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A mechanistic view of the particulate biodiffusion coefficient: Step lengths, rest periods and transport directions

by R. A. Wheatcroft[1], P. A. Jumars[1], C. R. Smith[2] and A. R. M. Nowell[1]

ABSTRACT

We link specific mechanisms of biogenous sediment mixing with the commonly used bioturbation coefficient (D_b) that describes their bulk effects. Using an isotropic, stationary, unbiased random walk model we mechanistically decompose the particulate bioturbation coefficient into the fundamental dimensions of length and time. The result shows that D_b depends directly on the square of the distance particles are moved (step length) and inversely on the elapsed time between movements (rest period). This new decomposition in terms of explicit mechanisms (i.e., animal activities), leads to scaling arguments that large, deposit feeding animals will in nearly all cases dominate biogenous mixing. Paradoxically, such animals often transport particles vertically in an advective fashion (e.g., conveyor-belt feeding), making the widespread fit of the diffusion equation to tracer profiles equivocal. Finite-difference simulations reveal that even in the complete absence of vertical diffusion, rapid diffusive horizontal mixing coupled with vertical advection can produce vertical profiles characteristic of diffusion. We suggest that near-surface horizontal mixing rates by animals far exceed vertical mixing rates in the same stratum and that this anisotropy may persist throughout the surface mixed layer. Thus, despite their apparently good kinematic fit, one-dimensional biodiffusion coefficients may not accurately describe the dynamics of sediment displacement, leading to errors in models of early diagenesis.

1. Introduction

Displacement of sediment grains by organisms (bioturbation) has major sedimentological and geochemical ramifications. The preservation of physical sedimentary structures is strongly influenced by sediment mixing rates (Moore and Scruton, 1957; Rhoads, 1974; Nittrouer and Sternberg, 1981). In addition, rates of organic matter degradation, the dissolution of various biogenic components ($CaCO_3$ and SiO_2) and pore-water concentration profiles of nearly all dissolved chemical species are materially affected by the intensity of bioturbation (Schink and Guinasso, 1977; Berner, 1980; Aller, 1982; Emerson, 1985; Rice and Rhoads, 1989). The rate of sediment mixing further influences microbial activity within the sediment (Yingst and Rhoads, 1980). When one considers the potentially important, yet little explored, feedbacks between

1. School of Oceanography WB-10, University of Washington, Seattle, Washington, 98195, U.S.A.
2. School of Ocean, Earth and Technology, University of Hawaii, Honolulu, Hawaii, 96822, U.S.A.

chemistry and biology, especially microbiology, the central role of the rate and mode of sediment mixing in early diagenesis immediately becomes apparent.

Bioturbation typically has been modeled quantitatively as a one-dimensional, (vertically) diffusive process. A coefficient is estimated by fitting regression lines to the down-core distribution of either impulsive or continuous tracers (Guinasso and Schink, 1975; Nozaki *et al.*, 1977). This coefficient is taken to be analogous to a standard Fickian diffusivity and is known as the biodiffusion coefficient or biodiffusivity (D_b). All of the myriad animal activities affecting the sediment (e.g., feeding, burrowing, tube building) are represented by D_b. Depicting all animal activities by a single coefficient, however, has shifted focus away from specific mechanisms of sediment mixing. Instead, much effort has been devoted to correlating the magnitude of D_b with other presumably important parameters (e.g., sediment accumulation rate or organic carbon flux, Cochran, 1985 and animal biomass, Matisoff, 1982). For several reasons, little predictive understanding of bioturbation has been gained.

First, D_b is an integrative measure of sediment mixing rate on temporal and spatial scales that are, in part, tracer dependent (Stordal *et al.*, 1985; Thomson *et al.*, 1988). The ancillary data with which D_b has been correlated are also time and space dependent, but it is not always apparent that there is a proper match between scales. Secondly, by definition bioturbation must focus on animals. Because diffusion coefficients are bulk measures of mixing that integrate all animal activities, however, it is difficult to link causes of variation in the mixing rate with specific forcings. Moreover, without a means to relate explicitly specific mechanisms of sediment mixing to the biodiffusion coefficient, the purely correlative approach runs the risk of confusing correlation with causation or of missing correlations obscured by interactions.

The need to better understand mechanisms of bioturbation has recently been made elegantly apparent in a series of papers by Boudreau (1986a, b; Boudreau and Imboden, 1987). His simulations showed that drastically different styles of sediment mixing (e.g., diffusive versus advective) can, given sufficient time, produce similar tracer profiles. This convergence does not mean that these mixing styles are functionally equivalent geochemically, however, because the reaction kinetics of many chemical species are markedly affected by the type of sediment mixing. Hence there is demonstrable need for a method that explicitly relates animal activities with their mixing consequences.

With this aim in mind, in this paper we decompose D_b into its constituents of step lengths and rest periods. After doing so, we briefly review animal activities that mix sediments and evaluate their likely relative importances based on extant data. We also take a critical look at the suitability of the diffusion analogy toward sediment mixing and conclude that in many cases a one-dimensional, vertical diffusion model may poorly describe biogenous mass transfer mechanisms. Yet, down-core profiles of most radiotracers (even short-lived ones) appear diffusive. Thus, a consequent purpose of ours is to suggest ways to reconcile this contradiction.

2. Decomposition of the biodiffusion coefficient

Diffusion coefficients were first proposed in the mid-1800's (Fick, 1855; Maxwell, 1860; Rayleigh, 1880), when scientists recognized that the integrated effects of the motion of individual "atoms" and "molecules" (these words are used in the 19th century sense) could be expressed in terms of the discrete variables of a length multiplied by a velocity. The appropriate length scale was postulated to be the average distance an atom moved before colliding with another and the speed was taken as the mean between collisions (Smoluchkowski, 1916; Einstein, 1926). The law of large numbers (ca. 10^9 collisions s^{-1}) and certain simplifications (e.g., neglecting changes in angular momentum and multi-atom collisions) permit this microscopic picture of molecular diffusion in terms of mean-free-paths and root-mean-square velocities (Jost, 1964; Cussler, 1984).

At about the same time as Fick's, Maxwell's and Lord Rayleigh's papers, a microscopic view of continuous processes (turbulence) was formulated by Boussinesq (1877). He proposed that a coefficient analogous to a viscosity could be used to relate the mean velocity gradient to the stress. The "eddy viscosity" was a function of the degree of turbulence in the fluid and its location in the flow. This early view of fluid mixing was expanded upon many years later by Taylor (1921), who demonstrated that the diffusion of a passive scalar in a fluid could be described by an "eddy-diffusion" coefficient analogous to the molecular diffusivity. Since then, many ways to decompose eddy diffusivities have been proposed, based mainly on higher-order characteristics of the mean flow (Launder and Spalding, 1972). The simplest and arguably most useful view of the eddy-diffusion coefficient, however, retains a kinetic-theory picture of diffusion in terms of a length scale times a velocity. This view of turbulence was introduced by Prandtl (1925) and is known as the mixing-length theory. In this view of eddy diffusivity, the velocity and length scales are coupled uniquely, reducing the number of unknowns to one. This reduction is accomplished by recognizing that the fluctuating velocity is proportional to the distance a parcel of fluid is moved, times the mean velocity gradient. Since the majority of the momentum is transported by the largest eddies, whose length scale is set by the maximal gradient of velocity, the boundary layer thickness is typically used as the length scale in estimating the eddy diffusivity.

It is the eddy-diffusive picture of mixing that historically has served as the analogy for bioturbation (Goldberg and Koide, 1962). Guinasso and Schink (1975) in their seminal paper expanded on the diffusion analogy and provided the first explicit decomposition of the biodiffusion coefficient. They followed the velocity-length scale approach, and provided a means to estimate these variables from biological data. They recognized that the parameter "population-level reworking rate" ($cm^3 \ m^{-2} \ yr^{-1}$) measured by benthic ecologists (e.g., Rhoads, 1963; 1967) could be simplified to have units of a velocity. The characteristic length scale of particle movement was, by analogy with Prandtl's mixing-length theory, taken to be the depth of the surface

mixed layer (L_b) ($=$ boundary layer thickness). Thus,

$$D_b = L_b V_c, \qquad (1)$$

where V_c is the population-level reworking rate (Guinasso and Schink, 1975).

For several reasons this approach breaks down when applied to bioturbation. First, in sediment mixing the velocity and characteristic length-scale are not coupled via any extant theory. This decomposition also implies that in sediment with a constant reworking rate (V_c) an increase in the thickness of sediment being reworked (L_b) results in a greater biodiffusivity. Clearly this conclusion is in error because the reworking rate, which provides the "power" for mixing, has not changed. Furthermore, although V_c has the correct dimensions of a velocity, it is inappropriate to divide the volume of sediment reworked by a unit of area to obtain the length scale of the velocity because the choice of the area and hence the directionality of the resultant length scale is completely arbitrary. Extracting a velocity from the discharge (volume area^{-1} time^{-1}) of a pipe is appropriate, by contrast, because the coordinate system is uniquely determined. In sediment mixing it is not.

