BIO-IRRIGATION INDUCED BY *ARENICOLA MARINA*: CLASSICAL ASSUMPTIONS VS. NUMERICAL MODELING

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The sediment irrigation due to pumping activity of the lugworm *Arenicola marina* is simulated numerically using a finite element approach. A detailed model of the flow field surrounding the L-shaped *Arenicola* burrow was constructed. The mucus lining of the burrow walls appears essential as a hydrodynamical barrier, i. e. to prevent short-circuits of the porewater flow and re-entry of anoxic porewater. In contrast to current ideas, *Arenicola*'s quicksand column turns out to have a rather minor effect on porewater flow and solute transport.

Introduction

Besides molecular diffusion, bio-irrigation comprises the most important transport process controlling the exchange of solute components between surface sediments and the overlying water column. 3D numerical simulations were performed in order to study sediment irrigation induced by the pumping activity of benthic organisms. The lugworm *Arenicola marina* was selected as the model organism, since it is highly abundant and active in coastal environments, and thus plays an important role in bio-irrigation.

Arenicola marina is a head-down deposit feeder inhabiting intertidal sand flats. This polychaete can represent more than half of the total biomass of all worm species in the tidal flat ecosystem (BEUKEMA & VLAS, 1979). The worm dwells in L-shaped burrows, which may reach a depth of 20-30 cm. When feeding, the worm resides in the lower part of the burrow called the ''gallery'' (see Fig. 1). It ingests sediment from the feeding pocket at the closed end of the gallery. This causes a downward motion of sediment and leads to the formation of the so-called quick-sand column. This cylinder of loosened sediment ends in the funnel, a depression on the sediment surface. The sediment is excreted at the open end of the burrow forming faecal mounds. The polychaete ventilates its tube by pumping oxygenated water from the overlying water body *via* peristaltic motions. This water enters the open end of the tailshaft, is pumped to the feeding pocket and then percolates to the surface through the sediment. The general assumption is that the water rises almost exclusively through the quicksand column. The validity of this assumption and the role of the tube wall insulation are assessed in this work.

Numerical methods

The emphasis in this modelling exercise lies on a proper description of (1) the flow field and (2) the reactive transport around the *Arenicola* burrow. The worm itself is modelled as a pump with a known flux *versus* pressure performance (RIISGARD et al., 1996). The porewater flow in the sediment is described by Darcy's law, which relates the velocity vector to the pressure gradient by:

$$\vec{v}_d = -(k/\eta)\nabla p ,\qquad(1)$$

where k denotes the permeability of the porous medium, η the porewater viscosity, and p the pressure; v_d is Darcy velocity (related to actual porewater velocity v as $v_d = \phi v$).
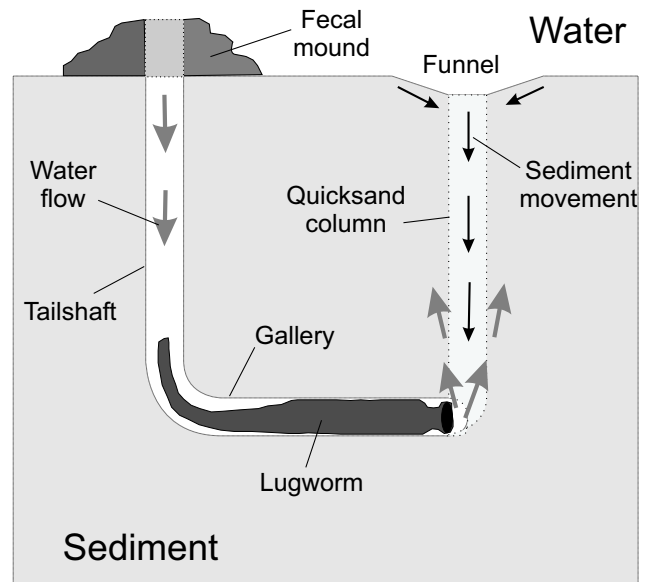

Fig. 1. Schematic drawing of the *Arenicola marina* L-shaped burrow, sediment movement and water flux.

