Diffusion in a lattice-automaton model of bioturbation by small deposit feeders

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ABSTRACT

The mixing of $^{210}$Pb and tagged particles is examined in a lattice-automaton model for bioturbation containing small deposit feeders. The values of the biodiffusion coefficient, $D_B$, calculated using typical biological parameter values, i.e., size, abundance, feeding and locomotion rates, are similar to those expected from marine sediments of a given sedimentation rate. Most biological parameters appear to exert primarily linear effects on $D_B$ values, while most nonlinearities seem to be model artifacts or failures of the assumptions in the basic $D_B$ model. The model highlights the importance of ingestion-egestion over simple particle displacement, as an agent of bioturbation.

The tagged particles are used to calculate root-mean-squared displacement plots, which are linear over long time spans, indicating diffusive behavior. However, initial trends on such plots are not usually linear, indicating that the calculated $D_B$ is time dependent for surprisingly long periods after the beginning of such experiments. The latter constitutes a warning to the interpretation of short-term tracer experiments where tagged-particles are salted onto the sediment-water interface and mixing is dominated by small deposit feeders.

1. Introduction

The mixing of surficial sediments by infauna and epifauna, a process widely known as bioturbation, alters fundamentally the fabric, the geotechnical properties, the distribution, the composition of the sedimentary components, and thus the nature of the geological record (e.g., Rhoads, 1974; Guinasso and Schink, 1975; Aller, 1982; Fisher, 1982; McCall and Tevesz, 1982). The fate of contaminants and pollutants in sediments can also be largely regulated by this process (e.g., Bosworth and Thibodeaux, 1990). Consequently, much effort has been expended to describe quantitatively (mathematically) the effects of bioturbation.

Based on the variability and random character of bioturbation, most common models
treat this mixing as a Fickian diffusion, usually in 1D, e.g., Goldberg and Koide (1963), Guinasso and Schink (1975), Boudreau (1986a), and Smith et al. (1993). In some situations, the diffusive model is clearly inappropriate as the biological motions are either directed (advective) or large scale, which has given rise to the formulation of nonlocal models, such as those proffered by Fisher et al. (1980), Boudreau (1986a,b, 1998), Robbins (1986), and Boudreau and Imboden (1987). Unfortunately, biology and ecology are, in truth, largely absent from all these models in that they contain neither direct representations of the organisms nor any true biological parameters, e.g., individual rates of ingestion or locomotion, population composition, or densities, etc., notwithstanding the efforts of Guinasso and Schink (1975), Boudreau (1986a, 1998), Wheatcroft et al. (1990), and Smith (1992) to alleviate that situation.

These diffusive and nonlocal models are deterministic and continuum representations of the properties of the solid sediment, not of the benthic ecology. However, attempts have been made to create representations that allow for the discrete, stochastic nature of the biology and its effects. Most of these are based on multi-dimensional “transition matrix” methods for moving the sediment particles (Hanor and Marshall, 1971; Foster, 1985; Trauth, 1998). The idea is to represent a sediment in 2D or 3D as an array of discrete sediment particles (possibly reactive) that are moved at each time step in these models according to a matrix of probabilities that are resolved with a random number generator. The result is a model with non-predictable outcomes that is capable of both local and nonlocal mixing and that can easily deal with multi-dimensional transport. The obvious shortcoming is that biological organisms are still absent and the probabilities are user inputs, rather than dynamic features of the model. Another technique to overcome the lack of biology has been the functional-group model advanced by François et al. (1997). While this model does contain real biological elements, they are static and the mode of mixing they produce is predetermined, e.g., diffusion; yet, it is certainly a step in the right direction. Finally, Risk et al. (1978) attempted to capture the effects of deep-burrowing shrimp on sediment composition and stratigraphy with a “rule-controlled” burrow model; while ingenious, the model again controlled the creation of burrows, without having any organisms actually present.

