicate that feeds with a mucous filter, varies seasonally. The composition of the feces provides qualitative information on the structure of the food web and on the seasonally changing role of different organisms in energy flow.

3.3 MATERIALS AND METHODS

3.3.1 GENERAL

Oikopleura vanhoeffeni was collected in March, June, and November 1990, and January 1991, while Calanus finmarchicus was collected in April, July and September of 1990, using the method described in Chapter 2.

3.3.2 ANALYSIS OF PELLET AND WATER COLUMN CONTENTS

Fresh, intact pellets were removed from the filter and pipetted into a beaker containing distilled water to rinse off salt crystals. The water containing the pellets was then passed through a 0.45 μm nylon filter (13 mm in diameter, Micron Separations Inc.). The filter with attached pellets was put through an ethanol dehydration series (50%, 70%, 85%, 95%, 100%), critical point dried and coated with gold (Turner, 1984). Contents of the pellets were viewed on a Hitachi S 570 scanning electron microscope (SEM) with the upper detector set at 15 Kv and an 8 mm working distance. After critical point drying, 50% of the pellets were pulled in half using double-sided tape before being mounted and coated with gold.

In each season, 6-8 fecal pellets from both Calanus finmarchicus and Oikopleura vanhoeffeni were examined at

3000X using SEM. 3000-5000 fields were scanned on O. vanhoeffeni pellets (average pellet area was 9.73×10^5 μm^2), and 500-700 fields were scanned on C. finmarchicus pellets (average pellet area was 1.42×10^5 μm^2). Photomicrographs were made of all phytoplankton species that appeared in > 20% of the fields and of those that were unique or rare. Intact cells were measured to the nearest 0.1 μm, and were identified to genus and/or species when possible. Taxa that appeared in > 50% of the fields were tabulated as "abundant", those that appeared in 20-50% as "common", and those that appeared in < 20% "rare".

When Calanus finmarchicus was collected, 180-ml samples were taken from the subsurface chlorophyll maximum (SCM) for microscopic analysis. Cell samples were stained with Lugol's iodine and fixed in 5% borate-buffered formaldehyde in seawater. 10-50 ml samples were allowed to settle for 48 h, followed by identification and counting at 200 and 400X using a Zeiss Axiovert 35 inverted microscope with phase contrast, following the method of Utermöhl (1958).

3.4 RESULTS

A complete species list of the contents identified from the fecal pellets of Calanus finmarchicus and Oikopleura vanhoeffeni is given in Table 3.1. The contents for both fecal types varied seasonally.

3.4.1 SPRING

In March, O. vanhoeffeni feces were full of diatoms (Fig. 3.1A) and chrysophytes (Fig. 3.1B). Dinoflagellates, silicoflagellates, coccolithophorids, choanoflagellates, ciliates and bacteria were "rare". Many cells were intact and diatom chains were observed. Cells ranged from 0.7-183 μm in least dimension in valve view, with most < 10 μm in size.

In April, broken diatom shells (Fig. 3.1C) dominated the contents of C. finmarchicus feces, including Skeletonema costatum (Fig. 3.1D), Chaetoceros spp., Thalassiosira spp. and Fragillariopsis spp. Intact cells ranged from 5-18 μm in least dimension. Chrysophyte and dinoflagellate remains were "rare".

The water sample was dominated by diatoms, primarily Thalassiosira spp. and Chaetoceros spp. (Table 3.2). Unidentifiable spheres < 2 μm in diameter were copious,

followed by choanoflagellates and chrysophytes. Ciliates and dinoflagellates were scarce. Total cell concentration was $1.58 \times 10^6\ \ell^{-1}$.

3.4.2 SUMMER

Broken and unidentifiable diatom frustules dominated fecal pellet contents of Oikopleura vanhoeffeni at the end of May and beginning of June (Fig. 3.2A). Individual cells ranged from 1-167 μm in least dimension in valve view. Dinoflagellate fragments were "common" (Fig. 3.2B & C).

At the end of June and early July, the pellet contents of Calanus finmarchicus were diverse. Broken diatom shells were "abundant" (Fig. 3.2A), but bacteria, choanoflagellates (Fig. 3.2D), cyanobacteria, dinoflagellates (Fig. 3.2B), and diatom cysts were "common". Intact cells ranged from 1-44 μm in least dimension.

Particles in the water were dominated by macroscopic flocs of "marine snow" (Table 3.2). Few intact diatoms were present. Spheres < 2 μm in diameter were the most prevalent live organisms. Gymnodinium spp., choanoflagellates and ciliates were present. Total cell concentration was $1.91 \times 10^5\ \ell^{-1}$.

3.4.3 FALL

In September, Calanus finmarchicus feces were dominated by nanoplankton, including ciliates (Fig. 3.3A), bacteria, cyanobacteria (Fig. 3.3B), choanoflagellates (Fig. 3.3C), cysts (Fig. 3.3D), cryptomonads, chrysophytes, diatoms (Fig. 3.3E) and dinoflagellates. Cells ranged from 0.5-87 μm in least dimension. Small diatoms were "rare".

Chrysophytes and unidentifiable spheres < 2 μm in diameter dominated the cells in the SCM (Table 3.2). Small (< 15 μm) and large (> 20 μm) ciliates were plentiful, as were choanoflagellates, gymnodinoid dinoflagellates and marine snow. Total cell abundance was $3.13 \times 10^5\ \ell^{-1}$.

In November, diverse nanoplankton species dominated the fecal pellets of Oikopleura vanhoeffeni. Coccolithophorids (Fig. 3.3F), choanoflagellates (Fig. 3.3G), chrysophytes, dinoflagellates (Fig. 3.3H), euglenoids (Fig. 3.3I), silicoflagellates (Fig. 3.3J), xanthophytes and cysts (Fig. 3.3K) were "abundant", and "rare" was a testate rhizopod (Fig. 3.3L), with many partially broken cells. Intact cells ranged from 0.9-57 μm in least dimension.

3.4.4 WINTER

Diatoms, including Skeletonema costatum, Chaetoceros spp. (Fig. 3.4A), and Arcocellulus cornucervis (Fig. 3.4B), and coccolithophorids (Fig. 3.4C) were the main components in the fecal pellets of O. vanhoeffeni in January. Chrysophytes, dinoflagellates, choanoflagellates and ciliates were "common" (Fig. 3.4D). Small cells appeared to be intact but many larger cells and chain-forming diatoms were cracked. Intact cells ranged from 1-66 μm in least dimension.

3.5 DISCUSSION

3.5.1 CAUSES OF SEASONAL DIFFERENCES IN THE CONTENT OF FECAL Pellets

The seasonal succession of phytoplankton and microbes is reflected in the changing composition of the feces of Oikopleura vanhoeffeni and Calanus finmarchicus. Large, chain-forming diatoms dominate phytoplankton biomass and numbers during the spring bloom in Newfoundland waters (Table 3.2). These autotrophic species deplete dissolved silica in surface waters by the end of May (Thompson, et al., 1986), resulting in a 200-fold decrease in diatom concentration by June and early July (Table 3.2). Bacterial activity is suppressed during the bloom due to low temperature and substrate levels (Pomeroy and Deibel, 1986; Pomeroy, et al., 1991). Phagotrophic and mixotrophic organisms are found in all seasons, though they predominate in the summer and fall as components of the microplankton and nanoplankton communities in coastal waters (Stoecker, et al., 1989; Paranjape, 1990). In my samples, unarmored dinoflagellates and ciliates together made up 12% and 9% of the cell numbers in the summer and fall respectively (Table 3.2). Thus, bacterial numbers and heterotrophic flagellate biomass track the seasonal cycle of water temperature, which peaks in the late summer and early fall (Powell, et al.

1987). In the late fall and winter, single-cell diatoms become abundant, most likely in response to increased vertical transport of essential, inorganic nutrients resulting from destabilization of the water column.

The content of the feces of both O. vanhoeffeni and C. finmarchicus reflects the phytoplankton succession and relative abundance of particle size classes available in the SCM at the time of sampling. Diatoms are the primary component of both animals' feces in the winter and spring, especially chain-forming Skeletonema costatum, Chaetoceros spp., Thalassiosira spp. and Fragillariopsis spp. (Figs. 3.1, 3.4). An assortment of nanoplankton species fill the feces in the fall (Fig. 3.3). Also abundant are amorphous mucous blobs which may be the remains of soft bodied plankters or marine snow. The large numbers of broken diatoms in the feces in the summer (Fig. 3.2) and the few intact diatoms found in the water column suggest that both O. vanhoeffeni and C. finmarchicus are feeding on marine snow derived from fragmented diatoms. I am not attempting to quantify the relative importance of armored vs. unarmored or autotrophic vs. heterotrophic plankters as a food source for copepods and appendicularians.

3.5.2 A CHANGING FOOD WEB: LINKS TO THE MICROBIAL LOOP

The fecal pellet contents of O. vanhoeffeni and C. finmarchicus follow a similar seasonal pattern. They are dominated by large diatoms in the spring (Fig. 3.1) and small nanoplankton and bacteria in the fall (Fig. 3.3). Summer and winter fecal pellets have an even mixture of large diatoms and small nanoplankton (Figs. 3.2, 3.4), thus showing seasonal shifts in food web structure (Fig. 3.5). This confirms the role of the oikopleurids as a "generalist" suspension feeder, and should result in a seasonal change from the flux of opal from diatoms in the spring (Fig. 3.1) to calcite from coccolithophorids in the fall (Fig. 3.3).

Sediment traps from Conception Bay show maximum copepod (C. finmarchicus) fecal pellet flux in September and October (McKenzie, et al., unpubl. obs.), indicating that they are able to consume the nanoplankton in early fall. The surprisingly high content of bacteria (Fig. 3.3) and nanoplankton in the fall C. finmarchicus feces raises the question of the validity of existing conceptual models of the classic food chain, from large (> 20 μm) diatoms to copepods to fish, and suggests it is time to look for mechanisms to explain how this consumption of bacteria and nanoplankton takes place.

My observations indicate that O. vanhoeffeni and C.

finmarchicus ingest large quantities of non-phytoplanktonic, food particles, generally overlooked in laboratory feeding studies and energy flow models. Marine snow is absent during the spring, but makes up 36% and 7% of the total particles in the summer and fall respectively (Table 3.2). Since these aggregates are large ($\geq$ 50 μm), they, together with attached particles, may be ingested by C. finmarchicus, creating an avenue for the vertical flux of bacterial biomass. These observations could also help explain the controversy over external vs. internal pellet decay (Honjo & Roman, 1978; Gowing & Silver, 1983; Alldredge, et al., 1987) by indicating a source (i.e. marine snow) for the internal bacteria found in some fecal pellets.

Previous studies have shown that C. finmarchicus is an indiscriminate, raptorial feeder, ingesting those particles present in greatest abundance (Cowles, 1979; Ishimaru, et al., 1988). Particles < 10 μm have been found in C. finmarchicus feces (Huntley, 1981; Ishimaru, et al., 1988), indicating that although this copepod is not able to filter particles of this size efficiently (Nival & Nival, 1976), such particles may be ingested when abundant and/or trapped within marine snow aggregates. There are reports of copepods and euphausiids eating ciliates, tintinnids, choanoflagellates, heterotrophic dinoflagellates and coccolithophorids (Berk, et al., 1977; Honjo & Roman, 1978;

found in the fecal pellets of C. finmarchicus and O. vanhoeffeni.

It is axiomatic that ciliates and phagotrophic protozoans represent the main link between microheterotrophs and copepods (Porter, et al., 1979; Sherr, et al., 1986). However, my observations indicate that both copepods and appendicularians are able to feed on bacteria, heterotrophic nanoflagellates and ciliates (Fig. 3.2, 3.3), and thus are capable of mediating a flow of energy out of the microbial loop. My observations also have important methodological implications, because the conventional dilution technique for determining the grazing pressure on bacteria and other picoplankton does not measure their consumption by metazoans, such as copepods and tunicates. This may result in the erroneous conclusion that the microbial loop is an energy sink.

Turner, 1984; Marchant & Nash, 1986; Tanoue & Hara, 1986; Ishimaru, et al., 1988), implying direct removal of biomass from the microbial loop.

Azam, et al. (1983) defined the microbial loop as the interaction between bacteria, flagellates and microzooplankton. Choanoflagellates are considered important bacteriovores and members of the microbial loop (Sherr, et al., 1986). Lorica remains from choanoflagellates were found in the feces of both O. vanhoeffeni and C. finmarchicus (Fig. 3.2, 3.3) and thus represent a direct link between macrozooplankton and the microbial loop. The lorica was frequently broken in my samples and the remains were often difficult to recognize. This fragility may explain the relatively few reports of choanoflagellate remains in fecal pellets of macrozooplankton.

Heterotrophic dinoflagellates are also important grazers on bacteria and phytoplankton, and provide an important food source for copepods (Klein Breteler, 1980). Protoperidinium depressum has been reported to feed on bacteria (Lessard & Swift, 1985), and many unarmored dinoflagellates are phagotrophic, forming important links in food chains (Kimor, 1981; Odate & Maita, 1990). Both P. depressum (Fig. 3.2) and unarmored dinoflagellates were

Table 3.1: Phytoplankton Content of Oikopleura vanhoeffeni and Calanus finmarchicus Fecal Pellets.

SPECIES	SPRING	SUMMER	FALL	WINTER
Bacillariophyceae				
Amphora spp.	Or		Cr	Or
Arcocellulus cornucervis	Oa		Oc	Oa
Bacterosira fragelis			Or	
Berkeleya sp.	Or			
Chaetoceros spp.	Ca	Oc, Cr		Oa
Cocconeis spp.	Or	Or, Cr	Oc, Cr	Oc
Coscinodiscus radiatus	Oa			
Cyclotella spp.			Or	
Fragillariopsis spp. F. curvata F. cylindrus	Oa		Oc	Oa
Gomphoneopis littoralis		Oc	Or	
Gomphoseptatum aestuarrii	Oc		Or	
Licmophora sp.	Oc			Or
Minidiscus trioculatus	Oa		Oa, Cr	Oc
Navicula spp.	Oc	Oc	Oc, Cr	Oc
Nitzchia sp.	Or, Cr			
Pleurosigma sp.	Or			

Continuation of Table 3.1

SPECIES	SPRING	SUMMER	FALL	WINTER
Pseudogomphonema kamtschaticum	Oc			
Pteroncola spp.	Oc		Oa	
Skeletonema costatum	Oa, Ca		Oa	Oa
Tabularia sp.	Or	Oc	Oc	
Thalassionema nitzschioides			Or	Oc
Thalassiosira spp. T. gravida T. minima T. pseudonana T. symmetrica	Oc, Ca	Oa, Cc	Oc	Oc
Pyrrhophyceae				
*Ceratium sp.			Or, Cr	
Gymnodinium sp.			Or, Cr	
Prorocentrum spp. P. balticum P. minima	Oc	Cc	Oa, Cc	Oc
Protoperidinium spp. P. depressum		Or		
Scripsiella sp.			Oa	
Chrysophyceae				
Dictyocha speculum	Oc		Oc	Or
Tetraparma sp.	Oa, Cr		Or	Or
Triparma stigata	Or			Or

Continuation of Table 3.1

SPECIES	SPRING	SUMMER	FALL	WINTER
Xanthophyceae				
Meringosphaera mediterranea			Oa	Oc
Haptophyceae				
Coccolithus pelagicus	Or		Or	Or
Emiliana huxeleyi	Oc		Or	Oa
Craspedophyceae				
Parvicorbicula sp.	Or			
Stephanoeca sp.			Or	
*Lorica bundles	Or	Cr	Oa, Cr	Oa
Tintinnidae				
Stenosemella steini	Oc			
Others				
Bacteria	Oc	Cr	Oc, Ca	Oc
Ciliates			Or, Ca	Or
Cyanobacteria		Cr	Cc	
Cysts	Or	Or, Cr	Oa, Ca	Or
Euglenoids	Oc		Oc	

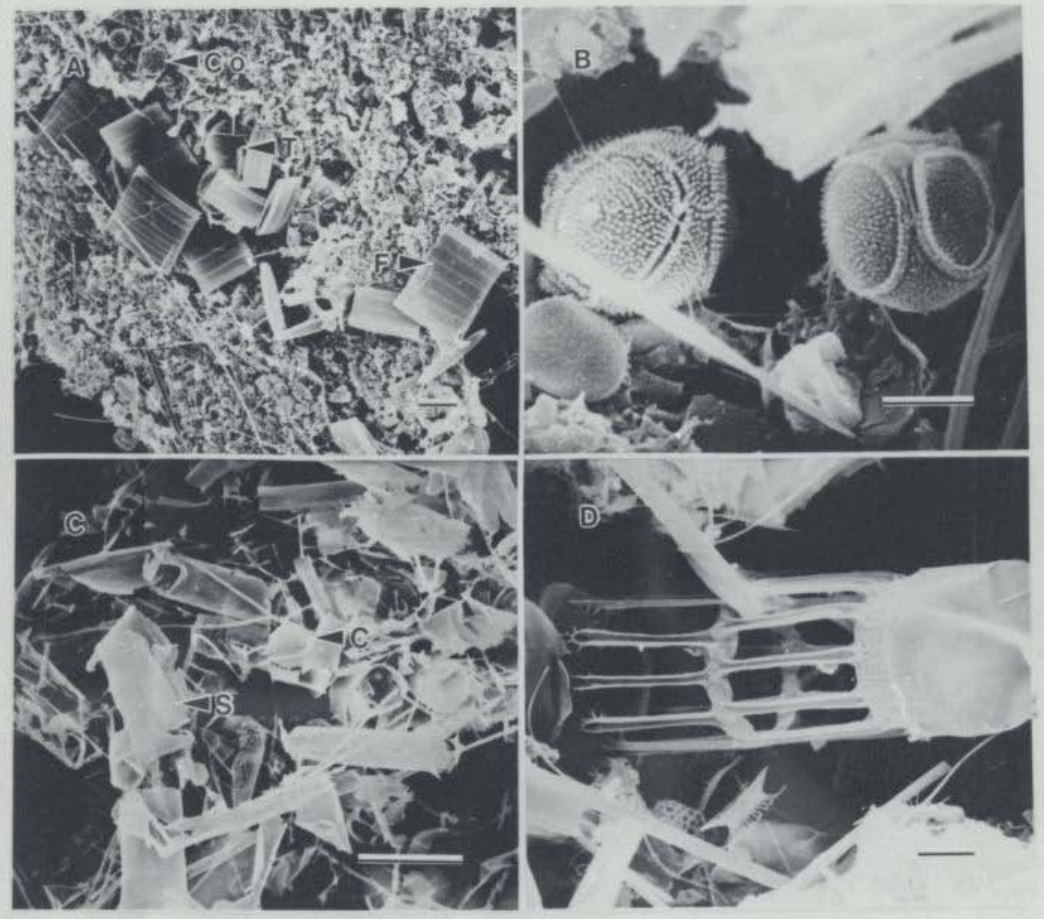
O= found in O. vanhoeffeni feces
C= found in C. finmarchicus feces
* fragments, identified by plate or surface morphology
a= abundant, found in > 50% of fields viewed
c= common, found in 20-50% of fields viewed
r= rare, found in < 20% of fields viewed

Table 3.2: Cell Counts of Water Samples from Conception Bay.

