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Burrow patchiness and oxygen fluxes in bioirrigated sediments

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ABSTRACT

Bioturbation plays a crucial role in benthic nutrient cycling in many sedimentary environments. Burrowing animals affect benthic–pelagic coupling by mixing sediment and porewater and increasing the effective area of diffusive exchange between oxidizing and reducing environments. Here, we report on a coupled laboratory-modeling experiment that explores organism distribution patchiness and its implications on sedimentary oxygen fluxes. Microcosms were established with three different arrangements of artificial burrows. Data from the laboratory were used to parameterize a three-dimensional diffusion–reaction model, and the impact of burrow distribution on benthic O_2 fluxes at the plot (decimeter) scale was assessed for a range of sediment reactivities representing a variety of benthic habitats. At high O_2 consumption rates, as seen in the microcosms, burrow spacing had little to no effect on sedimentary O_2 uptake; at intermediate rates, the overlap of oxic halos surrounding burrows and benthic O_2 uptake depended significantly on the burrow distribution pattern. Using observed relationships between benthic O_2 flux and oxygen penetration depth in marine sediments, we predict that burrow patchiness has its greatest impact in settings with benthic oxygen fluxes on the order of 1–10 mmol m^{-2} d^{-1}, typical for the continental shelf and slope. The biogeochemical heterogeneity caused by burrows also affects the interpretation of concentration measurements, and we present an estimate of the number of measurements needed to reliably estimate bulk O_2 concentrations in cohesive sediments as a function of organism density, measurement scale and sediment reactivity.

1. Introduction

Organisms that reside within sediments have significant impacts on the nature and properties of their benthic environment (Coleman and Williams, 2002; Meysman et al., 2006). The effects of benthic faunal bioturbation manifest themselves at the scale of individuals (Aller, 1980; Krantzberg, 1985) and may propagate to the scale of ecosystems when organism densities are sufficiently high (Waldbusser et al., 2004). The cumulative effect of burrowing organisms is well illustrated by the dramatic alteration of oceanic sulfur cycling during the Phanerozoic, caused by the evolution of burrowing across the Ediacaran/Cambrian transition (Canfield and Farquhar, 2009), or by the modern ecosystem engineering of bioturbating organisms (e.g. D'Andrea and DeWitt, 2009). However, when investigating ecosystem-level implications of bioirrigation, inferences from spatially averaged plot-scale measurements are often used to describe effects over larger scales. Such extrapolations may be impacted by unresolved localized features and small-scale variability (Schneider et al., 1997).

At the infaunal organism scale (mm-cm), the biogeochemical effects of benthic infaunal burrows in diffusion-dominated environments stem in large part from the creation of additional surface area for diffusive solute exchange between reduced porewater and oxidized overlying water (Aller, 1980). The balance of reaction and diffusion leads to sub-mm to cm-scale concentration and redox gradients across sediment-water interfaces, including burrow walls (Timmermann et al., 2006), which drive benthic solute exchange fluxes. A complex three-dimensional zonation of biogeochemical transformations results (Kristensen, 2001), and numerous studies have shown burrow effects on chemolithotrophy and abiotic redox reactions (Kristensen and Kostka, 2005) as well as coupled nitrification/denitrification (Kristensen, 1988). The seminal work of Aller (1980) on the radial diffusion model to describe the local burrow environment is an elegant approach that has proven adequate in many cases for capturing effects of infauna on sediment biogeochemistry by describing a complex spatial domain as a collection of equally-spaced cylindrical vertical burrows. This micro-environment approach allows for very fine scale (sub-mm to cm) and computationally efficient descriptions of the biogeochemical dynamics around burrows. However, the application of a constant inter-burrow distance may limit the ability of this model to predict benthic exchange fluxes if patchy infaunal distributions result in overlap of geochemical zones of influence between burrows.

Patchiness has long been recognized as a structuring agent of sediment properties and benthic communities (e.g. Levin, 1992; Underwood et al., 2000), and in a seminal work on spatial dynamics

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in the benthos, Morrisey et al. (1992) noted the variability of benthic infaunal populations across increasingly large (up to kilometers), nested spatial scales. However, the smallest sampling resolution considered by Morrisey et al. was that of core samples, capturing approximately 80 cm^2. In many settings, this may encompass numerous burrow structures in different spatial arrangements, exemplifying the disparity between the resolution at which benthic communities are sampled and the resolution at which animal-sediment interactions are studied or modeled. Thus, common coring or grab-type sampling does not address the question of how individual tube-building animals' spatial domains of biogeochemical influence interact (as they do ecologically, *sensu* Woodin, 1978), and what the biogeochemical consequences of these interactions are. Indeed, fine-scale patchiness as a factor shaping soft-sediment communities and as a potential driver of sediment biogeochemical processes has received only limited treatment.

Studies aimed at documenting the effects of density or burrow spacing on sediment chemistry have noted non-linear effects; for example, Marinelli (1994) and Marinelli and Williams (2003) found non-linear effects of burrow density on biogeochemical fluxes, and in sediment plug experiments mimicking evenly spaced burrows, Gilbert et al. (2003) report non-linear effects on denitrification with respect to burrow densities and inter-burrow distance. Such results represent important steps forward in more fully integrating the spatially explicit nature of life within marine sediments, and they emphasize the need to assess the implications of spatial variation in order to fully understand the intricacies of ecosystem interactions (e.g. Timmermann et al., 2006; Volkenborn and Reise, 2007).