The sediment porosity ϕ is assumed to be constant, whereas the effect of permeability is discussed below. Equation (1) is combined with the continuity equation for an incompressible fluid:

$$\nabla \cdot \vec{v}_d = 0 .\qquad(2)$$

Upon substitution of (2) into (1), one obtains

$$\nabla \cdot \left(-(k/\eta)\nabla p\right) = 0 \qquad(3)$$

This equation then is solved using the finite element approach implemented in the Chemical Engineering Module of FEMLAB® (COMSOL AB, 2002). The resulting output comprises the pressure field over the computational domain. Using equation (1), the sought-after flow field around the Arenicola burrow can be calculated.

This velocity field $\vec{v}_d$ can then be used as input in a reactive transport model for porewater solutes, described by the mass conservation equation

$$\frac{\partial c}{\partial t} + \frac{1}{\phi}\vec{v}_d \cdot \nabla c - D^* \Delta c - R = 0 ,\qquad(4)$$

where c is the concentration in the porewater, $D^* = D/(1-2\log\phi)$ the molecular diffusion coefficient corrected for tortuosity effects (BOUDREAU, 1996), and R is a production term due to chemical reactions. When modelling passive tracers, this reaction term should be set to zero.

The size of the computational domain roughly represents the average volume of sediment that is occupied by a worm on an intertidal flat (BEUKEMA & VLAS, 1979). Accordingly, a sediment block of the dimensions L 20 × W 20 × H 25 cm was selected, which corresponds to a density of 25 animals per square meter. The worm tube is placed in the middle plane of the sediment block, so that because of symmetry, only half of the domain needs to be modelled. The burrow is cylindrical and has a constant diameter of 5 mm. Fig. 2 shows the finite element mesh used in numerical simulations.

Flow patterns

In order to solve the flow field $\vec{v}_d$ from equation (3), one must implement appropriate boundary conditions. The bottom and

side walls of the sediment box are assumed impenetrable to flow. So, one effectively needs to prescribe the water exchange at the sediment-water interface (SWI) and at the interface between the burrow and the surrounding sediment (BSI). At the SWI this is rather straightforward: a constant hydrostatic pressure was applied (which was arbitrarily set to $p = 0$). The water exchange across the tube wall boundary however requires additional consideration.
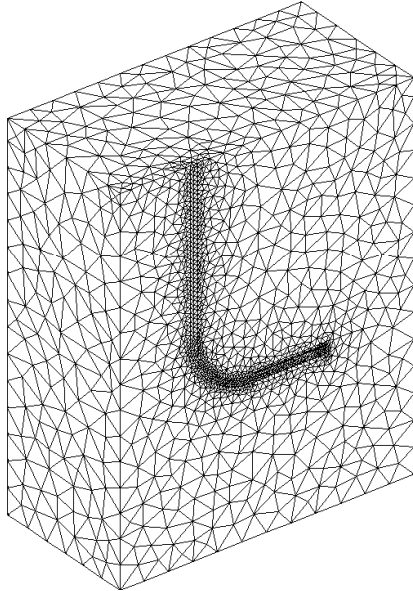

Fig. 2. Example of the finite element mesh used for the lugworm burrow and surrounding sediment.

The *Arenicola* burrow is surrounded by a mucus layer, which is presumably essential to prevent the structure from collapsing, but also to ensure the efficiency of peristaltic pumping (see below). To simulate the effect of a thicker mucus layer in the lower part of the burrow, the gallery is hydrodynamically insulated. In the computational domain it is surrounded by impenetrable solid cylinder. In contrast to the gallery, the mucus layer covering the tailshaft may be relatively thin. According to HÜTTEL (1990), sediment particles are cemented by mucus, forming a layer which is roughly 1 mm thick and which is relatively impermeable for the advective flux of porewater (but still allows oxygen to diffuse through the burrow wall). Actual data about the permeability of the mucus-lined walls is, however, not available. Thus, we consider here two limiting cases: fully permeable (continuity of the porewater flux) and completely impermeable walls (no flow condition across the burrow wall).

