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A particle introduction experiment in Santa Catalina Basin sediments: Testing the age-dependent mixing hypothesis

by William L. Fornes[1], David J. DeMaster[2] and Craig R. Smith[3]

ABSTRACT

The occurrence of "age-dependent mixing," a process by which recently deposited, food-rich particles undergo more intense bioturbation than older, food-poor particles, could dramatically alter patterns of organic-matter diagenesis in deep-sea sediments. To explicitly test for age-dependent mixing, an *in-situ* particle introduction experiment was conducted on the bathyal Santa Catalina Basin floor. Mixtures of radioisotope-tagged particles representing a food quality gradient were dispersed in small amounts on the seafloor and sampled over periods of 0 to 594 days. Introduced particle types were all similar in size and included fresh diatoms ("young" particles), surface sediments ("intermediate-age" particles), and particles from 30-cm deep in the sediment column ("old" particles). This approach permitted evaluation of particle mixing intensity for several particle "ages" and provided an independent check on mixing coefficients determined from naturally occurring radioisotopes ($^{234}Th_{xs}$ and $^{210}Pb_{xs}$). All particles experienced rapid (<6 h) transport into the upper 2 cm of the seabed resulting from passive deposition down burrows or extremely rapid bioturbation. Intense bioturbation on 4-d time scales included both biodiffusive and nondiffusive (bioadvective and nonlocal) transport. Bioturbation of tracers exhibited time (or "age") dependence in two ways: (1) Diffusive mixing intensity for all tracer types decreased with time (4-d $D_b = 293$ cm^2 y^{-1}, D_b at 520 d $= 2.6$ cm^2 y^{-1}), and (2) The nature of bioturbation changed over this period with more efficient bioadvection and nonlocal exchange giving way to slower diffusive mixing. Both changes are consistent with the age-dependent-mixing hypothesis. Biodiffusive mixing was not measurably selective, with no significant preference for a single particle type. In contrast, nondiffusive transport, likely caused by deposit-feeding cirratulid polychaetes, exhibited distinct particle selectivity, especially over 4-d time scales, with the diatom tracer transported most rapidly to depth. Degradation of the labile organic carbon in diatoms most likely led to decreasing selection of diatoms by deposit feeders until diatoms and "old" sediment particles experienced comparable mixing intensities.

1. Introduction

Bioturbation, i.e., mixing of sediment particles by organisms, occurs in nearly all marine sediments and significantly influences numerous physical, chemical and biological pro-

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cesses and characteristics in the seabed including stratigraphic preservation, nutrient fluxes, redox conditions, mineral dissolution rates, benthic community structure, pollutant and trace metal cycling, and organic carbon preservation (Schink *et al.,* 1975; DeMaster and Cochran, 1982; Kukert and Smith, 1992; Aller, 1994; Bromley, 1996; Wheatcroft and Martin, 1996). Therefore, understanding the rates and mechanisms of bioturbation will significantly improve knowledge of these important benthic processes.

Eddy diffusion, whereby particles undergo mixing at a rate proportional to a bioturbation coefficient, D_b, is often used to characterize bioturbation within the upper few centimeters of the sediment or the sediment mixed layer (Goldberg and Koide, 1962; Guinasso and Schink, 1975; Wheatcroft *et al.,* 1990). Although individual mixing events are nondiffusive, entailing unidirectional transport of material into an adjoining (bioadvection) or a nonadjacent (nonlocal mixing) sediment layer, the diffusive analogy often adequately describes overall mixing because tracer profiles integrate a large number of events over time and space (Boudreau, 1986; Wheatcroft *et al.,* 1990). The solution to the equation governing one-way, time-dependent biodiffusion of an instantaneous tracer pulse in a sediment mixed layer of constant porosity is

$$A(t) = \frac{I}{(\pi D_b t)^{1/2}} \exp(-z^2/D_b t), \tag{1}$$

where A is the activity of the radioisotope (dpm cm^{-3}), I is the total inventory in the sediment column (dpm cm^{-2}), z is depth relative to the sediment-water interface (cm), D_b is the (constant) bioturbation coefficient (cm^2 y^{-1}), and t is elapsed time (y) since the tracer was deposited at the sediment-water interface (Crank, 1975; Blair *et al.,* 1996). The boundary conditions used to generate Eq. (1) are as follows: for $t = 0$, $A = 0$ everywhere except at $z = 0$ where it approaches infinity, and for $t > 0$, activity goes to zero as z approaches infinity. The appearance of subsurface peaks in sediment profiles cannot be produced via diffusive mixing and are modeled as nondiffusive, nonlocal mixing processes operating simultaneously with and independently of diffusive mixing (Smith *et al.,* 1986/87; Pope *et al.,* 1996; Fornes *et al.,* 1999). Models of chemical processes in sediments generally assume that animals mix all particles uniformly (Smith *et al.,* 1993), implying that measurement of a single radiotracer suffices to characterize the rates of and controls on bioturbation in an environment. However, recent evidence suggests that the assumption of uniform mixing is erroneous and that bioturbation intensity varies with particle size, organic carbon content, specific gravity or position in the sediment column (Cammen, 1980; Lopez and Levinton, 1987; Smith *et al.,* 1993; Blair *et al.,* 1996; Levin *et al.,* 1997; Fornes *et al.,* 1999 and references therein).

