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MODELLING PARTICLE AND SOLUTE TRANSPORT IN SEDIMENTS INHABITED BY *ARENICOLA MARINA*. EFFECTS OF PYRENE ON TRANSPORT PROCESSES

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DIAGENETIC MODELLING
ARENICOLA MARINA
ADVECTIVE TRANSPORT
FEEDING FUNNEL
PYRENE

ABSTRACT. – Infaunal bioturbation (irrigation and particle mixing) significantly influences diffusion, advection and phase transfer of sediment constituents, thereby affecting net flux and catabolism of natural and anthropogenic sediment associated compounds. Hence, several types of bioturbation models have been developed to characterise and quantify effects of bioturbation. The present article presents two newly developed diffusion-advection models describing particle and solute transport caused by bioturbation by the lugworm *Arenicola marina*. Both models are described in cylinder coordinates allowing the existence of a feeding funnel which has not been included in previous bioturbation models, but is crucial for understanding particle and water transport induced by *A. marina*. Model output parameters describe the velocity of the particle burial rate due to the conveyorbelt feeding mode of *A. marina*, the size (and existence) of a feeding funnel, the velocity of the advective solute transport from feeding depth to the sediment surface caused by *A. marina* irrigation as well as the size of the area affected by advective solute transport. In combination with a microcosm tracer experiment the models were used to study the effects of pyrene (a 4-ringed polycyclic aromatic hydrocarbon) on particle and solute transport in bioturbated sediment by comparing model output parameters from pyrene contaminated and uncontaminated sediment. A sediment concentration of pyrene 900 ppb significantly affected particle bioturbation, reducing the subduction rate by 34% from 0.138 cm/day in uncontaminated sediment to 0.091 cm/day in contaminated sediment. Apparently pyrene had little but no significant effect on the advective transport of solutes (estimated to 42.52 ± 11.34 cm/day) and the size of the area affected by the transport of solutes (estimated to 11.78 ± 9.02 cm²) indicating that, sediment associated toxins affect feeding rate more than they affect irrigation for this organism.

MODÉLISATION DIAGÉNÉTIQUE
ARENICOLA MARINA
TRANSPORT ADVECTIF
CÔNE DE NUTRITION
PYRÈNE

RÉSUMÉ. – La bioturbation due à la faune intra-sédimentaire (irrigation et remaniement des particules) influence significativement la diffusion, l'advection et le transfert des diverses phases des constituants du sédiment, affectant ainsi le flux net et le catabolisme des composants naturels et anthropogéniques associés au sédiment. Ainsi plusieurs types de modèles de bioturbation ont été développés afin de caractériser et de quantifier les effets de la bioturbation. Cet article présente deux nouveaux modèles de diffusion-advection décrivant le transport des particules et des substances dissoutes dû à la bioturbation induite par le Ver *Arenicola marina*. Les deux modèles sont décrits à l'aide de coordonnées cylindriques prenant en compte l'existence d'un cône de nutrition qui n'a pas été pris en compte dans les modèles précédents, mais qui s'avère crucial dans la compréhension du transport des particules et des substances dissoutes liées à l'action de *A. marina*. Les paramètres des modèles décrivent la vitesse d'enfouissement des particules dues au mode de nutrition en "tapis roulant" de *A. marina*, la taille (et l'existence) du cône d'alimentation, la vitesse du transport advectif des solutés allant du niveau de nutrition vers la surface du sédiment et provoqué par l'eau injectée par *A. marina*, ainsi que la taille de l'aire affectée par le transport advectif des solutés. En combinaison avec une expérience à l'aide d'un traceur, en microcosme, les modèles ont été utilisés pour étudier les effets du pyrène (un hydrocarbure aromatique polycyclique) sur le transport des particules et des liquides dans des sédiments soumis à la bioturbation, en comparant les paramètres relevés dans les modèles provenant de sédiments contaminés et non contaminés par le pyrène. Une concentration de 900 ppb de pyrène dans le sédiment affecte significativement la bioturbation particulière, en ré-

duisant le taux de subduction de 34 %, et la vitesse de 0,138 cm par jour pour un sédiment non contaminé, à 0,091 cm par jour pour un sédiment contaminé. Apparemment, le pyrène a une faible influence, non significative sur le transport advectif des substances dissoutes (estimation : $42,52 \pm 11,34$ cm/jour) et sur la dimension de l'aire affectée par le transport des solutés (estimation : $11,78 \pm 9,02$ cm²), ce qui indique que les substances toxiques associées au sédiment affectent davantage le taux de nutrition que l'irrigation pour l'organisme.

INTRODUCTION

Sediment dwelling organisms significantly affect the physical, geochemical and diagenetic properties of marine sediments (e.g. Aller 1982, Andersen & Kristensen 1991). Through burrowing, feeding, respiration and locomotion activities infaunal organisms enhance particle and fluid transport both within the sediment and between the sediment and overlying water. Feeding and defecation enhance the resuspension of particles as well as increase the reworking rate within the sediment. Fecal pellets deposited at the sediment surface increase the sediment-water interface enhancing diffusional exchanges between overlying water and sediment. Also, burrows act as extended sediment surfaces increasing diffusive transport of solutes between overlying water and the surrounding porewater. The ventilation of burrows by infauna enhances both the flux of solutes into deeper layers of the sediment and the flux from sediment porewater to overlying water.

The biologically induced transport of particles and water has a major influence on sediment properties. Particle transport caused by reworking, tube construction, feeding and defecation change sediment structure and porosity, and may affect microbial and meiofauna communities (Findley *et al.* 1990). The increased transport of water enhances the flux of nutrients and oxygen (Marinelli 1994, Kristensen & Hansen 1999), thereby affecting sediment redox level, enhancing organic matter degradation (Banta *et al.* 1999, Kristensen & Holmer 2001) and stimulating microbial activities in the sediment (Van Duyl *et al.* 1992).

A variety of environmental factors such as sediment organic matter, sulfide and organic pollutants may affect infauna bioturbation activity (Lopez & Levinton 1987, Miron & Kristensen 1993, Timmermann & Andersen 2003). Petrogenic and pyrogenic polycyclic aromatic hydrocarbons (PAHs) are widespread organic pollutants known to be toxic to infauna (Swartz *et al.* 1990, Boese *et al.* 1999) resulting in decreased growth rates and changed particle mixing and irrigation pattern (Kure 1997, Augenfeldt 1980, Foss & Forbes 1997, Timmermann & Andersen 2003). Changes in infaunal bioturbation intensity and behaviour as a response to toxic stress can be expected to affect

the transport of particles and solutes within the sediment as well as exchange processes between sediment and overlying water. Contaminants may thus indirectly influence sediment biogeochemical and diagenetic processes as well as their own fate.

