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Experimental tests for particle size-dependent bioturbation in the deep ocean

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Abstract

The potential for particle size-dependent bioturbation rates was experimentally tested at 1,240 m in the Santa Catalina Basin (eastern Pacific). Spherical glass bead tracers in five size classes (8–16, 17–31, 32–62, 63–125, and 126–420 μm) were spread over the sediment surface and tube cored 997 d later. Downcore concentrations of glass beads were enumerated in each of the five size categories and Page's L-test was used to test the null hypothesis of equal vertical penetration of all size classes of tracer. In all cores the null hypothesis was rejected; finer tracers penetrated deeper into the sediment. In two of the three cores, vertical biodiffusivities were computed from concentration profiles of downcore tracers. These also showed size dependence, with biodiffusivities ranging from 1 cm^2 yr^{-1} for the 8–16-μm fraction to 0.1 cm^2 yr^{-1} for the 125–420-μm size class. These data demonstrate that vertical bioturbation rates are particle size-dependent in Santa Catalina Basin. The likely cause is preferential ingestion and downward transport of fine particles by deposit feeders.

Nearly all particles that reach the floor of the ocean are displaced several times by animals before they are buried to become part of the sedimentary record. This mixing of sediment or *bioturbation* has profound effects on a wide range of phenomena. Rates of organic matter decomposition, for example, as well as the dissolution of nearly all sedimentary constituents (e.g. $CaCO_3$ and SiO_2) are markedly influenced by the rate of sediment mixing (Berner 1980). Similarly, the distribution of solid and liquid phase nutrients is mediated by bioturbation, implying that there are likely to be strong feedbacks between the style and rate of mixing and the distribution of infauna. The displacement of sediment grains also destroys or blurs sedimentary signals (Wheatcroft 1990). Therefore, a better understanding of bioturbation, especially its rates, styles, and variability would benefit a wide range of aquatic disciplines.

In the past scientists have approached bioturbation from one of two directions. On the one hand, benthic ecologists (e.g. Rhoads 1967) have typically focused on a single species (usually from a shallow-water, temperate site) and observed rates and styles of sediment reworking under a range of conditions (e.g. changing temperature). Following nearly two decades of such autecologic studies there is a large body of literature (summarized by Thayer 1983; Wheatcroft et al. 1990) demonstrating that sediment displacement is tremendously complex. Deposit feeding and hence particle displacement rates have been shown to be temperature- (Rhoads 1967), particle-shape- (Whitlatch 1974), and particle-size- (Powell 1977) dependent. Moreover, there seem to be ontogenetic changes in a species' particle selectivity, as well as interactions between different environmental cues, that further complicate mixing.

The other approach to bioturbation has been taken primarily by geochemists who require a community-wide estimate of the sediment mixing rate to characterize the role of bioturbation as a mass transfer mecha-

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nism. This goal is achieved by making various simplifying models of bioturbation. Currently the most widely used model is based on an analogy with standard Fickian diffusion (Guinasso and Schink 1975; Wheatcroft et al. 1990). Community-wide mixing rates are obtained by measuring the vertical concentration profiles of various tracers and fitting theoretical profiles to the observed gradients. The best-fit curves contain various parameter values, one of which is biodiffusivity (D_b). This coefficient represents all of the myriad sediment-displacing activities of the benthos at a given site, and thus, much of the complexity observed by benthic ecologists is incorporated into D_b. An untested and extremely important question is whether that complexity will manifest itself in the community-wide measures of mixing (e.g. biodiffusivities) in a systematic and predictable manner. That is, is it necessary or even possible to explicitly incorporate biology into the biodiffusion coefficient?

This question is addressed by focusing on an issue that has a long history (considering the youthfulness of this field) in studies of bioturbation: the question of particle size dependence in deep-sea mixing rates. As previously mentioned, several autecologic laboratory studies have demonstrated preferential ingestion of fine particles by deposit feeders (*see* Taghon 1989). In addition, many head-down deposit feeders preferentially ingest fine-grained sediments resulting in biogenic graded bedding, whereby one passes from fine to coarse grains moving down into the sediment. These observations, however, have been made on a limited subset of animals, mainly temperate, shallow-water deposit feeders in sandy environments. To what extent these shallow-water observations apply to deep-sea bioturbation rates is presently unknown.

There is some inferential evidence that deep-sea mixing is indeed size-dependent. Several recent radioisotopic studies (DeMaster and Cochran 1982; Stordal et al. 1985) have reported disparities between mixing coefficients derived from various radionuclides (e.g. ^{210}Pb vs. ^{32}Si or ^{210}Pb vs. ^{239,240}Pu). In both cases the radionuclide that yielded the higher mixing rates was inferred to be associated with finer particles. Cochran (1985) also found a disagreement between mixing coefficients calculated from the profiles of the bomb-produced radioisotopes, ^{137}Cs and ^{239,240}Pu vs. ^{210}Pb. He suggested differential mixing of different-sized particles, but also stated that selective mobility of the radionuclides could not be ruled out. An additional independent line of evidence that suggests mixing is size-dependent comes from the studies of $CaCO_3$ ages in the mixing layer. Berger and Johnson (1978) hypothesized that discrepancies between ^{14}C- and δ^{18}O-derived dates might result from greater mixing of the bulk carbonate fraction relative to the large foraminiferans from which the oxygen record was derived.

An explicit test for size dependency in deep-sea mixing was made by Ruddiman et al. (1980). They measured the vertical dispersion of different-sized ash particles and, on the basis of visual comparisons of the concentration profiles, cautiously concluded that mixing was *not* size-dependent. Since then, their data have been statistically reanalyzed by Wheatcroft and Jumars (1987), who found that there was indeed greater mixing of the fine fraction. Although the results of their reanalysis and the inferential evidence discussed above qualitatively suggest mixing rates are size-dependent in the deep sea, the magnitude of the relationship is unclear. My primary goal here is to describe results of an a priori test for particle size-dependent bioturbation in the deep ocean. A secondary goal is to discuss animal activities that displace sediment within the context of their potential for particle size-dependent mixing.

Background

All animal activities that displace sediment have the potential to produce size-dependent transport rates. The direction of bias (i.e. preference for fine or coarse particles), however, often differs within and between activities; thus, there is the possibility that the integrated community-wide effect could be neutral. That is why tests for particle size-dependent mixing must be made in the field, where the summed activities of all animals in a given community can be assessed. Size-dependent mixing rates (particle migration, sensu Williams and Khan 1973) can be produced actively or passively. Passive particle migration often occurs in industrial mixing (Williams and Khan 1973; Stephens and Bridgwater 1978), where it is typically caused by spatial heterogeneity in the local strain rate and resultant porosity field. Some animal activities (e.g. burrowing) may cause passive particle migration. Most animal activities contain an active component, however, whereby the animal preferentially displaces particles of a given size.