The objective of this paper is to evaluate temporal changes in bioturbation rates with respect to particle food quality, which generally is a function of time since deposition (i.e., "age"), in quiescent deep-sea habitats. We present results from an *in situ* particle introduction experiment (or PIE, see Blair *et al.,* 1996; Levin *et al.,* 1997; Fornes *et al.,* 1999) conducted on the bathyal seafloor in Santa Catalina Basin, a site where tracer-
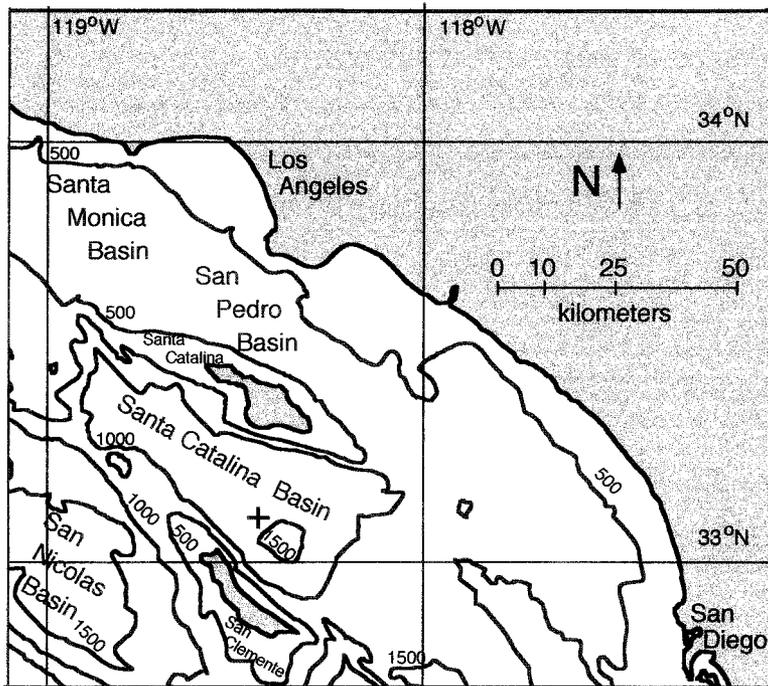
Figure 1. Bathymetric map of Santa Catalina Basin. Samples were collected during *Alvin* dives at 33°11′N, 118°26′W. Depth contours are in meters.

dependent mixing has previously been observed (Smith *et al.,* 1993). Our experiment, involving deployment and recovery of radioisotope-tagged particles on the seafloor via submersible, allowed examination of bioturbation over time scales unattainable with naturally occurring radiotracers (e.g., $^{234}Th_{xs}$ and $^{210}Pb_{xs}$). Specifically, we address the following questions: (1) How does passive deposition affect the distribution of recently deposited particles? (2) Does bioturbation intensity vary over time? And (3) Does selectivity for particles rich in labile organic matter significantly affect bioturbation? Addressing these questions will develop a more thorough understanding of bioturbation in quiescent deep-sea benthic habitats.

2. Materials and methods

a. Study site

The experiment was conducted at a depth of 1215 m in Santa Catalina Basin off the Southern California coast (Fig. 1). The organic-rich (3–4% C_{org}) sediments accumulate at a rate of ∼12 cm ky^{-1} (Fornes, 1999). The quiescent physical nature of the study area (<7 cm s^{-1} bottom currents) suggests that sediment mixing occurs mainly through biological mechanisms (Smith and Hamilton, 1983; Smith, 1986; Kukert and Smith, 1992).

Deposit feeders dominate the relatively abundant (17 individuals m^{-2}) megafaunal community (Smith and Hamilton, 1983; Miller *et al.,* 2000). Deposit feeders also constitute 90% of the macrofauna, which has a density of 6,000–10,000 individuals m^{-2} (Smith, 1986; Smith *et al.,* 1998). Large megafaunal mounds (10 cm high $\times$ 30 cm diameter), formed from echiuran fecal material, cover 1–2% of the seafloor (Smith *et al.,* 1986). Millimeter-scale biogenic structures including worm tubes and animal tracks cover much of the flat seafloor (Smith *et al.,* 1993).

b. Tracer preparation

Preparation of particles and radiotracers was similar to Blair *et al.* (1996), Levin *et al.* (1997) and Fornes *et al.* (1999). The particles chosen for tagging varied in presumed food quality and ''age,'' with diatoms representing young, organic-rich particles, ambient surface sediment (0–0.5 cm) representing particles of intermediate food quality and age, and deep sediments (from 30–30.5 cm in the sediment column) representing old (>1500 y based on 12 cm ky^{-1} sedimentation rate; Fornes, 1999), food-poor particles. The radioisotopes (^{139}Ce, ^{113}Sn and ^{88}Y) were selected as tracers because they are particle-reactive, easily detectable via gamma spectroscopy, and have short half-lives (108–138 d), preventing long-term environmental contamination.

A diatom, *Ditylum brightwellii* ($\sim$30–40 µm diameter), was cultured at a constant temperature (24°C) in closed containers of amended F/2 media in artificial seawater (Parsons *et al.,* 1989). *Ditylum brightwellii* cultures were vacuum-filtered, frozen and diluted to 1 L in artificial seawater. A ^{139}Ce solution (4.4 $\times$ 10^6 dpm mL^{-1} in 1N HCl) was added in 1-mL increments (45 mL total) and stirred overnight at 4°C. After centrifugation and dilution to 100 mL with artificial, unbuffered seawater, the slurry was split into 5-mL aliquots (equivalent to $\sim$9.8 $\times$ 10^6 dpm ^{139}Ce, 0.6 g SiO$_2$, and 0.025 g C$_{org}$). Following the addition of kaolin ($\sim$8 g per aliquot) to enhance settling efficiency, each sample was freeze-dried (Blair *et al.,* 1996; Levin *et al.,* 1997; Fornes *et al.,* 1999).

