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Modeling of advective solute transport in sandy sediments inhabited by the lugworm *Arenicola marina*

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ABSTRACT

Irrigation by the lugworm *Arenicola marina* has a major impact on solute transport and distributions in nearshore environments due to the subsurface injection of overlying water at depth (typically 15–20 cm) and the resulting advective water flow within the sediment back toward the sediment surface.

A mechanistic one-dimensional diffusion and advection model which emphasizes the injection and advective transport of solutes within the sediment not described in previous irrigation models was developed to describe irrigation by *A. marina*. The model was verified by comparing its results to measured pore-water tracer (Br) profiles and it is concluded that the model adequately described the experimental tracer profiles, including the characteristic subsurface peaks often observed in sediments inhabited by lugworms. There are three model output parameters, $P(t)$, κ and β , which contain biological information about irrigation. $P(t)$ is the pumping rate of *A. marina* [ml/h]. κ describes the ratio between the area of the advective transport zone (i.e. zone affected by the return advective transport of irrigation water) and the total area of the sediment core [dimensionless]. Finally, β is a measure of the increased effectively diffusive transport due to the presence of *A. marina* [cm²/h]. Pumping rates were estimated to 8.8–21.3 mL H₂O/g/h which are within the range of reported values for *A. marina*. Model calculations of κ were between 0.1 and 0.53, equivalent to areas of 5.5 to 29 cm², indicating that water was more or less locally transported to the sediment surface. In all simulations β was greater than 1 indicating that diffusion-like transport was enhanced by lugworms, affecting solute transport.

1. Introduction

The lugworm *Arenicola marina* is an important bioturbator in nearshore environments capable of mixing both sediment particles and water up to 30 cm below the sediment surface (Reise, 1985). *A. marina* is a head-down conveyor-belt feeder (Rhoads, 1974) feeding on sediment at depth, typically at 10–20 cm depending on worm size. Feeding activity results in vertical transport of particles downward in the sediment column as well as defecation at the water-sediment interface. Sediment particles are thus transported over long distances. Irrigation by *A. marina* results in water movement in the opposite direction of the particle transport. The worm irrigates the sediment by pumping oxygen-rich water

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down its J-shaped tube by peristaltic movements (Andersen and Kristensen, 1991). Water leaves the tube at the closed end where it is injected into the feeding pocket, resulting in an upward, advective transport of pore water (Wells, 1966; Rijken, 1979; Hüttel, 1990).

Bioturbation by *A. marina* can have major impact on marine habitats. Particle reworking and irrigation result in physical and chemical changes such as increased porosity due to funnel creation (Krantzberg, 1985) and increased oxygen penetration caused by the water current (Reise, 1985) which affect degradation of organic matter and lead to changes in the redox status of the sediment (Banta *et al.*, 1999). Bioturbation also stimulates nutrient fluxes (Krantzberg, 1985; Hüttel, 1990) and influences pH gradients by removing acidic metabolites (Reise, 1985).

The needs to characterize and quantify the effects of bioturbation in sediments have resulted in the development of several types of bioturbation models. The effects of infaunal irrigation on solute transport have generally been modeled using three different approaches (1) the diffusion analogy (Aller, 1982), (2) Aller's radial diffusion model (Aller, 1980a–c) and (3) the related nonlocal irrigation model (Emerson *et al.*, 1984; Boudreau, 1984). The diffusion analogy introduced by Goldberg and Koide (1962) is based on the assumption that the activity of sediment-dwelling and -irrigating organisms causes random movement of particles or solutes, resulting in a transport of particles or pore water along a concentration gradient in a similar manner as molecular diffusion. In these models, bioturbation is described and quantified by calculating an apparent enhanced diffusion coefficient that describes the increase in particle or solute transport relative to that expected from molecular diffusion alone (Guinasso and Schink, 1975; Aller, 1982; Wheatcroft *et al.*, 1990; Aller and Aller, 1992). Mathematical models based on the diffusion analogy can adequately describe situations only where the length scale for biological transport of material is less than the scale of the solute profile or where the mixing is approximately stochastic (Boudreau, 1996).

Exchange of material between nonadjacent points in the sediment, which is often the case for tube-dwelling organisms, cannot, however, be modeled as a diffusive transport since the transport distances are too great and the solute movement is not random. These cases can often be treated by nonlocal mixing models (Imboden, 1981) or radial diffusion models (Aller, 1982), which simulate situations where overlying water and solutes are pumped into an organism's tube and thus transported over large vertical distances, during and after which solutes are exchanged locally with the surrounding pore water by diffusion. In both models the effect of irrigation depends on and is calculated from the surface area of the worm's tube or burrow and the diffusion coefficient (Boudreau, 1984). The effects of irrigation by *A. marina* cannot, however, be characterized as diffusion but instead as direct injection of water and advective transport. Solute profiles resulting from irrigation by *A. marina* are often characterized by a subsurface solute peak (Rasmussen *et al.*, 1998) that results from the nonstochastic and nonlocal water transport caused by *A. marina*. Injected water returns to the sediment surface along the path of least resistance, usually within the feeding funnel (Hüttel, 1990), leading to a rapid, advective solute transport. This transport

Table 1. Input parameters (I , φ , W_w , r , PI) used in the irrigation model. See text for further explanation.

Profile number	Incubation time (h)	Porosity φ	[Br ⁻] in olw. start	[Br ⁻] in olw. end	Ww of lugworm (g)	Radius of tube (cm)	Pumping Interval (zone 2) (cm)
2a	1.20	0.32	12.7	11.3	0.6	0.15	17–18
2b	1.30	0.31	10.7	9.7	1.3	0.25	17–18
2c	1.26	0.33	13.3	11.2	3.6	0.30	19–21
2d	1.40	0.31	10.4	9.6	1.2	0.25	17–19 [†]
2e	1.60	0.3	13.1	9.8	3.8	0.30	25.5–27.5 [†]
2f	1.90	0.33	12.6	7.3	6.2	0.35 ^{††}	20–23.5

[†] Pumping interval is based on model fit and not observed depth of the lugworm.