In contrast to the above, Choi et al. (2001) have advanced a radically new type of model that overcomes these problems and that should allow us to better understand how biology, ecology and sediment mixing are quantitatively related. This model treats sediments as a random lattice of particles and recognizes organisms explicitly as a fundamental part of such a model, i.e., as automatons. An overview of the model is given in the next section, and details are available in Choi et al. (2001).

This new lattice-automaton bioturbation simulator (LABS) is a means of exploring quantitatively the connection between animal activities and mixing. The validity and acceptance of the model in the community of benthic scientists will depend on its validation; i.e., that the model can generate mixing parameter values from predicted tracer profiles that are similar to those seen in nature, given reasonable inputs for the biological
parameters. This paper aims to address this concern. Therefore, starting from values of observed ingestion and locomotion rates for an ecology of small deposit feeders; e.g., capitellid-like organisms, we generate tracer profiles and calculate equivalent biodiffusion coefficients, $D_B$. This derivation of $D_B$ values does not imply that the mixing in the model is truly diffusive, only that it is interpreted, without prejudice, using a diffusion model. Two types of tracers are considered: $^{210}\text{Pb}$ which is a decaying tracer (half-life = 22.3 yr) supplied at the sediment water interface, and a number tag on each particle in the simulation. As shown below, these two types of tracers supply different information about mixing rates.

2. Model overview

Details of LABS can be found in Choi et al. (2001). More succinctly, the LABS model represents sediment as a 2D-lattice (width $L$, depth $D$) of square holes. The number of squares in this array is determined by the dimensions of an individual square, which is an input parameter. A particular lattice hole must be filled with a “particle” of one of three different phases: pore water, solid sediment or—and this is a basic novelty of the LABS approach—organism. Surface sediments have traditionally been modeled as a two-phase environment, fluid and solids, whereas the organisms are treated as invisible agents that mediate the displacement of sediment grains and porewater packages. Our new LABS model directly incorporates the organisms as physical entities in the model; thus, organisms occupy some volume fraction of the sediment. (The effective incorporation of organisms into a traditional 1D reactive-transport model of sediments constitutes another new line of thinking and a more in-depth treatment of this topic can be found in Meysman (2001).)

In LABS an organism is defined as a collection of organism particles, occupying adjoining lattice squares and moving in a coherent manner, which is dictated by a set of biological movement rules. The surrounding sediment is modeled as a random collection of solid and porewater particles, occupying the other lattice positions. The main purpose of the LABS model is to investigate how sediment particles are moved around when the organisms are given behavior rules, particularly with regard to movement and sediment processing, based on actual biological information.

The model sediment particles are not true individual sediment grains, as that would be computationally onerous; instead they should be viewed as idealized bodies that are roughly comparable to the sediment parcels manipulated by organisms. In nature, deposit-feeding worms manipulate (move/ingest) packets of sediment of variable size, and these clumps of sediment are dynamic in that they can be broken up or recombined by the organisms or other processes; e.g., passage through an animal’s gut, compaction, etc. The LABS particles are predefined chunks of sediment that cannot be broken up or recombined. This further implies that there is no mixing or mass exchange at the boundaries of the clumps in LABS. The composition of the particle cannot change via small-scale mixing at the boundaries with adjacent particles, but only by chemical reaction or passage through an
animal’s gut. Therefore, particle displacement in our model is akin to the movement of tiles in the old order-the-numbers game, i.e., the 2-D precursor to the Rubik’s cube—see Choi et al. (2001) for illustrative figures. Nevertheless, we believe the absence of boundary mixing between particles leads to no significant problems.

Each sediment particle in LABS can have individually assigned chemical, biological and physical properties, e.g. food versus inert material, etc. Particles can be added to the model by sedimentation and removed by burial, while compaction guarantees the existence of a sediment-water interface and the slow disintegration of some biologically generated features.