Surface (0–0.5 cm) and older (30–30.5 cm) sediments were collected by multiple corer from Santa Catalina Basin and size fractionated by allowing the particles to settle for 15 min in artificial seawater (T $<$ 5°C). Particles remaining in suspension were decanted off and the settled sediment (grain size $>$ 20 µm but typically $<$ 63 µm) was set aside for tagging. Spike solutions of ^{113}Sn and ^{88}Y (both 4.4 $\times$ 10^6 dpm mL^{-1} in 1N HCl) were added in 1-mL increments to the 0–0.5 and 30–30.5 cm intervals, respectively. The activity of each sample (800 mg dry weight) was $\sim$9.8 $\times$ 10^6 dpm $\cdot$ aliquot^{-1}.

c. Field methods

On board ship one aliquot of each radioisotope-tagged particle was combined with 30 g of 32–63 µm glass beads (manufactured by Cataphote) in a ''tracer-shaker'' (a 1 L plastic container covered with a sliding base plate and 2 mm mesh window screening). Using the submersible *Alvin,* the particles in the ''tracer-shakers'' were emptied within a spreading canopy covering visually flat 40-cm $\times$ 40-cm plots (devoid of large biogenic features such

as pits or mounds) and allowed to settle for ~45 min, leaving a layer <1 mm thick (Levin *et al.,* 1997; Fornes *et al.,* 1999). Tracer addition equaled ~8 d of organic carbon flux and <2 y of net mass flux under ambient conditions (C_{org} flux = 0.019 g C · m^{-2} d^{-1} and mass flux = 0.32 g · m^{-2} d^{-1}, Fornes, 1999). Sampling of replicate plots occurred at one of 5 time intervals (0, 4, 74, 520, and 594 d) using an Ekman corer (20 × 20 cm cross section and 15 cm deep) partitioned into 4 subcores (10 × 10 cm cross section and 15 cm deep) as described in Smith (1986). One subcore per box core was allocated for radiochemical analysis and sectioned in 0.5-cm intervals to 2 cm and in 1-cm intervals below, discarding the outer 0.5 to 1.0 cm to lessen any downcore smearing. Samples were sealed in 125 mL Petri dishes and stored at room temperature.

d. Laboratory methods

An Ortec LOAX intrinsic Ge γ-detector was used to determine all radiotracer activities in the samples. The activities of ^{139}Ce, ^{113}Sn and ^{88}Y were measured at 169.9, 391.9, and 898.1 keV, respectively. After counting and correcting for self-absorption (Cutshall *et al.,* 1983), wet samples were weighed and dried (60°C) to determine dry bulk density and porosity. Detection limits were ~0.1 dpm g^{-1}. The profiles are reported in fractional inventory, a dimensionless value that normalizes the spatial heterogeneity inherent in tracer deployment and recovery.

Glass bead counting was performed at the University of Hawaii using a modification of the method of Smith and Kukert (1996). Dried samples were rehydrated in distilled water, sonicated, treated with 30% H_2O_2 and 7N HNO_3, passed through a 63 μm sieve, and retained on a 32 μm sieve to help separate the glass beads (32–63 μm) from the sediment. To obtain ≤2,000 bead counts, the total samples were split into $\frac{1}{16}$ to $\frac{1}{128}$ fractions using a MacLane Research Laboratories sediment sample splitter before counting on a dark-field dissecting microscope. Because of the labor of bead counting, bead profiles were obtained from only a subset of the PIE's.

3. Results and discussion

a. Time-zero distribution

The upper 2 cm contained nearly all of the tracer inventory in the time-zero treatment (Fig. 2). Although the profile shapes in the upper 2 cm were consistent with diffusive mixing, the D_b values (Table 1, derived from a least squares fit of Eq. 1) were much higher in the time-zero samples than typically measured in natural marine habitats (generally ≪ than 200 cm^2 y^{-1}; Smith *et al.,* 1993; Boudreau, 1994). Mechanistically decomposing D_b into a relationship between mixing step length, L, and rest period between mixing events, p, yields (Wheatcroft *et al.,* 1990):

