Vol. 182: 37–54, 1999 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published June 11

Macrofaunal processing of phytodetritus at two sites on the Carolina margin: *in situ* experiments using ^{13}C-labeled diatoms

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ABSTRACT: Tracer experiments using ^{13}C-labeled diatoms *Thalassiosira pseudonana* were carried out at two 850 m sites (I off Cape Fear and III off Cape Hatteras) on the North Carolina, USA, slope to examine patterns of macrofaunal consumption of fresh phytodetritus. Experiments examined the influence of taxon, feeding mode, body size and vertical position within the sediment column on access to surficial organic matter. δ^{13}C measurements were made on macrofaunal metazoans and agglutinating protozoans from background sediments and from sediment plots in which ^{13}C-labeled diatoms were deposited and then sampled 0.3 h, 1 to 1.5 d, 3 mo and 14 mo later. Significant between-site differences were observed in background δ^{13}C signatures of sediments, metazoans, and large, agglutinating protozoans, with values 2 to 3‰ lower at Site III than at Site I. Background δ^{13}C signatures also varied as a function of taxon and of vertical position in the sediment column at Site III. The background δ^{13}C value of carnivores was higher than that of surface-deposit feeders among Site I annelids, but no annelid feeding-group differences were observed at Site III. δ^{13}C data from short-term (1 to 1.5 d) experiments revealed rapid diatom ingestion, primarily by agglutinated protozoans and annelids at Site I and mainly by annelids at Site III. Selective feeding on diatoms was exhibited by paraonid polychaetes, especially *Aricidea* spp. Exceptionally high uptake and retention of diatom C also was observed in the maldanid *Praxillella* sp., the nereid *Ceratocephale* sp. and several other surface-deposit feeding polychaetes. After 14 mo, little of the diatom ^{13}C remained at Site III, but high concentrations of the tracer were present in annelids and agglutinating protozoans at Site I. At both sites, non-annelid metazoans and subsurface-deposit feeding annelids exhibited the least uptake and retention of diatom C. Our hypotheses that large-bodied taxa and shallow-dwelling infauna should have greatest access to freshly deposited organic matter were not borne out. Some small, deep-dwelling taxa acquired label more readily than large or near-surface forms. Differences in tracer fates between sites reflected greater vertical mixing at Site III. These results indicate heterogeneity in benthic processes along the Carolina margin, but suggest that labile organic matter is consumed quickly at both sites. Because most of the taxa found to consume freshly deposited diatoms in these experiments are typical of bathyal settings, we infer that phytodetritus reaching the seabed in margin environments is rapidly processed by protozoan and metazoan components of the benthic fauna.

KEY WORDS: Agglutinated protozoa · Bioturbation · δ^{13}C · Deposit feeding · Continental slope · Macrofauna · Polychaete · *Aricidea* · *Praxillella* · *Ceratocephale* · Tracer

INTRODUCTION

At one time the food supply of deep-sea organisms was assumed to consist largely of organic matter that rained down slowly through the water column, or of detrital seagrass and algae deposited on the deep seabed (e.g. Menzies & Rowe 1969, Schoener & Rowe 1970). It is now known that relatively fresh material, termed phytodetritus, is deposited seasonally or episodically in many places on the ocean floor. Photographic records or samples of phytodetritus exist for many parts of the North Atlantic (Billett et al. 1983, Lampitt 1985, Graf 1989, Hecker 1990, Theil et al.

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1990, Pfannkuche & Lochte 1993) and the north and central Pacific (Honjo 1982, Smith et al. 1994, Smith et al. 1996). Thus, many deep-sea benthic organisms must be exposed to phytodetritus. Even where phytodetritus has not been observed directly, it is common to find relatively intact diatoms in sediments (e.g. Aller & Aller 1986, Cahoon et al. 1994). Biological investigations into the fate of phytodetrital material have revealed rapid numerical or functional responses to phytodetrital deposition by bacteria (Lochte & Turley 1988), protists and foraminifera (Gooday 1988, 1993, Linke 1992, Linke et al. 1995, Drazen et al. 1998), metazoan meiofauna (Lambshead et al. 1995), macrofauna (Graf 1989, Blair et al. 1996, Levin et al. 1997) and megafauna (Smith et al. 1993, Campos-Creasey et al. 1994, Lauerman et al. 1997).

Although macrofauna (defined here as animals retained on a 300 µm mesh) are historically among the best studied faunal groups in the deep sea from a community perspective, relatively little is known about their trophic behaviors, including their access to and rate of consumption of phytodetritus. Often inferences about the feeding modes of deep-sea taxa are drawn from known behavior of shallow-water analogs or from morphological considerations (e.g. Fauchald & Jumars 1979, Levin et al. 1991). Only rarely has there been direct observation of gut contents or experimental assessment of feeding modes in taxa from deep water. Recently, the naturally occurring, short-lived radiotracer ^{234}Th has been used to examine the relative freshness of gut contents of deep-sea megafauna relative to surface sediments to assess selectivity for phytodetritus (Lauerman et al. 1997, Smith et al. 1998). Natural ^{14}C, a longer lived tracer, is being employed to determine the age of carbon in megafaunal and large macrofaunal organisms from deep-sea sediments (DeMaster et al. 1998). These approaches are nearly impossible to use with very small macrofauna or meiofauna in the deep sea.

Several investigations have employed isotopically labeled organic matter to evaluate carbon pathways and bioturbation *in situ*. The advantage of this approach is that the labeled carbon can be traced into animal guts and tissues directly. Widbom & Frithsen (1995) examined fates of ^{13}C-labeled phytodetritus in shallow-water mesocosms mimicking eutrophic conditions. Cahet & Sibuet (1986) used ^{14}C-labeled organic matter in dissolved and particulate form to track biochemical transformations at a 2000 m site in the Gulf of Gascogne, France.

As part of the present project, ^{13}C-labeled algae have been spread off Cape Hatteras on the North Carolina, USA, continental slope to examine short-term particle mixing and ingestion by infauna (Blair et al. 1996, Levin et al. 1997). Initial investigations have revealed rapid ingestion of freshly deposited algae by selected infauna, and rapid downward mixing to depths of 4 to 13 cm on time scales of 1 to 2 d (Blair et al. 1996, Levin et al. 1997). Based on visual observations and carbon isotopic signatures of animals and sediments, Levin et al. (1997) proposed that rapid subduction of fresh organic matter by maldanid polychaetes may be a keystone function which provides other deep-dwelling deposit feeders with highly labile food.

The present paper further examines the role of macrofauna in processing recently deposited organic carbon on the continental margin. Experiments were conducted to compare particle fates and macrofaunal access to freshly deposited diatoms at 2 locations on the North Carolina slope with contrasting carbon flux regimes and faunal assemblages. Isotopic evidence for labeled diatom carbon in animal tissues was examined within hours, 1 to 1.5 d, 3 mo and 14 mo after tracer placement. We also explored naturally occurring variations in carbon isotopic signatures between sites and among taxa.

Long-standing paradigms regarding the feeding activities of infauna were examined. Many of our investigations focus on annelids because they are the infaunal taxon most responsive to organic enrichment in shallow water (Pearson & Rosenberg 1978) and deep water (Levin & Gage 1998), because they are numerically dominant at our study sites (Schaff et al. 1992) and because their ecology in deep water is better known than that of many other taxa. We tested the null hypotheses that the rate or amount of diatom carbon ingestion is not a function of (1) single- versus multicelled organization (protozoans vs metazoans) or metazoan taxon (annelids vs non-annelids), (2) annelid feeding mode, (3) body size, or (4) vertical position in the sediment. Our initial predictions were that metazoans, surface-deposit feeding polychaetes, large-bodied taxa, and animals dwelling in the upper few cm of sediment should be the first to ingest the diatom tracer. We also were interested in determining whether there were specific taxa likely to exert exceptionally strong influence on the fate and distribution of freshly deposited organic matter at Sites I and III, with the idea that their presence might be used to help predict diagenetic processes and rates.

This work is part of a larger study (SLOPEX) aimed at understanding the biogeochemical processes that control the fate of different types of freshly deposited particles on the North Carolina slope. Radiotracer and isotopic studies of bioturbation and carbon transformations are reported elsewhere (Blair et al. 1996, Levin et al. 1997, Thomas 1998, Fornes et al. 1999). The present paper focuses specifically on macrofaunal uptake and retention of diatom carbon.

MATERIALS AND METHODS

Experimental design and logistics. A tracer mixture containing 95% ^{13}C-labeled marine diatoms *Thalassiosira pseudonana*, subsurface slope sediment (10 to 60 µm), and glass beads (105 to 149 µm) was placed on the seabed at 850 m sites off Cape Hatteras (Site III: 35° 23' N, 74° 50' W) and Cape Fear (Site I: 32° 55' N 76° 31' W) (Fig. 1). The diatoms (CCMP1335 clone, Provasoli-Guillard National Center for Culture of Marine Phytoplankton, Bigelow Laboratory) were cultured in the laboratory in artificial seawater amended with f/2 medium containing 95% ^{13}C-$NaHCO_3$. This produced a diatom carbon that was 95 ± 1% ^{13}C and had a $\delta^{13}C$ signature of ~ +1 700 000. Details of diatom preparation are given in Levin et al. (1997). *Thalassiosira pseudonana* was selected as the carbon source in our experiments because diatoms in this genus are present in sediments near our study sites (Cahoon et al. 1994) and they are typical of waters overlying continental margins.

Each particle type (diatoms, sediments, glass beads) was tagged with a different radiotracer (^{210}Pb for diatoms, ^{113}Sn for sediments and ^{228}Th for glass beads). The ^{13}C-labeled diatoms were freeze-dried onto the clay kaolin to enhance settling. The tracer mixture was spread with the 'Johnson SeaLink' submersible by releasing the material from a shaker device into a plexiglass box on the sediment surface, where it was allowed to settle for ~20 min. Removal of the box left a 40 × 40 cm plot covered by a layer of tracer particles 1 to 2 mm thick. Excess diatom carbon accounted for <1.1% of existing POC in surface sediments, so these were not intended to be enrichment experiments.