^{††} The tube radius of the large lugworm (2f) was calculated by extrapolating the relation between body weight and tube radius (see “input parameters”) to 6.2 gram since worms of this size were not within the range of worms used to estimate the body weight-tube radius relation.

can be mechanistically described neither as enhanced diffusion (Boudreau, 1986; Wheatcroft *et al.*, 1990) nor as nonlocal mixing (e.g. Martin and Banta, 1992).

The aim of this paper is to present a model that mechanistically simulates solute transport in sediments irrigated by *A. marina* and which emphasizes the effect of injection and advective transport within the sediment. Furthermore, we intended the model to provide biologically relevant parameters useful for, e.g., comparing the activities of different lugworms or different populations.

2. Methods

a. Experimental

The irrigation model described in this paper simulates solute transport in sediments inhabited by the lugworm *Arenicola marina*. The model was tested and output parameters estimated by fitting pore-water Br⁻ profiles from an experiment conducted by Rasmussen *et al.* (1998). As part of that study, dissolved Br⁻ was used as an irrigation tracer (Aller and Aller, 1992; Martin and Banta, 1992). Briefly, 10 mM KBr was added to water overlying the sediment cores (height 35 cm, inner diameter 8.2 cm, sediment height 25 cm, overlying water volume 250 ml) containing 1 lugworm (equivalent to a density of 190 m⁻²). The sediment used in these experiments was sandy with a low porosity (Table 1) and although the hydraulic conductivity was not measured, pore water drained easily, indicating that the sediment was very permeable. Lugworms ranged in size from 0.6 to 6.2 g wet weight (without gut contents). After incubating for 1.2–1.9 h, cores were sectioned in layers 0.5, 1, 2 or 3 cm thick, with thicker sections in the deeper sediment layers. For bioturbated sediments with an uneven sediment surface the location of the sediment surface was defined as the mean between the highest and lowest points at the end of the incubation. Given the irrigation pattern of *A. marina* with long periods of continuous pumping activity

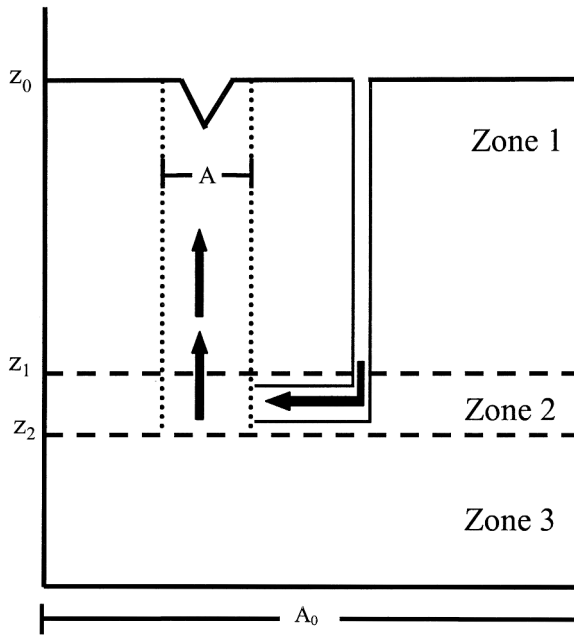


Figure 1. Conceptual description of the irrigation model. Arrows indicate the transport of water (and solutes) within the sediment due to irrigation by *Arenicola marina*. Solutes are injected from the overlying water into the sediment (zone 2) and transported from zone 2 to the sediment surface. Below the bioturbated zone (zone 3) solutes are affected only by diffusion. A_0 represents the total area of the sediment core while A represents the area affected by advective transport of water.

(40–50 min) and short periods of rest (a few min) (Krüger, 1966) the incubation times used (Table 1) were long enough to ensure a representative mean irrigation rate while still being short enough to avoid a steady state tracer concentration to be reached (Fig. 2).

Pore-water was centrifuged from each sediment section ($1500 \times g$ for 1 min) and filtered through a GF/C filter using scintillation vials with modified caps (Thomsen and Kristensen, 1997). Wet and dry sediment densities were determined for each sediment sample. Porosity (ϕ) was calculated based on water loss from a known volume of sediment after drying overnight at 105°C . Overlying water Br^- concentration at the beginning and end of the incubation as well as pore-water Br^- concentration in each sediment section was determined spectrophotometrically as described by Presley (1971).

b. Model construction

Irrigation by *Arenicola marina* is characterized by injection of overlying water into the sediment at feeding depth and transport of porewater from feeding depth to the sediment surface (Rijken, 1979; Hüttel, 1990; Riisgård and Banta, 1998). To describe these effects on solute transport we divided the sediment into three different depth zones (Fig. 1) where

lugworm irrigation has different effects on solute transport and thus is modeled differently.

The irrigation model is based on two central assumptions about lugworm irrigation.

1. All water transported into the tube of *Arenicola marina* is injected out into the surrounding sediment, at feeding depth (Fig. 1, zone 2). *A. marina* is a strong irrigator, the sediment in which it lives is sandy and permeable, and because characteristic subsurface tracer peaks are typically observed (e.g. Rasmussen et al., 1998), the assumption is believed to be valid.
2. Sediment porosity (φ) is constant over time during the irrigation measurement (but can vary with depth). Porosity undoubtedly changes after the initial introduction of *A. marina* to an experimental core, but after a short period (a few days to a week) a new steady state for porosity is established.

The consequence of these two assumptions about lugworm irrigation is that a model describing the effect of irrigation by *Arenicola marina* on solute transport must include a source term describing injection of the solution at feeding depth and an advective (i.e. directional) transport term describing return of the water injected at depth to the sediment surface, as assumption 2 precludes accumulation of water within the sediment.