$$D_b = L^2/2p. \tag{2}$$

A 1-cm step length (C. R. Smith, unpublished data), translates to a rest period of ~6 h for PIE 96-30 (D_b = 727 cm^2 y^{-1}; Eq. 1, Table 1). If macrofaunal density is 6000 individuals m^{-2},
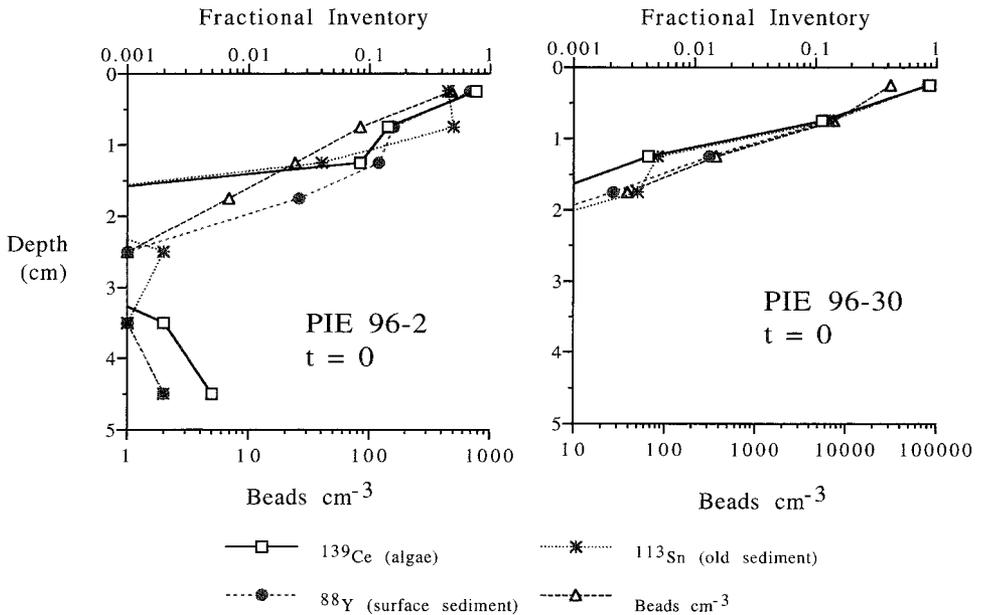
Figure 2. Plots of fractional inventory and bead concentration vs. depth for the PIE time-zero treatment. ^{139}Ce error bars are shown and were estimated from counting statistics.

the upper 2 cm (200 mL wet sediment) requires a sediment reworking rate of $\sim$5000 mL individual^{-1} y^{-1} to reproduce the profile, a rate much higher than steady-state values reported in other environments (96–400 mL individual^{-1} y^{-1}, Rhoads, 1974; Thayer, 1983).

Such rapid penetration of tracers has been observed in several other studies in shallow-water and deep-sea sites with wide ranges in the abundance and species composition of benthos (Wheatcroft *et al.,* 1994; Blair *et al.,* 1996; Levin *et al.,* 1997; Fornes *et al.,* 1999). Thus, this rapid initial penetration results either from widely distributed biological processes (e.g., rapid bioadvection of newly deposited sediment, Smith *et al.,* 2001) or from physical processes such as settlement around animal burrows, bottom roughness, physical mixing associated with core recovery, or passive infilling of vacated burrows. To minimize the effects of centimeter-scale bottom roughness, the flattest subcore in each plot was designated for radiochemical analysis and sectioned at the same angle as the surface relief. Some post-recovery mixing in the cores may have occurred during the time elapsed ($\sim$6 h) between recovery and sectioning. In addition to unavoidable jostling of *Alvin* during submersible recovery, rapid bioturbation may have caused deep initial transport of the tracers as well. Indeed, it is likely that a deposition pulse would elicit some response from the benthos, possibly inducing a ''snowstorm effect'' whereby animals responded to the added particles by reopening burrows and pulling some sediments downward in the process. In laboratory tracer addition experiments with natural assemblages of shallow-

Table 1. PIE Apparent D_b's (cm^2 y^{-1}). D_b values were obtained from a least-squares fit of Eq. 1. The values in parentheses represent D_b values below the TZH.

PIE	^{139}Ce	^{113}Sn	^{88}Y	Mean ± S.D.	Mean r^2
time zero					
96-30	620	800	760	727 ± 95	0.900 ± 0.070
$t = 4$ d					
96-5	250	360	350	320 ± 61	0.397 ± 0.014
96-8	200	280	320	267 ± 61	0.756 ± 0.084
	(409)	(584)	(651)	(548 ± 125)	(0.832 ± 0.140)
mean	225 ± 35	320 ± 57	335 ± 21		
$t = 74$ d					
96-13	43	13	23	26 ± 15	0.715 ± 0.031
	(59)	(29)	(49)	(46 ± 15)	(0.873 ± 0.099)
96-14	25	31	26	27.3 ± 3.2	0.851 ± 0.051
	(33)	(50)	(48)	(44 ± 9)	(0.961 ± 0.028)
96-16	25	22	22	23.0 ± 1.7	0.807 ± 0.062
	(31)	(35)	(33)	(32.8 ± 2.0)	(0.779 ± 0.110)
96-18	25	13	13	17.0 ± 6.9	0.742 ± 0.112
96-19	31	12	12	18 ± 11	0.766 ± 0.034
	(48)	(23)	(21)	(31 ± 15)	(0.871 ± 0.024)
mean	29.8 ± 7.8	18.2 ± 8.2	19.2 ± 6.3		
	(43 ± 13)	(34 ± 12)	(38 ± 13)		
$t = 520$ d					
96-24	0.9	0.9	1.1	1.0 ± 0.1	0.965 ± 0.008
96-25	5.1	3.0	4.3	4.1 ± 1.1	0.676 ± 0.035
	(10)	(7)	(8)	(8.3 ± 1.5)	(0.728 ± 0.075)
mean	3.0 ± 3.0	2.0 ± 1.5	2.7 ± 2.3		
$t = 594$ d					
96-12	2.5	1.0	0.8	1.4 ± 0.9	0.893 ± 0.126
	(5.1)				(0.746)

water benthos, Thomas (1998) found that passive infill was ejected from animal burrows within minutes. Even fauna that eventually pulled tracer down their tubes first cleared them, presumably to restore irrigation capabilities (Thomas, 1998). Concurrently, because relict burrows and tubes can act as vertical conduits, passive infilling may also be an important transport mechanism near the sediment-water interface (Aller and Aller, 1986; Smith *et al.,* 2001). The spreading canopy also possibly enhanced passive deposition by negating horizontal currents that foster nonperpendicular trajectories of settling particles (Yager *et al.,* 1993; Smith *et al.,* 2001).

