Fecal pellet production and diel migratory behavior by the euphausiid *Meganyctiphanes norvegica* effect benthic–pelagic coupling

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Abstract—Observations made during submersible dives revealed that high densities of fecal pellets (50–325 particles m^{-3}) accumulated at night in 5–24 m thick layers coincident with the pycnocline (15–30 m) within the Gulf of Maine and the canyons south of Georges Bank. These large, cylindrical (0.2 mm × 3–10 mm long) particles sank rapidly (*ca* 204 m d^{-1} ± 24 S.E.) and could transport substantial amounts of organic matter (7–12 mg C m^{-2} d^{-1}) to the bottom. Vertically migrating euphausiids, *Meganyctiphanes norvegica*, produced the pellets. These individuals represented only part of enormous aggregations (up to 10^4 individuals m^{-3}) of adults (25–35 mm long) that remained within 10 m of the seabed day and night and appeared to forage in the benthic boundary region. These discoveries reveal that environmental factors and zooplankton behaviors can influence the rate and amount of particle flux. Furthermore, the unexpected observations of prodigious, epibenthic stocks of krill disclosed the distribution of major food resources that have supported the centuries-old fisheries in this region.

INTRODUCTION

IN general, the amount of particulate matter in the oceans decreases exponentially below the productive photic zone (HARGRAVE, 1984). The relatively rapid (1–1000 m d^{-1}) sinking of heavy particles, like zooplankton fecal pellets, can contribute substantially to the vertical export of organic compounds and various elements (FOWLER and KNAUER, 1986). However, the amount of fecal matter produced and the rate at which this matter settles are known to vary in relation to a host of physical and biological factors, e.g. advection, viscosity, diet and decomposition. Consequently, mathematical models developed to predict regional and global flux rates of biogenic material require detailed information about the production and distribution of these important particles (HARGRAVE, 1985; MICHAELS and SILVER, 1988). Most of the existing data about particle flux have been based on *in situ* sampling with sediment traps, pump-supported equipment, optical techniques or scuba (URRERE and KNAUER, 1981; BISHOP *et al.*, 1985; LAMPITT, 1985; ALLDREDGE *et al.*, 1987). Data obtained from sediment traps and optical devices can be misleading in that the amount of material measured may be a mixture of particles transported by vertical sinking, lateral advection and periodic resuspension. Similarly,

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information derived from filtration systems may include both suspended and fast-sinking particles. Scuba assessments of the sizes, sources and sinking of particulate material are depth limited.

We report here another approach, the use of a technically advanced, manned submersible. Our water column research showed where and when fecal pellets were produced by the euphausiid *Meganyctiphanes norvegica*. We quantified the chemical composition and potential flux of these biogenic particles. Observations of feeding activity in the epibenthic regime by large populations of euphausiids were unexpected and suggest that pathways of particle transport via egested feces are complex.

MATERIALS AND METHODS

Field sampling

Fecal pellets and euphausiids were observed *in situ* with the JOHNSON-SEA-LINK submersible within the Gulf of Maine and along the southern edge of Georges Bank during July–August in 1983, 1984, 1985 and 1987 (Fig. 1). The submersible was not operational in 1986 but field measurements of primary productivity were conducted. Devices designed to sample fecal pellets for chemical and other measurements were available only in 1985 and 1987. Vertical depth profiles of temperature, conductivity and transmittance were recorded simultaneously at 1-s intervals with a data logging system attached to the submersible (TUSTING and SAINSBURY, 1984). In 1987, a Sea-Tech