Based on the classic diffusion-advection-reaction diagenetic equations (Berner, 1980) the general form of the irrigation model is given by:

$$\text{Zone 1: } \frac{\partial \varphi C}{\partial t} = \frac{\partial}{\partial z} \left(D \frac{\partial \varphi C}{\partial z} \right) + \frac{\partial (v \varphi C)}{\partial z} \quad (1)$$

$$\text{Zone 2: } \frac{\partial \varphi C}{\partial t} = \frac{\partial}{\partial z} \left(D \frac{\partial \varphi C}{\partial z} \right) + \frac{\partial (v \varphi C)}{\partial z} + S(t, z) \quad (2)$$

$$\text{Zone 3: } \frac{\partial \varphi C}{\partial t} = \frac{\partial}{\partial z} \left(D \frac{\partial \varphi C}{\partial z} \right) \quad (3)$$

where C is the solute concentration in a volume of pore-water (mM), φ is the porosity, $S(t, z)$ represents the source of solute due to injection of overlying water at feeding depth (mM/h), $v(t, z)$ is the velocity of the advectively recirculating water (cm/h) and $D(z)$ represent the apparent diffusion coefficient (incl. molecular diffusion) in the sediment (cm²/h).

The irrigation model includes the following initial and boundary conditions:

$$i. \text{ Initial condition. } \quad t = 0: C(z = 0) = C_{olw}(t = 0), C(z > 0) = C_{bg} \quad (4)$$

where $C_{olw}(t = 0)$ is the solute concentration in the overlying water (mM) after the addition of the tracer and C_{bg} is the measured background solute concentration in the sediment (~ 0.3 mM for Br⁻).

ii. *Boundary conditions.* $z = z_{\max}: \frac{\partial C}{\partial z} = 0, z = 0: C(t) = C_{olw}(t).$ (5)

The first condition is a closed boundary (there is no flux of solutes across the bottom of the sediment core) and the second states that the pore-water concentration at the sediment-water interface has the same concentration as the overlying water.

iii. *Continuity conditions.* $z = z_1: C_{zone 1} = C_{zone 2}, z = z_2: C_{zone 2} = C_{zone 3}.$

These conditions ensure continuity of solute concentration between the different vertical zones in the model.

Using the previously described assumptions it is now possible to express the source term $S(t)$, the advective transport term $v(z, t)$ and the apparent diffusion coefficient D in terms of relevant biological and physical parameters.

The first assumption is that *Arenicola marina* pumps water into the sediment at a given depth (zone 2). The amount of solute transported to the sediment column by the pumping activity of *A. marina* depends on two factors, the pumping rate, $P(t)$, and the solute concentration in the water injected at feeding depth, C_{inj} . Since *A. marina* injects overlying water into the sediment the solute concentration in the injected water equals the solute concentration in overlying water. Overlying water is, however, injected into the sediment with a time delay, τ , the time to pump water from the surface to the feeding pocket and replace the water in the lugworm's tube, hence $C_{inj}(t) = C_{olw}(t - \tau)$ and the source term is described by

$$S(t) = \frac{C_{olw}(t - \tau) \cdot P(t)}{V_{z_2 - z_1}} \quad (6)$$

where $V(z_2 - z_1)$ is the volume of water in zone 2 (l), τ is the time delay (h) which depends on the volume of the tube, $V_g(l)$, and the pumping rate, $P(t)$ (l/h). τ is defined as $\tau = V_g/P(t)$.

The second condition of our irrigation model is a steady porosity; hence water pumped into the sediment by *Arenicola marina* must return to the surface, creating a vertical flow within the sediment. The porosity assumption makes it possible to express the velocity (v) of the recirculating water in terms of pumping rates and the area through which the water flows (Eq. 7)

$$v(z, t) = \frac{P(t)}{A \cdot \phi} \quad (7)$$

where A describes the area (cm^2) of sediment particles and porewater over which the water is horizontally dispersed (area of advective column). This area depends on the physical structure of the sediment and how it is altered by *A. marina*.

Lugworms often create a feeding funnel with loose sand, with lower resistance and presumably greater water flow compared to the surrounding sediment, through which the

water is transported back to the surface (Hüttel, 1990). In this case, water will be locally transported to the surface with a higher velocity relative to situations where the flow is dispersed over a greater area. By introducing a factor, κ , which is the ratio between the area of the advective column (A) and the total area of the sediment column (A_o , Eq. 8), it is possible to determine whether the transport to the surface is localized in a small area or dispersed throughout the sediment column.

$$\kappa(z, t) = \frac{A}{A_o}. \quad (8)$$

κ can vary between 0 and 1. If κ is small, the water flow to the surface is localized indicating the presence of a feeding funnel. Larger values of κ indicate that the water is dispersed and not transported through a funnel. If κ equals 1, water is moving upward homogeneously in the entire horizontal level. The advective term describing solute transport from zone 2 to the surface is obtained by combining Eqs. 7 and 8.

$$v(t, z) = \frac{P(t)}{\kappa \cdot A_o \cdot \varphi}. \quad (9)$$

In practice, it is not possible to determine κ empirically because this factor depends on microscopic parameters such as physical structure of the sediment, porosity in each zone of the sediment as well as the activity and behavior of *A. marina*. It can, however, be estimated by fitting the model to the observed solute profile.