Regardless of the mechanisms driving the rapid tracer penetration, the 2-cm depth was designated as the time-zero horizon (TZH); the presence of tracers below this depth at later samplings indicated active biological mixing. The time-zero contribution to bioturbation estimates in cases where $t > 0$ can be seen where, due to a more vertical fit to Eq. 1, whole-core D_b values were consistently lower than D_b values determined after discounting values from 0–2 cm. Therefore, if the initial penetration to 2 cm was due to passive

Table 2. Fractional inventories (FI) below 2 cm (TZH).

PIE	Time (d)	^{139}Ce	^{113}Sn	^{88}Y	z_{max} (cm)	S_1 [a]	S_2 [b]
96-5	4	0.004	0.002	0.001	4–5	1.7	0.7
96-8	4	0.008	0.005	0.002	4–5	1.6	0.6
96-13	74	0.047	0.038	0.049	8–9	1.1	1.1
96-14	74	0.053	0.047	0.047	9–10	1.1	1.0
96-16	74	0.100	0.096	0.098	9–10	1.0	1.0
96-18	74	0.027	0.033	0.026	6–7	0.9	0.9
96-19	74	0.015	0.008	0.016	9–10	1.2	1.3
96-24	524	0.005	0.010	0.006	2–3	0.7	0.8
96-25	524	0.011	0.019	0.019	6–7	0.8	1.0
96-10[c]	590	0.030	0.050	0.212	7–8	0.3	1.6
96-12	590	0.014	0.016	0.020	5–6	0.8	1.1

[a] $S_1 = 3 * FI_{Ce}/(FI_{Ce} + FI_{Sn} + FI_Y)$.
[b] $S_2 = 2 * FI_Y/(FI_{Sn} + FI_Y)$.
[c] The large error bars associated with the data in PIE 96-10 precluded any meaningful interpretation of sediment mixing based on this replicate.

deposition and if one assumes that D_b exclusively describes active mixing (Table 1), then passive deposition will lead to an underestimate of bioturbation intensity.

b. Bioturbation

Assuming negligible sedimentation throughout the experiment, bioturbation should, over time, cause the tracers to penetrate below the TZH. Below-TZH fractional inventory increased with time when considering the 4-d and 74-d treatments ($p < 0.001$, Mann-Whitney test; Conover, 1999), but not when 500-d profiles were included (Table 2, $p > 0.25$, Kruskal-Wallis k-sample test; Conover, 1999). The lack of increased penetration between 74 and 520 d may be explained by reduced detection sensitivity for the short half-life radiotracers after ~5 half-lives. The loss of tracer from plots due to horizontal mixing may also have made the tracers more difficult to detect.

The 4-d treatment indicated rapid bioturbation in Santa Catalina Basin (Fig. 3). In PIE 96-5, the nearly vertical profile below 1.5 cm and the poor fit of the tracer data to Eq. 1 ($r^2 = 0.397 \pm 0.014$, Table 1) suggested nondiffusive transport or extremely rapid diffusive mixing. In PIE 96-8, the decrease of ^{139}Ce and ^{113}Sn with depth suggested some diffusive mixing, whereas the subsurface peaks in the ^{88}Y and glass-bead profiles suggested simultaneous nondiffusive transport. Similar to the time-zero treatment, the 4-d profiles generated extremely high (and probably unrealistic) D_b values (Table 1) compared to the general bioturbation literature, where D_b is typically $\ll 200$ cm^2 y^{-1} (Boudreau, 1994). Reproducing the observed profiles required an average sediment reworking rate of ~3000 mL individual^{-1} y^{-1}. Consequently, the D_b values are called "apparent" and should be used for comparative purposes only because there were probably insufficient transport events to simulate diffusive transport. The 74-d, 520-d, and 594-d treatment profiles could
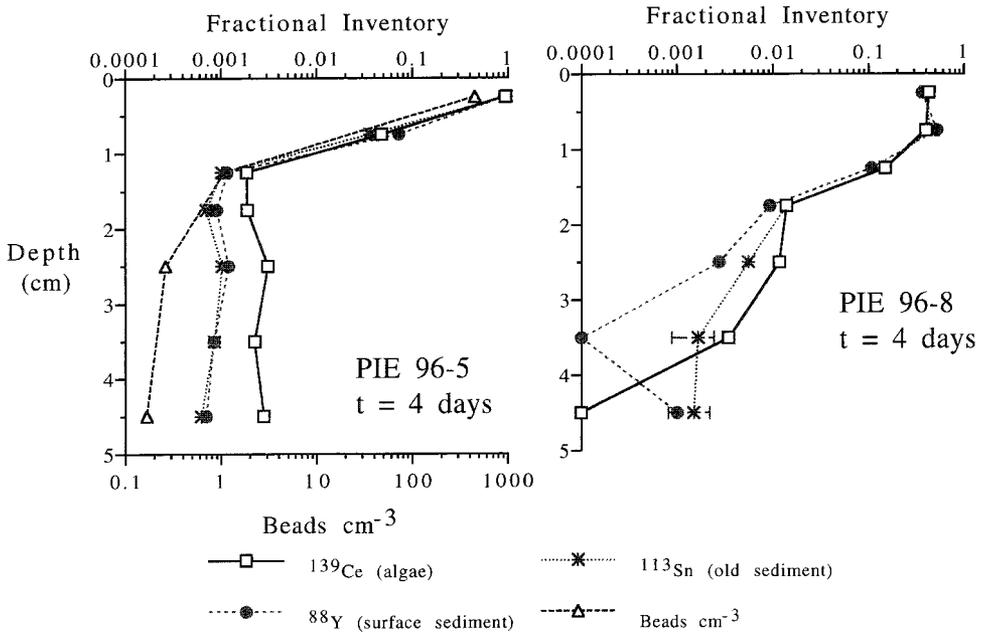
Figure 3. Plots of fractional inventory and bead concentration vs. depth for the PIE 4-day treatment. [139]Ce error bars are shown and were estimated from counting statistics.