Sediments were sampled by Ekman-style boxcore at varying intervals following tracer placement (Table 1). Short-term (1 to 1.5 d) experiments were conducted during August 1994 (at both sites) and October 1995 (Site I only). A 3 mo experiment was conducted from May to August 1994 at Site III only, and 14 mo experiments were conducted at both sites from August 1994 through October 1995. Background samples were collected and control (Time 0) experiments, sampled within 20 min of placement, were carried out in May and August 1994 and October 1995. Although we refer to these control treatments as Time 0 samples, core recovery and shipboard processing often took 1 to 4 h. Two or 3 replicate plots, ~5 m apart, were sampled for each location and time treatment (Table 1).

Sample processing. Each Ekman boxcore, sampled from an experimental plot or background sediment, contained four 7 × 7 × 15 cm subcores. These were stored on board ship in a cold room (4 to 6°C) until processing, usually within 2 to 3 h. One subcore from each boxcore was sectioned vertically at 0–1, 1–2, 2–5, 5–10 and 10–15 cm intervals, then sediments were sieved through a 300 µm mesh and preserved in 8% buffered formalin for subsequent quantification and identification of macrofauna.

A second subcore was sectioned at the same intervals and sediments were refrigerated (for up to several hours) until animals could be sorted live. On board the ship, living animals retained on a 300 µm sieve were removed with methanol-washed forceps, rinsed care-

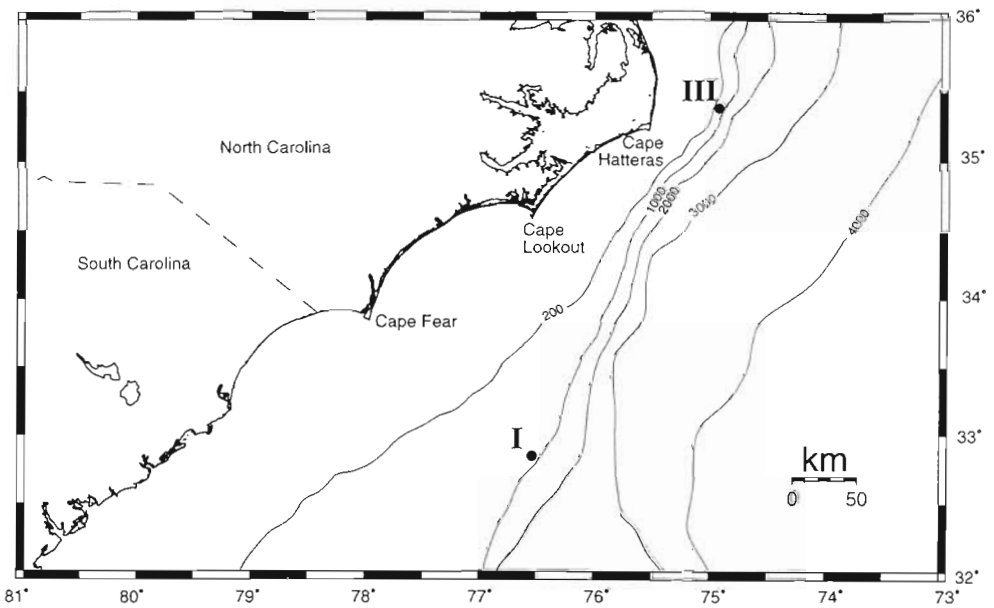

Fig. 1. Location of study sites on the North Carolina margin. Both sites are located in 850 m water depth

Table 1 Location, date, and replication of tracer experiments conducted on the North Carolina continental margin at 850 m. Replicate values for background samples indicate the number of Ekman cores collected. For the tracer treatments, replicate values indicate the number of 40 × 40 cm experimental plots sampled (1 Ekman core plot^{-1})

Time	Date	No. replicate plots	
		Site I	Site III
Background	May 1994	–	2
	Aug 1994	2	1
	Oct 1995	5	1
0 (<0.5 h)	May 1994	–	2
	Aug 1994	4	2
	Oct 1995	2	–
1 d	Oct 1995	4	–
1.5 d	Aug 1994	3	2
3 mo	May 1994–Aug 1994	–	2
14 mo	Aug 1994–Oct 1995	3	3

fully in filtered seawater, identified to the lowest taxonomic level possible (sometimes only family or order) and frozen at –20°C for later analysis of $\delta^{13}C$. For very small taxa (e.g. *Gobobulimina* sp., oligochaetes, nematodes), multiple individuals were pooled to form a single sample. In the laboratory, the frozen animals were dried *in vacuo*, acidified with sulfurous acid in silver boats, dried again *in vacuo* and combusted to CO_2 with a modified Carlo Erba CNS analyzer (Blair & Carter 1992). The isotopic composition ($^{13}C/^{12}C$) of the animal CO_2 was measured on a modified Finnegan MAT Delta E isotope ratio mass spectrometer (Hayes et al. 1977).

One subcore from each boxcore, destined for measurement of $PO^{13}C$ and $DI^{13}C$, was sectioned at 1 cm intervals to 7 cm, then at 2 cm intervals to 15 cm. Large infauna encountered during sectioning were removed for later $\delta^{13}C$ analyses. Mud from each interval was packed into 15 ml N_2-flushed centrifuge tubes and separated from porewater by centrifugation for 20 min at 5000 × *g*. Combustion and analysis of carbon isotopic composition of POC in the solid phase was performed as described above for animals, except that the acidification stage was done in beakers. The fourth subcore in each boxcore was sectioned for radiotracer and bead analyses. Most of the $PO^{13}C$, $DI^{13}C$, ^{210}Pb, ^{113}Sn, ^{228}Th and glass bead results are presented elsewhere (Levin et al. 1997, Fornes et al. 1999, Blair et al. in press).

Lifestyle and feeding mode classifications for macrofauna were based on information in Fauchald & Jumars (1979) and in Gaston (1987) as well as on direct observation of gut contents. Statistical comparisons among sites, exposure time treatments, and factors such as feeding group, body size, and vertical position were made by ANOVA, *t*-tests and linear regression using Statworks and JMP software. *A posteriori* pairwise testing following significant ANOVA results employed the Tukey Kramer HSD test. All error terms presented in the text and figures are standard errors.

$\delta^{13}C$ values presented here have been corrected for procedural organic contamination determined using blank analyses. Where possible, the ^{13}C content of the animals was corrected for natural (non-tracer) contributions using measurements of the same species collected from nearby background samples. In some instances, the concentration of tracer in macrofauna was expressed as the percent of total organic C in a specimen (tracer + animal) that existed as tracer (diatom) C. The percent tracer contribution allows us to relate tracer uptake to animal biomass, but can be misleading when some of the organism's carbon derives from ingested sediment. When the necessary background information was not available, the percent tracer was calculated using the regression:

$$\%\ C\ (\text{tracer}) = 0.0234 + 0.0014 \times \delta^{13}C$$

The regression was obtained from background-corrected samples.

RESULTS

Macrofaunal community structure

During the study period, metazoan macrofaunal densities were 2 to 3 times higher at Site III than at Site I (Fig. 2), a pattern noted consistently in previous years (Schaff et al. 1992, Blake & Grassle 1994). Site I densities were 10 271 ± 1139 (n = 9) and 8885 ± 971 ind. m^{-2} (n = 13) in August 1994 and October 1995, respectively. In contrast, Site III densities were 26 326 ± 4366 ind. m^{-2} (n = 5) in May 1994, 29 362 ± 3734 in August 1994, and 21 359 ± 3304 in October 1995. Although more of the macrofauna were collected below 5 cm at Site III (16.3% in 1994, 14.5% in 1995) than at Site I (6.6% in 1994 and 9.5% in 1995) (Fig. 2), these differences in vertical distribution were not statistically significant (1994: t_{15} = 1.930, p = 0.073; 1995: t_{14} = 1.266, p = 0.226).

Representation of major macrofaunal groups was similar at Sites I and III (Fig. 3), although dominant polychaete taxa differed between Sites I and III, as reported previously by Schaff et al. (1992). Additional information about the macrofauna at the 2 sites during 1994 can be found in Fornes et al. (1999). Agglutinating protozoa (foraminifera and xenophyophores), many of which are macrofaunal in size, were common at both sites but were not quantified in this study. Agglutinated protozoa were slightly more abundant and much more diverse at Site I (Hughes 1996, A. Gooday pers. comm.).

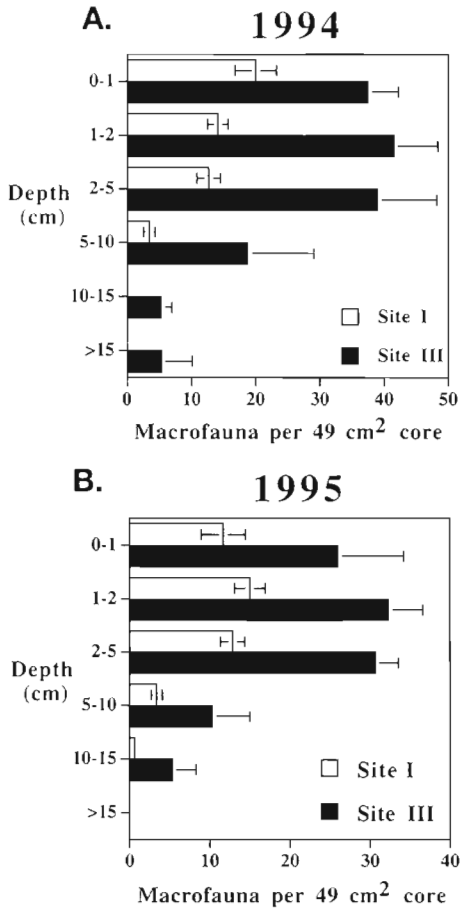

Fig. 2. Vertical distribution and abundance of macrofauna (>300 µm) collected during August 1994 and October 1995 at Sites I and III. Data are mean ±1 SE. Values are derived from pooled background and experimental cores listed in Table 1

The possible influence of experimental tracer additions on macrofaunal densities was examined by comparing (for each site separately) macrofaunal counts from cores collected in background sediments, Time 0 samples and the various short- and long-term exposure plots. No significant treatment effects on total macrofaunal density were observed at Site I ($F_{4,17} = 2.298$, p = 0.101) or Site III ($F_{4,6} = 0.945$, p = 0.499).