Fig. 3a shows the pattern of the streamlines in the case of fully permeable tailshaft walls. A significant fraction of the water volume pumped by the worm re-enters the burrow through the permeable walls of the tailshaft (about 40% of the total irrigation discharge). This porewater re-entering the burrow will be practically anoxic. Consequently, such short-circuits should have an adverse effect, since the worm's main reason for irrigating is to ensure an adequate oxygen supply for respiration (according to ZEBE & SCHIEDEK, 1996, *Arenicola marina* is able to extract between 32 and 40% of dissolved oxygen out of the incoming water). The flow pattern in the case of completely insulated burrow walls is illustrated in Fig. 3b.

Since the sediment used in this study has a uniform permeability, the porewater injected into the sediment at the end of the burrow spreads and rises to the surface over a rather large area. In particular, some flow lines head initially downwards from the injection point. This fact may be important, since it implies that the sediment layers below the burrows may also be affected by advective irrigation and not only by diffusive transport.

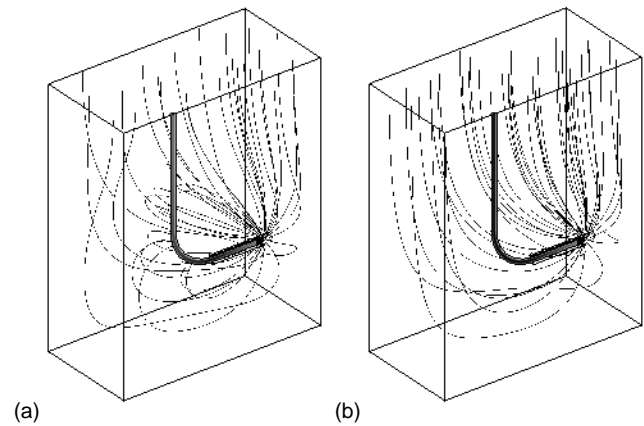(a)   (b)

Fig. 3. Flow lines of the porewater flow through the sediment with constant porosity arising in the cases of (a) permeable and (b) impermeable walls of the tailshaft.

Effect of permeability

In this work, we assume that the dependence of the volumetric water flow on the pressure of the lugworm's peristaltic pump follows the curve established by RIISGARD (1996) for a "standard" *Arenicola marina* specimen. Basically, when the worm experiences an increased back pressure, its pumping rate will diminish. The pumping pressure and corresponding flow rates, computed for the sediments with different permeability, are summarized in Fig. 4. The sediment permeability determines the pumping rate and, consequently, the available oxygen supply. Consequently, the insulation of the tailshaft walls should extend the habitat range of the lugworm into less permeable muddy sediments.

Passive transport modelling

A frequently used experimental method to evaluate irrigational transport is by means of passive tracer (see for example, TIMMERMANN *et al.,* 2002). Fig. 5 illustrates the computed vertical profiles of the passive tracer Br⁻ in a highly permeable sand after 1–5 hours of pumping activity for a "standard" *Arenicola marina* (RIISGARD, 1996). The tracer parameters as in TIMMERMANN *et al.* (2002) were used, i. e. the molecular diffusion coefficient of Br⁻ was calculated at a temperature $T = 10^{o}C$.