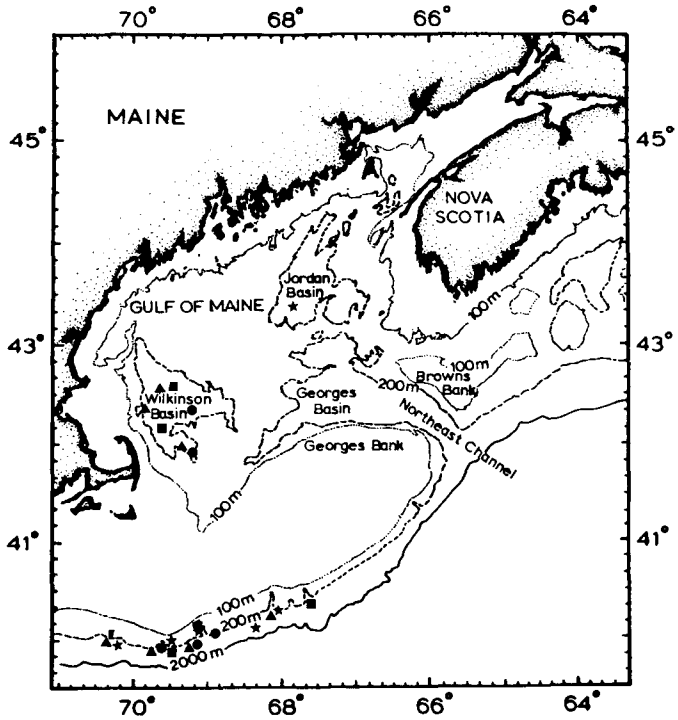

Fig. 1. Locations of submersible dive sites where epibenthic aggregations of the euphausiid *Meganyctiphanes norvegica* were observed, photographed or collected. (circle) 10–17 July 1983, (star) 9–19 August 1984, (triangle) 1–6 July 1985, (square) 13–18 September 1987. Bottom depths ranged from 200 to 800 m.

fluorometer was added to the environmental datalogger in order to obtain profiles of chlorophyll *a*.

Fecal pellets were collected using eight, cylindrical 7.5 l acrylic samplers (TIETZE and CLARK, 1986) mounted vertically along a linear framework just forward of the submersible's pressure hull (YOUNGBLUTH, 1984). The ends of each cylinder were sealed by a pair of lids that moved horizontally over the openings. Sieves consisting of 209-μm mesh plankton netting glued to 8-cm tall, acrylic frames (17 cm ID) were inserted into the bottom of each sampler. In use, the samplers' lids were partially opened during launching of the submersible. After launch, as soon as the samplers filled with water forcing out all residual air, the lids were closed. The submersible then descended to a depth just below a layer of fecal pellets, the lids were opened and the submersible was made positively buoyant. After traversing upwards through a layer of fecal pellets, the lids were closed, and the submersible descended again to a depth just below the layer. The sampling process was repeated 5–10 times. The total volume filtered by each sampler ranged from 1 to 3.7 m^3 depending on the vertical extent of a layer.

Sinking rates of freshly collected fecal pellets were measured at *in situ* temperatures onboard ship by introducing individual pellets into a gimballed, graduated cylinder (46 cm tall × 6 cm ID) filled with seawater. *In situ* estimates of these rates were calculated using the formula given by KOMAR *et al.* (1981)

$$\omega_s = 0.0790 \frac{1}{\mu} (\rho_s - \rho) g L^2 \left(\frac{L}{D}\right)^{-1.664},$$

where ω_s is the settling velocity, L and D are the mean fecal pellet length and diameter, ρ_s is the particle density (calculated from laboratory sinking rates), and μ and ρ are the fluid viscosity and density, respectively.

Microbial enumerations followed accepted procedures (DAVOLL and SILVER, 1986). Fixation techniques for scanning electron microscopy were standard (BLADES and YOUNGBLUTH, 1979).

The proportion of living microbial carbon in a fecal pellet was ascertained with fluorescence microscopy and calculated in the following manner: total number of organisms per pellet times volume per organism times a weight of carbon per unit volume specific for each type of organism (DAVOLL and SILVER, 1986) divided by the total carbon per pellet.

Stomachs of krill were excised and the contents prepared for chemical analyses. Care was taken to avoid the inclusion of chitinous matter from the stomach lining. Proximate chemical analyses employed standard methods (BAILEY and ROBISON, 1986).

Total organic carbon and nitrogen of dried (60°C), homogenated samples were measured using acetanilide as the standard. These analyses were conducted with a Perkin–Elmer Model 240 machine at 650°C. This temperature is below that for carbonate combustion (*ca* 700°C).