3. Input parameters

Currently, LABS provides a 2D representation of the sediment environment. In the simulations presented here, we always employ a lattice that is 50 cm wide ($W$) and 20 cm deep ($D$). This 2D planar model can be interpreted as a slice of a 3D-model, which has the thickness of the worm’s diameter and where the worm is restricted to movement within this 2D slice. The latter representation proves helpful in relating the 2D density of organisms in LABS to a corresponding 3D population density. This point is discussed at some length in Choi et al. (2001). One 2-mm diameter worm in the 2D model is equivalent to about 1000 individual worms m$^{-2}$ of sediment, i.e., 2 organisms per slice times 500 slices of 2 mm thickness for each square meter. More organisms scale linearly to this estimate, i.e., 2 worms = 2000 ind. m$^{-2}$, etc. The sediment supplied at the interface contains 3% organic matter, which the organism(s) actively seek and digest. Locomotion rates in the range of 1–80 cm d$^{-1}$ are considered below (e.g., Caron et al., 1996), as well as ingestion rates of 0–25 g sediment per g of body mass (e.g., Lopez and Levinton, 1987).

Mixed-layer depths were taken to be 14 cm for the numerical experiments with excess $^{210}$Pb and 20 cm for the tagged-particle experiments. The deeper mixed layer for the tagged-particle experiment removes the “bottom effect,” described later, in the tagged-particle experiments; i.e., because the tagged particles are conservative, they are more easily influenced by the bottom boundary condition and so the particle simulations can generate incorrect values for the mixing coefficient, using the simple model described below, if the mixed depth is too shallow. For the excess $^{210}$Pb studies, we further assumed that the animal had a linearly increasing chance to turn upward, the deeper the animal moved into the sediment, with a 100% chance at the base of the mixed layer. The deterministic model, used to extract mixing coefficient, $D_B$, from the $^{210}$Pb profiles assumes that $D_B$ is a constant (also see below), which is at variance with a decreasing chance of depth penetration. However, real bioturbating organisms in nature have a largely unquantified decreasing chance of depth penetration (e.g., McCall and Tevesz, 1982); yet, we routinely fit the constant $D_B$ model to natural profiles. To be consistent with normal practice, we also employ the constant $D_B$ model. In the case of the tagged-particle method, the decreasing chance of depth penetration is removed because the equations for extracting $D_B$ from the results of these experiments are strictly valid only for isotropic diffusion;
furthermore, as stated above, a deeper mixed layer is employed, whose base is reflective to animal motion.

4. Diffusion constants from excess $^{210}$Pb

The visualization of an example model output is shown in Figures 1 and 2. The top panel of each figure depicts the position of the solid particles as brown/gold dots, the water in blue-purple, and the bioturbating organism(s), with body in yellow and head in orange/red. The lower panels are the corresponding excess $^{210}$Pb activities, with a brighter blue indicative of higher normalized activity (brightest equals unit normalized activity) to dark blue for zero excess. The initial distribution is that expected for sedimentation and decay only at steady state.

Figure 1. Top: Initial ($t = 1$ day) random lattice of about 45,000 particles (brown dots) with a single capitellid-like worm (head in red and body in yellow) that is 3 cm long and about 0.2 cm in diameter. The worm searches for food (not color coded) and has a linearly decreasing chance of moving deeper into the sediment. The dimensions of the lattice are 50 cm by 15 cm, and the single worm in this 2D simulation is approximately equivalent to 1000 worms per square meter in a 3D world. Bottom: A color-coded 2D initial distribution of excess $^{210}$Pb, with brighter blue an indication of higher normalized activity (brightest equals unit normalized activity) to dark blue for zero excess. The initial distribution is that expected for sedimentation and decay only at steady state.

Furthermore, as stated above, a deeper mixed layer is employed, whose base is reflective to animal motion.
realization of the model is unique as a random seed is used to initialize the random number generator employed to place the particles and the organism(s). The excess $^{210}\text{Pb}$ on each particle is initially set to the value that would be expected at a given depth if only decay and advection (sedimentation, $0.01 \text{ cm yr}^{-1}$ in this case) are operative, with a normalized unit activity at the sediment-water interface. This tracer is continually supplied to the interface, associated with the sediment particle flux.

