

Biological Redistribution of Lake Sediments by Tubificid Oligochaetes: *Branchiura sowerbyi* and *Limnodrilus hoffmeisteri*/*Tubifex tubifex*

Gerald Matisoff^{*,1}, Xiaosong Wang², and Peter L. McCall¹

¹Department of Geological Sciences
Case Western Reserve University
10900 Euclid Ave.
Cleveland, Ohio 44106-7216

²South Florida Water Management District
3301 Gun Club Road
West Palm Beach, Florida 33406

ABSTRACT. Mechanisms and rates of sediment mixing by the largest oligochaete in Lake Erie, *Branchiura sowerbyi*, have been quantitatively investigated using a multiple ¹³⁷Cs tracer microcosm technique and compared with a mixture of the dominant tubificids, *Limnodrilus hoffmeisteri* + *Tubifex tubifex*. These worms feed head down in the sediment (up to 20 cm for *B. sowerbyi* and up to 10 cm for *L. hoffmeisteri*/*T. tubifex*) on organic-rich particles and deposit fecal pellets at the sediment-water interface (conveyor-belt feeding). Obliteration of tracer layers by these worms was attributed to mixing by both diffusive- and feeding-style (advective) processes. The downward velocities were 2.87 to 3.66 cm/d/100,000 indiv/m² for the cells with *B. sowerbyi* (~10 cm body length, 13 mg body mass) and 0.33 to 0.49 cm/d/100,000 indiv/m² for the cells with *L. hoffmeisteri* / *T. tubifex* (~5 cm body length, 1 mg body mass). These downward velocities correspond to sediment fluxes across the sediment-water interface of 66.4 to 86.4 g dry sediment/indiv/m²/yr in cells with *B. sowerbyi* and 5.91 to 9.09 g dry sediment/indiv/m²/yr in the cells with *L. hoffmeisteri* / *T. tubifex*. The differences between species was due to differences in biomass, with recycling rates of 5.11 to 6.65 and 5.91 to 9.09 g dry sediment/mg biomass/m²/yr for *B. sowerbyi* and *L. hoffmeisteri*/*T. tubifex*, respectively. Similarly, biomass normalized downward velocities were 806 to 1,028 cm/yr/kg biomass/m² and 1,205 to 1,789 cm/yr/kg biomass/m² for *B. sowerbyi* and *L. hoffmeisteri*/*T. tubifex*, respectively. Both *B. sowerbyi* and *L. hoffmeisteri* / *T. tubifex* feed selectively on organic-rich fine-grained particles and showed an increase in particle selectivity with an increase in population density. The particle selectivity factor values ranged from 1.0 to 2.5. Food competition at a higher population density might force these organisms to selectively feed on a smaller size range of sediments. The maximum feeding rate for *B. sowerbyi* (4,000 to 8,000 indiv/m²) ranged from 9.10 to 13.9 per yr at depths between 11.7 and 13.6 cm while the maximum biodiffusion coefficient, *D_b*, ranged from 0.78 to 1.02 cm²/yr at depths between 1.6 and 2.3 cm. The maximum feeding rate for *L. hoffmeisteri* / *T. tubifex* (20,000 to 40,000 indiv/m²) was 8.13 to 13.1 per yr at depths between 5.21 and 5.27 cm and *D_b* ranged from 0.20 to 0.72 cm²/yr at depths between 0.87 and 2.0 cm.

INDEX WORDS: Bioturbation, oligochaete, *Branchiura*, *Limnodrilus*, *Tubifex*, Lake Erie.

INTRODUCTION

Biological sediment mixing in lakes is species specific. In many places the most abundant species in a benthic community may not be the most important in terms of sediment mixing. Profundal infauna of most lacustrine environments are dominated by

molluscs, chironomids, oligochaetes, and amphipods (McCall and Tevesz 1982). Molluscs and oligochaetes, in particular, are known to mix sediment at depth (Fisher *et al.* 1980). For example, western Lake Erie is known to be subject to deep sediment mixing (Robbins *et al.* 1989) and some of that deep mixing may have been caused by suspension feeding unionids (McCall *et al.* 1986). However, poor water quality and the recent introduction

*Corresponding author. E-mail: gxm4@po.cwru.edu

of zebra mussels may be leading to their extirpation from the lake (Nalepa *et al.* 1996). Therefore, oligochaetes are likely to be the most important deep mixers in Lake Erie because they are abundant and because they are deep conveyor-belt deposit feeders (Robbins *et al.* 1979). While mixing by abundant limnodrilid and tubificid oligochaetes (Fisher *et al.* 1980), especially *L. hoffmeisteri* and *Tubifex tubifex*, have been studied (Krezoski and Robbins 1985), the less abundant, larger tubificid, *Branchiura sowerbyi*, has not been studied.

Quantifying oligochaetes mixing rates is very important to modeling mass transport and the fate of pollutants in sediments. There are several different techniques available to quantify mixing rates (Gerino *et al.* 1998). Here the results of *in vitro* particle mixing by *B. sowerbyi*, using radiotracer methods developed by Krezoski and Robbins (1985) and a model of nonlocal sediment mixing (Robbins 1986), are reported. These results are then compared to those obtained from the more abundant deposit feeding oligochaetes (mostly *L. hoffmeisteri*, some *T. tubifex*).

METHODS

B. sowerbyi and harbor worms (mostly *Limnodrilus hoffmeisteri* with some *Tubifex tubifex*) were collected by grab sampling bottom sediments in June 1993 from the western basin of Lake Erie and from Cleveland Harbor, respectively. The population densities of *B. sowerbyi* range from several hundred to several thousand per square meter. Population densities of harbor worms were not measured at the time of collection, but can exceed 25,000 indiv/m² in the western basin (Soster and McCall 1990). Adult *B. sowerbyi* and harbor worms have average body lengths and weight of about 10 cm and 13 mg/indiv and 5 cm and 1 mg/indiv, respectively (Soster 1984). These species construct burrows extending from the sediment-water interface to depths often greater than body length. *B. sowerbyi* burrows were found to a depth of about 20 cm; harbor worms burrowed to about 8 cm.

Sediment used in laboratory microcosms was sieved through a 500- μ m sieve without water added. The sediment was then defaunated by refrigeration for ~1 day. The defaunated sediment was maintained at room temperature (~20°C) in plastic bags until needed (~1 week).

Live worms were obtained by gently rinsing with tap water small quantities of sediment through a 1 mm mesh sieve. The worms retained in the sieve

were transferred into plastic boxes that contained Lake Erie mud and water. These boxes were then transferred into a 40-liter well-aerated aquarium and maintained at 12°C for about 2 to 10 days before the experiments began. All the animals were active when they were selected for the experiments.

¹³⁷Cs was used as the sediment tracer. Experiments showed that ¹³⁷Cs is strongly bound to illite particles with a $K_d > 5000$ (Robbins *et al.* 1979). It has a half-life of 30.2 years and a gamma-emitting energy of 662 KeV, sufficient to eliminate its adsorption by sediment. Microcosms containing multiple tracer layers were prepared using a method described by Krezoski and Robbins (1985). A layer of lake sediment was loaded into a microcosm (rectangular plastic cells 30 cm \times 5 cm \times 1 cm ID), then a submillimeter-thick ¹³⁷Cs-labeled illite tracer layer (~1 μ Ci) was laid atop the sediment. After the tracer particles settled, a layer of unlabeled lake sediment 1 to 2 cm thick was loaded atop the tracer layer. This process continued until the desired 5 to 7 tracer layers were added to each cell covering a total depth of 10 to 15 cm. The top tracer layer was at the sediment-water interface. The prepared cells were transferred into a 40-liter, temperature regulated (12°C) aquarium before the experiment started.

