JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research,* one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at https://elischolar.library.yale.edu/.

Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope

by L. Levin[1], N. Blair[2], D. DeMaster[2], G. Plaia[2], W. Fornes[2],
C. Martin[1] and C. Thomas[2]

ABSTRACT

In situ tracer experiments conducted on the North Carolina continental slope reveal that tube-building worms (Polychaeta: Maldanidae) can, without ingestion, rapidly subduct freshly deposited, algal carbon (^{13}C-labeled diatoms) and inorganic materials (slope sediment and glass beads) to depths of 10 cm or more in the sediment column. Transport over 1.5 days appears to be nonselective but spatially patchy, creating localized, deep hotspots. As a result of this transport, relatively fresh organic matter becomes available soon after deposition to deep-dwelling microbes and other infauna, and both aerobic and anaerobic processes may be enhanced. Comparison of tracer subduction with estimates from a diffusive mixing model using [234]Th-based coefficients, suggests that maldanid subduction activities, within 1.5 d of particle deposition, could account for 25–100% of the mixing below 5 cm that occurs on 100-day time scales. Comparisons of community data from the North Carolina slope for different places and times indicate a correlation between the abundance of deep-dwelling maldanids and the abundance and the dwelling depth in the sediment column of other infauna. Pulsed inputs of organic matter occur frequently in margin environments and maldanid polychaetes are a common component of continental slope macrobenthos. Thus, the activities we observe are likely to be widespread and significant for chemical cycling (natural and anthropogenic materials) on the slope. We propose that species like maldanids, that rapidly redistribute labile organic matter within the seabed, probably function as keystone resource modifiers. They may exert a disproportionately strong influence (relative to their abundance) on the structure of infaunal communities and on the timing, location and nature of organic matter diagenesis and burial in continental margin sediments.

1. Introduction

Pulsed delivery of organic matter to the continental margins and deep sea is now known to be widespread (Honjo, 1982; Lampitt, 1985; Hecker, 1990; Smith, 1994; Smith *et al.,* 1994; Gehlen *et al.,* 1996). However, the short-term, post-depositional processes and biological responses triggered by the delivery are poorly understood. Past studies have emphasized population-level responses by bacteria, protozoans and meiofauna to phytode-trital falls (reviewed in Gooday and Turley, 1990). There also are recent reports of

[1] Marine Life Research Group, Scripps Institution of Oceanography, La Jolla, California, 92093-0218, U.S.A.
[2] Department of Marine, Earth and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina, 27695-8208, U.S.A.

functional responses by macrofauna (Graf, 1989) and megafauna (Rice and Lambshead, 1994; Smith, 1994; Lauerman *et al.,* 1997). Aside from the report by Graf (1989) of rapid subduction of chlorophyll-rich fecal pellets by sipunculans on the Voring Plateau, there is limited understanding of macrofaunal responses to pulsed phytodetrital inputs or the influence of macrofauna on the diagenesis of organic matter delivered to the deep-sea floor.

Jumars *et al.* (1990) proposed that one expected response to organic pulses in the deep sea might be the downward transport and caching of such material by benthic fauna in the seabed. Rice and Rhoads (1989) discuss the role of bioturbating fauna in affecting the spatial distributions of the quality and quantity of detrital food and highlight the potential importance of subsurface injection of reactive organic matter to consumers foraging below the top few cm of sediment. Subsurface maxima of recently-deposited particles, indicative of nonlocal transport and possibly caching, are documented in several deep-sea systems where sipunculans or echiurans appear to be responsible (Smith *et al.,* 1986; Smith and Schafer, 1984; Graf, 1989; Jumars *et al.,* 1990). Recent work on the North Carolina slope implicates paraonid and scalibregmid polychaetes in rapid subduction of organic matter to 4–5 cm (Blair *et al.,* 1996).

Until recently, the fates of materials reaching the deep-sea floor were studied with naturally occurring radiotracer (e.g., ^{234}Th or ^{210}Pb; Smith *et al.,* 1994) and stable isotopic signatures (Suchanek *et al.,* 1985), plant pigments (Graf, 1989; Pfannkuche and Lochte, 1993) or anthropogenically produced materials (Guinasso and Schink, 1975; Van Dover *et al.,* 1992). Experimental emplacement of tracers provides a valuable means to characterize particle mixing and organic matter decomposition *in situ* over relatively short (hr to yr) time scales. Deliberate tracers used to study fates of inorganic particles include microtaggants® (Smith *et al.,* 1986; Levin *et al.,* 1991), glass beads (Wheatcroft, 1992), luminophores (Gerino *et al.,* 1994), and noble-metal tagged sediment (Wheatcroft *et al.,* 1994). Use of ^{13}C- and ^{14}C-labeled organic matter has proven successful in tracking the pathways of carbon within sediments, porewaters and animal tissues (Cahet and Sibuet, 1986; Widbom and Frithsen, 1995; Blair *et al.,* 1996).

Experiments reported in this paper employ a multiple tracer technique, in which ^{13}C-labeled diatoms and radio-labeled diatoms, sediments and glass beads are used to study the short-term transport of materials reaching the seabed off North Carolina. We demonstrate rapid, nonselective, subduction of freshly deposited diatoms and other surficial materials by maldanid polychaetes and show that this activity can account for a substantial fraction of the deep particle mixing that occurs at the study site. Through use of ^{13}C-labeled organic matter, we provide the first direct evidence that deep-dwelling infauna (below 5 cm) gain access to surficial material within a few days of deposition. These results build on previous observations of maldanid activities in the laboratory and in shallow water, providing knowledge of the magnitude and consequences of organic matter subduction activities on the continental slope. We propose that species responsible for the marked redistribution of labile organic matter within the sediment column may function as

keystone taxa in continental margin sediments and offer evidence from one site on the North Carolina slope.

2. Methods

A particle mixture containing [13]C- and ^{210}Pb-labeled diatoms (freeze-dried onto kaolin), [113]Sn-labeled local slope sediment (20–60 μm in size), and [228]Th-labeled glass beads (105–149 μm in size) was spread on the seafloor in August 1994 at a site off Cape Hatteras (35°23′ N 74°50′ W, water depth 850 m, Site III in Schaff *et al.*, 1992). Tracer particles were selected to represent a variety of natural particle types and sizes. The pelagic diatom, *Thalassiosira pseudonana,* was used because diatoms in this genus commonly are found in surface sediments on the NC slope and beneath other upwelling regions (Cahoon *et al.,* 1994). Sediment from the bottom (>15 cm) of boxcores collected near the study site was used to represent local sediment low in labile organic matter. Sand-size particles also were chosen because they comprise approximately 32% of the naturally occurring sediment at the study site (Kelchner, 1992) and are used by several polychaete taxa present, including maldanids, to construct tubes.