Numerical results were compared to data from experiments by TIMMERMANN *et al.* (2002) performed in sediment cores. Fig. 6 shows the fit of the experimental tracer profile (TIMMERMANN *et al.,* 2002; Fig. 2e therein) with the three-dimensional numerical simulation. The burrow end in these computations was located at a depth of 24.3 cm at the axis of the 30 cm deep sediment core. Thus, results of the three-dimensional simulation (assuming uniform sediment properties) closely resemble the experimental results. However, the simulation should be interpreted with caution. The sediment cores used by TIMMERMANN *et al.* (2002) had a relatively small diameter of 8.2 cm, which could lead to a significant "container effect" (given the size of an *Arenicola* burrow).
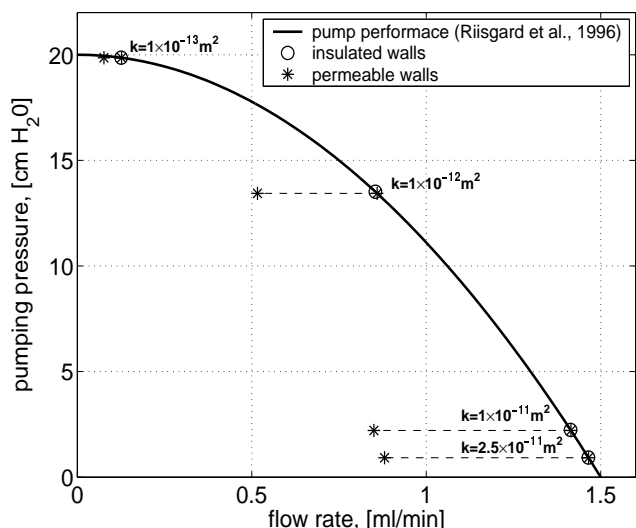
Fig. 4. Pumping pressure, achieved flow rates and influx from the water column (for permeable burrow walls only) computed for "standard" (RIISGARD *et al.*, 1996) *Arenicola marina* in the sediments with varying permeability.
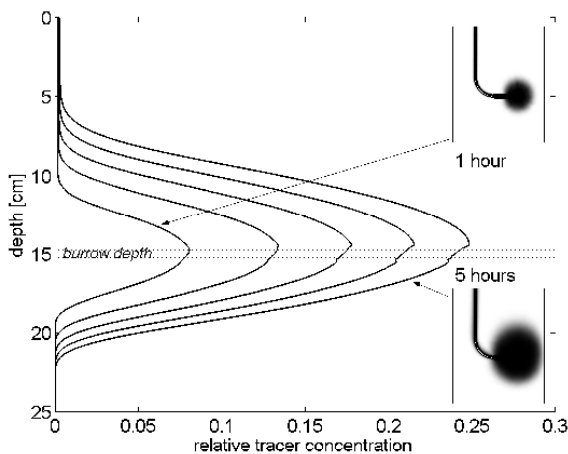

Fig. 5. Vertical profiles of advected passive tracer concentration after 1–5 hours of pumping of "standard" *Arenicola marina* (RIISGARD *et al.*, 1996).
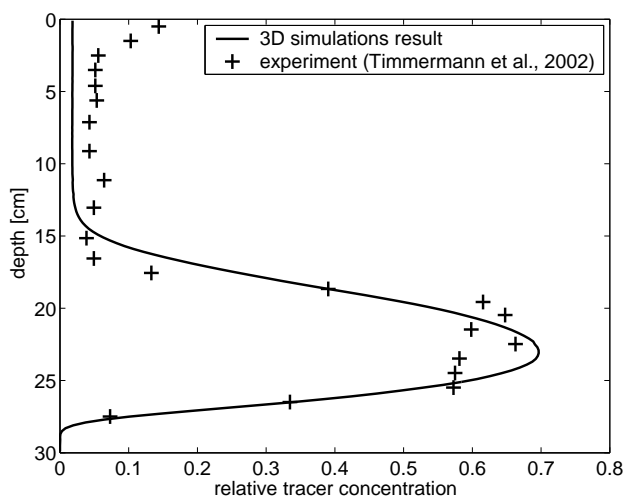

Fig. 6. Comparison of the vertical profile of a passive tracer from 3D simulations with the experimental data (TIMMERMANN *et al.,* 2002; Fig. 2e therein).