Recently, Boudreau (1986a) has derived a form of the diffusion equation that contains a biodiffusivity made up of the fluctuating component of the local advective velocity times the "typical distance particles are moved." This decomposition reflects the kinetic-theory picture of diffusion. Although dimensionally correct, the problem with applying this formulation to sediment mixing is that sediment particles spend most of the time sitting still. Gas molecules and fluid parcels are in constant motion; thus a velocity has ready meaning and is easily measured. In sediment mixing, mean particle velocities must be derived from very short periods of movement coupled with long periods of rest. Hence the mean particle velocity describes few particles at any given time.

A phenomenological review of sediment mixing aids in the selection of a useful decomposition. First, bioturbation is a discrete process. Particles are moved finite distances in specific directions. They then spend some length of time sitting still, after which they are again moved some distance, probably, but not always, in a different direction from the previous movement. Thus, from a mechanistic standpoint, if we knew the distance and direction particles were moved and the period of time between those movements we could accurately describe sediment mixing. Random walk models explicitly use these variables and can be extended in a continuum limit to produce the diffusion equation (Chandrasekhar, 1943; Feller, 1968; Berg, 1983; Ghez, 1988). We will initially focus on the simplest approach, a one-dimensional, isotropic random walk, and then generalize it.

Following Ghez (1988), envision points on a line separated by a distance, δ (Fig. 1a). Assign to each labeled point (site) a number of particles, N (i.e., N_k is the number of particles at site k). Particles can jump to adjacent sites with a frequency, Γ, that is independent of the site location. We further assume that the walk is homogeneous,
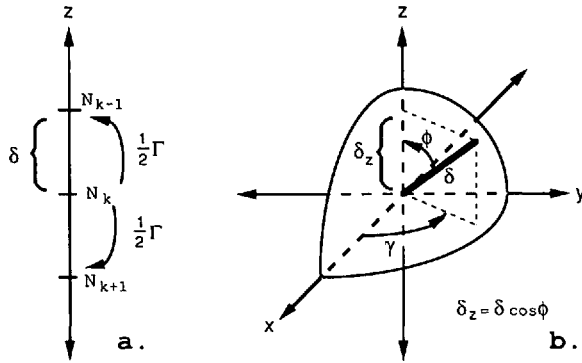
Figure 1. Coordinate axes for random walks. (a) Isotropic, one-dimensional case. A given number of particles, N_k, are located at sites k, separated by a unit step length, δ. Particles have a transition frequency, $\frac{1}{2}\Gamma$, of carrying out a specific jump. (Modified from Ghez, 1988.) (b) Three-dimensional, nonlattice case restricted to the positive octant of a sphere. Particles now step a unit length, δ, in a random direction from the origin. The mean vertical step length, $\langle \delta_z \rangle$, is the average of the function, $\delta \cos \phi$, weighted by an element of area (see text for details).

stationary and isotropic (i.e., Γ and δ are spatially and temporally invariant, and the probability of moving one step in either direction is identical and equal to $\frac{1}{2}$). To arrive at the time rate of change of particle numbers about the kth site, we compute all of the possible transitions to and from that site:

$$\frac{dN_k}{dt} = -\frac{1}{2}\Gamma(N_k) + \frac{1}{2}\Gamma(N_{k-1}) + \frac{1}{2}\Gamma(N_{k+1}) - \frac{1}{2}\Gamma(N_k). \qquad (2)$$

Rearranging, we arrive at a rate equation in terms of the particle distribution

$$\frac{dN_k}{dt} = \frac{1}{2}\Gamma(N_{k-1} + N_{k+1} - 2N_k). \qquad (3)$$

This linear difference-differential equation (similar to the centered-difference form of the numerical solution of the diffusion equation) describes the discrete distribution of particles at site k.

To find the local continuum analog to Eq. 3 two requirements must be met. First, the sites must be points on a real line. We will further assume, although it is not necessary, that these points are separated by a constant distance; this distance is the step length, δ. Secondly, an arbitrary function $\tilde{N}(z, t)$, that is continuous and differentiable must be introduced that interpolates the previous function $N_k(t)$ at sites $z = z_k$. Omitting the time variable, and expanding the interpolating function in a Taylor series around z_k, we obtain

$$\tilde{N}(z_{k\pm1}) = \tilde{N}(z_k) \pm \delta \frac{\partial \tilde{N}}{\partial z} + \frac{1}{2}\delta^2 \frac{\partial^2 \tilde{N}}{\partial z^2} + O(\delta^3), \qquad (4)$$

where the "O" has the meaning "terms of order ... and above". Because $\tilde{N}(z_k, t) = N_k(t)$, Eq. 4 becomes

$$N_{k+1} = N_k + \delta \frac{\partial N}{\partial z} + \frac{1}{2} \delta^2 \frac{\partial^2 N}{\partial z^2} + O(\delta^3) \tag{5a}$$

and

$$N_{k-1} = N_k - \delta \frac{\partial N}{\partial z} + \frac{1}{2} \delta^2 \frac{\partial^2 N}{\partial z^2} - O(\delta^3), \tag{5b}$$

where both sides of the expansion have been written out. Introducing Eqs. 5 into Eq. 3 and simplifying yields

$$\frac{\partial N}{\partial t} = \frac{1}{2} \Gamma \delta^2 \frac{\partial^2 N}{\partial z^2} + O(\delta^4). \tag{6}$$

If we introduce the traditional definition (Ghez, 1988):

$$D \equiv \frac{1}{2} \Gamma \delta^2, \tag{7}$$

neglect terms equal to or greater than 4th order, and state that the average concentration of particles per cell is, $C = N/\delta$, then Eq. 6 becomes

$$\frac{\partial C}{\partial t} = D \frac{\partial^2 C}{\partial z^2}. \tag{8}$$

This equation (Fick's second law), with additional terms to take into account sedimentation and chemical reactions, which are assumed to be more important than 4th order, is the basis for describing tracer concentration profiles in sediments and hence sediment mixing (Goldberg and Koide, 1962).

One-dimensional, isotropic diffusivity then, may be viewed as one-half of a squared step length times the frequency of steps (Eq. 7) or as

$$D = \delta^2/2\Omega, \tag{9}$$

where Ω is the amount of time between steps or "rest period" ($\Omega = \Gamma^{-1}$). Thus, the magnitude of a diffusivity depends on how far, on average, a particle moves, and on the period of time between movements. This relationship, known as the Einstein-Smoluchkowski relation, is the central connection between the microscopic details of particle motions and the bulk, macroscopic parameters relating to diffusion. It makes explicit what parameters influence the intensity of mass transfer due to diffusion and suggests why D_b might vary. In addition, it clarifies some of the potential limitations of the one-dimensional, isotropic diffusion analogy of sediment mixing.

a. Spatial and temporal variation. For a constant D_b to represent accurately the intensity of sediment mixing at a given site the step length and rest period must be spatially and temporally invariant over the scales of interest. In sediment mixing such invariance is not always the case. Mean step length may vary considerably on scales approaching the size of cores, ranging from several meters in the case of deep-burrowing thalassinid shrimp (Pemberton *et al.*, 1976) to fractions of particle diameters for near-surface meiofauna "shouldering aside" sediment grains (Cullen, 1973). Similarly, not all particles within the sediment are moved with equal frequency. Some near-surface particles may be in nearly constant motion, while others, especially at depth, may never move and simply transit the surface mixed layer at a speed equal to the sediment accumulation rate. This inhomogeneity of step length and rest interval means that either (1) the mixing is inherently nonlocal (Boudreau, 1986b) and the use of biodiffusivity to model mixing is inappropriate, or (2) a spatially varying biodiffusion coefficient is required. In the latter case, Eq. 8 takes the form

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial z}\left[D_b \frac{\partial C}{\partial z}\right]. \tag{10}$$

Previous authors have recognized the likelihood that D_b might vary spatially (Guinasso and Schink, 1975; Jumars, 1978), and a variety of models have been proposed in which D_b decreases as a function of depth in the sediment (Schink and Guinasso, 1977; Olsen *et al.*, 1981; Christensen, 1982; Kadko and Heath, 1984; Li *et al.*, 1985). The fit of these models, however, to the observed tracer profiles often is not significantly better than a simulation with a D_b independent of depth (Boudreau, 1986a; Robbins, 1986). It could be that mixing intensity remains essentially constant in the vertical, because both the rest period and step length increase with depth, the former due to decreasing animal abundance with sediment depth (Jumars, 1978; Hines and Comtois, 1985), the latter to increasing animal size with depth (e.g., Esselink and Zwarts, 1989).

