Running Head: Burrow Patchiness and Sediment O_2 Fluxes

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.

Key words: patchiness, bioturbation, benthic-pelagic coupling, sediment oxygen uptake

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 (Timmerman 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 et al. 1988). The seminal work of Aller (1980) on the radial diffusion model to describe the local

61 burrow environment is an elegant approach that has proven adequate in many cases for capturing
62 effects of infauna on sediment biogeochemistry by describing a complex spatial domain as a
63 collection of equally-spaced cylindrical vertical burrows. This micro-environment approach
64 allows for very fine scale (sub-mm to cm) and computationally efficient descriptions of the
65 biogeochemical dynamics around burrows. However, the application of a constant inter-burrow
66 distance may limit the ability of this model to predict benthic exchange fluxes if patchy infaunal
67 distributions result in overlap of geochemical zones of influence between burrows.
68 Patchiness has long been recognized as a structuring agent of sediment properties and
69 benthic communities (e.g. Levin 1992, Underwood et al. 2000), and in a seminal work on spatial
70 dynamics in the benthos, Morrisey et al. (1992) noted the variability of benthic infaunal
71 populations across increasingly large (up to kilometers), nested spatial scales. However, the
72 smallest sampling resolution considered by Morrisey et al. was that of core samples, capturing
73 approximately 80 cm^2. In many settings, this may encompass numerous burrow structures in
74 different spatial arrangements, exemplifying the disparity between the resolution at which
75 benthic communities are sampled and the resolution at which animal-sediment interactions are
76 studied or modeled. Thus, common coring or grab-type sampling does not address the question
77 of how individual tube-building animals' spatial domains of biogeochemical influence interact
78 (as they do ecologically, *sensu* Woodin 1978), and what the biogeochemical consequences of
79 these interactions are. Indeed, fine-scale patchiness as a factor shaping soft-sediment
80 communities and as a potential driver of sediment biogeochemical processes has received only
81 limited treatment.
82 Studies aimed at documenting the effects of density or burrow spacing on sediment
83 chemistry have noted non-linear effects; for example, Marinelli (1994) and Marinelli and

84 Williams (2003) found non-linear effects of burrow density on biogeochemical fluxes, and in
85 sediment plug experiments mimicking evenly spaced burrows, Gilbert et al. (2003) report non-
86 linear effects on denitrification with respect to burrow densities and inter-burrow distance. Such
87 results represent important steps forward in more fully integrating the spatially explicit nature of
88 life within marine sediments, and they emphasize the need to assess the implications of spatial
89 variation in order to fully understand the intricacies of ecosystem interactions (e.g. Timmermann
90 et al. 2006, Volkenborn et al. 2007).

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

99

100 **Methods**

101 *Laboratory Methods*

102 Laboratory microcosms were established in four 10 cm long by 10 cm wide by 20 cm
103 deep rectangular containers. These aquaria were filled with homogenized surface sediment
104 collected from a muddy-sand intertidal flat, Little Tom's Cove, VA, USA (lat = 37.886, lon =
105 75.345). The sediment was poorly sorted, with the following average properties across all
106 microcosms as determined by methods of Folk and Ward (1957): porosity 0.43 ± 0.01, mean

grain size 281.8 mm ± 6.7 and 0.50 ± 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 a density ρ of 400 per m^2 (e.g. Miron and Kristensen 1993, Volkenborn et al. 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 hours. 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 hours 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.

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 x 20 cm x 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:

153 $$0 = \nabla \cdot (D \nabla C) - k \frac{C}{C + K_m} \quad (1)$$

154 where C is the O_2 concentration. The effective diffusion coefficient D is estimated as $D = D_{mol}\phi^2$
155 (Ullman and Aller 1982), with a molecular diffusion coefficient D_{mol} of $1.73*10^{-9}$ m^2 s^{-1}. O_2
156 consumption was modeled using Monod kinetics with K_m set to 20 μM (Furukawa 2001). The
157 maximum sediment oxygen consumption rate k was determined from flask incubations, and
158 subsequently varied to assess the impact of both sediment reactivity and burrow distribution
159 patterns on O_2 distribution and exchange fluxes. At the sides and bottom of the model domain,
160 fluxes were set to zero, while an O_2 concentration of 220 μM was imposed at the sediment
161 surface and burrow walls as the artificial burrows were continuously flushed.
162 Model-generated concentration fields were used to assess the variability of measurements
163 expected in a bioturbated field setting. A random sampling algorithm was used to determine the
164 number of sampling points necessary to obtain a value within 5% of the actual average
165 concentration at a given depth (N_s). In order to obtain a value for N_s, the average oxygen
166 concentration in a depth horizon was determined analytically, and then the value of the sampled
167 concentration was averaged over n sampling points to provide a running average of the sampled
168 oxygen levels: $C(n)$. This value was tracked from a value of $n >> N_s$ down to a value of n such
169 that $C(n)$ is no longer within 5% of the true average. In order to account for variations in the
170 random sample locations, the determination of N_s was repeated multiple times within the plot
171 and averaged to give a plot value.
172
173
174
175