Quicksand column: importance?

The results presented above are obtained under the assumption of a homogeneous permeability in the sediment box. However, it is generally assumed that the water injected into the sediment rises to the surface mostly within a quicksand column of loosened sediment (see Fig. 1), which is supposed to have higher permeability than the surrounding sediment. This quicksand column is, however, rather narrow and has a typical width of about 5 mm (RIJKEN, 1979). This makes it unlikely that a significant portion of the porewater flux occurs through this narrow channel.

To assess the role of the quicksand column additional computational tests were performed. The model domain in these simulations was axisymmetric (this allows to use finer grids). A 5 mm wide quicksand channel was located at the axis of this sediment cylinder. The water is injected into the lower end of the quicksand column, and then moves up to the sediment surface. The sediment permeability linearly increases toward the centre of the quicksand channel, reaching a maximum value, which is 10 times higher than the permeability of the bulk sediment. Fig. 7 shows the distribution of passive tracer after pumping for one hour with a flow rate of 1.5 ml/min (sediment is assumed to have a porosity equal to 0.5) for the cases of uniform sediment permeability (left) and with the increased permeability of quicksand. The variation of the sediment permeability inside the rather narrow channel has a minor effect. In both cases most of the flux is carried in the surrounding bulk of undisturbed sediment. As a result, the tracer concentration profiles exhibit only a small difference: the presence of a quicksand column leads to the formation of a "finger" protruding from the growing tracer blob at the base of the quicksand channel.
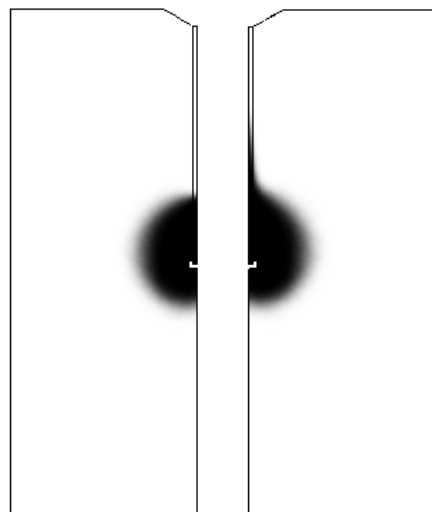

Fig. 7. The role of a quicksand: Passive tracer profiles after 1 hour of pumping without (left) and with a permeable quicksand channel present (right).

Reactive transport modelling

Pumping activity of the lugworm results in the injection of the oxygen-rich water into the sediment which otherwise would be anoxic at the burrow depth. Using the estimated oxygen consumption rate in the sediment, $R_i = 2.83 \times 10^3 \, \text{yr}^{-1}$, we can estimate the oxygen concentration patterns arising due to sediment irrigation by *Arenicola marina*. Fig. 8 shows the estimated relative oxygen concentration patterns arising in the sandy ($k = 2.5 \times 10^{-11} \, \text{m}^2$) and muddy ($k = 1 \times 10^{-13} \, \text{m}^2$) sediments. In these computations we assume that the burrow walls are insulated and neglect the downward diffusion of oxygen from

the water column through the sediment-water interface, since it is strongly counteracted by advective flux of the rising anoxic porewater.
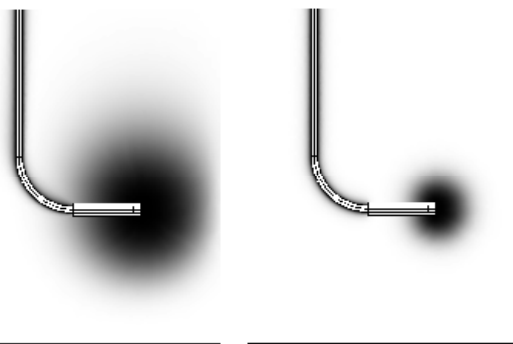

Fig. 8. Oxygen concentration patterns due to sediment irrigation by *Arenicola marina* estimated using the first-order oxygen consumption rate (see text) for the cases of sandy (left) and muddy sediment.