After the worms were introduced into the cells, the redistribution of sediment particles by the organisms was monitored by periodically vertically scanning the activity of ¹³⁷Cs in each cell with a NaI gamma detector. Vertical profiles of the ¹³⁷Cs activity were obtained at 0.2 cm intervals from 1 cm above the interface to a depth below the deepest tracer layer. The NaI gamma detector was coupled to a multi-channel analyzer (Fig. 1) and was protected from incident radiation by lead shielding 13 cm thick in front and 2.5 cm thick on the sides, except from a collimated slit 0.4 cm \times 5 cm in front extending the full width of a cell. The remaining shielding around the detector was provided from lead bricks. The detector was placed on an aluminum plate which was supported by four vertical screw rods and connected to a horizontal and vertical slider which was moved by two computer-operated stepper motors. The accuracy of repositioning was better than 0.01 mm. Since the cells were not disturbed during each scan, continuous migration of tracer-labeled particles could be measured. Sufficient counts were obtained in a single scan at each depth interval within 5 minutes. Scans were conducted on a daily basis for the first few days of the experiment and every 3 to 4 days after that until 10

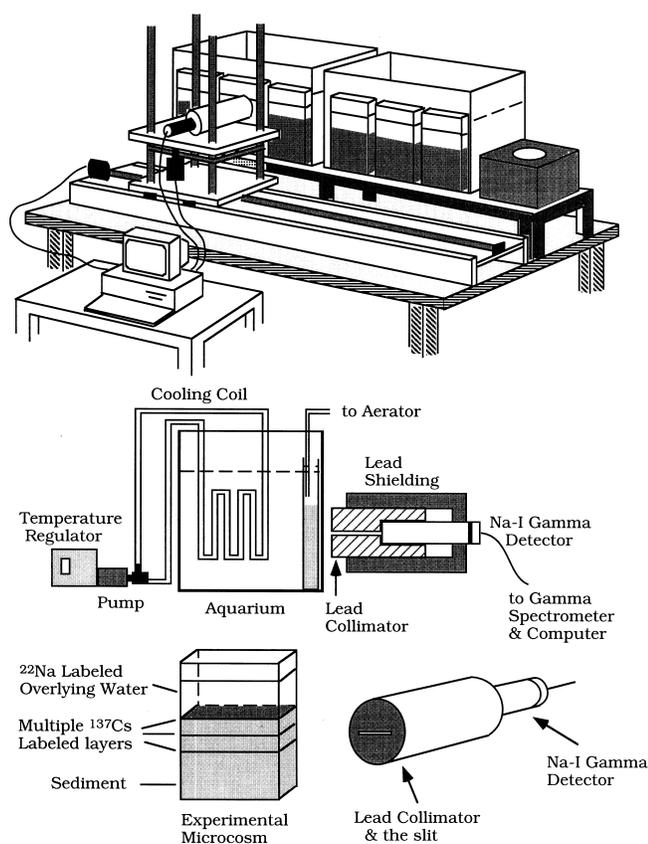


FIG. 1. Experimental gamma scan system. The top illustration shows the general layout of the equipment, the middle illustration shows a side view of the collimator/detector and the bottom figure illustrates the tracer layers in a microcosm and the slit in the collimator.

to 14 scans were completed for each cell in this 42-day experiment. Five experimental cells were used: 2 *B. sowerbyi* (4,000 indiv/m²), 4 *B. sowerbyi* (8,000 indiv/m²), 10 harbor worms (20,000 indiv/m²), 20 harbor worms (40,000 indiv/m²), and a control. The organism densities used in the experiments simulated natural to very high population densities. This helped facilitate the processes under observation without disturbing the system too much from natural conditions. The control cell served as a measure of the migration of ¹³⁷Cs caused by molecular diffusion through pore water. It was also used to monitor possible long-term electronic drift and changes of the efficiency of the detector system. Table 1 summarizes the experimental design.

Sediment porosity was measured using a ¹⁰⁹Cd gamma ray adsorption technique (Wang 1995)

based on the fact that the weak 0.088 MeV emission from the ¹⁰⁹Cd nuclide is partially attenuated when it penetrates through a sediment column. If the thickness of the sediment column and the detector geometry are fixed, then the attenuation of the ¹⁰⁹Cd gamma emission will be different for sediment having different porosities. An empirical relationship between ¹⁰⁹Cd activity and sediment porosity was determined which permitted evaluating the sediment porosity profiles non-destructively for all cells. In all organism-containing cells sediment porosity did not change significantly from surface to depth and ranged from 0.67 to 0.80. The cells with higher population densities had higher sediment porosities.

Model and Parameter Evaluation

Because *B. sowerbyi* and the worms from Cleveland Harbor (*L. hoffmeisteri* and *T. tubifex*) are conveyor-belt deposit feeders, quantitative interpretation of the mechanisms of sediment mixing by them was based on the model developed by Robbins (1986) and parameter evaluations were based on the procedures presented in Krezoski *et al.* (1984) and Krezoski and Robbins (1985). Robbins (1986) presents a governing equation for diffusive-style mixing with conveyor-belt feeding of a particle-bound radioactive tracer as

$$\frac{\partial \hat{C}}{\partial t} = \frac{\partial}{\partial Z} \left(D_b \frac{\partial \hat{C}}{\partial Z} \right) - \frac{\partial}{\partial Z} (\omega \hat{C}) - (\lambda + \gamma(Z)) \hat{C} \quad (1)$$

where

- \hat{C} = total tracer mass (g/cm³ bulk sediment),
- C = total tracer mass (g/g sediment solids)
- $\frac{\hat{C}}{\rho_s(1-\phi)}$
- ρ_s = mean density of the sediment solids (g/cm³),
- ϕ = porosity (cm³ water/cm³ bulk sediment) = $\phi(Z) = \phi_\infty + (\phi_0 - \phi_\infty) e^{-(\beta Z)}$,
- ϕ_∞ = porosity at depth,
- ϕ_0 = porosity at the sediment surface,
- β = constant which characterizes the rate of porosity change with depth,
- Z = sediment depth (cm) (positive downward),
- D_b = coefficient of diffusive mixing of bulk sediment by organisms (cm²/yr),
- ω = velocity of sediment solids relative to the interface (cm/yr),

TABLE 1. Experimental design, Gaussian model fitting results of the biodiffusion coefficient, D_b , Gaussian model fitting results of the tracer feeding rate, γ , and parameters used in the model simulations (Fig. 9).

| Model parameter | units | <i>B. sowerbyi</i> 4,000/m ² | <i>B. sowerbyi</i> 8,000/m ² | Harbor worms 20,000/m ² | Harbor worms 40,000/m ² | Description |
|-----------------|---------------------------|--|--|--|--|-------------------------------------|
| — | °C | 12 | 12 | 12 | 12 | Temperature |
| — | cm | 10 | 10 | 5 | 5 | Organism size |
| — | indiv/m ² | 4,000 | 8,000 | 20,000 | 40,000 | Population density |
| — | — | 6 | 6 | 5 | 5 | Number of tracer layers |
| ϕ_o | — | 0.80 | 0.67 | 0.80 | 0.80 | Sediment porosity at surface |
| ϕ_∞ | — | 0.79 | 0.67 | 0.80 | 0.80 | Sediment porosity at depth |
| β | 1/cm | 0.01 | 0.00 | 0.00 | 0.00 | Rate of porosity change |
| ρ_s | g/cm ³ | 2.50 | 2.50 | 2.50 | 2.50 | Density of sediment solids |
| R | g/cm ² /yr | 0.00 | 0.00 | 0.00 | 0.00 | Mass sedimentation rate |
| $t_{1/2}$ | yr | 30.2 | 30.2 | 30.2 | 30.2 | Tracer half-life |
| η | — | 2.0 | 2.0 | 1.0 | 1.5 | Particle selectivity factor |
| D_{max} | cm ² /yr | 0.78 | 1.03 | 0.72 | 0.20 | Maximum biodiffusion coefficient |
| D_b | cm ² /yr/indiv | 0.39 | 0.26 | 0.072 | 0.010 | Indiv. max biodiffusion coefficient |
| μ_{Db} | cm | 1.63 | 2.26 | 1.96 | 0.87 | Depth of biodiffusion |
| σ_{Db} | cm | 2.02 | 1.12 | 1.12 | 2.72 | Range of biodiffusion |
| γ_{max} | 1/yr | 9.10 | 13.86 | 8.13 | 13.11 | Maximum feeding rate |
| γ | 1/yr/indiv | 4.55 | 3.47 | 0.81 | 0.66 | Individual maximum feeding rate |
| μ_γ | cm | 13.62 | 11.74 | 5.21 | 5.27 | Depth of feeding |
| σ_γ | cm | 4.06 | 5.24 | 1.88 | 2.38 | Range of feeding |
| x | cm | 20 | 20 | 20 | 20 | Total simulation depth |
| dx | cm | 0.05 | 0.05 | 0.05 | 0.05 | Simulation depth increment |
| t | day | 365 | 365 | 365 | 365 | Total simulation time |
| dt | day | 0.1 | 0.1 | 0.1 | 0.1 | Simulation time increment |
| s | cm | 0.22 | 0.22 | 0.22 | 0.22 | Detector efficiency coefficient |

λ = radioactive decay constant for ¹³⁷Cs
(= 0.6932/ $t_{1/2}$) (1/yr),

$\gamma(z)$ = first order depth dependent feeding rate of
advectors on bulk sediments (1/yr).