The ^{13}C-labeled *Thalassiosira pseudonana* (CCMP1335 clone, Provasoli-Guillard National Center for Culture of Marine Phytoplankton, Bigelow Laboratory for Ocean Sciences) was cultured at 22°C in closed 9.5L Pyrex bottles containing a modified f/2 medium. Autoclaved, bicarbonate-free f/2 culture medium was amended with a filter sterilized solution of 99% ^{13}C-NaHCO$_3$ (Cambridge Isotopes) to create a final DIC concentration of 4 μM. The inocula for the cultures were grown on the same medium. The bottles were illuminated with fluorescent shop lights. The cultures were harvested via filtration when exponential growth ceased as indicated by the leveling off of the pH at 9.5–9.7.

Dried ^{13}C-labeled diatom material was combusted to CO_2 with a modified Carlo Erba CNS analyser (Blair and Carter, 1992). The CO_2 was trapped cryogenically and analyzed for ^{13}C-content on a modified Finnegan-MAT isotope ratio mass spectrometer (Hayes *et al.,* 1977). The masses 44 and 45 ($^{12}CO_2$ and $^{13}CO_2$ respectively) were monitored alternately in the least sensitive (pilot) cup of the mass spectrometer because of the extreme ^{13}C enrichment of the samples. The diatom carbon was 95% ± 1% [13]C.

Algae, slope sediment, and glass beads were tagged with gamma-emitting tracers (^{210}Pb, [113]Sn, and [228]Th, respectively) to permit their rapid detection following core recovery from the seabed. The half lives of these radioisotopes are 22 y, 118 d, and 1.9 y, respectively. The tracers are naturally particle-reactive and consequently remain with their original particulate phase even after deployment on the ocean floor. Experimental design avoided excessive sediment enrichment; labeled diatom carbon accounted for ≤1.1% of existing POC levels (1.6% C) in the upper 1 cm of sediment. We could not, however, quantify what fraction of the labile carbon pool the tracer represented.

The tagged particles were spread by submersible onto 40 × 40 cm plots ~5 m apart on the seafloor, and then were sampled using Ekman boxcores either within 30 minutes of

tracer spreading ($T = 0$, $n = 2$ plots) or after ~1.5 days ($T = 1.5$ d, $n = 3$ plots). Only two of the 1.5-day plots were sampled successfully; the boxcore failed in the third. A 1.5-day tracer exposure period was selected in order to capture initial transport events; earlier experiments at this site (Blair *et al.*, 1996; unpublished data) helped establish the appropriate time frame.

Ekman boxcores ($15 \times 15 \times 15$ cm) each contained 4 subcores (a–d). Sediments within the subcores were analyzed for (a) $\delta^{13}C$ of dissolved inorganic carbon (DIC) and particulate organic carbon (POC), (b) $\delta^{13}C$ of infauna sorted then frozen on board ship, (c) radiotracers and glass beads, and (d) infaunal abundance and composition. During sectioning of (a) and (c), care was taken to remove outer edges of each sediment interval to avoid tracer that might have been subducted along the subcore wall during insertion.

All cores were stored on board ship at ambient (*in situ*) temperature (4–6°C) until they could be subsampled. Subcores for POC/DIC measurements were sectioned at 1 cm intervals down to 7 cm, then at 2 cm intervals to 13 cm. When large infauna were encountered during sectioning of these subcores, they were removed and frozen for later $\delta^{13}C$ analyses. Radiotracer and bead subcores were sectioned at 0.5-cm intervals down to 2 cm, then at 1-cm depth intervals to 15 cm. Faunal subcores (b and d above) were sectioned at 0–1, 1–2, 2–5, 5–10, and 10–15 cm depth intervals. Sample processing was usually completed within 2–3 hours of coring.

Mud from each interval of the POC/DIC subcore was packed in 15 mL N_2-flushed polypropylene centrifuge tubes. Porewater was recovered by centrifugation for 20 minutes at 5000 rpm. The isolated porewater was filtered through 0.45 µm pre-rinsed Nylon membranes. One mL aliquots were sealed in vials with crimped red rubber stoppers (Wheaton) for the DIC analyses. The samples were stored frozen until analysis. The DIC samples were acidified with 0.2 mL of 1 M H_3PO_4, and the resulting CO_2 was stripped with helium, dried via passage through anhydrous magnesium perchlorate and Nafion® tubing (Perma-Pure), and then trapped cryogenically for isotopic analysis. Subsamples of the centrifuged sediment were used for the POC analysis. CO_2 for isotopic analysis was produced from the POC as described in Blair and Carter (1992). The $^{13}C/^{12}C$ content of the CO_2 from both the DIC and POC was measured on the modified Finnegan MAT Delta E isotope ratio mass spectrometer. $\delta^{13}C$ measurements of the DIC and POC from two background cores, collected within 10 m of the experimental plots, were made to correct for the natural occurrence of ^{13}C (Blair *et al.*, 1996).

Core sediments for $\delta^{13}C$ faunal analyses were sieved through a 300-µm mesh screen, then macrofauna were sorted live and identified, washed in filtered seawater, and frozen at $-20°C$. Fauna from subcores targeted for infaunal counts were sieved through a 300-µm screen prior to preservation in 8% buffered formalin and seawater.

In the laboratory, frozen animals were dried *in vacuo*, acidified with 4M HCl in silver boats, dried again *in vacuo*, and combusted to CO_2 with the modified Carlo Erba CNS analyzer (Blair and Carter, 1992). The isotopic composition of the CO_2 was measured as

described above. Preserved specimens (>300 μm) were sorted from sediments under a dissecting microscope at 12× magnification and later identified to species.

Gamma activities from the tracers were measured in the laboratory by placing a 125 ml petri dish containing wet sediment on an intrinsic germanium gamma detector (DeMaster *et al.,* 1994; Fornes, 1996). The energies of the gamma emitting isotopes were 46 keV (^{210}Pb), 392 keV (^{113}Sn), and 583 keV (^{228}Th via ^{208}Tl). The counting efficiencies for the various gamma energies were determined using a uraninite standard with all ^{238}U daughters in secular equilibrium. The ^{210}Pb and ^{228}Th activities in the experimental plots were corrected for naturally occurring ^{210}Pb and ^{228}Th, based on profiles from background sediment cores.

Glass beads were counted directly in selected cores to assess concordance of ^{228}Th emissions with bead abundance. To permit direct counts, bead samples were digested with H_2O_2 and HCl, then sieved to remove particles less than 63 μm and greater than 300 μm. Beads from each fraction were counted in three 20-ml aliquots taken from a one-liter cylinder during constant stirring. Glass beads were enumerated visually using a dissecting microscope (12–25× magnification). Counting precision was ~6% (Blair *et al.,* 1996).