In addition to processes directly caused by the presence of *A. marina*, the distribution of tracer throughout the sediment is affected by molecular diffusion and diffusion-like processes, e.g., sediment mixing from meiofauna (Aller, 1982; Emerson *et al.*, 1984; Forster *et al.*, 1995). We have chosen to describe the sum of these diffusion-like effects by the factor $\beta(z)$:

$$D(z) = \beta(z)D_{s, sed} \quad (10)$$

where $D_{s, sed}$ is the effective molecular diffusion coefficient of the solute in the sediment (adjusted for tortuosity) and $\beta(z)$ is a factor describing the increased diffusion (dimensionless). $D_{s, sed}$ for Br^- was estimated from data in Li and Gregory (1974) and the Stokes-Einstein equation (Applin and Lasaga, 1984) to $1.55 \cdot 10^{-5} \cdot \varphi(z)$ cm^2/sec under the given experimental conditions. The $\beta(z)$ -factor includes unknown processes such as small-scale mixing from meiofauna (Aller and Aller, 1992) and dispersion due to hydrodynamic flows within the sediment (Boudreau, 1997), which, depending on the scale of interest, can be modeled as being random and diffusion-like (Boudreau, 1997). It should be noted that $\beta(z)$ is dependent on depth in the sediment, $\beta(z) \geq 1$ and that $D(z)$ in Eq. 10 is analogous to the apparently increased biodiffusion coefficient (D_s) often used to describe enhanced diffusion due to small-scale mixing (Aller and Aller, 1992).

c. Input parameters

Six profiles from the experiments by Rasmussen *et al.* (1998) were simulated using the developed irrigation model. In the simulations radius, of the tubes of *A. marina* were estimated from a wet weight versus body radius relationship determined for *A. marina* using 20 individuals of different sizes (0.6–3.5 g, data not shown). A semi-log function was chosen since it gave the best fit and the regression equation was: $y = 0.16X + 0.23$ where y is body radius (cm) and X is \log_{10} (wet weight (g)), $R^2 = 0.51$, $p \leq 0.001$. The pumping zones (zone 2) were based on the observed location of the lugworm at the end of the experiment. In two cores (2d and 2e) it was not possible to simulate the experimental profiles from the observed locations of *A. marina*. The pumping zone was, therefore, changed and the locations used as input parameters are entered in Table 1. Changes in Br^- concentration in overlying water were assumed to be constant over time and were estimated from concentrations measured at the beginning and end of the incubation. Before reaching steady state, tracer concentration will appear linear as the main source of Br^- removal is due to *A. marina* irrigation. We have confirmed such linear changes in Br^- concentrations in other studies with lugworms (e.g. Rasmussen *et al.*, 2000).

d. Solution method

The model was solved numerically with the software program PDEase2[®] (Macsyma Inc.) using Finite Element Method (FEM) (Iserles, 1996). The best-fit parameters for each simulation were determined based on goodness of fit criterion by manually changing the parameters until the sum of squared residuals was minimized. The parameters were estimated one at a time starting with $P(t)$ then κ and finally β . Since each of these parameters is uniquely determined from the shape and size of the measured Br^- profiles, there is little chance that fitting one parameter affects the estimation of the others. The sequential fitting procedure and the relatively independent model parameters significantly reduces the risk of inaccurate parameter estimations due to local minima.

3. Results

Comparisons between simulated and measured tracer profiles (Fig. 2a–2f) showed that the developed irrigation model simulates the experimental tracer profiles well, especially the subsurface peak generated by the injection of overlying water at the feeding depth of *Arenicola marina*. The subsurface Br^- concentration was highest in the upper part of the peak because Br^- concentration in overlying water was highest at the beginning of the incubation (Table 1) and fell 10–42% over the incubation period.

A plot of residuals (difference between predicted and measured concentrations) versus depth in sediment (Fig. 3) indicates generally good agreement. Some large deviations were observed, however, in the top 2 cm of the sediment, while the deviations between predicted and measured data were much less deep within the sediment. Goodness-of-fit tests (χ^2) indicated no statistically significant differences between the simulated and experimental data for any of the profiles (Table 2).

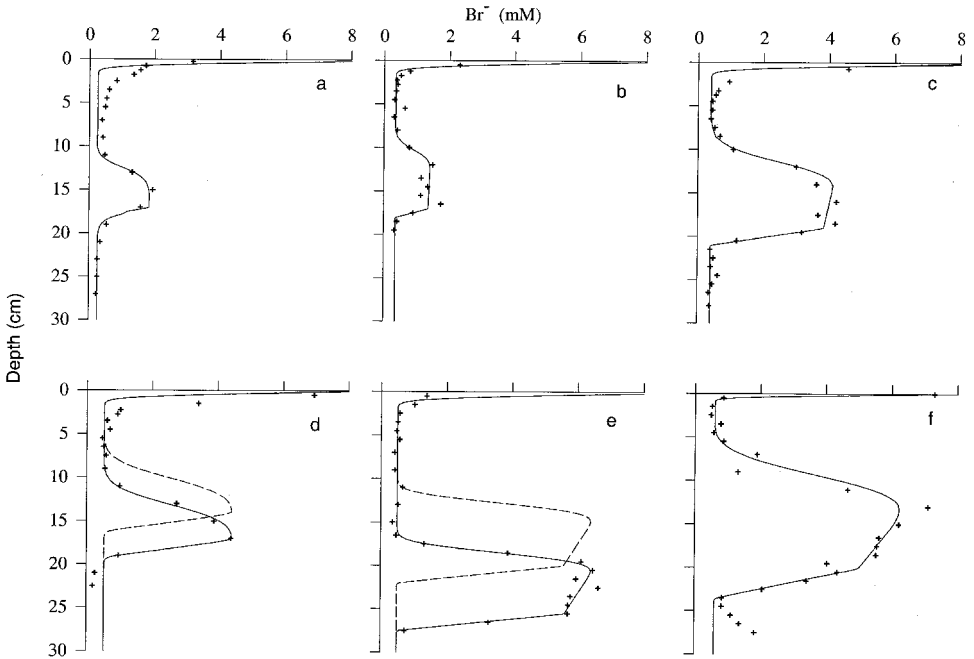


Figure 2. Measured (+) and predicted (—) pore-water Br^- concentration profiles from 6 sediment cores inhabited by *Arenicola marina*. Input and output parameters for profile 2a to 2f are presented in Table 1 and 2 respectively. Model fits for profiles 2e and 2f are shown based on the observed locations of the worms (dashed line) and an altered location of the worms (zone 2) that gave the best fits to the data (solid line).