Results

Microcosm and Model Fluxes

The laboratory microcosms showed relatively large oxygen uptake fluxes, on the order of 80 ± 5.6 mmol m^{-2} d^{-1}. The fluxes tended to be highest in the even arrangement and lowest when highly clustered (Fig. 1, Experimental), but these differences were not statistically significant (F = 1.34, p = 0.32). The maximum sediment O_2 consumption rate (k) was calculated to be $1.4*10^{-5}$ mol m^{-3} s^{-1} using least-square fitting.

Modeled sediment O_2 uptake ratios for the cornered and grouped arrangements relative to the even setting are shown in Figure 1, for reactivities ranging from $1.4*10^{-5}$ mol m^{-3} s^{-1} (in line with values reported for coastal sediments, Hall et al. 1989) to $1.4*10^{-8}$ mol m^{-3} s^{-1} (corresponding to deep ocean sediments, Wenzhoefer et al. 2001). Consistent with the experimental data, simulated fluxes are virtually identical in the three burrow arrangements at the value of k derived from the flask incubations. At lower reactivities, there are pronounced burrow arrangement effects, while at very high and very low values for k, there is no apparent effect of burrow distribution. At their most pronounced ($k = 1.38*10^{-7}$ mol m^{-3} s^{-1}), the effects due to arrangement can account for up to a 30% decrease in benthic flux when compared to an even burrow arrangement. While a reduction of the burrow radius and hence the burrow surface area leads to a smaller absolute O_2 flux, the same relative effect of burrow clustering on benthic O_2 uptake is also observed for smaller burrow radii (r = 2 mm; not shown). Similarly, variations in porosity affect the magnitude of benthic fluxes, but the same flux ratios are obtained using the lab-measured porosity of 0.43 or a value of 0.6, representative of fine sand or muddy sediments (cf. Volkenborn et al. 2010).

198 Modeled concentration fields for the different arrangements (Fig. 2) show the role of
199 burrows on O_2 spatial distribution patterns. Model cross-sections illustrate that different burrow
200 clustering patterns can result in different degrees of overlap between each burrow's oxygenated
201 zone; note in particular the lack of anoxic zones between burrows in the clustered model cross-
202 sections (Figs. 2b and c). The grouped and cornered distributions - reflecting many small groups
203 versus one large cluster respectively - show noted overlap in these cross-sections, a feature not
204 seen at the high reactivity and low oxygen penetration depth observed in the laboratory
205 microcosms.
206
207 *Patchiness and Sampling Reliability*
208 Model-obtained oxygen concentration fields were also used to assess sampling reliability
209 as a function of organism density, measurement scale, and sediment reactivity (Fig. 3). Although
210 the average sedimentary oxygen concentration was similar for all model settings, more sampling
211 points were needed in the cornered arrangement than in the grouped or even setting (Fig. 3 inset).
212 Increasing reactivity (k) necessitated a larger number of samples be taken to accurately measure
213 the average concentration in a given sediment horizon, as did lower organism density, expressed
214 by a length scale $L_D = 1/\sqrt{\rho}$, where ρ is the areal burrow density. For a given measurement
215 device of radius L_M, the number of sampling events (N_s) necessary to reliably reproduce the
216 average concentration in a select sediment depth interval peaks at high values for k and a low
217 measurement to density scale ratios ($P=L_M/L_D$). It can be approximated by (Fig. 3):

218 $$N_s = 62.84 \cdot e^{(1.94 \cdot 10^5 k - 6.3P)} \quad (2)$$

where k is in mol m^{-3} s^{-1}. As the rate of O_2 consumption decreases, the number of burrows increases or a larger measurement device is used, the calculated value for N_s drops quickly to only a few measurements.