PLANKTON CATEGORY	SPRING 6-4-90 (cell ℓ^{-1})	SUMMER 26-6-90 (cell ℓ^{-1})	FALL 27-9-90 (cell ℓ^{-1})
Total Cell Count	1.58×10^6*	1.91×10^5*	3.13×10^5*
< 2 μm Spheres	2.95×10^5 (19%)	1.07×10^5 (56%)	8.24×10^4 (28%)
2-5 μm Spheres	3.23×10^4 (2%)	**	**
> 5 μm Spheres	8.08×10^3 (.5%)	1.21×10^4 (6%)	1.03×10^5 (36%)
Chrysophytes	6.46×10^4 (4%)	1.45×10^4 (8%)	4.85×10^4 (17%)
Choanoflagellates	6.26×10^4 (4%)	1.06×10^4 (6%)	4.04×10^3 (1%)
Cryptophytes	2.22×10^4 (1%)	5.39×10^3 (3%)	4.04×10^3 (1%)
Cyanobacteria	2.02×10^3 (.1%)	1.62×10^3 (.8%)	4.04×10^3 (1%)
Phaeocystis sp.	2.50×10^3 (.2%)	**	**
Prasinophytes	8.08×10^3 (.5%)	1.62×10^3 (.8%)	8.08×10^2 (.2%)
Prymisophytes	2.42×10^4 (2%)	6.47×10^3 (3%)	4.85×10^3 (2%)
< 20 μm Ciliates	**	8.08×10^2 (.4%)	8.08×10^3 (3%)
> 20 μm Ciliates	1.41×10^4 (.9%)	1.24×10^3 (.6%)	2.00×10^2 (.06%)
Tintinnids	**	8.00×10^1 (.04%)	2.00×10^1 (.006%)
Diatoms	9.96×10^5 (63%)	5.55×10^3 (3%)	1.05×10^4 (4%)
Unarmored Dinoflagellates	4.24×10^4 (3%)	2.10×10^4 (11%)	1.62×10^4 (6%)
Armored Dinoflagellates	1.01×10^4 (.6%)	2.42×10^3 (1%)	3.33×10^3 (1%)
Marine Snow	**	1.10×10^5	2.34×10^4

* Total does not include marine snow
** There were none present in the sample

Figure 3.1: Spring Fecal Pellet Contents



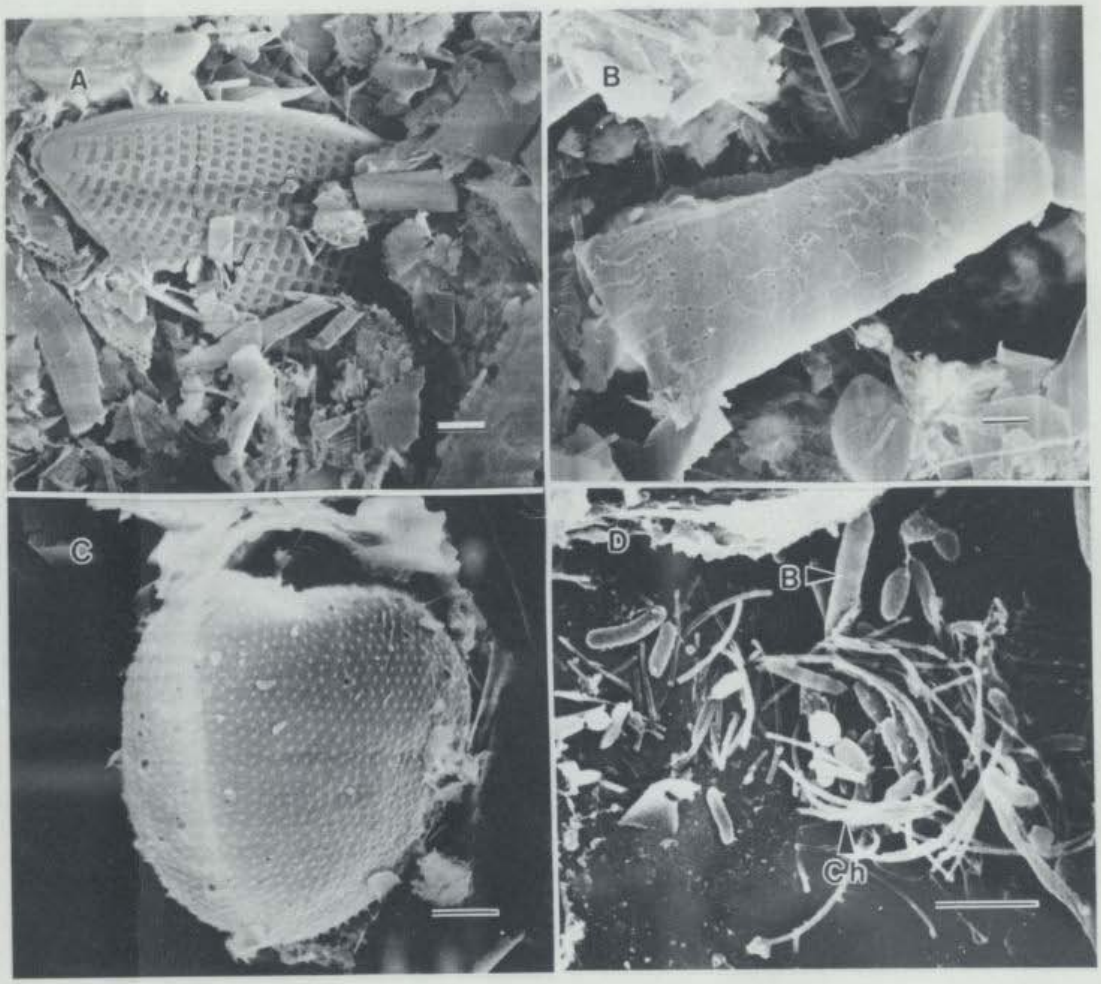
A. Overview of O. vanhoeffeni fecal pellet; F=Fragillariopsis sp. chain, Co=coccolithophore, T=Thalassiosira sp., scale bar= 20 μm.

B. Common chrysophyte, Tetraparma sp., scale bar= 1 μm.

C. Overview of C. finmarchicus fecal pellet; C=Chaetoceros sp., S=Skeletonema costatum, scale bar= 10 μm.

D. Dominant diatom, Skeletonema costatum, scale bar= 2 μm.

Figure 3.2: Summer Fecal Pellet Contents



A. Broken diatoms, common to both types of feces, scale bar= 2 μm.

B. Dinoflagellate plates, Protoperidnium depressum, scale bar= 2 μm.

C. Dinoflagellate, Prorocentrum minima, scale bar= 2 μm.

D. Bacteria (B) and choanoflagellate lorica remains (Ch) scale bar= 2 μm.

Figure 3.3: Fall Fecal Pellet Contents

A. Ciliate, scale bar= 2 μm.

B. Bacteria (B) and cyanobacteria, Anabeana sp. (A), scale bar= 2 μm.

C. Broken diatom and choanoflagellate lorica remains (Ch), scale bar= 2 μm.

D. Chrysophyte cyst, scale bar= 2 μm.

E. Diatom, scale bar= 2 μm.

F. Coccoliths from Emiliana huxleyi, scale bar= 2 μm.

G. Choanoflagellate, Stephanoeca sp., scale bar= 1 μm.

H. Common dinoflagellate, Scripsiella sp., scale bar= 2 μm.

I. Euglena sp., scale bar= 2 μm.

J. Silicoflagellate, Dictyocha speculum, scale bar= 2 μm.

K. Unknown cyst (Cy) and Meringoshpaera mediterranea (M), scale bar= 2 μm.

L. Testate rhizopod, Paulinella ovalis, scale bar= 1 μm.

Figure 3.3: Fall Fecal Pellet Contents

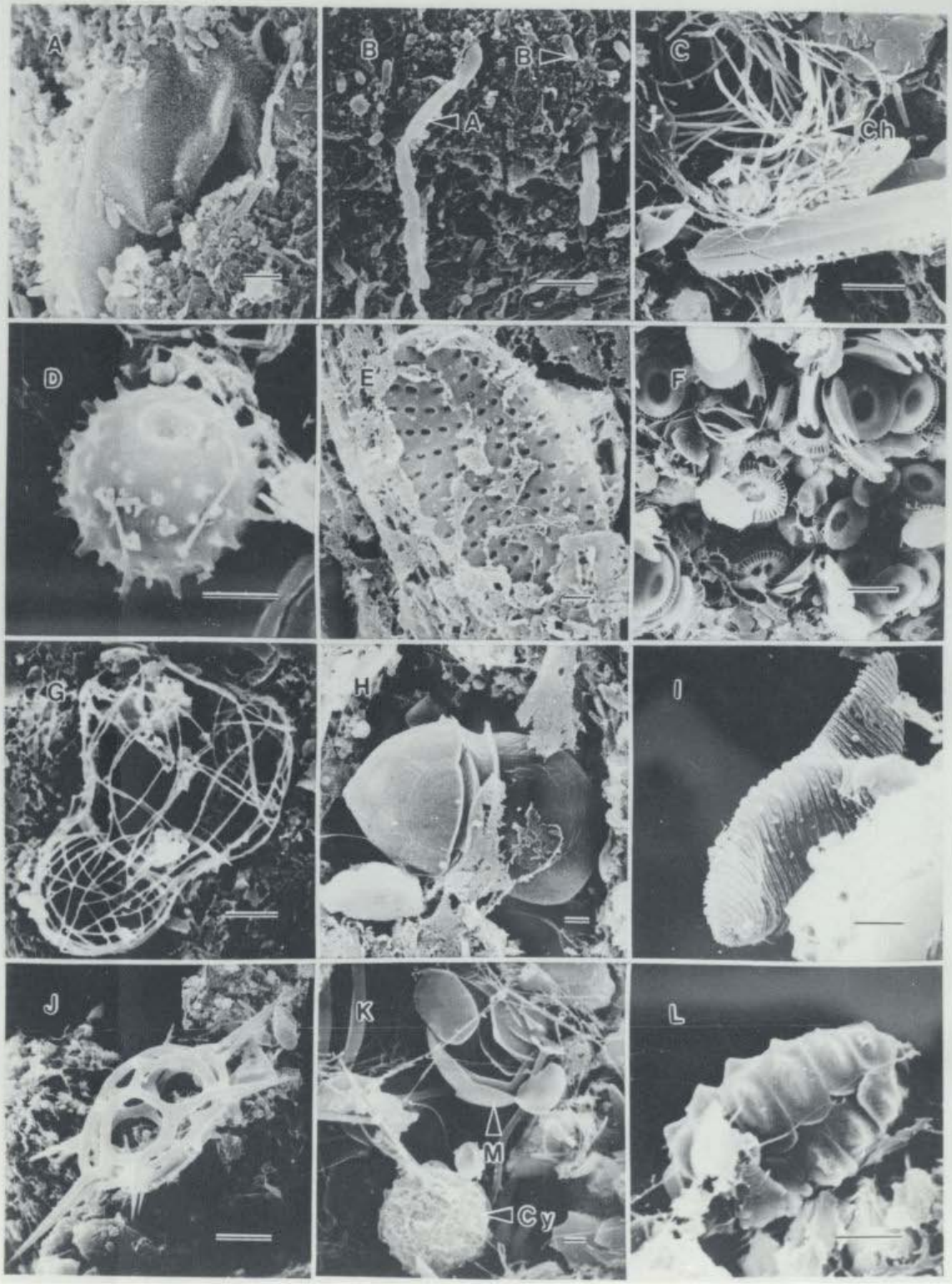


Figure 3.4: Winter Fecal Pellet Contents

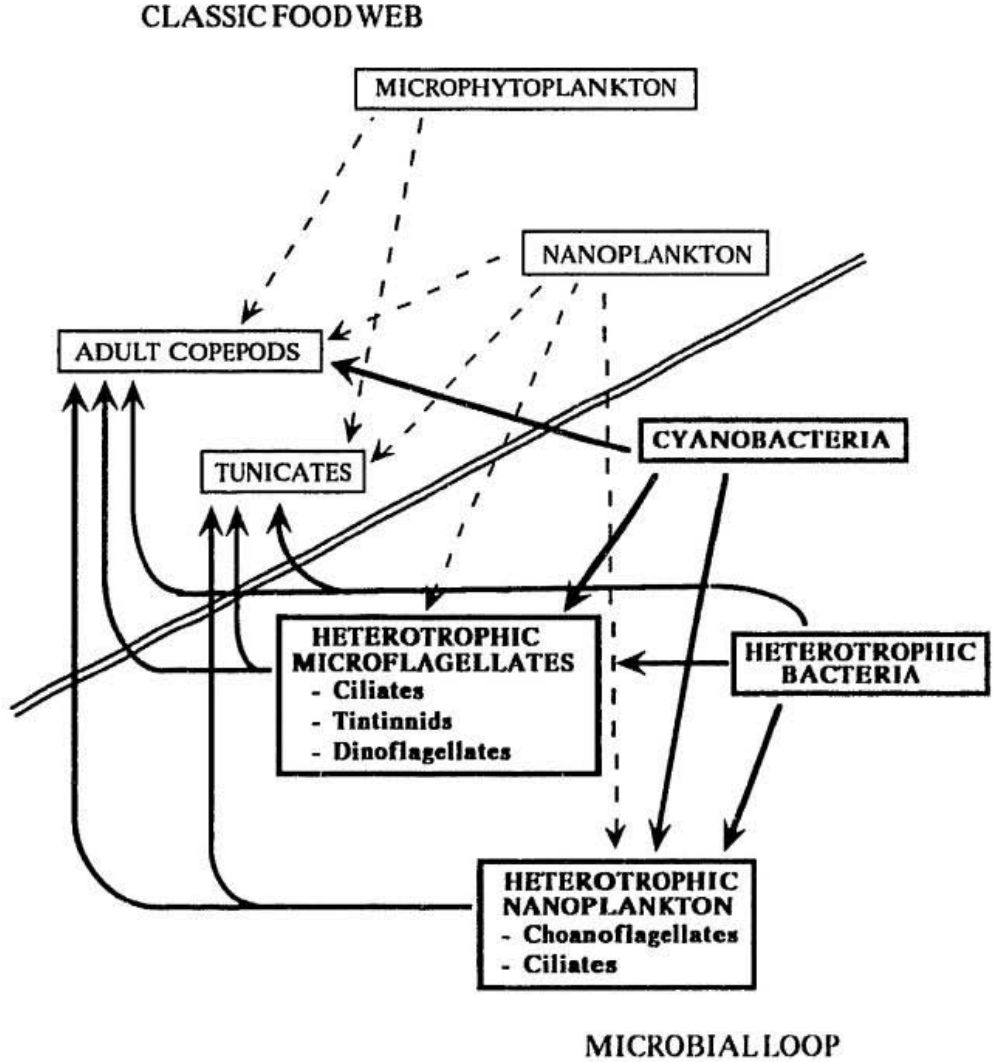
A. Overview of O. vanhoeffeni fecal pellet, C=Chaetoceros sp., N=Navicula sp., Ch=choanoflagellate lorica, scale bar= 5 μm.

B. Common diatom, Thalassionema nitzschioides, scale bar= 2 μm.

C. Coccoliths from Emiliana huxeleyi, scale bar= 2 μm.

D. Dinoflagellate, Prorocentrum sp. (P) and choanoflagellate lorica remains (Ch), scale bar= 2 μm.

Figure 3.5: Model of Zooplankton Food Web.
To the left of the double line and with dashed lines is the classic, diatom-based food web predominant in the spring. To the right of the double line and with solid lines is the microbial loop predominant in the fall.



CHAPTER 4

SEASONAL VARIATION IN FECAL PELLET DYNAMIC DENSITIES

4.1 ABSTRACT

The dynamic densities of fecal pellets from Oikopleura vanhoeffeni and Calanus finmarchicus were measured in an isosmotic density gradient. These are the first reported seasonal measurements of fecal pellet densities from two different types of macrozooplankters, a gelatinous, filter feeder and a crustacean, suspension feeder. Dynamic density ranges and medians were significantly different among seasons for both species, depending primarily on the type of phytoplankton ingested and its ability to be compacted. I termed this density the fecal pellet's dynamic density. Fall C. finmarchicus feces and winter O. vanhoeffeni feces filled with nanoplankters and soft bodied organisms were more tightly compacted (Packing Index (% open area) = 4 & 3.5% for C. finmarchicus & O. vanhoeffeni respectively) and more dense (1.19 & 1.23 g cm^{-3}) than spring feces filled with diatoms (Packing Index = 23 & 15% and 1.11 & 1.13 g cm^{-3}). This is opposite the results found using the conventional literature mass/volume relationship for feces, where spring diatom filled feces had a calculated density of 1.12-1.24 g cm^{-3} and fall feces containing nanoplankters had

a calculated density of 1.08 g cm^{-3}. This disparity can have important effects on calculated fecal pellet sinking velocities and on flux estimates. Based on the seasonal dynamic densities, fecal pellets filled with unarmored flagellates and nanoplankters have a greater potential for exiting the upper mixed layer and in contributing to the nutrient flux than do feces filled with diatoms.

4.2 INTRODUCTION

Fecal pellets can transport nutrients, pollutants and other particles from the euphotic zone to the benthos (Angel, 1984; von Bodungen, et al., 1987; Wefer, et al., 1988). Most studies have examined the sinking velocities (Fowler and Small, 1972; Small, et al., 1979) or nutrient composition (Johannes and Satomi, 1966; Bruland and Silver, 1981; Morales, 1987) of feces at a single point in time. From this work, estimates of pellet density and settling velocity have been calculated and used in conjunction with sediment trap data to determine the vertical flux of fecal pellets (Dunbar and Berger, 1981; Morris, et al., 1988; Lane, et al., submitted).

The difference between fecal pellet density and that of the surrounding water is an important factor in determining the settling velocity of pellets (Komar, et al., 1981). While still water sinking velocities are easily measured, the actual density of the fecal pellets has rarely been measured (Taghon, et al., 1984; Alldredge, et al., 1987). Dillon (1964) reported a value of 1.19 g cm-3 for copepod feces, although he did not report how he obtained this value. Density is most commonly estimated from measurements of mean volume and mean dry weight and calculated using a wet-to-dry weight ratio along with the mass/volume

relationship (Bienfang, 1980; Bruland and Silver, 1981). It is also possible to either measure or to calculate the settling velocity and back-calculate pellet density using the Komar, et al. (1981) equations for settling velocity of fecal pellets or the Stokes equation. These methods have resulted in a range of reported density values of 1.06-1.80 g cm-3 for crustacean zooplankton (Corner, et al., 1986 and ref. within).

Fecal pellet size, settling velocity and density vary with the type and amount of phytoplankton ingested (Dagg and Walser, 1986; Bienfang, 1980; Corner, et al., 1986), yet in flux models a constant density value is used; 1.19 or 1.22 g cm-3 for copepods (Dillon, 1964; Paffenhöfer & Knowles, 1979; Komar, et al., 1981) and 1.10 g cm-3 for salps (Bruland & Silver, 1981). These generalizations may result in misleading fecal pellet flux estimates.

In coastal Newfoundland waters, the succession of phytoplankters follow a seasonal cycle; diatoms dominate in the winter and spring while flagellates dominate in the summer and early fall. This is reflected in the contents of the fecal pellets of two of the major macrozooplankters in these waters, Oikopleura vanhoeffeni, a pelagic tunicate, and Calanus finmarchicus, a copepod (Chapter 3). O. vanhoeffeni is an indiscriminate filter feeder with no hard mouth parts, while C. finmarchicus is a raptorial suspension

feeder that "crushes" food. The purpose of this study was to measure the density of the fecal pellets from these two types of grazers over the year and to determine if seasonal changes in the diet were reflected in the density of the feces.

4.3 MATERIALS AND METHODS

4.3.1 GENERAL

Oikopleura vanhoeffeni was collected in June 1990 and January and March 1991 using methods described in Chapter 2. Twenty pellets were pipetted into each of four jars filled with 0.2 μm filtered sea water. Calanus finmarchicus was collected in June and September 1990 and April 1991 as described in Chapter 2. Twenty pellets were pipetted into each of six jars containing 0.2 μm filtered sea water. All jars with pellets were then transported to the North West Atlantic Fisheries Centre, where density analysis was done within 13 h of collection. No decay of the pellet membrane was observed during this time.

4.3.2 DENSITY ANALYSIS

The contents of each jar were poured into a 50 ml graduated centrifuge tube and centrifuged for 5 minutes at 2700 rpm (1500-1600 x g) on a Beckmann PJ6 Centrifuge. The supernatant was drawn off, leaving 5 ml in the tube. Each tube was then touched to a vortex mixer to resuspend the pellets.

Using a single-channel peristaltic pump and a 100 ml gradient mixer, the sea water and pellet mixture was

underlain with a 40 ml linear density gradient following the method of Schwinghamer, et al. (1991). Density gradients ranging from 1.02-1.20 or 1.41 g cm^{-3} were created using isosmotic colloidal silica (Nalco 1060) plus sucrose solution. The filled centrifuge tubes were balanced and centrifuged for 17 minutes at 2700 rpm (1500-1600 x g).

Using the densest Nalco 1060/sucrose solution (1.41 g cm^{-3}) to underlay the density gradient, 2 ml volumes were displaced upward, through the conical cap of the centrifuge tube (Schwinghamer, et al., 1991), into preweighed glass vials and capped. The vials and contents were then reweighed and the difference was the weight of the contents. The volume of the contents was double checked using a Hamilton syringe. Density of the contents and the included fecal pellets was calculated using a weight/volume ratio. Error using this method was found to be 0.01 g cm^{-3}.

The length and width of pellets from each density layer were measured under a Zeiss dissecting microscope. The volume, surface area and frontal cross sectional area were calculated for each pellet, assuming cylindrical shape for the C. finmarchicus fecal pellets and prolate spheroid shape for the O. vanhoeffeni feces. The densities for the pellets were regressed against the physical measurements to see if there were significant correlations between fecal pellet density and size.

Pellets were then prepared for SEM (scanning electron microscopy) to examine their contents using the method described in Chapter 3. A mean seasonal packing index (P.I.) for each fecal type was calculated on the percent open area in a cross-sectional view of the pellet in an electron micrograph. The open area was measured using a JAVA image analysis system. A cross-sectional view from six different fecal pellets from both O. vanhoeffeni and C. finmarchicus was analyzed, and the mean P.I. obtained for each feces type in each season.

4.3.3 CONVENTIONAL DENSITY DETERMINATIONS

The mean dry weight of fecal pellets from Calanus finmarchicus was found for each season by collecting 60 to 200 feces on a filter, and then converted to an average wet weight using the conversion factor of 4.4 (Fowler, 1977). The density was calculated using the average wet weight and the average volume for the feces in each season.

In another set of experiments, the sinking velocity, length, width and dynamic density of a group of feces was measured (Chapter 5). From these measurements the density of the fecal pellets was calculated using the equations of Komar, et al. (1981). Both types of estimated densities were compared to the measured dynamic densities.

4.4 RESULTS

4.4.1 SEASONAL DENSITIES

The dynamic density data in each season for both fecal types was not normally distributed (Shapiro-Wilk'W, $p < 0.001$, Fig. 4.1 & 4.2), so nonparametric analysis was done using Wilcoxon scores (for testing the ranges) and median scores (for testing the median). There were significant differences among the three seasons in the dynamic density ranges ($p < 0.01$) and medians ($p < 0.01$), for both O. vanhoeffeni and C. finmarchicus, (Table 4.1). The least dense pellets were found in the spring for both species and the most dense occurred in the fall for C. finmarchicus and winter for O. vanhoeffeni, with the largest ranges occurring in the fall and winter, (Fig. 4.1 & 4.2). In the spring, there was no significant difference in either the range ($p > 0.10$) or median ($p > 0.80$) dynamic densities between species. This was also true for fall C. finmarchicus and winter O. vanhoeffeni samples, range ($p > 0.30$) and median ($p > 0.90$). Summer samples had significant differences between the ranges ($p < 0.01$) but not between the medians ($p > 0.40$).

The measured median dynamic density of C. finmarchicus fecal pellets was compared to the predicted density calculated using the mean mass/mean volume. In the spring

the predicted density (1.12 g cm^{-3}) was similar to that measured in the density gradient (1.11 g cm^{-3}). However, the predicted density was substantially higher than the measured for the summer samples (1.24 g cm^{-3} vs. 1.12 g cm^{-3}) and lower than the measured for the fall samples (1.08 g cm^{-3} vs. 1.19 g cm^{-3}). The predicted fecal pellet density for both species, using the Komar, et al. (1981) equations were similar, 1.04 g cm^{-3} (O. vanhoeffeni) and 1.06 g cm^{-3} (C. finmarchicus). This was 5% lower than the measured dynamic density for C. finmarchicus in the spring, and 15% lower than the measured dynamic density for O. vanhoeffeni in the winter.