In four simulations (Fig. 2a, 2b, 2c and 2f) there was good agreement between the depth of the subsurface Br^- peak and the observed depth of the individual, suggesting that lugworms usually did not change their positions during irrigation measurements and core sectioning. In these situations it was possible to describe the Br^- profile from the observed location of the worm. In two cores (2d, 2e), lugworms apparently changed their positions prior to or during core sectioning since the observed position did not correlate with the subsurface Br^- peak. Consequently the model failed to predict the location of the subsurface peak (Fig. 2d and 2e) and it was necessary to change the position of zone 2 to get an adequate description of these profiles. Furthermore, we observed a second smaller Br^- peak beneath the first peak in profile 2f which probably arose because the lugworm changed its position within the sediment during the incubation and, therefore, had been pumping at another depth for a short while. This second peak was not accounted for in the estimation of the pumping rate in our model, which was, therefore, underestimated.

We estimated pumping rates for *Arenicola marina* between 10.5 and 61 ml/h (Table 2). Pumping rate ($P(t)$) showed a strong allometric relation with worm weight ($P(t) = 15.1 w^{0.76}$, $p \leq 0.008$) which is quite similar to allometric scaling observed for *A. marina*

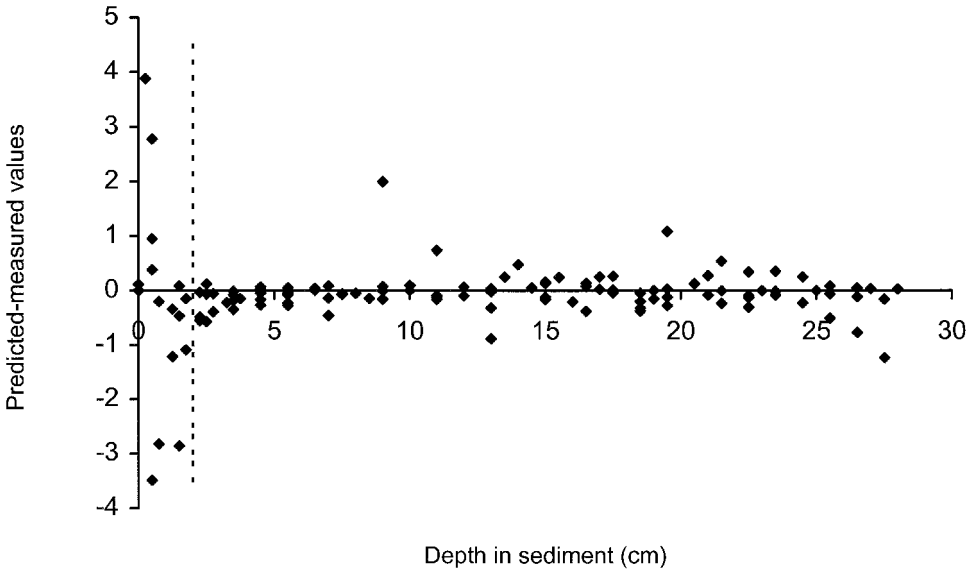


Figure 3. Plot of residuals, i.e. differences between model predicted and measured Br^- concentration, versus depth in sediment. Dashed line: 2 cm below sediment surface.

respiration where V_{O_2} (ml O_2/h) consumption scaled up to the 0.8 power of dry weight (Krüger, 1964). Also, calculated weight-specific pumping rates agreed with reported pumping rates for *A. marina* ranging between 10 and 20 ml/h/g (Krüger, 1966; Andersen and Kristensen, 1991; Riisgaard *et al.*, 1996). The parameter κ ranged between 0.1 and 0.53 which is equivalent to areas of 5.5 to 29 cm^2 per worm through which the water is advectively transported from zone 2 to the sediment surface (Table 2). Interestingly, κ did not show a significant allometric relationship to worm size ($\kappa = 0.18 w^{0.56}$, $p \leq 0.11$). Finally, an enhanced diffusive transport was detected in all sediment cores as indicated by β being much greater than 1 (Table 2). Large differences between profiles were observed, with β values ranging from 10 to 170, but the enhanced diffusional transport was not

Table 2. Output parameters in the irrigation model ($P(t)$, $P(t)$ per gram, κ , β) and the result of a χ^2 test for each core.

Profile number	$P(t)$ (ml/h)	$P(t)$ per gram (ml/h/g)	κ -factor	Area of advective zone (cm^2)	β -factor	p (χ^2 test)
2a	10.5	17.5	0.14	7.8	170	0.81
2b	11.5	8.8	0.10	5.5	20	1.0
2c	41.0	11.4	0.29	16.1	100	0.99
2d	25.5	21.3	0.40	22.2	50	0.30
2e	41.2	10.8	0.48	26.6	10	1.0
2f	61.0	9.8	0.53	29.4	50	0.99