This equation describes the time rate of change at any sediment depth of the total tracer concentration. The first term on the right hand side of Equation (1) accounts for diffusive mixing of bulk sediment by organisms. The second term accounts for tracer transport caused by advective processes. The model accounts for two advective processes: sedimentation and burial by conveyor-belt feeding. The last term on the right hand side of Equation (1) accounts for the loss (or gain) of the tracer at any depth by radioactive decay and advective feeding and includes particle selective feeding.

An accurate evaluation of each parameter based on a single profile from a single sediment core was practically impossible, because the resultant profile

was an integration of all processes occurring in the sediment. However, it was possible to extract information from the time series of scans to better constrain values for the parameters in Equation (1) which describe diffusive mixing and feeding (non-local mixing) and obtain estimates of their depth distributions.

Biological diffusive mixing of sediment results in a single tracer layer becoming wider and wider with time as the radiolabeled particles are mixed with adjacent unlabeled sediment (Robbins *et al.* (1979). An estimate of the spread at any time is obtained by determining the standard deviation of a Gaussian fitted to a peak (Krezoski and Robbins 1985). By determining the spreads of the peak at each scanned time, the rate of widening of the tracer layer is obtained by plotting the square of the standard deviations against time, and the corresponding biological diffusive mixing coefficient, D_b , at that depth is calculated from the slope of the resultant straight line

(McCall *et al.* (1995). In most cases, D_b is strongly depth dependent because organisms behaved differently at different depths and population density and organism type varied with depth which resulted in different mixing rates at different depths. By employing multiple tracer layers at different depths this depth dependency of D_b is determined. This process is repeated for all the tracer layers at different depths in a cell and the values of D_b are plotted versus depth to obtain the depth dependency of D_b (Matisoff 1995).

The effect of feeding on sediment mixing is either diffusive or non-diffusive, depending on the animal size and feeding behavior. For conveyor-belt deposit feeders, the most important effect is the removal of sediment particles from depth and their re-deposition on the surface (Robbins *et al.* 1979). This caused the sediment above the zone of feeding to be advected downward. The velocity of burial of tracer layers above the zone of feeding is determined by the repeated measurement of the position of the layers over time. This bulk sediment removal or feeding rate is different from the tracer feeding rate because the organisms may not necessarily feed on tracer particles at the same rate as they feed on unlabeled sediment particles. Instead, they have different values because the benthos preferentially select certain sizes or classes of particles and the fine grained tracer-labeled clay particles are preferentially selected compared to the bulk sediment. The downward velocities of the peaks are used to determine the particle selectivity factors using the method described in Krezoski and Robbins (1985).

The feeding rate (γ) is determined by measuring the rate of removal of labeled material from each layer. When tracer-labeled particles are removed from a tracer layer at depth and deposited onto the sediment surface, the activity in the tracer layer decreases which is reflected as a decrease in the area under the corresponding peak on the scanned profiles. Therefore, examination of the time series of the areas under individual peaks on the scanned profiles provides information on the rate of feeding and its distribution with depth. If the rate of feeding on bulk sediment particles is proportional to the rate of feeding on the tracer then the natural logarithm of the tracer concentration in a tracer layer (the area under the peak) when plotted against time is a straight line (Krezoski and Robbins 1985). The tracer feeding rate at the corresponding depth interval is determined from the slope of the line. This process is repeated for all the tracer layers at different depths in a cell and the obtained values of γ are

plotted versus depth to obtain the depth dependency of γ (Matisoff 1995).

After all the parameters were determined, the biological sediment mixing processes in the experimental cells were simulated with Equation (1) to evaluate individual sediment mixing processes as well as provide a prediction of the tracer profiles with extended mixing.

RESULTS

Both *B. sowerbyi* and the harbor worms immediately burrowed into the sediment to a depth equivalent to their body length (10 cm with *B. sowerbyi* and 5 cm with the harbor worms), then quickly extended their burrows to a depth of more than twice their body length. The worms displayed a conveyor-belt deposit feeding style (Rhoads 1974, Robbins *et al.* 1977), feeding head-down on fine particles at depth and depositing fecal pellets onto the surface. In all cases, a fine-grained brownish gray fecal pellet layer 5 to 8 cm thick formed on top of the surface during the 42-day experiment.

The scan results for selected times are shown in Figure 2. The positions of the tracer layers in each cell are well defined by corresponding activity peaks. Since the top tracer layer was initially at the sediment-water interface (SWI) its position on day 0 defines the SWI. Because the detector collimator slit has a finite width (0.4 cm), the detector response to a line source is a Gaussian that is broader than the actual thickness of the submillimeter line tracer source (Robbins *et al.* 1979). By 31 days the ^{137}Cs activity profiles in the cells containing organisms were highly modified, whereas no discernible changes had occurred in the control cell. Also shown in Figure 2 are the results of least squares Gaussian curve fits (lines) to the scan data, which provide estimates of peak position, peak spread or width, and the area under each peak. The scan profiles from the cells with worms showed some peak broadening with time. The biological diffusion mixing coefficient, D_b , can be estimated for each peak by first fitting a least squares straight line to the σ^2 versus t data for each peak and then calculating the value of D_b from the slope of the line (Fig. 3). As can be seen in Figure 3, the good linear relationships between σ^2 and t indicate that the values of D_b are well constrained.

The depth dependency of D_b in each cell was determined by plotting D_b versus mean depth of each peak. The parameter values are given in Table 1 and the curves are shown in Figure 4. D_b reached a

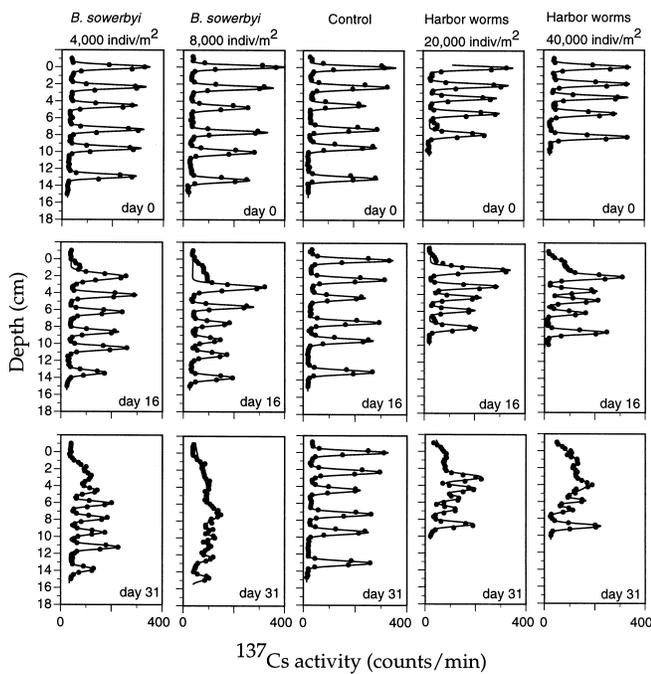


FIG. 2. ^{137}Cs activity distribution in the experimental microcosms containing *Branchiura sowerbyi* or *Limnodrilus hoffmeisteri*/Tubifex tubifex worms and in the control cell (no worms) over a time period of 31 days. Solid dots are measured activities. Lines are least squares multiple peak Gaussian curves.

maximum at about 2 cm and then decreased down-core to a non-zero value. D_b increased again to another maximum at ~ 9.5 cm in the cell with 8,000 *B. sowerbyi* /m² and at ~ 5 cm in the cell with 20,000 harbor worms/m². The second maximum was not observed in the other two cells. It can be seen in Figure 3 that the top tracer layer in the cell with 4,000 indiv/m² *B. sowerbyi* showed a decrease in D_b after 16 days. The decrease in D_b occurred because the top tracer layer gradually became buried and the newly added sediments at the surface caused it to compact so that the layer became thinner. This was also observed in the cell with 8,000 *B. sowerbyi* worms at times greater than shown on the graphs. On the other hand, by 31 days the top tracer layer was so smeared that it no longer defined a single layer (Fig. 2). At this point, measurements of the top tracer layer were fruitless.