Primary productivity was determined using the ^{14}C tracer technique with the radioactivity measured by scintillation counting (Searle Mark III). Metal-free techniques were employed (FITZWATER *et al.*, 1982). Samples of seawater were collected with Niskin bottles on a Kevlar wire tripped with Delrin messengers. Six depths were sampled (surface to 50 m at 10-m intervals) to include two collections in the mixed layer, one in the thermocline, one in the chlorophyll maximum layer just below the thermocline and

two below the mixed layer at the base of the photic zone (1% light level). Incubations were performed *in situ* for 6 h from sunrise to noon (LAN). Two 250-ml polycarbonate, screw-cap bottles inoculated with 20 μCi of $NaH^{14}CO_3$ were set with a time-zero blank at each sampling depth. The time-zero blank was used in place of a dark bottle incubation (R. EPPLEY, J. MARRA and D. REDALJE, personal communication). At the conclusion of the incubations, the photosynthetic production of nanoplankton and netplankton was measured following serial fractionation of 100-ml aliquots through 22-μm mesh Nitex and Whatman GF/F glass fiber filters at <25 mm Hg (GOLDMAN and DENNETT, 1985) and rinsed once with filtered (0.45-μm Millipore) seawater.

The abundance of euphausiids within epibenthic aggregations was estimated visually. The best quantitative data were obtained with 5-min transects. During each transect, the submersible moved at *ca* 0.7 kn in a horizontal direction about 10–15 m above the bottom with all lights extinguished or with the lamps dimmed. At 1-min intervals the lights were turned on or brightened for 5 s. In this brief period five estimates of nearest neighbor distances (MACKIE and MILLS, 1983), between euphausiids in haphazardly selected parts of the field in view, were recorded. Care was taken to make estimates of only those euphausiids that occurred in undisturbed water forward of the submersible's acrylic pressure hull.

RESULTS

Fecal pellets were seen on most dives and were especially abundant at those sites where the euphausiid *Meganyctiphanes norvegica* was numerous. These pellets often occurred in a discrete layer (*ca* 5–24 m in vertical extent). The position and breadth of the layer in the water column varied with the time of day. Between midnight and sunrise, the layer was located in the uppermost 14–40 m. The bulk of pellets in this early morning layer was coincident with the pycnocline (Fig. 2). Between sunset and midnight, such concentrations of pellets were absent at the density interface and were usually dispersed throughout the water column below the mixed layer.

The accumulation of fecal pellets at the pycnocline indicated that the relatively fast-sinking particles are often stalled. This suggests that, if the discontinuity is pronounced, it may facilitate lateral transport of particles such as proposed by MARTIN *et al.* (1987).

In 1987 we encountered a deep (192–213 m) layer of fecal pellets in Atlantis Canyon. This observation was unexpected as the position of this layer did not coincide with a physical or chemical discontinuity and the bottom depth was 550 m. The relative abundance and chemical composition of pellets in this layer were within the range of data recorded for pellets at shallower depths elsewhere. All of this information suggested that krill may have remained below the mixed layer to feed. Water column data support this conclusion in that there was an unusually warm surface water mass (*ca* 23°C) characteristic of an intrusion by a warm-core Gulf Stream ring (COX and WIEBE, 1979).

Fecal pellet abundance averaged 325 ± 29 S.E. pellets m^{-3} within the layers during the 1985 cruise. This density was *ca* six times higher than that recorded in 1987 (Table 1). However, because the 1987 layer had a greater vertical extent, the mean number of pellets within the water column (pellets m^{-2}) differed by *ca* four times between the 2 years. The pellets were relatively large, cylindrical rods (0.2 mm OD × 3–10 mm long) and golden-brown in color.