Background isotopic signatures

Carbon isotopic signatures ($\delta^{13}C$) of sediments were consistently heavier at Site I (–18.6 ± 0.2, [n = 38, 0 to 14 cm]) than at Site III (–21.2 ± 0.1, [n = 26, 0 to 12 cm]) by nearly 3‰ (Blair et al. 1994). This between-site difference is reflected in heavier background $\delta^{13}C$ signatures of annelids ($t_{27} = 6.72$, p < 0.00001), non-annelid metazoans ($t_{22} = 2.09$, p = 0.048), and agglutinated protozoans ($t_{36} = 2.48$, p = 0.018) at Site I than at Site III. Average annelid $\delta^{13}C$ values, –16.5 ± 0.3 at Site I (n = 16) and –19.0 ± 0.2 at Site III (n = 30), were more than 2‰ heavier than those of the sediments at each site. Agglutinating protozoans, with tests of sediment particles, exhibited $\delta^{13}C$ signatures closer to those of the ambient sediments (–18.7 ± 0.2 at Site I [n = 25] and –20.0 ± 0.1 at Site III [n = 5]). Non-annelid metazoans had values between annelids and agglutinating protozoans (–18.2 ± 0.6 at Site I [n = 7] and –19.8 ± 0.8 at Site III [n = 8]). Within-site statistical comparisons of the 3 major taxonomic groups revealed significantly heavier $\delta^{13}C$ values in annelids than non-annelids or protozoans at Site I ($F_{2,70} = 26.62$, p <0.00001), but no differences at Site III ($F_{2,19} = 0.38$, p = 0.687). All of these signatures are indicative of a largely phytoplankton-based food chain (Fry & Sherr 1984).

$\delta^{13}C$ signatures in annelids (polychaetes and oligochaetes) collected from background sediments were examined for effects of vertical distribution and presumptive feeding mode. At Site I, no statistically

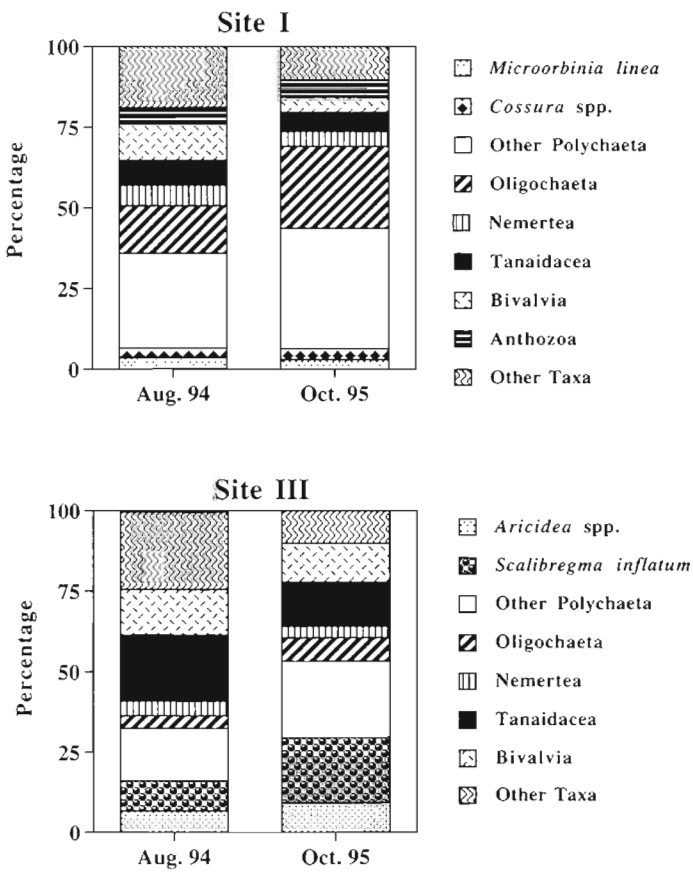

Fig. 3. Taxonomic composition of macrofauna (>300 µm) collected at Sites I and III near the beginning (August 1994) and end (October 1995) of the study. The 2 most abundant genera at each site are shown, along with other major taxa. Data are derived from pooled background and experimental cores listed in Table 1

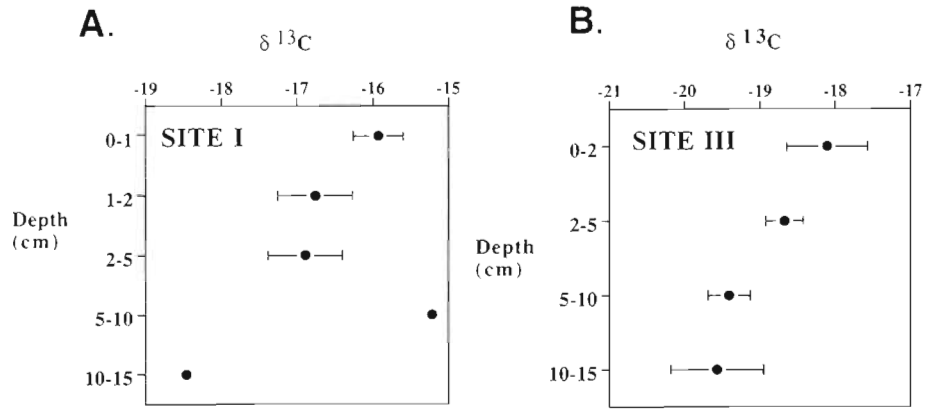

Fig. 4. Average background $\delta^{13}C$ signatures of annelids (±1 SE) collected from different vertical fractions within the sediment column at (A) Site I and (B) Site III. Background samples from 1994 and 1995 were pooled. Background POC $\delta^{13}C$ profiles (0 to 12 cm) are nearly vertical at Site I ($\delta^{13}C$ = −18.3 to −18.7) and Site III ($\delta^{13}C$ = −21.1 to −21.5)

significant differences in annelid $\delta^{13}C$ values were observed as a function of depth in the sediment column (Fig. 4A); however, only 2 individuals were obtained from below 5 cm. Within Site III sediments, average annelid $\delta^{13}C$ signatures exhibited considerable variation, but became lighter downcore (Fig. 4B). Annelids collected from the upper 2 cm had heavier $\delta^{13}C$ values (−18.11 ± 0.54) than those from the 5 to 10 cm fraction (−19.41 ± 0.28) (t_{16} = 2.17, p = 0.045) and the >10 cm fraction (−19.57 ± 0.61) (t_{11} = 5.11, p = 0.062).

Annelid $\delta^{13}C$ signatures did not vary as a function of feeding mode at Site III, but feeding group differences were evident at Site I ($F_{3,14}$ = 3.63, p = 0.048) (Fig. 5). Surface-deposit feeders at Site I exhibited lighter $\delta^{13}C$ signatures (−17.5 ± 0.5) than carnivores (−15.8 ± 0.4). Average values for the 4 feeding groups surface-deposit feeders, non-traditional surface-deposit feeders (3 taxa which were unexpectedly found in our experiments to take up large amounts of tracer: paraonids, maldanids and the nereid *Ceratocephale* sp.), subsurface-deposit feeders and carnivores were between −19.5 and −18.8 at Site III and between −17.5 and −15.3 at Site I (Fig. 5).

Within a site, average background $\delta^{13}C$ signatures differed slightly among species or taxa (Fig. 6). For most taxa, $\delta^{13}C$ signatures within a site were remarkably consistent. However, considerable variation was observed for bivalve $\delta^{13}C$ values at both sites (Fig. 6). Since bivalves were not identified to family, genus or species prior to analysis, it is probable that several taxa with different feeding modes, lifestyles or fractionation characteristics were grouped together. Despite interspecific variation in carbon isotopic signatures within a site, there was very little overlap in metazoan background $\delta^{13}C$ signatures between Sites I and III (Fig 6). Where the same genera or families occurred at both sites (e.g *Bathysiphon*, Maldanidae), they exhibited different $\delta^{13}C$ signatures, reflecting the general bulk sediment offset between sites.

$\delta^{13}C$ values greater (heavier) than −15 were never observed in background fauna at either site (Tables 2 & 3). In our evaluation of the tracer experiments, $\delta^{13}C$ values ≥−14 encountered in animals exposed to labeled diatoms were considered as evidence that organisms had ingested or otherwise obtained ^{13}C derived from our diatom tracer.

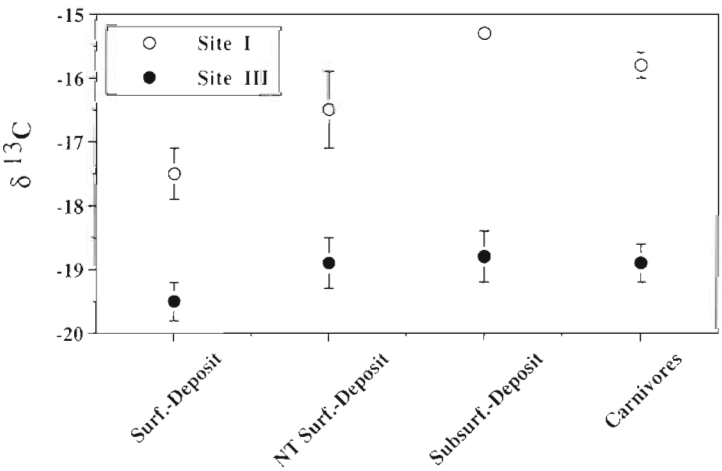

Fig. 5. Average background $\delta^{13}C$ signatures (±1 SE) of annelid feeding groups collected at Sites I and III. Background samples from 1994 and 1995 were pooled. Surf.-Deposit = surface-deposit feeders; NT Surf.-Deposit = non-traditional, surface-deposit feeders and includes 3 taxa found in our experiments to ingest large amounts of diatom tracer: paraonids, maldanids and the nereid *Ceratocephale* sp.; Subsurf.-Deposit = subsurface-deposit feeders. Carnivores includes animals that may also be scavengers or omnivorous