The top tracer layer in the control cell only had 0.05 cm downward migration due to sediment compaction, whereas the tracer layers in the cells with

organisms, especially those near the sediment-water interface, have significant downward migration (Fig. 5). The continuous, linear downward migration rates during the entire experiment indicate that the organisms did not “run out of food” during the experiment and that the feeding rates were constant during the experiment and were unaffected by food supply. In 31 days the top tracer layers in the cells with 4,000 indiv/m² and 8,000 indiv/m² *B. sowerbyi* moved down 4.54 cm and 7.12 cm, respectively. This corresponds to downward migration velocities of the top tracer layers of 53.1 ± 1.87 cm/yr and 83.8 ± 2.56 cm/yr, respectively. In the cells with 20,000 indiv/m² and 40,000 indiv/m² harbor worms, the top tracer layers moved down 3.06 cm and 4.05 cm, respectively, or at downward velocities of 36.4 ± 0.97 cm/yr and 49.8 ± 1.85 cm/yr, respectively. These velocities are much higher than those caused by compaction in the control cell (~ 0.4 cm/yr) and illustrate the magnitude of sediment recycling by the worms. The greater slopes in the tracer layers near the surface indicate higher downward migration rates than those lower in the sediment. The downward migration rates are also greater in the cells with higher population densities. These downward velocities were used to calculate particle selectivity factors (Krezoski and Robbins 1985) and the values are given in Table 1.

Except in the control cell the area under each peak in Figure 2, which represented the total activity of ^{137}Cs in the layer, decreased with time (Fig. 6). This occurred because feeding by the organisms on sediment particles resulted in some of the ^{137}Cs labeled illite particles being removed from the tracer layer and transferred onto the surface, resulting in a decrease in the total activity in a tracer layer. Because the rate of feeding on bulk sediment particles was proportional to the rate of feeding on the tracer, the natural logarithm of the tracer activity in a tracer layer (the area under the peak) when plotted against time was a straight line whose slope was the tracer feeding rate at that depth. The rate of decrease in peak area is different at different depths, indicating that the feeding rate is depth dependent (Fig. 7). All cells showed a maximum feeding rate below the surface. For example, the observed depth of maximum feeding for *B. sowerbyi* was at about 13 cm, whereas it was at 5.2 cm for the harbor worms (Table 1). The depth distributions of the feeding rates varied from cell to cell, but they all were approximated as a Gaussian distribution using a least squares technique (Fig. 7, Table 1). However, the functional form used to describe

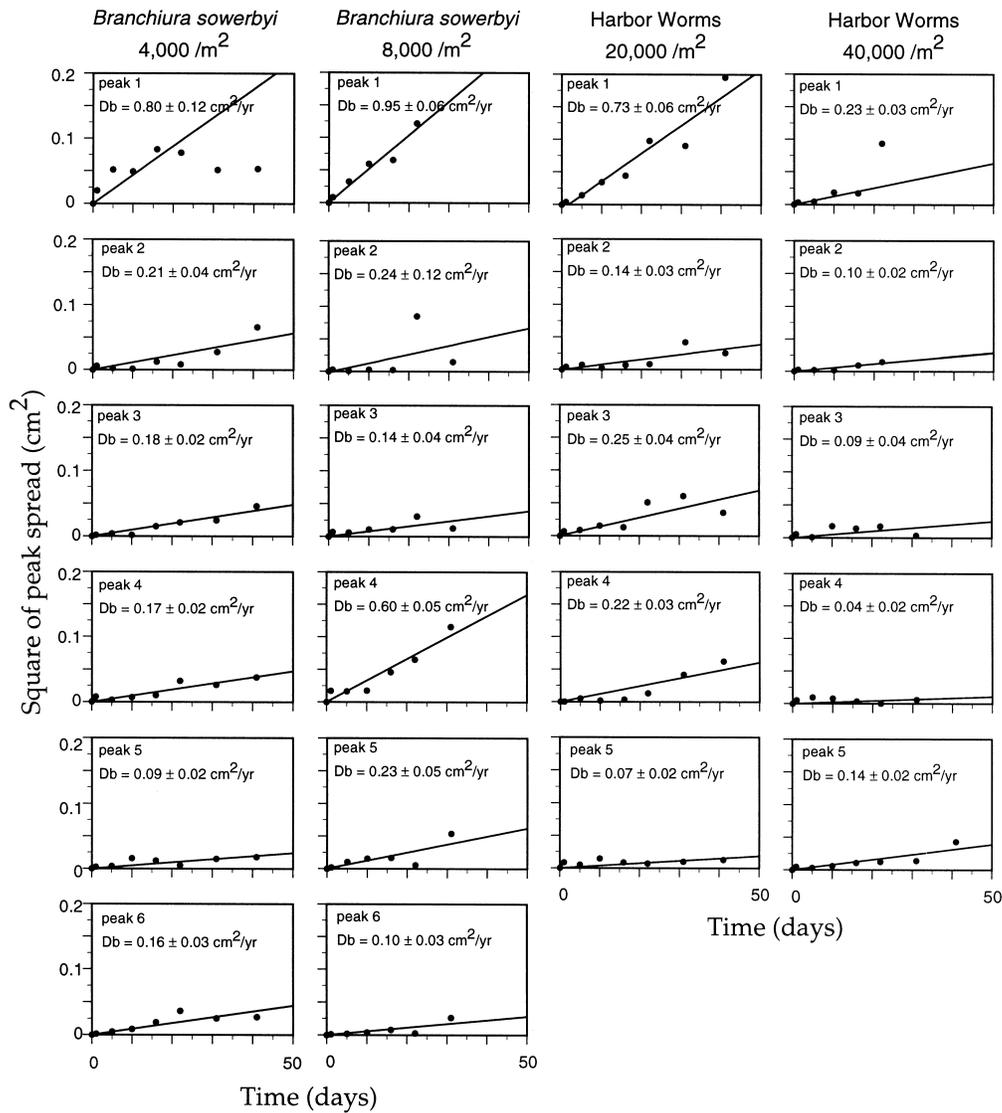


FIG. 3. Square of peak spread versus time in the cells containing *Branchiura sowerbyi* or *Limnodrilus hoffmeisteri*/Tubifex tubifex (harbor worms). The solid dots are the peak widths calculated from the experimental measurements. Straight lines are least squares fits to the data.

the depth dependency of feeding was arbitrary. In the control cell, no significant changes in peak area were observed (Fig. 2). Therefore, no further treatment was done for the control cell.

Mathematical Model

Both biodiffusion and feeding affect particle mixing. To gain some insight into the sensitivity of tracer profiles to the two styles of mixing, simulations using the mixing model (Eq. 1) were con-

ducted with a range of model parameters. Simple 2-layer diffusive mixing was simulated by assigning $\gamma = 0$ and using a D_b that was constant in the top 10 cm. The obliteration of a profile during 30 days of mixing are shown in Figure 8. The 2-layer mixing model (i.e., $\gamma = 0$) is shown for each of the three values of D_b ($D_b = \text{constant}$ over the top 10 cm), while the rest of the curves show the simulations of Equation (1) for a range of values in both D_b (distributed depth distribution, Robbins 1986) and γ

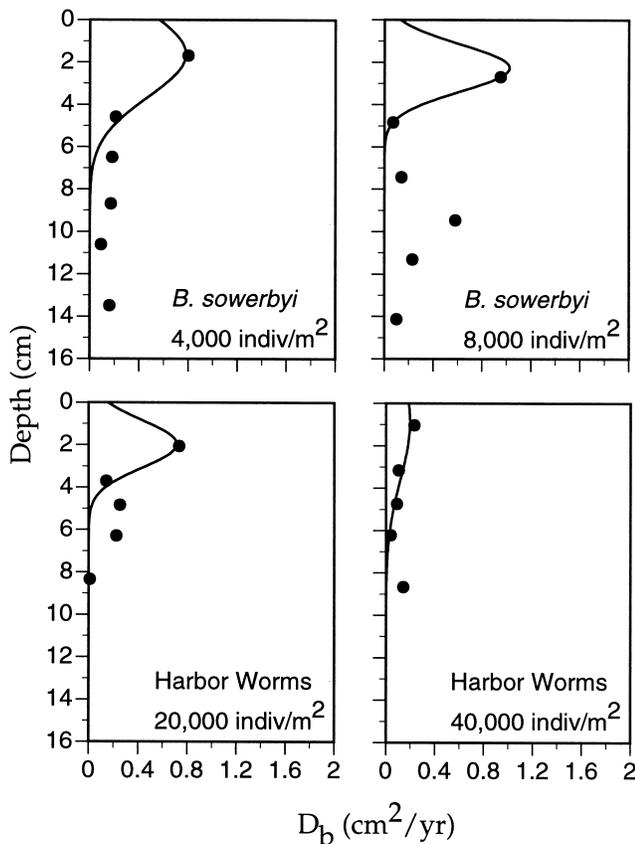


FIG. 4. Biodiffusion coefficient as a function of depth in the experimental cells. The solid dots are biodiffusion coefficients calculated from the slope of the lines in Figure 3. Lines are least squares Gaussian fits to the data.