Calculated settling velocities of pellets, based on data from hydrographic profiles and

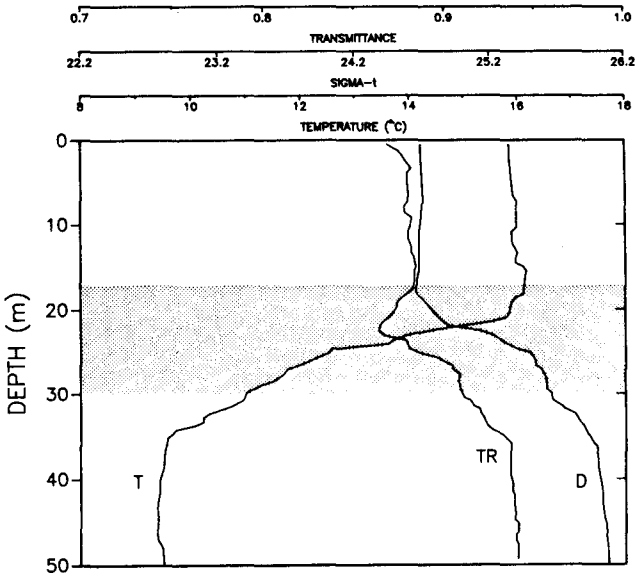

Fig. 2. Examples of an accumulation (300 fecal pellets m^{-3} within the stippled area) of euphausiid fecal pellets near a pycnocline. Dive 1107, 40°21.55'N latitude, 68°08.86'W longitude, 4 July 1985.

Table 1. *Mean values* (± S.E.) *of fecal pellet data including abundance, breadth of layer, sinking rate, carbon content and carbon flux*

Fecal pellet data	1985	1987
Abundance (pellets m^{-3})	325 ± 29 (n = 6)	52 ± 18 (n = 12)
Breadth of layer (m)	14 ± 3 (n = 6)	24 ± 6 (n = 12)
Sinking rate (m d^{-1})	200 ± 25 (n = 25)	211 ± 21 (n = 30)
Carbon content (μg $pellet^{-1}$)*	2.6 ± 1 (n = 6)	5.8 ± 1 (n = 12)
Carbon flux (mg C $m^{-2}d^{-1}$)	12 ± 3 (n = 6)	7 ± 1 (n = 12)

*n, Pooled samples of 300–400 pellets per sample.

in situ sinking rates measured under shipboard laboratory conditions and integrated to account for physical/chemical differences throughout the water column, averaged 206 ± 22 S.E. m d^{-1} (Table 1). These data indicate that pellets produced in the mixed layer could settle to the deep basins in the Gulf of Maine at 240 m in about 1 day (28 h). If all of the pellets collected in the layers near the pycnocline were to reach the sea floor, the accumulated abundance would be *ca* 1200–4600 pellets m^{-2} d^{-1}.

Fluorescence microscopy indicated that the fecal material contained a variety of microbial populations. The abundance (cells $pellet^{-1}$) of the major live microbes was enriched considerably above concentrations in seawater (Table 2). However, living microbial carbon accounted for only 0.1% of the average fecal carbon content (3–6 μg C $pellet^{-1}$). Scanning electron microscopy of the pellets showed only a few recognizable particles (phytoplankton tests and zooplankton exoskeletons) interspersed among masses

Table 2. Mean abundance (± S.E.) of microbes on fecal pellets and enrichment factor relative to background seawater concentrations

Microbe taxon	Abundance (cells pellet^{-1})	Enrichment factor
Eucaryotic autotrophs (<10 μm)	$1.3 \pm 0.2 \times 10^{-3}$ (n = 24)	×9200
Coccoid cyanobacteria	$7.5 \pm 1.0 \times 10^{-4}$ (n = 24)	×20,000
Heterotrophic bacteria	$1.2 \pm 0.3 \times 10^{-5}$ (n = 24)	×1200

Table 3. Fecal pellet proximate chemical composition expressed as mean percentage of the dry weight (± S.E.). n, Pooled samples of 300–400 pellets per sample

Chemical component	1985 (n = 6)	1987 (n = 12)
Ash	75.9 ± 0.6	72.8 ± 2.0
Protein	4.5 ± 0.4	6.2 ± 1.0
Carbohydrate	2.1 ± 0.3	2.6 ± 0.5
Lipid	0.4 ± 0.1	0.5 ± 0.2
Chitin	no data	5.1 ± 1.3
Carbon	5.1 ± 1.0	11.0 ± 2.0
Nitrogen	0.9 ± 0.1	1.1 ± 0.1
C:N (weight)	5.7	10.0

of unidentifiable amorphous, granular matter. These data were consistent with proximate chemical analysis that revealed the feces to be high in ash content and low in organic components (Table 3). The carbon values for fecal pellets noted in Table 3 represent natural variation since the same methods were used in all determinations. Contamination from carbonate was unlikely since all samples were combusted at 650°C (TELEK and MARSHALL, 1974). The additional measurement of chitin in 1987 was made to check if carbon chemically bound in chitin might account for a high C/N ratio. The relatively small amount of chitin and its C/N ratio of 7 suggested that chitin was not a bias for the pellets collected in 1987.

