

Trophic dynamics in antarctic benthic communities. I. In situ ingestion of microalgae by Foraminifera and metazoan meiofauna

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ABSTRACT: Benthic microalgal production and the ingestion and subsequent metabolism of algal carbon by Foraminifera and several metazoan meiofauna were measured in situ in McMurdo Sound, Antarctica. The benthic microalgal community was dominated by the diatom *Amphora antarctica*. Microalgal biomass and production were 15 ± 4.8 mg chl *a* m^{-2} (mean \pm SD) and 6.0 ± 1.9 mg C $m^{-2} d^{-1}$, respectively. Weight-specific ingestion rates of microalgae by the foraminifers *Astrammmina rara* and *Astrorhiza* sp. were ca 2.5 to 3.5 ng C mg wet wt⁻¹ d⁻¹; these rates were 2 to 3 times lower than those of the burrowing anemone *Edwardsia meridionalis*, small polychaetes and clams. All the meiofauna examined appeared to biosynthesize new cellular material from the ingested algal carbon. The patterns and rates of polymer synthesis differed significantly for the protozoan and metazoan meiofauna: Foraminifera synthesized 2 to 5 times more protein and 3 to 5 times less lipid than metazoans. The different patterns of polymer synthesis of the meiofauna likely reflect differences in prey preference, metabolic rates, and the pathways and rates of digestion of the ingested prey. This study suggests that there may be differences in the patterns of metabolism and trophic status of co-occurring meiofauna.

INTRODUCTION

Foraminifera are ubiquitous in marine benthic environments, including the deep sea and polar oceans. The total test-free biomass of Foraminifera in the deep sea can be greater than all other taxa combined (Hessler 1974, Smith et al. 1978, Bernstein & Meador 1979, Snider et al. 1984). In McMurdo Sound, Antarctica, Foraminifera are conspicuous components of the soft bottom meiofaunal community (Dell 1972, DeLaca et al. 1980, DeLaca 1986a, b, DeLaca & Bernhard unpubl.). They can attain large sizes (≥ 38 mm; DeLaca et al. 1980) and comprise a significant proportion of the meiofaunal community (Dayton & Oliver 1977, DeLaca et al. 1980, Bernhard 1987). Despite their high abundance, the trophic position and the concomitant energy and material flux through Foraminifera is largely unknown (DeLaca 1982). Here we examine the in situ rates of ingestion and patterns of assimilation of naturally occurring benthic microalgae by several large species of antarctic foraminifers and associated meiofaunal metazoans.

Particle ingestion and nutrient assimilation by

benthic Foraminifera has been measured in the laboratory (Lee et al. 1966, Lee 1980) and for a few temperate salt marsh species in the field (Lee & Muller 1973). Foraminifera can ingest diverse prey, however, some species show prey selectivity (Boltovskoy & Wright 1976, Lee et al. 1988): for example, in the laboratory Foraminifera readily consumed several species of small pennate diatoms, unicellular green algae and several species of bacteria, whereas other species of algae and bacteria and cyanobacteria, yeast, dinoflagellates and chrysophytes were either not ingested or were ingested less readily (Lee et al. 1966, 1988, Lee 1974). Furthermore, some larger species of agglutinated Foraminifera can capture and consume metazoan prey including copepods and cumaceans (Winter 1907, Christiansen 1971).

Recent laboratory investigations of benthic Foraminifera from the Ross Sea, Antarctica show them to ingest diatoms and bacteria and assimilate dissolved organic carbon (DOC) (DeLaca et al. 1980, 1981, DeLaca 1982, Alexander & DeLaca 1987, DeLaca unpubl.). Although these results suggest that Foraminifera are potentially important to the trophic

dynamics of shallow-water antarctic food-webs (DeLaca et al. 1980, Bowser et al. 1986, DeLaca 1986a, b, Alexander & DeLaca 1987), studies of the in situ rates and patterns of ingestion and growth are lacking. For a substrate to support growth, it must be metabolized and used for the biosynthesis of new cellular material. Thus, the measurement of ingestion or assimilation of a particulate or dissolved substrate alone is insufficient to evaluate whether that substrate is used for growth. For organisms, such as Foraminifera, where the techniques are not available to measure the growth in situ (for review see DeLaca 1986b), an alternative approach is necessary. The research presented here examined the in situ rates of ingestion of microalgae and the subsequent patterns of metabolism and polymer biosynthesis by benthic Foraminifera and associated meiofauna.