Several irrigation and particle mixing models have been developed (e.g. Goldberg & Koide 1962, Berner 1980, Aller 1980a, Boudreau 1997). Such models can be used to study effects of e.g. contaminants on transport of solutes and particles in bioturbated sediments. Most commonly, the transport of both solutes and particles are described by one dimensional biodiffusion models (e.g. Guinasso & Schink 1975, Aller 1982), incorporating all animal activities affecting the sediment into a single biodiffusion coefficient (D_B for particle mixing and D_s for solute transport). This simple approach is appropriate when the transport is local i.e. the length scale of the biological transport of material is much less than the scale of a tracer profile or where the transport processes are approximately stochastic in nature (Boudreau 1986).

To describe particle transport between non-adjacent points in the sediment one dimensional diffusion-advection models have been used (e.g. Gerino *et al.* 1994, Boudreau 1997). These models describe the upward or downward transport of sediment caused by ingestion and defecation from infauna by a single velocity parameter v estimated from experimental tracer profiles. Non-local solute transport is often described by a one-dimensional non-local mixing model with a single non-local exchange parameter (α) or a two dimensional radial diffusion model (Aller 1980a-c). Both models simulate situations where solutes are pumped into an organism's tube and thus are transported over long vertical distances after which the solutes are exchanged with the surrounding porewater by diffusion. These models cannot mechanistically describe bioturbating activities by the conveyorbelt feeding polychaete *Arenicola marina*, the common lugworm, due to the complexity of this polychaete's borrow (i.e. different lateral and vertical zones) and characteristic advective transport processes. The lugworm was chosen as experimental animal in the present study because it is an important bioturbator, both for irrigation and particle mixing, and a functional keystone organism in coastal areas (Grimm 1995, Forbes & Kure 1997). Accordingly, the objectives of this work were 1) to

develop mechanistic models describing transport of particles and solutes in sediments inhabited by *A. marina* and 2) to use these models in combination with tracer based methods to study the effects of pyrene on particle and solute transport in bioturbated sediment.

The models developed in this paper are extensions of existing 1 dimensional models describing particle transport caused by conveyorbelt feeders (e.g. Boudreau 1997, Francois *et al.* 1997) and advective solute transport caused by *A. marina* irrigation (Timmermann *et al.* 2002). The extended models are described in cylinder coordinates which makes it possible to include the feeding funnel crucial for transport processes induced by *A. marina* bioturbation.

MATERIALS AND METHODS

Sediment collected at St. Havelse, an intertidal site in Roskilde fjord, Denmark, was wet sieved (< 1 mm) in the field to remove macrofauna and other large material and kept at 4 °C for 2 weeks. To contaminate sediment, pyrene (98%, Aldrich) dissolved in acetone was added slowly to 1 L of air dried sediment during stirring. Wet sediment was added successively until a nominal pyrene concentration of 900 ppb was reached and mixed for 3 hours. Uncontaminated sediment was mixed with acetone for 3 hours as well. Maximum acetone concentration was 0.8ml/kg.

5 pyrene contaminated and 5 uncontaminated microcosms in polypropylene cores (inner diameter 8.4 cm, sediment volume 1500 ml) were established and designated +pyr and -pyr respectively. 500 ml of millipore filtered seawater diluted with demineralised water to 15 ‰ salinity were added to each microcosm. The microcosms were aerated with aeration stones and kept at 15 °C in the dark (experimental conditions).

Lugworms collected at Store Havelse were acclimated for one week in sieved sediment under experimental conditions. On experimental day zero, lugworms incubated overnight in aerated seawater for gut-emptying were weighed (mean \pm std wet weight 1.66 ± 0.17 g), and one lugworm was added to each microcosm equivalent to a density of 190 ind./m².

Particle mixing: To be able to trace particle movements, ⁵¹Cr as ⁵¹CrCl₃ in 0.5 M HCl (Dupont, spec. act. 13.8 mBq/mg) was added to 4 ml 0.5 M HCl + 2 ml 1.0 M NaOH and then added to two blue cap bottles containing pyrene contaminated or uncontaminated sediment slurries to give approximately 10,000 cpm/g sediment. The ⁵¹Cr-sediment slurries were then mixed for 24 hours using an electric mixer. In each microcosm fecal casts were removed and the sediment surface levelled before 30 g of ⁵¹Cr-labeled sediment was added to the overlying water to settle on the sediment surface and form a layer of approximately 5 mm.

Water transport: Water transport within the sediment was measured using Br⁻ as a solute tracer, by adding

10 mM KBr to the overlying water of each microcosm as described by Aller & Aller (1992). In microcosms without *A. marina* KBr was added approximately 30 hours before harvesting the microcosm, while KBr was added 2 hours before harvesting microcosms with *A. marina* to compensate for the extensively increased water flux due to *A. marina* irrigation.

Fecal production: Fecal production, an estimate for feeding rate, was measured every 4-5. day by collecting fecal pellets deposited at the sediment surface 6 to 8 hours after the surface had been carefully levelled. The ⁵¹Cr concentration in feces was quantified by γ -counting in a Packard Cobra II auto-gamma counter, and feces material was returned to the cores by carefully adding it to the overlying water to settle on the sediment surface.

Irrigation: Water exchange rates between overlying water and sediment were calculated using a model described by Timmermann & Andersen (2003). Briefly, carrier-free ¹⁰⁹Cd (CdCl₂ in 0.5M HCl, spec. act. 1.30 mCi mg⁻¹, Dupont) was added to the overlying water in each microcosm to give approximately 2000 cpm/mL. Overlying water samples (2 ml) taken every 30 min during the first 3 hours, then once per hour for 4 hours and finally after 24 hours were γ -counted. These data allowed calculation of the ¹⁰⁹Cd removal rate from overlying water (Timmermann & Andersen 2003). Removal rates in cores without worms are caused by sorption of Cd⁺⁺ to particles at the sediment surface whereas the irrigation by *A.marina* enhances the ¹⁰⁹Cd removal from the water due to the pumping of overlying water into the sediment, which increases the sorption of ¹⁰⁹Cd. The difference between removal rates in microcosms with and without lugworms was used to calculate irrigation rates for each worm.

Core sectioning: On day 10, 19, 29, 38 and 51 the sediment core of one microcosm from each group (+/- pyr) was sectioned at intervals of 0.5 to 2 cm increasing with depth. The position of the worm was noted. Each sediment section was weighed and porosity calculated based on water loss after drying a known volume of sediment. Sediment particles and porewater was separated by centrifugating (1000 rpm, 10 min and 10 min. at 1500 rpm) bulk sediment in double centrifuge tubes with a Whatman GF/C filter in between (Thomsen & Kristensen 1997). Sediment particles were analysed for ⁵¹Cr by γ -counting subsamples from each sediment section. Because of the different γ energies of the isotopes, they could be counted without interference (5-35 keV for ¹⁰⁹Cd and 240-400 keV for ⁵¹Cr) (data not shown). Interstitial Br⁻ concentration in each sediment section and in overlying water was determined spectrophotometrically as described by Presley (1971) however in one core it was not possible to detect Br⁻ above background level indicating that no extra Br⁻ had been added.