(localized depth distribution, Robbins 1986). For large values of either D_b or γ , the profiles are completely obliterated within the zone of mixing. Conversely, for small values of D_b and γ the profiles remain relatively undisturbed. For values of D_b and γ in the range of those derived in the experiments ($D_b \sim 1.0 \text{ cm}^2/\text{yr}$; $\gamma = 10/\text{yr}$) it can be seen that the profiles are modestly disturbed, with the effects of feeding more significant than the effects of diffusive mixing (compare $D_b = 0.0 \text{ cm}^2/\text{yr}$ and $\gamma = 5.0/\text{yr}$ with $D_b = 1.0 \text{ cm}^2/\text{yr}$ and $\gamma = 0.0/\text{yr}$). How the profiles were obliterated differs in the two styles of mixing. Diffusive mixing broadens the peaks and raises the background activity until the peaks coalesce and blend into the background, whereas feeding decreases the peaks and raises the background until the peaks can no longer be detected above the background.

In the cells with organisms, D_b was strongly depth dependent (Fig. 4). This indicates that use of a constant D_b is insufficient to depict the real mechanisms of biological sediment mixing. On the other hand, the depth distribution of D_b varied from cell to cell indicating that the functional form of D_b may be organism or population density dependent. Selection of the functional form for D_b was somewhat arbitrary. For example, it is reasonable to assume that D_b will be proportional to the vertical distribution of the population density, that is, an exponential form might be appropriate. Or, mixing may occur over a restricted depth range about a feeding zone or a mixed population may have organisms of a variety of sizes. In these cases, a Gaussian function might be more suitable for describing the depth distribution of D_b . It has been shown that some tubificid oligochaetes have a maximum feeding rate well below the sediment-water interface (Fisher *et al.* 1980, McCall and Tevesz 1982). Mixing of this type may be better described as Gaussian. Therefore, for the purposes of obtaining a depth dependent functional form for D_b a Gaussian was fit to the data.

The parameters values (Table 1) were substituted into the sediment mixing model (Eq. 1) to simulate the sediment mixing processes that occurred in the organism-containing cells. The simulation results are shown in Figure 9. In general, the model simulation results mimic the measured tracer profiles in each cell fairly well which suggests that the assumptions and the mathematical treatment were reasonable. Some discrepancies occurred between the model simulation results and the measured tracer profiles. As seen in Figure 9, the feeding rate, γ , used in the model simulation was slightly overestimated for the two cells with *B. sowerbyi* worms (model simulated peaks had higher downward migration rates than the measured rates) as was the particle selectivity factor (model simulated peak areas decreased faster than the measured areas). For the cells with the harbor worms, the γ seemed well estimated, but the particle selectivity factor, η , was slightly overestimated (Fig. 9). These discrepancies are mostly due to the error obtained by assuming a single Gaussian functional form for the sediment feeding rates and biodiffusion rates. The model simulations were conducted after all the parameters had been determined, not by fitting the model to the measured data. The close match between the modeling results and the measured profiles indicates that the model very well described the mixing processes.

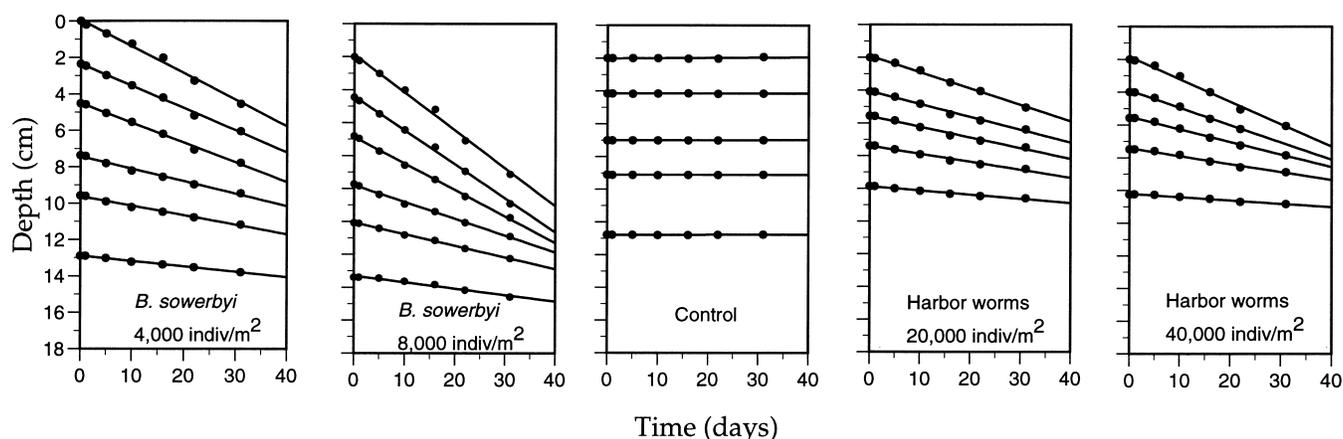


FIG. 5. Tracer layer positions versus time for all tracer layers in all microcosms. Solid dots are measured peak positions. Straight lines are least squares fits to the data.

DISCUSSION

Figures 2 and 5 show that the tracer layers in the cells with organisms exhibited downward migration during the experiment. Sediment particles injected at depth were deposited on the surface causing the downward migration of sediment. Therefore, it is possible that sediments could be recycled through the feeding zone many times before ultimate burial below the zone of feeding. Where the sediment is inhabited by dense populations of these organisms, any contaminants deposited onto the sediment surface would be extensively recycled within the surficial sediment for further resuspension and redistribution.

The downward velocities in each cell may be compared to each other by normalizing the rates to the number of individuals in the experiment. These velocities at 20°C are 3.66 and 2.87 cm/d/100,000 indiv/m² for the cells with 4,000 and 8,000 *B. sowerbyi*/m², respectively, and 0.49 and 0.33 cm/d/100,000 indiv/m² for the cells with 20,000 and 40,000 *L. hoffmeisteri*+*T. tubifex*/m², respectively. These subduction velocities agree well with those reported by various authors for *T. tubifex* and *L. hoffmeisteri* (0.10 to 0.68 cm/d/100,000 indiv/m²) (McCall and Tevesz 1982, Table III). However, the subduction velocities determined for *B. sowerbyi* in this study (2.87 to 3.66 cm/d/100,000 indiv/m²) are considerably greater than recycling rates previously reported for any other freshwater oligochaete. This recycling can be calculated as a sediment flux across the sediment-water interface and is 66.4 to 86.4 g dry sediment/indiv/m²/yr in cells with *B. sowerbyi*, and

5.91 to 9.09 g dry sediment/indiv/m²/yr in cells with harbor worms. Using average biomasses of 13 mg/indiv for *B. sowerbyi* and 1 mg/indiv for harbor worms, the recycling fluxes are comparable: 5.11 to 6.65 g dry sediment/mg biomass/m²/yr for *B. sowerbyi* and 5.91 to 9.09 g dry sediment/mg biomass/m²/yr for *L. hoffmeisteri* / *T. tubifex*. These results indicate that although *B. sowerbyi* recycles more sediment than the smaller species of oligochaetes, this is a consequence of its larger size.

Unlike the other tracer layers, the peak area of the top tracer layer in the cells with organisms increased in the first 15 to 20 days (Fig. 6). This initial increase in peak area is caused by the surface deposition of tracer-labeled particles by the worms during conveyor-belt feeding on subsurface tracer-labeled particles. Later, when the top tracer layer migrated down into the feeding zone, organisms started to feed on the sediments in this layer. As a result, the activity or the peak area of this tracer layer started to decrease. This also indicates that tubificid oligochaetes fed mostly at depth, not at the surface.