4.4.2 PELLET CHARACTERISTICS

For Calanus finmarchicus, fecal pellet volume was significantly different in each season (Fig. 4.3), while for Oikopleura vanhoeffeni, spring fecal pellet volume was significantly different from summer and winter (Fig. 4.4). The largest pellets occurred in the spring for both animals and were filled with diatoms. Analysis of covariance was used to see if a volume to density correlation existed for either C. finmarchicus or O. vanhoeffeni. Measured seasonal volumes for each density value were regressed against the observed seasonal dynamic densities. There was no

significant Season x Density interaction ($p > 0.07$), yet a significant Season variation ($p < 0.01$) occurred for both C. finmarchicus or O. vanhoeffeni, which prevented further analysis. If the fall data set was taken out of the above analysis for C. finmarchicus, there was no significant Season variation ($p > 0.40$) but there was a weak correlation between volume and density ($p = 0.05$).

Seasonal variations in fecal pellet length, width and shape (L/D) occurred (Table 4.2). Individual data sets for both C. finmarchicus and O. vanhoeffeni were analyzed to see if any relationships between dynamic density and particle size could be found. For each season and for each species, the measured dynamic densities were regressed against the mean lengths, mean widths, mean L/D and mean volumes of the fecal pellets for each density value. Mean values were used to decrease the variation of the dependent variable. The same results were obtained when the raw data was used. In five out of six cases, no significant linear relationship was found. There were significant correlations between fecal pellet dynamic density and length ($p < 0.01$), width ($p < 0.05$) and volume ($p < 0.01$) for the winter O. vanhoeffeni sample.

Examination of the feces with the scanning electron microscope revealed differences in the size and type of material ingested in each season. Intact centric and chain-

forming diatoms dominated the spring O. vanhoeffeni fecal pellets (Fig. 4.5A), while masticated, spine and chain forming diatoms filled the spring C. finmarchicus feces (Fig. 4.5B). In the summer, the feces of both species were filled with crushed diatom fragments, mucous "blobs" and dinoflagellate remains (Fig. 4.5C & D). In the fall, C. finmarchicus feces were packed with nanoplankton, bacteria, ciliates, dinoflagellates and a few diatoms (Fig. 4.5F). A mixture of cracked diatoms, coccolithophores, silicoflagellates and dinoflagellates filled the winter O. vanhoeffeni feces (Fig. 4.5E). These seasonal differences in content resulted in different mean seasonal packing indices (i.e. percent free space) for each feces type (Table 4.3). Spring feces from both species were less compact, i.e. they had more open space per unit area. The fall and winter fecal pellets were the most compact. A negative relationship was found between the seasonal median dynamic density and the mean seasonal packing index, i.e. as the density increased the packing index (percent free space) decreased (Figs. 4.6A & B).

4.5 DISCUSSION

4.5.1 CONTROLS ON THE SEASONAL DENSITY OF FECAL PELLETS

Significant seasonal differences occurred among the ranges and median dynamic densities for C. finmarchicus and O. vanhoeffeni. Length, width and volume of the feces also varied seasonally, but in 90% of my data sets, I found no relationship between dynamic density and fecal pellet size or shape. The amount of food present and the type of food ingested has been found to affect the size and density of copepod fecal pellets (Beinfang, 1980; Dagg & Walser, 1986).

In coastal temperate waters, phytoplankters follow a seasonal succession from diatoms to small flagellates (Neilson & Richardson, 1989). In coastal Newfoundland waters I found (Chapt. 3) small centric diatoms, Thalassiosira spp. and Minidiscus triculatos, and pennate diatoms, Navicula spp. and Fragillariopsis spp. are abundant in the early spring. As the spring bloom progresses, chain and spine-forming Skeletonema costatum and Chaetoceros spp. dominate the water column. After the bloom ends, gymnodinoids, chrysophytes and marine snow become abundant. Early in the fall, ciliates, cysts, chrysophytes and marine snow are the most common. By January a fairly diverse phytoplankton population occurs including coccolithophores, silicoflagellates, chrysophytes, dinoflagellates and single

celled diatoms.

This change in phytoplankton community structure is clearly reflected in the fecal pellet contents (Chapter 3). It appears that this change in phytoplankton also affects fecal pellet dynamic density. Contrary to Bienfang (1980), I found that the fecal pellets filled with diatoms had the lowest dynamic density. The compactness of pellet contents rather than the primary density of the components has the greatest influence on fecal pellet density. The hard shells of diatoms and diatom spines cause more empty space (P.I.= 11-25%, Fig. 4.5), while nanoplankton and soft bodied species are packed in the feces with few empty spaces (P.I.= 3.5-5%, Fig. 4.5).

The fact that the opposite results are found for the predicted densities, using the mean mass/mean volume relationship, may be due to the nature of the particles within the feces. Diatom frustules will weigh more than bacteria or marine snow. Thus the predicted densities in this study and Bienfang's (1980) suggest more the "gravimetric density", that due to the weight of the component particles. The dynamic density has important implications for settling velocity models and the potential vertical nutrient flux of fecal pellets.

4.5.2 IMPLICATIONS ON SEASONAL DENSITY VARIATIONS

Seasonal changes in fecal pellet dynamic densities could result in changes in the flux of nutrients and particulate matter to the benthos. The densest fecal pellets of O. vanhoeffeni were found in January, (median=1.23 g cm^{-3}); they contained many coccolithophores, resulting in a potentially large flux of calcium carbonate to the benthos. Measured settling velocities of 80-500 m day^{-1} were found for O. vanhoeffeni fecal pellets in February (Chapter 5), suggesting that these fecal pellets can exit the upper mixed layer.

Analysis of sediment trap samples revealed that the largest number of copepod fecal pellets appears in the fall (McKenzie, et al. unpubl. data), when the pellets are the densest (median=1.19 g cm^{-3}). These pellets are filled with nanoplankton, ciliates and bacteria, implying that seasonally the microbial loop in temperate waters may be linked to the benthos through copepods (Chapter 3). This result is in contrast to the modelling work of Michaels and Silver (1988), which suggests that the microbial loop is only important to the vertical particle flux when swarms of gelatinous zooplankton are present.

The significant variation in pellet volume and density between the spring and fall and winter samples implies that

there are two very different populations of fecal pellets. This agrees with previous studies which found that copepod pellets vary in volume with the type and amount of food offered (Bienfang, 1980; Dagg & Walser, 1986). Tunicates are known to be indiscriminate filter feeders (Alldredge & Madin, 1982). Yet, a constant fecal pellet density value can not be assumed for the year for tunicates. My results agree with others which suggest that C. finmarchicus can be an indiscriminate suspension feeder, consuming particles which occur in the greatest abundance regardless of size (Cowles, 1979; Ishimaru, et al., 1988).

The seasonal variation in fecal pellet dynamic density has important implications for flux models. The flux of fecal pellets is influenced by the sinking rate and decay rate of the pellets and by the zooplankton community structure (Hofmann, et al. 1981; Noji, 1991). Using a single, average density may lead to erroneous estimates of seasonal variation in pellet flux. Using the literature value of 1.22 g cm^{-3} for copepod fecal pellet density (Komar, et al. 1981), a seasonal variation in sinking velocity of 10 m day^{-1} is found, yet this settling velocity is 2-3 times higher than that predicted for all seasons using the median or modal dynamic density values in my study, (Table 4.4). The opposite is found for O. vanhoeffeni, for which the use of a reported salp fecal

median density gives maximum rates 37% lower than that found using the full range of densities. This difference becomes more pronounced for fall and winter feces where the range of dynamic densities is greater, and using the median value gives maximum settling velocities that are $\geq$ 40% lower than that found using the full range of density values. Thus using one density value for the year and within one season can lead to miscalculating the potential of the feces to leave the upper mixed layer.

pellet density of 1.10 g cm^{-3} (Bruland & Silver, 1981) gives settling velocities 2-5 times lower than those predicted using the median and modal values from this study.

My data suggest that fall and winter fecal pellets have the greatest potential for leaving the upper mixed layer and contributing to verticle particle flux. This is substantiated by sediment trap samples which show maximum copepod fecal pellet flux from August to October, and maximum oikopleurid fecal pellet flux in December (McKenzie, et al. unpubl. data) The need to know accurately the seasonal dynamic density ranges of the fecal pellets is important in determining the actual potential role that feces may play in particulate flux. Using the equation for copepod fecal pellet settling velocity from Chapter 5, and the densities and fecal pellet sizes reported here, I can calculate sinking velocities. Using the median dynamic density value for the spring (1.11 g cm^{-3}), results in 12 m day^{-1} settling velocity range (13 - 25 m day^{-1}) but if the minimum and maximum dynamic densities (1.07 & 1.16 g cm^{-3}) are used a 32 m day^{-1} settling velocity range is obtained (7 - 39 m day^{-1}). Using the literature value of 1.22 g cm^{-3} gives a predicted settling velocity range of 28 m day^{-1} (28 - 56 m day-1). Changing the density of the fecal pellet by 10% (my median value vs. literature) can result in a 55 - 80% change in the predicted sinking velocity, and using one

Figure 4.1: Seasonal Density Distribution of Oikopleura vanhoeffeni Fecal Pellets.

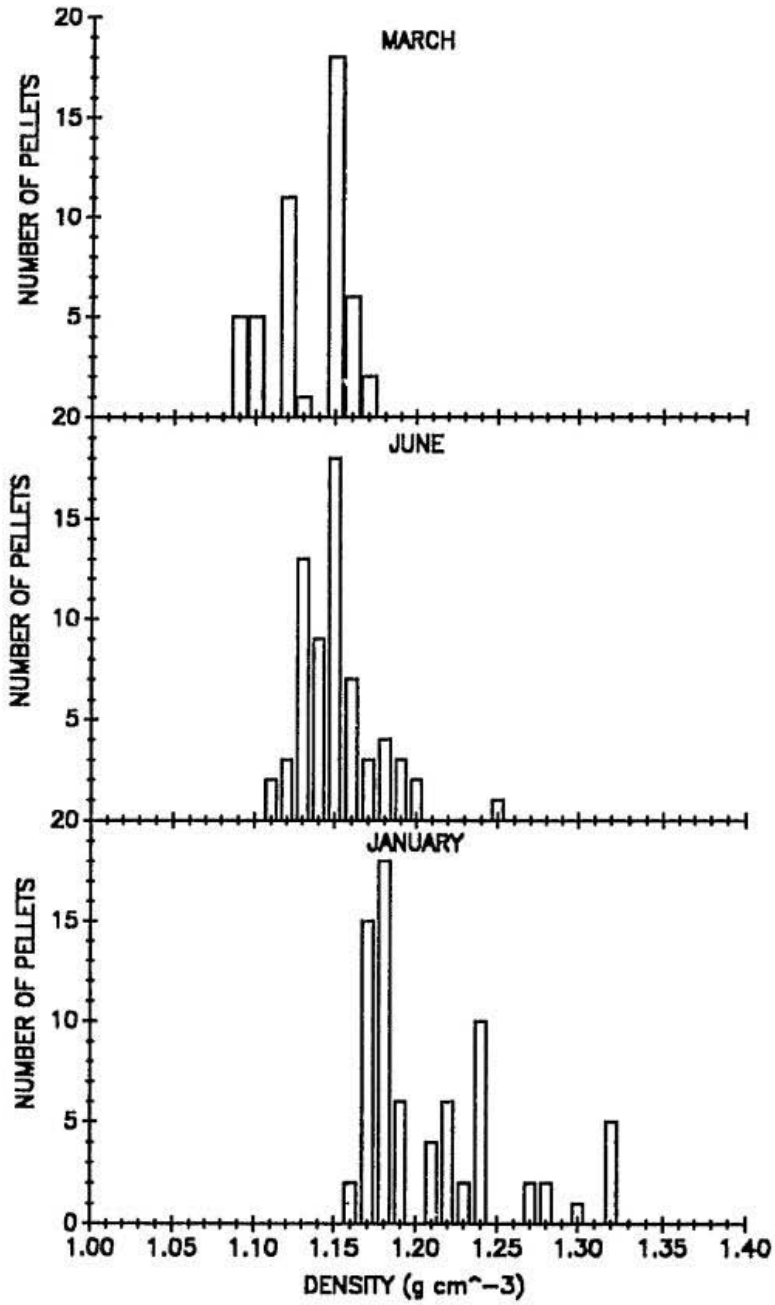


Figure 4.2: Seasonal Density Distribution of Calanus finmarchicus Fecal Pellets.

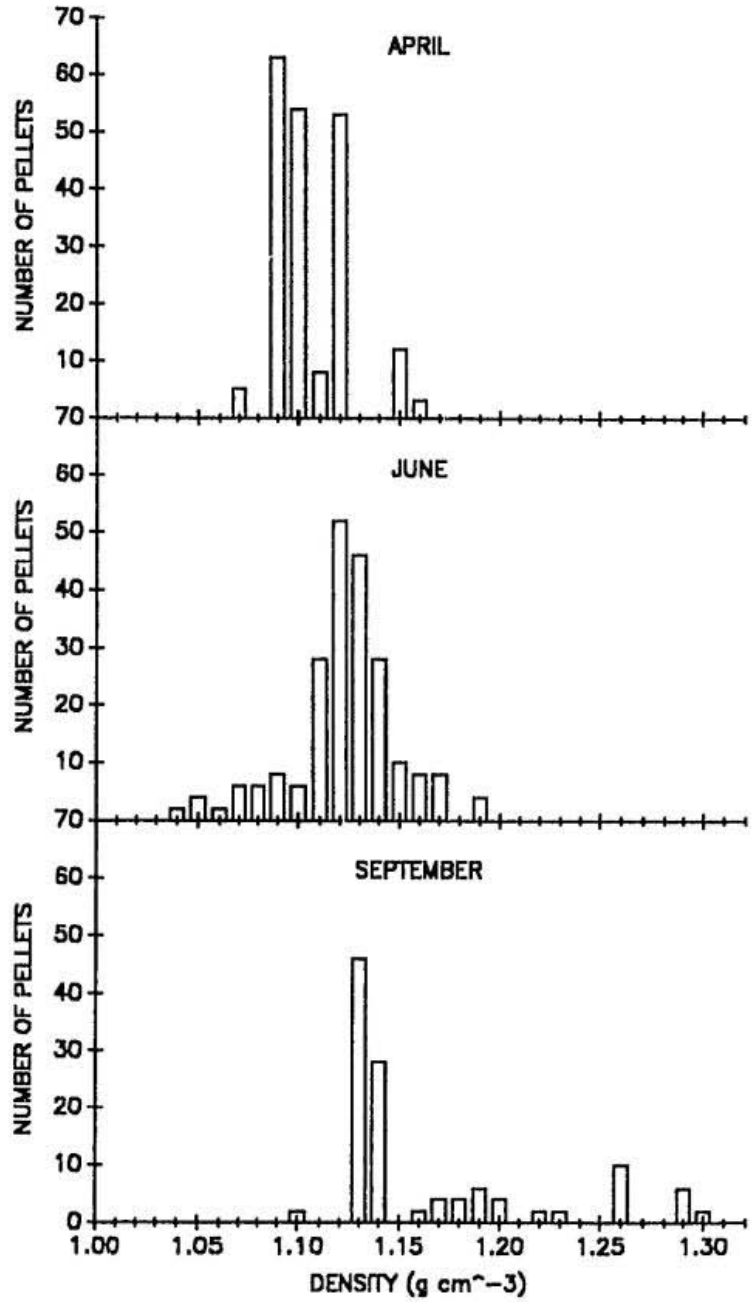


Table 4.1: Seasonal Values of Fecal Pellet Densities for *Oikopleura vanhoeffeni* and *Calanus finmarchicus*.

SEASON	N	RANGE g cm^{-3}	MEDIAN g cm^{-3}	MEAN g cm^{-3} $\pm$SD	MODE g cm^{-3}
SPRING					
O. vanhoeffeni	48	1.09-1.17	1.13	1.13$\pm$.02	1.15
C. finmarchicus	287	1.07-1.16	1.11	1.11$\pm$.02	1.09
SUMMER					
O. vanhoeffeni	65	1.11-1.25	1.16	1.15$\pm$.02	1.15
C. finmarchicus	219	1.04-1.19	1.12	1.12$\pm$.03	1.12
FALL					
C. finmarchicus	131	1.10-1.30	1.19	1.17$\pm$.05	1.13
WINTER					
O. vanhoeffeni	73	1.16-1.32	1.23	1.21$\pm$.04	1.18

Table 4.2: Mean Seasonal Pellet Lengths, Widths, Shapes (L/D) and Volumes for Oikopleura vanhoeffeni and Calanus finmarchicus.

SEASON	LENGTH(μm) $\bar{x}$ ±SD	WIDTH(μm) $\bar{x}$ ±SD	L/D(μm) $\bar{x}$ ±SD	VOLUME(μm^3) $\bar{x}$ ±SD
SPRING				
O. vanhoeffeni	1011±362	306±99	3.3±2.5	$5.22\pm4.90X10^8$
C. finmarchicus	564±167	69±13	8.2±2.0	$2.26\pm1.37X10^6$
SUMMER				
O. vanhoeffeni	534±158	201±79	2.7±1.2	$1.11\pm1.37X10^8$
C. finmarchicus	326±124	70±19	4.7±3.0	$1.45\pm1.21X10^6$
FALL				
C. finmarchicus	312±110	58±14	5.4±4.9	$9.31\pm8.19X10^5$
WINTER				
O. vanhoeffeni	529±179	171±70	3.1±3.5	$8.71\pm11.8X10^7$

Figure 4.3: Mean Seasonal Calanus finmarchicus Fecal Pellet Volume. Error Bars Represent 95% Confidence Intervals.

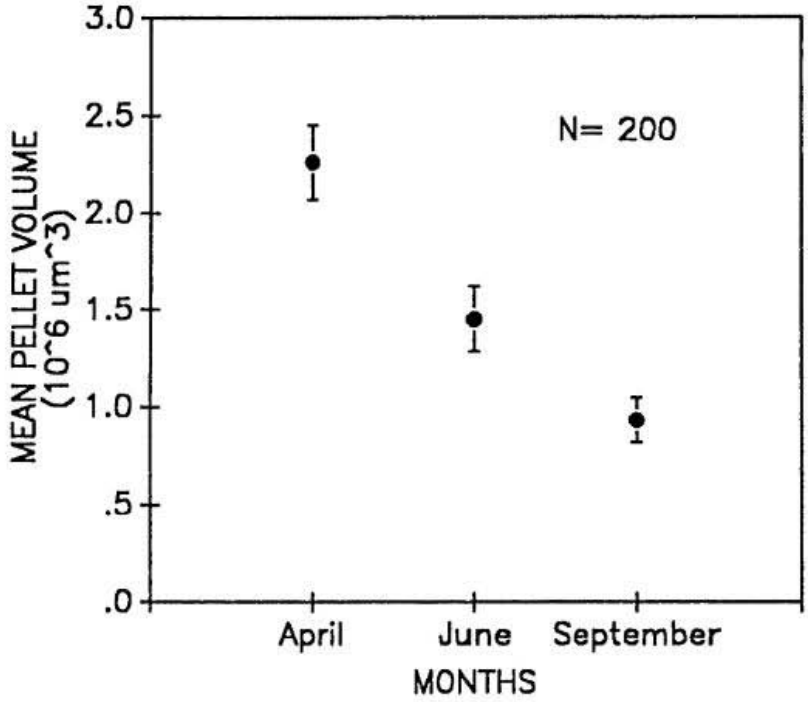


Figure 4.4: Mean Seasonal Oikopleura vanhoeffeni Fecal Pellet Volume. Error Bars Represent 95% Confidence Intervals.

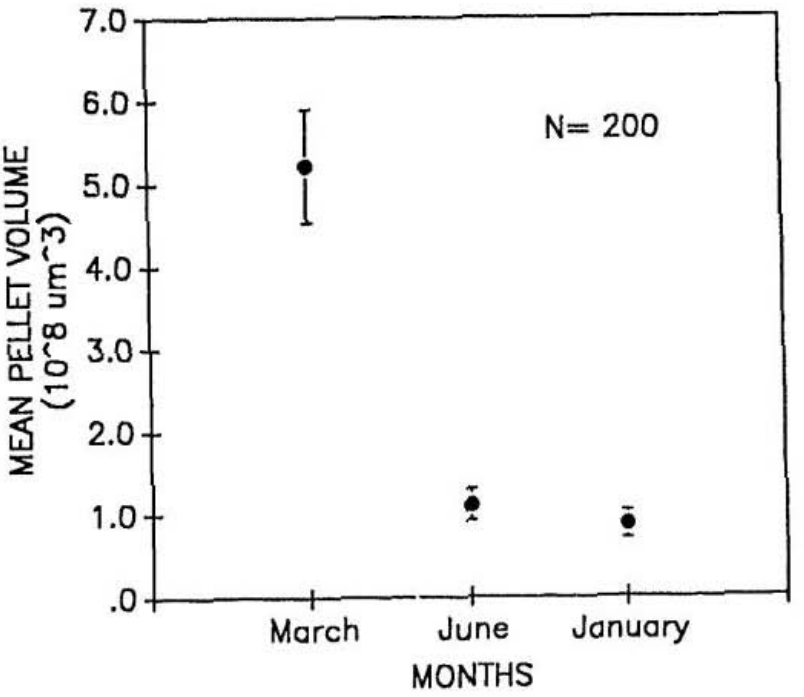


Figure 4.5: Seasonal Content and Packing of Copepod and Tunicate Fecal Pellets.

A. Overview of spring O. vanhoeffeni fecal pellet, Ce= centric diatom. Scale bar= 3 μm.

B. Overview of spring C. finmarchicus fecal pellet, C= Chaetoceros spine, S= Skeletonema costatum spines. Scale bar= 3 μm.