Figure 2 is the condition in the model 100 yr into the simulation, i.e., five times the half-life of $^{210}\text{Pb}$, in order to assure an averaged steady state. The $^{210}\text{Pb}$ has penetrated significantly deeper than with advection acting alone, as a result of the bioturbation. This 2D view illustrates the heterogeneity that continues to exist, even in a purported steady state. Such heterogeneity agrees with that observed in detailed 3D $^{210}\text{Pb}$ measurements at a somewhat large scale within a box core taken by Smith and Schaffer (1984).

The 2D distribution in Figures 1 (lower) or 2 (lower) can be integrated laterally to produce a 1D excess $^{210}\text{Pb}$ profile, similar to that sampled by conventional means in sediments. Examples are provided in Figure 3 as a time series from the initial advection-
decay profile to that at steady state for diffusion-advection-decay at 100 yrs. Note that the sediment-water interface is initially at $x = 4$ cm, relative to an arbitrary datum in the water column. With time, the $^{210}$Pb appears to move up into the water column.

Figure 3. Typical evolution (0–100 years) of laterally averaged $^{210}$Pb depth-profiles taken from results such as those given in Figure 2. The sediment-water interface is initially at $x = 4$ cm, relative to an arbitrary datum in the water column. Top: Infauna does not ingest-egest, but does burrow through the sediment. Bottom: Infauna ingests and defecates sediment as well as moving it by burrowing. The deeper penetration of the $^{210}$Pb in the latter case is the result of the nonlocal nature of the ingestion-egestion process.
because mounds are formed, which “lift” the sediment-water interface into the water column (closer to the $x = 0$ datum).

The amount of data in these profiles is far greater than normally available in field samples; however, we decided to employ these data-rich profiles, rather than averaging to typical sample sizes in order to achieve acceptable statistics on the correlations that follow. In addition, we do not utilize data below a normalized activity of about $10^{-2}$ in the following analysis as that value represents a typical analytical limit on real profiles of excess $^{210}$Pb. On the other hand, no attempt has been made to smooth out the model-generated variability in the profiles. Notice also that the profiles in Figure 3 develop sharp interface gradients, which are not consistent with Fickian mixing. These gradients may constitute an artifact of the uneven surface; however, the theory of internal nonlocal mixing, as developed in Boudreau and Imboden (1987), predicts the appearance of sharp interface gradients in such circumstances, and those in Figure 3 may be expressions of that phenomenon. Nevertheless, we will treat our profiles as if they were the results of Fickian processes.

For constant average porosity, the conservation equation for a tracer subject to Fickian diffusion, advection by sedimentation and decay is (Berner, 1980)

$$D_B \frac{d^2C}{dx^2} - w \frac{dC}{dx} - \lambda C = 0$$

(1)

where $C$ is the excess $^{210}$Pb activity, $x$ is depth relative to the sediment-water interface, $w$ is the sedimentation velocity, and $\lambda$ is the decay constant for the tracer. Furthermore, usual practice is to ignore the contribution from sedimentation (i.e., technically, $w^2 \ll 4D_B\lambda$), which is generally justified, and to treat the mixed layer as infinite. The model then simplifies to

$$D_B \frac{d^2C}{dx^2} - \lambda C = 0$$

(2)

which has the well-known solution

$$C(x) = C(0) \exp[-(\lambda/D_B)^{1/2}x]$$

(3)

where $C(0)$ is the tracer concentration at the sediment-water interface (i.e., unity in our case). Eq. (3) was fit to results like those in Figure 3 for Year 100. The lower curved part of these profiles are not included in the fits because they are always below the $10^{-2}$ normalized activity cut-off. Fits were done by nonlinear regression, rather than linearizing by logarithmic transformation, as the former gives weight to the larger values of activity where the errors are smaller (Mulsow et al., 1998).