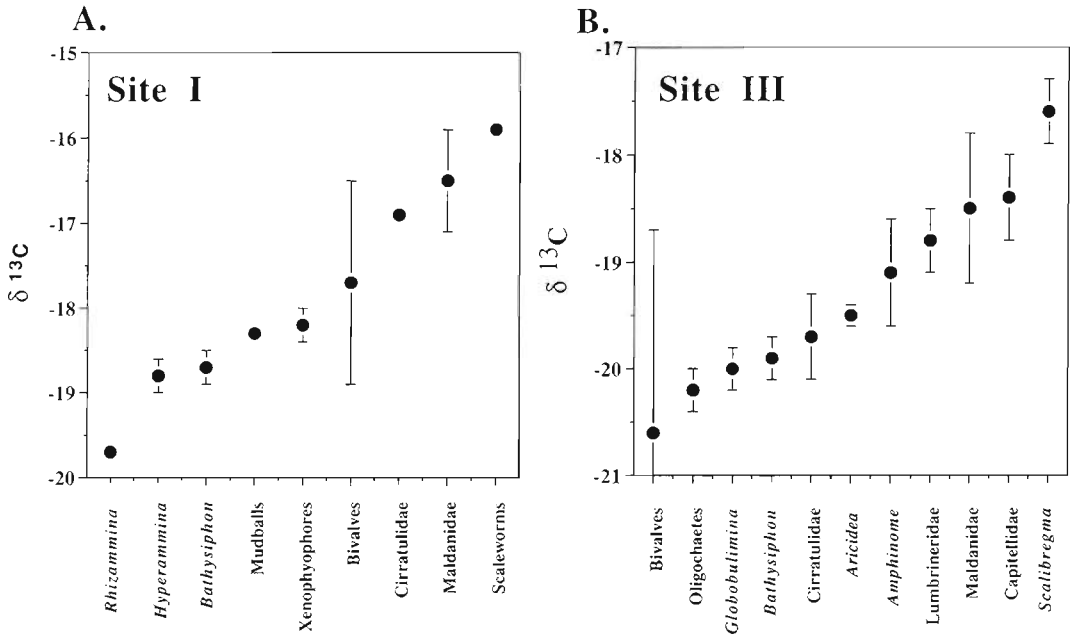

Fig. 6. Average background $\delta^{13}C$ signatures (±1 SE) of individual infaunal taxa, genera or species at (A) Site I and (B) Site III. The first 5 taxa shown for Site I are agglutinated sarcodine protozoans (foraminifera and xenophyophores). At Site III, *Bathysiphon* is an agglutinated foraminiferan and *Globobulimina* is a calcareous foraminiferan that also accretes sediments

Diatom ingestion as a function of time, site, and taxon

Time 0

Time 0 samples were intended to provide information about passive movement of tracers and artifacts associated with the experimental protocol. In Time 0 samples, the upper 2 cm of sediment contained over 97% of the labeled diatom C ($PO^{13}C$) at Site III (Levin et al. 1997) and over 99% of the diatom at Site I, suggesting that only a small fraction of the tracer was transported passively down tubes or burrows. However, during recovery and processing of cores, some infauna apparently ingested the labeled diatoms. Ingestion may have occurred immediately within the seabed, in cores on the submersible, or in dishes after sectioning, prior to sorting of organisms.

At Site I, 17% of metazoans (5 out of 30) appeared to ingest or otherwise obtain tracer in Time 0 samples (Table 2). These included a gastropod ($\delta^{13}C$ = 40.8), 3 polychaetes (a lumbrinerid, $\delta^{13}C$ = −9.7; a nephtiid, $\delta^{13}C$ = −9.3; and a paraonid, $\delta^{13}C$ = −3.7), and a bivalve ($\delta^{13}C$ = −9.2). The average $\delta^{13}C$ signature (±1 SE) of the remaining metazoans was −16.4 ± 0.4 (n = 25). Thirty-eight percent (11) of the 29 agglutinating protozoans analyzed in Time 0 samples from Site I exhibited elevated $\delta^{13}C$ signatures indicating tracer uptake (average $\delta^{13}C$ for these 11 was −10.0 ± 1.8). Only 1 of these (a komokiacean-like mudball) had a value >0.0 ($\delta^{13}C$ = 5.1). For the protozoans, there is no way to determine whether elevated signatures resulted from ingestion, active incorporation of labeled diatoms into agglutinated tests, or passive adhesion of tracer to tests. The remaining 18 agglutinated protozoans had an average $\delta^{13}C$ signature of −17.6 ± 0.3.

Of the metazoans analyzed from Time 0 samples at Site III, only 1 had $\delta^{13}C$ heavier than −14, the ampharetid polychaete *Melinna* sp. ($\delta^{13}C$ = 90.0). The average value for the others was −20.0 ± 0.6 (n = 20) (Table 3). A single Time 0 protozoan from Site III, *Bathysiphon filiformis*, had a $\delta^{13}C$ value of −20.9, consistent with background values.

Early in the study some Time 0 animals from Site I were left in dishes overnight before sieving. We suspect that the increased incidence of tracer uptake by Time 0 animals at Site I relative to Site III reflects the longer time required for processing samples, rather than a greater tendency to eat fast.

1 and 1.5 d

Short-term experiments (1.0 and 1.5 d at Site I and 1.5 d at Site III) revealed between-site differences in tracer uptake by organisms and among-taxon differences within sites (Fig. 7, Tables 2 & 3).

Site I. Agglutinated protozoans were among the most active organisms at Site I (Fig. 7). Of the 29 protozoan specimens examined following 1 d exposure to

Table 2. $\delta^{13}C$ signatures of macrofaunal metazoans and protozoans collected from experimental plots at Site I exposed to ^{13}C-labeled diatoms for Time 0 (<4 h) and 1 d, 1.5 d, or 14 mo periods. $\delta^{13}C$ values greater than –14.0 were considered to reflect ^{13}C-labeled diatom uptake

	Time 0	1 d	1.5 d	14 mo
Annelida				
Melinna sp.		166.59		
Capitellidae	–16.04	–15.65		147.78
	–15.94			–12.72
	–17.51			–14.39
	–15.11			–12.35
Cirratulidae	–17.17	47.03	–14.61	1025.02
		–15.35		944.54
Flabelligeridae			–10.85	4357.14
Sabellaridae			393.80	
Aurospio sp.	–15.51		7.18	
Terebellidae	–17.01			
Terebellides sp.	–16.94			190.53
	–17.85			
Maldanidae	–16.99	–13.43		249.22
	–16.67	–15.36		215.92
	–14.37			–8.52
	–16.94			–13.14
	–16.99			246.67
	–16.67			
Ceratocephale sp.		20.77		
		317.54		
Paraonidae	–3.69		–18.12	
Aricidea sp.				213.09
Lumbrineridae	–9.68			
Nephtiidae	–9.30		–12.32	
Onuphidae	–17.78	–5.21		–17.02
Opheliidae	–16.50			–6.50
Phyllodocidae		–14.01		
Mystides sp.				385.08
Polychaete (unid.)				–18.38
Oligochaeta	–19.51		–18.01	–14.06
	–18.78			
	–15.86			
Other Metazoa				
Aplacophora			–16.47	
Bivalvia	–9.17	–16.24		
	–14.21			
Holothuria				12.82
Gastropoda	–15.16	–15.44		16.59
	40.77			
Isopoda		18.44		
Unknown	–16.30	–15.05		
Ophiuroidea			–3.47	
Ostracoda		–12.69		
		–12.42		
Porifera			36.18	
Red anenome				–12.21
Nemertea	–18.53			
Tanaidacea	–15.92	–15.50		22.72
				63.96
Turbellaria		13.84	–16.20	
			–16.39	

	Time 0	1.0 d	1.5 d	14 mo
Protozoa				
Allogromids	–17.98	82.61	–19.51	–16.43
		–18.72		–17.50
		–17.34		
Aschemonella-like		–17.22		
Astrorhiza sp.	–19.20	–15.45		
Astrorhiza-like		380.16		21.95
		161.60		1818.31
Bathysiphon rufum		132.18	10.51	
		469.37	345.10	60.10
		–16.16	766.83	25.32
			926.14	–6.36
			–12.86	63.86
			107.78	
			–14.98	
			56.70	
			144.18	
Bathysiphon spp.	–14.26			
	–9.78			
	–17.54			
	–15.73			
	–16.17			
	–12.17			
	–9.76			
	–18.05			
	–13.58			
	–17.75			
Indet. tubular foram.		121.51		–9.82
Hyperammina	–16.57	68.90		69.95
	–16.57	–11.05		43.82
				21.14
				–25.61
Mudballs	–7.03	7.55		–19.21
(komokiacian?)	–17.27	–1.00		–16.01
	–18.15	–18.47		–16.18
	–17.93	–18.12		3.10
Mudballs (with tubes)	5.10		39.92	
	–18.77		–1.33	
	–18.96		–23.86	
	–19.40		–19.04	
		30.55	–5.92	3.10
		305.51	–6.95	–15.10
				–17.77
Occultammina sp.	–16.04			
	–17.78			
	–16.04			
	–17.78			
Pelosina sp.	–20.15	30.55		
	–11.67			
Rhizammina		46.57		–2.87
		–3.94		–18.32
		–16.39		484.14
Xenophyophores				
Psammina sp.		6.89		–11.24
		–12.39		–18.78
		–16.46		–19.72
		54.92		
Tubular species		148.13		–16.61
(near *Occultammina* sp.)		–14.11		–15.10
		–17.22		
Other xenophyophores			38.65	
			–18.32	
			–24.50	

tracer (1995 experiments), 59% (17) had $\delta^{13}C$ values indicative of tracer uptake and 9 of these contained >0.1% diatom carbon (>1 µmol diatom C $mmol^{-1}$ organism C). The average $\delta^{13}C$ value for all specimens was 62.2 ± 23.5 (range −18.7 to 469.4, n = 29). In the 1.5 d experiment, 68% of the specimens (13 out of 19) took up tracer, with 5 containing >0.1% diatom C. The average $\delta^{13}C$ value for all specimens in this experiment

Table 3. $\delta^{13}C$ signatures of macrofaunal metazoans and protozoans collected from experimental plots at Site III exposed to ^{13}C-labeled diatoms for Time 0 (<4 h) and 1.5 d, 3 mo or 14 mo periods. $\delta^{13}C$ values greater than −14.0 were considered to reflect ^{13}C-labeled diatom uptake