C. Overview of summer O. vanhoeffeni fecal pellet showing broken diatoms. Scale bar= 3 μm.

D. Overview of summer C. finmarchicus fecal pellet showing diatom fragments. Scale bar= 3 μm.

E. Overview of winter O. vanhoeffeni fecal pellet, D= diatom, Co= coccolith. Scale bar= 3 μm.

F. Overview of fall C. finmarchicus fecal pellet, D= diatom, B= bacteria. Scale bar= 3 μm.

Figure 4.5: Seasonal Content and Packing of Copepod and Tunicate Feces.

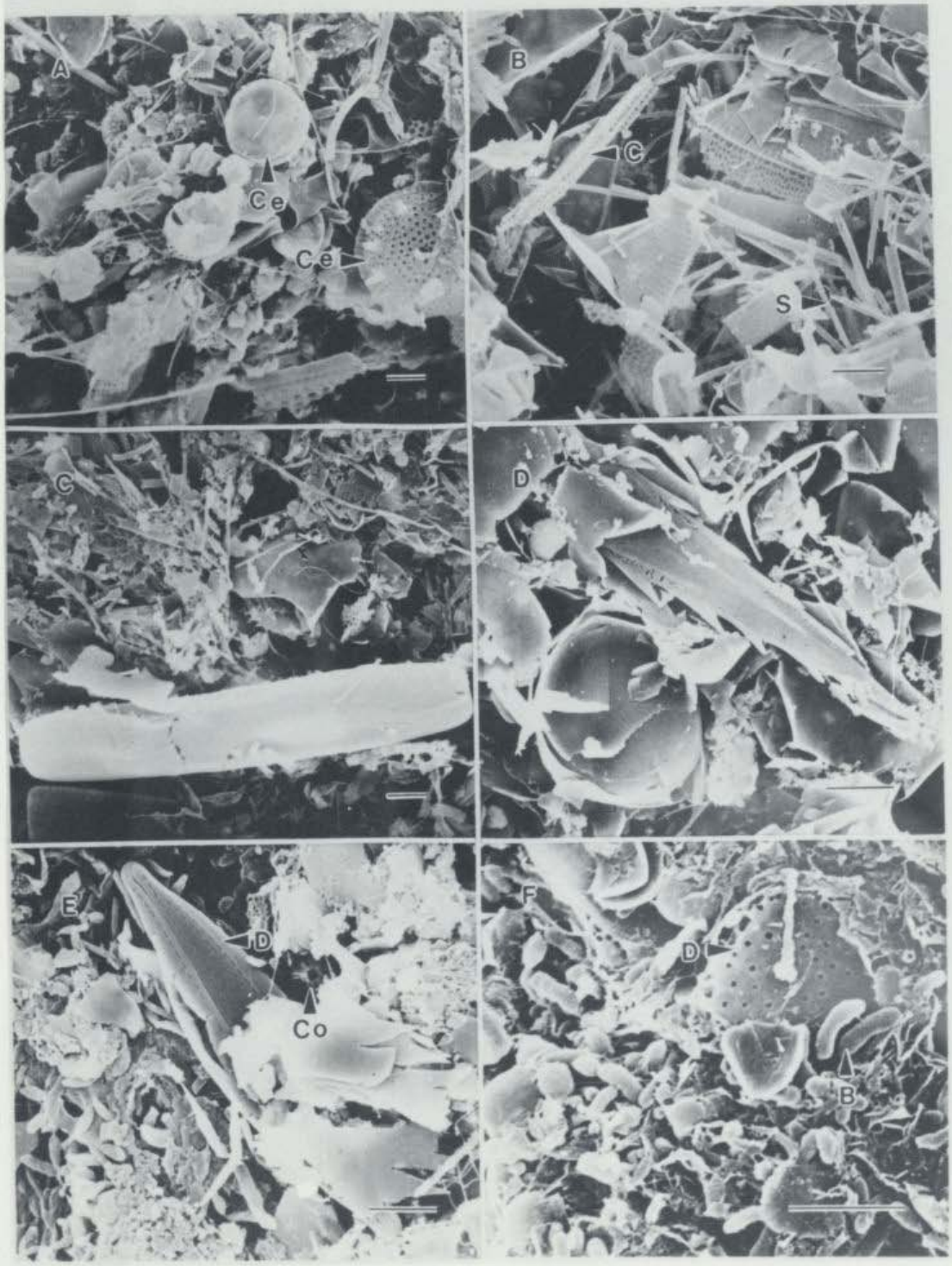


Table 4.3: Mean Seasonal Packing Index for *Oikopleura vanhoeffeni* and *Calanus finmarchicus* Fecal Pellets.

SEASON	PELLET INDEX	
	O. vanhoeffeni %open ± SD	*C. finmarchicus* %open ± SD
SPRING	12 ± 5%	25 ± 6%
SUMMER	11 ± 5%	15 ± 3%
FALL	**	5 ± 2%
WINTER	3.5 ± 2%	**

** No samples taken

Packing Index (P.I.)= $\frac{\text{Area open}}{\text{Total area}} \times 100$

Figure 4.6: Relationship Between Seasonal Median Density and Mean Seasonal Packing Index. Error Bars Represent Standard Deviations.

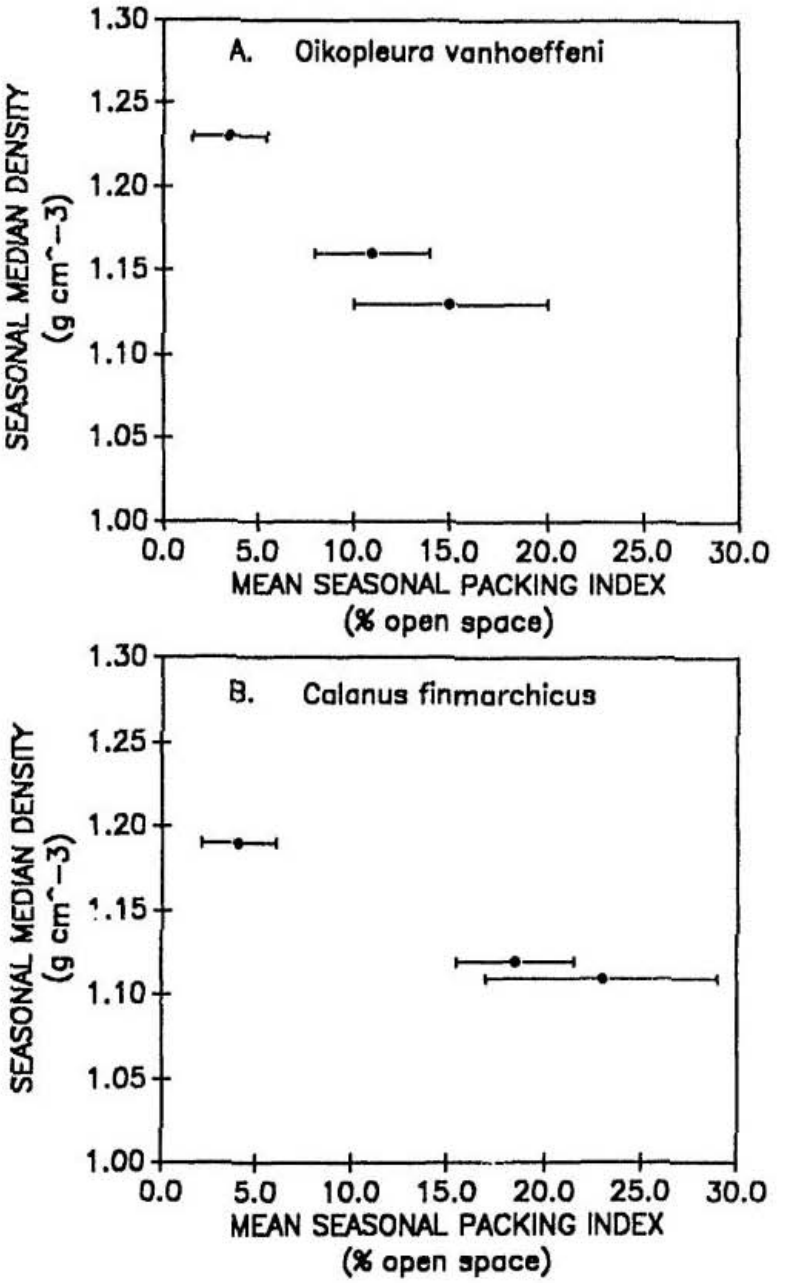


Table 4.4: Test for Seasonal Settling Velocities Using One Density Value.

	SETTLING VELOCITY			
DENSITY ($g\ cm^{-3}$)	**SPRING** ($m\ day^{-1}$)	**SUMMER** ($m\ day^{-1}$)	**FALL** ($m\ day^{-1}$)	**WINTER** ($m\ day^{-1}$)
Literature				
1.22 (C.f.)	40.8	48.3	39.9	**
1.10 (O.v.)	123.9	51.1	**	40.0
Mean Value[1]				
C.f.	18.5	24.2	29.9	**
O.v.	170.4	83.1	**	86.2
Mode Value[1]				
C.f.	14.4	24.2	21.9	**
O.v.	201.4	83.1	**	72.6

**No samples taken
C.f.= C. finmarchicus
O.v.= O. vanhoeffeni
[1]Values taken from Table 1, this study

CHAPTER 5

THE DETERMINATION AND COMPARISON OF STILL WATER SINKING VELOCITIES OF FECAL PELLETS FROM A COPEPOD AND A TUNICATE

5.1 ABSTRACT

The still water settling velocities of the fecal pellets from a pelagic tunicate, Oikopleura vanhoeffeni, and a copepod, Calanus finmarchicus, were measured in a modified settling column. After inverse transformation of the C. finmarchicus data to insure normality, width and frontal cross sectional area were positively correlated with the settling velocity. While no transformations were needed for the O. vanhoeffeni data, length, width, volume and surface area were positively correlated with the settling velocity. Measured settling velocities were 3-10 times lower than predicted values from literature equations, leading me to develop equations based on my data. Both fecal types sank at low Reynold's numbers ($\leq$ 3.6) and followed Stokian principles. For O. vanhoeffeni the settling velocity (W_s) is equal to;

$$W_s = .002 \frac{1}{\mu} (\rho_s - \rho) g D_n^{2.0} \left(\frac{L}{D}\right)^{.331}$$

and for C. finmarchicus;

$$W_s = .028 \frac{1}{\mu} (\rho_s - \rho) g L^{1.8} \left(\frac{L}{D}\right)^{-1.759}$$

where μ is the viscosity of the water, ρ_s is the fecal pellet density, ρ is the density of the water, g is gravity (981 g cm^{-1}), D_n is the diameter of an equivalent sphere, L and D are the length and diameter of the fecal pellet. These equations explained 84% of the variance for O. vanhoeffeni pellets and 70% of the total variance for C. finmarchicus pellets. The 2-20 fold faster sinking velocities of the O. vanhoeffeni fecal pellets indicate that these feces have a greater potential in exiting the upper mixed layer and contributing to the vertical particle flux than do copepod feces.

5.2 INTRODUCTION

Aggregates, either fecal pellets or marine snow, are important vectors in the transport of nutrients, amino acids, lipids, radionuclides and pollutants from the euphotic zone (Angel, 1984; Krishnaswami, et al., 1985; Smetacek, 1985; Bathmann & Liebezeit, 1986; Matsueda, et al., 1986). Fecal pellets from zooplankton are also considered to be important food sources for other zooplankton through coprophagy and coprohexy (Paffenhofer & Knowles, 1979; Lampitt, et al., 1990, Noji, et al., 1991) and for microbes and heterotrophic flagellates through degradation (Gonzàlez & Biddanda, 1990). The role that fecal pellets from macrozooplankton play in nutrient cycling is controlled in part by their settling velocity and sinking behavior. Are they able to sink out of the upper mixed layer or are they recycled there? Does their settling behavior enhance their opportunities to become entangled with marine snow?

Accurate determination of sinking velocity is important for flux models and to understand the role that aggregates may play in nutrient cycles. Numerous studies have been done on the sinking velocity of copepod, euphausiid, salp, and doliolid fecal pellets and of marine snow (Turner, 1977; Small, et al., 1979; Bruland & Silver, 1981; Angel, 1984;

Alldredge & Gotschalk, 1988 & 1989; Deibel, 1990). Sinking velocity has been found to depend on water temperature and on the concentration and type of available food particles (Bienfang, 1980; Fowler & Knauer, 1986).

The sinking velocity of a fecal pellet is dependent on its shape, size and density relative to the surrounding water's density and viscosity (Janke, 1966; Komar, et al., 1981). Equations that predict the settling velocity of fecal pellets under different conditions have been developed, based on the settling behavior of glass rods, quartz particles or sand grains (Janke, 1966; Komar, 1980). The accuracy of these models for predicting actual sinking velocities of fecal pellets has not been tested. Komar, et al. (1981) showed that the equations he developed for cylindrical and ellipsoid particles (Komar, 1980), produced values that agreed with the sinking velocity trends of copepod and euphausiid fecal pellets.

The purpose of this study was to measure and compare the settling velocities of fecal pellets from the copepod, Calanus finmarchicus, and the tunicate, Oikopleura vanhoeffeni, and examine their depedence on physical characteristics of the fecal pellets. The density, length and width of each fecal pellet was measured, which allowed me to compare observed settling velocities to those predicted using current equations from the literature

(Komar, et al., 1981), and to test the accuracy of these equations for extremely low temperatures.

5.3 MATERIALS AND METHODS

5.3.1 GENERAL

Oikopleura vanhoeffeni was collected in February, 1991 using the methods described in Chapter 2. Pellets were collected after half an hour and the lengths and widths were measured to the nearest 10.0 μm, using an ocular micrometer on a Zeiss dissecting microscope. Pellets were then transferred to a 5 ml vial for density and sinking experiments.

Calanus finmarchicus was collected in April, 1991 using the methods described in Chapter 2. The animals were kept alive in the laboratory for three weeks by changing the water every 6-12 h. Pellets were measured as above and then pipetted into 5 ml vials for density and sinking determination.

The density of individual fecal pellets was determined using a continuous density gradient technique with colloidal silica and sucrose solution (Schwinghamer, et al., 1991; Chapter 4). The density for C. finmarchicus fecal pellets was measured prior to sinking experiments while the density for O. vanhoeffeni pellets was measured after sinking experiments. C. finmarchicus fecal pellets were gently rinsed with 0.2 μm filtered seawater to wash off any density gradient solution prior to being sunk. To ensure that no

colloidal silica and sucrose from the density gradient mixture was adhering to the feces, nine fecal pellets were sunk prior to having their density determined. No difference was found between these methods (Wilcoxon paired t test, $p > 0.60$). Examination of the pellets on a scanning electron microscope revealed no difference in appearance between pellets whose density was determined prior to being sunk and those that were never put in the density gradient solution. All sinking experiments were done within 2 h of collecting the fecal pellets.

5.3.2 SINKING VELOCITY DETERMINATION

Fecal pellets were sunk individually in a modified settling column (SETCOL), consisting of an inner square chamber with an inside width of 20 cm and a height of 1 m (Fig. 5.1). A funnel was located 20 cm from the top. The bottom of the chamber consisted of another funnel that led down to a clamped hose through which pellets could be retrieved. This chamber was filled with 0.2 μm filtered seawater (0° C, salinity = 32 ppt, density = 1.0213 g cm^{-3}) and set inside a 40 cm wide water jacket containing flowing seawater. One side of the outer chamber had a glass panel to allow better viewing of the feces. Black garbage bags were hung on two sides of the column to prevent light

reflection. A 50 cm ruler was fixed to an outer wall of the inner chamber to mark timing intervals.

Pellets were injected with a pipette just below the water surface at the top and fell 20 cm before passing through the funnel. The purpose of this funnel was to try and eliminate turbulence caused by the pipette. Beginning 15 cm below the funnel, each pellet was timed using a stop watch over 5 intervals of 5 cm each. If possible, the pellet was retrieved through the hose at the bottom funnel and either saved for density determination or prepared for scanning electron microscopy.

5.4 RESULTS

The feces from Oikopleura vanhoeffeni were dark brown, a prolate spheroid shape and sank at rates 2-20 times faster than the cylindrical Calanus finmarchicus feces (Table 5.1 5.2). Feces from both zooplankters sank in a diagonal orientation and rotated (i.e. cork screwed). Reynold's numbers for O. vanhoeffeni fecal pellets were generally above the Stokes range (Re= 0.3 - 3.6), while C. finmarchicus feces were within the Stokes range (Re = 0.01 - 0.05).

Being able to accurately predict the sinking velocity of fecal pellets from easily measured physical characteristics is important for modeling the role of feces in nutrient flux. The settling velocity for O. vanhoeffeni fecal pellets was found, using linear regression, to be positively correlated with volume (r^2 = 66, p = .015), surface area (r^2 = 76, p = .005), length (r^2 = 86, p = .001) and width (r^2 = 51, p = .048), while after inverse transformation to insure normality the settling velocity for C. finmarchicus pellets was positively correlated with the feces frontal cross-sectional area (r^2 = 27, p = .019) and the width (r^2 = 32, p = .009). The feces of both animals were filled with diatoms, eliminating the variability in sinking velocity due to food type (Bienfang, 1980). These

differences in settling velocity correlations could be due to the differences in the shape and size of the fecal pellets (Table 5.1 & 5.2).

Previous studies have generated modified Stokes equations to predict the sinking velocity of fecal pellets and of marine snow (Komar, et al., 1981; Carder & Steward, 1986; Alldredge & Gotschalk, 1988). I proceeded to test my measured sinking velocities against predicted values generated in several ways. First, predicted values were obtained using the Stokes equation for a sphere

$$W_s = \frac{1}{18} \frac{1}{\mu} (\rho_s - \rho) g D_n^2 \qquad (Eq. 1)$$

where μ and ρ are the water viscosity (18.8×10^{-3} g cm) and density (1.0213 g cm^{-3}), ρ_s is the fece's density (g cm^{-3}), g is the acceleration of gravity (981 cm s^{-2}), and D_n is the equivalant spherical diameter (cm), i.e. the diameter of a sphere having equal volume and density to that of the fecal pellet. Second and third predicted values were generated by using Komar's (1980) equations for a cylindrical and an ellipsoid particle. For a cylinder

$$W_s = 0.0790 \frac{1}{\mu} (\rho_s - \rho) g L^2 \left(\frac{L}{D}\right)^{-1.664} \qquad (Eq. 2)$$

where L is length of the cylinder (cm) and D is its diameter (cm). For an ellipsoid

$$W_s = \frac{1}{18} \frac{1}{\mu} (\rho_s - \rho) g D_n^2 E^{.380} \qquad (Eq. 3)$$

where E is equal to the shape factor defined by Janke (1966)

$$E = D_s \left(\frac{D_s^2 + D_i^2 + D_l^2}{3} \right)^{-.5} \qquad (Eq. 4)$$

where D_s, D_i and D_l are the shortest, the intermediate and the longest axial diameters (cm).

The values obtained using these equations are reported in Tables 5.2 and 5.3. Measured sinking velocities were regressed against predicted values and the resulting model examined for 1.) a significant F value and normally distributed residuals 2.) an intercept not significantly different than zero and 3.) a slope not significantly different from one. The slopes were significantly different from one in all regressions and predicted values overestimated the measured settling velocity by 2-100 times (Table 5.2 & 5.3). This lead me to try and modifiy Stokes equation to better predict the sinking velocity for both copepod and tunicate fecal pellets at -1 to 0° C.

5.4.1 DEVELOPMENT OF SETTLING VELOCITY EQUATIONS

The data sets for O. vanhoeffeni and C. finmarchicus were randomly split in half into a predictor and tester set. Four subsets were tried for both the predictor and tester sets, with all subsets giving the same equations and having a total variance ± 5 m day^{-1}. To determine if I could use Stokian principles for both types of feces I calculated the drag coefficient using Komar & Taghon's (1985) equation

$$C_d = \frac{4}{3} \frac{(\rho_s - \rho)}{\rho} \frac{(g\, D_n)}{W_m^2} \qquad (Eq.\ 5)$$

where W_m is the measured settling velocity (cm s^{-1}). The log of C_d was regressed against the log of the Reynold's number, where $Re = W_m\, D_n/\mu$, for each type of fecal pellet (Fig. 5.2 & 5.3). This yielded the following equation for O. vanhoeffeni

$$C_d = 382.1\, Re^{-1.1} \qquad (Eq.\ 6)$$

and for C. finmarchicus

$$C_d = 99.08\, Re^{-1.07} \qquad (Eq.\ 7)$$

The linear relationship between the inverse Reynold's number and the drag coefficient is indicative of Stokian behavior (Tritton, 1977). The Reynold's numbers for O. vanhoeffeni were slightly above the accepted Stokes range but based on the C_d to Re relationship, I treated both types of pellets in the same way. The observed settling velocities were compared to those of equivalent spheres, resulting in a modified Stokes equation. After transforming equation 1 to its log-log form to learn the value of the constant and the power on D_n, I regressed

$$Log \left(\frac{W_s \mu}{(\rho_s - \rho)\ g} \right) \ vs \ Log \ D_n$$

For O. vanhoeffeni, this resulted in

$$W_s = .004 \ \frac{1}{\mu} \ (\rho_s - \rho) \ g \ D_n^2 \qquad (Eq.\ 8)$$

and for C. finmarchicus

$$W_s = .005 \ \frac{1}{\mu} \ (\rho_s - \rho) \ g \ D_n^{1.8} \qquad (Eq.\ 9)$$

I next took the same approach as Komar (1980) in trying to get a modified Stoke's equation that included a shape factor (Eq. 2). That is, I wanted an equation in the form of

$$W_s = k \frac{1}{\mu} (\rho_s - \rho) g \lambda^2 f(\delta) \qquad (Eq. 10)$$

where k will be a constant, λ is a fecal pellet size scale (i.e. length or width) and $f(\delta)$ is a function of fecal pellet shape (L/D). Length, width and nominal diameter were sequentially tried for λ, with length and nominal diameter giving similar goodness-of-fit for both feces types. I regressed the log-log form of equation 10

$$Log \left(\frac{W_s \mu}{\rho_s - \rho} g \lambda^2 \right) vs \; Log \left(\frac{L}{D} \right)$$

This yielded the following equations for O. vanhoeffeni

$$W_s = .002 \frac{1}{\mu} (\rho_s - \rho) g D_n^2 \left(\frac{L}{D} \right)^{.331} \qquad (Eq. 11)$$

$$W_s = .010 \frac{1}{\mu} (\rho_s - \rho) g L^2 \left(\frac{L}{D}\right)^{-1.030} \quad (Eq. 12)$$

and for C. finmarchicus

$$W_s = .026 \frac{1}{\mu} (\rho_s - \rho) g D_n^2 \left(\frac{L}{D}\right)^{-.407} \quad (Eq. 13)$$

$$W_s = .028 \frac{1}{\mu} (\rho_s - \rho) g L^{1.8} \left(\frac{L}{D}\right)^{-1.759} \quad (Eq. 14)$$

Equations 8, 11 and 12 for O. vanhoeffeni and equations 9, 13 and 14 for C. finmarchicus were then tested against the tester set of data. The six equations had no intercepts significantly different from zero and had no slopes significantly different from one. Equations 11 and 14 explained more of the variance (r^2 = 84 & 70% respectively) than the other four equations, indicating that shape has a measurable influence on sinking velocity.