Through multiple numerical experiments and fittings as described above, we were able to explore the relations between $D_B$ and the biological parameters and settings in our automaton model. Figure 4 illustrates the influence of the number of organisms for two different feeding rates. Each data point in this figure, as in all graphs that follow, is the
mean of three model outcomes with an associated error bar. If the error bar is not apparent, it is smaller than the symbol for the data point. Figure 4 shows that $D_B$ is not a simple function of the number of organisms. At the low end of the feeding rates the relationship is hyperbolic, perhaps indicative of a saturation effect, while it is linear at the higher feeding rate. The latter behavior may also become hyperbolic, but we consider larger numbers of organisms unrealistic in this case. Saturation occurs at these low feeding rates because the organisms quickly satiate themselves and do not move a lot more sediment. As important as the trends in Figure 4 is the range of $D_B$ values generated by the model, i.e. 0.1–0.7 cm$^2$ yr$^{-1}$. Such values are typical of sediments at this sedimentation rate (Boudreau, 1994). We wish to emphasize that in no way did we manipulate the input parameters to obtain these $D_B$ values; the biological parameters were those found in the literature and simply plugged into the model.

Figure 5 displays the results from varying the feeding rate for a single 2D organism ($\sim$1000 3D organisms m$^{-2}$). The data indicate a slow rise in $D_B$ above a rate of about 2.5 g (g body)$^{-1}$ d$^{-1}$ and a rapid rise in this parameter as the rate approaches zero. This result at
first confused us, as we expected a continued fall below \(2.5 \text{ g (g body)}^{-1} \text{ d}^{-1}\), i.e. no mid-value minimum. Eventually we came to realize that the minimum and the rise as zero is approached is a model-generated artifact.

Logically, as the ingestion rate falls, so should the mixing rate. However, the egestion rate is linked to the ingestion rate, so that as the feeding rate falls, so does the defecation frequency. The latter fact means that a worm will travel much farther before defecating than if it were to feed at a faster rate, because locomotion is independent of feeding in our model. Thus, a worm with a small ingestion rate can ingest a small amount of \(^{210}\text{Pb}\)-rich material at the surface and re-deposit it quite deep into the sediment because of the long lag between ingestion and egestion; a fast-feeding worm cannot do so. The effect is to make \(^{210}\text{Pb}\) penetrate further than at faster feeding rates, i.e., a nonlocal transport (see Boudreau, 1986b; Boudreau and Imboden, 1987). Nevertheless, we consider this to be a model artifact in the way feeding and defecation are related and not necessarily reflective of any actual behavior; as such, we believe the linearity of the above \(2.5 \text{ g (g body)}^{-1} \text{ d}^{-1}\) is more representative of the expected relationship.

The discussion immediate above highlights the relative impact on \(D_B\) of eating-defecating versus simply displacing particles. If we return to Figure 3, two sets of excess...
$^{210}$Pb profiles are displayed: the top diagram was generated without ingestion-egestion of particles (i.e., need for food shut off), while the bottom figure results from ingestion and delayed egestion (i.e., animals fill to proscribed extent before defecating). Ingestion-egestion causes deepening of the profile by facilitating transport and implies a considerably larger $D_B$.