METHODS

Samples were collected in mid-December 1984 from Explorers Cove, an embayment of New Harbor on the western side of McMurdo Sound (DeLaca 1982). Using SCUBA, replicate 6.5 cm diameter cores were collected in diatom-rich sediments at ca 20 m. This sampling protocol did not disturb the superficial sediment layer. Experiments were conducted within 2 h of collection of cores. Niskin bottles (5 l) were deployed through holes in the ice and samples were collected at 4 m intervals between the base of the ice and 20 m. Incident and downwelling light (photosynthetically active radiation between 400 and 700 nm) was measured with a quantum photometer (Li Cor Lambda Model LI-185B) equipped with surface (Model LI-190SB) and sub-marine (Model LI-192) sensors, respectively.

Radiolabelling experiments. Replicate ($n = 6$) cores were inoculated with $\text{NaH}^{14}\text{CO}_3$ to a final activity of ca $1 \mu\text{Ci ml}^{-1}$ in the overlying water and incubated in situ at the collection site. At ca 12 and 24 h, cores were harvested and four 3.5 cm^2 subsamples were taken from each core. The subsamples from each core were pooled, suspended in 10 ml of filtered seawater and duplicate aliquots from each were (1) preserved in 2% buffered formalin for the identification and enumeration of microalgal species; (2) filtered onto Whatman GF/F glass-fiber filters and extracted in 90% acetone to fluorometrically determine chlorophyll *a* (Teitjen 1968); and (3) filtered onto GF/F glass-fiber filters to measure ^{14}C incorporation by the benthic microalgal community. Filters were digested with 0.2 N perchloric acid for 24 to 48 h to solubilize cellular material and to convert residual ^{14}C -bicarbonate to $^{14}\text{CO}_2$ (Rivkin et al. 1989). The incorporation of ^{14}C and the chl *a* content of the dominant species were determined from separate

aliquots using the single-species technique (Rivkin & Seliger 1981, Rivkin & Putt 1987).

After the microalgae were sub-sampled, the overlying water was removed and the core was extruded. Foraminifera and selected metazoan meiofauna isolated from the upper 2 to 3 cm of the core were washed by transferring through 5 serial washes of $0.2 \mu\text{m}$ membrane filtered, ambient temperature seawater (DeLaca 1986b). The sarcodes of Foraminifera were dissected from their tests and the wet weights of sarcodes and meiofauna were determined with a Cahn electrobalance (Model 28). Sarcodes and meiofaunal metazoans were digested in 2.0 N NaOH for 24 h prior to counting of radioactivity. Examination of samples confirmed that the sarcodes and metazoan tissue were solubilized by this treatment.

^{14}C Carbon accumulated by microalgae and meiofauna in killed (cores incubated with 1% final concentration HgCl_2) and darkened controls was negligible. This implies that abiotic uptake of carbon by microalgae or meiofauna did not occur and that the meiofauna did not directly assimilate inorganic carbon (Montagna 1983, Montagna & Bauer 1988).

Polymer synthesis. The pattern of synthesis of polymers were determined for the microalgal community, the dominant algal species and individual meiofauna. After incubating in situ for ca 12 and 24 h, the radioactive carbon incorporation into lipids, low molecular weight compounds (LMW), polysaccharides and proteins was measured by serial solvent extraction as described by Roberts et al. (1955) and Morris et al. (1974) as modified by Rivkin (1985). Specific polymer classes were extracted based on their relative solubilities in different solvents (Hitchcock 1983, Rivkin 1985), thus macromolecules were separated into functionally rather than metabolically defined classes of compounds. Lipids and LMW compounds were extracted into the chloroform and methanol-water layers, respectively, with the chloroform-methanol-water solvent system (Bligh & Dyer 1959). Polysaccharides were solubilized by heating 5% trichloroacetic acid (TCA) at 95 to 100°C for 60 min. Proteins remained in the insoluble residue (however see Smucker & Dawson 1986). The sum of the radioactivity in the individual solvent fractions was 83 to 115% of the activity in the unextracted samples. To facilitate the comparison of labelling patterns among the different organisms (microalgae, protozoans and metazoans) and incubation times, we presented the data as percent incorporation. This presentation allows the patterns of polymer synthesis and allocation to be compared despite differences in the net ^{14}C -uptake rates. The percent incorporation in each fraction (representing different polymer classes) was:

$$\% \text{ Incorp.} = \frac{100 \times (\text{dpm in the polymer fraction})}{\text{Sum of the dpm in all fractions}}$$