Deibel's (1990) study and those in my study were produced by gelatinous, filter-feeding zooplankton. The volume of the feces was similar, yet Deibel found $W_s \propto Vol^{.32}$ and $W_s \propto Diam^{.96}$ while I found $W_s \propto Vol^{.62}$ and $W_s \propto Diam^{2.0}$. The density of these two types of feces may have been different. My study had values of 1.17-1.23 g cm^{-3}, while Deibel presumed his were $\leq$ 1.10 g cm^{-3}. The appearance of the feces may also help explain some of these differences; the doliolid feces resemble marine snow (Deibel, 1990) while the oikopleurid feces in my study are compact cylinders.

That the settling velocity of O. vanhoeffeni fecal pellets is correlated with surface area while the settling velocity of C. finmarchicus feces is correlated with frontal cross-sectional area is probably attributable to differences in the fecal pellet shapes. O. vanhoeffeni produces ovoid pellets, with L/D ratios of 1.9 - 5.8, while C. finmarchicus produces feces that are cylidrical, L/D = 6.5 - 12.8, (Table 5.1 & 5.2). Surface properties of the two types of feces may vary, which could affect settling behavior (Chase, 1979). Both feces are covered by a peritrophic membrane, though O. vanhoeffeni's appears thinner and may be a mucous sheet rather than a chitinous membrane. The sides of the fecal pellets are not streamlined due to protruding phytoplankton remains and attached bacteria and flagellates (González & Biddanda,

5.5 DISCUSSION

5.5.1 SETTLING VELOCITY AND BEHAVIOR OF COPEPOD AND TUNICATE FECES

The settling velocities I measured for C. finmarchicus are generally lower than those reported in the literature for calanoid feces, yet most studies are done at 15 - 20° C, while my study was done at -1° C (Honjo & Roman, 1978; Small, et al., 1979; Bienfang, 1980). The rates I obtained are similar to those measured in the spring in the middle Atlantic Bight by Lane, et al. (submitted). These low sinking velocities suggest that the spring feces are recycled in the upper water column. This agrees with previous studies that found small fecal pellets are recycled in the upper water column (Hofmann, et al., 1981; Small, et al., 1987), and with sediment trap work done in Conception Bay, Newfoundland, in April, in which few copepod feces are found (McKenzie, et al. unpubl. data). The high sinking velocities of O. vanhoeffeni fecal pellets indicate that these fecal pellets have a greater potential in exiting the upper mixed layer and in contributing to the nutrient flux than do copepod feces.

The higher Reynold's numbers found for the O. vanhoeffeni fecal pellets agree with those found by Deibel (1990) for doliolid pellets. Both the fecal pellets in

1990; McKenzie unpubl. obs.), which may have great effect on their orientation and settling behavior. The fecal pellets were diagonally oriented and rotated as they sank. Turner (1977) found this same rotating behavior for Pontella meadii fecal pellets.

The orientation and rotating behavior of the fecal pellets may affect their ability to form aggregates. Alldredge and McGillivary (1991) found that attachment probability of marine snow particles increases with increasing volume, surface area of contact and collision velocity. The diagonal orientation and rotation of the feces should increase the apparent surface area of contact, i.e. the encounter radius. Aggregates or marine snow play an important role in the transporting of particulate matter from the surface to deep water (Silver & Alldredge, 1981; Smetacek, 1985; Alldredge & Gotschalk, 1988 & 1989; Passow, 1991). The ability of small fecal pellets to form aggregates would enhance the probability of their being transported from the upper mixed layer.

5.5.2 MEASURED VS. PREDICTED SETTLING VELOCITIES

Current equations in the literature for predicting settling velocity of fecal pellets provide accurate trends for my data but overestimate the actual sinking velocities (Tables 5.3 & 5.4). This inaccuracy has important implications for flux estimates and for determining the role of fecal pellets in pelagic and benthic nutrient cycles.

The modified Stokes equations I derived differ from those of Komar (1980) only in their constants and the power to which the shape factor is raised. The equations for both copepod and tunicate feces have the settling velocity proportional to the square of the nominal diameter, as is found in Stokes relationships. My results agree with other studies which found shape important to the settling velocity and that drag increases with decreasing Reynold's number (Janke, 1966; Komar & Reimers, 1978; Komar, 1980; Komar, et al., 1981; Komar & Taghon, 1985).

The higher settling velocity for the tunicate feces agrees with previous studies that report the importance of feces from gelatinous filter feeders to the nutrient and particle flux (Bruland & Silver, 1981; Matsueda, et al., 1986; Bathmann, 1988). Using my equations to get predicted seasonal settling velocities for O. vanhoeffeni and C. finmarchicus fecal pellets indicate that both spring and

early summer copepod fecal pellets (5 -40 m day^{-1}) are likely to be recycled in the upper mixed layer while tunicate feces (80 - 700 m day^{-1}) and fall copepod feces (25 - 95 m day^{-1}) have a greater potential for leaving the upper mixed layer and contributing to nutrient flux.

Figure 5.1: SETCOL Used in Fecal Pellet Sinking Experiments

H= Height of column, 100 cm

I= Water inflow in outer water jacket

O= Water outflow in outer water jacket

P= Pressure cap in outer water jacket

R_1= 50 cm ruler

R_2= Hose to retrieve fecal pellets

W_1= Width of inner column, 20 cm

W_2= Width of outer water jacket, 40 cm

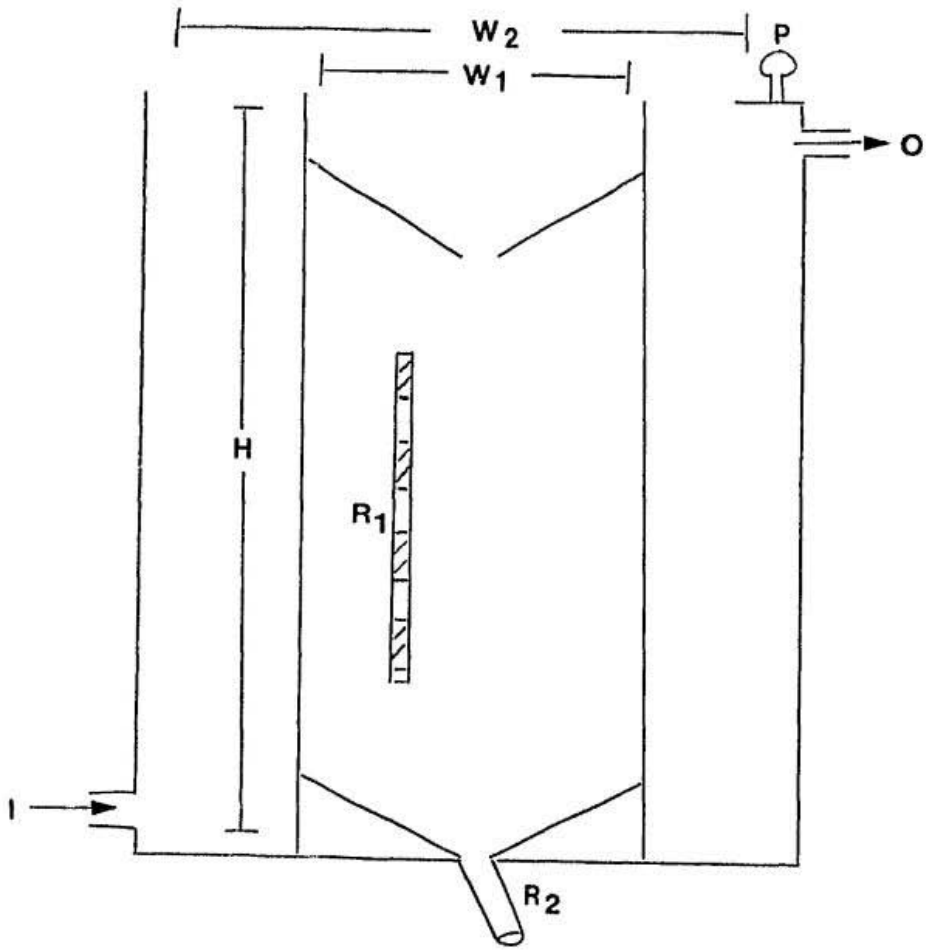


Table 5.1: Physical Measurements of Oikopleura vanhoeffeni Fecal Pellets used in the SETCOL.

PELLET NUMBER	LENGTH cm	WIDTH cm	D_n cm	L/D cm	DENSITY g cm^{-3}	VELOCITY cm s^{-1}
1	.140	.03	.09	4.7	1.29	.4579
2	.105	.03	.09	3.5	1.18	.3369
3	.140	.04	.13	3.5	1.22	.5184
4	.042	.02	.06	2.0	1.28	.1468
5	.065	.02	.06	3.3	1.22	.0864
6	.100	.03	.08	3.3	1.15	.2592
7	.130	.04	.11	3.3	1.23	.3715
8	.102	.04	.10	2.6	1.18	.2592
9	.140	.03	.09	4.7	1.21	.4567
10	.057	.03	.07	1.9	1.25	.1020
11	.100	.03	.08	3.3	1.24	.3578
12	.130	.04	.11	3.3	1.19	.2789
13	.105	.03	.09	3.5	1.27	.6780
14	.140	.04	.13	3.5	1.26	.6543
15	.043	.02	.06	2.2	1.27	.1406
16	.130	.04	.11	3.3	1.21	.3297

** The first 8 are the reported tester set.

Table 5.2: Physical Measurements of Calanus finmarchicus Fecal Pellets used in the SETCOL.

PELLET NUMBER	LENGTH cm	WIDTH cm	D_n cm	L/D cm	DENSITY g cm^{-3}	VELOCITY cm s^{-1}
1	.10	.010	.03	10.0	1.09	.0228
2	.10	.009	.03	11.4	1.09	.0242
3	.12	.011	.03	10.2	1.09	.0285
4	.08	.010	.03	8.3	1.09	.0315
5	.08	.006	.02	12.8	1.10	.0119
6	.10	.009	.03	11.4	1.09	.0249
7	.07	.010	.02	6.5	1.09	.0242
8	.07	.010	.02	6.5	1.08	.0209
9	.09	.011	.03	8.4	1.10	.0303
10	.10	.010	.03	10.0	1.09	.0223
11	.09	.010	.03	9.0	1.09	.0210
12	.10	.009	.03	11.4	1.08	.0174
13	.12	.010	.03	12.0	1.10	.0330
14	.08	.007	.02	11.4	1.09	.0121
15	.08	.006	.02	11.4	1.10	.0130
16	.07	.010	.02	6.5	1.09	.0234
17	.10	.010	.03	10.0	1.09	.0241
18	.10	.011	.03	9.1	1.09	.0312

**The first 9 are the reported tester set.

Table 5.3: Measured and Predicted Sinking Velocities for *Oikopleura vanhoeffeni* Fecal Pellets.

PELLET NUMBER	W_m (m day^{-1})	W_s (m day^{-1})	W_c (m day^{-1})	W_e (m day^{-1})	W_p (m day^{-1})
1	457.92	6431.7	1216.1	3746.6	477.1
2	336.96	3718.7	820.9	2591.3	236.1
3	518.40	9561.3	2166.8	6938.3	595.0
4	146.88	2452.4	658.0	2009.8	126.9
5	86.40	2130.7	477.7	1464.8	132.0
6	259.20	2443.4	514.5	1603.2	162.2
7	371.52	7401.9	1608.1	5107.8	479.3
8	259.20	4792.2	1124.3	3574.5	286.8

W_m is the measured settling velocity

W_s is the predicted settling velocity using Stokes equation for a sphere (Eq. 1).

W_c is the predicted settling velocity using Komar (1980) equation for a cylinder (Eq. 2).

W_e is the predicted settling velocity using Komar (1980) equation for an ellipsoid (Eq. 3).

W_p is the predicted settling velocity using my equation (Eq. 11).

**This table includes only the predictor data set

Table 5.4: Measured and Predicted Sinking Velocities for *Calanus finmarchicus* Fecal Pellets.

PELLET NUMBER	W_m (m day^{-1})	W_s (m day^{-1})	W_c (m day^{-1})	W_e (m day^{-1})	W_p (m day^{-1})
1	22.86	592.7	60.2	303.3	26.3
2	24.22	497.0	48.2	241.9	20.8
3	28.54	758.3	76.7	384.8	32.6
4	31.50	522.3	56.4	287.0	26.0
5	11.98	315.9	29.4	147.4	13.1
6	24.96	497.0	48.2	241.9	20.8
7	24.24	445.9	52.1	267.4	25.7
8	20.90	37.9	44.3	227.5	21.9
9	30.36	769.4	82.7	419.2	37.1

W_m is the measured settling velocity

W_s is the predicted settling velocity using Stokes equation for a sphere (Eq. 1).

W_c is the predicted settling velocity using Komar (1980) equation for a cylinder (Eq. 2).

W_e is the predicted settling velocity using Komar (1980) equation for an ellipsoid (Eq. 3).

W_p is the predicted settling velocity using my equation (Eq. 14).

**This table includes only the predictor data set

Figure 5.2: Regression of the Log of the Drag Coefficient on the Log of the Reynold's Number (r=.95).

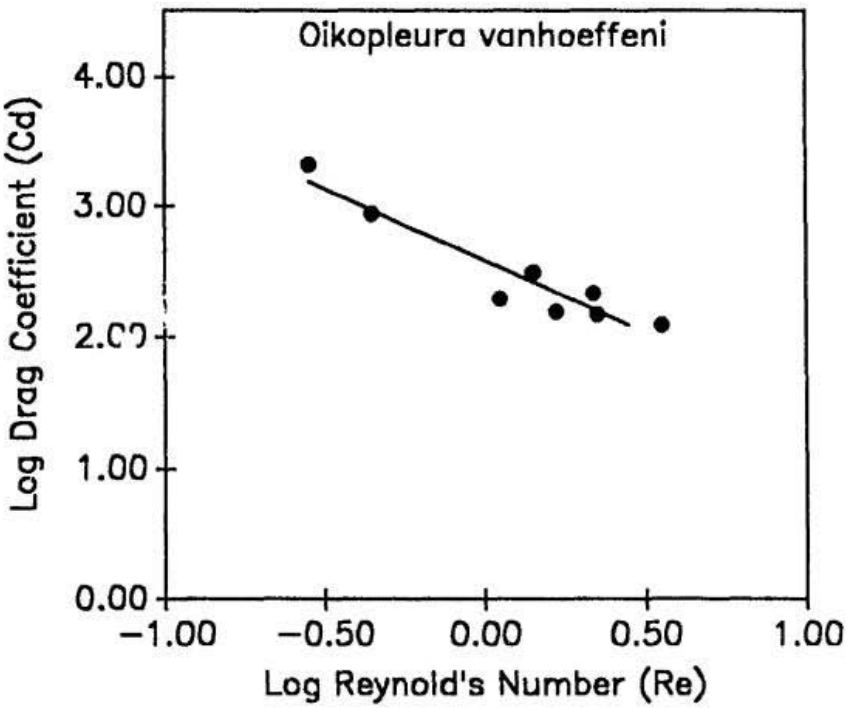
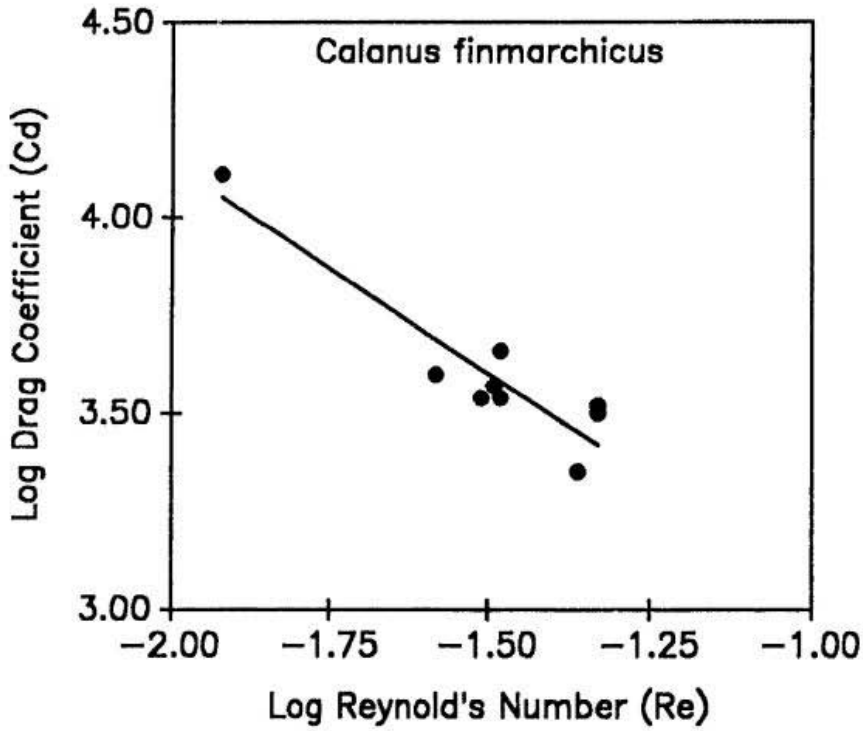


Figure 5.3: Regression of the Log of the Drag Coefficient on the Log of the Reynold's Number (r=.92).



CHAPTER 6

SEASONAL DEGRADATION OF CALANUS FINMARCHICUS FECAL PELLETS: IMPLICATIONS FOR VERTICAL PARTICLE FLUX

6.1 ABSTRACT

The decay rate of Calanus finmarchicus fecal pellets was measured in the laboratory and field in April, July and October. Water temperature ranged from -1° to 10° C. Differences in decay rate for the fecal pellets were found between the laboratory and field. In the field, fecal pellets in all three months were completely degraded (i.e. fragmented) or the POC and Si content was reduced by at least 50%, within 2 weeks. Dissolved free amino acids were released into the surrounding water as the feces were fragmenting. Spring feces have the greatest potential for transporting particulate silicate, while October feces have the greatest potential for transporting particulate organic carbon from the upper mixed layer. This means that seasonally, the microbial loop can contribute to the vertical carbon flux, as fall feces were filled with bacteria and ciliates.

6.2 INTRODUCTION

In recent years, the role of fecal pellets as transporters of nutrients from the euphotic zone has been debated (Hofmann, et al., 1981; Krause, 1981; Corner, et al., 1986 and ref. within; Bathmann, et al., 1987; Martens & Krause, 1990). Are medium sized fecal pellets (1 mm > x > 100 μm in length) recycled in the upper water column or are they able to sink to the benthos? Sediment trap work from the Antarctic, Atlantic and Pacific oceans shows a decrease in fecal pellet numbers with depth suggesting that they are recycled in the upper water column (Bishop, et al., 1978; Knauer, et al. 1979; Urrère & Knauer, 1981; von Bodungen, et al., 1987). McCave (1975) reported that only large, rapidly sinking particles contribute to the vertical particle flux. More recent work suggests that marine snow aggregates are responsible for transporting particles to the benthos (Smetacek, 1985; Alldredge & Gotschalk, 1989). However, since fecal pellets are frequently found in marine snow they may still play an important role in transporting nutrients from the surface.

The rate at which pellets are degraded by bacteria, protists and zooplankton, and the rate at which nutrients leach out of them, controls how long they are a nutrient source. González and Biddanda (1990) found that bacteria

and protists together had the greatest impact on decay rate. Other studies have shown that copepods can eat the peritrophic membrane or the fecal pellets themselves, or cause fragmentation of the feces (Paffenhöfer & Knowles, 1979; Hofmann, et al., 1981; Skjoldal & Wassmann, 1986; Lampitt, et al., 1990; Noji, et al., 1991). Temperature has been found to have a positive effect on decay rate (Honjo & Roman, 1978; Turner, 1979; Roy & Poulet, 1990). Jumars, et al. (1989) suggested that 90% of the DOC (dissolved organic carbon) in small fecal pellets (diameter < 100 μm) leached out within 2 seconds of excretion. Gonzàlez and Biddanda (1990) found that after 16 days the C/N value present was similar to that present initially, implying that the C/N value is not a good indicator of particle age or nutritional potential. Other possible indicators of nutritional value are lipid or amino acid content.

The composition of amino acids within fecal pellets is more complex than that found in the animals' diet (Poulet, et al., 1986). Both amino acids and lipids in fecal pellets decrease with depth, suggesting that these compounds are quickly utilized by microbes (Wakeman, et al., 1984; Matsueda, et al., 1986). Roy and Poulet (1990) found that a majority of the amino acids within fecal pellets steadily decreases during decay. Both bacteria and heterotrophic flagellates take up dissolved free amino acids (DFAA)

(Andersson, et al., 1985; Flynn & Fielder, 1989; Kirchmann, et al., 1989 & 1990).