3. Results

After 1.5 d on the seabed, all three deliberately placed particle types were present in the sediment column to depths of at least 10–13 cm. Subsurface maxima of diatoms (reflected in profiles of labeled diatom C and ^{210}Pb), slope sediment, and glass beads were observed at 3–5 cm, 5–7 cm and especially at 9–13 cm depths (Figs. 1A, 2). Tracer peaks were present below 10 cm in 3 of 4 subcores examined (the POC and radiochemistry subcores from plot 94-26 and the POC subcore from plot 94-25). A distinct peak in labeled diatom C also was present in porewater DIC sampled from 9–13 cm, and finer scale deflections in the DIC curves are evident at 3–4 and 5–6 cm (Fig. 1B inset). The association between subsurface peaks in the DIC and POC profiles suggests that the DIC was produced by *in situ* respiration in that depth interval, rather than by irrigation, which would smear DIC profiles. Subsurface maxima of diatom C and gamma-tracers were absent in $T = 0$ samples. In Time 0 cores the upper 2 cm of the seabed contained more than 89% (DI^{13}C) and 97% (PO^{13}C) of the labeled diatom C (Fig. 1), and over 97% of ^{210}Pb, ^{113}Sn, and ^{228}Th activities. The percent of PO^{13}C label found below 5 cm in the sediment column was 0.07% and 0.6% in the two $T = 0$ cores and 13% and 6% in the two $T = 1.5$-d cores. The difference between the $T = 0$ and 1.5-d profiles suggests that a time-dependent, active process was responsible for rapid, downward advection of particles. We feel it is unlikely that passive transport down tube or burrow openings could account for the large differences observed (Fig. 1A), although passive movement of tracer may have occurred during the course of the experiment. Despite heterogeneity among subcores and plots in amount and depth of vertical particle transport, the three particle types generally moved in concert within the seabed (Fig. 2). The mechanism responsible for rapid subduction of particles appears to be nonselective over the range of particle quality and texture tested.
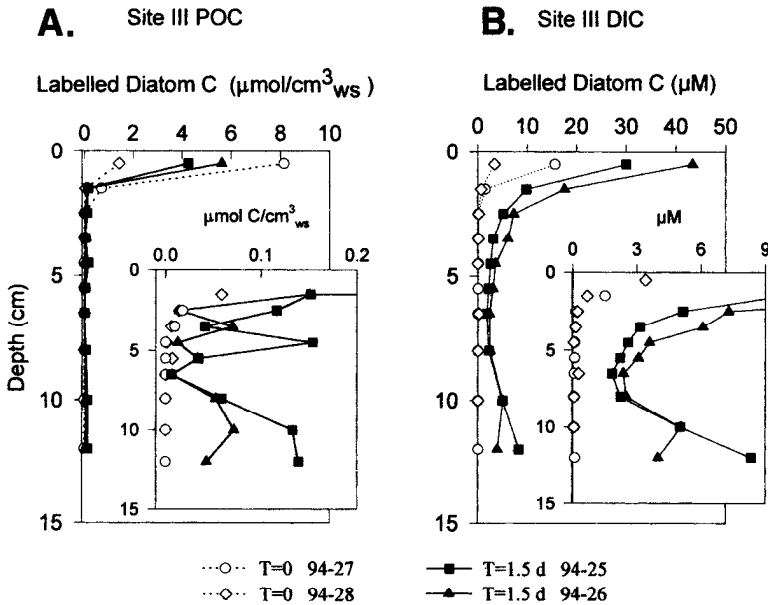
Figure 1. Depth profiles of ^{13}C-labeled diatom carbon in the (A) particulate organic C and (B) dissolved inorganic C fractions shortly after tracer introduction at the sediment surface. Each symbol represents data from a different experimental plot. $T = 0$ plots (94-27 and 94-28), which served as procedural controls, were in contact with tracer for up to 2–3 hours due to the time required for retrieval and processing. $T = 1.5$-d plots (94-25 and 94-26) were in contact with tracer for 33–36 h. Concentrations are reported in terms of total C ([13]C + [12]C) derived from the 95% ^{13}C-labeled diatom. The insets depict data for the 1–13 cm vertical fractions on a magnified concentration scale. Note that data points below 7 cm represent 2 cm-thick vertical intervals.

Two shipboard observations indicated that maldanid polychaetes (bamboo worms in the genus *Praxillella*) were responsible for tracer subduction. The white tracer mixture, which is readily distinguishable by eye from ambient sediment, filled the gut of a maldanid from one subcore (subcore b). In subcore a from the same plot (94-25), tracer was observed in a feeding cavity at the base of a maldanid tube 13 cm below the sediment surface, although the tube occupant showed no evidence of ingestion (Fig. 3). In this subcore, 13% of the solid-phase, labeled diatom C was found below 7 cm, and 5.7% of the total was in the 11–13 cm interval. The ratios of gamma activity (Pb/Sn = 8–9, Pb/Th = 4–5 and Sn/Th = 0.5–0.6) were similar in sediments from the feeding cavity (11–13 cm) and in surface (0–0.5 cm) sediments, providing additional evidence for nonselective particle transport by maldanids (Fornes, 1996).

Because δ^{13}C values of ambient infauna are consistently between -28 and -17 at our site (Table 1, Blair *et al.*, 1996), ingestion of 95% ^{13}C-diatoms by infauna is readily apparent in our experimental samples analyzed for δ^{13}C (Table 1). Annelids comprised 80% of the macrofauna below 5 cm, yet none of them (>5 cm) collected from $T = 0$ plots had δ^{13}C values indicative of tracer ingestion (Table 1). However, one surface-deposit
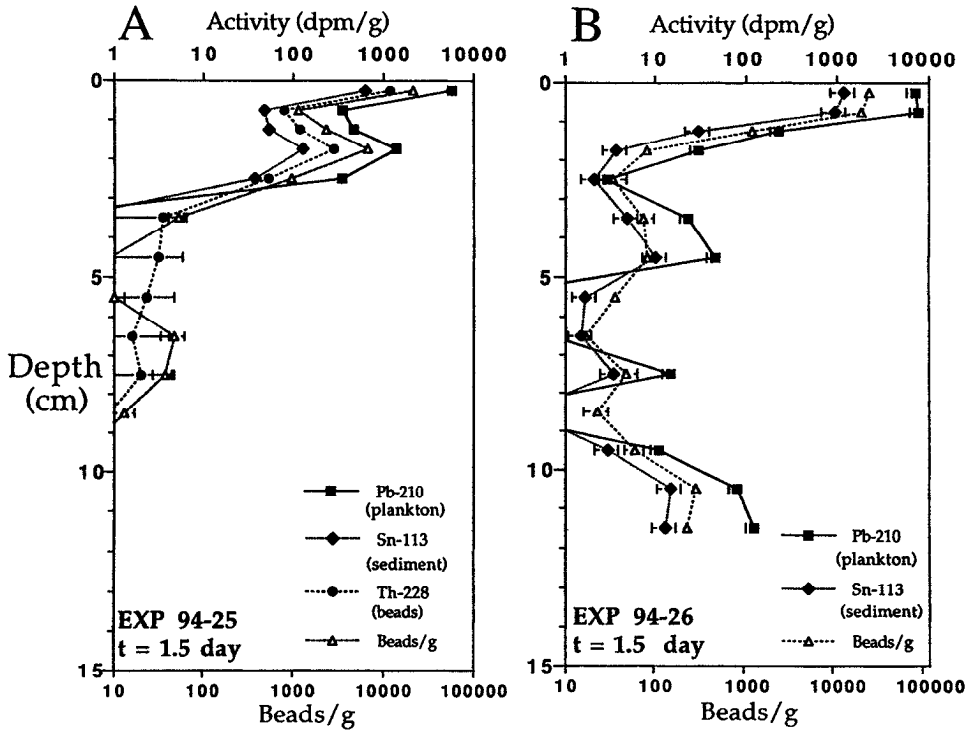
Figure 2. Depth profiles of [210]Pb (spiked on *Thalassiosira* = plankton), [113]Sn (on slope sediment), and [228]Th (on glass beads 105–149 μm) or actual glass bead count 1.5 days after introduction of tracer particles. (A) Plot 94-25, (B) Plot 94-26. Note: in 94-26 glass beads were not labeled with [228]Th. In (A) radiotracers were measured down to 12 cm but values below 9 cm were near 0 dpm/g.