For about 100 burrow openings per m^2 and assuming a sediment oxygen demand on the order of 1 x 10^{-5} mol m^{-3} s^{-1}, sediment cores present a reliable average concentration-measuring tool, though missing the underlying variability within the sediment. Microelectrodes, on the other hand, may require repeated deployment to obtain a measure of the average porewater concentration (e.g. Jørgensen et al. 2005). Moreover, N_s increases with decreasing oxygen penetration depth, because a larger number of points is needed to ensure the probe samples within a burrow's oxic zone. Decreasing reactivities lead to more uniform O_2 concentration fields, decreasing the number of necessary sampling points. Finally, burrow arrangement also has an effect on N_s as can be seen in the different values for the even, grouped, and cornered arrangements (Fig. 3 inset); the distribution effect is more pronounced at higher reactivities, in contrast to the trends seen for flux values.

Discussion

Benthic Flux

Burrowing infauna affect the biogeochemical structure of their sedimentary habitat and consequently elemental cycling, and can govern benthic exchange fluxes (see e.g. Kristensen 2000, 2001 for reviews). In the diffusion-dominated settings studied here, burrow formation increases the benthic flux simply by means of the increased surface area for exchange between porewater and overlying water, making burrow density the master variable affecting benthic exchange for a given type of macrofaunal community. The flux accentuation, however, is

242 dependent on the concentration gradient at the burrow walls; treating burrows as simple
243 extensions of the sediment-water interface ignores the impact of the potential overlap of the oxic
244 halos of neighboring burrows.

245 The degree of overlap of the oxygenated zone around burrows also depends largely on
246 the sediment reactivity. At the reactivity seen in the microcosm sediment, the oxygenated halos
247 do not overlap, because the inter-burrow distance is large relative to the oxygen penetration
248 depth. However, when the sediment is less reactive, O_2 penetrates deeper into the sediment, and
249 burrows' oxic zones can begin to interact with each other. Different burrow arrangements show
250 different degrees of overlap at moderate reactivity (Fig. 2). At these values for k (on the order of
251 10^{-6} mol m^{-3} s^{-1}), there is a clear trend of decreasing fluxes with increasing overlap (Fig. 1), so
252 that sediment oxygen uptake in the even setting is higher than in the grouped arrangement, which
253 is in turn higher than in the cornered setting. Finally, as the reactivity decreases even more, the
254 oxygen penetration depth is always large relative to the burrow spacing used here; the diffusive
255 flux approaches zero and there is no detectable pattern due to arrangement. Trends in settings
256 with lower burrow densities are similar to those discussed above, except that as the average
257 burrow spacing is increased, a larger oxygen penetration depth (i.e. a lower reactivity) is
258 necessary for oxic zones to overlap.

259 In addition to differences due to burrow wall properties (Aller 1983) and burrow
260 geometry (Koretsky et al. 2002), overlap of oxygenated regions surrounding burrows and the
261 variation of such overlap in a patchy burrow distribution explains why benthic flux may not scale
262 linearly with organism density or surface area (e.g. Marinelli and Williams 2003). However, the
263 scale of this variation – centimeters – is rarely considered in ecological studies but can have
264 significant effects on benthic oxygen uptake, which is often used as a proxy for whole sediment

metabolism. Our model simulations suggest that ignoring the patchiness of burrow distributions can alter such estimates up to approximately 30%.

Concentration and Variability

The presence of irrigated burrows generates fine-scale heterogeneity that can have a strong influence on the structuring of sediment microbial communities (Marinelli et al. 2002, Fenchel and Finlay 2008). In bioirrigated settings, a large number of single point measurements with microelectrodes may be necessary to capture the sediment's spatial variability, e.g. due to oxic microniches that form within bioturbated zones. Burrowing organisms impact not only large-scale benthic exchange fluxes but also finer-scale solute distribution in the sediment, and therefore affect sampling requirements: in a highly heterogeneous environment, it takes significantly more measurements to obtain an accurate value of the "average" concentration. This effect is also directly linked to the scale in question, emphasizing the need for a scale-based measure of patchiness.