During *tube building,* many invertebrates (especially polychaetes) exhibit scrupulous selection of particles based on various attributes (e.g. shape, specific gravity, or size). Field observations of the polychaete *Owenia fusiformis* have revealed concentrations of tabular grains of hornblende in its tube at least 25-fold over ambient levels (Fager 1964). Similarly, in laboratory tests the same species displayed a 100% preference for angular over spherical glass particles (Self and Jumars 1988). Whitlatch and Weinberg (1982) observed strong selection of larger particles by the tube-building pectinarid polychaete *Cistenides gouldii.* Other species of tube-building, shallow-water polychaetes, however, exhibit a weak preference toward finer particles (Self and Jumars 1988). Thus, the integrated effect of various tube builders on particle size-dependent mixing will likely depend on the species composition of that community and is difficult to predict a priori. Until it can be shown otherwise, in the equitable communities characteristic of the deep sea, tube building will be considered to have a neutral effect on particle migration. *Test-building* protistans (e.g. foraminiferans and xenophyophores), however, display strong selection for coarse particles (pers. obs.). In many deep-sea settings protistans dominate macrofaunal biomass; therefore one might expect greater residence times of coarse particles in the surface mixing layer.

Animal *locomotion* (e.g. crawling and burrowing) has the potential to produce *passive,* size-dependent vertical mixing. In cohesionless, polydisperse systems of particles undergoing industrial mixing, two types of gravitationally forced vertical migration occur. The first is downward migration of fine particles (termed *percolation,* Williams and Khan 1973), due to the greater tendency of the fines to settle into voids created in the moving particle matrix. This process in turn results in a second upward migration of coarse particles because the weight of coarse particles causes an increase in pressure below it that stops the particle from moving downward. As particles are jostled, more fines fall under the coarse particles and are locked into position (Williams and Khan 1973). Thus, the coarse particles migrate upward. Elements of the coarse-particle migration mechanism have been used to explain the tendency for Mn nodules to remain at the sediment surface (Sanderson 1985) and the observed upward migration of very coarse glacial debris in deep-sea sediments (McCave 1988). The difference in particle sizes in both systems was large (~100–1,000-fold), however, so the likelihood of passive particle migration in more equitably sized deposits is unclear.

Several independent lines of reasoning suggest that if there is any passive particle migration due to locomotion it should be toward greater *downward* transport of the coarse fraction. First, sediments in nature are not subject to the high-frequency vibrations experienced in industrial mixing. Thus, localized high shear zones that result in enhanced particle migration rates (Williams and Khan 1973) are not likely to form. More importantly, most marine sediments are not cohesionless. Rather, they are complex mixtures of wet, cohesive, organically bound particles. Thus, downward percolation of fine particles is unlikely in aqueous sediments where the gravitational force on fine particles could be balanced by cohesive or adhesive forces. Only coarse (but not too coarse; Sanderson 1985; McCave 1988) particles are likely to display preferential downward migration due to burrowing, since for them gravity overcomes the cohesive-adhesive bonds. This effect was demonstrated by Clifton (1984) who observed that the burrowing mechanism of a nephytid polychaete fluidized the sediment enough to allow the coarser and denser particles to settle lower in the deposit. That sediments in general may be fluidized enough to allow coarse-particle migration or at least reorientation is tentatively supported by observations by Chernow et al. (1986), who explained the minimal influence of bioturbation on magnetic fabrics by invoking similar fluidization. Thus, if burrowing has any effect on particle migration it may be toward preferential downward movement of the coarse fraction.

Preferential downward transport of coarse particles due to the activities of *surface-crawling animals* is also likely. There is a higher probability for crawlers to contact large particles, due solely to geometrical considerations. Thus, larger particles are more likely to be pushed into open tubes and burrows where they are transported downward (Wheatcroft et al. 1990). Again, particles that are very large relative to ambient sediments will be avoided completely by crawling animals.

Of all animal activities, *deposit feeding* has been postulated to be the dominant sediment transport mechanism (Thayer 1983; Wheatcroft et al. 1990). Thus, if preferential mixing of particles occurs, it is most likely due to this activity. The direction of particle size preference is also most clear for this animal activity. Deposit feeders on the whole actively select and thus displace finer particles. The reasons are both behavioral and morphological. First, the long-standing observation that, at a given water depth, deposit-feeder standing stock increases with decreasing particle size of the deposit suggests that more food is to be found in finer sediments (Sanders 1960). With decreasing particle size, the ratio of grain surface area to grain volume increases, providing the potential for more food per unit of grain volume (assuming that most food is surface associated). Quantitative measures of the relationship between sediment surface area and microbial abundance and organic C (DeFlaun and Mayer 1983) support this explanation down to particle sizes of ~10 μm. The above observations were put into an optimal foraging context by Taghon et al. (1978) who predicted that deposit feeders should, under most conditions, preferentially ingest small particles.

There have been numerous empirical studies of particle selection, as well as a priori tests of size selectivity (e.g. Taghon 1982). The most frequent finding is of preferential selection for smaller particles (*see* Taghon 1989). More recent experimental studies with glass beads of varying sizes and specific gravities and animals from several phyla support earlier findings of peak selectivity for small particles (10–20 μm) (Self and Jumars 1988).

There are exceptions to the pattern of greater selection of the fine fraction, whereby coarser particles are ingested preferentially (e.g. Whitlatch 1974; Fenchel et al. 1975; Whitlatch and Weinberg 1982). In some instances, enhanced selection of the coarse fraction occurs when the majority of food is associated with that size class (e.g. diatoms, Fenchel et al. 1975). In other cases it is probably caused by morphological constraints of the specific feeding appendage (Whitlatch and Weinberg 1982). In any case, selection for coarse particles is the exception, and deposit feeding normally will result in enhanced displacement of fines.

A higher displacement frequency (or shorter rest period in the nomenclature of Wheatcroft et al. 1990) for fine particles does not necessarily mean that they will penetrate farther into the sediments in a given unit of time because, at least in shallow-water environments, many deposit feeders (both surface and subsurface types) egest material on the sediment surface. The ramifications of such mixing have been explored, via first-order Markov models, by Jumars et al. (1981), who found that under some circumstances fine-grained particles will be preferentially kept in the surface mixing layer. Thus it is conceivable that coarse particles will penetrate into the sediment at faster rates.