Figure 6 displays our results with respect to the effect of locomotion speed at constant ingestion rate for a single organism, but with two different values of the mixed-layer depth, i.e., 10 and 14 cm. With a 14 cm bioturbated layer, the effect of locomotion is decidedly linear and the values of $D_B$ are in the expected range. When the mixed depth is decreased to 10 cm, the predicted $D_B$ values are initially identical to the 14 cm case, but deviate to higher values at faster movement rates. This deviation from the expected is a model artifact, but not one associated with LABS, but with Eq. (3). Eq. (3) assumes that the mixed layer is essentially infinite in extent; however, with a 10 cm mixed layer and larger locomotion rates, the tracer can be transported to that depth before it decays. Thus, the mixing of the $^{210}$Pb “feels” the bottom, which is a reflective boundary, and consequently,
there is more excess $^{210}\text{Pb}$ at each depth between 0–10 cm than would be expected if the bioturbated layer was of infinite extent. More excess $^{210}\text{Pb}$ means a shallower slope than expected and fitting Eq. (3) to this data produces a $D_B$ value larger than the actual value. This explains the trends in Figure 6 and is a warning to all attempting to model excess $^{210}\text{Pb}$ data; specifically, Eq. (2) has two solutions, an exponential that decays and one that grows with depth. The growing component of the complete solution to Eq. (2) may occasionally need to be retained, along with the familiar decaying component, if the isotopic profile is influenced by a finite depth of mixing.

Figure 7 illustrates the substantial effect of nonlocal transport by ingestion-egestion on the apparent $D_B$ as a function of locomotion velocity up to 80 cm d$^{-1}$. This result indicates that literature-reported $D_B$ values are complex composite measures of the type of mixing taking place in sediments and attempts to give them simple mechanistic interpretations based on Fick’s First Law, e.g., Guinasso and Schink (1975), Boudreau (1986a) and Wheatcroft et al. (1990), will always prove to be somewhat unsatisfactory.

Finally in this section, the influence of body width for a single animal is illustrated in Figure 8. A linear trend is observed, and this results from the fact that the feeding rate is linearly proportional to the mouth size, i.e., body width in our model. Overall, the most important determinants of $D_B$ appear to be ingestion-egestion, locomotion rates and numbers of organisms, followed by body width and egestion frequency, with a surprisingly small effect from feeding rate itself, at least for a single 2D organism.
5. Tagged-particle analysis

One of the wonderful benefits of the LABS model is that the particles employed in the model can be their own tracers. What we mean by this statement is that the particles can have unique identities and their movements can be followed during the course of a numerical experiment. There is value in knowing the displacement of the particles, i.e., distance traveled from their original position, as diffusion can be defined on the basis of particle displacements, as well as through more traditional tracers like excess $^{210}\text{Pb}$.

Jost (1964; reproduced in Boudreau, 1997) gives a lucid account of the basis for this methodology. If each particle in a system subject to true isotropic Fickian diffusion (self-induced or externally via organisms) is tagged and the displacement of these particles is measured with time, then the mean-squared displacement of the population of particles, $\overline{\Delta^2}$, should follow the equation (e.g., Berg, 1983; Wheatcroft, 1991)

$$\overline{\Delta^2} = 4D_B t$$  \hspace{1cm} (4)

in 2D, where $t$ is the time since the beginning of the simulation and where the left-hand side of Eq. (4) is calculated as,
\[ \bar{\Delta^2} = \frac{1}{n} \sum_{i=1}^{n} (\Delta_i)^2 \]  

where \( \Delta_i \) is the displacement of particle \( i \) at time \( t \), and \( n \) is the total number of moving particles. Eq. (4) indicates that the root of the mean-squared displacement (RMS displacement) is linear in the square-root of time. Wrigley et al. (1990) have considered the validity of Eq. (4) when some of the movements are to nonadjacent points and found that it continues to hold although the interpretation of \( D_B \) becomes more complex. In addition, Wheatcroft (1991) has some evidence that mixing in real sediments may not be isotropic; however, care was taken to ensure isotropy in our numerical experiments.

LABS allows easy tagging of particles via assignment of individual number labels and subsequent calculation of their RMS displacements. Results of this type of calculation are provided in Figures 9 and 10 as functions of locomotion speed, for mixing by mechanical displacement only (Fig. 9); i.e., no ingestion-egestion, and with a normal rate of ingestion-egestion (Fig. 10). Note that the panels to the right in each figure are enlargements for early time values (<400 days), not separate results.