Modelling *A. marina* bioturbation

Arenicola marina lives in porous sandy sediments in a j-shaped tube reaching from the sediment surface to the bottom of the feeding funnel. The lugworm is a head down, conveyor belt feeder (Rhoads 1974) ingesting large quantities of sediment at feeding depth (typically 15-30 cm) and defecating at the sediment surface. The sediment removed at depth is replaced by sediment fal-

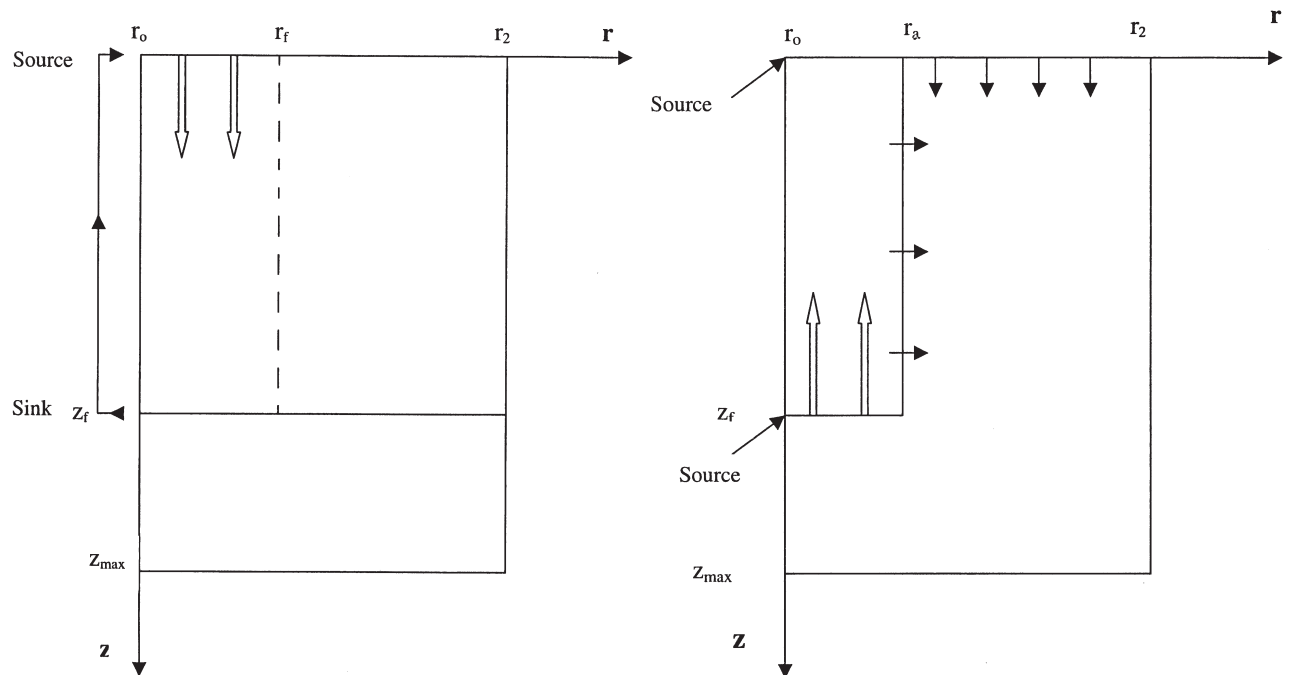


Fig. 1. – On the left. Particle transport due to feeding activity of *Arenicola marina*. Particles are ingested at feeding depth (z_f) and defecated at the sediment surface (z_0) creating a downward transport of particles (open arrows). r is the radial direction with $r=0$ placed in the center of the feeding funnel. r_f is radius of the feeding funnel, r_2 is radius of the sediment core and if no feeding funnel is created then $r_f=r_2$.

Fig. 2. – On the right. Solute transport due to irrigation activity of *Arenicola marina*. Overlying water is injected into the sediment at feeding depth (z_f) and solutes are advectively transported from feeding depth back to the overlying water (open arrows). r_a is radius of the advective zone (i.e. zone affected by advective transport). Diffusive transport (black arrows) from the sediment surface as well as radial diffusion between the advective zone and surrounding pore-water is also possible.

ling down the feeding funnel resulting in a vertical downward transport of particles from sediment surface to the feeding depth (Rhoads 1974). Irrigation by *A. marina* results in a transport of water in the opposite direction of the particle transport. Overlying water is pumped into the tube and injected directly into the sediment. The water injected returns to the overlying water, presumably through the feeding funnel (Huttel 1990) resulting in an advective transport of porewater from feeding depth to the sediment surface.

Particle mixing model: In the field *A. marina* often creates feeding funnels observable by eye and the particles may thus fall down this funnel. When held in the laboratory a funnel is however seldomly visible and often not formed (Rijken 1979). In these situations particles are transported downward in the total sediment core area. To cover both situations (i.e. with and without a feeding funnel) the particle mixing model is described in cylinder coordinates (see Fig. 1) which, contrary to the 1-D conveyor belt model described by Boudreau (1997), allows horizontal differences (i.e. the existence of a feeding funnel). Generally, the concentration of an inert particle tracer (e.g. luminophores) can be described by the conservation equation (Berner 1980):

$$\frac{\partial C_s}{\partial t} = \nabla \cdot (D_s \nabla C_s) + \nabla \cdot (\mathbf{u}_s C_s) \quad (1)$$

where C_s is the particle tracer concentration, first term represent particle diffusion-like transport processes caused by e.g. meiofauna and the second term describes the advective transport processes; i.e. the downward transport of particles. \mathbf{u}_s is the velocity of the particles sinking downwards in the sediment and D_s the apparent biodiffusion coefficient. ∇ is a differential operator which, in cylinder coordinates is defined as

$$\nabla C_s = \left(\frac{\partial C_s}{\partial r}, \frac{\partial C_s}{\partial z} \right) \text{(gradient) and}$$

$$\nabla \cdot \mathbf{v} = \left(\frac{1}{r} \frac{\partial}{\partial r} (r v_r) + \frac{\partial v_z}{\partial z} \right) \text{(divergence).}$$

Using knowledge about *A. marina* behaviour the velocity of the sinking sediment particles \mathbf{u}_s can be expressed in terms of biologically relevant and easily measurable parameters such as feeding rate. Since the void created by ingestion is continuously filled with sinking particles the velocity of these particles are determined by the volume of material removed by ingestion, V_f , as well as the area through which the particles sink, $\pi(r_f)^2$, which can be the feeding funnel in the field or the entire microcosm. Hence the velocity can be described as

$$\mathbf{u}_s = \begin{cases} \left(0, \frac{V_f}{\pi r_f^2}\right), & \text{if } 0 \leq r \leq r_f \text{ and } 0 \leq z \leq z_f \\ (0, b), & \text{if } r_f \leq r \leq r_2 \text{ and } 0 \leq z \leq z_f \\ (0, 0), & \text{otherwise} \end{cases} \quad (2)$$

where V_f is the defecation rate (cm³/hour), r_f is the radius of the feeding funnel and b is an *ad hoc* parameter (cm/hour) allowing different transport velocities in and outside the feeding funnel. When a distinct feeding funnel is created (i.e. $r_f < r_2$) the b -parameter can be estimated from measured tracer profiles (see result section). When $r_f = r_2$ no distinct feeding funnel is present and particles are transported downward over the entire sediment area with a velocity predictable from the easily measurable defecation rate, V_f . Note that the 1. component of \mathbf{u}_s is always 0 since there is no lateral advective particle transport. Below feeding depth \mathbf{u}_s is also 0 i.e. no advective transport below the worm.