The variability within a sedimentary O_2 concentration distribution comes from two primary sources: the consumption of O_2 in the sediment and the presence of burrows as a source of lateral heterogeneity. Model-obtained information can be used to assess this variability and predict the number of measurement events necessary to capture an accurate picture of O_2 in the benthos (N_s; Fig. 3). However, while determination of the measurement- to density-scale ratio (P) is straightforward, sediment reactivity (k) may not be as easily obtained in the field directly. It is thus useful to relate the reactivity to the oxygen penetration depth (L_{O2}), which may either be measured directly, constrained from measurements in comparable environments, or visually assessed based on observed color changes in sediment cores (Diaz and Trefry 2006). Assuming a

rate of O_2 consumption (k) constant with depth, as is approximately the case if reoxidation of reduced metabolites is significant near the O_2 penetration depth (Glud et al. 1994), it can be approximated as (Cai et al. 1996):

$$L_{O2} \approx \sqrt{(2\phi DC)/k} \quad (3)$$

Thus, Equation 2 can be approximated by:

$$N_S = 62.84 \cdot e^{(3.88 \cdot 10^5 \phi DCL_{O2}^{-2} - 6.3P)} \quad (4)$$

C is the bottom-water concentration of oxygen (in mol m^{-3}), D is the effective diffusion coefficient (m^2 s^{-1}), and L_{O2} is the oxygen penetration depth in meters. Because the probability of encountering a burrow is related to not only abundance but also burrow size, the estimation of N_s is impacted by changes in burrow radii: smaller burrows are less likely to be encountered, and thus the calculation of N_s will slightly underestimate the true extent of variability in the sediment oxygen distribution when used with very small burrows.

Scaling up and ecological context

Understanding the small-scale effects of patchy distributions on oxygen dynamics is important where scaling up from an 'average' burrow is not sufficient. Our data show that burrow arrangement has negligible effect on sediment O_2 uptake in settings with small O_2 penetration depths, which are characteristic for benthic environments with a high sediment load and rapid remineralization of organic matter. Similarly, in entirely oxic sediments such as in the deep sea, burrow grouping is inconsequential for benthic O_2 uptake. The areas most likely to be impacted by burrow patchiness are those where burrow spacing is on the same order of magnitude as the scale over which biogeochemical gradients are evident. For organism densities similar to those investigated here, patchiness has most impact in settings with oxygen penetration

311 depths on the order of centimeters, indicative of intermediate reactivities. For O_2 penetration
312 depths of 1 cm, a typical flux is on the order 2 mmol m^{-2} d^{-1} (estimated as $F_{O_2} = 2\phi D[O_2]/L_{O_2}$; Cai
313 et al. 1996). This is well within the range where bioturbation is a significant contributor to total
314 O_2 uptake (Meile and Van Cappellen 2003) and corresponds to water depths typical for the
315 continental shelf and slope (Wijsman et al. 2002).
316 If patchiness is to be considered as an important community variable when scaling up, it
317 is crucial to have measures that relate directly to the scale of observation, and account for
318 clustering. The ratio of measurement scale and characteristic burrow spacing (*P*) yields insight
319 into the relative probability of encountering burrow structures and is easily estimated in the field;
320 however, it does not reflect the actual organism *arrangement*. Some arrangement information is
321 reflected in the Clark-Evans Index, but because it considers only the nearest neighbor for each
322 organism, the cornered and grouped arrangements in this particular study are not distinguished
323 despite the differences in sediment biogeochemistry evident in the benthic O_2 fluxes (Fig. 1). As
324 a more concise measure of patchiness we propose a normalized probability (*Q*) of encountering
325 one or more burrow openings with a measurement device of a given sampling radius.
326 Normalization by the probability for a uniform random distribution of the same density removes
327 the impact of burrow density, similar to the Clark-Evans index. This measure emphasizes
328 oxygenated burrow microenvironments as a critical factor for sediment biogeochemistry in
329 predominantly anoxic coastal sediments, and it offers the improvement of explicit consideration
330 of both observation scale and increased sensitivity to subtle changes in burrow arrangement. For
331 instance, for a measurement scale of 2 cm, the grouped and cornered distribution, which are
332 characterized by the same Clark-Evans index, have *Q*-values of 0.8 and 0.6, respectively.