feeder, the ampharetid polychaete *Melinna* sp., present in the 2–5 cm fraction of a $T = 0$ core, appeared to have consumed tracer (Table 1). In the 1.5-day experiments, all of the maldanids (*Praxillella* sp.) sampled from 2 to 10 cm in the sediment column ($n = 5$ individuals) had $\delta^{13}C$ values indicative of labeled diatom ingestion. Below 10 cm only 1 of 4 maldanids appeared to ingest labeled diatoms (Table 1). In the fraction containing the largest, most heavily labeled maldanid (plot 94-25, subcore b, 5–10 cm), maldanid tubes and 5 other infaunal taxa (nematodes, oligochaetes and paraonid, lumbrinerid and ampharetid polychaetes) also showed extensive $\delta^{13}C$ enrichment (Fig. 3, Table 1), indicating tracer incorporation. In some taxa (e.g., oligochaetes and nematodes) the deeper dwelling organisms were more heavily labeled than those closer to the sediment surface (Table 1).

The $\delta^{13}C$ and radiotracer data, combined with visual observations of tracer in a maldanid feeding cavity at 13 cm, indicate that *Praxillella* sp. can transport surface particles to depths >10 cm within 1.5 days of deposition. Based on preserved samples, *Praxillella* sp. density at the study site was estimated to average (± 1 SE) 689 ± 259 individuals m^{-2}. This species comprised 2.3% of the total macrofauna >300 μm (density $29,351 \pm 3,732$
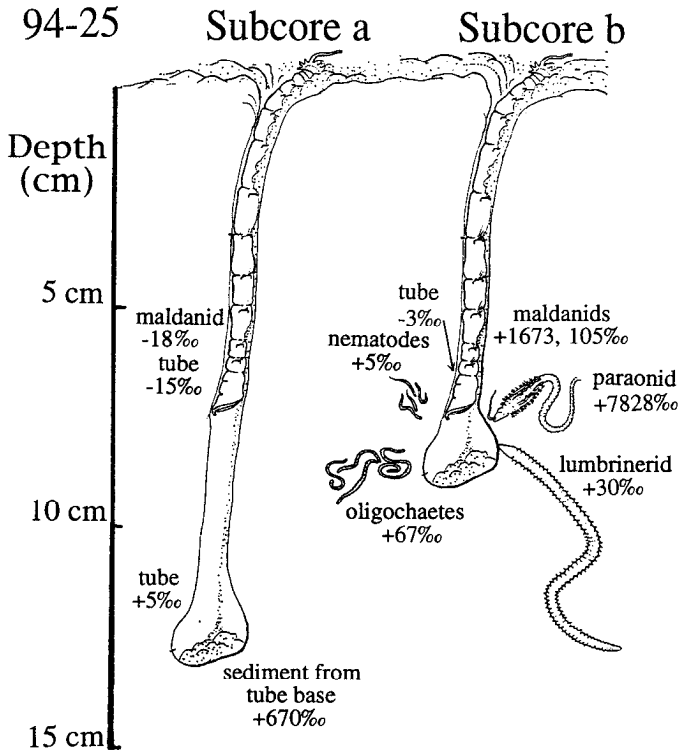
Figure 3. A schematic representation of possible events in experimental plot 94-25, based on $\delta^{13}C$ values observed 1.5 days after deposition of 95% ^{13}C diatoms. In subcore 'a' uningested tracer was present in the feeding cavity of *Praxillella* sp. (Polychaeta: Maldanidae), although the maldanid and its tube exhibited little tracer enrichment. Hoeing is a likely subduction mechanism, but some passive transport may have occurred. In subcore 'b' the maldanids were enriched in ^{13}C as were other subsurface feeders living 5–10 cm deep in the sediment column. Ingestion of 95% ^{13}C diatoms is indicated by $\delta^{13}C \geq -16‰$ in animals. Note $\delta^{13}C$ values are shown only for the 5–10 cm fraction; see Table 1 for other fractions. Maldanids shown hoeing sediments were collected from the 5–10 cm fraction.

individuals m^{-2} in our study plots). Although maldanid individuals were distributed throughout the sediment column to 20 cm (Fig. 4A), the upper 5 cm contained only juveniles (1st setiger width <0.25 mm), while the anterior ends of large individuals (1st setiger width >1.5 mm) occurred only below 5 cm (Fig. 4B). These larger individuals appear to be responsible for most of the tracer subduction.

4. Discussion

a. Magnitude of subduction effects. The maldanid subduction activities documented by our experiments may account for a significant fraction of the particle mixing that takes place at the study site. One means to evaluate the maldanid contribution to mixing is to

Table 1. $\delta^{13}C$ (‰) of metazoan macrofauna from background sediments and experimental plots in August 1994. Data are listed by vertical position (cm) within the sediment column. When a sample contained more than one individual, the number of individuals is given in parentheses. Two replicate plots were sampled for each exposure period. 'a' and 'b' refer to separate subcores within a single boxcore (see text). * indicates background samples collected in 1990.