	Time 0	1.5 d	3 mo	14 mo
Annelida				
Melinna sp.	90.05	1159.58		
Cirratulidae	−19.73		−17.30	−3.86
			−19.24	−17.80
Chaetozone sp.				−18.28
Trichobranchidae	−19.12	−16.70		−12.06
Terebellides sp.	−26.00		3.38	−8.89
			−17.91	−6.28
			−15.28	−15.92
				23.57
				−16.20
Cossuridae				−17.49
Cossura sp.				1812.00
Maldanidae	−28.52	141.23	−19.53	−15.78
	−19.81	64.43	−19.11	−16.89
	−21.50	45.00	−15.88	
	−18.03	17.05	−17.40	14.67
	−19.76	−17.15	−17.08	−16.82
	−18.78	50.61	−16.86	−15.14
	−19.10	105.02		−17.40
		552.66		−16.43
		1672.65		−15.24
		104.65		
		−17.83		
		−18.68		
		147.69		
		−18.45		
Praxillella sp.				−15.14
Ceratocephale sp.			−11.21	447.09
				354.55
				37.34
Aricidea quadrilobata	−19.37			
	−15.97			
	−19.24			
	−19.24			
	−19.80			
Aricidea spp.		1461.16	−17.15	
		2780.96	−10.24	−18.28
		7828.20	1686.06	3.75
				−18.16
				−12.82
				−17.97
				−14.19
				32.91
Levinsenia sp.				51.77
				63.77
Capitellidae				−17.26
Oligochaeta	−20.14	−25.23		−16.29
		67.44		−1.22
		−20.18		−4.40

	Time 0	1.5 d	3 mo	14 mo
Annelida (cont.)				
Scalibregma inflatum		−3.99	−12.90	−17.18
			−4.72	−16.97
				−18.18
				−16.69
				−15.56
				−6.63
				−17.65
				−17.53
				−17.37
				−17.84
				−16.93
				−18.64
				−1.43
				−16.89
				−18.22
Lumbrineridae	−19.43	−16.25	−19.31	−15.87
	−18.15	−12.07	−18.31	−18.43
		−18.72	−15.21	−16.98
		29.72	−18.65	−16.98
			−18.41	−17.41
			−17.92	−17.90
			−18.78	
Onuphidae				−17.81
Hyalinoecia sp.				−18.50
Other Metazoa				
Amphipoda		−19.50		−18.44
Aplacophora		17.34		−25.39
Bivalvia		18.45	−18.25	−17.41
		49.61		−16.63
				−16.87
Gastropoda	−18.51			
Bubble snail				−1.23
Copepoda				−19.66
Isopoda				−20.66
Nematoda	−20.26	−17.25		
		5.36		
Nemertea				−16.80
Opisthobranchia		−14.34		
Polinices sp.				−18.35
Scaphopoda				12.39
Tanaidacea		−2.80		−18.71
				−20.22
Turbellaria				−15.69
Protozoa				
Bathysiphon sp.				−17.68
				−17.22
Bathysiphon filiformis	−20.90		−19.80	
Globobulimina sp.		1.71		−19.88
		−11.54		−28.63
		−9.32		−27.23
				−16.78

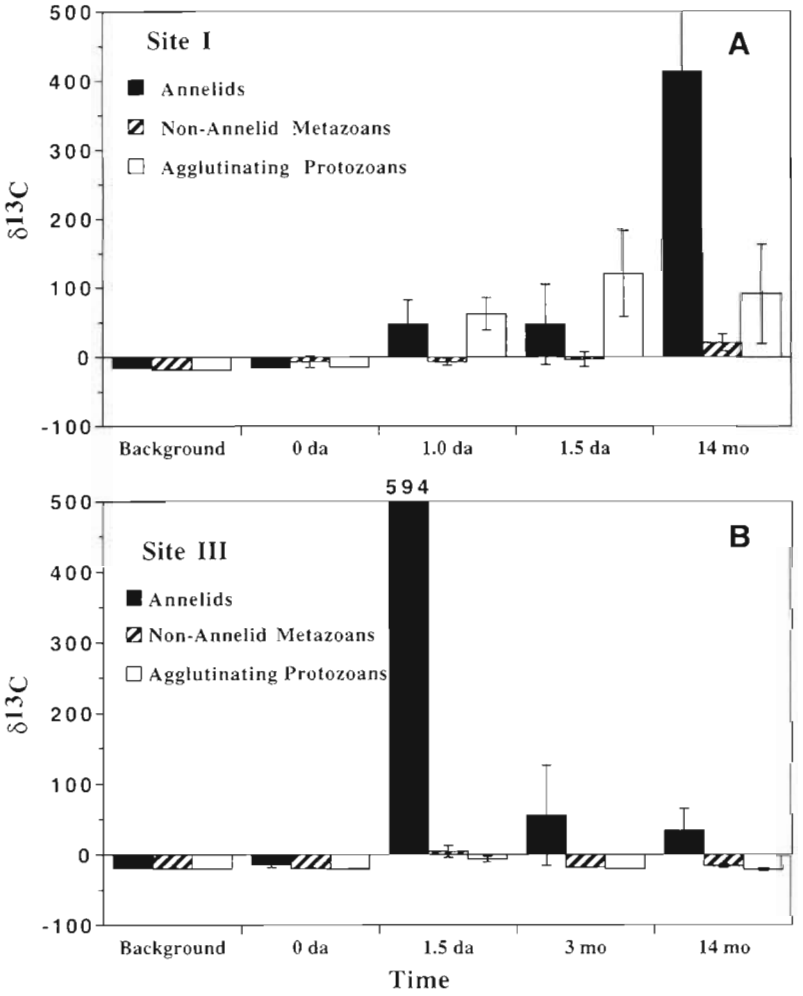

Fig. 7 Average $\delta^{13}C$ signatures (±1 SE) of annelids, other metazoans and agglutinating protozoans at (A) Site I and (B) Site III as a function of time since emplacement of ^{13}C-labeled diatoms. Background samples are from ambient sediments not exposed to tracer

was 120.5 ± 62.4 (range −23.9 to 926.1, n = 19) The agglutinated protozoans containing the greatest amount of tracer C (>0.1%) included an allogromid, *Pelosina* sp., *Hyperammina* sp., an astrorhizinid-like foraminiferan, *Bathysiphon rufum*, and tubular xenophyophore fragments (Table 2).

Annelids were also active tracer ingesters at Site I (Fig. 7); 60% (6 out of 10) and 57% (4 out of 7) of the annelids ingested labeled diatoms in the 1.0 and 1.5 d experiments, respectively. Of these, 4 contained ≥0.1% diatom C: a sabellarid polychaete ($\delta^{13}C$ = 393.8, 0.57% diatom C), the nereid *Ceratocephale* sp. ($\delta^{13}C$ = 317.5, 0.47% diatom C), the ampharetid *Melinna* sp. ($\delta^{13}C$ = 166.6, 0.26% diatom C) and a cirratulid polychaete ($\delta^{13}C$ = 47.0, 0.1% diatom C). For all annelids examined, average $\delta^{13}C$ values were 47.3 ± 35.0 (n = 10) in the 1 d experiment and 46.7 ± 57.9 (n = 7) in the 1.5 d experiment.

Non-annelid metazoans were much less active consumers of the labeled diatoms at Site I. The average $\delta^{13}C$ value for specimens was −6.9 ± 5.1 (n = 8; range −16.2 to 18.4) in the 1 d experiment and −3.3 ± 10.2 (n = 5, range −16.5 to 36.2) in the 1.5 d experiment. Forty-six percent of the 13 specimens examined had isotopic signatures indicative of tracer ingestion, but none contained ≥0.1% diatom C. The most active tracer consumers were an isopod, a turbellarian and a sponge (Table 2).

Site III. A detailed account of ^{13}C-labeled diatom uptake by macrofauna following 1.5 d exposure at Site III is given by Levin et al. (1997). However, this account did not compare annelids to other taxa, nor examine the overall incidence of tracer uptake, so these issues will be the focus here. Annelids were the primary consumers of ^{13}C-labeled diatoms after 1.5 d (Fig. 7, Table 3). The average $\delta^{13}C$ value for the 27 annelids sampled was 594 ± 307 (range −18.7 to 7828). Tracer ingestion was observed in 63% of individuals (17), with 10 of these (all paraonids *Aricidea* spp. and maldanids *Praxillella* sp.) having body concentrations of ^{13}C diatoms ≥0.1%. The 3 *Aricidea* spp. collected had tracer body loads of 11.0, 3.9 and 1.8% diatom C, and 1 *Praxillella* sp. had 2.3% diatom C. The average $\delta^{13}C$ signatures for non-annelid metazoans was 4.6 ± 8.3 (n = 8), with 38% ingesting tracer but none having >0.1% diatom C (Table 3). Only 3 protozoans, all *Globobulimina* sp. (a calcareous foraminifer), were sampled and all exhibited isotopic evidence of minor tracer uptake ($\delta^{13}C$ = −6.4 ± 4.1) (Table 3).

3 mo

The 3 mo tracer experiment, conducted at Site III between May and August 1994, was the first experiment deployed. Diatoms were spread without use of a settling agent (i.e. kaolin). As a result, little of the tracer mixture actually reached the seabed. Approximately 10% of the ^{210}Pb but only 1.1 ± 1.0% of the ^{13}C-diatom tracer was recovered after 3 mo (Fornes 1996). Twenty-five percent of the annelids sampled in

this experiment (6 out of 24) exhibited isotopic signatures indicative of tracer uptake, including *Ceratocephale* sp. most likely *C. loveni*, *Aricidea* spp. (most likely *A. quadrilobata* or *A. fragilis*), *Scalibregma inflatum* and *Terebellides* sp., but only 1, *Aricidea* sp., exhibited high concentrations of tracer C ($\delta^{13}C$ = 1686, 2.4% diatom C). The only non-annelids collected in this experiment, a single bivalve, and a single foraminifer, *Bathysiphon filiformis*, exhibited no evidence of tracer ingestion.

14 mo

Site I. Fourteen months after tracer emplacement, annelids appeared to be the taxon at Site I that retained the greatest amount of diatom C (Fig. 7A, Table 2). The average $\delta^{13}C$ value for annelids was 414 ± 230 (n = 19, range −18.4 to 4357), with 79% of specimens (15 of 19) exhibiting isotopic evidence for tracer uptake. Ten of these had >0.1% diatom C and 3 had >1% diatom C (Table 2). The greatest ^{13}C concentrations (>0.1% diatom C) were found in cirratulids, maldanids, *Aricidea* spp., the trichobranchid *Terebellides* sp., the phyllodocid *Mystides* sp. and a flabelligerid. Those taxa exhibiting no isotopic evidence of tracer diatom ingestion were oligochaetes and capitellid and onuphid polychaetes.