Tracer profiles for the experimental cells were simulated for times extending beyond the length of the experiment. The tracer profiles for the two cells with *B. sowerbyi* worms were nearly identical after 365 days (Fig. 9). This suggests that even though the population densities in these two cells are different, the resultant effect of the biological mixing by *B. sowerbyi* on sediment properties after a long time period is the same. The predicted tracer profiles in the two cells with the harbor worms look slightly different after 365 days. For the cell with

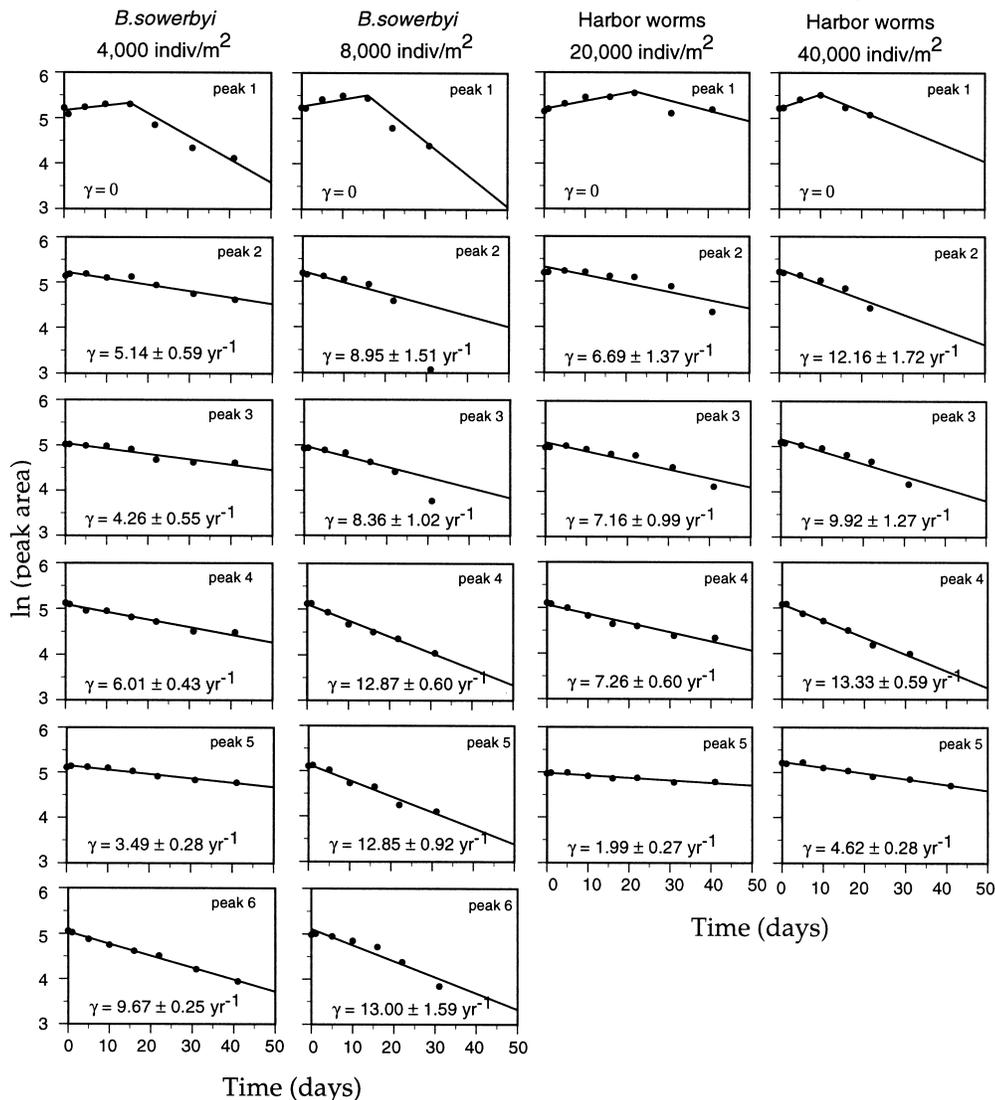


FIG. 6. Tracer peak area versus time in the microcosm cells containing *Branchiura sowerbyi* or *Limnodrilus hoffmeisteri*/*Tubifex tubifex* (harbor worms). The solid dots are the peak areas calculated from the experimental measurements. Straight lines are least squares fits to the data.

8,000 indiv/m² harbor worms, more tracer is retained in the upper 6 cm of the sediment column. The tracer-labeled particles are more evenly distributed within the top 9 cm of the sediment column in the cell with 4,000 indiv/m² harbor worms. This occurs because the cell with a higher population had a higher sediment feeding rate and a higher particle selectivity factor, so that the tracer-labeled particles were recycled within the feeding zone (< 6 cm) at a higher rate. Tracer profiles in these two cells even-

tually become similar because there is no external sedimentation in these experiments. However, in a natural setting, profile shapes could be different depending upon the organism types, population densities, and sedimentation rates. The mixing process in both cells will approximate a steady-state condition, but it will take a shorter time for the higher population cell to reach this steady-state condition. If there were external sedimentation and some of the tracer were continuously buried, the cell with the higher

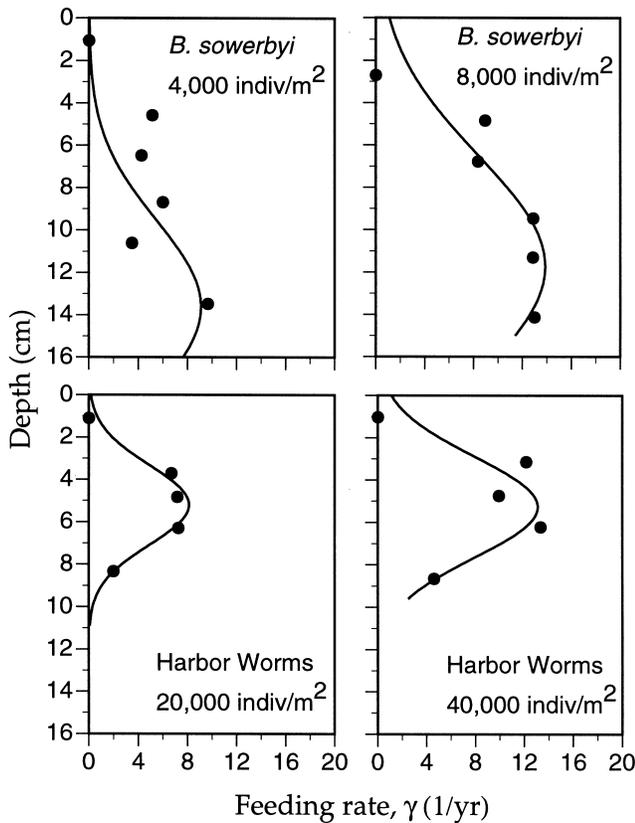


FIG. 7. Feeding rate as a function of depth in the experimental cells. The solid dots are feeding rates calculated from the slopes of the lines in Figure 6. Lines are least squares Gaussian fits to the data.

population density will have more tracer retained within the feeding zone. Figure 9 shows that after 365 days the tracer layers in the cell with 20,000 indiv/m² harbor worms are homogenized within the feeding zone, but in the cell with 40,000 indiv/m² harbor worms more than 70% of the tracer labeled particles are retained in the upper 6 cm sediment column after 365 days.

Although the tubificid oligochaetes used in these experiments intensively mixed the sediment, the obliteration of the peaks occurred more by loss of the peak to background signal than by overlapping of peaks by broadening. This indicates that mixing by diffusive processes were subordinate to mixing induced by feeding. In the two cells containing *B. sowerbyi* worms, the biodiffusion coefficient, D_b , ranged from 0.09 to 0.95 cm²/yr. In the cells with the harbor worms, D_b ranged from 0.04 to 0.73 cm²/yr. By comparison, the molecular diffusion coefficient of ¹³⁷Cs in the control cell was 0.04 ± 0.01 cm²/yr. Values for D_b in the Great Lakes obtained by using geochemical tracers (Robbins *et al.* 1979, Christensen and Bhumia 1986, Fukumoni *et al.* 1992) ranged from 0.02 to 12 cm²/yr, and in the western basin of Lake Erie, Robbins *et al.* (1978) calculated a mixing rate of 1 cm²/yr. These field-derived values are in agreement with the results of this study in which organism densities similar to those in the field were used.