Similarly, changes in the abundance or size structure of a benthic community over time could affect the estimated biodiffusivity. If changes in local community structure occur on time scales that are similar to the decay period [half-life/0.693 (Boudreau, 1986a)] of a given radioisotope, the system is nonstationary (unsteady), and measured D_b's could be in considerable error. Changes occurring over much shorter or longer time intervals than the decay period are either averaged into or do not materially affect the computed biodiffusivity. A particularly problematic time interval is the seasonal to annual one, since it is close to the decay period of two commonly used radiotracers, ^{234}Th and ^{7}Be. In shallow water, seasonal variations in animal abundance and size, in response to yearly reproductive cycles, could yield significant variations in the step length (as mean animal size increases) and rest period (as more animals recruit), resulting in a variable D_b. There is evidence for seasonal variation in carbon flux to the deep sea (Billett *et al.*, 1983) and in the ability of certain animals (Foraminifera, Gooday, 1988; Sipunculida, Graf, 1989) to respond to this food pulse. Thus, it would

not be too surprising to find temporal variation in deep-sea biodiffusivities as well; even though the one study (DeMaster *et al.*, 1985) that has addressed temporal variation has not found it.

b. Multidimensional mixing. A more troublesome aspect in relating biological activities to sediment mixing models is that animals move particles in all three dimensions. The diffusion equation (Eq. 8) is easily extended to take this multidimensionality into account, becoming

$$\frac{\partial C}{\partial t} = D \nabla^2 C, \tag{11}$$

where ∇^2 is the three-dimensional Laplacian operator, $\partial^2/\partial x^2 + \partial^2/\partial y^2 + \partial^2/\partial z^2$ and D is spatially invariant. Because geochemical gradients are thought to be steepest in the vertical and depth in the sediment is associated with time, models of early diagenesis are typically one dimensional (vertical) (Berner, 1980). Moreover, without manipulations it is possible to estimate only *vertical* biodiffusion coefficients since the input of particle-adsorbed radionuclides or other natural tracers (microtektites or volcanic ash) is thought to be horizontally quasi-uniform. This fact does not imply absence of lateral mixing, but only that deliberate experiments must be performed to address its importance.

Our decomposition of D_b, presented above, is also based on a one-dimensional model. In order to use biological data to estimate population-level biodiffusivities from Eq. 9 (discussed below), a correction factor must be introduced that resolves the distance particles are moved in the z-direction. We proceed by assuming that animals move particles isotropically. Steps are still of unit length, but now they can project in any direction from a given site. For the sake of simplicity we restrict our analysis to the positive octant of a sphere (Fig. 1b), and ask what is the average z-component, $\langle \delta_z \rangle$, of an infinite number of rays of unit length (δ) projected from the origin? This problem can be considered a question of coordinate transformations, whereby in passing from Cartesian to spherical coordinates, $\delta_z = \delta \cos \phi$. Before averaging, this function must be weighted by an element of area ($dA = \delta\, d\phi\, \delta \sin \phi\, d\gamma$) that takes into account "latitudinal" variations in the surface area of a sphere. Thus, the function becomes

$$\langle \delta_z \rangle = \frac{2}{\pi} \int_0^{\pi/2} \cos \phi \sin \phi\, d\phi\, d\gamma, \tag{12}$$

which yields $\langle \delta_z \rangle = 0.5\delta$. The result is the same for the average x and y displacements since the system is isotropic. Eq. 9 now becomes, for movement in the vertical direction, $D_b(z) = \langle \delta_z \rangle^2/2\Omega$.

c. Anisotropic mixing. There are strong reasons (given below) that the assumption of isotropy is wrong, and that horizontal mixing coefficients might be much greater than

vertical D_b's at a given site. Whereas for isotropic diffusion, D_b is a scalar quantity, for anisotropic mixing the diffusion coefficient becomes a second-order tensor (having nine components), and Eq. 11 is expanded to (Jost, 1960; Crank, 1975):

$$\frac{\partial C}{\partial t} = D_{xx} \frac{\partial^2 C}{\partial x^2} + D_{xy} \frac{\partial^2 C}{\partial x \partial y} + D_{xz} \frac{\partial^2 C}{\partial x \partial z}$$

$$+ D_{yx} \frac{\partial^2 C}{\partial y \partial x} + D_{yy} \frac{\partial^2 C}{\partial y^2} + D_{yz} \frac{\partial^2 C}{\partial y \partial z} \tag{13}$$

$$+ D_{zx} \frac{\partial^2 C}{\partial z \partial x} + D_{zy} \frac{\partial^2 C}{\partial z \partial y} + D_{zz} \frac{\partial^2 C}{\partial z^2}$$

assuming the diffusivities remain spatially constant. The off-diagonal (interaction) terms represent the rate of mass transfer in one direction due to the component of the concentration gradient in another direction. By assuming that variables are horizontally uniform, which in the absence of persistent unidirectional water currents seems warranted, and recalling the mixed derivative theorem, Eq. 13 can be simplified to the two-dimensional case

$$\frac{\partial C}{\partial t} = D_{xx} \frac{\partial^2 C}{\partial x^2} + (D_{zx} + D_{xz}) \frac{\partial^2 C}{\partial x \partial z} + D_{zz} \frac{\partial^2 C}{\partial z^2}. \tag{14}$$

Further treatment of anisotropy in studies of Fickian diffusion (Jost, 1960; Crank, 1975), heat transfer (Carslaw and Jaeger, 1959), and turbulent mixing (Fischer *et al.*, 1979) proceeds by recognizing that the diffusivity tensor is symmetric. Symmetric tensors have the unique property that a transformation can be made so that the coordinate axes coincide with the principal axes of diffusion, thus reducing the contribution of the interaction terms to zero (Jost, 1960; Aris, 1962; Corrsin, 1974; Crank, 1975). This transformation reduces Eq. 14 to the two-dimensional diffusion equation

$$\frac{\partial C}{\partial t} = D_{xx} \frac{\partial^2 C}{\partial x^2} + D_{zz} \frac{\partial^2 C}{\partial z^2}, \tag{15}$$

where $D_{xx} \neq D_{zz}$. Previous models of bioturbation (e.g., Guinasso and Schink, 1975; Berner, 1980; and many others) assume that there is only a mean gradient of natural tracers (e.g., radionuclides or ash particles) in the vertical direction ($\partial C/\partial x = 0$). Therefore, the first term in Eq. 15 is also disregarded, since diffusion is strictly a gradient operator (i.e., no gradient, no diffusion).

Neglecting horizontal mixing may no longer be possible, however, since recent studies (e.g., Smith and Schafer, 1984) have demonstrated that horizontal gradients of radionuclides (^{210}Pb) can be as great as vertical ones. This finding is not surprising,

considering the biogenic roughness of the sediment-water interface, and the sensitivity of particle deposition and hence radioisotope activity to such surface roughness (Levin *et al.*, 1986). Small-scale variability in tracer penetration rates, due to variation in animal abundance (Jumars, 1978), insures that such lateral heterogeneity persists down into the sediment (Smith and Schafer, 1984). Thus, the distribution of particle-adsorbed radioisotopes is more akin to that found for various solutes (Aller, 1982), and thus the effects of horizontal mass transfer can no longer be neglected.

Finally, although the transformation that allows one to disregard the interaction terms is mathematically correct, it is not sufficient for the conclusion that, at least in sediment mixing, those terms do not exist. We cannot assume *a priori* that a biodiffusion tensor would be symmetric. There are no published data that would allow one to evaluate whether the interaction terms exist or judge the importance of the horizontal diffusivity in Eq. 15, so we will explore these issues below.

d. Correlated motion. The canonical form of the random walk model and its continuum limit, the diffusion equation, also require that particles move independently; i.e., that there is no correlation between steps. In sediment mixing, however, during short time periods a particle has a tendency to behave as it did in the period immediately before, and adjacent sediment grains are more likely to be moved in the same directions and over the same distances than widely separated particles. Thus, on small temporal and spatial scales particle motions are partially correlated. Correlated continuous motion has been treated at length in classical turbulence studies, where the Lagrangian autocorrelation function is used to set the length and time scales over which motions of water parcels are alike (Taylor, 1921). Similarly, Goldstein (1951) has derived a temporally correlated random walk model that converges, in its continuum limit, to the so-called telegraph equation [see Boudreau (1989) for a detailed discussion of this equation within the context of bioturbation]. Systems displaying correlated movement can be approximated, however, by the much simpler diffusion equation if the length and time scales over which particle movements are correlated is small relative to the length and time scales of observation (Taylor, 1921; Barber and Ninham, 1970; Corrsin, 1974; Okubo, 1980).