Treatment Experiment no. Subcore	Background	T = 0 (94-27)	T = 0 (94-28)	T = 1.5 d (94-25) a	T = 1.5 d (94-25) b	T = 1.5 d (94-26) a	T = 1.5 d (94-26) b
Polychaeta							
Maldanidae (*Praxillella* sp.)							
0–2					−17.1	+45.0	+17.0
						+64.4	
2–5			−28.5		+105.0	+552.7	+50.6
			−21.5				
5–10			−18.0	−17.8	+1673		+141.2
					+104.7		
10–15	−17.1	−19.8			−18.5		+147.7
0–15 cm	−18.0						−18.7
Maldanid Tubes							
2–5			−20.8		+143.6		
5–10			−21.2	−15.2	−3.3		−10.2
10–15		−20.0		+5.2			
Sediment at base of maldanid tube				+670			
Lumbrineridae							
2–5	−18.0						
5–10	−18.4	−19.4			+29.7		−16.3
	−19.3	−18.2					−12.1
	−19.4						−18.7
Paraonidae (*Aricidia quadrilobata*)							
0–1					+1461		+2781
2–5	−19.3	−19.4	−19.2				
	−19.4	−16.0	−19.2				
5–10	−19.7		−19.8		+7828		
Ampharetidae (*Melinna* sp.)							
0–1	−19.7						
2–5		+90.0					
5–10				+1160			
Trichobranchidae (*Terebellides* sp.)							
2–5	−18.9*		−26.0				−16.7
5–10		−19.1					
Scalibregmatidae (*Scalibregma inflatum*)							
0–2	−17.5				−4.0		
	−18.0*						
Cirratulidae							
5–10	−20.6		−19.7				
	−20.7						

Table 1. (Continued)

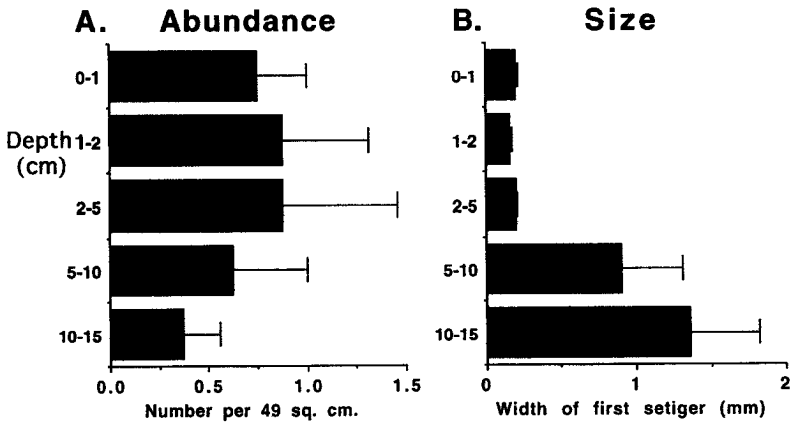| Treatment Experiment no. Subcore	Background	$T = 0$ (94-27)	(94-28)	$T = 1.5$ d (94-25) a	(94-25) b	(94-26) a	(94-26) b
Oligochaeta							
2–5					−25.2		
5–10	−20.5				+67.4 (9)		
	−21.1*						
10–15	−20.2 (17)		−20.1 (6)		−20.2 (15)		
	−20.5						
	−23.5*						
Nematodes							
2–5	−20.5				−17.2 (30)		
5–10			−20.3 (50)		+5.4		
Tanaids							
2–5					−2.8 (6)		
Amphipods							
5–10							−19.5
Aplacophorans							
0–1					+17.3		
Bivalves							
0–1	−24.5						
1–2							+18.5
2–5					+49.6		
Gastropoda							
0–1			−18.5				
2–5 (opisthobranch)					−14.3		

Figure 4. Properties of *Praxillella* sp. at the study site as a function of depth in the sediment column. Mean + 1 SE [$n = 8$ subcores (49 cm² × 15 cm deep) each from a separate boxcore]. (A) Abundance of anteriors with prostomium. (B) Size of *Praxillella* sp. measured as width of the first setiger.

compare the fraction of the labeled tracer subducted below 5 cm in 1.5 d (presumably maldanids dominate this process) with the fraction expected below 5 cm after diffusive mixing over different periods. We used a particle mixing model (Guinasso and Schink, 1975; Blair *et al.*, 1996), assuming (a) only diffusive mixing, (b) instantaneous deposition on the sediment surface of a 1-mm thick pulse of tracer mixture containing 54 μmol C cc^{-1} of ^{13}C diatom (the amount in plot 94-25), and (c) a diffusive mixing coefficient (D_b) ranging from 12–30 cm^2 yr^{-1}, the range for this site reported by DeMaster *et al.* (1994) based on naturally occurring excess ^{234}Th profiles. This model yielded no detectable tracer below 5 cm at 40 hr (the approximate duration of our experiments). Using the lower (12 cm^2 yr^{-1}) and upper (30 cm^2 yr^{-1}) estimates of D_b for this site (DeMaster *et al.*, 1994), the diffusive mixing model predicts that 5% to 23% of the tracer will be mixed below 5 cm after 100 days (the approximate time scale over which ^{234}Th profiles are integrated). Thus, maldanid subduction activities over 1.5 d, which moved 6% of the tracer below 5 cm in 1 plot and 13% in another, could account for 25% to 100% of the deep transport estimated for 100-day time scales. The major uncertainties in this calculation involve how much of the material subducted rapidly by maldanids is returned to the sediment surface as feces, and at what rate. These parameters currently are unknown.

b. Effects of particulate subduction by maldanids. Though most maldanid polychaetes are head-down, conveyor-belt feeders that transport subsurface sediments upward, several shallow water genera in the subfamily Euclyminae appear to drag fresh surface material down their tube into the feeding cavity prior to ingestion (Mangum, 1964; Kudenov, 1978; Weinberg, 1978; Dobbs and Whitlatch, 1982). Craig and Lopez (1996), using x-ray dense particles, demonstrated *in situ* that within 9 days of particle deposition, the sandflat maldanid *Clymenella torquata* creates pockets of surface material in feeding cavities 20 cm below the seabed. Blake and Hilbig (1994) predicted that maldanids should be able to transport organic matter from the surface to deeper sediment layers on the North Carolina slope. This behavior, described here for *Praxillella* sp., which is also a euclyminid, could explain previous reports of viable diatoms present to depths of 14 cm in sediments near our study site (Cahoon *et al.*, 1994).

Once the material resides at depth, it may become accessible to infauna and microbes, thereby enriching what is normally considered to be a poor quality diet for organisms dwelling deep in the sediment column (Rice and Rhoads, 1989; Jumars *et al.*, 1990). Maldanid subduction of diatoms could explain the occurrence of heavily-labeled, subsurface-deposit feeders 5–10 cm beneath the sediment surface, while some individuals closer to the sediment surface were unlabeled (Table 1). We cannot discount the possibility that some of the infauna traditionally considered to be subsurface-deposit feeders traveled to the surface to obtain the ingested tracer, although their small size makes this unlikely over such short time periods.

Maldanid activities influence the redox balance of the seabed and may enhance the rates of subsurface microbial processes. Irrigation by maldanids injects O$_2$ into the sediment

column which oxidizes reduced Fe, thus producing the rust-coloration of their tube linings (Blair *et al.,* 1994). Other reduced diagenetic products, such as S^-, and CH_4, are probably oxidized as well along the sediment-tube wall interface (Blair *et al.,* 1994; Fuller, 1994). The oxygenation of the seabed by the maldanids is limited to a small portion of the subsurface (≈ 1–15 cm) sedimentary volume. Given the observed density of maldanids, and assuming a diameter of 0.5 cm for each tube and its oxidized rind, which is an observed upper limit, less than 1.4% of the subsurface volume (to 15 cm) is aerobic due to maldanid irrigation.