D_b reached a maximum at about 2 cm in all cells

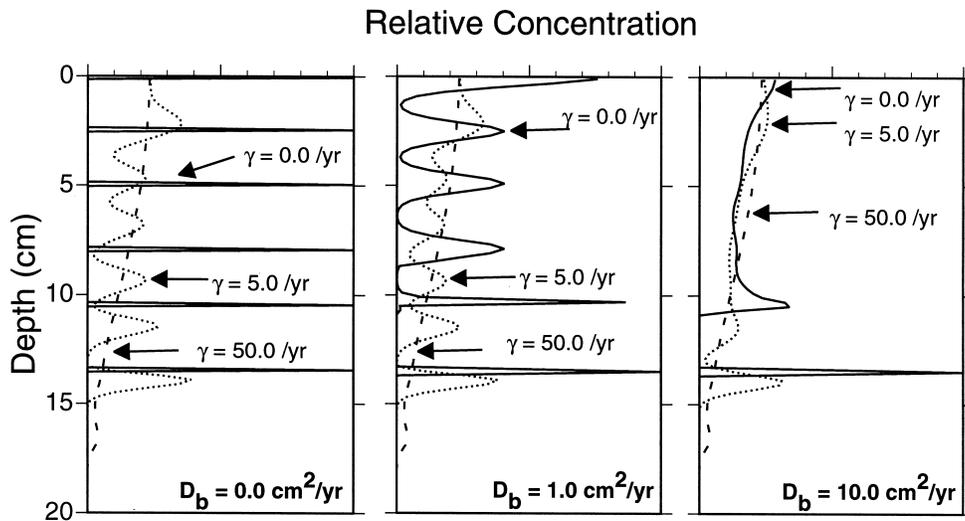


FIG. 8. Sensitivity of tracer profiles to variations in the diffusive mixing coefficient, D_b , and the feeding coefficient, γ . Simulation conditions: mixing depth = 10 cm; D_b = constant (when $\gamma = 0$) or is distributed ($\gamma \neq 0$); feeding depth = 10 cm; feeding distribution = localized, spread = 5 cm.

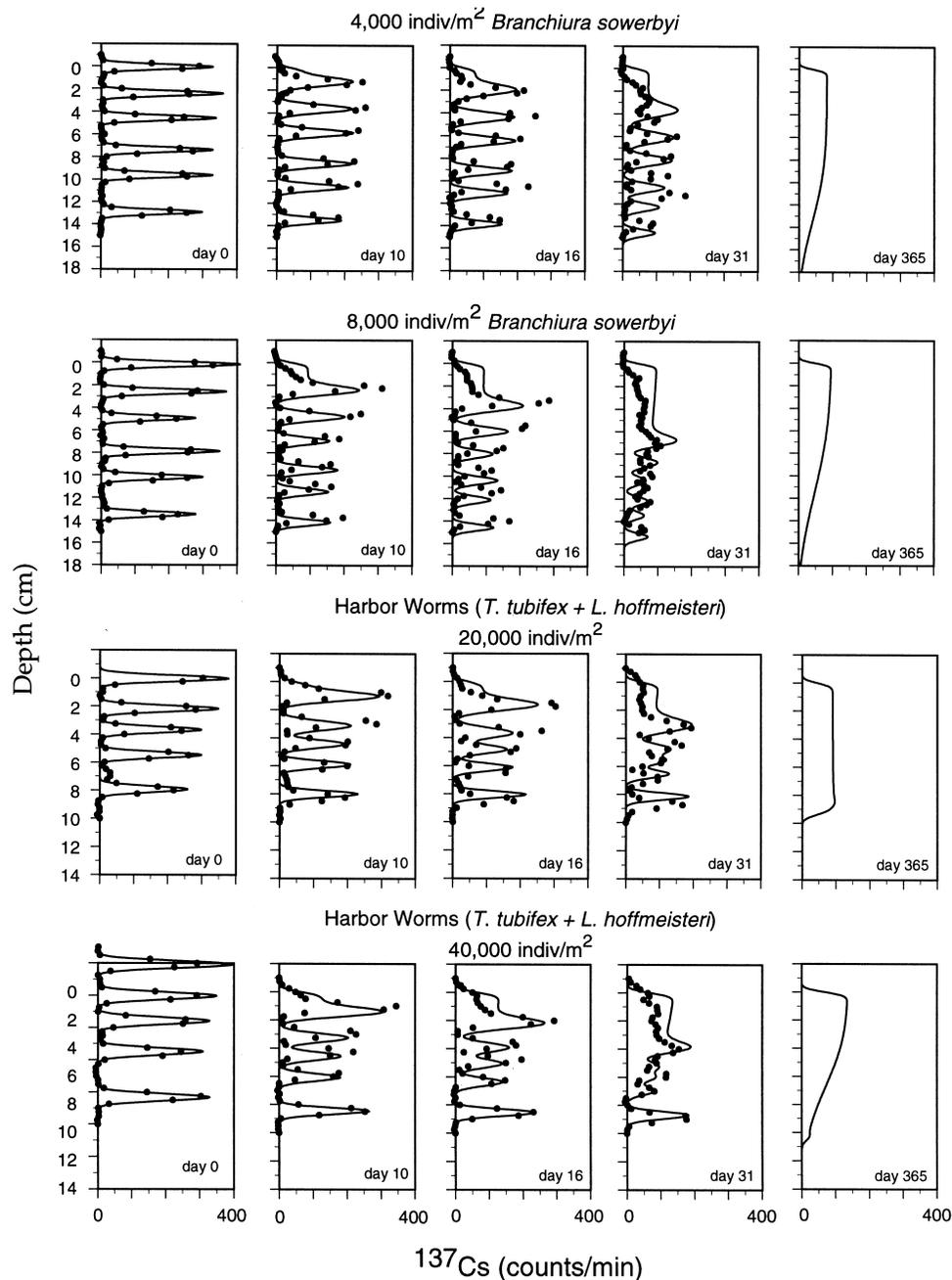


FIG. 9. Model simulations of the ^{137}Cs activity profiles in the microcosm cells containing *Branchiura sowerbyi* or *Limnodrilus hoffmeisteri*/*Tubifex tubifex* (harbor worms). The solid dots are measured activities. Lines are model simulations using Eq. (1) and the independently determined parameter values listed in Table 1.

with organisms and a secondary, deeper maximum was observed in some of the cells. There are two reasons for D_b to exhibit a maximum at 2 cm. First, the maximum mixing might be caused by the initial locomotion and burrowing of the organisms when

they were introduced into the cells. Second, differential downward migration and heterogeneous compaction of the sediment above the feeding zone may have created a mixing maximum artifact. It was observed that sediments near the center of the cell

moved down faster than those near the cell walls because of frictional drag between the sediment and the cell walls. As a consequence, the tracer layers were bent downward in the center of the layer, with greater bending the closer the tracer layers were to the surface. The effect of this bending of the tracer layers on a scanned profile appeared to the detector as a widening of the tracer layers. The D_b maximum lower in the sediment is likely from feeding activities at the bottom of the feeding zone. The use of a single Gaussian to characterize the depth distribution of D_b results in a poor fit between the model and the data, especially for the cell with 8,000 indiv/m² *B. sowerbyi*. Two Gaussian functions, with one centered about the 2 cm depth mixing maximum and one centered about the lower D_b maximum caused by feeding would fit the data significantly better. However, this curve fitting is somewhat unimportant because the magnitude of mixing by diffusive processes is relatively small compared to the mixing by feeding. In fact, the distribution of D_b does not have to be very well defined because its contribution to modification of the scanned profiles was small relative to the advective processes.

The depths of maximum feeding in the cells with 8,000 indiv/m² *B. sowerbyi* (11.74 cm) and with 20,000 indiv/m² harbor worms (5.21 cm) matched the depths of the lower D_b maximum very well. The depth of maximum feeding in the cell with 4,000 indiv/m² *B. sowerbyi* was 13.62 cm, which is also very close to the depth of the increased D_b observed for the bottom tracer layer (~13.5 cm). In the cell with 40,000 indiv/m² harbor worms the increased D_b in the bottom tracer layer was at a depth of about 8.7 cm, whereas the maximum feeding occurred only at a depth of about 5.27 cm. It is not clear what caused this discrepancy. It might be due to the higher population density in this cell, or, because the D_b value was so low even a small number of individual random movements might have caused a relatively large increase in the value of D_b . These results suggest that much of the diffusive mixing is a consequence of feeding processes.

The difference in the depth of maximum feeding between these two species may be attributed to their different sizes. Tubificid worms tend to feed at depths close to their body lengths, and since *B. sowerbyi* (~10 cm) was larger than the harbor worms (~5 cm) it fed deeper and over a much wider vertical range than the harbor worms. However, other factors such as population density may also contribute to the feeding depth range.