In sediment mixing, rough estimates of the former can be obtained by considering the maximal volume of sediment moved *en masse* to be the gut volume of the largest deposit feeder that moves particles diffusively, which is of order 1 cm^3 for deep-sea animals. This volume is likely an overestimate, since most deposit feeders do not fill their guts in one "bite" (Penry, 1988). The time period over which particle movements are correlated can be approximated by the rest period, Ω. Lacking reliable data on this parameter, especially from the deep sea, we can provide estimates of it by knowing D_b and using a range of mean step lengths from a given site [see Boudreau (1989) for a similar argument]. For example, if we use published values of D_b measured in the deep sea (0.01 to 100 $cm^2 yr^{-1}$), and select a mean step length of 0.5 cm, then rest periods
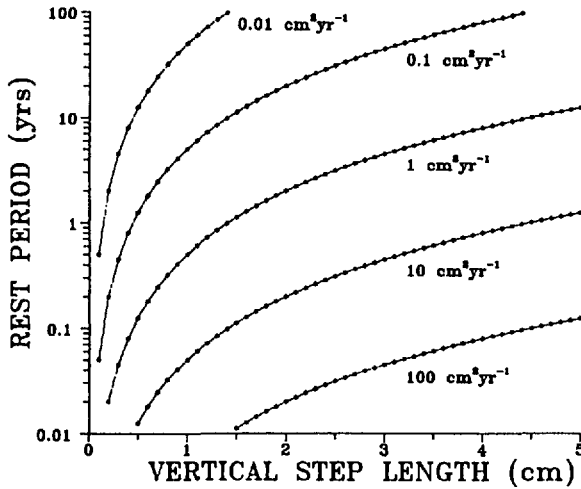
Figure 2. Particle rest period plotted as a function of vertical step length (δ_z) over the range of biodiffusivities typically measured in the ocean.

from 0.5 d to > 10 yr are obtained (Fig. 2). A larger mean step length will result in longer rest periods for the same mixing coefficient.

Characteristic length and time scales of observation are constrained by the volume of sediment needed to make radioisotopic measurements (> 10 cm^3) and the minimal radiotracer half-life (24 d for ^{234}Th). Thus, at most sites, because of the coarse resolution of sediment samples, the spatial constraint is not a difficulty, although especially small samples could be sensitive to the most recent deposit-feeding activities. The time constraint is more problematic. Using short-lived radioisotopes (^{7}Be or ^{234}Th) to estimate mixing rates in slowly stirred sediments may be inappropriate. [See Boudreau (1986a; 1989) for a different approach that reaches a similar conclusion.]

3. Animal activities that mix sediment

As with many new models, extant data are not entirely adequate to test our approach. Information pertaining to rest periods (Ω), step lengths (δ) and particle transport directions are mainly anecdotal and in the case of the latter two parameters often missing. Moreover, those data that do exist are highly biased toward large-bodied animals living in mid-latitude, intertidal or shallow-subtidal, sandy environments. There are virtually no data available concerning sediment reworking modes in the deep sea, yet most studies that have estimated D_b are from those depths. We hesitate to apply what is known about animal activities in shallow water directly to deep-sea taxa without cautioning the reader that the unique environment of the deep sea may elicit undocumented behaviors (Jumars *et al.*, 1990). As our knowledge of biogenous sediment mixing activities in both shallow and deep water increases, however, it will be possible to use the decomposition presented herein to reassess the relative importance

of various animal activities. As a first approximation, we show how to extract the relevant information and then review important sediment mixing activities within the context of step lengths, transport directions and rest periods.

Biological interest in sediment mixing derives either from the standpoint of sediment disruption as a disturbance mechanism (e.g., Brenchley, 1981; Thayer, 1983; C. R. Smith *et al.*, 1986) or as a surrogate measure of deposit-feeding rate (e.g., Cammen, 1980). Much research has focused on measuring, usually in the laboratory, on an individual animal basis, mass or volume of sediment moved per unit of time. This metric is labeled "individual reworking rate" (Rhoads, 1963; 1967; Myers, 1977; Grant, 1983; Thayer, 1983). Population-level reworking rates are obtained by multiplying individual rates by animal densities in the field. This approach may introduce some unknown amount of error, however, because individual reworking rate may not be independent of animal density (see Miller and Jumars, 1986) and the laboratory measurements are not always made under realistic field densities. Nonetheless, the approach is useful for some aspects of benthic ecology. A volumetric reworking rate is not particularly valuable from the standpoint of the diffusion analogy of sediment mixing, however, because it lacks an appropriate length scale.

The population-level reworking rate can be more usefully expressed as, in the present context, the rest period, Ω. This quantity is obtained by dividing the population-level reworking rate $[L^3 L^{-2} T^{-1}]$ into the volume of potentially handled sediment per unit of seafloor area $[L^3 L^{-2}]$. To do so it is necessary to estimate the depth of sediment over which an animal contacts particles during a given activity. Although there are few dependable data on this subject, rough estimates may be obtained by using the maximal sediment depth at which a specific animal occurs.

To obtain estimates of population-level biodiffusivities for a given animal activity, it is also necessary to select an appropriate step length. For one-dimensional mixing models only the component of movement in the selected dimension is of interest. For multidimensional models, when isotropy is not a valid assumption, transport direction must also be specified. If the animal activity moves particles isotropically (not often the case), then the correction factor derived in Section 2b must be used to obtain estimates of a step length appropriate to a one-dimensional mixing coefficient. As will become evident shortly, there are few reliable data concerning step lengths and transport directions. Thus, in most cases it is not possible to calculate population-level biodiffusivities from the extant literature. Those contained in Table 1 should be looked upon only as examples of what will be possible when more data become available concerning modes and rates of sediment mixing. Furthermore, caution is required when step lengths are greater than ~2 cm since the mixing may no longer be diffusive, but instead be nonlocal (Boudreau, 1986b).

a. Deposit feeding. The bulk ingestion and subsequent egestion of particles from within or upon the sediment—subsurface or surface deposit feeding—is in nearly all

Table 1. Population-level reworking rates and estimated biodiffusivities due to various forms of deposit feeding and locomotion (crawling or burrowing) in both the horizontal (x) and vertical (z) directions. Entries enclosed in parentheses were estimated based on all available information.

Taxon	Pop. Rwk Rate $cm^3m^{-2}d^{-1}$	Rwk. Depth cm	Rest Period d	Step Length x cm	Step Length z cm	Pop. D_b x cm^2	Pop. D_b z $cm^2 yr^{-1}$	Reference
Deposit Feeding								
Euzonus mucronata	1.4×10^5	(15)	1.1	1.2	1.2	240*	240	Kemp (1987)
Oreaster reticulatus	112	0.3	27	(3)	0	61	0	Scheibling (1982)
Pectinaria californiensis	34	5	1500	(3)**	5	(1)	3	Nichols (1974)
Locomotion								
Armandia sp.	(1×10^5)	1	0.1	0.025	0.025	0.2	0.2	Tamaki (1985)
Paraphoxus spinosus	(3200)	2	6	0.1	0.1	0.5	0.5	Myers (1977)
Memoma ventricosa	2000	6	30	(4)	(0.5)	97	1***	Chesher (1969)
Bathybembix bairdii	52#	0.5	96	(1)	(0.25)	2	0.1	This study

*Probably an overestimate, since the population-level reworking rate is based on an abnormally fast gut clearance time of 3 min.
**Information on animal orientation is from Gordon (1966).
***Supplemented by information from Hammond (1982).
#Crawling rate data from Wheatcroft et al. (1989), population density data from Smith and Hamilton (1983).

cases the dominant particle mixing activity (Aller, 1982; Thayer, 1983). Several factors contribute to the validity of this generalization. First, in nearly all muddy-bottom environments, deposit feeders are the most abundant macrofaunal group (Sanders, 1960), especially in the deep sea, where up to 80% or more of the macrofauna make their living by ingesting sediments (Jumars and Gallagher, 1982). Deposit feeders depend on some as yet unknown combination of particle-surface associated microbes, nonliving organic matter and meiofauna to support them. Metabolizable material typically makes up much less than 5% by volume of the sediment ingested (Lopez and Levinton, 1987). Deposit feeders cope with these low levels of organic matter by processing extremely large volumes of sediment per unit of time. Most ingest

several times their body weight per day (Table 1 in Lopez and Levinton, 1987), resulting in short rest periods relative to other mixing mechanisms.

Not only does deposit feeding yield high individual processing rates, but ingested sediment is often moved a long way. Little is gained metabolically by ingesting recently egested sediment, so deposit feeders morphologically or behaviorally separate sites of food collection and egestion. Particles moved during deposit feeding often are transported at least the length of the animal, resulting in relatively large step lengths (Table 1). Displacement lengths may be even greater if the animal is a tentaculate surface deposit feeder or moves while feeding (Kemp, 1987).