The ingestion of particles at feeding depth is modelled as a particle sink at z_f . This sink is automatically included in the description of \mathbf{u}_s which is discontinuous at z_f (it becomes zero below the feeding depth, eqn 2). The consequence of this discontinuity is that the model lets particles disappear when they reach the feeding depth, which is consistent with the biological process where the worm ingests particles at feeding depth hence removes them from that part of the system.

At the sediment surface particles are defecated by the lugworm inducing a source at $z = z_0$. The tracer concentration in feces (C_f) determines the concentration at the sediment surface and this source can be included in the boundary condition:

$$C_s^{z_0} = C_f = (1 - A_x)C_s^{z_f} \quad (3)$$

where C_f is the contaminant concentration in feces, A_x is the assimilation efficiency and $C_s^{z_f}$ is the contaminant concentration in ingested sediment (i.e. concentration at feeding depth). In this experiment the ⁵¹Cr concentration in feces was measured during the experiment however the concentration was below detection limit (data not shown), hence this boundary condition was $C_s^{z_0} = 0$.

The remaining spatial boundaries (i.e. $z = z_{max}$, $r = r_2$ and the symmetry axis $r=0$) are closed and described by

$$\frac{\partial C(r, z_{max})}{\partial z} = 0, \quad \frac{\partial C(r_2, z)}{\partial r} = 0, \quad \frac{\partial C(r=0, z)}{\partial r} = 0 \quad (4)$$

At the beginning of the experiment ⁵¹Cr was added as a layer (0.5 cm) at the sediment surface and this initial condition is described by

$$C_s(t=0) = \begin{cases} C_0 & \text{if } z \leq 0.5 \\ 0 & \text{otherwise} \end{cases}$$

where C_0 is the concentration of ⁵¹Cr in the contaminated toplayer added to the sediment surface at the beginning of the experiment.

Solute model: Water transport caused by *A. marina* irrigation is characterised by the injection of overlying water into the sediment at feeding depth and advective transport from feeding depth to the sediment surface presumable through the feeding funnel (Aller 1982, Martin & Banta 1992, Risgaard & Banta 1998, Huttel 1990, Timmermann *et al.* 2002).

The solute model is also described in cylinder coordinates to allow advective transport in a limited horizontal area (e.g. a feeding funnel). Previously published cylinder (or radial) models with focus on the tube construction have been used to describe solute transport in irrigated sediments (Aller 1980a-c) which is appropriate if diffusion from the burrow is the dominant transport process. In contrast, solute transport in sediments inhabited by *A. marina* is dominated by advection in a limited area of the sediment (funnel) and this transport process is orders of magnitudes larger than diffusional transport from the tube and feeding funnel to the surrounding sediment (e.g. Timmermann *et al.* 2002).

The transport of solutes and the model geometry is described in figure 2. It should be noted that the depth and area of the feeding funnel in the particle model and the zone affected by advective solute transport (designated the advective zone) need not necessarily be the same.

The injection of overlying water and solutes at feeding depth is described by a source term:

$$C_{pw}(t, r < r_a, z = z_f) = C_{olw}(t) \quad (5)$$

where $C_{pw}(t, r < r_a, z = z_f)$ is the porewater concentration at feeding depth within the advective zone and C_{olw} is the tracer concentration in overlying water. This term describes situations where porewater at feeding depth is replaced by overlying water.

The boundary condition at the sediment surface is also a source and described by

$$C_{pw}(t, r, z = 0) = C_{olw}(t) \quad (6)$$

which states that the porewater at the sediment surface has the same tracer concentration as the overlying water.

The tracer distribution within the sediment is affected by diffusion and transport processes caused by the irrigation process by *A. marina*. In general these transport processes are described by

$$\frac{\partial C_{pw}}{\partial t} = \nabla \cdot (D_{pw} \nabla C_{pw}) + \nabla \cdot (\mathbf{u}_{pw} C_{pw}) \quad (7)$$

where C_{pw} is the porewater solute concentration, the first term represents the diffusion-like transport processes and the second describes the advective transport of solutes. D_{pw} is the apparent diffusion coefficient often designated D_s (e.g. Aller 1980b) and \mathbf{u}_{pw} is the velocity of the solutes transported within the advective zone.

By assuming that porosity is constant over time the water injected into the sediment must return to the sediment surface. Under this assumption the velocity of recirculating water \mathbf{u}_{pw} can be expressed in terms of pumping rates and the area through which the water flows.

$$\mathbf{u}_{pw} = \theta_a \left(0, \frac{P(t)}{\pi r_a^2 \phi}\right), \quad \theta_a = \begin{cases} 1 & \text{if } 0 \leq r \leq r_a \wedge 0 \leq z \leq z_f \\ 0 & \text{otherwise} \end{cases} \quad (8)$$

where $P(t)$ is the the pumping rate (ml/h), ϕ is the porosity and r_a is radius of the advective zone. θ_a describes the area affected by the advective transport of solutes.

In addition to transport processes directly caused by the irrigation of *A. marina* other transport processes such as molecular diffusion, sediment mixing from meiofauna (Aller 1982, Forster *et al.* 1995) and hydrodynamic dispersion (Boudreau 1997) affect the distribution of solutes. These small scale transport processes can, depending on scale of interest, be treated as diffusion like (Boudreau 1986, Aller & Aller 1992) and modelled as $D_{pw} = \beta D_m$ (Timmermann *et al.* 2002) where D_m is the

effective molecular diffusion coefficient of Br⁻ in sediment (corrected for tortuosity) and β is a factor describing the enhanced diffusion due to e.g. meiofauna (no dimension). D_m was estimated to $1.55 \cdot 10^{-5}$ cm²/sec using Li & Gregory (1974) and the Stoke-Einstein equation (Applin & Lasaga 1984).

The only boundary open for flux of matter is the boundary at the sediment surface described in equation 6. The rest of the boundaries are closed and described as the boundaries for the particle model (eqn 4).

Addition of Br⁻ to the overlying water prior to core sectioning gives the initial condition which is described by:

$C_{pw}(t = 0, r, z = 0) = C_{olw}$ and $C_{pw}(t = 0, r, z > 0) = C_{bg}$ where C_{olw} is the concentration of Br⁻ in the overlying water after addition of the tracer and C_{bg} is the background Br⁻ concentration in the sediment.