be largely simulated by diffusive mixing (Figs. 4 and 5). The probable large number of mixing events encompassed by this time scale most likely satisfied criteria for the diffusion analogy (Boudreau, 1986; Wheatcroft *et al.,* 1990). Reproducing these profiles required an average sediment reworking rate on the order of $\sim$300 mL individual^{-1} y^{-1} or less. Nondiffusive, nonlocal mixing events remained evident in the 74-d treatment with subsurface peaks in PIE's 96-16 and 96-19 (Fig. 4).

A negative correlation between D_b and treatment duration was apparent ($p \ll 0.001$, Table 1). Naturally occurring radioisotope data from the Santa Catalina Basin show a similar pattern of decreasing D_b with time scale, providing confidence in our modeling efforts for both types of tracers. Mean D_b values ($\pm$S.E.) were 11 ± 7 cm^2 y^{-1} for ^{234}Th$_{xs}$ (100-d time scale, $n = 9$) and 0.6 ± 0.1 cm^2 y^{-1} for ^{210}Pb$_{xs}$ profiles (100-y time scale, $n = 13$; Fornes, 1999). Similarly, *in situ* tracer experiments in North Carolina continental slope sediments displayed rapid (<1.5 d), centimeter-scale, vertical transport of recently-deposited particles followed by a gradual reduction in mixing intensity over the next 430 d (Fornes *et al.,* 1999; Blair *et al.,* 2001). Our doubt that the $\leq$4-d treatment D_b values resulted from biodiffusive mixing raises the question of the suitability of the diffusive analogy on very short time scales. However, the significance of the negative correlation between D_b and time scale persisted when D_b values corresponding to $t < 74$ d time scales were excluded ($p = 0.002$). Our results suggest that bulk transport to depth decreases over time and that diffusive mixing intensity continues to decline after several months. Both
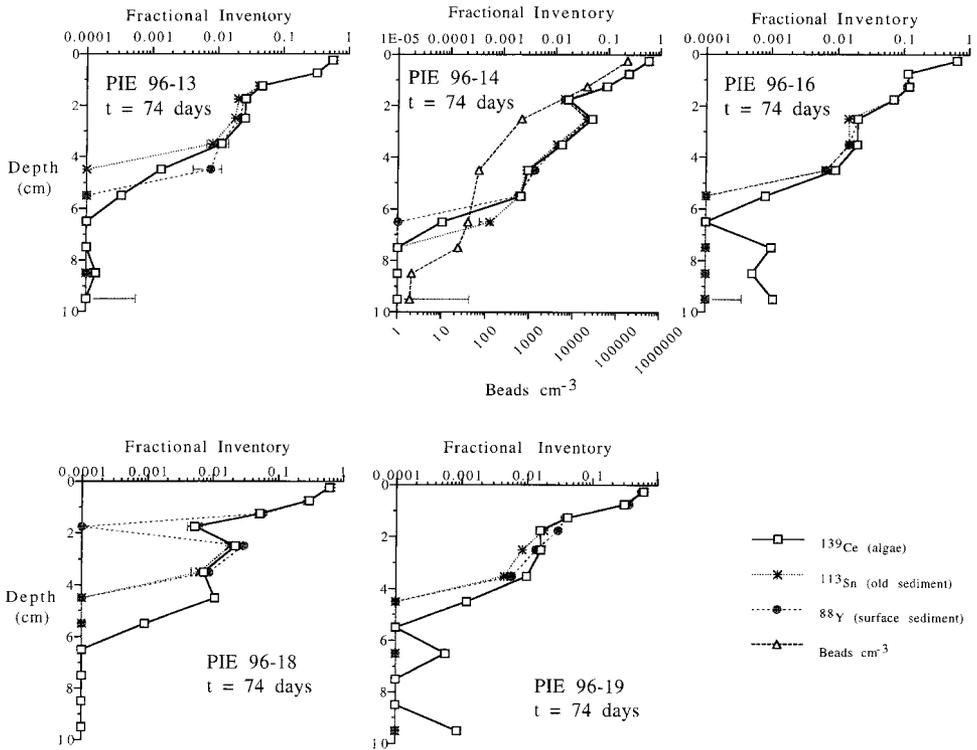
Figure 4. Plots of fractional inventory and bead concentration vs. depth for the PIE 74-day treatment. [139]Ce error bars are shown and were estimated from counting statistics.

results are explicitly predicted by the age-dependent-mixing hypothesis (Smith *et al.,* 1993).

c. Particle selectivity

The ability of deposit feeders to select particles of high food quality is well established (Lopez and Levinton, 1987; Billett *et al.,* 1988; Thiel *et al.,* 1988/89; Graf, 1989; Lauerman *et al.,* 1997; Miller *et al.,* 2000; Smith *et al.,* 2001). As labile organic carbon decays away in "young" particles, e.g., in our diatom tracers, the food quality of these particles should decline. The age-dependent-mixing hypothesis predicts that such particles will be less frequently ingested, and bioturbated less intensively, over time as food quality declines (Smith *et al.,* 1993; Fornes *et al.,* in prep.). To examine particle selectivity in our tracer experiments, we evaluated: (1) apparent D_b values of each tracer at each time scale, and (2) the inventories of tracers below the TZH as a function of time.