A complicating aspect of deposit feeding is the phenomenon of particle selectivity, leading to particle-dependent rest periods and step lengths. Many deposit feeders cope with the low organic content of sediments by actively or passively selecting a certain class of particles. Because food is generally particle-surface associated, many deposit feeders enhance the surface area-to-volume ratio of ingested sediment by selecting the fine fraction (Taghon *et al.*, 1978; Mahaut and Graf, 1987; Wheatcroft and Jumars, 1987; Self and Jumars, 1988). Others may select larger grains (Whitlatch, 1974) when these grains contain the majority of utilizable food. One might think that selective deposit feeders will have lower feeding rates and thus longer rest periods than nonselective deposit feeders, but selective feeders still handle large volumes of particles. Particles that are handled in the course of feeding, but not ingested are called "pseudofeces." Current estimates are that greater than 80% of the particles handled by some deposit feeders are rejected as pseudofeces (Nichols, 1974; Bender and Davis, 1984; and others). Particle selection may occur at the point where the feeding appendage (e.g., tentacle or siphon) contacts particles (Jumars *et al.*, 1982), in which case step lengths are small and there is little mixing, or it may occur at the mouth (Miller, 1984), yielding significant step lengths.

There are numerous specific styles of deposit feeding (Fig. 3a-f), some of which are likely to be quantitatively more important in determining vertical biodiffusivities than others, mainly because of the direction in which sediment is moved. Some animals displace large volumes of sediment per unit of time without materially affecting the vertical mixing rate by restricting their activities to a single depth stratum (Fig. 3a, c). For example, the relatively high population-level biodiffusivity calculated for the surface deposit feeding asteroid *Oreaster reticulatus* (Table 1) only affects the upper 0.3 cm of sediment, and particles are moved predominantly in the horizontal. Similarly, tentaculate surface deposit-feeding polychaetes move particles long distances in the horizontal, but very little in the vertical (Fig. 3c), since shallow-water species generally defecate on the surface. Thus, these deposit feeders contribute little to vertical biodiffusivities, but their activities could yield high horizontal mixing rates.

There are other deposit feeders, however, that feed at one depth in the sediment and defecate at another (Fig. 3d–f), potentially effecting high vertical mass transport rates. The majority of these animals (i.e., of the observed shallow-water "representatives"),
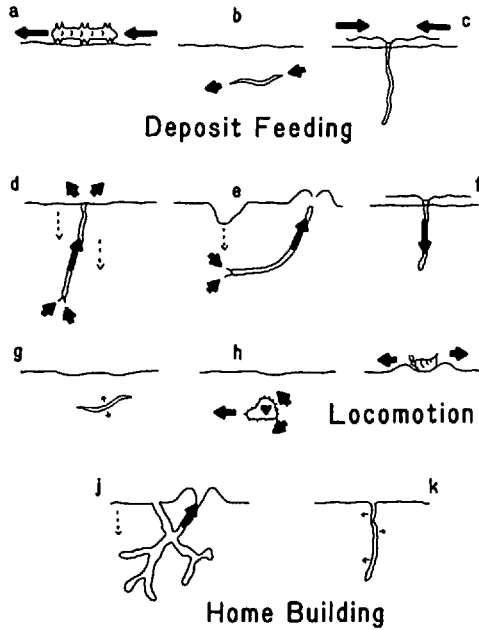
Figure 3. Schematic cartoons of the dominant sediment mixing activities discussed in the text. (a) Mobile surface deposit feeder (e.g., some holothuroids and gastropods). (b) Mobile subsurface deposit feeder (e.g., some polychaetes and echinoids). (c) Sessile, surface deposit feeder (e.g., some polychaetes and echiurans). (d) Conveyor-belt or head-down deposit feeder (e.g., maldanid polychaetes and some holothuroids). (e) Funnel-feeding deposit feeder (e.g., arenicolid polychaetes, some holothuroids and enteropneusts). (f) "Reverse conveyor-belt" deposit feeder, an animal that feeds at the surface and defecates at some depth in the sediment (e.g., the polychaete genus *Polycirrus* and some sipunculans). (g) Radial, subsurface burrower (e.g., many polychaetes). (h) Axial burrower that moves by transporting sediment along the axis of its body (e.g., heart urchins and many crustaceans). (i) Surface crawler (e.g., gastropods, many echinoderms, and crustaceans). (j) Burrow excavator (e.g., decapod crustaceans and many other taxa). (k) Tube builder (many taxa). Arrows denote transport direction and relative magnitude.

known as conveyor-belt or funnel feeders (Fig. 3d–e), move sediment from some depth within the sediment and deposit it on the surface (e.g., arenicolid or maldanid polychaetes). This type of feeding results in a series of convective loops since sediment from above presumably caves in to fill the newly created feeding voids. It seems safe to assume that this caving in results in mass balance over the rest period. Other animals [e.g. the polychaetes *Tharyx acutus* and members of the genus *Polycirrus* (Myers, 1977; Rice, 1986) and some sipunculans (J. N. Smith *et al.*, 1986; Graf, 1989)], feed at the surface and egest feces at depth (Fig. 3f). Although these latter animals are much less common, at least in shallow water, because they transport radioisotopically "hot" sediment from the surface to some depth they could influence the measured isotope profiles far in excess of their actual contribution to mass transfer. Of all deposit-feeding
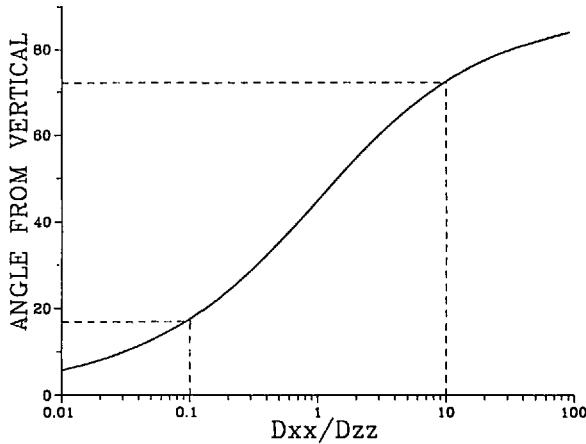
Figure 4. The ratio of horizontal to vertical biodiffusivities (D_{xx}/D_{zz}) as a function of the direction sediment is moved. Note that for angles from approximately 20 to 70 degrees from the vertical the difference between biodiffusivities is an order of magnitude or less.

modes, the effects of downward movement of surficial sediments may look least diffusive, since gravity will not act to move material in the opposite direction. Communities dominated by this activity may be relatively easy to identify from their radionuclide profiles (J. N. Smith *et al.*, 1986).

Our preceding discussion might have left the reader with the impression that deposit feeders move sediment *either* horizontally or vertically, and not simultaneously in both directions. Usually this impression is wrong. For example, the head-down deposit feeder *Pectinaria californiensis* typically transports sediment nearly equal distances in the vertical and horizontal (Gordon, 1966), resulting in similar biodiffusivities (Table 1). For transport directions from approximately 20 to 70 degrees from the vertical (Fig. 4), horizontal and vertical D_b's differ by an order of magnitude or less. Significant anisotropic biodiffusion occurs only when transport directions are nearly purely horizontal or vertical. We can think of few deposit feeders that during feeding move sediment only vertically *in a diffusive manner*, whereas there are numerous examples (Fig. 3a–c) of deposit feeders, especially surface deposit feeders, that move particles only horizontally (Table 1). Because the known deposit feeders (Fig. 3d–f) that do move material predominantly in the vertical direction do so with extreme directional bias, those styles of mixing are not diffusive and are more appropriately modeled as advective or nonlocal transport (Aller and Dodge, 1974; Boudreau, 1986b; Rice, 1986; Robbins, 1986). Interestingly, over very long time intervals (i.e., $>> \Omega$), the tracer concentration-depth profiles produced by advective mixing can be very similar to "diffusive" profiles (Aller and Dodge, 1974; Boudreau, 1986b).

b. Locomotion. This activity includes surface or subsurface movement in getting from point A to point B without the use of permanent tubes or burrows (i.e., the animal is in

direct contact with loose particles). Reasons for moving include deposit feeding, predator avoidance, prey search, or simply adjustment of an animal's living position. Although there exist few data concerning sediment reworking rates due to locomotion, in general particle displacement due to this activity is not likely to be as important as deposit feeding, especially below the sediment-water interface. Subsurface burrowing is the most energetically expensive means of locomotion, including flight (Trevor, 1978). The high cost of burrowing is due to the drag imposed by the sediment-water mixture, which increases with depth in the sediment because water content decreases and lithostatic pressure increases. We suspect this cost is why few animals spend much time moving through the sediment, especially at sediment depths in excess of 5 cm. A result of the high cost of burrowing is relatively long particle rest periods that increase with depth. At some depth within the sediment (depending on grain size, sorting and other variables) lithostatic pressure will exceed some critical value and the costs of burrowing will exceed gains from it. The nearly constant mixed-layer depths in deep-sea sediments of approximately 10 cm estimated by various means (Berger and Johnson, 1978; Thomson *et al.*, 1988) may reflect this phenomenon (Jumars and Wheatcroft, 1989).