Treatment of data and statistical analysis: The models described in the previous sections were solved numerically with the finite element method using the computer program PDEase2[®] (Macsyma Inc.).

To compare the radial model results with the measured profiles model results were averaged in radial direction. Hence for each depth z_j the average pyrene concentration was calculated using the formula

$$\bar{C}_{z=z_j} = \frac{\sum_{i=1}^n C_{ij} \cdot (r_i^2 - r_{i-1}^2)}{r_n^2}$$

where C_{ij} is the pyrene concentration at (r_i, z_j) and where r designates radial distance from center of the cylinder (i.e. $r_0 < r_1 < \dots < r_n$). r_0 is the center and r_n the radius of the cylinder.

In both models one or more model parameters were estimated from the measured tracer profiles. The best fit parameters for each simulation were determined based on least squares criterion by manually changing the parameters until the sum of squared residuals was minimized. The rest of the parameters were estimated from either literature values or independently measured values and described in table I.

Differences in model output parameters from +pyr and -pyr treatments were tested with Students *t*-test.

RESULTS

Particle mixing

To compare model results with the measured ⁵¹Cr profiles the particle transport model was solved with the input parameters from Table 1. Comparison between model simulations and measured ⁵¹Cr profiles (Fig. 3) showed that the model was able to describe the characteristic subsurface tracer concentration peak resulting from the non-diffusional conveyorbelt feeding mode of *Arenicola marina*. Also, the downward transport of the contaminated layer was reflected quite well in the model. In the +pyr group where the independently measured fecal production rates were used as model input parameters the good agreement between model and measured profiles indicated that the velocity of the downward transport (i.e. $|u_s|$) is predictable using *A. marina* fecal production as model input parameter.

The model in the form without feeding funnel (i.e. $r_f = r_2$) was not able to predict the double peak observed at day 10 (with pyrene). The second peak observed at depth is probably caused by particles falling down a feeding funnel (whereas the upper peak is due to burial by fecal pellets). The situation where particles fall down a feeding funnel was simulated letting $r_f < r_2$ (i.e. there is a feeding funnel) and by allowing two different transport velocities (i.e. $b \neq V_f / \pi r_f^2$), see eqn 2. Both r_f and b were ad-hoc estimated from the measured ⁵¹Cr-profile and the best fit parameters were 2.5 cm² and 1.3 cm/day respectively. The rest of the profiles were without a distinct feeding funnel (i.e. $r_f = r_2$).

Figure 4 demonstrates that the cylinder model could describe the measured double peak profile which is not possible using a 1 dimensional model. Also, the good agreement between the model and the profile suggests that this double peak was in-

Table I. – Input parameters used in the simulations.

	Feeding rate, f(t), ml/h	Pumping rate, P(t), ml/h	Area of advective zone, r_a , cm	Feeding depth, z_f , cm
Day 10 – pyr	0.28 [*]	10 [*]	1.5 [*]	10.0 [♣]
Day 19 – pyr	0.25 [*]	7.2 [*]	1.1 [*]	13.4 [♣]
Day 29 – pyr	0.28 [*]	-	-	12.3 [♦]
Day 38 – pyr	0.35 [*]	22.0 [*]	1.7 [*]	11.0 [♦]
Day 51 – pyr	0.44 [*]	18.0 [*]	1.7 [*]	16.5 [♦]
Day 10 + pyr	0.23 [♦]	25.0 [♦]	2.2 [*]	14.0 [♦]
Day 19 + pyr	0.11 [♦]	3.7 [♦]	1.3 [*]	12.8 [♣]
Day 29 + pyr	0.21 [♦]	-	-	13.0 [♦]
Day 38 + pyr	0.21 [♦]	40 [♣]	3.2 [*]	14.5 [♦]
Day 51 + pyr	0.28 [♦]	25.6 [♦]	2.3 [*]	12.2 [♦]

♦: Independently measured parameters

♣: Parameters were changed to give better fit

♠: Parameters were estimated from the profiles

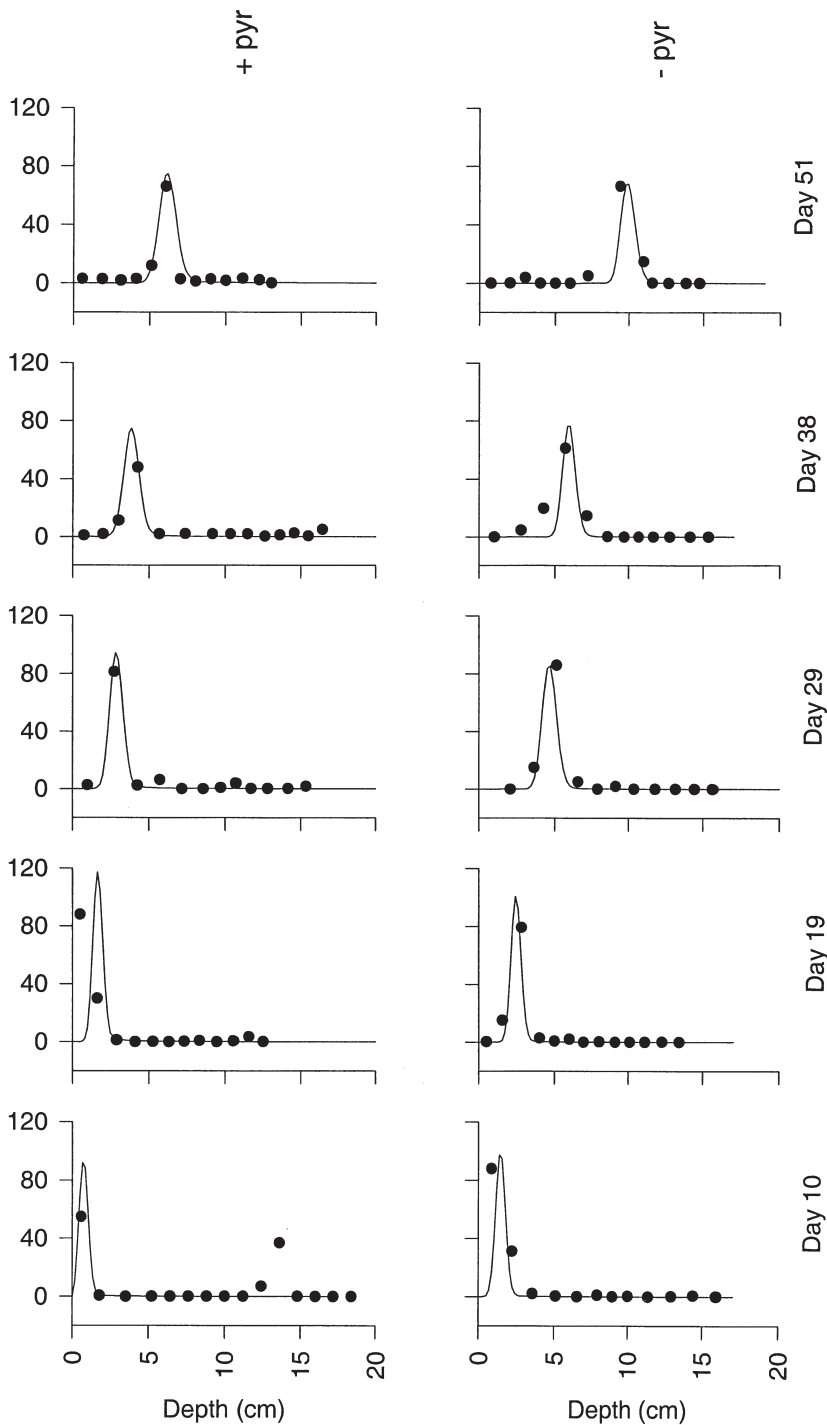


Fig. 3. – Measured (circle) and simulated (line) ⁵¹Cr-profiles from sediments with (+pyr) and without (–pyr) pyrene.