Study site

The study site (33°12′N, 118°30′W) is at 1,240 m on the floor of Santa Catalina Basin (SCB), a bathyal basin in the California borderland tectonic province. SCB sediments consist of clayey-silts with a mean disaggregated diameter of ~4 μm. The coarse fraction (>62 μm) is composed of radiolarians, foraminiferans, quartz, and lithic fragments. Bottom water is sufficiently well oxygenated (0.4 ml liter^{-1}) and organic C flux high enough to support an abundant and reasonably diverse bottom fauna (Jumars 1976; Smith and Hamilton 1983; C. Smith et al. 1986).

The macrofauna is dominated by members of the polychaete families Paraonidae, Cirratulidae, and Cossuridae (Jumars 1976; C. Smith et al. 1986). There is very little natural history information on these groups, especially from the deep sea. Limited observations on shallow-water congenerics suggest that many of these worms are deposit feeders, which studies of gut contents from SCB animals support (Penry and Jumars 1990). The megafauna is strongly dominated (>99%) by the epifaunal brittle star *Ophiophthalmus normani* (Smith and Hamilton 1983). This animal is probably an omnivore, capable of deposit and suspension feeding, as well as preying on various meiofauna. It is highly mobile and probably responsible for the high near-surface horizontal bioturbation rates measured in this basin (Wheatcroft 1991). Other epibenthic megafauna consists of two species of gastropod and various echinoderms (e.g. holothuroids, asteroids, and ophiuroids) (Smith and Hamilton 1983). Although it has not been sampled in box cores, there is evidence (visual observations, photographs, and large mounds and broad surface depressions) for the presence of a subsurface echiuran worm that mixes particles advectively (C. Smith et al. 1986; Smith in press). Thus, treatments in this study were located away from the mounds-depression complexes to avoid the complications of large-scale (>10 cm) advective mixing.

Field and laboratory procedures

The tracers used in this study are spherical glass beads ranging in size from 8 to 420 μm. To isolate the effect of size on bioturbation rate, I held other attributes of the particles such as specific gravity (2.4) and surface roughness (very smooth) constant. The beads were spread on the sediment surface with the DSV *Alvin* and "salt shakers": 1-liter freezer containers with plastic screening (1.2-mm mesh) across their openings. Aluminum-T handles were bolted to the sides of the bead spreaders for manipulation by *Alvin*. At the sea floor, the bead spreaders were removed from the basket in an upright position, held ~50 cm off the bottom and upended. Continual shaking by the manipulator arm for 1–2 min dispersed ~200 ml of beads onto ~1 m^2 of seafloor. The use of more sophisticated devices that purportedly yield monolayers of tracer particles on the sediment surface is unnecessary because only the vertical *gradient* of particle concentration is of interest. Moreover, such devices undoubtedly disturb the near-surface infauna and epifauna to a much greater extent than the bead spreader described here.

Treatments of two different durations were deployed. A long-term experiment was initiated on 5 February 1985 (dive 1,512) and cored 997 d later on 30 October 1987 (dive 1,937) with 6.7-cm-i.d.-diameter acrylic tube corers. A second, short-term treatment was introduced on 12 December 1986 (dive 1,779) and cored 319 d later on 31 October 1987 (dive 1,938). A control experiment, consisting of bead spreading followed by immediate coring, was performed on 10 November 1987 (dive 1,949). Details of the navigation system used to relocate and core the small-scale treatments on the deep-sea floor are given elsewhere (Wheatcroft 1991).

On the surface, cores were processed within 4 h by siphoning the supernatant water and placing the corers onto extruders. After extruding a vertical interval of 1 cm, a thin (0.5 mm) sheet of metal was used to vertically isolate the uppermost slab of mud. A 4.2-cm-diameter plastic fence was then pressed into the center of the subsample and the outer ring of mud discarded. The central disk of mud, ostensibly free of vertical contamination, was then transferred to a sample bottle. The approximately equal-volume samples (14 cm^3) were collected to ~10-cm depth.

The method used to enumerate the tracers consists of randomly settling grains onto microscope slides where they can be counted (method of Moore 1973 as modified by Laws 1983). The samples were sonicated in their bottles for 3 min with a 250-W Vibracell ultrasonicator. Pretests showed that this step completely disaggregated all fecal pellets and other aggregates without affecting the glass beads. After transfer to 600-ml beakers, samples were split into three subsamples, each 2/27 (7.4%) of the total sample. These replicate subsamples were sieved through 62-μm Nytex screens. The >62-μm fraction was sieved onto 8-μm Nuclepore polycarbonate filters and transferred onto 5 × 7.5-cm glass slides to await counting. The <62-μm fraction was poured into 3,000-ml beakers filled with tapwater, stirred vigorously, and allowed to settle for 30 min (*see* Moore 1973). Calculations with Stokes' law suggest that two-thirds of the 8-μm particles would have transitted the 15 cm of water in the beakers in that time. The supernatant water was then siphoned to below the microscope slide stages (*see* text-figure 1 of Laws 1983), and 250-W infrared heat lamps were positioned above the stages. Evaporation of the remaining water was complete in <1 h. The slide preparation technique yielded randomly distributed samples, as indicated by χ^2 test for agreement with a Poisson distribution (Sokal and Rohlf 1981) on randomly selected slides.

The <62-μm fraction was counted with a Zeiss compound microscope (25× with 10× oculars) and transmitted light. To minimize subjectivity I assigned subsamples random letters and counted blindly in an arbitrary order. Only after counting all depth intervals from a given core were the results tallied. Six stratified random transects were made across each slide, and the glass beads that were at least halfway within a 280-μm wide ocular grid were counted into one of three size classes: 8–16, 17–31, and 32–62 μm. Counting each of the two slides in each beaker resulted in 36 transects. They formed the basis of the size-specific particle concentrations and the standard errors at each depth level. The coarse fraction was counted into two size fractions (63–125 and 126–420 μm) on the glass slides with the Zeiss microscope (10× with 10× oculars).

Numerical and statistical methods

The transects yielded an estimate of the number of tracers (±1 SE, $N = 36$) in each of five size classes at each depth interval. Within each core the results were summed to provide an estimate of the total inventory of glass beads of that size. The size-specific inventory was then used to normalize the number counts from each depth interval; thus, concentrations reported in the ensuing tables and figures represent the proportion (i.e. relative concentration) of the total number of beads of that size class at that depth interval estimated in each core.