Those animals that do move frequently (e.g., subsurface deposit feeders or predators) are constrained by the expense of burrowing to minimize the volume and distance of sediment displaced. Over evolutionary time, this constraint (among others) has resulted in many low-aspect ratio infauna (i.e., low body width-to-length ratios). Because in many cases burrowing is effected by moving sediments radially (Trueman and Ansell, 1969), particles are moved relatively small distances (approximately the radius of the animal) (Table 1). The net distance moved may be even less because particles often collapse back into the void vacated by the animal (Frey and Howard, 1972). Thus, the majority of animals moving through sediments are likely to do so rarely and minimize the amount and distance sediment is displaced (Fig. 3g), resulting in long rest periods and short step lengths, a combination that results in low population-level biodiffusivities (Table 1).

There are, of course, exceptions to this generalization. Many hard-bodied subsurface burrowers (e.g., heart urchins or mole crabs) move through the sediment using various specially adapted appendages that transport particles from the front of their bodies to the back ("axial" burrowers, Fig. 3h) (Trueman and Ansell, 1969). Because these animals can be large, they displace large volumes of sediment per unit of time and they move it relatively long distances ($\geq$ body length). These animals may produce significant horizontal and vertical mixing rates (Table 1), although there are few data that address transport direction. Because animals typically have preferred living depths in the sediment, however, it is likely that they spend more time moving horizontally than vertically. Therefore we would expect that particle movement due to axial burrowers will be predominantly horizontal.

Animals moving on the sediment surface (Fig. 3i) also displace large volumes of sediment per unit of time. In general epifauna are larger and more numerous than

animals in any other thin (< 0.5 cm) depth interval, and it is energetically less costly to move about on the sediment surface than within sediments (although there are other costs, i.e., predation). Thus, epifauna are potentially more mobile than infauna, and contact a smaller volume of particles per unit of area, resulting in shorter rest periods. Particles, however, are again mainly transported laterally by epifauna (e.g., *Bathybembix bairdii*, Table 1).

Mobile epifauna, as well as surface deposit feeders, may influence vertical mixing rates indirectly, however. Most soft bottoms are riddled with open tubes and burrows that are predominantly vertical. As epifauna move about or forage on the sediment surface they push sediment into these open burrows, thus, "piping" recently deposited, radioisotopically hot sediment to depth. In terms of its effect on sediment mixing this process is equivalent to the reverse conveyor-belt feeders discussed earlier and is one example of the interaction between horizontal and vertical mixing that we explore in the discussion.

c. Dwelling-structure construction. Many animals construct lined or unlined structures that serve as homes. Tubes and burrows come in a variety of shapes and sizes that reflect not only the size of the producers, but also depend on factors such as substrate consistency (Rhoads, 1970) and prevailing current direction (Barwis, 1985). To facilitate discussion we will, following Lee and Swartz (1980), make a distinction between burrows and tubes, although we recognize there is a continuous gradation between them, and possible need for more than two end members. Burrows differ from tubes in that the former have diameters significantly greater than the inhabitant, and particles are moved from some depth in the sediment to the surface (Fig. 3j). Tubes, by contrast, are much closer to the diameter of the inhabitant, and are produced by the animal selecting suitable particles from the surface (usually) and incorporating them into the lining (Fig. 3k). Tubes are generally more permanent features requiring considerable investment of time (energy) during construction and maintenance. Some adult tube builders are incapable of producing new domiciles, and thus live within a single tube their entire lives. Burrows are more ephemeral features and an animal may construct hundreds during its lifetime. In terms of their contributions to sediment mixing rates, burrow builders frequently move large volumes of sediment per unit of time over fairly large vertical distances, while tube builders move less sediment less frequently and over shorter distances.

In some settings burrow excavation may dominate biogenous mass transport. On many tropical tidal flats and shallow subtidal areas thalassinid shrimp occur at high population densities and excavate large volumes of sediment to a depth of 2-3 m (Pemberton *et al.*, 1976; Suchanek, 1983; Branch and Pringle, 1987). As one example of their prodigious mixing rates, Branch and Pringle (1987) report population-level reworking rates of approximately 12 kg m^{-2} d^{-1} for the sand prawn *Callianassa kraussi*. As portions of the burrow system are abandoned by the inhabitant the burrow

walls either collapse, filling the void from the sides, or surface sediment falls into the abandoned tunnels. In either case, the net effect is that burrow excavation of this sort is, from a sediment mixing standpoint, very similar to conveyor-belt deposit feeding. Particles are initially moved from some depth to the surface, where due to continued subsurface excavation they are subducted downward (Fig. 3j).

A problem with thalassinid shrimp and other deep burrow-excavating animals is that they are difficult to sample by conventional methods (i.e., trawls, grabs or corers). For example, in Catalina Basin, a bathyal site in the California borderland, the bottom is covered by large (> 30 cm diameter) mounds that indicate significant subsurface excavation (C. R. Smith *et al.*, 1986). Yet, not a single probable mound-producer has been collected in well over 100 (20 × 20 × 30 cm) cores from the area (C. R. Smith, unpublished data). Thus, these deep-excavating animals may go unnoticed in conventional faunal surveys, yet materially affect the rate and style of sediment mixing at a given site.

There is an additional complication related to tube and burrow building that may require unique treatment. In Section 2d we discussed the phenomenon of temporal correlation, and concluded that at least for most shallow-water environments (where mixing rates are ≥ 10 cm^{2}yr^{-1}) the correlation time (rest period in Fig. 2) is short relative to the observational time scale. By incorporating particles in tubes or burrow linings, however, animals may immobilize (i.e., correlate) particles for times approaching the decay period of a given radiotracer. Accurate measurements of tube and burrow lifetimes are not available, but personal observations on tidal flats and via time-series photographs suggest that tubes may persist for a year or more. Thus, the use of short-lived radioisotopes such as ^{234}Th or ^{7}Be to characterize mixing rates in areas of high tube density must be viewed with caution. Because mixing is probably restricted to regions between tubes, it may be desirable to separate the two fractions for analysis.

d. Incidental movement. Incidental movement is not an animal activity *per se*, and we can provide no estimates of consequent biodiffusivities. We believe that this phenomenon has potentially important implications. By giving it a name we hope to call more attention to it. Incidental movement is any type of particle displacement that occurs as an indirect result of the activities discussed above. For example, while the siphon of a surface deposit feeding bivalve (e.g. *Macoma*) sucks in sediment it frequently dislodges particles but does not ingest them. Similarly, as an animal burrows through the sediment it displaces a given area of sediment based on its cross section, but it also indirectly moves sediment several particle-diameters away. Incidental particle movement then, occurs at high frequencies, being associated with all other animal activities, involves small step lengths and is quasi-random. In short, it fulfills all of the necessary criteria that describe a diffusive process. Incidental movement may be the key in eliminating correlation between particle paths, because it separates adjacent particles

between deposit-feeding events. It may be another reason that vertical diffusion models work in the absence of identifiable animal activities that move particles diffusively in that direction.

4. Discussion

Our decomposition of the biodiffusion coefficient and subsequent survey of animal activities that mix sediment has several immediate consequences. First, it is now possible unambiguously to discuss how specific external forcings (e.g., water temperature or organic carbon flux) affect the magnitude of D_b by focusing on the effect these forcings may have on step lengths and/or rest periods. We can also make scaling arguments, based on shallow-water data on ingestion rates, concerning the relative contributions of various size classes of deposit feeders to the overall mixing rate. Finally, we are forced to address the issue of how to model vertical mass transport accurately, when we know that movement occurs in three dimensions and is often vertically advective.

a. Water temperature. Because invertebrates are poikilothermic, variations in water temperature may result in changes in metabolic activity. Short-term shifts to warmer temperatures, within limits, generally result in higher metabolic activity, requiring an increase in caloric intake per unit of time. One way of fulfilling this requirement is to feed at a faster rate, thus reducing the mean particle rest period. Several well constrained, shallow-water, mid-latitude studies of a variety of deposit feeders support the trend of increased individual ingestion (or egestion) rate with increasing water temperature (Rhoads, 1963; Hargrave, 1972; Hylleberg, 1975; Cadée, 1976; 1979; Myers, 1977; Powell, 1977; Kudenov, 1982). Note that these studies treat only within-individual variation in feeding rate for animals that normally experience a wide range in water temperature. One cannot draw the apparently obvious conclusion that because of reduced temperatures in the deep sea individual and thus population reworking rates will also be low. Due to temperature compensation (Somero *et al.*, 1983), metabolic rates of deep-sea animals in food-rich areas may be comparable to those of their shallow-water relatives.