deed caused by particles falling down a feeding funnel. It is however not possible to predict such profiles beforehand since the simulation requires a tracer profile to estimate r_f and b .

In order to detect an effect of pyrene on the vertical ⁵¹Cr distribution the estimated particle transport velocities from the model, u_s , were compared

in a students *t*-test, which showed a significantly lower ($p=0.037$) subduction rate in contaminated sediments than in non-contaminated sediments (Table II). The subduction rate was estimated to be 0.091 ± 0.027 cm/day in pyrene contaminated sediment compared to 0.138 ± 0.033 cm/day in non-contaminated sediment. Hence pyrene reduced the subduction rate by 34%.

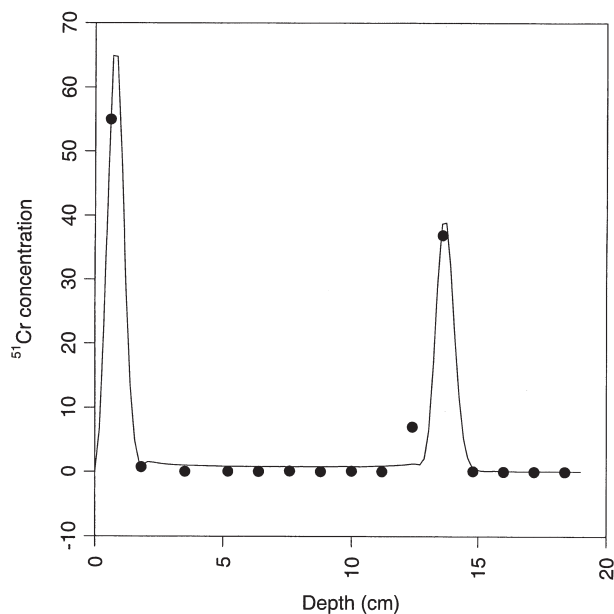


Fig. 4. – Measured (circle) and simulated (line) ^{51}Cr -profile (day 10, +pyr). In the simulation particles were allowed to fall down a feeding funnel with a radius estimated to 2.5 cm and with an estimated velocity of 1.3 cm/day.

Solute transport

The solute model was solved using the input parameters described in table I. Comparison between model predicted and measured Br⁻ profiles (Fig. 5) showed that the model was able to describe the measured profiles including the Br⁻ concentration peak observed at *A. marina* feeding depth. Unfortunately the measured profiles were too coarse at the top cm of the sediment to give a good diffusion profile.

Apparently the use of a mean pumping rate estimated from ^{109}Cd -fluxes was appropriate to model

the Br-profiles although in one profile (day 38, +pyr) the specific pumping rate during the Br⁻ incubation (2 hours) seemed to differ from the mean pumping rate measured during the entire experimental period (7 weeks) and better model descriptions were obtained when this parameter was changed as described in the “treatment of data” section.

In 5 simulations the measured subsurface Br⁻ concentration peak correlated very well with the observed location of the lugworm. In 3 cores better model descriptions were obtained by changing the location of z_f suggesting that these lugworms had changed their positions prior to or during core sectioning.

The radius of the advective zone, r_a , was estimated between 1.1 and 3.2 cm equivalent to areas of 3.8 and 32.2 cm². Hence in all cores r_a was less than the radius of the core (4.2 cm) indicating that the water was locally transported towards the sediment surface. The sediment volume affected by advective solute transport (i.e. $\pi (r_a)^2 z_f$) was between 51 and 467 cm³ accounting for approximately 3.4 to 31% of the total sediment volume.

It should be noted that in the core with a distinct feeding funnel (day 10, +pyr, Fig. 4) the radius of this funnel (r_f) was estimated to 2.5 cm using the particle model whereas the radius of the advective zone r_a in this core was estimated to 2.2 cm (Table I) using the solute model, which is a good agreement, strongly indicating that solutes in this core were transported within the feeding funnel.

In order to detect an effect of pyrene on solute transport the calculated velocity of the water transport $|u_{pw}|$ as well as the area of the advective zone ($\pi (r_a)^2$) were compared with a student's *t*-test (Table II). The test showed that while the parameter was lower, there was no significant difference in porewater transport velocity $|u_{pw}|$ between contaminated and non-contaminated sediment ($p=0.13$). Similarly, the area affected by advective solute transport was not significantly affected by pyrene ($p=0.24$).

Table II. – Model output parameters (mean \pm standard deviation) from pyrene contaminated and uncontaminated sediments as well as the result from the student's *t*-test.

Model parameter	Without pyrene	With pyrene	Probability
Particle velocity (u_s) cm/day	0.138 \pm 0.033	0.091 \pm 0.027	$p=0.037$
Porewater velocity (u_{pw}) cm/day	48.70 \pm 10.77	36.35 \pm 9.08	$p=0.13$
Area affected by advective solute transport (πr_a^2) cm ²	7.25 \pm 2.49	16.3 \pm 11.36	$p=0.17$