Two paths were used to arrive at an overall comparison of particle size-specific mixing intensity. The first method simply compares the weighted-mean depth of the concentration profiles between size classes. More intensely displaced size fractions should be, on average, moved farther down into the sediment, yielding larger weighted-mean depths. This technique makes no assumptions about how (e.g. biodiffusion or advection) the particles arrive at their observed destinations.

The second method of analysis uses the diffusion analogy of bioturbation to arrive at a biodiffusion coefficient representative of the intensity of vertical particle displacement (Guinasso and Schink 1975; Wheatcroft et al. 1990). Long-term sediment accumulation rates in SCB (Schwalbach and Gorsline 1985) suggest that during the maximal length (997 d) of this experiment <0.5 mm of sediment would have accumulated. Thus, sedimentation can be neglected as a vertical mass transfer mechanism, and the conservation equation for a nondecaying, particulate tracer undergoing diffusive mixing is

$$\frac{\partial C}{\partial t} = D_b \frac{\partial^2 C}{\partial z^2}, \tag{1}$$

where C is tracer concentration, t is time, and z is depth into the sediment. Downcore porosity variations have been neglected. For an instantaneous, plane source (i.e. at $t = 0$, $C = 0$ at $z > 0$ and $C = 1$ at $z = 0$), with reflection at a boundary (i.e. $\partial C/\partial z = 0$ at $z = 0$) the solution to Eq. 1 is (Crank 1975)

$$C(z) = \frac{1}{(\pi D_b t)^{1/2}} \exp(-z^2/4D_b t). \tag{2}$$

The biodiffusion coefficient that yields the best-fit concentration profile was computed by iteratively solving Eq. 2 with different values of D_b. The resultant theoretical concentration profiles were then compared to

Table 1. Normalized glass bead concentrations for each size class in the three cores.

Depth (cm)	Size class (μm) 8–16	17–31	32–62	63–125	126–420
			Core 1,937-1		
0–1	0.368	0.529	0.612	0.470	0.741
1–2	0.270	0.374	0.331	0.452	0.231
2–3	0.140	0.051	0.032	0.030	0.021
3–4	0.083	0.024	0.007	0.034	0
4–5	0.052	0.012	0.007	0.007	0
5–6	0.052	0.007	0	0.004	0.007
6–7	0.026	0.004	0.010	0.001	0
7–8	0.008	0	0	0.002	0
8–9	0	0	0	0	0
			Core 1,937-2		
0–1	0.484	0.834	0.846	0.896	0.983
1–2	0.124	0.051	0.049	0.029	0.017
2–3	0.088	0.027	0.022	0.026	0
3–4	0.071	0.017	0.010	0.002	0
4–5	0.082	0.028	0.019	0.010	0
5–6	0.056	0.032	0.043	0.033	0
6–7	0.028	0.004	0	0.002	0
7–8	0.024	0.004	0.007	0.001	0
8–9	0.042	0.004	0.005	0.001	0
			Core 1,937-3		
0–1	0.340	0.489	0.607	0.694	0.792
1–2	0.295	0.259	0.187	0.123	0.034
2–3	0.193	0.195	0.149	0.103	0.044
3–4	0.098	0.030	0.029	0.042	0.070
4–5	0.050	0.024	0.028	0.034	0.060
5–6	0.013	0.002	0	0.001	0
6–7	0.012	0	0	0	0
7–8	0	0.001	0	0	0
8–9	0	0	0	0	0

the observed data, and the biodiffusivity that yielded the smallest median residual was chosen. The best-fit technique is analogous to a logarithmic transformation in that it assigns an equal weighting to all depth intervals and thus removes the disproportionate influence of near-surface concentrations.

Statistical comparisons between either the weighted mean displacement (method 1) or the best-fit biodiffusivity (method 2) of each size class were performed with various nonparametric tests. Page's modification of the ordered alternative test (Hollander and Wolfe 1973) was used to test the null hypothesis of no differences between treatments (i.e. tracer sizes) on various attributes (i.e. D_b or mean vertical displacement) against the alternative of a natural ordering of treatments with respect to the attributes. A nonparametric test for correlation, Spearman's ρ, was used to test for significance between computed mixing rates and particle size.

Results

In all three of the long-term cores (the short-term experiment was missed during attempted recovery) there are strong indications of an increase in mixing intensity with decreasing tracer size. In each core, there is an increasing fraction of fine tracer relative to the coarser beads at increasing sediment depths (Table 1). Page's L-test for ordered alternatives rejects the null hypothesis of equal depth-weighted means for the various tracer size fractions at a high level of significance ($P = 0.001$) (Table 2). The control core, on the other hand, revealed that <0.1% of any tracer size class penetrated through the surface (0–1 cm) layer. These results suggest that, whatever the mechanism of mass transfer, it is not likely a sampling artifact and it is particle size-dependent.

In two (1,937-1 and 1,937-3) of the three cores the vertical concentration profiles can be fitted with the biodiffusive model of sediment mixing (Eq. 1 and 2). Vertical biodif-

Table 2. Summary of depth-weighted mean displacements (z_i, in cm) for each size class. In parentheses are the within-core ranks used to compute Page's L-test for ordered alternatives. The null hypothesis is $z_5 \leq z_4 \leq z_3 \leq z_2 \leq z_1$ and the alternative is $z_5 > z_4 > z_3 > z_2 > z_1$; R_i is the rank sum of each size class.

Core	Size class (μm) 8–16	17–31	32–62	63–125	126–420
1,937-1	1.98(5)	1.15(3)	1.01(2)	1.18(4)	0.78(1)
1,937-2	2.30(5)	1.01(4)	1.00(3)	0.82(2)	0.52(1)
1,937-3	1.81(5)	1.35(4)	1.18(3)	1.11(2)	1.07(1)
	$R_5 = 15$	$R_4 = 11$	$R_3 = 8$	$R_2 = 8$	$R_1 = 3$