Hoeing activities counterbalance the effect of irrigation by delivering reactive organic matter to the anaerobic subsurface. While O_2 is evidently present throughout the maldanid tube, it may be absent or at very low levels in the feeding chamber because of its dead end location and its high concentration of labile carbon. The dollop of tracer found at the base of one of the maldanid tubes (plot 94-25, subcore a) was in intimate contact with what appeared to be anoxic (or at least nonoxidized) mud, and was not in the oxidized tube. Consumption of the subducted material by other subsurface deposit feeders distributes it into the surrounding anoxic sediment.

Both irrigation and hoeing are likely to stimulate microbial activity (Aller, 1982; Dobbs and Whitlatch, 1982). Maldanids clearly enhance aerobic activities along a narrow zone surrounding their tubes and may help fuel anaerobic processes in the horizon near the base of their tubes. It is unclear whether the net effect of maldanid subduction enhances aerobic or anaerobic reactions, although anaerobic diagenesis is especially important in this region of the North Carolina slope where deep-dwelling maldanid populations are greatest (Schaff *et al.,* 1992; Blair *et al.,* 1994; Levin *et al.,* unpublished data). In addition to influencing the redox chemistry, maldanid subduction may act to aid preservation of O_2-sensitive organic compounds by carrying them closer to the base of the mixed layer and reducing exposure to O_2 (Hedges and Keil, 1995). Once the particles bearing these compounds are delivered to depth, they are more likely to be buried below the zone of biological mixing (Jumars *et al.,* 1981). Even though subducted diatom carbon is oxidized rapidly in our experiments, we cannot address the preservation issue directly because of the absence of the necessary compound-specific analyses.

Maldanid injection of fresh organic matter into subsurface sediments may be a widespread phenomenon. Maldanids in the genus *Praxillella* are known from the Pacific and Atlantic Oceans (Balcom, 1981; Hilbig, 1994), and the family Maldanidae is widely distributed on continental margins in all oceans (e.g., Balcom, 1981; Thompson and Jones, 1987; Hyland *et al.,* 1991; Schaff *et al.,* 1992; Blake and Grassle, 1994; Levin, unpublished data). For example, Hilbig (1994) reports over 25 species of maldanid polychaetes on the slope off North and South Carolina, including 3 species in the genus *Praxillella.* Maldanid densities in margin environments do not typically exceed 800 m^{-2}, according to the references cited above, and maldanids usually comprise <3% of the total macrofaunal individuals at a site. However, maldanid polychaetes are often among the largest, deepest-dwelling species present (K. Green, pers. comm.), so that even at low densities

their subsurface injection activities are likely to be ecologically and biogeochemically significant.

c. Subduction of surface particles as a keystone function in the deep sea. We propose that species responsible for redistributing labile organic matter deep within the sediment column, including *Praxillella* sp., may function as keystone taxa (sensu Mills *et al.*, 1993) in deep water and therefore modify the community structure of the seabed assemblage. They are likely to exert an effect on the infaunal community organization of margin sediments much greater than might be predicted from their numbers or biomass. The shallow water maldanid *Clymenella torquata* has been suggested to alter community structure through tube building, feeding, or irrigation activities (Weinberg, 1983; Fuller, 1994). The direct effects of organic matter subduction on infaunal animals are not known. However, experiments by Dobbs and Whitlatch (1982) suggest that *C. torquata* can stimulate microbial activity at depth in the sediment column. Subduction of reactive organic matter could influence many community attributes including: (a) temporal and spatial distribution of subsurface-deposit feeders (b) abundance, body size, and vertical range of infauna within the sediment column, (c) representation of various infaunal feeding groups, foraging strategies or lifestyles [e.g., commensalism, gardening], and (d) the distribution of different microbial metabolic processes in time and space. Similar community-level effects have been demonstrated for animals that modify sedimentary structures, chemistry and texture (Rhoads, 1974; Posey, 1990), but the effects of redistributing organic matter have not been explored directly.

Although we have no direct experimental evidence that maldanids exert the community effects listed above, data consistent with our hypotheses are found in (1) comparisons of two North Carolina slope sites with and without maldanids, (2) comparisons of processes at our Hatteras study site at times when maldanids were abundant and rare, and (3) comparisons among cores in which maldanid densities varied. For example, in 1988–89 our study site off Cape Hatteras (Site III) exhibited higher bacterial abundances and a larger fraction of the macrofauna below 5 cm than at an 850 m site 280 km to the south (Site I, east of Charleston, South Carolina) (Schaff *et al.*, 1992). Maldanid densities recorded were 621 individuals m^{-2} at Site III and 0 individuals m^{-2} at Site I (Schaff *et al.*, 1992).

In a tracer study we conducted at Site III in 1991 with ^{13}C-labeled *Chlorella*, algal carbon was subducted to 4–5 cm over 1.5 d, with a subsurface peak at 2–3 cm (Blair *et al.*, 1996). At that time maldanid densities were less than one-sixth (93 ± 50 individuals m^{-2}) those in the present study, possibly due to interannual variation or a small shift in sampling location of a few hundred meters. All maldanids present in 1991 were small individuals living in the uppermost 2 cm of sediment. Nonlocal transport in the 1991 experiments appeared to be caused by paraonid and scalibregmid polychaetes (Blair *et al.*, 1996). In those experiments we did not find extensive uptake of tracer by small infauna dwelling below 5 cm (as in the present study), although a large nereid (*Ceratocephale lovenii*) found below 10 cm was labeled (Blair *et al.*, 1996). The contrasting results for the two sets of

experiments are consistent with the idea that adult maldanid subduction can supply organic carbon to other deep-living species.

Enhancement of subsurface-deposit feeding population densities and a deepening of their activity zone may result from the maldanid subduction behavior. In the present study we observed a positive relationship between maldanid density and the density of other (nonmaldanid) macrofauna in preserved samples ($r^2 = 0.528$, $P = 0.040$, $n = 8$). In one subcore with 5 *Praxillella* sp. present below 5 cm, over 50% of the 241 individuals in the core also were present below 5 cm. The deep-dwelling taxa included tanaids, bivalves, paraonid and scalibregmatid polychaetes and oligochaetes. In the other 7 subcores examined, all of which had only 0 or 1 maldanid present below 5 cm, the proportion of infauna dwelling below 5 cm was 9.04% $\pm$ 2.38%. Thus, the maldanid *Praxillella* sp. appears to promote (*sensu* Reise, 1985) or facilitate infauna on the continental slope. Although underlying mechanisms are not always well known, facilitation of infauna by species constructing tubes or burrows is a common and important phenomenon in shallow water (reviewed in Rhoads, 1974; Reise, 1985; Posey, 1990) and probably also in the deep sea (Aller and Aller, 1986).