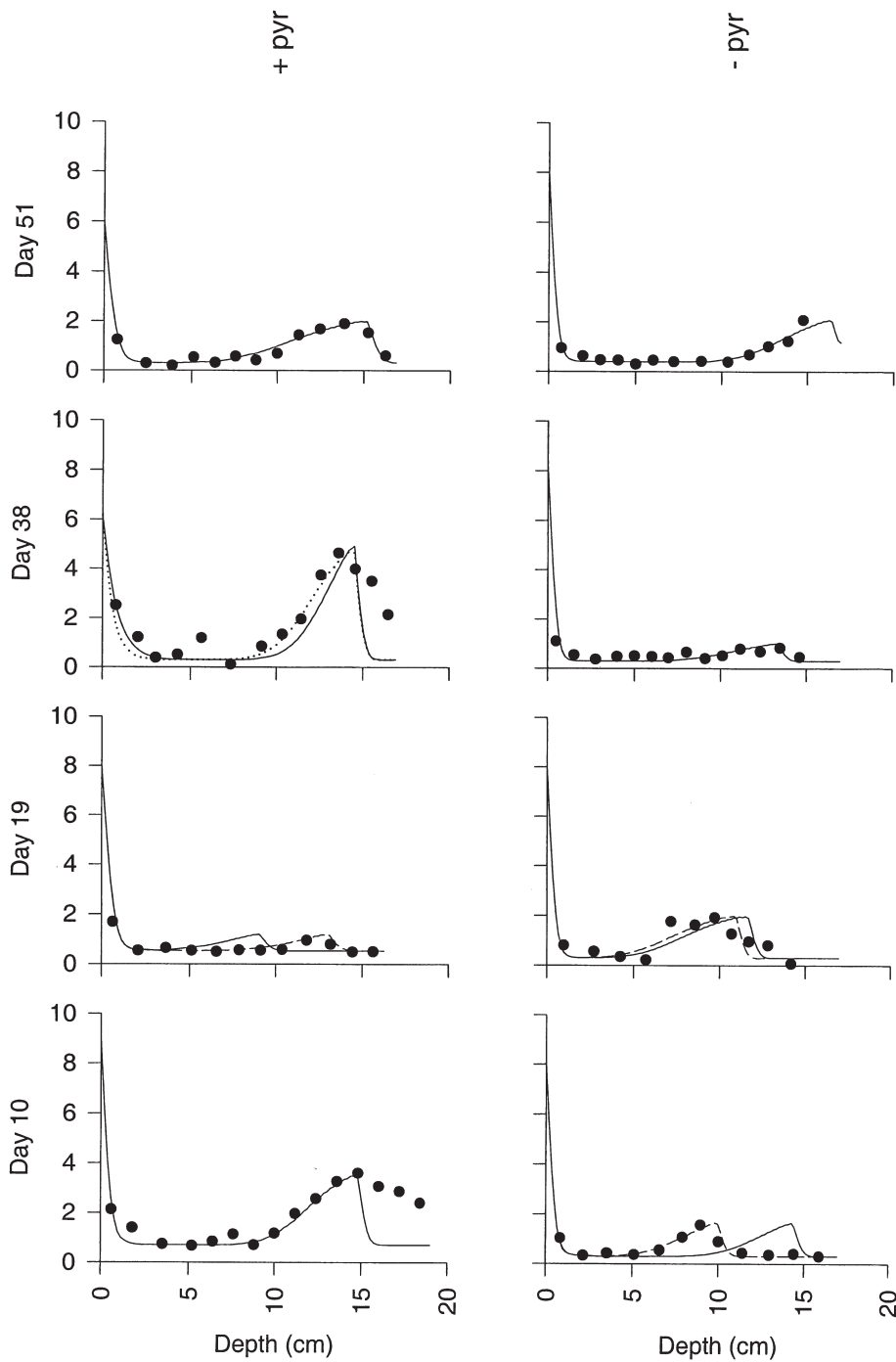


Fig. 5. – Measured (circle) and simulated (line) Br⁻ profiles from sediments with (+pyr) and without (-pyr) pyrene. Solid lines are simulations using empirical data. Dashed and dotted lines represent simulations where the location of the lugworm and the pumping rate were changed to give better fits (see text for explanation).

DISCUSSION

Particle mixing

Biological particle mixing is often considered analogous to eddy diffusion and described by a single biodiffusion coefficient, D_B . This description is appropriate when mixing is random or small scaled compared to the scale of the profile (Boudreau 1986). Bioturbation induced by conveyor belt feed-

ers is however a non-local bioadvective process which can not adequately be described by biodiffusion models (Boudreau 1986). This feeding mode results in the burial of a tracer containing toplayer and the appearance of a distinct subsurface tracer maximum (e.g. Madsen *et al* 1997) as observed from the ⁵¹Cr profiles in this study.

Reverse conveyorbelt feeding (Wheatcroft *et al.* 1994, Francois *et al.* 1997) and sedimentation (Rice 1986) can however also give rise to

subsurface particle tracer peaks. The effects of these processes on tracer distribution differ however from the effects from conveyorbelt feeders in dynamics and time scale. The effects of reverse conveyorbelt feeders which ingest particles at the sediment surface and defecate at some depth result in the appearance of a subsurface peak at defecation depth but contrary to conveyorbelt feeders this peak moves upward with time (Francois *et al.* 1997). Sedimentation is also described by advective transport (Rice 1986) and results in a subduction of a tracer containing toplayer. The rates are however orders of magnitudes lower than subduction rates induced by e.g. *A. marina*.

The particle model described in this paper is able to reproduce the characteristics of conveyor belt feeding namely the appearance of a subsurface peak and the downward movement of this peak. Apparently it is possible to predict the subduction rate by expressing the advective velocity in terms of bioturbation parameters (feeding rate). The advantages is that the subduction rate is predictable using a non-destructive method (feces production measurements) to estimate the subduction rate compared to normal situations where the subduction is estimated (based on best fit) from the tracer profiles which is a destructive method.

Although a distinct feeding funnel apparently was created in only one core (day 10, +pyr) the result from this core indicates that effects of particle mixing by *A. marina* may be different in different lateral zones. If a feeding funnel is created particles may fall down this funnel at high rates but over a small area leaving the surroundings unaffected by particle transport. In situations with no feeding funnel particle transport affects a larger area but the transport velocity is much lower. In sediment cores as those used in this experiment feeding funnels and thus fast particle transport are seldomly observed hence a 1 dimensional model is often appropriate. However 2 (or 3) dimensional models as the model presented in this paper are needed to describe the phenomena of particles falling down a funnel which is characteristic for the feeding mode of *A. marina*, especially in natural conditions.

Unfortunately it was not possible to verify the description of the particle sink (caused by *A. marina* ingestion) at feeding depth since the particle tracer did not reach feeding depth during the experimental period. This sink is only a true description if *A. marina* is a non-selective deposit feeder which is the normal characterisation of this animal (Beukema 1976). Particle selectivity is however very common among deposit feeders and may occur on the basis of e.g. size, shape and surface texture (Self & Jumars 1978, Taghon 1982). Depending on the tracer used selective conveyorbelt feeders may either enhance or reduce tracer concentration at feeding depth. Tracer concentration

increases if the animal avoids the tracer (as observed with glass beads) and decreases if the tracer is preferentially consumed (could be the case with particle sorbed tracers since deposit feeders often prefer small particles which contain high concentrations of particle sorbed tracer). To confirm the description of the particle sink the experiment should have been run for at least 90 days.

Solute transport

The solute transport model described in this paper was able to simulate the distribution of solutes within bioturbated sediment including the subsurface concentration peak often observed in sediments inhabited by lugworms. Apparently the size and location of this peak was predictable from *A. marina* pumping rate and the observed location of the lugworm.