A higher population density caused a higher feeding rate, which resulted in a higher recycling rate of the sediments about the feeding zone. This is supported by the data from experiments with different animal densities. The top tracer layer in the cell with 8,000 indiv/m² *B. sowerbyi* worms moved down 7.12 cm during the experiment, whereas it only moved down 4.54 cm in the cell with 4,000 indiv/m² *B. sowerbyi* worms. Similarly, in the cells with 40,000 indiv/m² and 20,000 indiv/m² harbor worms, the top tracer layer moved down 4.05 and 3.06 cm, respectively. Although the population densities in the cells containing harbor worms were much higher than that in the cells with *B. sowerbyi*, there was less downward migration because the individual harbor worms were smaller and had a lower feeding rate. This result indicates that a dominant species in terms of population density may not necessarily be the dominant species in terms of sediment mixing.

An increased population density resulted in greater values of γ , D_b , and η . Using the determined γ and D_b , the downward migration or burial rate of sediment due to feeding was calculated for each cell using various particle selectivity factors, η , and compared with the measured tracer layer burial rates. The rates from the two cells with *B. sowerbyi* agreed best with a particle selectivity factor of 1.5 to 2.0, which indicated that the worms preferentially fed on tracer-labeled fine illite particles. A particle selectivity factor of 1.5 was obtained in the cell with 40,000 indiv/m² harbor worms, but the data from the cell with 20,000 indiv/m² harbor worms was best described using a particle selectivity factor of 1.0. These results are in general agreement with the observations of McCall and Fisher (1980) that oligochaetes usually ingest organic-rich materials which are often associated with fine-grained sediment particles, and those of Krezoski and Robbins (1985) who obtained a feeding selectivity factor of 1.7 for the conveyor-belt deposit feeding Lumbriculid oligochaetes. These results also indicate that when the population density is low, the worms feed equally on tracer-labeled and non-labeled sediment particles, but when the population is high they tend to selectively feed on organic-rich tracer-labeled particles because of competition for food.

A major difference between the cells with the different types of oligochaetes is that the tracer layers were mixed and homogenized to much deeper depths in the cells with *B. sowerbyi* than in the cells with the harbor worms. The larger size of *B. sower-*

byi was responsible for this. The implication of this is that in places where most of the bottom-dwelling organisms are short conveyor-belt deposit feeders, pollutants that are introduced into the system would be expected to be retained and recycled within a shallow depth zone and be frequently available for resuspension. On the other hand, in places where most of the bottom-dwelling organisms are larger conveyor-belt species, pollutants will be retained in the surficial mixing zone for a longer period of time.

In conclusion, experiments using tracer-labeled particles permitted comparison of the rates and depth distribution of diffusive and advective particle reworking by conveyor-belt oligochaetes. Although the population densities in the cells containing harbor worms were much higher than those in the cells with *B. sowerbyi*, there was less downward migration because individual harbor worms were smaller and had lower feeding rates. This result indicates that the most abundant species in a benthic community may not necessarily be the dominant species in terms of sediment mixing, and, in this case, reworking rates were comparable on a biomass basis. Mixing by diffusive processes was subordinate to mixing induced by feeding. Sediments could be recycled through the feeding zone many times before ultimate burial below the zone of feeding. Where the sediment is inhabited by dense populations of these organisms, any contaminants deposited onto the sediment surface would be extensively recycled within the surficial sediment for further resuspension and redistribution. The higher the population density the higher the feeding rate and particle selectivity, so that more tracer is retained within the feeding zone. These results also indicate that when the population density is low, the worms feed equally on tracer-labeled and non-labeled sediment particles, but when the population is high they tend to selectively feed on organic-rich tracer-labeled particles because of competition for food.

ACKNOWLEDGMENTS

Reviews by Mark Green and Josephine Aller greatly improved the paper. This work was supported by EPA contract R-817278-01-0.

REFERENCES

- Christensen, E. R., and Bhumia, P. K. 1986. Modeling radiotracers in sediments: Comparison with observations in Lakes Huron and Michigan. *J. Geophys. Res.* 91:8559–8571.
- Fisher, J. B., Lick, W. J., McCall, P. L., and Robbins, J. A. 1980. Vertical mixing of lake sediments by tubificid oligochaetes. *J. Geophys. Res.* 85:3997–4006.
- Fukumoni, E., Christensen, E. R., and Klein, R. J. 1992. A model for ^{137}Cs and other tracers in lake sediments considering particle size and the inverse solution. *Earth Planet. Sci. Lett.* 114: 85–99.
- Gerino, M., Aller, R.C., Lee, C., Cochran, J.K., Aller, J.Y., Green, M.A., and Hirschberg, D. 1998. Comparison of different tracers and methods used to quantify bioturbation during a spring bloom: $^{234}\text{thorium}$, luminophores and chlorophyll a. *Estuar. Coast. Shelf Sci.* 46: 531–547.
- Krezoski, J. R., and Robbins, J. A. 1985. Vertical distribution of feeding and particle-selective transport of ^{137}Cs in lake sediments by Lumbriculid Oligochaetes. *J. Geophys. Res.* 90(C6): 11,999–12,006.
- _____, Robbins, J. A., and White, D. S. 1984. Dual radiotracer measurement of zoobenthos-mediated solute and particle transport in freshwater sediments. *J. Geophys. Res.* 89(B90): 7937–7947.
- Matisoff, G. 1995. Effects of bioturbation on solute and particle transport in sediments. In *Metal Contaminated Aquatic Sediments*, ed. H. Allen, pp. 201–272. Ann Arbor Press.
- McCall, P. L., and Fisher, J. B. 1980. Effects of tubificid oligochaetes on physical and chemical properties of Lake Erie sediments. In *Aquatic Oligochaete Biology*, pp. 253–317, ed. R. O. Brinkhurst and D. G. Cook. New York: Plenum Press.
- _____, and Tevesz, M. J. S. 1982. The effects of benthos on physical properties of freshwater sediments. In *Animal-Sediment Relations*, pp. 105–176, ed. P.L. McCall and M.J.S. Tevesz. New York: Plenum Press.
- _____, Matisoff, G., and Tevesz, M. J. S. 1986. The effects of a unionid bivalve on the physical, chemical, and microbial properties of cohesive sediments from Lake Erie. *Amer. J. Sci.* 286:127–159.
- _____, Tevesz, M.J.S., Wang, X., and Jackson, J.R. 1995. Particle mixing rates of freshwater bivalves: *Anodonta grandis* (Unionidae) and *Sphaerium striatinum* (Pisidiidae). *J. Great Lakes Res.* 21: 333–339.
- Nalepa, T. F., Hartson, D.J., Gostenik, G.W., Fanslow, D.L., and Lang, G. A. 1996. Changes in the freshwater mussel community of Lake St. Clair: from Unionidae to *Dreissena polymorpha* in eight years. *J. Great Lakes Res.* 22:354–369.
- Rhoads, D. C. 1974. Organism-sediment relations on the muddy sea floor. *Oceanogr. Mar. Biol. Ann. Rev.* 12:263–300.
- Robbins, J. A. 1986. A model for particle-selective transport of tracers in sediments with conveyor-belt deposit feeders. *J. Geophys. Res.* 91(C7):8,542–8,558.
- _____, Krezoski, J. R., and Mozley, S. C. 1977. Radioactivity in the sediments of the Great Lakes: Post-depositional redistribution by deposit-feeding organisms. *Earth Planet. Sci. Lett.* 36:325–333.

- _____, Edgington, D. N., and Kemp, A. L. W. 1978. Comparative ^{210}Pb , ^{137}Cs , and pollen geochronologies of sediments from Lakes Ontario and Erie. *Quaternary Res.* 10: 256–278.
- _____, McCall, P. L., Fisher, J. B., and Krezoski, J. R. 1979. Effect of deposit feeder on migration of ^{137}Cs in lake sediments. *Earth Planet. Sci. Lett.* 42: 277–287.
- _____, Keitly, T., White, D.S., and Edgington, D.N. 1989. Relationships among tubificid abundances, sediment composition, and accumulation rates in Lake Erie. *Can. J. Fish. Aquat. Sci.* 46:223–231.
- Soster, F. M. 1984. Colonization by benthic invertebrates in western Lake Erie following sediment disturbance. Ph.D. dissertation. Case Western Reserve University. Cleveland, OH.
- _____, and McCall, P. L. 1990. Benthos response to disturbance in western Lake Erie: field experiments. *Can. J. Fish. Aquat. Sci.* 47(10): 1970–1985.
- Wang, X. 1995. Biogenic Mass Transport in Great Lakes Sediments. Ph.D. dissertation. Case Western Reserve University. Cleveland, OH.

Submitted: 19 August 1998

Accepted: 13 December 1998

Editorial handling: Michael J. S. Tevesz