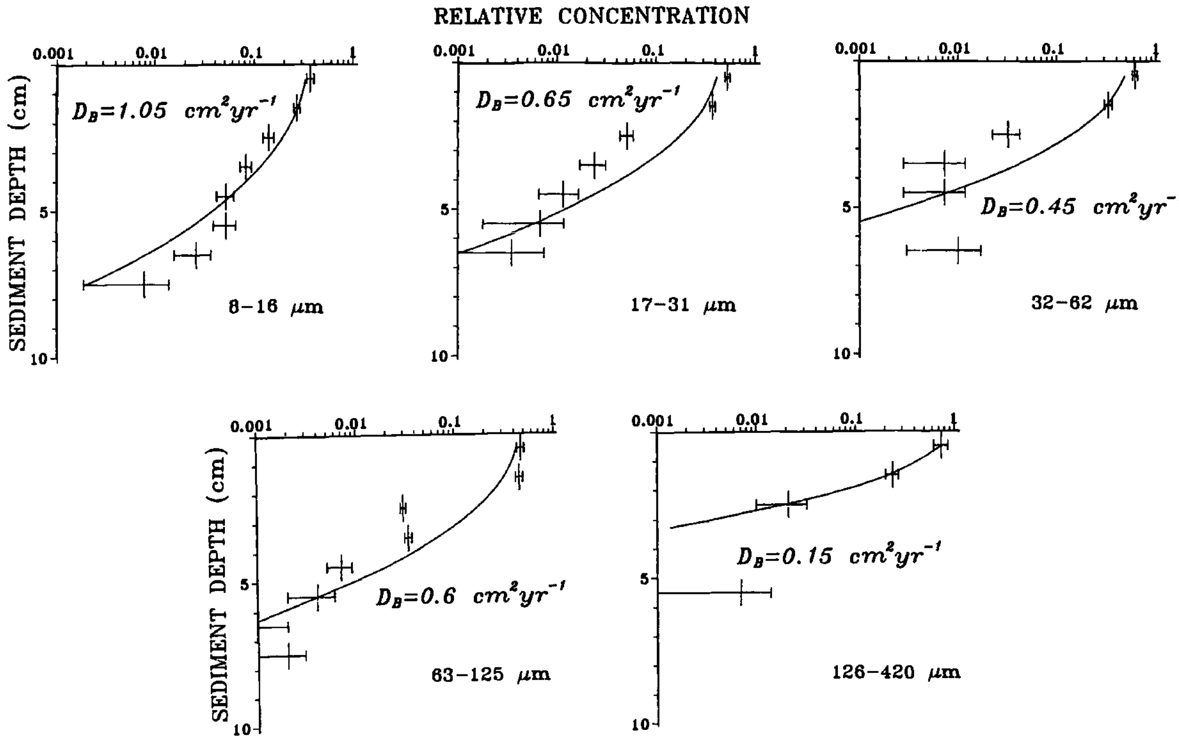

Fig. 1. Core 1,937-1: Observed vertical profiles of tracer concentration (±1 SE, $N = 36$) for each size class. The solid lines represent the theoretical concentration profiles of the best-fit biodiffusivities.

fusivities for core 1,937-1 range from 1.05 cm^2 yr^{-1} for the 8–16-μm fraction to 0.15 cm^2 yr^{-1} for the coarse (126–420 μm) fraction, a variation of about an order of magnitude (Fig. 1). Intermediate tracer size fractions yield intermediate D_b values, although the trend is not monotonic. The 63–125-μm size class of tracers penetrates deeper into the sediment and yields a D_b greater than the next smaller size class of tracers (Fig. 1). A similar trend in D_b values was found in core 1,937-3 (Fig. 2). In that core, the finest tracer (8–16 μm) yields a biodiffusivity of 0.95 cm^2 yr^{-1}, whereas the 63–125-μm fraction yields a D_b of 0.45 cm^2 yr^{-1}. Note that the coarsest fraction of tracer in core 1,937-3 does not display a diffusive profile (Fig. 2), but instead shows a subsurface peak in concentration.

In contrast to the overall good fit of the tracer concentration data in cores 1,937-1 and 1,937-3 to various biodiffusivities, data from core 1,937-2 do not conform to a simple biodiffusive model. In all but the coarsest tracer fraction (which yields a D_b of 0.05 cm^2 yr^{-1}), there is a local subsurface peak in concentration at a sediment depth of 4–6 cm (Table 1, Fig. 3). There are at least two possible mechanisms that could account for such a pattern. First, the glass beads may have fallen into open burrows or tubes when spread initially onto the sediment surface or later were pushed into tubes or burrows by mobile epibenthic megafauna (e.g. the brittle star *O. normani*). If this mechanism was responsible, any preferential transport of a size class should tend toward the coarser fraction for reasons discussed above. The second mechanism is via a process termed reverse conveyor-belt deposit feeding (figure I-3f, Wheatcroft et al. 1990), whereby particles are ingested at the surface and egested at some depth in the sediment. Such a nonlocal transport mechanism has been proposed by J. Smith et al. (1986) to account for subsurface peaks in ^{239,240}Pu and ^{210}Pb profiles in NE Atlantic sediments. At their site the responsible animal is likely a sipunculan worm, which is the macrofaunal community dominant and is known to feed in a reverse conveyor-belt mode (Rutgers van der Loeff and Lavaleye 1986). In SCB