Total primary productivity in the Gulf of Maine in 1986 and 1987 was *ca* 2–6 times higher than the rate reported by TOWNSEND and CAMMEN (1985) (Table 4). The relatively high values measured in 1986 and 1987 were similar to the levels of primary productivity found on Georges Bank in 1978 (DAGG and TURNER, 1982). Integrated Chl *a* values were similar for all 4 years (Table 4).

Meganyctiphanes norvegica was seen within the 15 m portion of the water column above the sea floor on most of the dives (65 of 72 dives). The dives occurred near and within Wilkinson and Jordan Basins in the Gulf of Maine and in the following canyons south of Georges Bank; Atlantis, Veatch, Hydrographer, Walker, Oceanographer and Lydonia (Fig. 1). On many occasions visual estimates of krill abundance were not possible due to the presence of a particle-rich, nepheloid layer. In these instances, when krill were numerous, only a minute or two passed before huge numbers of individuals were attracted to the lights on the submersible. Transect data (Table 5) indicated that the mean abundances of krill within large epibenthic aggregations ranged from 105 to 2857 individuals m^{-3}. Distances between individuals were as close as 5 cm in portions of some aggregations, *ca* 10 individuals m^{-3}. In 1984 epibenthic aggregations were encountered

Table 4. *Range of primary productivity and chlorophyll* a *concentrations. Mean values* (± S.E.) *of integrated productivity and number* (n) *of consecutive daily* in situ *incubations given in parentheses*

Location (date)	Maximum primary productivity (mg C m^{-3} h^{-1})	Integrated productivity (mg C m^{-2} d^{-1})	Integrated Chl *a* (mg m^{-2})
Georges Bank*	1.5–3.5	723–817	25–50
(Oct. 1978)	(surface max)	(770 ± 47; n = 2)	
Wilkinson Basin†	0.3–0.8	172	36
(Aug. 1983)	(deep max)		
Jordan Basin‡	5.0–9.5	371–953	16–38
(Sept. 1986)	(surface max)	(700 ± 172; n = 3)	
Wilkinson Basin‡	1.5–3.6	258–880	34–38
(Sept. 1987)	(surface max)	(600 ± 116; n = 4)	

* DAGG and TURNER (1982), † TOWNSEND and CAMMEN (1985), ‡ this study.

Table 5. *Mean abundances* (± S.E.) *of the euphausiid* Meganyctiphanes norvegica *within epibenthic swarms in the Gulf of Maine and canyons south of Georges Bank*

Date	Latitude Longitude	Time of day	Depth (m) of transects	Distance (m) above bottom	Abundance (individuals m^{-3})	n
10 Jul. 1983	43°31.8′ 69°34.2′	2115–2126	140–149	8	495 ± 160	2
12 Jul. 1983	42°34.0′ 69°13.7′	0333–0344	205–215	10	471 ± 163	2
14 Jul. 1983	40°06.8′ 68°50.5′	2230–2248	254–260	9	2857 ± 1134	3
16 Jul. 1983	39°54.3′ 69°34.7′	0004–0015	382–394	12	230 ± 137	2
13 Aug. 1984	41°42.9′ 69°14.9′	0032–0102	157–168	6	10 – 100	*
17 Aug. 1984	40°09.5′ 68°25.5′	0305–0505	274–415	8	10 – 1000	*
2 Jul. 1985	42°27.9′ 69°27.1′	0134–0145	220–253	10	176 ± 138	2
3 Jul. 1985	42°00.8′ 69°15.0′	0152–0203	167–201	5	105 ± 24	2
22 Sep. 1987	39°54.1′ 69°35.7′	0742–0825	456–488	9	373 ± 120	4
23 Sep. 1987	40°25.1′ 67°49.5′	2212–2223	365–396	10	434 ± 168	2

n, number of 5-min transects.
* Point estimates.

only in the southern part of Wilkinson Basin and an area near Oceanographer Canyon. Transects were not conducted at these two sites but estimates of nearest neighbor distances made at various times during the dives, indicated that the abundances of krill were comparable to data from other years.