333 However, for measurements encompassing several burrow clusters, Q does not distinguish
334 between arrangements, similar to R.
335 Given the importance of burrow arrangement for the diffusive oxygen flux, patchiness
336 likely also plays a role in other elemental cycles, particularly of redox sensitive species. For
337 example, Gilbert et al. (2003) showed a pronounced stimulation of coupled denitrification related
338 to inter-burrow spacing. Although the extent of oxygen penetration is a primary driver in the
339 various redox reactions within sediments, other elements will be sensitive to spatial scales
340 dependent on their respective reaction rates. For example, ventilation of burrows stimulates opal
341 dissolution by removing silicic acid from porewaters, and the response of burrowing organisms
342 to the presence of burrows in their vicinity alters these silica dynamics (Marinelli 1994).
343 Differences in organism distributions may also explain the lack of strong relationships between
344 species density and nitrogen and phosphorous concentrations (e.g. Ieno et al. 2006).
345 Extrapolating these impacts to the field scale – and taking into account the presence and impact
346 of patchiness documented here – suggests that patchiness can be an important factor for
347 biogeochemical fluxes and benthic-pelagic coupling.
348 The finding of unexpected non-additive density effects on benthic nitrogen, phosphorous
349 and oxygen flux (Michaud et al. 2009) highlights the potential importance of arrangement and
350 the need for measures that capture small-scale (centimeter) variations in burrow grouping
351 patterns. This recent finding indicates that organism distribution is a factor leading to net
352 community effects diverging from simple "sum-of-parts" aggregations, and suggests that
353 effective study requires consideration of both organism ecology and distribution in terms of
354 biogeochemical functioning (Waldbusser et al. 2004, Norling et al. 2007, Michaud et al. 2009).
355 The distribution of larger burrow structures has been shown to have a controlling influence on

356 the distribution of smaller burrowing organisms (Woodin 1978), potentially via the oxygenation
357 of otherwise anoxic sediments (Marinelli 1994), and the findings of this study provide
358 mechanistic evidence for such biogeochemical connectivity.
359
360 **Conclusions**
361 One way in which infauna ecosystem engineers structure their habitat is through
362 alterations of the physical or spatial structure, e.g. by establishing (semi-)permanent burrows
363 which affect biogeochemical zonation and benthic exchange fluxes. The spatial distribution
364 pattern, or patchiness, can be a significant factor in the creation of habitats and hence the benthic
365 community structure.
366 Combining microcosm experiment with permanently flushed artificial burrow structures
367 and reactive transport modeling, we showed that in diffusion dominated settings, it is possible to
368 quantitatively describe the relationship between burrow distribution, organism density, sediment
369 reactivity, and sediment oxygen demand. At high reactivity, burrow spacing has no impact on
370 benthic O_2 demand because all oxygen is consumed in close vicinity of the burrow walls.
371 However, as reactivity decreases and oxygen penetration into the sediment increases, such as the
372 case on the continental shelf, oxic zones surrounding burrow overlap and significant effects on
373 dissolved oxygen fluxes can be observed.
374 Our findings highlight the importance of spatial arrangement in some sediment habitats,
375 suggesting that fully understanding the role of the benthic community in elemental cycling
376 requires consideration of not only organisms' effects on their environments, but also the
377 inextricable feedback between these organisms and the ecological context in which they live.
378

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487

Figure legends

Figure 1: Modeled and experimental flux in the grouped and cornered burrow distributions relative to the fluxes from the setting with an even burrow distribution ($F^{O_2} / F^{O_2}_{Even}$) for a range of benthic habitats.

Figure 2: Model results showing O_2 concentration at 5 cm depth for a medium reactivity (k = 1.37 * 10^{-6} mol m^{-3} s^{-1}) for the **(A)** even **(B)** grouped and **(C)** cornered arrangement. Sketches at the top represent the three burrow arrangements, while the bottom half shows the sediment columns with the cross section of the O_2 concentration fields. The scale bar equals 10 cm.

Figure 3: Contour plot of N_s as a function of reactivity and L_M/L_D based on sampling at a 5 cm depth within the model domain. **Inset:** Actual values of N_s (Circles, squares, and triangles denote the microcosm values for the even, grouped, and cornered distributions, respectively) versus values predicted by equation 6; trendline indicates the 1:1 line.