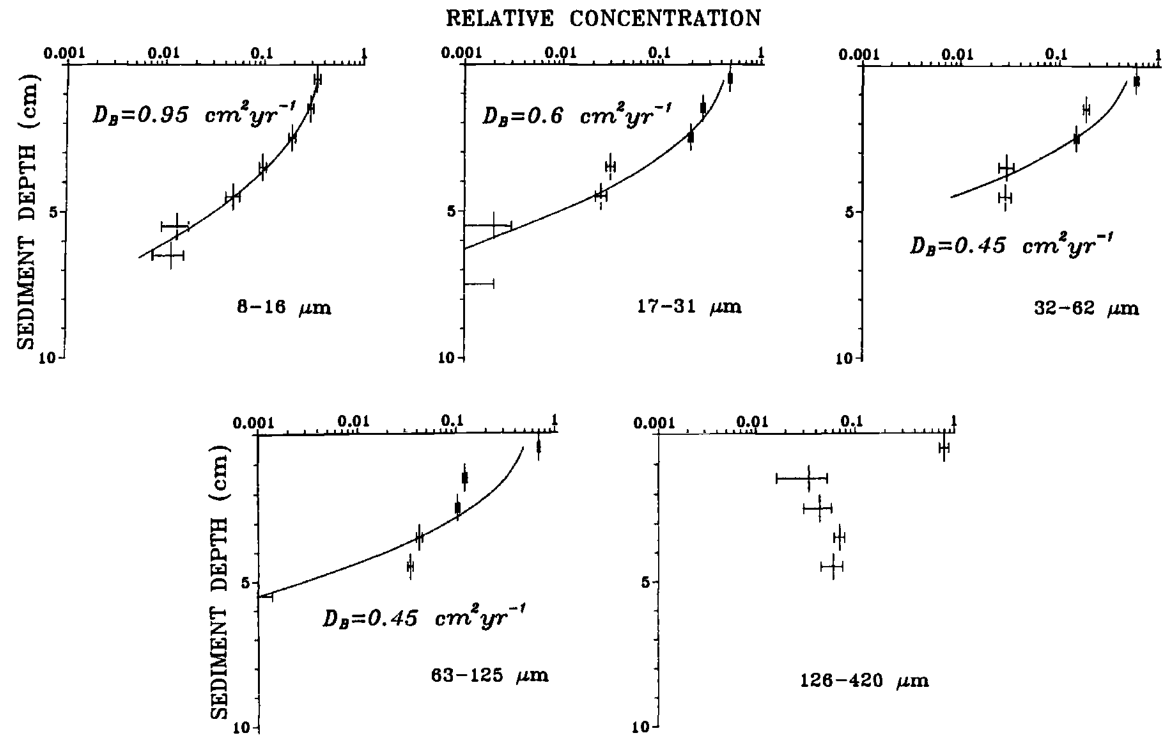

Fig. 2. As Fig. 1, but for core 1,937-3. The coarse fraction (126–420 μm) could not be fitted with a simple biodiffusive model.

it is more difficult to nominate a responsible species, but it is interesting to note that ~6% of SCB macrofauna are members of the cirratulid polychaete genus *Tharyx* (C. Smith et al. 1986). Congenerics in shallow water have been observed to feed in a reverse conveyor-belt mode (Myers 1977). Regardless of what mechanism is responsible, the data themselves suggest preferential selection of the finer fraction, since there is a weak trend of increasing tracer concentration in the 4–6-cm depth interval with decreasing particle size (Table 1).

Even though it is not possible to fit a simple vertical biodiffusivity to the data from core 1,937-2, several lines of evidence support greater mixing intensity of the fine fraction in this core as well. First, the depth-weighted concentration increases with decreasing particle size (Table 2). Second, the shapes of the profiles qualitatively match those produced by J. Smith et al. (1986). They derived a coupled biodiffusion-reverse conveyor-belt model that yields a suite of theoretical concentration profiles that are very similar to the core 1,937-2 data. In all of their simulations there is a similar, subsurface peak. The interesting point is that with increasing background biodiffusive mixing rates, the subsurface peak broadens vertically and decreases in magnitude (figures 6–10, J. Smith et al. 1986). This peak broadening and damping appears to occur in core 1,937-2 as well (Fig. 3), where there is an increase of ~16-fold from the 3–4-cm interval to the 5–6-cm interval in the coarse (63–125 μm) fraction, but succeedingly lesser increases (4-fold and 2-fold) at finer tracer sizes. Thus, there is sound evidence that biodiffusion rate increases with decreasing tracer size in this core as well.

Page's *L*-test for ordered alternatives is again used to test the null hypothesis (Table 3) of equal D_b values against the alternative of a predetermined unidirectional trend in biodiffusivities (Hollander and Wolfe 1973). Due to fewer data points, the results are less significant than the outcome of the weighted-mean displacement data, but the null hypothesis is still rejected ($P = 0.04$). Thus, there would seem to be a statistically significant trend in the size-specific mixing rates

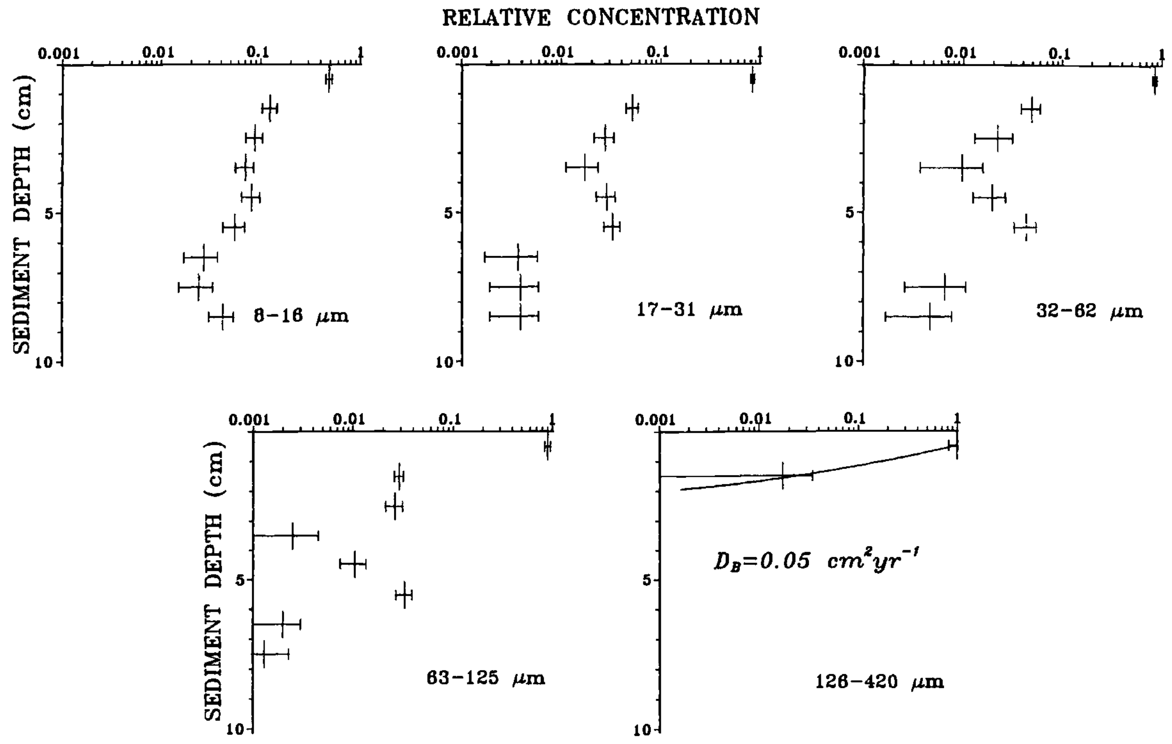

Fig. 3. As Fig. 1, but for core 1,937-2. The solid line in the 126–420-μm fraction is the theoretical concentration profile for the best-fit biodiffusivity. Profiles of the other tracer size fractions could not be fitted with a simple biodiffusive model.

(Fig. 4). A nonparametric measure of correlation, Spearman's ρ, was used to separately test for negative correlation between particle size and D_b in cores 1,937-1 and 1,937-3. The test yields values of Spearman's ρ of -0.90 and -0.95, which are significant at the 0.05 and 0.01 levels. Fisher's method of combining independent probabilities (Sokal and Rohlf 1981) provides an overall test of significance. The results indicate a negative correlation between particle size and biodiffusivity that is significant at $P < 0.01$. Bioturbation is particle size-dependent in SCB.