Based on the above findings one might also be tempted to expect the community-wide mixing rate to mimic seasonal temperature fluctuations. We know of only one study that has addressed temporal variation in D_b from a location subject to significant temperature variations. Martin and Sayles (1987) computed biodiffusivities from excess [234]Th profiles that show a strong seasonal dependence over a two-year period in Buzzards Bay. The maximal D_b (25 cm^2 yr^{-1}) occurred during June, while minimal values (5 cm^2 yr^{-1}) were measured during winter. The pattern was not perfectly in phase with water temperature, however, suggesting that additional factors that change seasonally (e.g., animal abundance and size or nutrient flux) affect mixing intensity.

b. Animal size. Our decomposition of D_b in terms of step lengths and rest periods also allows explicit evaluation of the influence of individual animal size on bioturbation rates. Specifically, scaling arguments allow assessment of the relative importance of different size classes to population- or community-level biodiffusivities. Cammen (1980) has demonstrated that for 19 species of shallow-water deposit feeders from several different phyla, ingestion rate (IR) scales roughly with body size:

$$IR \propto M^{0.75}, \tag{16}$$

where M is the mass of an individual. If, as argued above, deposit feeding dominates particle displacement, particle rest periods will be inversely proportional to ingestion rate. Thus, the effect on Ω for a given size class of deposit feeders will be

$$1/\Omega \propto M_k^{0.75} N_k, \tag{17}$$

where M_k is the individual body mass of animals in size class k and N_k is the number of individuals of size class k per unit of sediment area or volume. If body growth is isometric (i.e., body proportions remain constant during growth), then body length (L_k) can be substituted for mass

$$1/\Omega \propto ((L_k^3)^{0.75} N_k) = (L_k^{2.25} N_k). \tag{18}$$

For particle displacements due to deposit feeding, step length (δ) can usually be approximated by body length. Therefore, D_b for size class k is

$$D_b \propto \frac{\delta^2}{\Omega} \propto (L_k^2) (L_k^{2.25}) N_k, \tag{19}$$

$$D_b \propto L_k^{4.25} N_k. \tag{20}$$

Thus, assuming isometric growth, an order of magnitude increase in body length produces approximately a 10^4-fold increase in the per-individual contribution to the biodiffusivity. In addition, because biomass scales as L^3, a 10-fold increase in body length yields an approximately 20-fold increase in mixing rate per unit of biomass. Thus, large animals may be an order of magnitude less abundant than smaller ones (or comprise one-half their biomass) and still dominate community-level mixing rates.

How realistic is the isometric-growth assumption; do deposit feeders generally maintain a constant length-to-width ratio through life? In fact, allometric growth is often the rule among deposit feeders, and body length-to-width ratios often *increase* with increasing body size (Penry, 1988; Esselink and Zwarts, 1989), yielding a disproportionate enhancement of step length (δ). Thus, large deposit feeders are even more likely to control community-level mass transport rates, even if their numerical abundance or biomass is relatively small. Because Cammen's (1980) data are for shallow-water deposit feeders only, the numerical value of the exponent in Eq. 20 may

differ for deep-sea animals. We feel safe in predicting, however, that it will be some number greater than 2, maintaining the disproportionate importance of large deposit-feeding animals.

A final note of caution is in order here concerning the issue of local (i.e., diffusive) versus nonlocal (i.e., advective) mixing. As the mean vertical step length increases particles are transported over larger portions of the gradient of interest. At some point diffusion is no longer an accurate descriptor of this type of mixing and nonlocal models (Boudreau, 1986b; Boudreau and Imboden, 1987) must be employed. The point at which a given step length shifts from being local to nonlocal is not clear-cut, however. As is the case throughout this paper, the reader must judge for oneself if the animal activity of interest moves particles quasi-diffusively.

c. Horizontal and vertical interactions. Our review of specific mechanisms of sediment mixing also indicates that bioturbation may not be isotropic. In the deep sea, the predominance of surface deposit feeders and mobile epifauna suggests that, at least in the uppermost 1-2 cm of the sediment, horizontal mixing rates will exceed vertical rates. An initial piece of supporting information is that surface features (i.e., tracks and trails) disappear much more quickly than one would expect if one simply applied the vertical biodiffusion coefficient in the horizontal (Wheatcroft *et al.,* 1989). We are currently processing samples that will provide the first estimates of horizontal biodiffusion coefficients, and thus will have more to say on this issue in a later communication (Wheatcroft, 1990). In addition, those animal activities that do move sediment vertically often are not diffusive but are better modeled as advective (e.g., conveyor-belt feeding or burrow excavation). The importance of these two observations, although of unknown generality at this time, deserves additional discussion.

If $D_{xx} \gg D_{zz}$ in Eq. 15, how is vertical mass transport rate affected [i.e., does the tracer penetration rate (Cussler, 1984) change significantly]? Although Eq. 15 is not difficult to solve analytically (Carslaw and Jaeger, 1959; Crank, 1975), we chose to address the equation numerically so that we could more easily accommodate additional terms. We used an explicit finite-difference approach (e.g., Richtmeyer and Morton, 1967; Mitchell and Griffiths, 1980; Smith, 1985). The forward in time, centered in space algorithm we used rapidly converges (i.e., has a small discretization error) and is stable over the time intervals of interest provided relatively small diffusivities are used (Smith, 1985). The highest mixing coefficient used in our simulations is thus 1 cm^2 yr^{-1}. Abundant measurements (see Matisoff, 1982 for a summary) indicate that D_b's of up to two orders of magnitude greater occur in the ocean. Because we scaled other transport parameters (i.e., advective velocity) to D_b our results should generalize to these larger D_b values as well.

To address our initial question we ran four simulations in which D_{xx} was 0, 0.01, 0.1 and 1.0 cm^2 yr^{-1} and D_{zz} in any one column of the 16 × 20 matrix varied about a mean of 0.01 cm^2 yr^{-1} with a standard deviation of 0.005 cm^2 yr^{-1} (Fig. 5a). All simulations
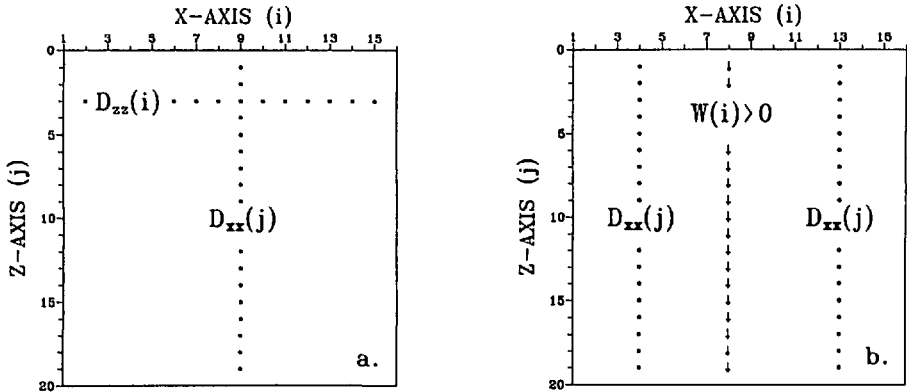
Figure 5. Schematic diagrams of the finite-difference simulations. (a) Vertical diffusivities (D_{zz}) for each column are Gaussian randomly distributed about a selected mean with a pre-selected standard deviation. Horizontal diffusivities (D_{xx}) for each row are either constant or decay with depth. Computational grid is 16×20, which pre-tests showed was large enough to minimize boundary effects. Solutions progress forward in time and space based on prescribed initial and boundary conditions. Final concentration at a given depth is computed by averaging the central 10 cells of each row. (See text for additional details.) (b) Advection (constant with depth) only occurs in column 8 of the matrix, D_{xx} is as before, $D_{zz} = 0$.

were run for equal time periods, after which the tracer concentration at any given depth was calculated by averaging the central 10 columns of the matrix. Boundary and initial conditions were concentration $= C = 100$ at $z = 0$ for $t \geq 0$ and $C = 0$ at $z > 0$ for $t = 0$. Note that these conditions correspond to a nondecaying tracer that is continuously supplied to the surface. Thus, our simulations are not directly comparable to either impulsive tracers (e.g. microtektites or ^{137}Cs) that possess time-varying boundary conditions or continuously supplied, decaying tracers (e.g., ^{210}Pb or ^{234}Th) that reach a steady state. This fictitious case, however, best shows the contribution of additional terms to the penetration rate of the tracer. Adding a decay term to simulate ^{210}Pb, for example, will change the tracer concentration at all depths, but not the shape of the profile and hence the computed D_b.