Caution should be exercised in equating an increased percent incorporation with an increased net synthesis. When comparing different experimental conditions, incubation times or organisms, an increase in the percent ^{14}C incorporation into a polymer fraction can be interpreted as an increase in the rate of polymer synthesis only when the product of the percent incorporation and the total ^{14}C uptake is higher (see Table 2).

In situ planktonic production. Replicate ($n = 3$) 1 l samples were collected onto Whatman GF/F filters for the fluorometric assay of chlorophyll *a* (Rivkin et al. 1989). Daily primary production was measured during 24 h in situ incubations as previously described by Rivkin et al. (1989). Water samples were inoculated with ca $0.5 \mu\text{Ci ml}^{-1}$ of $\text{NaH}^{14}\text{CO}_3$ and replicate (3 light and 1 dark) 1 l bottles were incubated at 5 depths between the base of the sea-ice and the 20 m bottom. An additional incubation bottle was lowered to 20 m and immediately retrieved. The carbon fixed during transit to depth was subtracted from all in situ incubations.

Radioactivity counting. Radioactivity was counted using a Beckman liquid scintillation spectrometer (Model LS-6800) with Biofluor as the scintillant. All counts were corrected for quench from sediments, oxidizing agents and solvents by the external standard method and for background. Counting efficiency was 70 to 88 % and counting times were adjusted to provide a standard error of the count of $< 8\%$.

Population structure. The abundances of Foraminifera and meiofaunal metazoans were determined by randomly placing 100 cm^2 (10 cm square) cores into the sediment. The locations of the cores relative to one another, to depth and to local topographic and biological features were noted. The upper 2 cm of the sediment was washed through nested sieves (5.0, 1.0, 0.5 and 0.067 mm apertures) and the Foraminifera and selected species of meiofaunal metazoans retained on the 0.5 mm and 0.067 mm sieves were identified and counted immediately. The abundance of the larger arborescent foraminifera were counted in situ in 400 cm^{-2} quadrants (DeLaca et al. 1980).

RESULTS AND DISCUSSION

Microalgal production and biomass

During the austral summer, benthic diatoms grow to a maximum depth of ca 30 m in Explorers Cove. Chlorophyll *a* concentrations and daily production in the sediments were $15.0 \pm 4.8 \text{ mg chl } a \text{ m}^{-2}$ (mean \pm SD, $n = 18$) and $6.0 \pm 1.9 \text{ mg C m}^{-2} \text{ d}^{-1}$ (mean \pm SD, $n = 18$), respectively (Table 1). The microalgal community was dominated by *Amphora antarctica* and there were $6.0 \pm 0.75 \times 10^7$ *A. antarctica* m^{-2} . Other

Table 1. Microalgal biomass ($\text{mg chl } a \text{ m}^{-2}$) and primary production ($\text{mg C m}^{-2} \text{ d}^{-1}$) in the benthos (20 m) and plankton of Explorers Cove, New Harbor during mid-December

	Benthos	Plankton
Chlorophyll <i>a</i>		
Range	11–35	0.22–1.3
Mean \pm SD	15 ± 4.8	0.69 ± 0.26
Production		
Range	3.4–8.2	0.30–0.45
Mean \pm SD	6.0 ± 1.9	0.37 ± 0.10

taxa present in lower abundances were *Trachyneas aspera*, *Amphiprora kufferathii*, *Fragilariopsis* sp. and *Nitzschia* sp. *A. antarctica* had $180 \pm 22 \text{ pg chl } a \text{ cell}^{-1}$ (mean \pm SD, $n = 5$) and a daily production of $76 \pm 11 \text{ pg C cell}^{-1} \text{ d}^{-1}$ (mean \pm SD, $n = 18$): based upon the standing stock of chlorophyll *a* and rate of primary production of the microalgal community and the species-specific biomass and productivity of *A. antarctica*, this one taxa contributed ca 70 to 75 % of the chlorophyll *a* and primary production in the sediments.