Calanus finmarchicus, a raptorial suspension feeder, is a major macrozooplankter in coastal Newfoundland waters. The purpose of my study was to determine the rate of decay of C. finmarchicus fecal pellets in the laboratory and in the field in April, July and October. The decay rate was measured by determining pellet membrane state, bacterial numbers in the feces and in the water, particulate organic carbon and particulate biogenic silicate content of the feces, and dissolved free amino acid composition of the water.

6.3 MATERIALS AND METHODS

6.3.1 GENERAL

Calanus finmarchicus was collected in April, July, September-October 1990 and April 1991 using the methods described in Chapter 2. The animals were kept alive in the laboratory for 1.5 weeks by changing the water every 6-12 h. 1 h after each water change, fecal pellets were gathered using the method in Chapter 2.

6.3.2 TEST OF THE DECAY TUBES

The fecal pellets were decayed in 210 ml PVC tubes. The tubes were 10 x 5 cm and had either 20 μm nitex mesh at each end (these will be referred to as open) or a PVC cap (these will be referred to as closed). The purpose of the open tubes was to allow water flow and the exchange of bacteria and nanoflagellates. Performance of the open tubes was tested by suspending them in a water flow of 2, 5, and 10 cm s^{-1}, injecting a drop of fluorescent rhodamine dye in front, and then timing how long it took for the drop to pass through the tube. Another performance check was done by hanging a tube filled with a solution of rhodamine dye in a water table at flow speeds of 2, 5 and 10 cm s^{-1}, and taking a sample every five minutes for an hour. In all current

speeds flow occurred through the open tubes. To ensure that pellets were not being broken mechanically, 10 pellets were put in each of 35 tubes. Seven tubes were then hung in each of the 3 current speeds (5, 10, 20 cm s^{-1}), and 7 tubes were placed in 0.2 μm filtered still seawater and 7 tubes were placed in unfiltered still seawater. A tube was retrieved from each treatment every two days and the pellet membranes examined. The pellets in flowing water did not fragment sooner than the pellets in still water, implying no mechanical break-up of the fecal pellets at current speeds up to 20 cm s^{-1}. This is in excess of the maximum 10 cm s^{-1} currents that occur in the field (DeYoung & Sanderson pers. comm.).

6.3.3 DECAY EXPERIMENT SETUP

Four experimental setups were deployed in the field with a corresponding four setups in the laboratory. Seven open tubes were filled with 20 μm filtered seawater and 20 fecal pellets, and suspended in still water at ambient seawater temperature in a 12 h light dark cycle in the laboratory for two weeks in April, July and October. A complimentary set of seven open tubes was deployed at a depth of 20 m in Logy Bay, Newfoundland (47° 37.85'N, 52° 39.52'W). Deployment of the tubes in the field was done

by SCUBA divers. The tubes were attached to a 10-pronged, 0.5 m diameter wheel array with large rubber bands made from innertube. The wheel was attached to a taught-wire mooring anchored in 50 m of water. Tubes were retrieved from the field by SCUBA divers and from the laboratory every second day and the pellet membranes observed and photographed. A corresponding seven closed tubes were filled with 20 μm filtered seawater and 20 fecal pellets and incubated in parallel in the laboratory and field.

Simultaneously, another set of seven open and seven closed tubes were filled with 20 μm filtered seawater and 60 to 100 fecal pellets, and incubated in the laboratory and field as above. These feces were monitored for changes in bacteria numbers, and particulate organic carbon (POC) and particulate silicate (Si). A tube from each open and closed set in the laboratory and field was retrieved every two days for two weeks and the fecal pellets analyzed, with triplicate samples taken every fourth day. Triplicate water samples from outside and inside the decay tubes were analyzed for bacteria numbers and dissolved free amino acid (DFAA) composition.

6.3.4 PHYSICAL MEASUREMENTS

Pellet state refers to the appearance of the peritrophic membrane and the integrity of the pellet. Pellets were classified as having an intact membrane, a 50% degraded membrane, or a 100% degraded membrane, or they were fragmenting into smaller pieces. Upon retrieval of the tubes, the fecal pellets were fixed in a 5 ml vial with 2% glutaraldehyde. Later, 10-20 pellets were put on a slide and viewed under a Zeiss Axioplan Microscope. The pellets were photographed under both transmitted light and phase contrast. The proportion of intact membrane was estimated (100, 50 or 0%). Also catalogued was when fragmentation of the feces occurred.

Triplicate 4 ml water samples were stained with DAPI for bacteria counts, and filtered onto 0.2 μm Nuclepore filters and rinsed with 2 ml of 0.2 μm filtered seawater (Porter & Feig, 1980). Bacteria were counted using a Ziess Inverted Microscope with epifluorescent illumination and the mean for triplicate samples was taken with less than 5% variation found between the maximum and minimum counts. Using the graphic estimation method of Cassell (1965) allowed for a 95% confidence limit on each individual count.

Every second day three feces were saved for bacteria counts along with a blank. The samples were corrected for

the blank and averaged. Fecal pellets for bacteria counts were pipetted into 2.5 ml centrifuge tubes and fixed with 0.5 ml of 5% buffered formaldehyde. Before analysis, 1.5 ml of tetrasodium pyrophosphate was added to each tube and the solution sonicated for 8 s at a power setting of 2 (Heat Systems-Ultrasonics, Inc.; Velji & Albright, 1986). The solution was stained with DAPI and filtered onto a 0.2 μm Nuclepore filter and counted as above.

6.3.5 CHEMICAL ANALYSIS

For particulate silicate (Si) analysis, 20-30 fecal pellets were measured (length & width) using an ocular micrometer in a Zeiss dissecting microscope, and pipetted with a plastic pipette onto 0.2 μm Nuclepore filter and rinsed with 0.2 μm filtered seawater. Each filter was then frozen in 4.5 ml polypropylene tube until further analysis. Blanks were prepared by rinsing filters with 0.2 μm filtered seawater.

The Si samples were thawed and hydrolysed with 4 ml of 0.5% Na_2CO_3, then capped and heated for 3 h in a water bath at 85° C. After being refrigerated overnight, 4 ml of Na_2CO_3 was used to rinse the tube and combined with the initial amount in a plastic beaker. The resulting solution was brought to a pH of 3.4 with 0.5 N HCl. The volume was

made up to 10 ml with distilled water, and 4.5 ml were saved in a plastic tube. Analysis was continued as for dissolved silicate (Strickland & Parsons, 1972).

Particulate organic carbon (POC) was measured using a Hewlett Packard CHN Analyzer for the July and October samples, and a Perkin Elmer 2400 CHN Elemental Analyzer for the April samples. 40-70 fecal pellets were measured (length & width) using a Zeiss dissecting microscope, pipetted onto a 13 mm Whatman GFF/C filter, rinsed with 0.2 μm filtered seawater and frozen until analysis on the CHN analyzer. Blanks were prepared with each sample.

Water for DFAA analysis was frozen immediately upon retrieval. DFAA's were measured using a Varian aerograph HPLC model 502000 and the OPA method of Lindroth and Mopper (1979).

6.4 RESULTS

The rate of decay appeared similar in all seasons in the field open experiment, although differences in the rate of decay were observed in the laboratory open experiments. Rate of decay is referring to the time required for the fecal pellet's membrane to degrade and the pellet to fragment, or to the time required for the decrease of $\geq$ 50% of the POC and Si in the feces. Bacteria numbers in the feces and surrounding tube water were lower in the field than in the laboratory. Percent composition of aspartic acid (ASP), glutamic acid (GLU) and threonine (THR) varied between the field and laboratory experiments. Decay rate, bacteria counts and DFAA composition were similar in all seasons for the closed experiments in the field and laboratory. Pack ice came into Logy Bay in April and prevented diving during the two week decay study, therefore only initial and final values are reported.

6.4.1 RESULTS OF THE PELLET STATE MEASUREMENTS

Pellet state refers to the degree to which the peritrophic membrane is degraded, and to when the pellet fragments. In the field open experiments, over half of the feces had membranes that were $\geq$ 50% degraded by day 2 in

July (6° C) and day 4 in October (10° C) (Fig. 6.1A & B). While in the laboratory open experiments, this occurred by day 6 in July and day 10 in October (Fig. 6.2A & B) and in the closed experiments this occurred by day 2 in July and day 8 in October (Fig. 6.3A & B). It was never observed in the laboratory open or closed experiments in April (-1° C) (Fig. 6.4A & B).

Fragmenting of some of the feces occurred on day 4 in both July and October in both the field open and laboratory open experiments (Fig. 6.1). In the field open experiment in April, 90% of the feces were fragmented by day 16, while no fragmentation was observed during the laboratory open experiment but some occurred by day 4 in the laboratory closed experiment (Fig. 6.4).

6.4.2 NUTRIENT CONTENT OF THE FECES

Decay of fecal pellets was also observed by measuring the change in the particulate silicate (Si) and particulate organic carbon (POC) concentrations ($\mu g\ \mu m^{-3}$) in the feces. In the field open experiments, Si concentrations decreased by $\geq$ 50% by day 14 in July and day 16 in October, while POC concentrations decreased by $\geq$ 50% by day 6 in October (Fig. 6.5A & B). In April, both Si and POC had decreased by $\geq$ 50% by day 16 (Table 6.1). In all set ups in July, POC was

undetectable by my methods after day 0. In the laboratory open experiments, Si had decreased by $\geq$ 50% by day 12 in April, day 6 in October and no change in concentration was seen in July (Fig. 6.6A & B, Table 6.1). While in the closed experiments, Si decreased by day 2 in April, day 14 in July and day 8 in October (Fig. 6.7A & B, Table 6.1). POC decreased by $\geq$ 50% in the laboratory open experiments by day 4 and by day 16 in the closed experiments in October (Figs. 6.6 & 6.7). POC concentrations dropped on day 8 in the laboratory open and on day 6 in the closed experiment in April, they then increased until final concentrations equalled initial concentrations (Figs. 6.6 & 6.7).

6.4.3 BACTERIA MEASUREMENTS

Bacteria in the feces doubled on day 4 in July and day 2 in October, and then declined in the field open experiments (Fig. 6.8A) while bacteria numbers in the water within the tubes peaked on day 4 in both July and October and had slight increases on days 12 and 14 (Fig. 6.8B). Bacteria numbers within the tubes were compared to bacteria numbers in the bay. For both July and October, levels outside the tubes were constant over the 2 week study and the numbers similar to those within the tubes, excluding day 4 when bacteria numbers doubled within the tubes.

In the laboratory open experiments, bacteria numbers peaked on days 4 and 12 in April and doubled on day 2 in July and day 4 in October (Fig. 6.9A). Bacteria in the tube water peaked on days 4 and 10 in April, day 4 in July and days 4 and 14 in October (Fig. 6.9B). In the surrounding water bacteria seemed to cycle on a 2 to 4 day pattern in all seasons and excluding April, the numbers were similar to those in the tube water. In April, bacteria numbers were 1.5-2 times lower in the surrounding water than in the tube water. Bacteria numbers were 1.5 - 3 times higher in the feces, tube water and surrounding water in the laboratory experiments than those found in the corresponding field experiments (Figs. 6.8 & 6.9). In all seasons in the closed experiments, bacteria numbers in the feces doubled on days 8 to 12 (Fig. 6.10A). Bacteria in the tube water peaked on days 4 and 12 in July and October but never increased in April (Fig. 6.10B).

6.4.4 DISSOLVED FREE AMINO ACID MEASUREMENTS

In the field and laboratory open experiments total percent composition of individual DFAA in the water both within the tubes and outside was similar (Table 6.2), though total concentrations over the two week study were 80% (July) and 30% (October) higher within the tubes than in the

surrounding water in the field, and 13% (April), 0% (July) and 40% (October) higher within the tubes in the laboratory open experiments. The elevated levels within the tubes were due to the peaks in DFAA on days 2 and 6 in July and days 2 and 16 in October in the field (Fig. 6.11A), and day 4 in April, days 6, 10-14 in October in the laboratory (Fig. 6.11B). Comparing field and corresponding laboratory open experiments, total DFAA concentrations within the tube water were 50% higher in the field in July, while in October they were 70% higher in the laboratory. The percent composition of ASP, GLU and THR varied between the field open experiments and both the laboratory open experiments and the closed experiments, (Table 6.2).

6.5 DISCUSSION

6.5.1 SEASONAL FLUX POTENTIAL OF *CALANUS FINMARCHICUS* FECAL PELLETS

The rate of decay of fecal pellets in the open experiments is different between the laboratory and field. Complete degradation, or at least the loss of $\geq$ 50% of the nutrient content of the feces, occurred within two weeks in the field in April, July and October (Table 6.1), while water temperature ranged from -1° C to 10° C. In the laboratory the rate of decay appeared related to the temperature of the water, as no decay was seen in April (-1° C) and $\geq$ 50% of the pellets were degraded in October (10° C). Sediment trap studies have found copepod feces and other small fecal pellets in deep water (Honjo & Roman, 1978; Urrère & Knauer, 1981; von Bodungen, et al., 1987), yet recent work has shown that small and medium sized fecal pellets are recycled in the upper water column (Krause, 1981; Hofmann, et al., 1981). Aggregates and marine snow are important vectors in the particle and nutrient flux from the euphotic zone (Angel, 1984; Smetacek, 1985; Conover, et al., 1986). The inclusion of calanoid feces in marine snow could explain how they can be transported to depth.

The seasonal potential contribution of Calanus finmarchicus fecal pellets to the particulate flux appears

to be controlled not by how fast the feces decay, but by their ability to sink out of the upper mixed layer, either individually or in marine snow. The potential seasonal contribution to the nutrient flux will depend on the initial nutrient content of the feces. Silicate concentrations in the feces were still higher after two weeks in April then they were initially in the fall, while the opposite was found with POC, (Table 6.1). Using my equation for copepod fecal pellet sinking velocity (Chapter 5) and the density data from Chapter 4, predicted fecal pellet sinking velocities of 5 - 35 m day^{-1} for April and 25 - 95 m day^{-1} for October were calculated. This suggests that spring copepod feces are not likely to transport silicate out of the upper mixed layer but that the microbial loop could be important seasonally in transporting carbon from the upper mixed layer as the fall feces were filled with bacteria and ciliates (Chapter 3). This is substantiated by the finding of copepod feces in sediment trap samples in Conception Bay, Newfoundland in August - October (McKenzie, et al., unpubl. obs.).

It is axiomatic that bacteria play a role in the releasing or remineralization of the nutrients in fecal pellets. Gonàlez and Biddanda (1990) found that bacteria and protists together had the greatest impact on the decay rate of fecal pellets. Could the role of bacteria and

heterotrophic flagellates in remineralizing feces vary seasonally in subarctic waters? Choanoflagellates, known bacteriovores, are abundant early in the Newfoundland spring bloom (McKenzie, unpubl. data) and have been found on the surface of feces (Gonzàlez & Biddanda, 1990; McKenzie unpubl. obs.).

Previous work done during the spring bloom in Conception Bay, Newfoundland, shows very low bacterial numbers and activity (Pomeroy and Deibel, 1986). More recent work suggests that it is the level of substrate that controls the activity of bacteria at -1° C (Pomeroy, et al., 1991). This relationship between substrate levels (DFAA) and bacteria numbers is more obvious in the July and October closed experiments (Figs. 6.10 & 6.12). The peaks in DFAA concentrations in the open experiments (Fig. 6.11) occur at the same time that feces with $\geq$ 50% degraded membranes or fragmenting pellets are found, suggesting that the feces are releasing DFAA into the water (Fig. 6.1 & 6.2). The initial colonization of bacteria and heterotrophic flagellates on the feces may cause breakage of the membrane and release of DFAA (Cho & Azam, 1988). Since substrate levels are low in the water column in the spring (Helleur, et al., unpubl. obs.), fecal pellets may represent small microcosms of energy. The slow sinking velocities (5 - 35 m day^{-1}) and the "rapid" decay of these feces suggests that spring

copepod fecal pellets are recycled in the upper water column. This is substantiated by sediment trap samples in which few copepod feces are found (McKenzie unpubl. obs.).

6.5.2 COMPARISON OF DECAY SETUPS

One purpose of my work was to compare laboratory and field decay rates for Calanus finmarchicus fecal pellets. Open and closed setups were used to determine the effect of water exchange. Contamination due to contact with the container walls was possible in all set ups. Gowing and Silver (1983) pointed out that this may result in faster decay rates in laboratory studies compared to those occurring in nature. Hence, the rates I obtained may be maximal, but I feel that the results and processes observed are accurate descriptions of the decay of C. finmarchicus fecal pellets in coastal Newfoundland waters, although they may more accurately depict the decay of feces within marine snow than as a free falling pellet.

The closed experiments in the laboratory and field gave similar data for each month, with the rate of decay intermediate between the field and laboratory open experiments. Bacteria numbers in the closed experiments are lower then in open experiments (Figs. 6.8-6.10) and DFAA concentrations tend to decrease in surrounding water.

Whenever pellets fragment and release DFAAs, there is a brief resurgence of bacteria. This is followed by a decrease in DFAAs and bacteria numbers, indicating the importance of substrate levels for bacteria (Keller, et al., 1982; Pomeroy, et al., 1991).

The open experiments permitted the exchange of nutrients, bacteria, and nanoplankton between tube water and the surrounding water. The degree to which this exchange occurred is unknown since the bacteria numbers in the tube water are different from those in the surrounding water (Fig. 6.8 & 6.9). This difference is more pronounced in the laboratory than in the field. In July and October, bacteria numbers are higher in the laboratory than field, suggesting the possibility for enhanced decay in the laboratory. The feces in the open experiments appear to be affecting the "local" water within the tubes in terms of bacteria numbers. Peaks of bacteria in the tube water occur at the same time as pellets are fragmenting, implying that the feces are releasing bacteria into the surrounding water. Gonzalez and Biddanda (1990) found a similar result when they decayed feces in running North Sea water.

The differences in the decay rate between the set ups have important implications for determining accurate fecal pellet decay rates and understanding the role of fecal pellets in the water column. Previous studies have been

done in the laboratory under various conditions, from still water to revolving plankton wheels or running water (Honjo & Roman, 1978; Turner, 1979; Gowing & Silver, 1983; Gonzàlez & Biddanda, 1990; Roy & Poulet, 1990). The rates of decay that I found in my laboratory open and closed experiments agree with previous studies that showed increased decay with increased temperature (Turner, 1979; Roy & Poulet, 1990). The rate of Si and POC loss from the feces in the field open experiments may have been dependent on temperature, but this can not be determined from my data set. The overall decay rates for the feces in the field open experiments exceed those found in laboratory studies (Honjo & Roman, 1978; Turner, 1979; Roy & Poulet, 1990; this study). The content of C. finmarchicus fecal pellets varies seasonally, with fall feces being filled with bacteria (Chapter 3). This is reflected in the 2-3 fold higher number of bacteria present in the fall decay study (Figs. 6.8-6.10). Whether it is the content of the feces, the water temperature, or microbe and flagellate numbers in the water column that control the decay rate can not be determined from my study. Different DFAA composition and relative percentages are found between field open and both laboratory open and closed experiments (Table 6.2), suggesting different decay processes between the field and laboratory. More work needs to be done on the seasonal decay rate of fecal pellets in the field and on the

processes that control this decay.

6.5.3 CONCLUSIONS

Differences in the decay rate of Calanus finmarchicus fecal pellets occur between the field and laboratory. In the field, fecal pellets in April, July and October are completely decayed or have lost $\geq$ 50% of their nutrient content within two weeks (Table 6.1). The extent to which these fecal pellets can contribute to the nutrient flux will depend on their ability to sink out of the upper mixed layer. Calculating sinking velocities for C. finmarchicus fecal pellets reveals that fall feces (25-95 m day^{-1}) sank at velocities ca. 2-20 times higher than those in the spring (5-35 m day^{-1}) and summer (10-40 m day^{-1}), indicating that fall feces have a greater potential in exiting the upper mixed layer. Thus, the role of C. finmarchicus fecal pellets in the water column may vary seasonally, with spring and early summer feces tending to be recycled in the upper water column. Fall feces are filled with bacteria and nanoplankton (Chapter 3) suggesting that the microbial loop can contribute seasonally to the nutrient flux via copepod feces.

Figure 6.1: Pellet State Measurements in the Field Open Experiments.

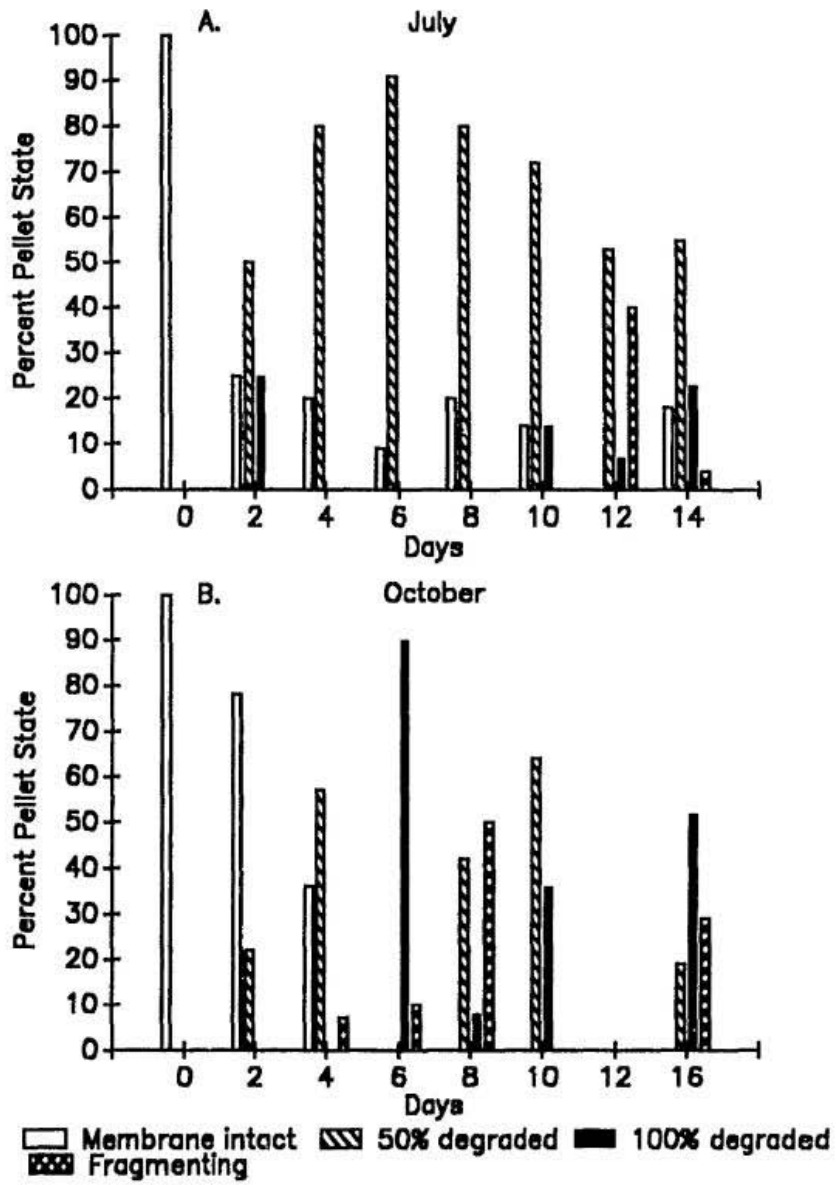


Figure 6.2: Pellet State Measurements in the Laboratory Open Experiments.