These figures are highly informative. Firstly, the values of the \( D_B \) calculated from these plots with Eqs. (4) and (5) are given in Table 1. Without ingestion-egestion, the \( D_B \) are much smaller than obtained with ingestion-egestion. The larger mixing intensities with ingestion are the result of the nonlocal transport, and this effect is pronounced, i.e., a factor of approximately two and a half orders of magnitude. Thus, simply moving small worms through sediments results in modest mixing, while large effects can result from their feeding activities.

Next, there is a disparity between the \( ^{210}\text{Pb} \)-based and displacement-based \( D_B \) values, both with ingestion; i.e., compare the values on the y-axis in Figures 4–7 with those in Table 1. These differences arise for two reasons. Firstly, the displacements include movements in both the lateral and vertical directions; thus, a lateral displacement that would not affect the laterally-averaged \( ^{210}\text{Pb} \) profiles is nevertheless counted in Eq. (4). This makes the displacement-based estimates larger. Secondly, the \( ^{210}\text{Pb} \) results were obtained with a linearly decreasing chance of penetrating deeper, while no such restriction was placed on the displacement simulations; this too tends to generate larger \( D_B \) values in the displacement case. Furthermore, the constraint that an animal burrowing downward has a special chance to turn upward, while a laterally moving animal has a simple random chance of deviating either up or downward, will lead to anisotropy in the model \( D_B \) and could in part explain the anisotropy observed by Wheatcroft (1991) in his seeding experiments. (Note also that the \( D_B \) at 40 cm d\(^{-1}\) with ingestion is not larger than that at 20 cm d\(^{-1}\), which indicates an effect that we do not as yet understand.)

In addition to the above, the plots in both Figures 9 and 10 are not linear for “early times” (see the right-hand panels), and more so at lower locomotion speeds. The deviations are more obvious in Figure 10, but they are present in Figure 9 and occur over roughly the same period, i.e., in the first 100 days. This outcome may have important implications for
Figure 9. Root-mean-squared (RMS) displacement of particles in the LABS model as a function of the square-root of time, in this case with no ingestion-egestion simply pushing of particles during burrowing. If the displacement process can be described as diffusion, the results from the model will plot linearly. The plots on the left show the behavior over about $10^4$ days, while those on the right illustrate early behavior, i.e., less than 400 days. The plots are linear over the long term, but deviate somewhat on short time scales. If a line appears in the right-hand diagrams, it is the continuation of the regression in the corresponding left-hand diagram. Error bars are obtained from 3 independent realizations of the model. The $D_b$ values calculated from these plots can be found in Table 1.
Figure 10. Same type of plot as in Figure 9, but with ingestion-egestion operative, in addition to simple displacement of particles during burrowing. Again the plots are linear over long time frames, but over the initial 100 days they can deviate strongly from linearity, especially at slow locomotion speeds. $D_B$ values calculated from the initial short time results would be time dependent. The reason for the nonlinearity is discussed in the text. (Specific input parameters: worm width = 0.2 cm, length = 1.2 cm, ingestion rate = 1 g g$^{-1}$ d$^{-1}$, and injection selectivity = 0.7.)
experimental studies where small deposit feeders dominate the ecology. Specifically, our results imply that $D_B$ values calculated from the spread of a surface-deposit of tagged particles will be a function of time for periods up to 100 days.