Although the relationship between D_b and radioisotope half-life observed by Smith *et al.* (1993) suggests that labile particles may undergo more intense biodiffusive mixing than refractory particles, tracer-specific apparent D_b values from the 4-d treatment indicated no

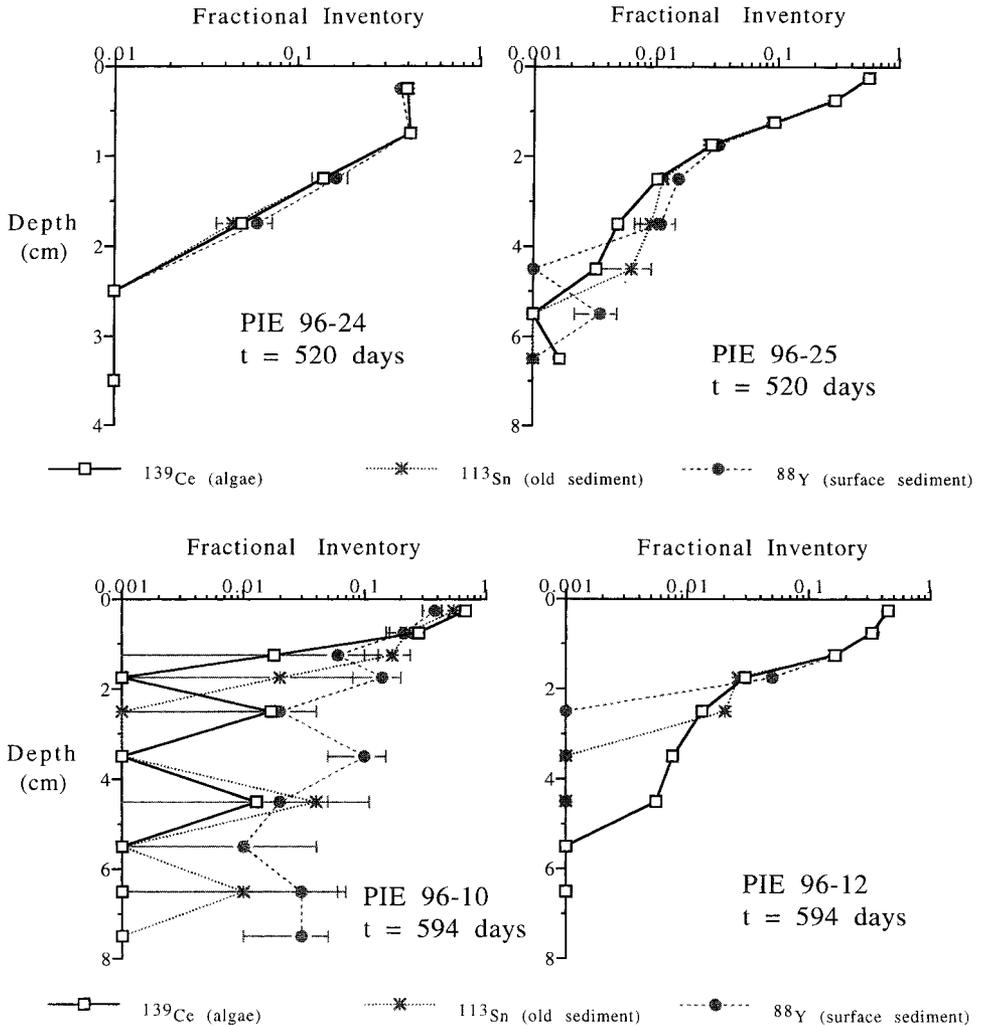Figure 5. Plots of fractional inventory vs. depth for the PIE 520-day and the 594-day treatments. [139]Ce error bars are shown and were estimated from counting statistics.

significant food-quality effect ($p = 0.14$, Kruskal-Wallis k-sample test). Additionally, diffusive mixing exhibited at most a marginally significant particle effect in the 74-d treatment ($p = 0.10$, Kruskal-Wallis k-sample test) and no significant effect in the 524-d treatment ($p = 0.9$, Kruskal-Wallis k-sample test). Admittedly, these tests were low in power as a result of small sample size. Nonetheless our data indicate that diffusive mixing in Santa Catalina Basin was at best a moderately particle-selective process. It may be that processes other than deposit feeding (e.g., tube building and burrowing) contribute substantially to bioturbation in Santa Catalina Basin (Wheatcroft *et al.,* 1990), and these

processes, particularly burrowing, are not particle selective. Over 75% of the Santa Catalina Basin macrofaunal community is made up of burrowing species (Kukert and Smith, 1992), and the most abundant animal, the paraonid polychaete *Levinsenia oculata,* moves horizontally through spiral burrows (Fauchald and Jumars, 1979). Thus, there is considerable potential for burrowing activity to yield nonselective mixing of Santa Catalina Basin sediments.