In contrast to an abundance of euphausiids frequently encountered near the bottom, we normally observed only a few individuals in the mixed layer at night. This apparent absence of high density aggregations is probably related to several factors acting separately or in concert. For example, the distribution of krill may be more dispersed in the evening; the number of krill that actually migrate upward at night may be relatively small; and these krill may spend only a few hours in the mixed layer.

The depths where krill aggregated in the water column were determined during descents to the sea floor by making horizontal transects at 30-m intervals with submersible lights turned on and off for several minutes. In several instances, krill were recorded

Table 6. Proximate chemical composition of gut contents of shallow- and deep-living euphausiids Meganyctiphanes norvegica. *Chemical components are expressed as mean percentage of the dry weight* (± S.E.)

Capture depth (m)	Ash	Protein	Lipid	Carbohydrate	Chitin
40 (n = 12)	13.6 ± 0.3	23.8 ± 2.1	27.0 ± 1.1	2.4 ± 0.1	3.4 ± 0.1
500 (n = 12)	21.2 ± 0.5	19.8 ± 2.2	23.1 ± 1.0	1.9 ± 0.1	2.4 ± 0.1

as numerous. During most of these observations krill were migrating upward or downward and were not strongly attracted to the lights of the submersible.

The difference between the sums of the organic components of euphausiid gut contents (Table 6) and the actual total organic content estimated by ashing is presumably due to refractory material, i.e. carbohydrate (LAWRENCE and MCCLINTOCK, 1988) and protein (SIBUET and LAWRENCE, 1981).

DISCUSSION

In spite of the low organic content, fecal material released from the krill *M. norvegica* could supply *ca* 10 mg C m^{-2} d^{-1} to the benthic community. This biomass represented 1–6% of the daily primary production in the mixed layer, depending on which year's total primary productivity values were used (Table 4). If oxidized completely, the average amount of fecal material would yield an oxygen consumption rate of 3 ml O_2 m^{-2} d^{-1}, i.e. at least 2% of the total benthic community respiration (SMITH and HINGA, 1983). These estimates are conservative. Variation in the carbon content of fecal pellets (3–18% dry wt) and the abundance of epibenthic euphausiids (10–10^4 individuals m^{-3}) indicated that carbon flux could easily be an order of magnitude greater.

Assuming a gut evacuation rate of 1–2 h and a daily grazing cycle of 8 h in the mixed layer (WILLASON and COX, 1986; HEYRAUD, 1979), about 7–68 euphausiids m^{-3} could have produced the mean number of pellets observed near the pycnocline. This estimate of population abundance supported our visual observations that in most cases only a portion of the euphausiids aggregated near the bottom actually migrated upward at night into the mixed layer. Data from dual beam sonar (420 kHz, JEFFERTS *et al.*, 1987), mounted on the JOHNSON-SEA-LINK submersible in 1987, also confirmed the abundance of epibenthic aggregations of zooplankton (*ca* 800 targets 10^{-3}) within the size range of *M. norvegica* (Oceanographer Canyon, GREENE *et al.*, 1988).

The deep-living cohorts in the benthic boundary region usually had full stomachs and appeared to be foraging when observed, i.e. feeding on resuspended particulate material in the epibenthic nepheloid layer and possibly on the flocculent "fluff" layer at the sediment–water interface. Proximate chemical analyses of material in the guts of deep-living krill revealed higher ash content and lower levels of organic components (protein, lipid, carbohydrate and chitin) than material in the guts of krill captured near the surface (Table 6). These differences lend support to our observations that deep-living euphausiids are foraging in the epibenthic region, and may recycle, at least in part, previously egested debris (i.e. fecal pellets). However, a diet based solely on detrital material is unlikely to meet the metabolic requirements of this species (MCCLATCHIE, 1985).