Discussion

The strength of the negative relationship observed between sediment mixing rate and particle size requires a discussion of potential artifacts in the deployment and enumeration of the tracers. Artifacts could be introduced during three phases of this investigation: bead spreading, coring, and counting. During their initial deployment

Table 3. Summary of particle size-specific biodiffusivities (D_b, cm^2 yr^{-1}). In parentheses are the within-core ranks used to compute Page's L-test for ordered alternatives. Note that the 126–420-μm fraction has been excluded from this analysis. ND indicates that a biodiffusion coefficient could not be fitted to the observed concentration profile. Table 2 gives the explanation of null and alternative hypotheses.

	Size class (μm)				
Core	8–16	17–31	32–62	63–125	126–420
1,937-1	1.05(4)	0.65(3)	0.45(1)	0.60(2)	0.15
1,937-2	ND	ND	ND	ND	0.05
1,937-3	0.95(4)	0.60(3)	0.45(1.5)	0.45(1.5)	ND
	$R_4 = 8$	$R_3 = 6$	$R_2 = 2.5$	$R_1 = 3.5$	

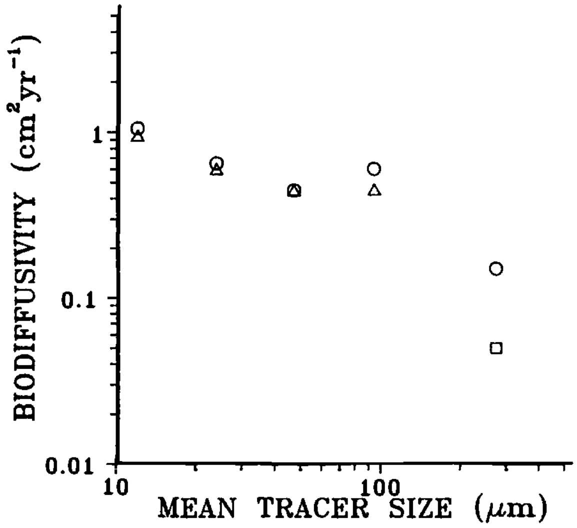

Fig. 4. A log-log plot of observed particle size-specific biodiffusivities vs. mean tracer size. Core 1,937-1—○; core 1,937-2—□; core 1,937-3—△.

from the bead spreaders, settling velocities of the tracers would differ considerably. Thus, there is the possibility of differential initial penetration into the sediments. Any such bias would be toward greater penetration of the coarse tracers, but it is unlikely that penetration would exceed the 1 cm necessary to reach the next lowest depth interval. Although the leading edge of the tube corers is beveled to minimize vertical subduction of sediment, invariably some surface sediment is entrained downward. If this effect occurred, it would also favor subduction of the larger tracers because of their greater per-particle area. As detailed in the methods section and demonstrated by the control core, however, discarding the outer ring of sediment at each depth interval seemed to minimize problems with vertical subduction. If more coarse tracers were somehow missed during counting at greater depths in the sediment, then the patterns observed might be artifacts. Again, any potential bias is most probably in the opposite direction (i.e. counting of coarse particles relative to fines was favored at increasing depth). This direction of bias is because the tracers were counted if and only if they were unequivocally identified as glass beads. Because of decreasing porosity with greater depth resulting in greater amounts of very fine silt and clay, the smaller glass beads were more easily masked. Thus, one would expect that with increasing depth the finer tracers would be missed more often relative to the coarse fractions. All of these arguments suggest minimal artifacts due to the experimental setup and that vertical bioturbation in SCB is strongly particle size-dependent.

Earlier it was argued that deposit feeding is the only animal activity that unequivocally favors preferential mixing of finer particles. Thus, the results reported here lend support to previous contentions (Thayer 1983; Wheatcroft et al. 1990) that deposit feeding dominates particle transport in the abyss. The strength and even direction of the relationship still remains surprising, however, given the textural complexities of marine sediments and the feeding mechanics of deposit feeders. Marine sediments in general, and SCB sediments in particular, are complex mixtures of fecal pellets of various sizes and shapes, organically bound aggregates, living and dead protistans and other skeletal components, as well as various rock and mineral fragments ranging in size from <1 μm to 1–2 mm. When this complex mixture is processed at the high rates (0.1 to >20 Hz, Miller 1984; R. F. L. Self pers. comm.) typical of most deposit feeding, any selection on the basis of a single cue (i.e. size) is remarkable.

Particle selection by deposit feeders is at least a two-step process (Jumars et al. 1982; Whitlatch 1989) made up of the probability of contact followed by the probability of retention. For surface deposit feeders that pat the sediment with various types of feeding appendages, there is a greater probability of contacting larger particles due purely to the greater per particle area they cover relative to fine particles (Jumars et al. 1982). The same is true to a lesser degree for subsurface gulpers (Whitlatch 1989) that ingest a discrete mouthful of sediment. Thus, because the probability of contact favors larger particles over small ones, the probability of retention must be the dominant mechanism operating to explain the results here. The mechanics leading to retention are less easily generalized and depend on particle size as well as on other factors including shape (Whitlatch 1974), specific gravity and surface roughness (Self and Jumars 1978), organic coating (Taghon 1982), and the adhesive strength of mucus covering the feeding appendage (Jumars et al. 1982). The results reported here strongly suggest that particle size is a dominant cue in retention, because *only* particle size (and its derived variables, e.g. surface area or volume) varied in this experiment.

Recall from the discussion above that many shallow-water deposit feeders egest material on the sediment surface, thus a possibility was that fines would be preferentially kept in the surface mixing layer. In experiments similar to this one performed in the abyssal Panama Basin, coarse particles (~80 μm) penetrated deeper into the sediment than fines (R. B. Whitlatch pers. comm.). The likely explanation for this pattern is that deposit feeders (surface or subsurface) in Panama Basin egest material on the sediment surface. In contrast, the results reported here demonstrate that fine particles penetrate farther into the sediment and suggests that surface egestion is not prevalent in SCB.