During these experiments, mid-day irradiances incident at surface of the sea-ice and at 20 m were 1100 to 1300 and 1 to $3 \mu\text{E m}^{-2} \text{ s}^{-1}$, respectively. Benthic algae can adapt to very low irradiances (Palmisano et al. 1985, Rivkin & Putt 1987). For example, carbon uptake by *Amphora antarctica* isolated from 18 to 20 m near McMurdo Station on the west side of McMurdo Sound saturated at ca $6 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Rivkin & Putt 1987). The rates of photosynthesis and chl *a* cell^{-1} of *A. antarctica* from near McMurdo Station and New Harbor were similar.

Ingestion of microalgae by meiofauna

Since the complex sedimentary environment both constrains the behavior and influences the efficiency of prey capture of meiofauna, studies which are conducted under laboratory conditions may not accurately reflect the in situ rates and patterns of particle ingestion. In this study, the ingestion of radiolabelled algal carbon by Foraminifera and several common metazoans were measured under in situ conditions of light, temperature, and predator and prey abundance and orientation. Since the protozoa and meiofauna as well as their microalgal prey were incubated in cores to which ^{14}C was added, the radioactivity within both the algal and consumer trophic compartments increased concurrently. The rates of ingestion of ^{14}C -labelled microalgae by the Foraminifera and metazoan meiofauna were determined by the 3 compartment model of Daro (1978) as modified by Roman & Rublee (1981) and Montagna (1984). We did not

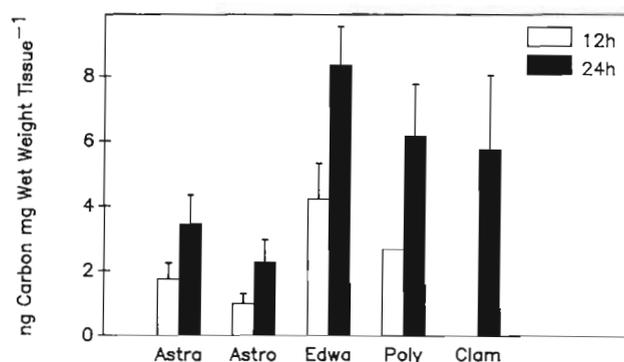


Fig. 1. Weight-specific incorporation rates of ^{14}C -labelled microalgae by the Foraminifers *Astrammima rara* (Astra) and *Astrorhiza* sp. (Astro), the burrowing anemone *Edwardsia meridionalis* (Edwa), a small polychaete (Poly) and clam. Meiofauna were assayed after 12 and 24 h in situ incubations. Error bars are standard deviations ($n = 5$ to 11 individuals assayed)

measure rates of respiration, excretion or the recycling of ^{14}C -labelled compounds by the meiofauna. Therefore, the ingestion rates measured over the 12 to 24 h incubations were minimum estimates.

Weight-specific ingestion rates of the Foraminifera *Astrammima rara* and *Astrorhiza* sp. ranged from ca 2.5 to 3.5 ng C mg wet wt⁻¹ d⁻¹ (Fig. 1). The rates of uptake for the burrowing anemone *Edwardsia meridionalis*, polychaetes and clams were 2 to 3 times greater than the Foraminifera (Fig. 1). Ingestion rates were approximately linear during the experiments. For example, the accumulation of radiolabelled algae after 24 h was ca twice that measured after 12 h. The relatively uniform rate of ^{14}C accumulation suggested that the ingestion rate was not limited by prey concentration and the Foraminifera and meiofauna were not adversely affected by the experimental manipulations. Ingestion rates were also measured for 2 large arborescent Foraminifera, *Notodendroides antarctikos* and an as yet undescribed species within the family *Notoanthoides* (DeLaca unpubl.). Due to their complex morphology, their sarcodes were not dissected and weights were not determined. These Foraminifera ingested 37 ± 4 and 33 ± 6 ng C ind.⁻¹ d⁻¹, respectively.