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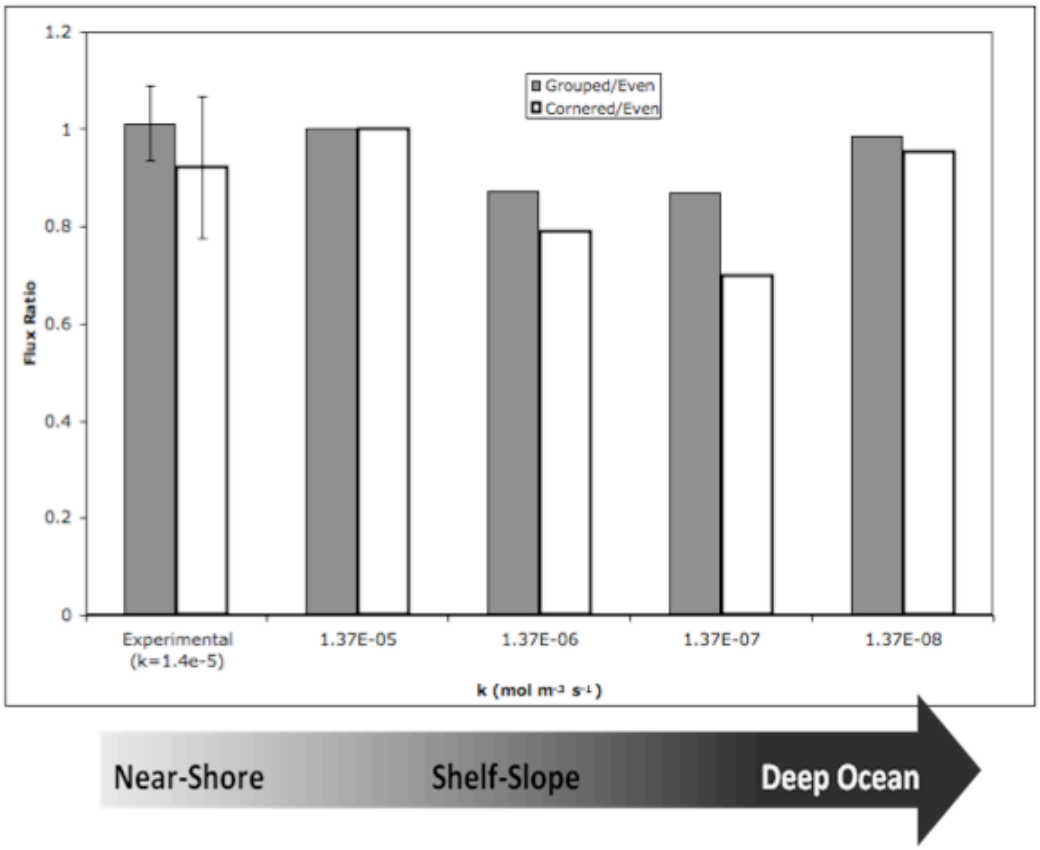

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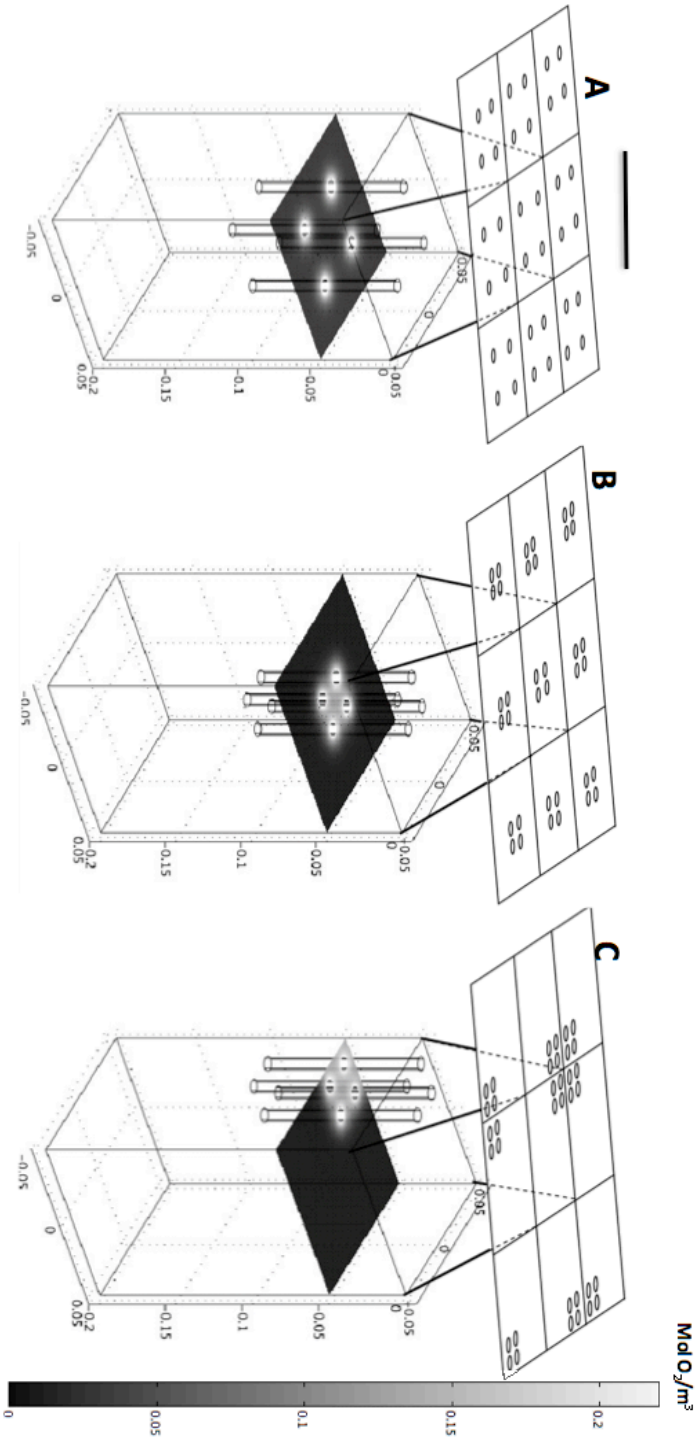
505 Figure 1