Agglutinated protozoans also had high $\delta^{13}C$ signatures (average 90.9 ± 71.8, range −25.6 to 1818, n = 26), indicating extensive tracer uptake and retention. Fifty-four percent (14 out of 26) specimens examined exhibited $\delta^{13}C$ signatures above background levels (≥−14) but only 4 of these had >0.1% diatom C. These were specimens of *Bathysiphon rufum*, *Rhizammina*, *Hyperammina*, and an astrorhizinid (Table 2).

All of the non-annelid metazoans examined (n = 5) exhibited elevated $\delta^{13}C$ signatures (average = 20.8 ± 12.3), but only a single tanaid had body concentrations of diatom C >0.1%. In general the non-annelid metazoans appeared to be the group least likely to ingest or retain large amounts of diatom C.

Site III. Little diatom ^{13}C remained in most animals at Site III after 14 mo (Fig. 7B, Table 3). Among annelids, the average $\delta^{13}C$ value was 34.1 ± 30.8 (n = 59, range = −18.5 to 1812). Thirty-two percent of the animals (19 of 59) exhibited evidence of tracer uptake, with 4 individuals having >0.1% diatom C (2 *Ceratocephale* sp., the paraonid *Levinsenia* sp., and *Cossura* sp.). The non-annelid metazoans had low $\delta^{13}C$ signatures, on average (−15.2 ± 2.5, range −25.4 to 12.5, n = 14) (Table 3). Of the 6 protozoans examined, none showed evidence of diatom C uptake ($\delta^{13}C$ = −21.2 ± 2.2) (Table 3).

Statistical analyses of changes in average annelid $\delta^{13}C$ signatures over time (1-way ANOVA) revealed no significant differences among exposure times >0 d at Site I, but a significant decrease from 1.5 d to 14 mo exposure at Site III ($F_{2, 110}$ = 4.477, p = 0.010).

Influence of annelid feeding group on diatom ingestion

The $\delta^{13}C$ signatures of annelid feeding groups varied at both sites (Fig. 8), but statistical differences among feeding groups were evident mainly at Site I. Surface-deposit feeders as well as paraonid, maldanid and nereid polychaetes (termed here non-traditional surface-deposit feeders) were primary tracer consumers (Fig. 8). As discussed above, exceptionally high $\delta^{13}C$ signatures were observed for many individuals in this latter group (Tables 2 & 3). Of all the taxa examined, *Aricidea* spp. consistently exhibited the heaviest $\delta^{13}C$ signatures, especially in the Site III short-term experiments. Subsurface-deposit feeders (excepting the maldanids, which were placed in another group) rarely exhibited $\delta^{13}C$ above background levels at either site. Carnivorous annelids had $\delta^{13}C$ signatures elevated above background levels only at Site I after 14 mo (Fig. 8).

Because tracer uptake was highly variable within each feeding group, with some individuals showing no evidence of diatom C ingestion in each group at any time (Tables 2 & 3), few statistical differences were observed in average $\delta^{13}C$ among annelid feeding groups, with the exception of Site I after 14 mo exposure (1-way ANOVA: $F_{3,14}$ = 3.25, p = 0.054). A 2-way ANOVA for feeding mode and time revealed a nearly significant feeding mode effect at Site I ($F_{3, 23}$ = 2.52, p = 0.077), where surface-deposit feeder signatures were more positive than those of carnivores (Tukey Kramer HSD, p = 0.011) (Fig. 8).

Influence of body size on diatom ingestion

Effects of taxon body size on diatom ingestion were examined for metazoans in the short- and long-term experiments at Sites I and III. Regressions of average body size (dry weight) versus average percent diatom C across taxa suggest that tracer ingestion was unrelated to taxon body size following 1.5 d exposure (Site I: r^2 = 0.09, p = 0.408, n = 10 taxa; Site III: r^2 = 0.02, p = 0.653, n = 12 taxa), and 14 mo exposure (Site I: r^2 = 0.05, p = 0.514; n = 12 taxa; Site III: r^2 = 0.01, p = 0.669, n = 24 taxa). A positive relationship between metazoan body size and diatom ingestion was observed in the Site I, 1.0 d experiment (r^2 = 0.615, p = 0.0003, n = 16 taxa). However, removal from the analysis of a single large *Ceratocephale* sp. that ingested a large amount

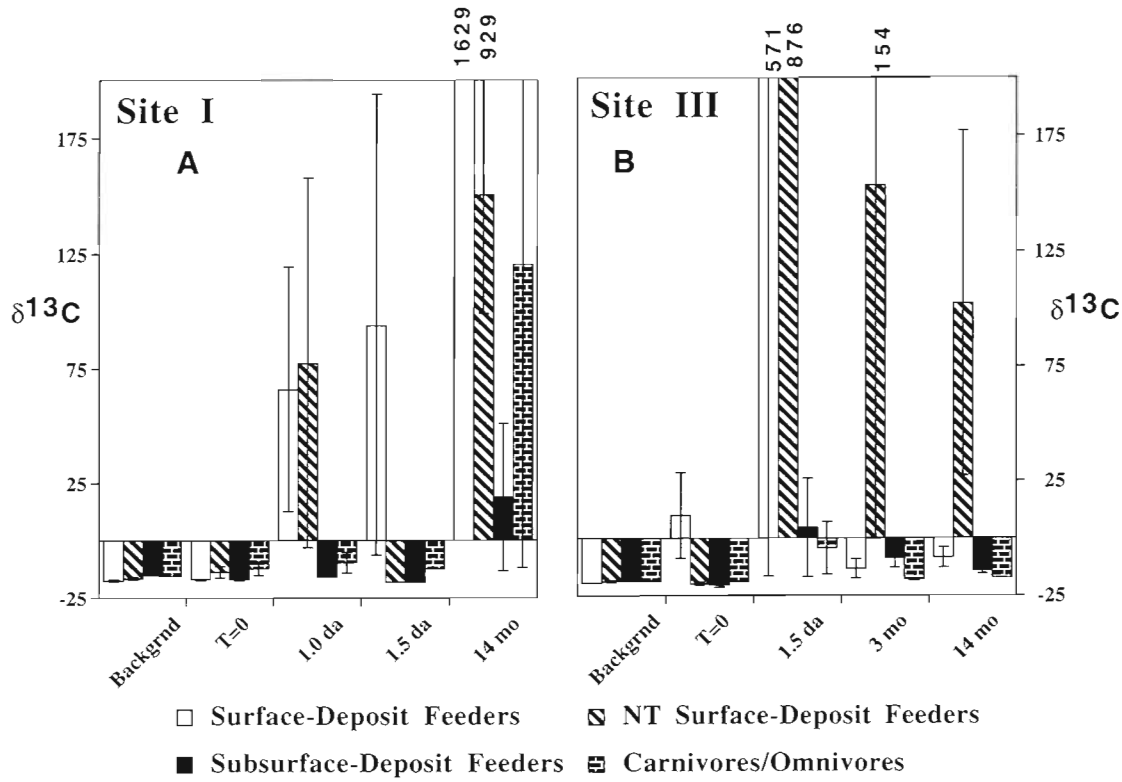

Fig. 8. Average $\delta^{13}C$ signatures (±1 SE) of annelid feeding groups at (A) Site I and (B) Site III as a function of time since emplacement of ^{13}C-labeled diatoms. NT surface-deposit feeders include 3 taxa found to consume tracer rapidly: paraonids, maldanids and the nereid *Ceratocephale* sp. Backgrnd = ambient annelids from sediments not exposed to tracer. Time 0 = annelids from control samples cored within 15 min of tracer placement and processed within 1 to 4 h. Other times represent the period between tracer emplacement on the seabed and sampling

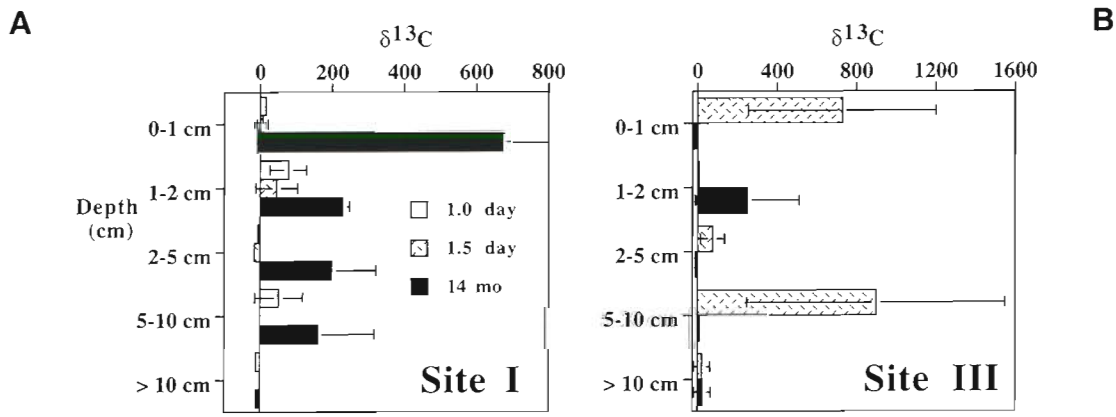

Fig. 9. Average $\delta^{13}C$ signatures (±1 SE) as a function of depth in the sediment column for metazoans collected from plots with ^{13}C-labeled diatoms after differing time periods at (A) Site I and (B) Site III

of tracer left no relationship between body size and tracer ingestion among the remaining taxa ($r^2 = 0.03$, $p = 0.524$, $n = 15$ taxa). Extensive diatom uptake was observed in both large taxa, such as *Praxillella* sp. and *Ceratocephale* sp., and small taxa, such as *Aricidea* spp. and cirratulids, while some relatively large individuals (e.g. a trichobranchid polychaete) did not consume tracer.

We examined within-taxon effects of body size on diatom uptake in 3 abundant taxa at Site III, including

2 major diatom consumers, *Aricidea* spp. and *Praxillella* sp., and 1 minor consumer, *Scalibregma inflatum*. Regressions of average dry weight against % diatom C were not significant for *Aricidea* spp. (14 mo experiment) and maldanids (1.5 d and 14 mo experiments), but a positive correlation between weight and diatom ingestion was observed for *Scalibregma* after 14 mo ($r^2 = 0.33$, $p = 0.0005$, $n = 33$). No other taxa were collected in sufficient numbers at either site for this analysis.