A variety of other infaunal taxa redistribute labile organic matter downward within the seabed. Conveyor-belt feeders, such as orbiniid polychaetes in the genus *Scoloplos,* effectively bury surface material by covering it with sediments removed from deeper sediment layers (Rice, 1986). The shallow-water lugworm *Abarenicola* transports surface material down its feeding funnel into its burrow (Hylleberg, 1975; M. Mayer, pers. comm.). *Amphitrite ornata,* an intertidal terebellid polychaete, subducts surface material to depths of >20 cm for tube construction (Aller and Yingst, 1978). Recently another terebellid, *Polycirrus eximius,* has been shown to rapidly transport x-ray dense barite from the surface into its burrow (Starczak *et al.,* 1996). Certain shallow-water calianassid shrimp bury algae and seagrass in their burrows (Suchanek, 1983). We might expect deep-water relatives of these shallow-water taxa to exhibit similar behaviors.

There is no question that redistribution of organic matter by deep-water taxa can occur immediately in response to pulsed deposition of detrital material. Deep-sea holothurians are known to utilize freshly deposited organic matter (Suchanek *et al.,* 1985; Smith *et al.,* 1993; Lauerman *et al.,* 1997; C. Smith and D. DeMaster, pers. comm.). A rapid response by sipunculans to the deposition of feces rich in chlorophyll *a* was observed in the Voring Plateau, with mixing to 9 cm within 8 days (Graf, 1989). The observations presented here, in which 6–13% of fresh ^{13}C-labeled diatom carbon was carried below 5 cm in 1.5 d, indicate a possible shorter time-frame for deep, downward transport. Maldanid polychaetes appear to distribute fresh surface deposits nonselectively in a vertically heterogeneous fashion, creating hotspots of "high-quality" organic matter that are patchy in 3 dimensions and also vary over time.

Subduction of surface materials by maldanids is certain to enhance the vertical penetration of pollutants into the continental margin seabed and to alter rates of organic matter burial. Because the slope environment receives a substantial portion of the carbon deposited on the ocean floor, maldanid subduction activities that can account for 25–100%

of short-term particle mixing in this setting are likely to have significant ecological and biogeochemical consequences that merit further quantification.

REFERENCES

Aller, J. Y. and R. C. Aller. 1986. Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. J. Mar. Res., *32*, 755–790.

Aller, R. C. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water, *in* Animal-sediment Relations, P. L. McCall and M. J. S. Tevesz, eds., Plenum Press, New York, 53–101.

Aller, R. C. and J. Y. Yingst. 1978. Biogeochemistry of tube-dwellings: A study of the sedentary polychaete *Amphitrite ornata* (Leidy). J. Mar. Res., *36*, 201–254.

Balcom, B. J. 1981. Results of the 1975–78 BLM Baseline studies and analysis program: Subtidal benthic environments of the southern California Bight. Bureau of Land Management, Pacific OCS. BLM-YN-P/T-81-009-1792.

Blair, N. E. and W. C. Carter. 1992. The carbon isotope biogeochemistry of acetate from a methanogenic marine sediment. Geochim. Cosmochim. Acta, *56*, 1247–1258.

Blair, N. E., L. A. Levin, D. J. DeMaster and G. Plaia. 1996. The short-term fate of fresh algal carbon in continental slope sediments. Limnol. Oceanogr., *41*, 1208–1219.

Blair, N. E., G. R. Plaia, S. E. Boehme, D. J. DeMaster and L. A. Levin. 1994. The remineralization of organic carbon on the North Carolina continental slope. Deep-Sea Res., *41*, 755–766.

Blake, J. A. and B. Hilbig. 1994. Dense infaunal assemblages on the continental slope off Cape Hatteras, North Carolina. Deep-Sea Res., *41*, 875–900.

Blake, J. A. and J. F. Grassle. 1994. Benthic community structure on the U.S. South Atlantic slope off the Carolinas: Spatial heterogeneity in a current dominated system. Deep-Sea Res., *41*, 834–874.

Cahet, G. and M. Sibuet. 1986. Activife biologique en domaine profond: transformations biochimiques *in situ* de composés organiques marqués au carbone-14 à l'interface eau-sédiment par 2000 m de profondeur dans le golfe de Gascogne. Mar. Biol., *90*, 307–315.

Cahoon, L. B., R. A. Laws and C. J. Thomas. 1994. Viable diatoms and chlorophyll *a* in continental slope sediments off Cape Hatteras, North Carolina. Deep-Sea Res., *41*, 767–782.

Craig, N. and G. Lopez. 1996. Mechanisms and scales of particle mixing in dense patches of the head down deposit feeder *Clymenella torquata*. EOS, *76*, OS69 (Abstract).

DeMaster, D. J., R. H. Pope, L. A. Levin and N. E. Blair. 1994. Biological mixing intensity and rates of organic carbon accumulation in North Carolina slope sediments. Deep-Sea Res., *41*, 735–753.

Dobbs, F. C. and R. B. Whitlatch. 1982. Aspects of deposit-feeding by the polychaete *Clymenella torquata*. Ophelia, *21*, 159–166.

Fornes, W. 1996. Bioturbation and particle transport in Carolina slope sediment: A radiochemical approach. M.S. Thesis, North Carolina State University, Raleigh, NC.

Fuller, C. M. 1994. Effects of porewater hydrogen sulfide on the feeding activity of the subsurface deposit-feeding polychaete, *Clymenella torquata*, Leidy. J. Mar. Res., *52*, 1101–1127.

Gehlen, M., C. Rabouille, U. Ezat and L. Guidi. 1996. Dynamics of the early diagenetic reactions: A time series study of deep-sea sediments in the Mediterranean. EOS, *76*, OS170. (Abstract).

Gerino, M., G. Stora and J. P. Durbec. 1994. Quantitative estimation of biodiffusive and bioadvective sediment mixing—in situ experimental approach. Oceanologica Acta, *17*, 547–554.

Gooday, A. J. and C. M. Turley. 1990. Response by benthic organisms to inputs of organic material to the ocean floor: A review. Phil. Trans. Roy. Soc. Lond., *33*, 119–138.

Graf, G. 1989. Bentho-pelagic coupling in a deep-sea benthic community. Nature, *341*, 437–439.

Guinasso, N. L. and D. R. Schink. 1975. Quantitative estimates of biological mixing rates in abyssal sediments. J. Geophys. Res., *80*, 3032–3043.

Hayes, J. M., D. J. DesMarais, D. W. Peterson, D. A. Schoeller and S. P. Taylor. 1977. High precision stable isotope ratios from microgram samples. Adv. Mass Spectrometry, *7*, 474–480.

Hecker, B. 1990. Photographic evidence for rapid fluxes of particles to the seafloor and their transport down the continental slope. Deep-Sea Res., *37*, 1773–1782.