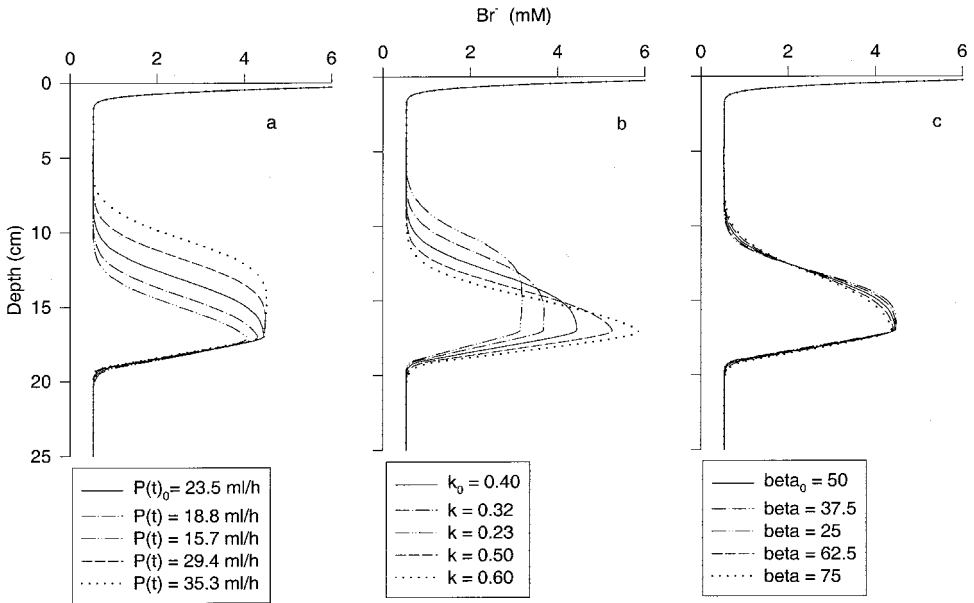


Figure 4. Model sensitivity to the output parameters: (a) pumping rate $P(t)$, (b) κ , the ratio between the area of water transport and the area of sediment core and (c) the apparent diffusion factor $\beta(z)$. The initially fitted parameter is given by the subscript 0. Parameters were then increased and decreased by 25% and 50%.

related to worm size ($\beta = 61.7 w^{-0.43}$, $p \leq 0.47$). The observed enhanced diffusion coefficients agreed well, however, with reported values, which typically range between 10 and 100 times greater than molecular diffusion (Aller, 1982).

a. Parameter sensitivity

Sensitivity of the model to variations in both input and output parameters was tested by changing the parameters one at a time and observing the change in the simulated profiles (Fig. 4). Sensitivity of the output parameters is an indication of the precision with which these parameters can be estimated. A highly sensitive parameter guarantees precision in estimating the values when fitting the data.

Solute concentration was much more sensitive to $P(t)$ and κ than to $\beta(z)$. Even small changes (20%) in these first two parameters altered the form of the profile substantially. This result limits the risk of errors in estimating κ and $P(t)$ because incorrect choices of these parameter values would lead to profiles quite different from those observed. In contrast, changes of up to 200% in β did not significantly alter the modeled profile, indicating that the choice of β is not well constrained. The chances for errors in estimating κ and $P(t)$ were further reduced because κ and $P(t)$ have different effects on the shape of the simulated profile. Changes in pumping rate result in a different amount of tracer

injected into the sediment and thus change the area under the profile curve. At high pumping rates, the maximum tracer concentration is independent of the pumping rate and the profile becomes “flat” and more spread out. The effect of κ is the opposite. Changes in κ do not affect the area under the tracer curve but result instead in a change in the maximum tracer concentration. The maximum tracer concentration is always dependent on κ . These different effects on the modeled tracer profile make it impossible to compensate for an incorrectly estimated pumping rate through changes in κ and vice versa. There are, however, similarities between the effects from $P(t)$ and κ on the advective transport of solutes which depends on both $P(t)$ and κ . At low pumping rates and large values of κ the advective transport becomes insignificant and diffusive processes dominate, leading to bell-shaped profiles. At high pumping rates and small κ values in contrast, advective transport dominates and the profiles become flat.

Most of the input parameters t_p , $\varphi(z)$, C_{otw} and the radius of the sediment cores are easy to measure and are without significant uncertainties, so no sensitivity tests were conducted for these input parameters. The remaining input parameters, the pumping interval (zone 2) and the lower depth of zone 2 (z_2) are, however, subject to uncertainties, and thus sensitivity tests were conducted.

The sensitivity tests for the size of the pumping interval (zone 2, Fig. 5a) show that uncertainties in determining the pumping interval have little effect on the profile. Changes in the size of the pumping interval do, however, affect the shape of the profile, especially the Br^- gradient from the depth of maximum penetration to the depth of maximum concentration. With small pumping intervals the gradient is steeper and a plateau is observed, while with larger pumping intervals, the profile becomes more bell shaped. The size of the pumping interval also has a minor effect on the estimation of κ . For example, κ will be underestimated by approximately 13% if the pumping interval is overestimated by 50%.

The simulated profiles are extremely sensitive to changes in the location of zone 2 (Fig. 5b). Change of location does not affect the shape of the profile but results in a displacement of the whole profile, which cannot be compensated for by changes in the other parameters. Hence, if the modeled depth of the maximum Br^- concentration does not coincide with the observed depth of the maximum tracer concentration, then the observed location of the lugworm could not have represented the pumping depth during the incubation (i.e. the worm moved during core sectioning).