Here, we report on a coupled laboratory-modeling approach toward gauging the importance of burrow spatial arrangement on sediment biogeochemical fluxes. A microcosm experiment using artificially irrigated burrow mimics was conducted to illustrate the effect of burrow patchiness on sediment oxygen fluxes. Finite-element reactive-transport modeling was used in tandem with the laboratory experiments to explore the effects of oxygen consumption rate and burrow arrangement on sediment biogeochemistry. This approach allows us to apply a mechanistic description to identify under what conditions burrow patchiness may be an important community level parameter in cohesive sediments.

2. Methods

2.1. Laboratory methods

Laboratory microcosms were established in four 10 cm long by 10 cm wide by 20 cm deep rectangular containers. These aquaria were filled with homogenized surface sediment collected from a muddy-sand intertidal flat, Little Tom's Cove, VA, USA (lat = 37.886, lon = 75.345). The sediment was poorly sorted, with the following average properties across all microcosms as determined by methods of Folk and Ward (1957): porosity (ϕ) 0.43 ± 0.01, mean grain size $281.8\ \text{mm} \pm 6.7$ and $0.50 \pm 0.25\%$ fines (passing a 75 mm sieve). Sediment was added to a depth of about 15 cm, leaving 5 cm of overlying water. Sediment was allowed to settle for one day before burrow structures were added by core replacement.

Artificial burrows with an inner radius of 0.4 cm and length of 10 cm were constructed of Magna nylon filter paper (0.45 μm filter) surrounded by 125 μm nominal sieve opening Nitex to provide structure, and were cinched at the bottom. Four burrows were placed in each microcosm, resulting in an areal density ρ of 400 per m^2 (e.g. Miron and Kristensen, 1993; Volkenborn and Reise, 2007), in three different arrangements (Fig. 2, top): even, grouped, and cornered. These arrangements represent an approximately uniform burrow distribution, many small and evenly-spaced burrow clusters, and widely-spaced large clusters of burrows, respectively. In the even arrangement, burrows were aligned in a square with roughly 2.5 cm between burrows located roughly 3 cm from the edge of the aquaria. In the grouped treatment burrows were approximately 0.5 cm apart and 4 cm from the edge of the aquaria. The cornered treatment had the same inter-burrow distances, but all burrows were within 1.5 cm of the corner of the microcosm. The Clark-Evans Indices (Clark and Evans, 1954), defined as $R = 2\bar{r}\sqrt{\rho}$, where $\bar{r}$ is the average distance to the nearest neighbor within the plot, of these plots are 1.6, 0.8 and 0.8, respectively (where $R = 1$ in a uniform random distribution and $R = 2$ in a completely uniform arrangement).

After artificial burrows were added to microcosms, the microcosms were placed in a seawater bath that was fed from a filtered, recirculating seawater system with a temperature of 22 °C and salinity of 33. Artificial burrows were flushed with a 12 channel peristaltic pump (Masterflex Computerized Drive, Model 75550-60), one channel per burrow, at a rate of 1 ml min^{-1} per burrow. The irrigation tubes were run through the acrylic lids and sealed with silicon, with one return line that fed each of the four pump channels per microcosm, so that microcosms could be sealed to measure fluxes of oxygen while water was being irrigated into burrows without contact to atmosphere. Except for the peristaltic tubing, all tubing used externally of the microcosms was low gas permeability, silver-embedded tubing (Tygon Silver Antimicrobial Tubing) to prevent atmospheric contamination and limit microbial biofilms inside tubing. When fluxes were not being measured, the tops of microcosms were propped open by 3–5 cm and vigorous mixing of the seawater bath ensured exchange between sediment and water bath, while allowing for irrigation of burrows. Flux measurements were performed in August 2009 and run over the course of 2 h. The experiments were repeated 4 times, and oxygen levels in the overlying water were monitored using a Thermo-Orion O_2 probe. Oxygen flux was determined by fitting a slope to the measured oxygen levels in the microcosm water.

To determine O_2 consumption rates and kinetic rate constants, sediment flask incubations were run separately. Sediment was removed from the microcosms at the end of the experiment and sealed in a flask. O_2 concentrations were measured every half-hour for six hours, and again at 26 and 30 h using a Thermo-Orion 4-Star oxygen meter and probe. Winkler titrations and spectrophotometric analyses of oxygen were also used to verify accuracy of the oxygen electrode.

2.2. Modeling approach

Reactive transport simulations were set up to mimic the laboratory microcosms, with 4 cylindrical burrows distributed according to the even, grouped, or clustered settings. For simulations with a lower organism density, the domain was extended to 20 cm × 20 cm × 20 cm, with inter-burrow distances increased proportionally. The O_2 concentration field was computed taking into account diffusion and reaction, and run to steady state:

$$0 = \nabla \cdot (D \nabla C) - k \frac{C}{C + K_m} \quad (1)$$

where C is the O_2 concentration. The effective diffusion coefficient D is estimated as $D = D_{mol}\phi^2$ (Ullman and Aller, 1982), with a molecular diffusion coefficient D_{mol} of $1.73 * 10^{-9}\ m^2\ s^{-1}$. O_2 consumption was modeled using Monod kinetics with K_m set to 20 μM (Furukawa, 2001). The maximum sediment oxygen consumption rate k was determined from flask incubations, and subsequently varied to assess the impact of both sediment reactivity and burrow distribution patterns on O_2 distribution and exchange fluxes. At the sides and bottom of the model domain, fluxes were set to zero, while an O_2 concentration of 220 μM was imposed at the sediment surface and burrow walls as the artificial burrows were continuously flushed.