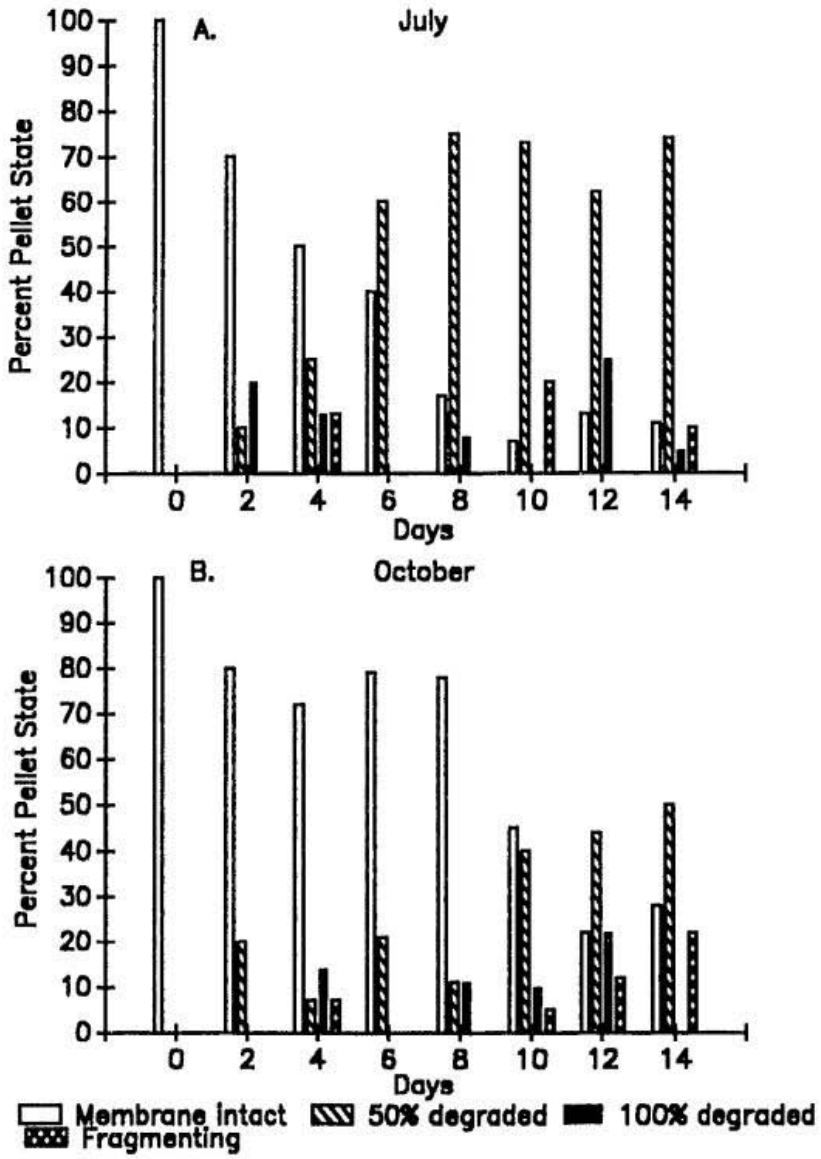


Figure 6.3: Pellet State Measurements in the Closed Experiments.

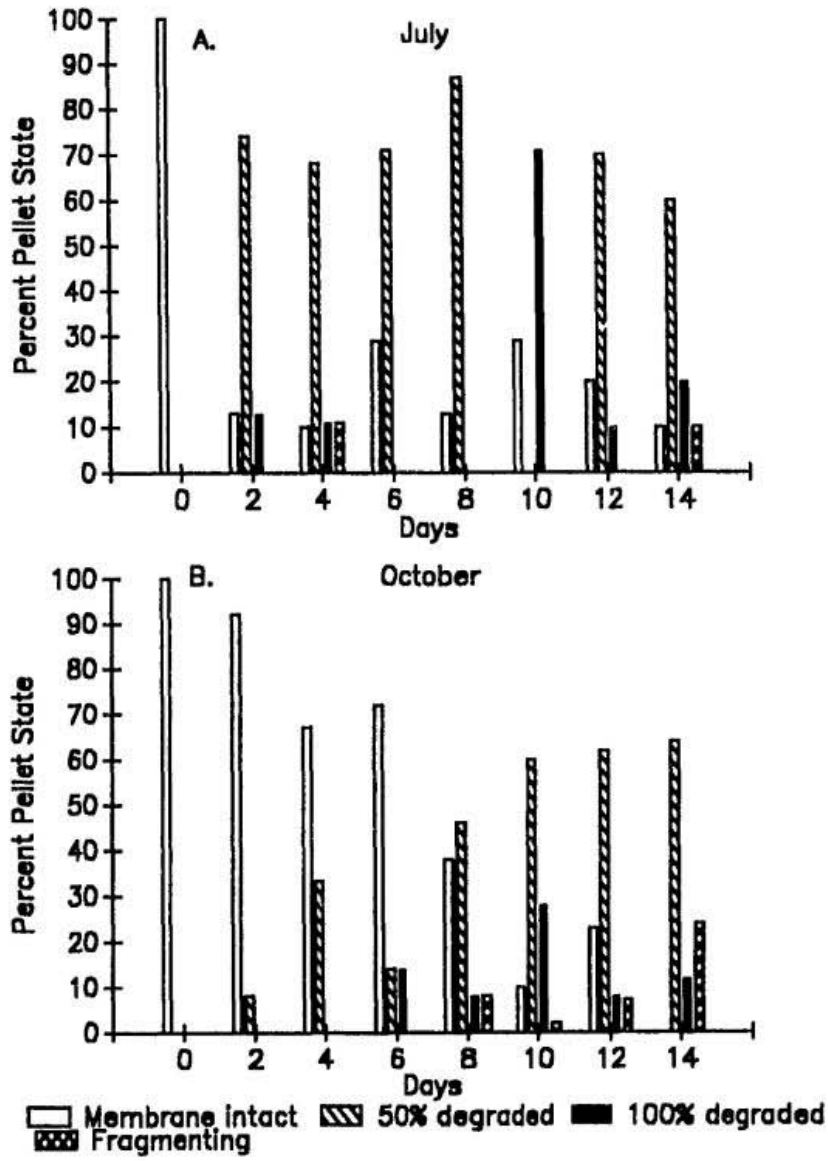


Figure 6.4: Pellet State Measurements in the Spring Laboratory Open and Closed Experiments.

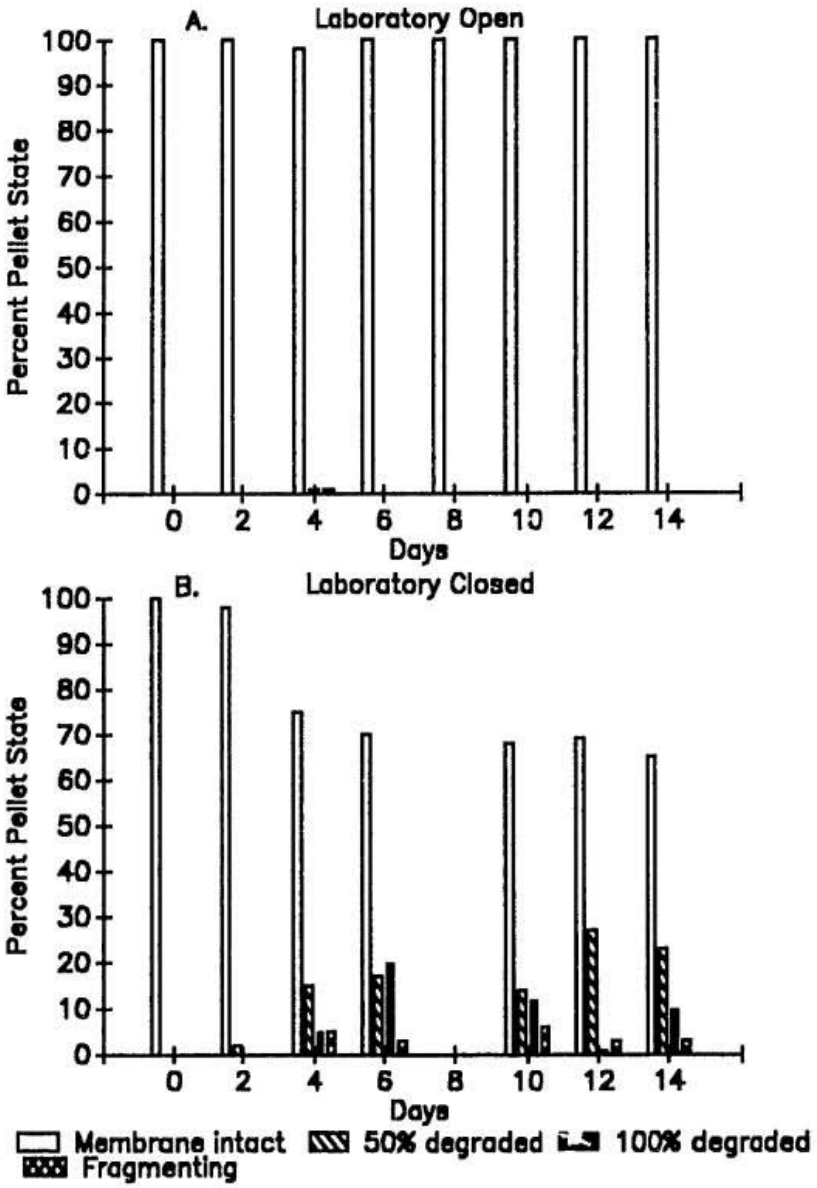


Figure 6.5: POC and Silicate Concentrations in the Feces in the Field Open Experiments. Error Bars Represent Standard Deviations (n=3), Triplicate Samples Were Taken Every 4 Days.

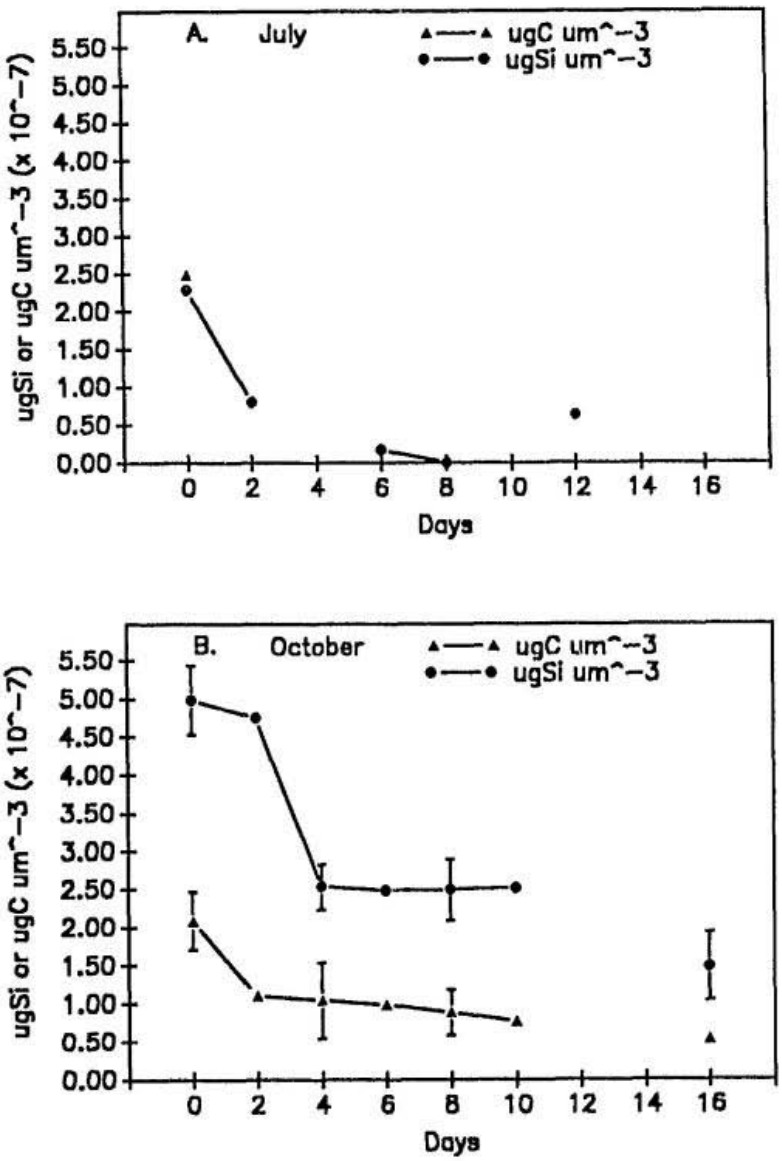


Table 6.1: Initial and Final Seasonal Concentrations of Particulate Organic Carbon (POC) and Particulate Silicate in the Feces.

DECAY SETUP		APRIL $\mu g\ \mu m^{-3}$	JULY $\mu g\ \mu m^{-3}$	OCTOBER $\mu g\ \mu m^{-3}$
FIELD OPEN				
POC	i=	3.4×10^{-7}	2.5×10^{-7}	2.1×10^{-7}
	f=	1.4×10^{-8}	**	5.4×10^{-8}
Si	i=	2.0×10^{-6}	2.3×10^{-7}	5.0×10^{-7}
	f=	5.4×10^{-7}	6.6×10^{-8}	1.5×10^{-7}
LABORATOY OPEN				
POC	i=	4.2×10^{-7}	2.0×10^{-7}	2.0×10^{-7}
	f=	3.8×10^{-7}	**	7.1×10^{-8}
Si	i=	2.0×10^{-6}	2.3×10^{-7}	5.5×10^{-7}
	f=	6.5×10^{-7}	3.5×10^{-7}	1.5×10^{-7}
CLOSED				
POC	i=	4.3×10^{-7}	2.6×10^{-7}	1.7×10^{-7}
	f=	5.5×10^{-8}	**	8.3×10^{-8}
Si	i=	2.1×10^{-6}	2.2×10^{-7}	4.9×10^{-7}
	f=	4.1×10^{-7}	6.8×10^{-8}	1.0×10^{-7}

i = initial concentration
f = final concentration

Figure 6.6: POC and Silicate Concentrations in the Feces in the Laboratory Open Experiments. Error Bars Represent Standard Deviations (n=3), Triplicate Samples Were Taken Every 4 Days.

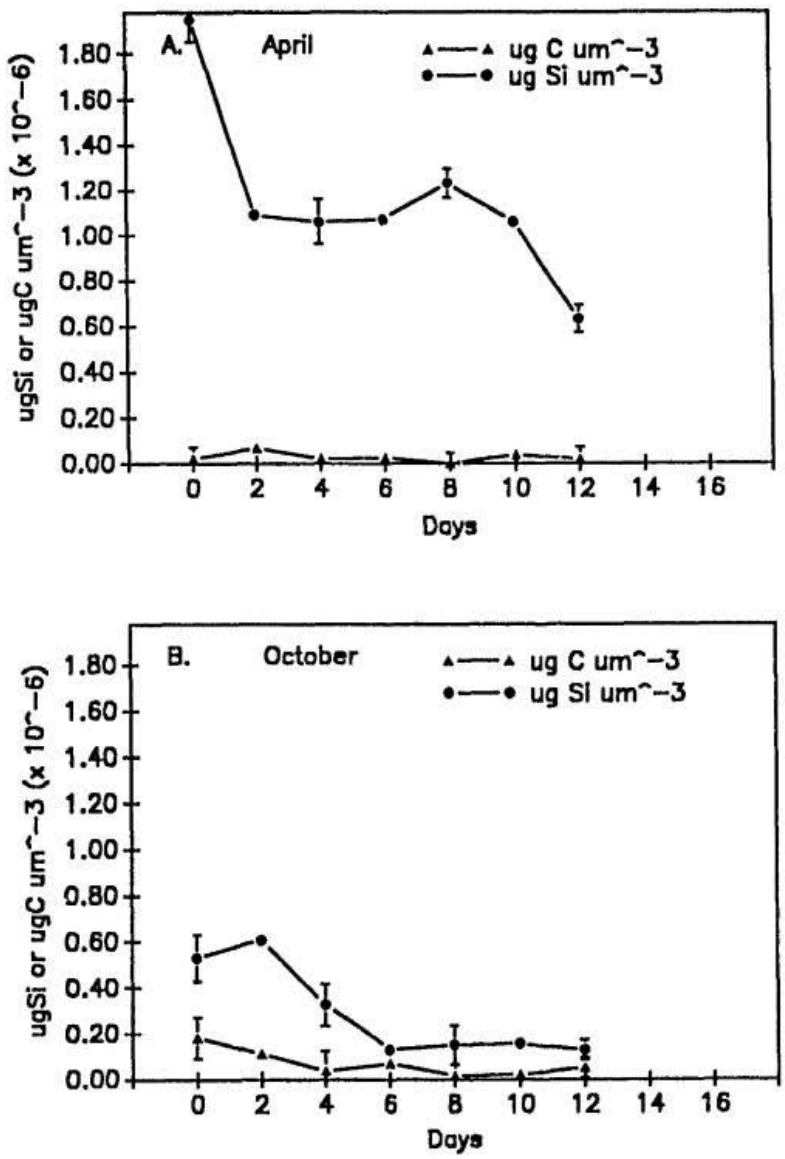


Figure 6.8: Bacteria Counts in the Feces and Tube Water in the Field Open Experiments. Error Bars Represent Standard Deviations (n=3).

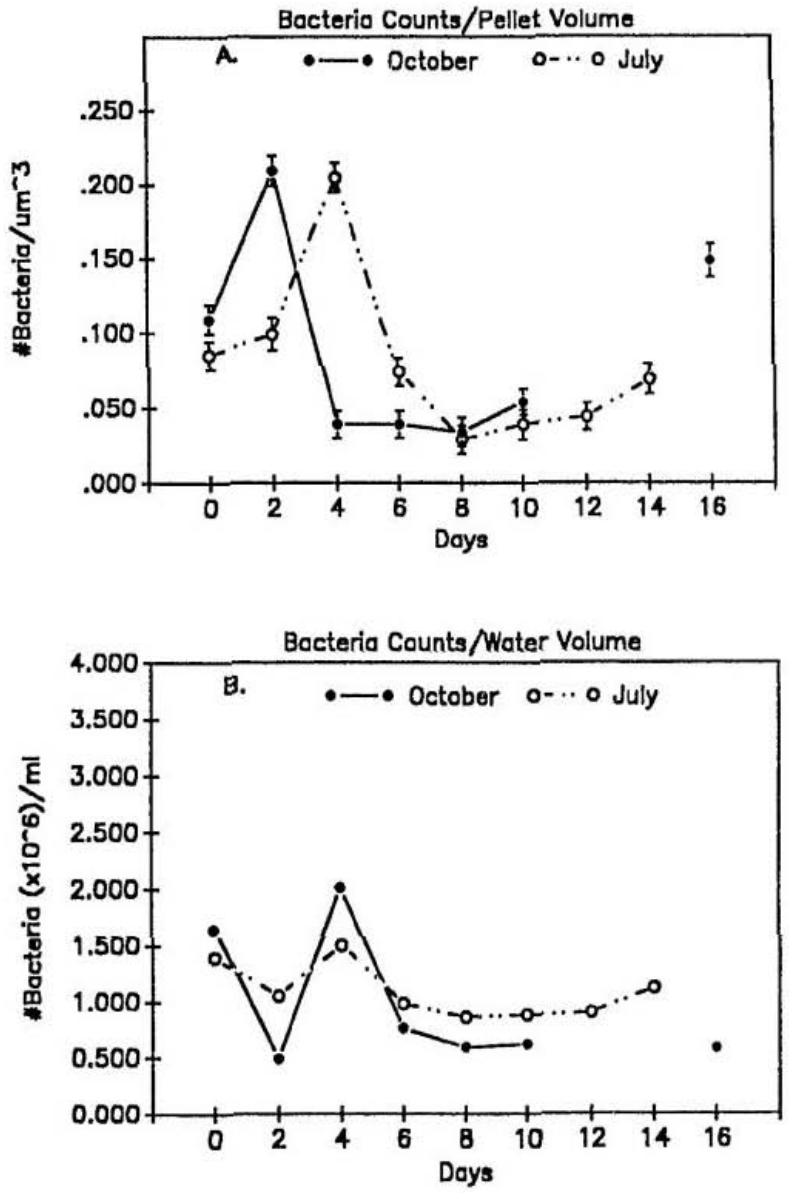


Figure 6.7: POC and Silicate Concentrations in the Feces in the Closed Experiments. Error Bars Represent Standard Deviations (n=3), Triplicate Samples Were Taken Every 4 Days.