4. Discussion

The model developed in this paper describes how irrigation by the lugworm *Arenicola marina* affects solute transport, including the injection of overlying water into the sediment and the upward advective transport of solutes within the sediment. Neither of these features, characteristic for actively irrigating head-down deposit feeders in porous sediments (e.g., arenicolids, maldanids, pectinariids), are included in the more common irrigation models such as the radial diffusion model (Aller, 1980a-c) or the 1D nonlocal

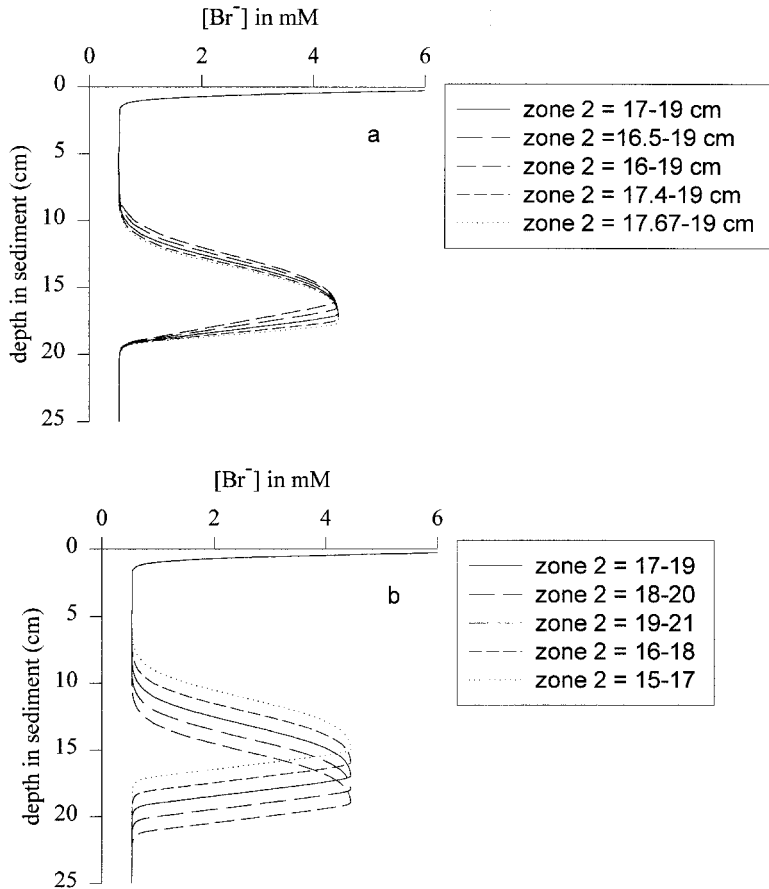


Figure 5. Model sensitivity of the input parameters: (a) the size of zone 2 and (b) the location of zone 2. The initially fitted parameter is given by the subscript 0. Parameters were then increased and decreased by 25% and 50%.

irrigation model (Emerson *et al.*, 1984). These models assume that diffusion or diffusive-like transport of solutes away from the tube of the organism is the only significant solute transport process. In contrast, injection and the rapid advective transport of water and solutes dominate solute transport in our model, and this transport is not controlled by concentration differences between overlying water and pore water but depends instead on solute concentration in overlying water and water flow within the sediment caused by *A. marina*. Diffusive transport processes are included in our model, but are of minor importance relative to advective transport. The existing diffusive or nonlocal mixing models and our advection-based irrigation model represent two end-members of a continuum of the effects of tube dwelling, irrigating fauna on solute transport in sediments. Our model describes situations where the transport of solutes within sediments is caused by

injection and following advective transport of water and solutes, often the case in sandy, porous sediments. The nonlocal model and Aller's radial model both describe situations where diffusion around the worm tube is the dominant transport processes, which more often is the case in muddy sediments or where burrows do not open directly into the sediments. It is evident that our irrigation model adequately describes solute tracer profiles resulting from irrigation by *Arenicola marina*, including the subsurface peak generated by injection and advective transport of overlying water within the sediment. Furthermore, the explicit description of the injection and advective transport of overlying water provides useful and meaningful physiological and ecological parameters such as the lugworm's pumping rate, $P(t)$, and κ , which indicates the presence and size of a feeding funnel.

The estimated pumping rates are based on the assumption that all water transported into the tube of *A. marina* is injected into the surrounding sediment at feeding depth. This assumption is supported in part by e.g. Riisgård *et al.*'s (1996) analysis of *A. marina*'s pumping mechanism, which showed no sign of backflow. Also, our estimated pumping rates are in good agreement with often reported values (Kruger, 1966; Andersen and Kristensen, 1991; Riisgård *et al.*, 1996), indicating that the model assumptions are valid and that model estimation using Br^- as a solute tracer is a reliable method to determining pumping rates for *A. marina*. If there had been a significant backflow, i.e. *A. marina* did not inject all of the water into the sediment, pumping rate would have been significantly underestimated by the model.

By determining κ , it is possible to estimate the size of the advective area by which the water is transported toward the sediment surface relative to the total sediment surface area. In all cores $\kappa < 1$ hence water was never dispersed over the total core area. Small values of κ were observed in 2a and 2b indicating that the water in these cores was transported more locally to the surface (5.5–7.8 cm²) than in other profiles (16–29.4 cm²). Not surprisingly, κ was positively related to pumping rate ($r = 0.87$, $p \leq 0.012$); hence at higher pumping rates water tended to be dispersed over a greater area. *Arenicola marina* often creates observable feeding funnels in the field. When held in the laboratory this funnel is seldom visible, however, and often not formed (Rijken, 1979). Injected water returning to the sediment surface is often assumed to be transported within the feeding funnel due to high porosity and low resistance (e.g. Hüttel, 1990). Subsequent experiments and modeling studies have shown that the advective area often is smaller than the area of the feeding funnel defined here as the area of advective downward particle transport (Timmermann, 2001).

Given the relatively small size of core tubes used in the experiment conducted by Rasmussen *et al.* (1998) it is possible that the core tube wall influenced the advective flow of water and thus the value of κ . If the injected water and tracer hits the core wall, the advective upward flow will presumably be faster (and κ smaller) than with no wall present. Two lines of evidence suggest that this effect was not a major problem in this experiment, however. First, we observed that while lugworm burrows were often close to the core wall, lugworms were located toward the center of the sediment cores. Given that the area of the

advective zone was much smaller than core area ($\kappa < 0.6$) the influence from the wall on tracer profiles should have been minimal. Second, tracer profiles from larger experimental microcosms with *A. marina* (Banta, unpub. data) indicated that the advective zone often was smaller than in this experiment which is the opposite of what would be expected if the core tube walls limited the lateral dispersion of water. Thus we believe that the core tube wall had only a minor effect if any on water and tracer flow and thus on the estimated values of κ . Note that the estimated values of κ do describe the advective area whether or not the solute flow was affected by core tube wall and thus adequately describe the solute transport as it occurred in the modeled sediment cores.