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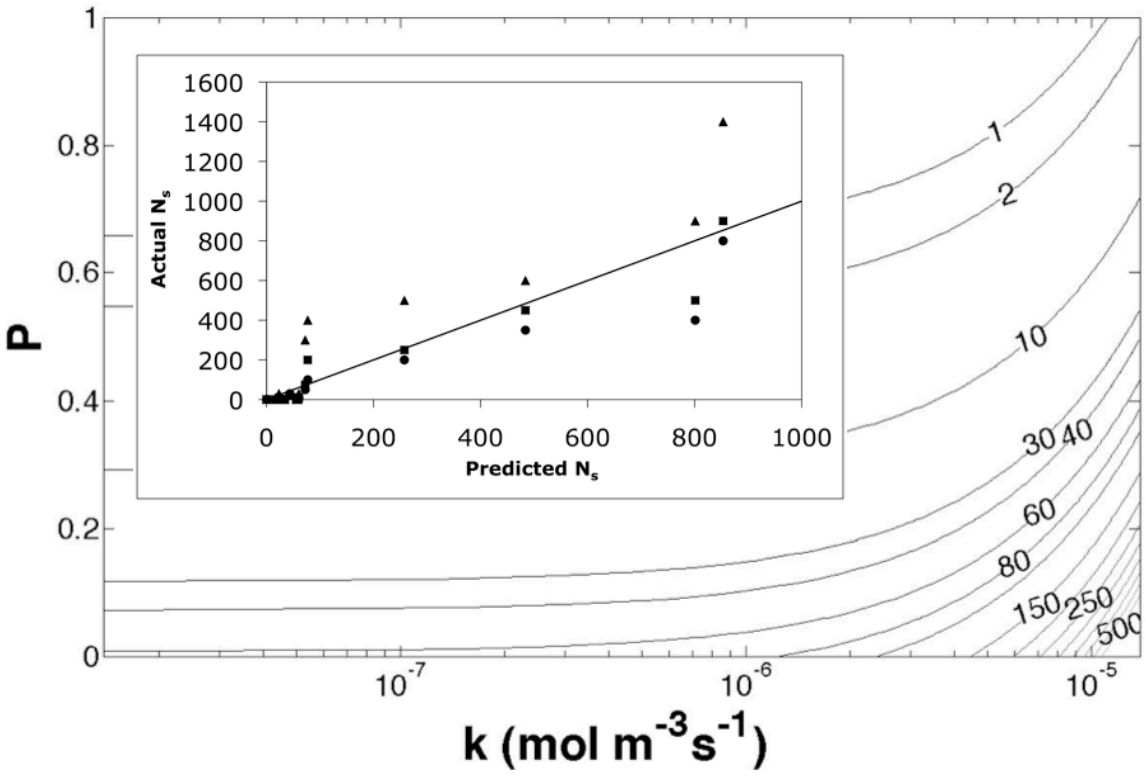
507 Figure 2



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510 Figure 3