Influence of vertical distribution on diatom ingestion

Initial access to ^{13}C-labeled diatoms was predicted to be greatest for animals dwelling in the upper few cm of the sediment column. This was not observed at either site (Fig. 9). Though near-surface animals sometimes had very positive $\delta^{13}C$ signatures within the upper 1 or 2 cm in the short-term experiments, this was also the case for various animals collected deeper, particularly in the 5 to 10 cm fraction (Fig. 9). Labeled animals collected in the 5 to 10 cm fraction included *Aricidea* spp., *Praxillella* sp., *Melinna* sp., a lumbrinerid, and an oligochaete at Site III and *Ceratocephale* sp. at Site I. This indicates that some deep-dwelling individuals were able to access fresh, surficial organic matter very rapidly. $\delta^{13}C$ variances were sufficiently high within vertical fractions that significant differences between fractions were not observed at Sites I or III for either 1.0 or 1.5 d experiments. After 14 mo, very high diatom C incorporation at Site I was observed in animals in the top cm, although average $\delta^{13}C$ values were not significantly different among fractions ($F_{4,17} = 0.266$, $p = 0.895$). At Site III, where little of the signal remained, vertical differences in $\delta^{13}C$ were observed only between the 1 to 2 and 2 to 5 cm fractions ($F_{4,70} = 2.284$, $p = 0.069$; Fig. 9).

DISCUSSION

Background carbon isotopic signatures

Between-site differences in ambient sediment $\delta^{13}C$ are substantial, though both sites reflect organic matter inputs primarily from marine phytoplankton. The more negative sediment and animal isotopic signatures at Site III may have several causes. One possibility is that the marine plankton $\delta^{13}C$ signatures may differ in the south and mid-Atlantic Bights (Blair et al. 1994). Alternatively, greater terrigenous input from Chesapeake Bay and other nearby bays may drive $\delta^{13}C$ signatures down, as terrigenous organic matter is often 5 to 10‰ lighter than marine organic matter (Blair et al. 1994 and citations within). Site I is further from continental sources of terrestrial C and does not have the focusing mechanisms acting at Site III. Variable contributions of ^{13}C-enriched marine grasses (e.g. *Spartina* or *Zostera*, $\delta^{13}C = -12$ to -15; Fry & Sherr 1984) to these sediments is not expected to be an important controlling factor of $\delta^{13}C$.

More negative $\delta^{13}C$ annelid values with depth (Fig. 4) may result from dietary differences that arise by active particle selection (e.g. Hentschel 1998), or from changes in the $\delta^{13}C$ of available carbon with depth in the sediment column. Based on DIC fluxes and production, Thomas (1998) suggested that the labile C on the Cape Hatteras slope has a $\delta^{13}C$ value of -18 ± 1, despite a bulk C signature of -21.2 ± 0.1. This $\delta^{13}C$ value for labile carbon is more similar to that observed for background annelids as a group (–19.0) and for annelids in surface sediments (–18.1) than is the bulk sediment signature, which varied little downcore. The tendency for annelids below 2 cm to exhibit $\delta^{13}C$ values < -18 at Site III (Fig. 4B) could indicate that the deeper forms utilize more recalcitrant material buried within the sediments.

Causes for differences in background $\delta^{13}C$ signatures among taxa within each site (Fig. 6) are unknown. Possible explanations include (1) selective ingestion and/or assimilation of organic materials with distinctive isotopic compositions and (2) taxon-specific fractionation. Hentschel (1998) observed 1 to 3 ‰ differences in $\delta^{13}C$ values for several co-occurring, deposit-feeding, tidal-flat polychaete species, but was unable to distinguish between explanations (1) and (2) above. Incorporation of organic parts other than soft tissues in the analysis may account for some of the differences observed between non-annelid metazoans (which often have exoskeletons) and annelids. Since it was impossible to separate protoplasm from the agglutinated test for analyses of agglutinating protozoans, the isotopic signature of this group includes organic matter associated with sediments and other particles forming the test.

Initial response of macrofauna to phytodetritus

The initial fate of the ^{13}C-labeled diatoms within animals reflects bioenergetic partitioning of new food. This food can be (1) immediately burnt for energy, with diatom carbon released as $^{13}CO_2$ and thus present only in the gut, (2) stored as reserve energy for later use, or (3) used to form tissues. In the short-term experiments we are unable to distinguish whether elevated $\delta^{13}C$ signatures result from the presence of diatom ^{13}C tracer in organism guts, energy reserves, tissues, or agglutinated tests (for protozoans). Isotopic signatures $\geqslant -14$ of some animals in Time 0, 1.0 d and 1.5 d exper-

iments (Tables 2 & 3) indicate that certain infauna are capable of very rapid uptake of freshly deposited phytodetritus. This appears equally true at Sites I and III, though the identity of consumers differs. Laboratory feeding experiments indicate that in at least some of the species the diatoms are converted to biomass. One to 6% of the animals' amino acids are replaced with uniformly ^{13}C-labeled amino acids from the diatoms after 1.0 to 1.5 d (Thomas 1998).

The percentage of annelids and non-annelid metazoans acquiring diatom C in the 1 d and 1.5 d experiments did not differ between the 2 sites, although the intensity of uptake varied (Fig. 7). We speculate that the lack of diatom ingestion by the non-annelid metazoans at both sites may reflect either the lack of deposit feeding (e.g. carnivory) or competition from agglutinated foraminifera and/or annelids.

Rapid ingestion of fresh phytoplankton material by agglutinating protozoans has been observed in experimental systems (Altenbach 1992) and inferred in natural settings (Heeger 1990, Thiel et al. 1990, Gooday et al. 1992a,b, Drazen et al. 1998). Agglutinated protozoans at Site I were large and 5 to 6 times more abundant than the metazoan macrofauna (Hughes 1996, A. Gooday unpubl. data). We have observed naturally occurring, green phytodetrital aggregates in surface sediments from Site I, suggesting that infauna have periodic access to phytodetritus. Gooday and coworkers have proposed that large, surface-dwelling, agglutinating foraminifera, which appear to be common beneath productive waters, may be primary consumers of phytodetritus (Gooday et al. 1992b), perhaps outcompeting metazoan macrofauna for this resource (Gooday et al. 1996). Drazen et al. (1998) observed increased density and biomass of agglutinated foraminifera 4 wk after phytodetrital input in the abyssal Northeast Pacific. The large, agglutinated foraminiferan at Site III, *Bathysiphon filiformis*, is known, based on protoplasmic inclusions, to ingest diatoms and other phytoplankton (Gooday et al. 1992a). Although significant tracer ingestion by Site III *B. filiformis* was not observed in the present study, several smaller members of the genus at Site I (mainly *B. rufum*) contained large amounts of diatom C (Table 2).

Longer-term retention of tracer

In the longer term (14 mo) studies, it is likely that elevated $\delta^{13}C$ signatures reflect incorporation of diatom ^{13}C into energy reserves, tissues or protoplasm (rather than guts). Significant retention of tracer C by animals at Site I is suggested by high $\delta^{13}C$ values in many annelids and agglutinated protozoans (Fig. 7A, Table 2). Over 10% of the original tracer ^{210}Pb and 4% of the tracer ^{13}C deposited was still present in sediments at Site I after 14 mo (Blair et al. in press). Similar retention of tracer C was not observed at Site III, where only 2% of the original tracer ^{210}Pb and <1% of the tracer ^{13}C remained in sediments, and few infauna exhibited elevated $\delta^{13}C$ signatures (Blair et al. in press; Fig. 7B, Table 3). Tracer loss at both sites was either a product of removal by currents (Blake & Grassle 1994), or resuspension and erosion resulting from animal activities. Megafaunal densities are higher on the slope off Cape Hatteras than off Cape Fear (Hecker 1994). We observed fish and crabs feeding in experimental plots at Site III shortly after tracer placement and animal tracks were visible in some plots prior to sampling. Of the organic carbon that remained in the experimental plots, about half was oxidized at both sites. Oxidation throughout the 14 months was probably mediated primarily by microorganisms.

Controls on macrofaunal access to phytodetritus

Variation among animals

We originally hypothesized that greatest consumption of the tracer diatoms should be by those animals that are (1) surface-deposit feeders, (2) exhibit large body size, or (3) dwell very near the sediment-water interface. Surface-deposit feeding annelids were clearly active sediment ingesters at both sites, although variation in uptake by this group was enormous (Fig 8). Of all taxa examined, paraonid polychaetes, especially *Aricidea* spp., were most likely to have fed selectively on the labeled diatoms. These animals are small and a large fraction of the individuals occur 2 to 5 cm into the sediment column (Blake 1994, this study). Yet they apparently have immediate access to surface organic matter. They also were one of the most abundant taxa at Site III (Fig. 3). Diatom feeding has been reported in a shallow-water paraonid, and consumption of foraminifera has been noted for deep-water forms (Fauchald & Jumars 1979). Paraonids were one of the few groups to exhibit enhanced densities in the presence of biogenic pits on the North Carolina slope at Site II, an 850 m station located between Sites I and III (Schaff & Levin 1994). It is likely that paraonids, which are common in many deep-sea assemblages, exhibit opportunistic or flexible feeding behavior, taking advantage of diatoms when they are present.

Maldanid polychaetes *Praxillella* sp. were observed, both visually and isotopically, to ingest large quantities of diatom tracer. Maldanids are generally considered

to be head-down, conveyor-belt feeders that consume deep sediments and defecate at the surface. However, they are capable of hoeing surface deposits into their feeding cavities deep in the sediments, resulting in downward mixing of surficial organic matter (Dobbs & Whitlatch 1982, Levin et al. 1997). Based on tracer experiments, Levin et al. (1997) proposed that subduction of organic matter by maldanids may serve a keystone function in bathyal sediments, promoting microbial activity, enhancing organic matter diagenetic processes and providing organic-rich food to deep-dwelling infauna. The positive isotopic signatures of many infauna 5 to 10 cm in the sediment at Site III after 1.5 d (Fig. 9) has been attributed to the redistribution of tracer by maldanids (Levin et al. 1997).