Hedges, J. I. and R. G. Keil. 1995. Sedimentary organic matter preservation: An assessment and speculative synthesis. Mar. Chem., *49*, 81–115.

Hilbig, B. 1994. Faunistic and zoogeographical characterization of the benthic infauna on the Carolina continental slope. Deep-Sea Res., *41*, 929–950.

Honjo, S. 1982. Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin. Science, *281*, 883–884.

Hyland, J., E. Baptiste, J. Campbell, J. Kennedy, R. Dropp and S. Williams. 1991. Macroinfaunal communities of the Santa Maria Basin on the California outer continental shelf and slope. Mar. Ecol. Progr. Ser., *78*, 147–161.

Hylleberg, J. 1975. Selective feeding by *Abarenicola pacifica* with selective notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. Ophelia, *14*, 113–137.

Jumars, P. A., L. M. Mayer, J. W. Deming, J. A. Baross and R. A. Wheatcroft. 1990. Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. Phil. Trans. R. Soc. Lond. A, *331*, 85–101.

Jumars, P. A., A. R. M. Nowell and R. F. L. Self. 1981. A simple model of flow-sediment-organism interaction. Mar. Geol., *42*, 155–172.

Kelchner, C. 1992. Organic-rich depositional regimes, North Carolina slope: Evaluating source sites and sediment transport pathways. M.S. Thesis. North Carolina State University, Raleigh, NC.

Kudenov, J. D. 1978. The feeding ecology of *Axiothella rubrocincta* (Johnson) (Polychaeta: Maldanidae). J. Exp. Mar. Biol. Ecol., *31*, 209–221.

Lampitt, R. S. 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep-Sea Res., *32*, 885–898.

Lauerman, L. M. L., J. M. Smoak, T. J. Shaw, W. S. Moore and K. L. Smith Jr. 1997. ^{234}Th and ^{210}Pb evidence for rapid ingestion of settling particles by mobile epibenthic megafauna in the abyssal NE Pacific. Limnol. Oceanogr., (in press).

Levin, L., S. Childers and C. Smith. 1991. Epibenthic, agglutinating foraminiferans in the Santa Catalina Basin and their response to disturbance. Deep-Sea Res., *38*, 465–483.

Mangum, C. 1964. Activity pattern in the metabolism and ecology of polychaetes. Comp. Biochem. Physiol., *11*, 239–256.

Mills, L. S., M. E. Soule and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. Biosci., *43*, 219–224.

Pfannkuche, O. and K. Lochte. 1993. Open ocean pelago-benthic coupling: Cyanobacteria as tracers of sedimenting salp faeces. Deep-Sea Res., *40*, 727–737.

Posey, M. H. 1990. Functional approaches to soft substrate communities. How useful are they? Rev. Aq. Sci., *2*, 343–356.

Reise, K. 1985. Tidal Flat Ecology, Springer Verlag, Berlin.

Rhoads, D. C. 1974. Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Annu. Rev., *12*, 263–300.

Rice, A. L. and P. J. D. Lambshead. 1994. Patch dynamics in the deep-sea benthos: The role of heterogeneous supply of organic matter, *in* Aquatic Ecology: Scale, Pattern and Process, P. S. Giller, A. G. Hildrew and D. G. Raffaelli, eds., Blackwell Scientific Publications, 469–497.

Rice, D. L. 1986. Early diagenesis in bioadvective sediments: Relationships between the diagenesis of beryllium-7, sediment reworking rates and the abundance of conveyor-belt deposit feeders. J. Mar. Res., *44*, 149–184.

Rice, D. L. and D. C. Rhoads. 1989. Early diagenesis of organic matter and the nutritional value of sediment, *in* Ecology of Marine Deposit Feeders, G. Lopez, G. Taghon and J. Levinton, eds., Springer Verlag, New York, 59–97.

Schaff, T., L. Levin, N. Blair, D. DeMaster, R. Pope and S. Boehme. 1992. Spatial heterogeneity of benthos on the Carolina continental slope: Large (100-km)-scale variation. Mar. Ecol. Progr. Ser., *88*, 143–160.

Smith, C. R. 1994. Tempo and mode in deep-sea benthic ecology: Punctuated equilibrium revisited. Palaios, *9*, 3–13.

Smith, C. R., P. A. Jumars and D. J. DeMaster. 1986. *In situ* studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. Nature, *323*, 251–253.

Smith, C. R., R. H. Pope, D. J. DeMaster and L. Magaard. 1993. Age-dependent mixing of deep-sea sediments. Geochim. Cosmochim. Acta, *57*, 1473–1488.

Smith, J. N. and C. T. Schafer. 1984. Bioturbation processes in continental slope and rise sediments delineated by Pb-210, microfossil and textural indicators. J. Mar. Res., *42*, 1117–1145.

Smith, K. L. Jr., R. S. Kaufmann and R. J. Baldwin. 1994. Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern North Pacific Ocean. Limnol. Oceanogr., *39*, 1101–1118.

Starczak, V., R. A. Wheatcroft and C. A. Butman. 1996. Particle subduction by a surface deposit-feeding polychaete worm. EOS, *76*, OS160 (Abstract).

Suchanek, T. H. 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. J. Mar. Res., *41*, 281–298.

Suchanek, T. H., S. L. Williams, J. C. Ogden, D. K. Hubbard and I. P. Gill. 1985. Utilization of shallow-water seagrass detritus by Caribbean deep-sea macrofauna: $\delta^{13}C$ evidence. Deep-Sea Res., *32*, 201–214.

Thompson, B. E. and G. F. Jones. 1987. Benthic macrofaunal assemblages of slope habitats in the southern California borderland. Allan Hancock Found., New. Ser., *6*, 1–21.

Van Dover, C. L., J. F. Grassle, B. Fry, R. Garritt and V. Starczak. 1992. Stable isotope evidence for entry of sewage-derived organic material into a deep-sea food web. Nature, *360*, 153–156.

Weinberg, J. R. 1988. Detritus on sediment surface enhances growth of *Clymenella torquata*, a head-down feeding, tubicolous polychaete. Ophelia, *29*, 187–197.

Weinberg, J. R. and R. B. Whitlatch. 1983. Enhanced growth of a filter-feeding bivalve by a deposit-feeding polychaete by means of nutrient regeneration. J. Mar. Res., *41*, 557–569.

Wheatcroft, R. A. 1992. Experimental tests for particle size-dependent bioturbation in the deep ocean. Limnol. Oceanogr., *37*, 90–104.

Wheatcroft, R. A., I. Olmez and F. Pink. 1994. Particle bioturbation in Massachusetts Bay: Preliminary results using a new deliberate tracer technique. J. Mar. Res., *52*, 1129–1150.

Widbom, B. and J. B. Frithsen. 1995. Structuring factors in a marine soft bottom community during eutrophication—an experiment with radio-labeled phytodetritus. Oecologia, *101*, 156–168.