There are grounds to believe that deposit feeders in the deep ocean in general do not egest material on the sediment surface, and that Whitlatch's results are exceptional. The reasons behind this tentative assertion are twofold: first, in most areas of the deep sea, including SCB, near-bottom current velocities are not sufficient to remove fecal pellets placed on the sediment surface. Thus, over time the animal would fill its feeding area with feces and this would likely have a negative impact, because, at least in shallow water, there is some evidence that accumulation of feces adjacent to an animal's tube depresses the feeding rate of that animal (Miller and Jumars 1986; C. A. Butman pers. comm.). Shallow-water currents are sufficiently vigorous to remove pellets, thus avoiding this complication. The second reason that deep-sea deposit feeders may not egest material on the sediment surface is that there may be some benefit in sequestering feces from other heterotrophs (Jumars et al. 1990). The easiest way to do this is to place material at some depth within the sediment, because most animals live in the upper few centimeters of sediment. Subsequently the animal can return to reingest this material and the accompanying microbial community that may have flourished in the steep geochemical gradients that surround macrofaunal tubes and burrows (Aller and Aller 1986).

It is also conceivable that the present experiment, although long (997 d) by most standards, was not of sufficient duration for particles to move into the zone where head-down deposit feeders might have been feeding. Thus, the fine particles never were returned to the surface. The rate of bioadvective overturn may be much higher at Whitlatch's site in Panama Basin. Although all of the above arguments are plausible they remain speculative and underscore two important points. First, present knowledge of the natural history of deep-ocean animals is generally lacking. Thus, we are often faced with the unsatisfactory situation of applying information concerning sediment displacement activities derived from shallow-water species to their deep-ocean cousins. Given that the deep ocean is in some ways fundamentally different than any shallow-water site, it is reasonable to expect novel behaviors or at the very least shifts in the importance of various ethologies (Jumars et al. 1990). The second, equally important point is that bioturbation is highly variable in the deep sea. Simple, one-dimensional diffusive models that treat all particles the same will not accurately portray the transport kinetics of deep-sea deposits. Sediments in the deep ocean show both large- and small-scale spatial changes in mixing mode and rate. The next generation of early diagenetic models must strive to incorporate greater biological realism (cf. Smith in press).

Results obtained here can be generalized tentatively to other marine environments. Vertical biodiffusivities are likely to be even more dependent on particle size in deeper abyssal, oligotrophic areas, whereas in shallow-water sediments mixing rates may be independent of particle size. Two observations are offered to support these conjectures. First, the whole premise of size-dependent mixing rests on the assumption that food for deposit feeders is surface associated, and, because finer particles have greater surface areas per unit of sediment volume, more food is associated with them. If there are other sources of food (e.g. plant detritus), then trends in those food sources might influence the degree of size selectivity. Thus, the observed decreases in the amount of terrestrial plant detritus with increasing depth and distance from land suggest that particle size selective pressures may increase in deeper waters. That is, in shallow continental shelf sediments an appreciable amount of food for deposit feeders is not strictly controlled by surface area-to-volume ratios. In such settings, other cues, such as specific gravity or surface texture may dominate over particle size. Secondly, there is reason to believe that the decreasing size of abyssal animals (Jumars et al. 1990) may influence overall selectivity, since, at least for shallow-water species, larger animals seem to exhibit less particle size selectivity (Self and Jumars 1988).

Particle size-dependent mixing has ramifications for the redistribution of various particle-associated radionuclides and their resultant biodiffusivities, although in a more equivocal manner than one might initially assume. Recall that several earlier studies comparing biodiffusion coefficients derived from various sources rationalized differences in observed mixing rates by invoking particle size-dependent mixing. For example, DeMaster and Cochran (1982) argued convincingly that the higher D_b values derived from ^{210}Pb compared to ^{32}Si profiles were due to the association of ^{210}Pb with the clay fraction, whereas ^{32}Si was associated primarily with large, slowly mixed radiolarians. Similarly, recently reported differences in mixing rates derived from ^{210}Pb and ^{230}Th profiles vs. D_b values computed from the penetration rate of planktonic foraminiferans into a recently emplaced turbidite were explained as resulting from greater mixing of the radionuclides associated with the fines relative to the larger Foraminifera (Thomson et al. 1988). Both scenarios are supported by the findings of this study. It is less easy to invoke particle size-dependent mixing to reconcile differences in ^{210}Pb- and ^{239,240}Pu-derived biodiffusivities (Stordal et al. 1985), because these radionuclides are generally associated with the particles of the same size. They do, however, possess different decay periods. It may be that a recently proposed (Smith et al. unpubl.) process, termed age-dependent mixing, has a greater effect on D_b values derived from radionuclides with similar distributions of particle size. Age-dependent mixing postulates that radionuclides with shorter half-lives are associated with labile organic matter for a greater proportion of their lives (Smith et al. unpubl.). Thus, they are more intensively mixed relative to longer lived radiotracers. Clearly, much additional work is needed to assess the prevailing cues for particle selection and hence displacement. This study indicates unequivocally that particle size is an important one.

The implications of particle size-dependent mixing are clearest for studies of deep-sea biostratigraphy and paleoclimatology. From the viewpoint of these disciplines, bioturbation acts as a low-pass filter that blurs and alters the apparent timing and amplitude of recorded oceanographic, biostratigraphic, and climatologic events (Loubere 1989; Wheatcroft 1990). Recently, attention has been devoted to removing the effects of sediment mixing from stratigraphic signals (Berger et al. 1978; Schiffelbein 1985). These unmixing or deconvolution algorithms use estimates of mixing-layer thickness (L_b) and the biodiffusivity (D_b) to parameterize an impulse response function that is in turn used to deconvolve the signal of interest (Schiffelbein 1985). An explicit assumption is that L_b and D_b, and thus the impulse response function, do not vary among sedimentary constituents. The results obtained in this study suggest that such assumptions are not tenable. Mixing rate decreases by at least a factor of four between tracer sizes from $\sim$20 to 200 μm suggesting similar differences in mixing rates of different sized microfossils. There is also the strong possibility, although this study did not address it, that mixing rates and mixing-layer thicknesses of still larger (0.5–2 mm) microfossils are even less. Thus, future attempts at deconvolving the mixing function and modeling the effect bioturbation has on microfossil microhabitats should take into account this added complexity and may even profit from the explicit inclusion of size-dependent bioturbation rates.

In closing, it is important to reiterate the main conceptual point of this paper. Bioturbation can and must be approached from both viewpoints discussed in the introduction (i.e. from species-specific, autecologic studies *and* community-wide studies). Only by using what is known concerning individual styles and rates of sediment reworking to formulate and test hypotheses regarding various aspects of bioturbation as represented by community-wide measures of mixing (e.g. biodiffusivities) will a better understanding of sediment mixing evolve.

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