Effect of irrigation on oxygen penetration depth

As shown above, the irrigational pumping of *Arenicola* will drastically change the pattern and magnitude of the porewater velocity in the sediment, but also near the sediment-water interface. It is of interest to estimate how these increased porewater velocities will influence the transport of oxygen across the SWI. The steady-state reactive transport of oxygen in the thin sediment layer just under the sediment-water interface may be described by the one-dimensional conservation equation

$$-v\frac{\partial c}{\partial z} + D^*\frac{\partial^2 c}{\partial z^2} - R_1 c = 0 , \qquad (5)$$

The general solution of equation (5) is of the form

$$c = c_0 \exp(-z/d) , \qquad (6)$$

where the coefficient $d > 0$ has the physical meaning of penetration depth. Substituting expression (6) into the equation (5) yields a second order algebraic equation with respect to d^{-1}. Taking its positive root we obtain an expression for the oxygen penetration depth as a function of upward porewater velocity, diffusion coefficient and reaction rate:

$$d = \frac{2D^*}{v + \sqrt{v^2 + 4D^* R_1}} \qquad (7)$$

In the absence of the porewater flow ($v = 0$) the penetration depth becomes $d_0 = \sqrt{D^*/R_1}$. In the case of no irrigation (7) yields an estimate for penetration depth $d_0 \approx 3$ mm. In the case of irrigation, the upward Darcy velocity is of the order of $v_d = 2 \times 10^3$ cm/yr, leading to a penetration depth decrease to 0.5 mm.

Conclusions

The three-dimensional finite element simulations were performed to study the sediment irrigation due to pumping activity of the lugworm *Arenicola marina*. The results show that lining of the burrow walls is essential to prevent short-circuit of the flow lines in the sediment, drawing anoxic porewater into the burrow and, thus, hampering the oxygen supply. Thus, burrow lining not only mechanically reinforces the burrow walls but also helps to extend the habitat range of the lugworm towards less permeable, muddy sediments.

The results of the numerical simulations indicate that the presence of a quicksand channel containing loosened sediment (sediment from upper layers sinking towards the feeding pocket, where it is being ingested by lugworm) with supposedly higher permeability has a rather moderate effect on the porewater fluxes. Most of the total flux is carried in the bulk of relatively undisturbed sediment, reaching the surface over a wide area.

References

BEUKEMA, J. J. & DE VLAS, J. (1979) Population parameters of the lugworm, *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res., **13**, 331–353.

BOUDREAU, B. P. (1996) The diffusive tortuosity of fine-grained unlithified sediments. Geochim. Cosmochim. Acta, **60**, 3139 – 3142.

COMSOL AB (2002) FEMLAB Chemical Engineering Module. COMSOL AB, Tegnérgatan 23, SE-111 40 Stockholm, Sweden.

HÜTTEL, M. (1990) Influence of the lugworm *Arenicola marina* on porewater nutrient profiles of sand flat sediments. *Mar. Ecol. Prog. Ser.* 62, 241–248.

RIISGARD, H. U., BERNSTEN, I. & TARP, B. (1996) The lugworm (*Arenicola marina*) pump: characteristics, modelling and energy cost. Mar. Ecol. Prog. Ser., **138**, 149–156.

RIJKEN, M. (1979) Food and food uptake in *Arenicola marina*. Neth. J. Sea Res., **13**, 406–421.

TIMMERMANN, K., CHRISTENSEN, J. H. & BANTA, G. T. (2002) Modeling of advective solute transport in sandy sediments inhabited by the lugworm *Arenicola marina*. J. Mar. Res., **60**, 151–169.

ZEBE, E. & SCHIEDEK, D. (1996) The lugworm *Arenicola marina*: a model of physiological adaptation to life in intertidal sediments. Helgoländer Meeresunters., **50**, 37–68.

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