Polymer labelling patterns

During this study, we concurrently measured the patterns of polymer synthesis by the microalgal assemblage (Fig. 2A), by the diatom *Amphora antarctica* (Fig. 2B) and by the several species of Foraminifera and metazoan meiofauna (Fig. 3). There were significant ($p = 0.05$) differences in the labelling patterns of the microalgae (Fig. 2) and the meiofauna and among the Foraminifera and the metazoans (Fig. 3).

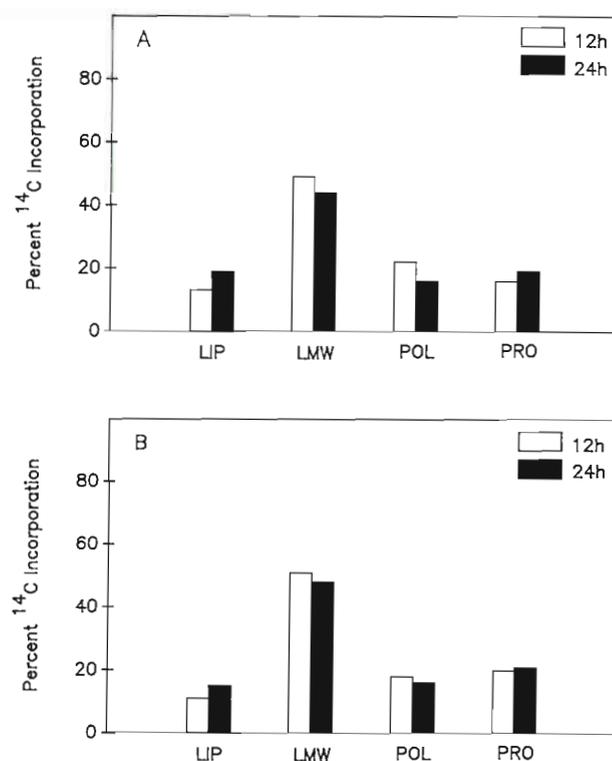


Fig. 2. Pattern of incorporation of $\text{NaH}^{14}\text{CO}_3$ into lipids (LIP), low molecular weight compounds (LMW), polysaccharides (POL), and proteins (PRO) by (A) the natural benthic microalgal assemblage and (B) *Amphora* sp. during 12 and 24 h in situ incubations

The labelling patterns of the microalgal assemblage (Fig. 2A) and *Amphora antarctica* (Fig. 2B) were identical. Further, there was no significant difference (Student's t test, $p = 0.05$) in the percentage of ^{14}C in the different polymer fractions at 12 and 24 h (Fig. 2). This suggests that isotopic equilibrium among the polymer pools was reached within 12 h (Hitchcock 1983, Smith & Geider 1985, Rivkin 1989). Between 10 and 20% of the ^{14}C was incorporated into the lipid (LIP), polysaccharide (POL) and protein (PRO) fractions and ca 50% was incorporated into LMW compounds.

The ^{14}C -labelling patterns of the Foraminifera and metazoan meiofauna differed significantly (analysis of variance [ANOVA], $p = 0.05$) from their benthic algal prey. Labelling patterns of the algae and meiofauna would be qualitatively similar if (1) the ^{14}C were directly incorporated by epifaunal algae rather than the meiofauna (Teitjen 1971); (2) the algae in the food vacuoles of the Foraminifera or gut of the metazoan meiofauna were retained but not digested; or (3) the meiofauna digested the algae without transforming the algal polymers. The significant difference in labelling patterns of the algae and the meiofauna (Figs. 2 and 3) suggests that the Foraminifera and metazoan meiofauna