An apparently enhanced diffusive transport was observed in all cores as indicated by $\beta > 1$. Also, large differences in β were observed, probably due to differences in sediment structure and meiofauna activity. Uncertainties in estimating this parameter (low sensitivity) could explain much of the observed variation. In any case, β played only a minor role in solute transport in the zones affected by advective flow. Also, β is not a precisely mechanistic term and, in fact, could be excluded over the time scales simulated here without significant reduction in the model's descriptiveness. We chose, however, to include β in the model since it does describe small-scale random processes. Furthermore, β allows direct comparison to diffusion-like transport coefficients used in other models. Finally, including β ensures that this model can be more easily generalized to other species, longer incubation times and other sediment types where diffusion-like processes may be more important. Note, including β in modeling the profiles did not affect the estimation of the other model output parameters.

Even though our irrigation model adequately simulates solute transport in bioturbated sandy sediments, the choice of a one-dimensional (1-D) geometry limits the applicability of our model. In a 1-D model, it is not possible to describe heterogeneity in the horizontal plane. As a consequence, it is not possible to model the diffusion of tracer from the overlying water into the sediment due to the fact that the upward advection term in the model operates in the entire cross-sectional area of the sediment and overwhelms any downward-diffusive transport. Net diffusive transport of solutes from overlying water down into the sediment was observable in the Br^- profiles (top 2 cm) indicating that there must be areas in these sediment cores where no upward advection occurs. This is also supported by the fact that $\kappa < 1$ in all cores. What was observed in the measured solute profiles is thus a weighted average of these two sediment areas, i.e., with and without advective solute transport. That diffusive transport was evident at the sediment-water interface and indicates that all solute transport processes occurring in these bioturbated sediments cannot be adequately described in a single 1-D model. This combination of processes can be included either by developing a 2-D version or using two 1-D models, one describing the advective zone in the feeding funnel and one describing the zone around the feeding funnel affected only by diffusive processes. A weighted average of solute profiles from these two 1-D models would then describe the measured solute profiles. Note, however, that the deep advective transport of solutes due to irrigation by *Arenicola marina*

results in rapid solute transport over much greater distances than the processes occurring at the sediment surface and thus advective transport dominates solute transport in sediments inhabited by *A. marina*.

Other geometric simplifications were made in order to keep our model simple. Both the position and size of zone 2 were assumed to be constant during the incubation period. Hence we do not account for any change in worm position during the experiment. Lugworms are usually stationary, only occasionally moving to new areas and establishing new burrows (Wells, 1963; Brey, 1991). The tracer profiles and the subsequent modeling indicated, however, that worms in a few cases changed position during the tracer incubation or just prior to core sectioning. Whether this was a result of experimental manipulations or animal behavior remains uncertain.

The source term in our irrigation model adds tracer to a given depth in the sediment due to injection of overlying water by the lugworm. In the case of *Arenicola marina* this is a more mechanistically correct description compared to the apparent source term used in nonlocal mixing models as water and solutes are injected and not transported diffusively into the sediment from the worm burrow. This formulation does, however, limit the application of our irrigation model since it can describe only situations where solute concentrations in overlying water are greater than pore-water concentrations and cannot simulate situations where solutes are “flushed” out of the sediment due to injection of overlying water with lower solute concentrations than found in pore water. The advantage of this formulation is, however, that the pumping rate, $P(t)$, is uniquely determined from the amount of Br^- injected into the sediment (the source term $S(t)$). Furthermore, once the pumping rate is estimated, the velocity (v) of the water transported toward the surface only depends on κ , which then can be uniquely determined. If the model had no source term, both $P(t)$ and κ would need to be determined from the observed advection velocity, and an independent measurement of one of these parameters is required to get unique values for both $P(t)$ and κ . We recommend that an overlying water tracer such as Br^- be used to uniquely determine $P(t)$ and κ , after which these parameters can be used to model pore-water flushing or other phenomena of interest. It should be noticed that the model parameters can only be fit from tracer incubations run for a limited period. To determine $P(t)$ and κ it is essential to “catch” a subsurface tracer peak. Advective lugworm irrigation will eliminate this peak given sufficient time, creating a uniform tracer distribution (e.g. Hüttel, 1990). z_f can still be determined, however. Based on the pumping rates and other model parameters we have observed here, incubation time needs to be less than a few hours to allow adequate parameter fit.

5. Conclusion

We have developed and applied a model that adequately and mechanistically correctly describes solute transport from the overlying water into the sediment and its advective flow back to the sediment surface due to irrigation by the lugworm, *A. marina*. The advantages of this model are that it is a relatively simple one-dimensional model that emphasizes the

important role of advective transport in irrigated, porous sediments. Furthermore, the model parameters have physiological and ecological relevant interpretations. The model cannot, however, describe solute transport in heterogeneous sediments subjected to advective irrigation in some areas and diffusive transport in others due to its simple one-dimensional formulation. Also, it can only model solute transport in the case where solute concentrations are greater in the overlying water in comparison to porewater concentrations. Thus it is more appropriate for modeling situations where the overlying water is a source of a tracer or other solutes (e.g., oxygen or a pollutant) or for determining irrigation parameters for other use. Even with these shortcomings, we believe that this model represents an important contribution to modeling of bioturbation and irrigation as it more correctly describes solute transport processes in bioturbated porous sediments, where advective transport is important, compared to existing irrigation models based on diffusive transport processes surrounding worm burrows.

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