This early time dependence is not an artifact of the model, e.g., from initial conditions; instead, it is an inherent property of (Fickian) diffusive processes. There are a number of references on the topic, e.g., Csanady (1973), and this is discussed by Meysman (2001) in a diagenetic context. The essential point is that Eq. (4) is not valid at “early” times. The correct form for Fickian diffusion can be derived from the fact that the diffusion coefficient, which results from random (local) motions, is related to the change in the standard deviation, i.e., $\Delta^2$, of the particle distribution with time, i.e.

$$D_B(t) = \frac{1}{4d}\frac{\Delta^2}{dt}. \quad (6)$$

In turn, the standard deviation can be calculated by the equation

$$\Delta^2 = 4D_B \int_0^t R(\tau)(t - \tau)/t_c d\tau \quad (7)$$

where $t$ is time, $\tau$ is an increment of time, $t_c$ is the de-correlation/relaxation time, $D_B$ is the usual constant biodiffusion coefficient, and $R(\tau)$ is the autocorrelation function. $R(\tau)$ is a estimate of the correlation between the position of a particle at time $t$ and at a subsequent time $t + \tau$. The constant $t_c$ is a measure of the “half-life” for correlation between movements; i.e., beyond a few $t_c$ values, motions are no longer correlated. The importance of $t_c$ in a bioturbational context has previously been discussed by Boudreau (1989), who cautions that it may be large for bioturbation, i.e., the time elapsed between movements of the same particle may be weeks or months.

For a Markov process, like Fickian diffusion, (Csanady, 1973)

$$R(\tau) = \exp(-\tau/t_c). \quad (8)$$

Combining these equations,

$$D_B(t) = D_B[1 - \exp(-t/t_c)] \quad (9)$$
and this is the form that should appear in Eq. (4). This latter simple result shows that $D_B(t)$ starts at zero and increases to an asymptotic value in about $5t_c$. This is the behavior in our model. In other contexts such as solute diffusion or turbulent mixing, we often can ignore this time dependence because for molecular diffusion $t_c$ is far less than microseconds (see Boudreau, 1989), while for turbulence $t_c$ is a few hundred seconds (Csanady, 1973). The time dependence is most often a curiosity in these other fields; yet, for bioturbation experiments where small deposit feeders dominate, time dependence is an important matter, as seen in our experiments.

At first the above result may appear to contradict experiments where a tracer that is deposited at the sediment-water interface can rapidly appear at depth, suggesting an initial high $D_B$ value (e.g., Fornes et al., 1999). That is not the case, however, as the early mixing in these situations is usually dominated either by subsurface defecators or tracer transport down pre-existing tubes/burrows. Our model does not contain such processes and examines the pure end-member case of a population of small deposit feeders. Nevertheless, experimentalist should be on guard for this effect.

Finally, the fact that the period of the time dependence is roughly the same with and without ingestion-egestion reflects the similar time constraints on both motion and eating of benthic organisms in this model. We are unsure if this holds in nature.

6. Conclusions

The dual aims of this paper were to validate the lattice-automaton model (LABS; see Choi et al., 2001) and to gain new insight into the bioturbational process due to small deposit feeders. We have gained success on both counts.

Biodiffusion coefficients extracted from simulated excess $^{210}$Pb and from particle displacement studies and generated with commonly accepted rates of ingestion and locomotion are similar to those seen in nature. This result validates the basic functioning of LABS and should encourage its use for other investigations of bioturbation, benthic ecology and even sediment-water interactions.

Using $^{210}$Pb as a tracer, the model predicts mostly linear relations between $D_B$ values and various biological parameters, such as number of organisms, feeding rates, locomotion speeds, and width of organisms. Deviations from linearity are seemingly due to saturation effects, e.g., number of organisms at low feeding rates, or model artifacts, e.g., very low feeding rates with long lag times for egestion or “bottom” effects. The most important influence of the value of $D_B$ appears to be the presence/absence of ingestion-egestion.

The tagged-particle approach produced generally linear RMS-displacements versus square-root of time, as expected for a diffusive process. Exceptions occur at early times, when the plots are curved and indicative of time dependence in $D_B$. The latter is consistent with the theory of Fickian diffusion. Furthermore, ingestion-egestion leads to $D_B$ values that are much greater than by particle displacement alone, and by comparison with the lead-based results, we suggest that mixing coefficients measured in natural sediments will appear to be anisotropic, as indicated in the study by Wheatcroft (1991).
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