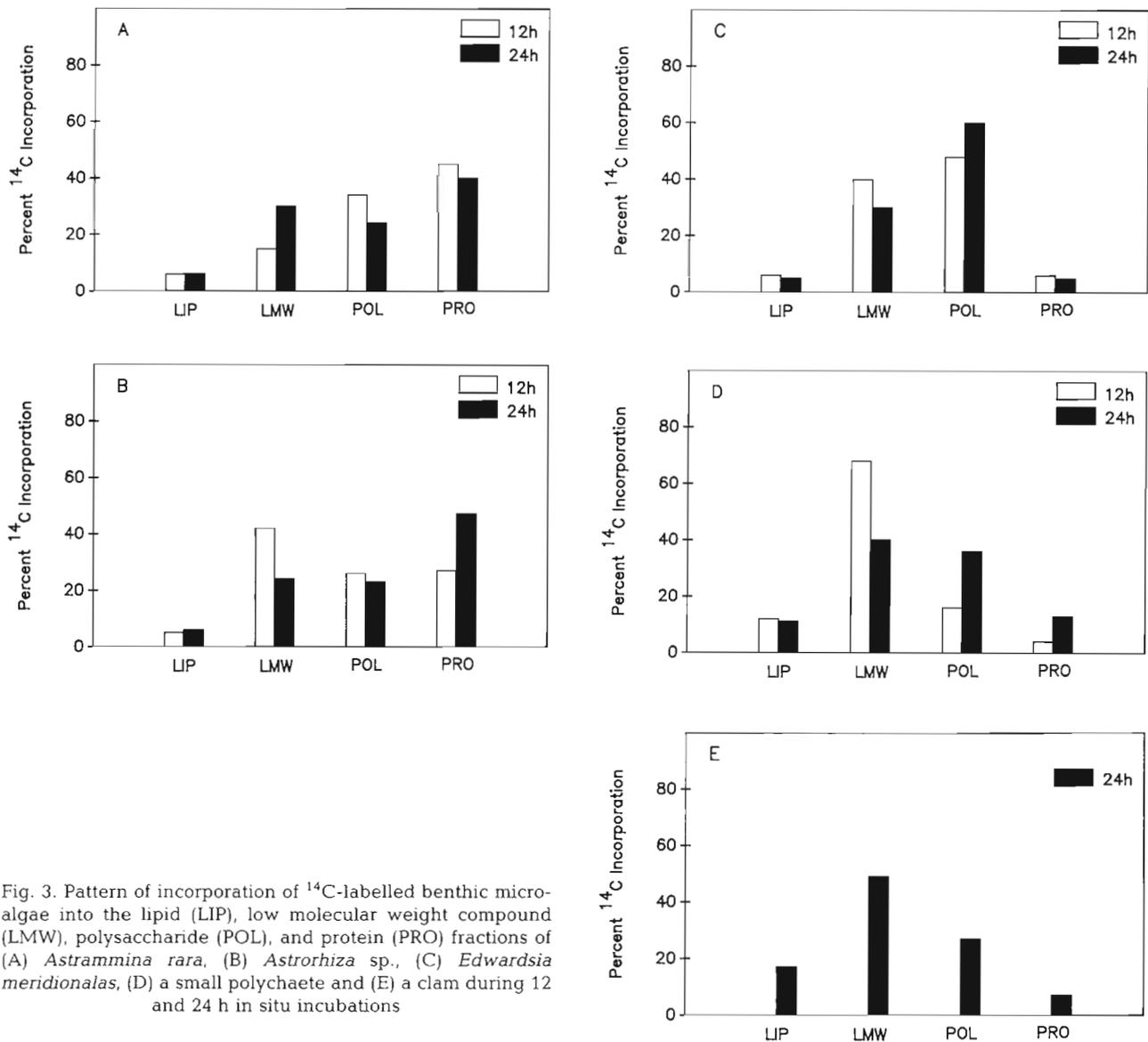


Fig. 3. Pattern of incorporation of ^{14}C -labelled benthic microalgae into the lipid (LIP), low molecular weight compound (LMW), polysaccharide (POL), and protein (PRO) fractions of (A) *Astrammima rara*, (B) *Astrorhiza* sp., (C) *Edwardsia meridionalis*, (D) a small polychaete and (E) a clam during 12 and 24 h in situ incubations

metabolized the algal carbon and used it to synthesize new cellular material. In Foraminifera < ca 10 % of the ingested algal ^{14}C -carbon was recovered from LIP, 20 to 40 % was recovered from LMW compounds and POL and 30 to 50 % was recovered from PRO (Fig. 3A, B). There was a reallocation of ^{14}C among polymer pools between 12 and 24 h, however the patterns were species-specific (Fig. 3A, B). In contrast to the Foraminifera, most (80 to 90 %) of the algal ^{14}C was recovered from POL and LMW compounds and ca 10 % was recovered from LIP and PRO in *Edwardsia meridionalis* (Fig. 3C) and the polychaete (Fig. 3D). The polychaete reallocated ^{14}C from LMW compounds to POL (Fig. 3D) during the 12 to 24 h interval. The ^{14}C labelling patterns for the clam was measured after 24 h only (Fig. 3E) and they were similar to the other metazoan.