Model estimates showed that the radius of the advective zone in all cores was smaller than radius of the sediment core (i.e. $r_a < r_2$) indicating that water was transported locally towards the sediment surface. However, in the majority of cores water was not transported towards the sediment surface within a feeding funnel since $r_a \neq r_f$ probably because real feeding funnels were not created. In the one core where a feeding funnel was observed the area of the advective zone was approximately the same as the area of the feeding funnel (i.e. $r_a \approx r_f$) indicating that the water in this case actually was transported within the feeding funnel. In nature where feeding funnels are often created it is thus likely that the water is transported towards the surface through this funnel as hypothesised by e.g. Huttel 1990.

Neither the injection, advective transport nor radial heterogeneity characteristics for solute transport induced by *A. marina* irrigation are adequately described by the common irrigation models such as the enhanced biodiffusion models, the radial diffusion model (Aller 1980a-c) and the non-local irrigation model (Emmersen *et al.* 1984). The hitherto only model accounting for the injection and advective transport of solutes was described in Timmermann *et al.* (2002). The solute transport model in the present article is an extension of that advective irrigation model. The model developed here differs from the model in Timmermann *et al.* (2002) by being described in cylinder coordinates, allowing inclusion of an area affected by advective transport in the geometry. As a consequence it is possible to model the spatial heterogeneity between advective solute transport in the advective zone (which sometimes equals the feeding funnel) and diffusional transport in sediment surrounding this zone/funnel. It is also possible to model diffusive transport of solutes from the overlying water into the sediment simultaneously with an advective

solute transport in the opposite direction as well as lateral diffusion which is not possible in the 1D model (Timmermann *et al.* 2002). Also, the injection of water at feeding depth is described differently in this model compared to the 1D model. The injection term in the 1D model adds tracer to the porewater at feeding depth which makes it unable to simulate situations where solutes are flushed out of the sediment. The injection term in the cylinder model is described as a replacement of porewater with overlying water at feeding depth (eqn 5) allowing one to describe the flushing effects as well as study the spatial heterogeneity between solute transport in the feeding funnel and transport in sediment surrounding the funnel.

The actual tube of the worm is however not included in the geometry and diffusive solute transport between tube water and porewater is thus not described in this model. In sediments where solute transport is dominated by injection and rapid advection of overlying water within the sediment molecular diffusion is of minor importance and in these situations it is reasonable to focus on the advective transport in the feeding funnel and not diffusion from the tube. In non porous sediments or with more weakly irrigating species, diffusion from the tube may likely dominate solute transport. This situation can be adequately described by the tube model by Aller (1980a-c) however. Although it is not possible to include the worm borrow in the geometry of the model developed in this paper, solute exchange between the tube and surrounding porewater can be included using a non-local apparent source term which can be expressed in terms of animal community parameters (Sandnes *et al.* 2000) and which is the 1D equivalent to Aller's radial diffusion model (Boudreau 1984).

The good agreements between simulated and measured particle and solute tracer profiles indicate that the models actually describe effects of lugworm bioturbation on particle and solute transport processes within the sediment. It is thus possible to use the models to translate tracer profiles into quantitative model parameters and use these parameters to detect significant differences due to e.g. contaminants. Furthermore, the biologically relevant parameters used in the models make the interpretation of the output parameters relatively straight forward. It is thus possible to test the effects of various factors such as contaminants on transport velocities and size of the bioturbated zone. It is of course possible to test effects on transport processes using other methods suitable for quantifying tracer profiles such as fitting known analytical functions to tracer profiles (e.g. Madsen *et al.* 1997), measure the distance from sediment surface to a tracer maximum or measure the area under a tracer profile etc. Such empirical approaches can however seldomly translate the results to real physical effects on transport processes

in the sediment. This requires models that mechanically describe transport processes.

Effects of pyrene on particle and solute transport

Sublethal concentrations of organic pollutants affect infauna bioturbation (Timmermann & Andersen 2003, Pécseli *et al.* 2002) as well as subduction rates. Gilbert *et al.* (1994) found that the rate of tracer burial by *Nereis diversicolor* was reduced by 77% in sediment contaminated with crude oil compared to uncontaminated sediment, and Madsen *et al.* (1997) observed a 19% reduction in subduction rate when *Capitella* sp. 1 was exposed to fluoranthene. In the present study, pyrene exposure resulted in a 34% lower subduction rate compared to uncontaminated sediment. Burial of particles due to large conveyor-belt species such as *A. marina* results in subduction rates of 28-48 cm/year which exceeds even high subduction rates of 1-3 cm/year in some coastal areas due to sedimentation from the water column (Olsen *et al.* 1981). Considering the importance of bioturbation compared to sedimentation for burial rates, a reduced biological subduction rate may significantly influence sediment processes such as organic matter recycling and the fate of organic pollutants (Kure & Forbes 1997).

The reduced subduction rate in pyrene contaminated sediment is causally related to a decreased feeding rate. Kure (1997) found reduced feces production in *A. marina* exposed to fluoranthene. Also, reduced feces production was observed for the related *Abarenicola pacifico* when exposed to oil contaminated sediment (Augenfeld 1980).

By reducing the feeding rate *A. marina* may reduce the intake of particle associated pyrene and thus reduce its own pyrene exposure. Kure (1997) found a close relation between the amount of fluoranthene passing the gut of *A. marina* and fluoranthene found in the tissue. This indicates that the worm to some extent may control its own contaminant exposure by regulating the feeding rate.

Apparently solute transport was not significantly affected by pyrene although transport velocities seem to be higher in non-contaminated sediments compared to contaminated sediment. Toxic effects of PAH's and other contaminants on infauna irrigation activity have, however been, detected in other studies (Timmermann & Andersen 2003, Miron *et al.* 1994). Miron *et al.* (1994) observed increased irrigation rates in *Nereis virens* exposed to low Hg concentrations (30 ppb) whereas the rate decreased at higher concentrations (300-3000 ppb). When *A. marina* was exposed to oil contaminated sediment there was a slight but not significant tendency for *A. marina* irrigation to increase whereas feeding rate was significantly reduced in contaminated sed-

iment (Pécseli *et al.* 2002). Apparently, feeding rate is more sensitive to toxicants than irrigation. Several PAH's exert narcotic effects on invertebrates leading to decreased feeding rates (More *et al.* 1989). It is however not clear if the narcotic effects also affect irrigation. On the other hand infauna are able to change their feeding rates as response to sediment quality such as content of organic matter (e.g. Taghon & Jumars 1984) and also avoidance behaviour as a response to contaminants has been observed (Møhlenberg & Kiørboe 1983, Landrum *et al.* 1991). A decreased feeding rate in contaminated sediment may thus indicate that infauna are able to avoid contaminants by decreasing their sediment ingestion.

Since infauna often play important roles for transport processes within the sediment, effects of contaminants leading to changed bioturbation activity may have profound effects on geochemical and diagenetic sediment processes as well as the fate of contaminants. A toxic response resulting in decreased subduction rates as observed in this study may enhance contaminant removal since contaminants stay longer at the sediment surface where degradation and desorption to overlying water is possible (Madsen *et al.* 1997, Kure & Forbes 1997) indicating a strong link between effects and fate of contaminants in bioturbated sediments.

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