If age-dependent-mixing were occurring through nondiffusive processes, young, food-rich tracer particles (i.e., our diatoms) should have penetrated below the TZH more rapidly than food-poor particles (our sediments), especially during the early time intervals (4 and 74 d). To examine any such differential penetration, selectivity indices (i.e., the ratios of fractional inventory) for the penetration of tracer below the TZH were calculated for each time interval as follows:

$$S_1 = \frac{3 * Ce}{Ce + Sn + Y} \tag{3}$$

$$S_2 = \frac{2 * Y}{Sn + Y} \tag{4}$$

where Ce, Sn and Y are the total fractional inventory below the TZH for the respective radioisotope (Table 2). The S_1 index was used to evaluate preferential penetration of the diatoms particles relative to other tracers added, whereas the S_2 index was used to evaluate preferential penetration of surface sediment relative to deep sediment. Values of S_1 and S_2 (Table 2) were tested against the null hypothesis $S_i = 1$ with a *t*-test; age-dependent mixing resulted if $S_i > 1$. The S_1 values (for sediments below the TZH) suggest that the diatoms experienced more rapid penetration than either sediment tracer in the 4-d treatment ($p = 0.02$, *t*-test). Preferential diatom penetration decreased over time (74-d treatment, $p = 0.15$, *t*-test; 520-d treatment, $p > 0.5$, *t*-test; all treatments, $p = 0.03$, Kruskal-Wallis *k*-sample test), supporting the age-dependent-mixing hypothesis that mixing intensities for initially food-rich particles will converge over time with those for bulk sediments. The S_2 values do not follow the same trend as S_1. Surface and deep sediments penetrated similarly in all treatments ($p \geq 0.4$), although the 74-day treatment indicated a slight increase in surface-sediment selectivity ($p = 0.07$, Kruskal-Wallis *k*-sample test).

Our data suggest that age-dependent-mixing was most strongly manifested through nondiffusive mechanisms such as nonlocal exchange or bioadvective transport. In particular, differential rapid "mixing" of young particles appears to have occurred through rapid initial subduction of particles very recently deposited at the sediment-water interface. This subduction was modestly selective for food-rich particles (i.e., diatoms) especially on 4-d time scales. The most likely animals responsible for this selective subduction in Santa Catalina Basin are cirratulid polychaete worms, especially those in the genus *Tharyx.* In the deep-sea, *Tharyx* species are believed to feed on surface particles with mucus-covered tentacles, and then egest the particles as they burrow through the sediment column

(Wheatcroft *et al.,* 1990). Such cirratulids were abundant in our PIE treatments (450 m^{-2}) with over 93% occurring below the top centimeter of sediment (Smith and DeMaster, unpublished data). In our 0–4 d PIE samples, we collected *Tharyx* with tracer particles (glass beads) in the guts as deep as 5–6 cm deep in the sediment column. Because cirratulids are one of the most abundant macrofaunal taxa in deep-sea (Jumars and Gallagher, 1982; Paterson *et al.,* 1998), such rapid, particle-selective subduction of fresh, food-rich particles (e.g., phytodetritus) may be widespread in bathyal and abyssal sediments (cf., Pope *et al.,* 1996; Stephens *et al.,* 1997). Rapid subduction of recently deposited tracer particles has also been documented on the North Carolina slope, where maldanid polychaetes "hoed" particles to depths of ≥12 cm within days (Levin *et al.,* 1997; Fornes *et al.,* 1999; Blair *et al.,* 2001). In contrast to our results in Santa Catalina Basin, however, particle subduction by maldanids did not show even modest selectivity among tracers of different quality and presumed food value (Levin *et al.,* 1997; Fornes *et al.,* 1999; Blair *et al.,* 2001). This difference in subduction selectivity likely reflects differences in the modes of particle pickup or entrainment. The mucus-mediated adhesion of particles onto tentacles allows selection based on particle size, specific gravity, surface texture, and organic coating (literature summarized in Smith *et al.,* 1993); in contrast, simple hoeing should allow little opportunity to select particles by other than position at the sediment-water interface. Thus, rapid subduction by cirratulid polychaetes is expected to exhibit selectivity based on particle quality while hoeing by maldanids is not.

4. Conclusions

Particle-introduction experiments with radioisotope-tagged particles of varying food-quality (and "age") offer a valuable approach for study of the mechanisms and rates of bioturbation over a broad range of time scales (in this case 0 to 594 days). Our experiments in Santa Catalina Basin indicate that, following a sedimentation pulse, deposited particles may penetrate 1–2 cm into bathyal sediments within hours. This rapid penetration results from passive, gravitational mechanisms and/or from extremely rapid bioturbation. On a time scale of days, nondiffusive transport supercedes diffusive processes, whereas after a period of months, bioturbation converts to processes apparently diffusive in nature. Our data also suggest that age-dependent bioturbation (i.e., differential particle mixing as a function of time since deposition) occurs in Santa Catalina Basin sediments by way of both biodiffusion and nonlocal/bioadvective transport. Biodiffusive mixing intensity of tracers decreased with time after deposition and did not appear to be particle selective. Nondiffusive bioturbation was selective for diatoms, with selectivity decreasing over time; the decrease in selectivity appears to have mirrored the decay of labile organic carbon within the diatoms. Future studies of deep-sea sediments must consider the quality (e.g., age, labile-organic-carbon content) and sediment position of particles to accurately assess bioturbation processes and their effects on sediment diagenesis.

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