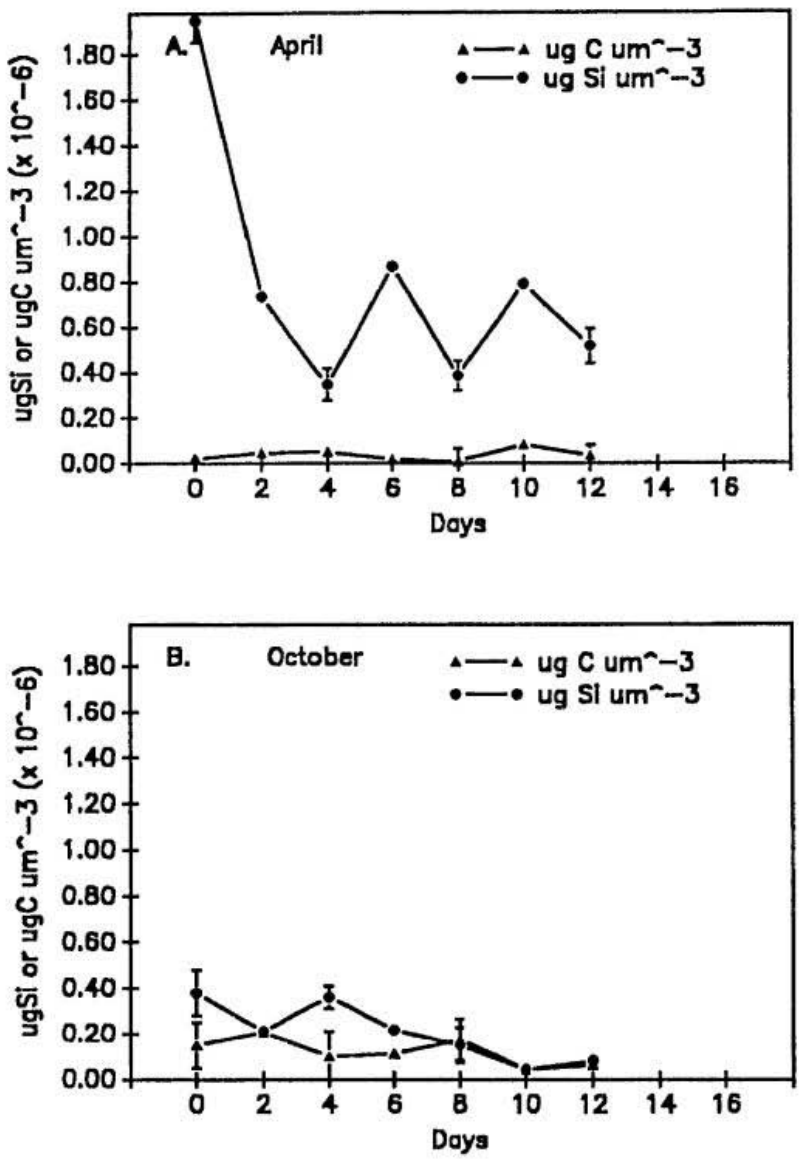


Figure 6.9: Bacteria Counts in the Feces and Tube Water in the Laboratory Open Experiments. Error Bars Represent Standard Deviations (n=3).

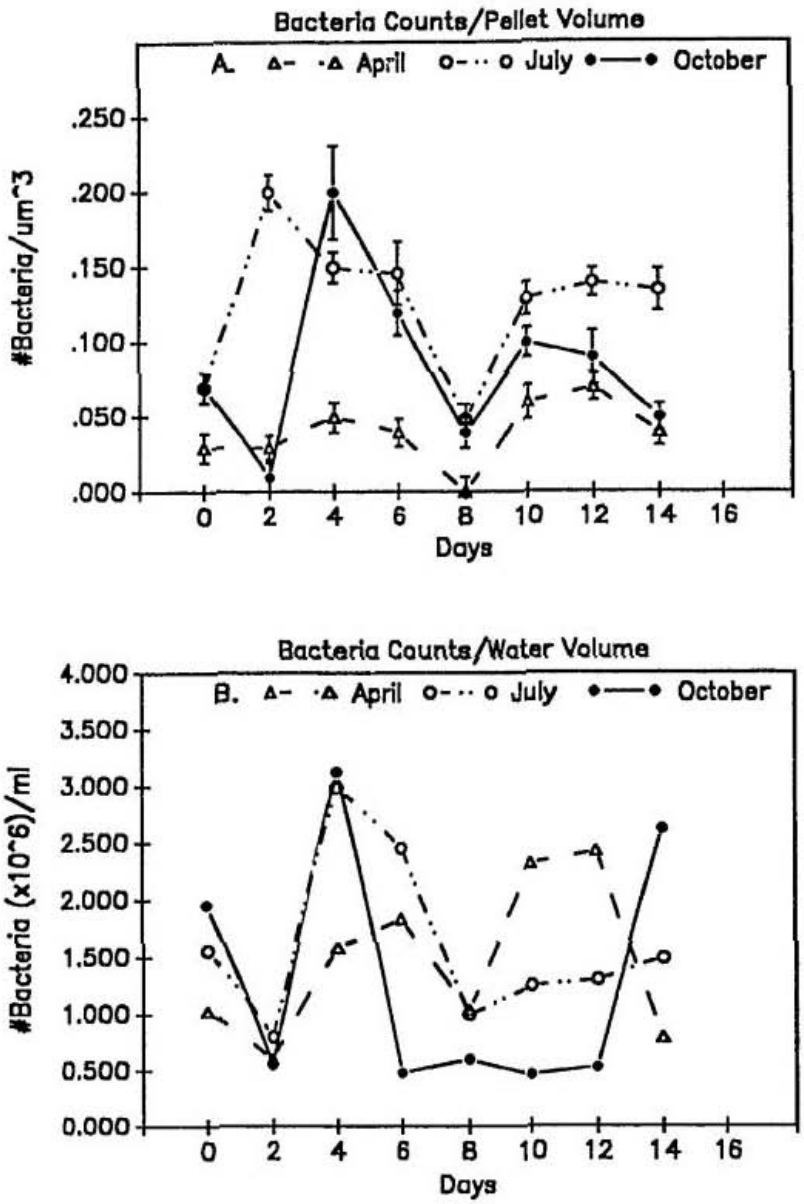


Figure 6.10: Bacteria Counts in the Feces and Tube Water in the Closed Experiments. Error Bars Represent Standard Deviations (n=3).

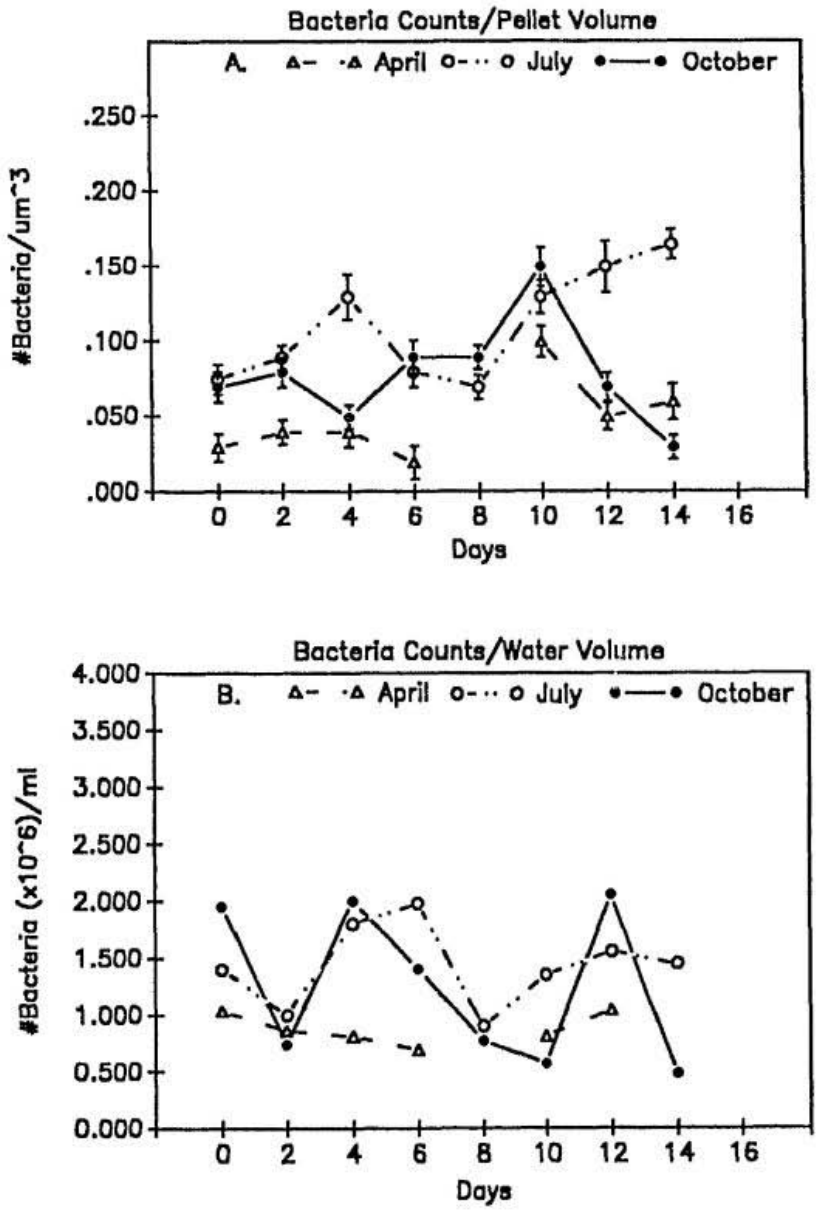


Table 6.2: Seasonal Percent of DFAA Composition in Tube and Surrounding Water.

SEASON	AMINO ACID										
DECAY SETUP	**ASP**	**GLU**	**ASN**	**SER**	**GLY**	**THR**	**AAT***	**MET**	**VAL**	**ILE**	**LEU**	**LYS**
Spring-Lab. Open												
Tube Water	19	18	6	11	8	3	13	5	3	2	1	11
Ambient	22	20	3	9	8	2	21	3	2	0	0	10
Spring-Closed												
Laboratory	16	6	2	19	12	3	17	7	4	4	1	9
Summer-Field Open												
Tube Water	26	14	2	17	10	7	14	5	5	0	0	0
Bay Water	24	12	1	16	13	5	15	8	6	0	0	0
Summer-Lab. Open												
Tube Water	24	25	1	14	9	1	16	7	3	0	0	0
Ambient	22	27	2	13	8	2	14	7	4	0	1	0
Summer-Closed												
Field	23	24	1	13	9	0	14	9	7	0	0	0
Laboratory	24	20	2	16	9	0	16	7	5	0	1	0
Fall-Field Open												
Tube Water	22	11	1	15	14	18	10	4	2	2	1	0
Bay Water	24	4	0	18	12	13	12	5	2	6	3	1
Fall-Lab. Open												
Tube Water	28	7	0	21	13	2	16	5	3	2	1	2
Ambient	27	11	0	17	13	1	18	7	4	1	.5	.5
Fall-Closed												
Field	28	13	0	18	13	1	15	5	3	3	1	0
Laboratory	30	7	0	23	10	0	15	6	4	2	1	2

*AAT is a group composed of ARG, ALA, TYR

Figure 6.11: DFAA Concentrations in the Tube Water in the Field and Laboratory Open Experiments. Error Bars Represent Standard Deviations (n=3), Triplicate Samples Were Taken Every 4 Days.

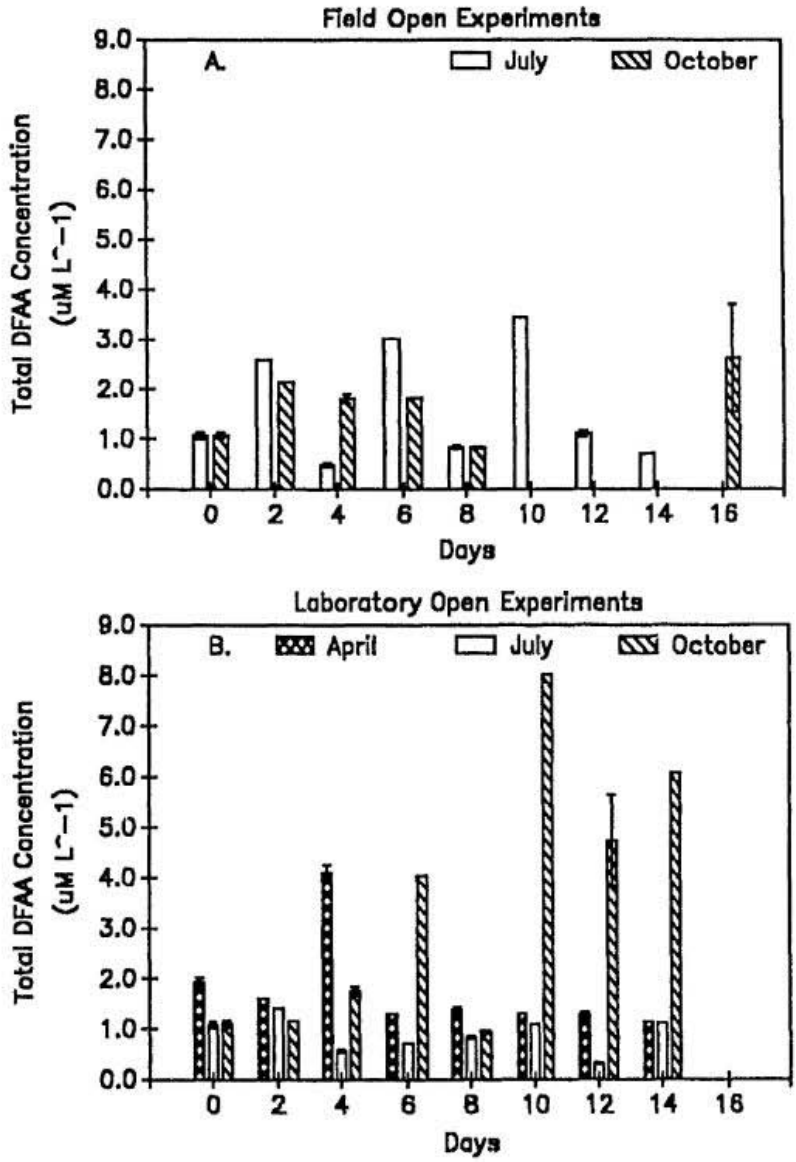
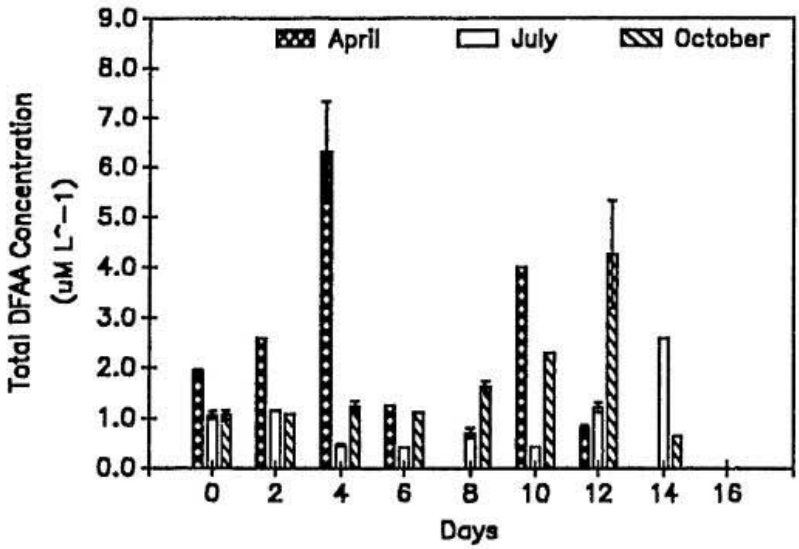


Figure 6.12: DFAA Concentrations in the Tube Water in the Closed Experiments. Error Bars Represent Standard Deviations (n=3), Triplicate Samples Were Taken Every 4 Days.



CHAPTER 7

GENERAL CONCLUSIONS

7.1 FECAL PELLET POTENTIAL TO CONTRIBUTE TO THE NUTRIENT FLUX

The seasonal potential of fecal pellets to leave the upper mixed layer and contribute to the nutrient flux can vary. It is controlled not by how fast the feces decay, but by the type of phytoplankton ingested, which affects their dynamic density and nutrient content. Changes in the composition of the fecal pellets reflect the relative succession of particles available in the water column (Figs. 3.1-3.4, Table 3.1 & 3.2). This agrees with previous studies in which both gelatinous filter feeders and crustacean copepods have been found to be nonselective suspension feeders (Poulet, 1978; Cowles, 1979; Alldredge & Madin, 1982; Deibel & Turner, 1985; Ishimaru, et al., 1988). Fall Calanus finmarchicus fecal pellets are filled with bacteria and ciliates (Fig. 3.3), indicating that both copepods and tunicates can ingest members of the microbial loop. The inclusion of bacteria and nanoplankton into C. finmarchicus fecal pellets may have be due to their feeding on marine snow. These changes in feces composition reflect a change in the predominance of the "classic" diatom-based

food chain in the spring to one based on the microbial loop in the fall (Fig. 3.5).

The changes in the phytoplankton content of the feces reflect changes in the food web structure and affect their dynamic density. The dynamic density is that which is controlled by the compactness of the component particles. Thus, feces filled with nanoplankton and bacteria have lower packing indices (P.I.= 3.5-5%) than pellets filled with diatoms (P.I.= 11-25%; Table 4.3), and they have corresponding higher densities (Table 4.1). This change in fecal pellet content results in significant differences in the seasonal range and median density for both C. finmarchicus and O. vanhoeffeni (Table 4.1). These results contradict values reported by Bienfang (1980) and values obtained using conventional literature methods (Chapter 4). The dynamic density of the fecal pellets has important implications in accurately determining the potential capabilities of feces to leave the upper mixed layer and to contribute to the vertical nutrient flux. My results indicate that zooplankton fecal pellets filled with bacteria and nanoplankton have a greater potential in leaving the upper mixed layer than do those filled with diatoms, thus the microbial loop may be important seasonally in contributing to the vertical nutrient flux.

7.2 SEASONAL FLUX OF FECAL PELLETS

The flux of fecal pellets is controlled in part by the settling velocity of the fecal pellets and by their ability to be transported out of the upper mixed layer (Noji, 1991). Seasonal changes in the fecal pellet density have important implications for flux models. The settling velocity of a fecal pellet is dependent on its shape and density relative to the surrounding water's density and viscosity (Janke, 1966; Komar, et al., 1981). Both C. finmarchicus and O. vanhoeffeni fecal pellets have low Reynold's numbers and follow Stokian principles. The measured settling velocities were compared to predicted values using literature equations (Komar, et al., 1981) and were found to be substantially lower than predicted (Table 5.3 & 5.4). Empirical settling velocity equations that are modified Stokes equations were developed to better predict the settling velocity of copepod and tunicate feces (Chapter 5).

The high measured settling velocities for O. vanhoeffeni fecal pellets (80-500 m day^{-1}) compared to those for C. finmarchicus (11-35 m day^{-1}) suggest that tunicate feces are better able to contribute to the nutrient flux in coastal Newfoundland waters than are copepod feces. This agrees with other studies that have found feces from gelatinous zooplankton contribute significantly to the

vertical nutrient flux (Bruland & Silver, 1981; Silver & Bruland, 1981; Madin, 1982; Matseuda, et al., 1986; Bathmann, 1988). Using the equations developed in Chapter 5 and the density data from Chapter 4, predicted seasonal settling velocities for C. finmarchicus were calculated. Spring and summer feces sink at velocities (5-40 m day^{-1}) that suggest they are likely to be recycled in the upper mixed layer, while fall feces sink at 25-95 m day^{-1}, indicating a greater potential for leaving the upper mixed layer and for contributing to the nutrient flux. Both copepod and tunicate feces sink in a diagonal orientation and rotate. This behavior may enhance their ability to form aggregates and be transported out of the upper mixed layer.

The magnitude of the seasonal flux of fecal pellets is controlled not only by their biomass and settling velocity but by their decay rate and nutrient content. In the field, the decay rate of C. finmarchicus fecal pellets was found to be independent of season (Chapter 6), suggesting that in nature, temperature alone does not control the decay rate of feces. This is in contrast to that which has been found in the laboratory (Turner, 1979; Roy & Poulet, 1990). There is a need to look at the seasonal, biological, in situ mechanisms of degradation of fecal pellets. What affects decay of feces and can it vary seasonally? As the fecal pellets decay and fragment they release DFAAs into the

surrounding water, indicating that fecal pellets can be a good source of DOM (dissolved organic matter).

7.3 CONCLUSIONS

1. Fecal pellet potential to contribute to the vertical nutrient flux is controlled not by how fast they decay but by their ability to leave the upper mixed layer, either individually or in marine snow.
2. The ability of feces to leave the upper mixed layer is controlled primarily by the type of phytoplankton ingested and its ability to be compacted. The compactness of the feces' contents affects their dynamic density and thus their settling velocity.
3. The content of the feces reflect the seasonal phytoplankton succession and illustrate a changing food web structure, from the "classic" diatom-based food chain in the spring to one based on the microbial loop in the fall, for both tunicates and copepods.
4. The 2-20 times higher measured settling velocities of O. vanhoeffeni fecal pellets indicate that these feces are more likely to leave the upper mixed layer and contribute to the nutrient flux than are copepod feces.
5. The high settling velocities (80-500 m day^{-1}) and the large number of coccolithophores in the fall O. vanhoeffeni

fecal pellets suggests that these feces are able to transport inorganic carbon (calcite) from the surface water to the benthos.

6. Predicted seasonal sinking velocities of C. finmarchicus fecal pellets indicate that fall feces have the greatest potential of exiting the upper mixed layer and in contributing to the nutrient flux. Thus, the microbial loop could be seasonally important to the vertical carbon flux via copepod feces.

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