Ceratocephale, a common genus in deep water (Fauchald & Jumars 1979), also was a significant tracer consumer. Shallow-water nereids are known to consume diatoms and algae, but many nereids are considered omnivores (Fauchald & Jumars 1979). Our observations provide the first confirmation that deep-water nereids may consume phytodetritus. Most of the other annelid taxa exhibiting high concentrations of diatom C (cirratulids, a flabelligerid, an ampharetid, and a cossurid) are recognized as surface-deposit feeders (Fauchald & Jumars 1979), but the cossurids might be expected to feed subsurface, because of their deep-dwelling habits.

Other factors affecting phytodetritus uptake

Body size appears to have little influence on infaunal access to phytodetritus. Our body size measure, dry weight, is not ideal, because some individuals may have had sediment present within their guts. However, sediment-filled guts would probably not obscure the 1 to 3 orders of magnitude differences in size observed among and within species. Several of the most active diatom consumers were large-bodied annelids, including *Praxillella* sp., *Ceratocephale* sp. (probably *C. loveni*), lumbrinerids and *Melinna* sp. These animals apparently do not outcompete the smaller paraonids, cossurids, cirratulids and tanaids for labile organic matter. Particle size may influence animal ingestion and subsequent particle mixing (Wheatcroft 1992). The diatom-kaolin aggregates were probably relatively large, but this does not appear to have been a problem for small-bodied taxa such as paraonids or tanaids. Some of the diatom ^{13}C present in animals after 14 mo was probably transformed into microbial C prior to ingestion, and thus was consumed as particles smaller than the diatoms.

Vertical position within the sediment column was a poor indicator of animal access to surficial deposits, even after just a few days (Fig. 9). Infauna may migrate vertically within the sediments during recovery and sectioning of cores, especially subsurface deposit-feeders (Blake 1994, Thomas 1998). However, we suggest most taxa probably do not change greatly their positions relative to one another during core recovery and processing. Either vertical distributions do not reflect feeding locations of infauna, or deep-dwelling fauna rapidly obtained freshly deposited material at depth in the sediment column. For the smaller infauna, proximity to large subducting animals such as maldanids may provide access to labile food resources 5 or more cm beneath the sediment surface (Levin et al. 1997).

Implications of tracer studies

Observed patterns of macrofaunal tracer consumption have significant implications concerning bioturbation and carbon diagenesis. The paraonid, nereid and maldanid polychaetes generally live deep in the sediment column (>2 cm) and were most abundant at Site III. A result of their extensive feeding activity is rapid downward mixing of surficial deposits. From 74 to 80% of the diatom C remaining in sediments at Site III after 14 mo was present below 2 cm in the sediment column. In contrast, much less vertical mixing of tracer was observed at Site I (Fornes et al. 1999), where dominant consumers were agglutinating protozoans and surface-feeding polychaetes, taxa which presumably do not bioturbate extensively. Of the tracer remaining in sediments at Site I after 14 mo, only 23% was present below 2 cm. ^{234}Th-based estimates of bioturbation (D_b), made prior to our experiments, reflect lower diffusive mixing rates at Site I than at Site III (Schaff et al. 1992, DeMaster et al. 1994). Observed patterns of tracer uptake by metazoan and protozoan infauna are consistent with this difference. We note that D_b values also reflect the frequency and magnitude of non-local transport, which differed in our tracer experiments at Sites I and III.

^{14}C analyses of animal tissues indicate that the carbon assimilated by macrofauna on the North Carolina slope is essentially all bomb-^{14}C labeled (future ages) relative to ambient surface sediments that have ages of 400 to 2000 yr (DeMaster et al. 1998). Our experiments demonstrate that metazoan and protozoan benthos can rapidly consume phytodetritus reaching the margin floor, with some taxa exhibiting greater access to the material than others. Presumably naturally occurring phytodetritus is some of the youngest carbon available to slope sediments, and those species which preferentially consume it (e.g. paraonids) should have the youngest ^{14}C ages.

CONCLUSIONS

Within-site differences in background $\delta^{13}C$ values among different major taxa, among annelid species, and among individuals at different depths in the sediment column, suggest that all infaunal individuals do not consume (or assimilate) the same carbon sources. The ubiquitous distribution of the dominant diatom consumers in this study, agglutinating foraminifera, paraonid, maldanid, cirratulid and nereid polychaetes, indicates that rapid phytodetritus consumption is likely to occur within hours to days of deposition in well-oxygenated, bathyal settings. Because propensity to ingest phytodetritus appears to be taxon specific, rather than a function of traditional feeding guilds, body size or vertical distribution, a detailed understanding of species identity and behavior (natural history) may be necessary for prediction of particle fates in deep water.

Differences in phytodetritus consumers and their behavior between Sites I and III, located 180 km apart, appear responsible for different rates of particle mixing and modes of organic matter diagenesis. Anaerobic degradation is more important at Site III than at Site I (Blair et al. 1994). While the difference is due at least in part to the higher sediment and organic carbon deposition rates at Site III, the bioadvection to depth in the seabed of fresh phytodetritus will increase the relative importance of subsurface, largely anaerobic reactions as well (Blair et al. 1996, Levin et al. 1997).

Lack of metazoan numerical response to natural phytodetrital input in the deep sea has been noted previously (Gooday & Turley 1990, Gooday et al. 1996), but functional and reproductive responses are now documented (Graf 1989, Lauerman et al. 1997, Smith et al. 1998). Experimental placement of dead plant material on the deep-sea floor has elicited a wide range of responses, often including macrofaunal density enhancement and/or appearances of uncharacteristic species (e.g. Levin & Smith 1984, Grassle & Morse-Porteous 1987, Snelgrove et al. 1992, 1994). Our experiments have shown that unaltered slope assemblages can rapidly ingest and vertically mix fresh phytodetritus down into the sediment column, but that the tempo and mechanisms of mixing are heterogeneous among locations. This heterogeneity will affect the cycling of organic matter on continental slopes, where much C is deposited. The extent to which rapid faunal processing of phytodetritus involves species interactions such as facilitation or competition and the geochemical consequences of these responses remain a matter of speculation until further experimentation occurs.

Acknowledgements. We greatly appreciate the skilled contributions of the crews, pilots and captain of the RV 'Edwin Link' and 'Johnson SeaLink' submersibles, without which our experiments could not have been performed. We thank the many scientific participants of SLOPEX 94 and 95, in particular W. Fornes, D Talley, A. McCray, C. DiBacco, and J. Crooks. Additional technical assistance was provided by T Pease, W. Savidge, E.Clesceri, S. Boehme, D. Dinsmore, D. Savidge, R. Pope, C. Reimers, R. Collman, D. Daley, D. Beauregard, G. Taylor, M. Becker, and G. Checkley. A. Gooday and 4 anonymous reviewers provided helpful comments on this manuscript. The research was supported by grants from the NOAA National Undersea Research Program at Wilmington, North Carolina, and the National Science Foundation (OCE 93-11711 and OCE 93-01793).

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: August 10, 1998; Accepted: February 1, 1999
Proofs received from author(s): June 1, 1999

Vol. 182: 55–67, 1999 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published June 11

Diatom fluxes to the deep sea in the oligotrophic North Pacific gyre at Station ALOHA

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ABSTRACT: Planktonic diatoms are important agents of vertical transport of photosynthetically fixed organic carbon to the ocean's interior and seafloor. Diatom fluxes to the deep sea were studied for 2 yr using bottom-moored sequencing sediment traps located in the vicinity of the Hawaii Ocean Time-series (HOT) program station 'ALOHA' (22° 45' N, 158° W). The average flux of empty diatom frustules was around 2.8×10^5 cells m^{-2} d^{-1} in both years, except in late summer when it increased approximately 30-fold. Flux of cytoplasm-containing diatom cells was much lower (about 8×10^3 cells m^{-2} d^{-1}) but increased 500-fold in late July 1992 and 1250-fold in August 1994. *Mastogloia woodiana* Taylor, *Hemiaulus hauckii* Grunow and *Rhizosolenia* cf. *clevei* var. *communis* Sundström were the dominant diatom species observed during the July 1992 event, with the former 2 species again dominant in August 1994. The 1994 summer flux event occurred about 3 wk after a documented bloom of *H. hauckii* and *M. woodiana* in the mixed-layer and a simultaneous increase in vertical flux of these species. This surface flux signal was clearly detectable at 4000 m, suggesting rapid settling rates. A further indication of very high sinking speeds of the diatoms was the much larger proportion of cytoplasm-containing cells in the bottom-moored traps during the 2 summer events. Cells of *H. hauckii* and *R.* cf. *clevei* var. *communis* frequently contained endosymbiotic cyanobacteria with heterocysts (cf. *Richelia*), similar to the cells of these species in the mixed-layer. Our data show for the first time that diatoms containing nitrogen-fixing cyanobacteria contribute directly to the vertical flux of organic matter to the deep sea in the oligotrophic regions. The peak of diatom flux coincided with a significant flux increase of biogenic silica in both years. During periods of rapid sinking, the vertical flux of diatom assemblages out of the uppermost water column seems to be more important than the diatom flux out of the deep chlorophyll maximum layer (DCML). Aggregate formation may be responsible for the fast sinking of the diatoms.

KEY WORDS: Biogenic silica · Bottom-moored sediment traps · Deep sea · Diatoms · Vertical particle flux

INTRODUCTION

Diatoms appear to be a very important phytoplankton group for new production in the ocean (Brzezinski & Nelson 1995, Dugdale et al. 1995, Dugdale & Wilkerson 1998). Vertical flux of particulate organic matter (POM) into the ocean's interior arises in the form of fecal pellets, carcasses of zooplankton, detritus and intact phytoplankton cells. Bottom deposition of diatom cells and other phytodetritus have been observed even at abyssal depths (Billett et al. 1983, Smith et al. 1996).

In the subtropical oligotrophic (low standing stocks of nutrients and biomass) gyres, diatom populations do not achieve high cell abundances, unlike prokaryotes and eukaryotic nanoflagellates which dominate the phytoplankton populations in these areas (Olson et al. 1990, Letelier et al. 1993, Malone et al. 1993, Campbell et al. 1997). Among the microphytoplankton, the filamentous cyanobacterium *Trichodesmium* spp. has received special attention, partly due to their striking presence at the sea surface under certain environmental conditions and partly due to their quantitative role in the biogeochemistry of oligotrophic oceans because

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