As a check of the accuracy of the simulations we solved the one-dimensional case (i.e., $D_{xx} = 0$) analytically (Crank, 1975), to compare with the numerical solution. The results (Fig. 6a) show that the numerical algorithm we used accurately simulated the equation of interest. Truncation errors (i.e., difference between analytical and numerical results) are less than 0.5% for all depths. More importantly, addition of horizontal mixing does not significantly influence the vertical tracer penetration rate (Fig. 6b). The spread of concentrations at any one depth falls within the envelope of error associated with radionuclide measurements. The result is not surprising, but it rules out the possibility that the diffusive appearance of most radionuclide profiles stems from much stronger horizontal mixing "contaminating" the vertical component of diffusion.

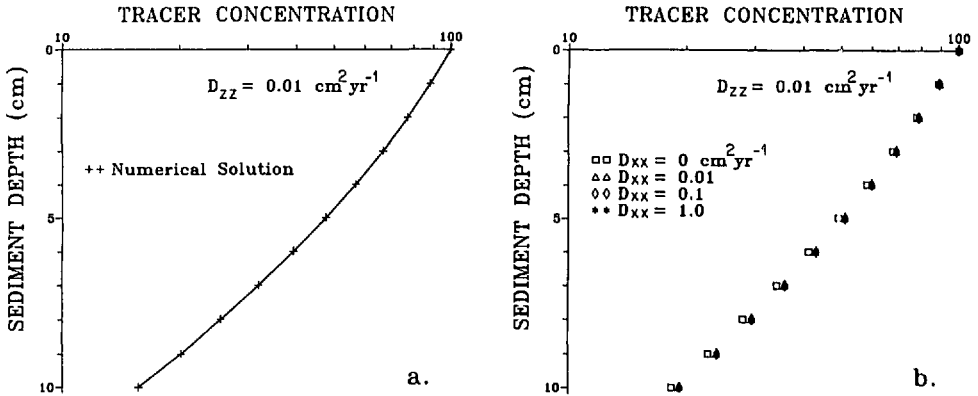TRACER CONCENTRATION   TRACER CONCENTRATION

Figure 6. (a) Tracer concentration (arbitrary units) as a function of depth in the sediment. Solid line is the analytical solution of the one-dimensional diffusion equation for $D_{zz} = 0.01$ cm^2 yr^{-1}. Symbols denote the numerical solution. The truncation error is less than 0.5% for all depths. (b) Tracer concentration as a result of coupling a vertical diffusivity (0.01 cm^2 yr^{-1}) with different D_{xx}'s.

A more appropriate question, in light of the examples provided in Section 3 and Figure 3d–f and j, is whether horizontal mixing in concert with vertical advection will produce a vertically diffusive profile. The relevant equation is now

$$\frac{\partial C}{\partial t} = D_{xx} \frac{\partial^2 C}{\partial x^2} + D_{zz} \frac{\partial^2 C}{\partial z^2} - W \frac{\partial C}{\partial z}, \tag{21}$$

where W is a vertical advection velocity (cm yr^{-1}). We again used the finite-difference approach with the same boundary and initial conditions, but now $D_{zz} = 0$. To simulate the likely scenario of a large deposit feeder causing vertically advective movement of sediment separated by areas of sediment with no advection, we allowed only the middle column of the matrix to be advective at 0.01 cm yr^{-1} for all depths (Fig. 5b). We then ran two sets of simulations, in the first D_{xx} was constant with depth and was 0.01, 0.1 and 1.0 cm^2 yr^{-1}. In the second simulation, D_{xx} decreased with depth as, $D_{xx} = D_{sx} (1/z)$, where D_{sx} = surficial horizontal diffusivity and z = depth in sediment (1 to 20 cm). Surface diffusivities were 1.0, 0.1 and 0.01 cm^2 yr^{-1}.

The results demonstrate that horizontal mixing coupled with vertical advection can, in the complete absence of vertical biodiffusion, produce diffusive-looking profiles (Fig. 7a–b). Specifically, the two cases with constant $D_{xx} = 1.0$ and 0.1 cm^2 yr^{-1} can be matched fairly well by a profile generated using a D_{zz} of 0.001 cm^2 yr^{-1}, whereas the profile generated by a $D_{xx} = 0.01$ cm^2 yr^{-1} can be produced using a $D_{zz} = 0.002$ cm^2 yr^{-1}. Similar claims can be made for the two larger depth-dependent D_{xx}'s displayed in Figure 7b. Interestingly, for both scenarios (depth-dependent and independent D_{xx}), as the horizontal mixing rate increases the vertical penetration rate of tracers decreases.
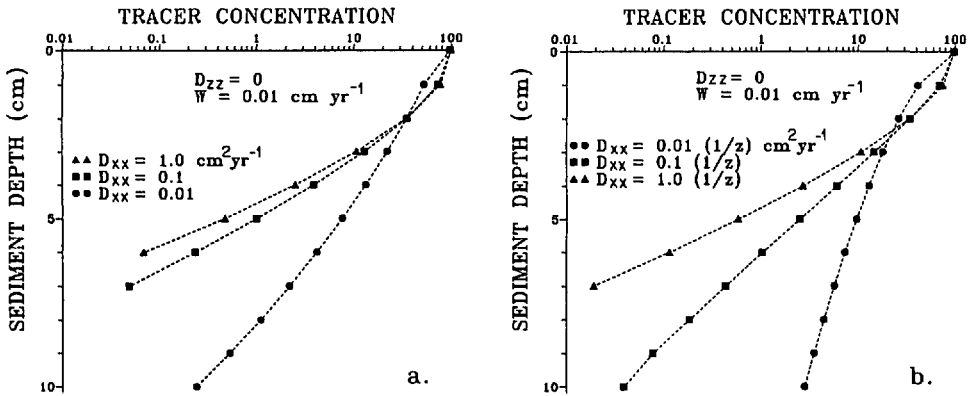
Figure 7. Tracer concentration (arbitrary units) as a function of depth in the sediment. (a) D_{xx} is constant with depth in the sediment. (b) D_{xx} decreases with depth.

This trend occurs because the higher D_{xx}'s remove high-concentration tracer from the advective column into zones lacking vertical transfer mechanisms. For the case of depth-decreasing D_{xx} starting at a surface value of 0.01 cm^2 yr^{-1} horizontal mass transfer is so small that the advective signal is retained in the tracer profile.

The reason that horizontal mixing makes the vertical profile look diffusive is easy to understand. In the absence of horizontal or vertical biodiffusion, motion of particles can be characterized by one mean velocity, and there is no way of decorrelating particle motions. Horizontal mixing moves particles in both directions between the vertically stationary surrounding sediment and the subducting (due to advection) column. It thereby increases the variance in apparent subduction velocities and distances, decorrelating particle motions vertically as well as horizontally.

These results are of interest for at least two reasons. First, these simulations demonstrate that once again different combinations of sediment mixing can look vertically diffusive. Previously, simple advective mixing (Aller and Dodge, 1974; Boudreau, 1986b; Robbins, 1986) and nonlocal symmetric mixing (Boudreau and Imboden, 1987) were shown to result in vertically diffusive profiles. It appears that very few combinations of sediment mixing modes do not result in vertical tracer profiles that can be fit with biodiffusion coefficients. [One documented exception is advective, reverse conveyor-belt feeding, (J. N. Smith *et al.*, 1986).] This convergence of product (i.e., tracer profiles) from divergent processes is dangerous because it may mislead one to model biogenous mass transport as diffusive when it is not. Secondly, because higher levels of horizontal mixing more effectively remove particles from zones of advection, they result in lower tracer penetration rates and hence lower apparent vertical D_b's (Fig. 7a). Thus, vertical biodiffusion coefficients may in some cases underestimate the intensity of diffusive mass transfer in the sediment, as well as erroneously portray the actual transport mechanisms.

5. Conclusions

Bioturbation is a discrete process. Hence the eddy-diffusion analogy borrowed from studies of turbulence can be misleading, especially when a microscopic decomposition of the mixing coefficient is sought. Previous decompositions of D_b using a velocity and a length scale have been in error due to the incorrect use of the mixed layer thickness as the length scale and the arbitrary definition of the velocity. In this paper, via Taylor series expansions, a one-dimensional, isotropic random walk model has been used to link the microscopic and macroscopic (or bulk) features of bioturbation. Considering mixing coefficients in terms of step lengths, rest periods and transport directions helps clarify some of the potential limitations of the one-dimensional diffusion analogy to sediment mixing and allows explicit discussion of mixing mechanisms. Specifically, scaling arguments demonstrate that in nearly all cases deposit feeding will dominate biogenous mixing. Consideration of the actual styles of deposit feeding indicates that sediment mixing may be highly anisotropic, with horizontal transfer rates dominating. Moreover, those deposit feeders that do move sediment vertically often do so advectively. Finite-difference simulations demonstrate that horizontal diffusive mixing in concert with vertical advection can yield vertically diffusive-looking profiles. Future models of sediment mixing must address the fact that many mechanisms of sediment displacement are not diffusive yet they can combine to produce apparently diffusive tracer profiles.

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