The patterns of synthesis (i.e. the product of the

percentage ^{14}C in the polymer and the total ^{14}C ingested), as well as the percentage incorporation of ^{14}C into the polymers, differed among the meiofauna (Table 2, Fig. 3). The greatest difference was for PRO (Table 2). For example, the ingestion rates of algal carbon by Foraminifera were lower than the metazoans (Fig. 1). However during the same incubation interval, the Foraminifera synthesized 2 to 5-fold more PRO and 2 to 4-fold less LIP than the metazoans (Table 2): the metazoans synthesized predominately POL and LMW compounds (Table 2).

Community structure

The rates and patterns of ingestion of microalgae were measured for meiofauna which were abundant

Table 2. Synthesis of lipids, low molecular weight compounds (LMW), polysaccharides and proteins from radiolabelled algal prey by benthic Foraminifera and metazoan meiofauna. Synthesis calculated as the product of the percent ^{14}C incorporation into that polymer and the net carbon incorporation. Each value is the mean of 4 to 6 determinations and the coefficients of variation were 12 to 20 %. Data are ng polymer C mg^{-1} wet wt tissue for 12 and 24 h incubations. ND: not determined

Meiofauna	Lipids		LMW		Polysaccharides		Proteins	
	12 h	24 h	12 h	24 h	12 h	24 h	12 h	24 h
<i>Astrammia rara</i>	0.172	0.206	1.441	0.234	0.892	0.789	0.926	1.612
<i>Astrorhiza</i> sp.	0.136	0.136	0.339	0.678	0.768	0.542	1.017	0.904
<i>Edwardsia meridionalis</i>	0.499	0.416	3.332	2.499	3.998	4.998	0.499	0.417
Polychaete	0.738	0.675	4.182	2.214	0.984	2.214	0.246	0.799
Clam	ND	0.972	ND	2.803	ND	1.544	ND	0.400

and representative of the benthic soft bottom community on the west side of McMurdo Sound. The abundances measured here (Table 3) were similar to those reported previously. The numerical dominant meiofauna in Explorers Cove are Foraminifera, small infaunal polychaetes, clams and crustaceans (Oliver 1979, DeLaca et al. 1980, DeLaca unpubl.); the meio- and small macro-epifauna is dominated by arenaceous arborescent Foraminifera (especially *Notodendrodes antarctikos*: DeLaca et al. 1980), various tube dwelling metazoans, and *Edwardsia meridionalis* (Dayton & Oliver 1977, Oliver 1979).

CONCLUSIONS

The patterns of biomass distribution and primary production by planktonic and benthic microalgae in McMurdo Sound are temporally and spatially variable (Bunt 1964, Dayton & Oliver 1977, Dayton et al. 1986, Rivkin & Voytek 1987, Rivkin 1990). Primary production and the abundance of benthic infauna are reported to be significantly higher on the east side (e.g. near McMurdo Station) than the west side (i.e. New Harbor) of McMurdo Sound (Dayton & Oliver 1977, Dayton et al. 1986, Barry 1988). The circulation patterns in the western Ross Sea and McMurdo Sound result in an advection of water with relatively high concentrations

Table 3. Abundances (mean \pm SD; no. ind. m^{-2}) of protozoan and metazoan meiofauna in Explorers Cove at the time microalgal ingestion was measured (n = no. of cores examined)

Meiofauna	Mean	SD	n
<i>Astrammia rara</i>	821	378	24
<i>Astrorhiza</i> sp.	129	155	24
<i>Edwardsia meridionalis</i>	233	53	24
Polychaeta	467	282	24
Clams	254	23	24
<i>Notodendrodes antarctikos</i>	97	56	12
Unnamed Notoanthoides	119	26	16

of particles along the east side of the McMurdo Sound. A countercurrent of nearly particle-free water originating under the Ross Ice Shelf flows along the west side of McMurdo Sound (Dayton & Oliver 1977, Lewis & Perkins 1985, Barry & Dayton 1988). Hence, allochthonous inputs of biomass to the benthos in New Harbor are very low.