Our direct observations of *M. norvegica* near the sea floor also support scattered, anecdotal data from the trawls and submersibles (BIGELOW, 1928; PERES *et al.*, 1957;

TREGOUBOFF, 1961; MAUCHLINE, 1980), which have suggested that epibenthic aggregation and near-bottom feeding by this species occur in nearshore waters from the western North Atlantic to Mediterranean seas. If consumption of biogenic detritus in the epibenthic region is common among these euphausiids, this species constitutes a substantial, heretofore unidentified grazing force that may account for considerable repackaging and bioturbation. Assuming that epibenthic populations feed more or less continuously, those individuals that migrate vertically each night may introduce recycled biogenic and inorganic materials back into the mixed layer when they release fecal pellets.

Krill represent only one of several zooplankton species that can act to biologically transform and vertically transport organic matter out of particle-rich layers. Greater emphasis on investigations in plumes of highly turbid water that flow along thermohaline density surfaces in the water column (GARDNER, 1989) or that develop from resuspension events near the sea floor (WALSH *et al.*, 1988) are likely to improve estimates of particle chemistry and flux. Future studies of spatial and temporal variability of particle biomass and composition in these zones should emphasize the interplay of diel feeding/migratory behaviors (LONGHURST and HARRISON, 1988), seasonal productivity maxima (TOWNSEND and CAMMEN, 1988) and water flow patterns.

The detection of prodigious epibenthic aggregations of euphausiids is also significant with regard to higher trophic level dynamics throughout the region studied. We and other investigators (P. AUSTER, R. COOPER, R. JONES, R. LANGTON and J. UZMANN, personal communication) have seen demersal fishes (*Gadus morhua*, *Pollachius virens*, *Merluccius bilinearis*, *M. albidus*, *Urophycis tenuis*, *U. chuss*) and squids (*Loligo pealei* and *Illex illecebrosus*) feeding on epibenthic populations of euphausiids. These preliminary observations of foraging by cod, hake, polluck and squid weaken the hypothesis that these zooplankton may avoid predation by living near the bottom and support fisheries data that indicate *M. norvegica* is an important food resource for commercial groundfish species (BOWMAN and MICHAELS, 1984; GROSSLEIN and AZAROVITZ, 1982).

Marine mammals, such as fin-whales (*Balaenoptera physalus*), are known to feed almost exclusively on euphausiids, presumably on patches of high (at least 17 g m^{-3}, *ca* 60 individuals m^{-3}) biomass (BRODIE *et al.*, 1978). Unpublished data from plankton net tows made in the Gulf of Maine/Georges Bank region (Marine Monitoring Assessment and Prediction Program) have indicated that euphausiid densities in the study area average less than 1 m^{-3} and range up to 50 m^{-3}. However, direct observations and sampling of surface swarms of *M. norvegica* in the Bay of Fundy have shown that patch densities can average 2.8 ± 0.5 S.E. × 10^5 individuals m^{-3} (NICOL, 1986). Acoustic backscattering data (120 kHz), recorded during the daytime in the Gulf of St. Lawrence, revealed that krill, primarily *M. norvegica*, can average 97 ± 20 S.E. individuals m^{-3} between 100 and 300 m where depths reach 225 m (SAMEOTO, 1983). Our observations also confirm that epibenthic populations of this euphausiid occur in aggregations dense enough to supply daily food rations required by fin-whales. Subsurface feeding on high-density euphausiid stocks has been reported for other whales [*Balaenoptera musculus*; SCHOENHERR (1988) and *Eubalaena australis*; HAMNER *et al.* (1988)].

Consequently, by virtue of enormous densities, daily migrations, and widespread distribution in nearshore waters, populations of *M. norvegica* probably impact benthic productivity over a broad geographic area in the North Atlantic Ocean in at least three ways: (i) as sources of biogenic particles (fecal pellets, molts and carcasses), (ii) as

bioturbators and transporters of resuspended and flocculent sediments and (iii) as prey for demersal predators.

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