Autochthonous inputs of carbon to the benthos of Explorers Cove and New Harbor are from in situ phytoplankton, ice and benthic microalgae production. Planktonic biomass and in situ planktonic production in New Harbor during the austral summer was 0.30 to 3.0 mg chl a m^{-2} (Table 1 and Dayton et al. 1986) and 0.37 $\text{mg C m}^{-2} \text{d}^{-1}$ (Table 1), respectively; this was up to 3 or 4 orders of magnitude lower than the biomass and production on the west side of McMurdo Sound (for review see Rivkin 1990). Ice algal biomass and production can be high near McMurdo Station (Palmisano & Sullivan 1983, Grossi et al. 1987), however ice algal communities in Explorers Cove have not been studied. Ice algal growth is irradiance limited (Grossi et al. 1987) and in Explorers Cove, where sea-ice typically persists for several years (DeLaca unpubl.), the irradiances at the ice-seawater interface are much lower than at the base of the 1-yr ice near McMurdo Station. This fundamental difference in the characteristics of the sea-ice on the east and west sides of McMurdo Sound may result in much lower ice algal biomass and production in Explorers Cove than on the east side of McMurdo Sound. During the early austral summer, the benthic microalgal biomass and production was 5 to 20 times greater than planktonic biomass and production (Table 1). Thus, benthic microalgal production may represent the primary input of autochthonous carbon to the benthos in New Harbor.

The benthic microalgal biomass measured here was similar to the 18 to 145 mg chl a m^{-2} reported for New Harbor during November and December 1975 by Dayton et al. (1986) and was significantly lower than the chlorophyll a from similar depths near

McMurdo Station (Dayton et al. 1986). Benthic production measured in Explorers Cove (Table 1), however, was 10 to 20 times lower than was reported in 1975 (2.4 to 62 mg C m⁻² d⁻¹; Dayton et al. 1986). The ice conditions in 1975 and 1984 differed and may have resulted in higher downwelling irradiances during 1975 (Dayton et al. 1986, Dayton pers. comm.). Alternatively, production measurements in 1975, which were based on short mid-day incubations of shaken sediment, may have disrupted the habitat of the benthic algae and overestimated daily in situ production. The rates of production we report for New Harbor were based on 24 h in situ incubations of undisturbed cores and thus accurately represent daily production.

The trophic dynamics of the meiobenthic and microbial communities are closely coupled (Coull 1973, Fenchel 1978, Gerlach 1978, Teitjen 1980). Benthic algae and bacteria are ingested by polar and temperate protozoan and metazoan meiofauna (Teitjen 1980, Rieper & Flotow 1981, Admiraal et al. 1983, Montagna 1984, Alexander & DeLaca 1987, Lee et al. 1988 and references therein). In this study, benthic microalgal production and the ingestion and subsequent metabolism of algal carbon by a natural meiofaunal community were measured under in situ conditions of light, temperature and predator and prey abundance. Hence, the results of this study can be extrapolated to the natural environment. These observed in situ patterns of polymer synthesis suggest that the ingested benthic microalgae were used for the biosynthesis of complex polymers and for growth by meiofauna. There were significant differences in the weight-specific rates of ingestion and the patterns of metabolism among the meiofauna. The rates of ingestion by Foraminifera were lower than the other meiofauna examined. However, Foraminifera synthesized 2 to 5 times more protein and 3 to 5 times less lipid than that of the metazoan meiofauna (Table 2). The differences in the patterns of polymer synthesis of the co-occurring meiofauna may reflect differences in prey selectivity and preference, in metabolic and growth rates, or in pathways and rates of digestion of the ingested prey. The distinct patterns of polymer synthesis suggest that the chemical composition, the nutritional value and trophic status of the different meiofaunal taxa may also differ.

Acknowledgements. We thank Drs P. A. Anderson, M. R. Anderson and Mr D. E. Gustafson for comments on early drafts of the manuscript, K. M. Smith for graphics, and J. Bernhard, K. Miller and W. Stockton for assistance with the SCUBA diving. The staff of the National Science Foundation and the ITT Antarctic Services provided logistic support in the Antarctic. This research was supported by NSF grants DPP 8314607, 8520278 and OCE 8516214 to R.B.R. and DPP 8305475 to T.E.D. University of Maryland, Center for Environmental and Estuarine Studies contribution no. 2118.

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