

Response to Anonymous Referee #1

We express our gratitude to Anonymous Referee #1 for his/her useful comments. Our response to the reviewer's comments and the corresponding revision are described in detail below. The numbers of pages, lines, equations, tables and figures are those in the revised manuscript unless otherwise described.

Comment 1:

“Validation: The model presentation introduces features that generally make sense, such as behavior tied to the presence of O₂ or the reactivity of organic matter. However, what is lacking is a rigorous validation of the results, which of course is rather challenging. A key concern is the limited discussion what organisms the model represents. LABS was a novel way of looking at organisms that move sediment around. Are these the same organisms that govern the distribution of O₂? Arguably, the most pronounced impacts on O₂ in contemporary sediments are not caused by moving around sediment blocks but by the flushing of burrows, injection of fluid into the subsurface or similar activities. Thus, organisms other than the ones studied with eLABS, or other activities (e.g. pumping, rather than directional movement of infauna) by the organism studied may set the O₂ distribution. Under these conditions, feedbacks other than that between movement and oxygenation considered in eLABS (which in the applications shown here possibly represents the 'simple small deposit feeders, resembling capitellids' referred to in Choi et al. 2002) may be dominant, and limit the ability of the model to capture the connections between food, air and organism.”

Response:

Simulated values of biodiffusion coefficients and oxygen fluxes are well within the observed ranges (Section 3.1). Thus, we consider that eLABS yields reasonable results, comparable to modern observations. While we agree that further confirmation of the model's validity would be desirable, experimental data that can be directly compared in detail with the model's settings and results is not available and thus further confirmation of the model's validity is not currently feasible.

According to Jumars and Wheatcroft (1989, In: Productivity of the Ocean: Present and Past (eds. W. H. Berger, V. S. Smetacek and G. Wefer), pp. 235-253), deposit feeders are responsible for most of sediment bioturbation for most of the time. Therefore, we consider the choice of the organism for the present study reasonable (a deposit feeder which resembles a capitellid and whose body size and ingestion rate are within the observed ranges described by Cammen (1980), Kemp (1987) and Lopez and Levinton (1987)). Although the details of the organisms (species) that are responsible for bioturbation can change with time and space (e.g., Aller, 2001; Kristensen et al., 2012; Tarhan et al., 2015), a strength of eLABS is that we can also change the burrow density and feeding rates by changing rules that govern organism behavior and biological parameters of the

organism (e.g., Fig. 2).

Flushing of burrows and injection of fluid into the subsurface are likely to be important in permeable sediment (e.g., Huettel and Webster, 2001). Such phenomena require relatively strong water flows above sediment. However, direct simulation of such strong flows would be difficult because a higher grid resolution would be required. Therefore, instead of direct simulation, we formulated the governing equation for oxygen with an effective diffusion term so that it includes the effect of oxygen mixing caused by turbulent flows above the seawater-sediment interface, i.e., an eddy diffusion term in addition to the term for molecular diffusion. The strength of eddy diffusion can be changed with shear velocity (e.g., Fig. 4e), which is related to the current strength in the water column above the modeled sediment (e.g., Pope et al., 2006).

To simply and implicitly enable a pumping action, the model has been updated (v0.2) so that the constant water flows imposed when an organism ingests or egests sediment particles can be increased by an arbitrary factor. Simulations where the water flows imposed at the time of ingestion/egestion are increased by factors between 10^2 and 10^4 suggest that greater oxygen can be introduced into sediment as a result of enhanced advective water flows and that this causes a significant increase in infaunal respiration flux, similar to the case with a high shear velocity. This similarity is reasonable given that both simulations implicitly employ increased contributions of advective water flows to oxygen mixing into sediment.

Changes in manuscript (Page numbers/Line numbers):

The need for a further validation of the model was additionally described in Section 4 (P/16/L32-P17/L1-2).

We mention that a variety of organisms can be responsible for bioturbation and, because of this, LABS is beneficial due to its ability to simulate various biological parameters that control organism behavior (P2/L25-27, P4/L31).

We have now clarified that flushing of burrows and injection of fluid into the subsurface can be implicitly simulated by increasing shear velocity (P12/L19-21).

We have added an appendix which shows results of simulations where water flows imposed at the time of ingestion/egestion are increased by factors between 10^2 and 10^4 (Appendix E, P19/L2-14). We mention that the simulation where advective flows contribute significantly to oxygen mixing leads to bioturbation results similar to those in the case where shear velocity is high and reference Appendix E (P12/L30-31).

Comment 2:

“Implementation: The calculation of the oxygen concentration is conducted on a grid that is occupied by water/organism particles with a general advection-diffusion-reaction equation (e.g., Boudreau, 1997) (EQ. 2). This is necessary as in the model there is no O₂ in the (zero porosity) in the solid cells,

yet no organic matter (M) in the fluid phase. However, nothing is stated what the size of this large scale grid is that represents average solid and fluid concentrations, or how exactly u and D are computed in the sediment.”

Response:

The calculation of oxygen and organic matter is conducted directly on the eLABS grid, i.e., by using individual eLABS grid cells as the finite difference grid cells. Thus, a value of organic matter concentration is assigned to each sediment grid cell while an oxygen concentration is assigned to each water/organism grid cell. Calculation of organic matter degradation is conducted wherever two grid cells of water/organism and sediment are located next to one another and degradation rate information is shared between the two grid cells to be reflected in the calculations of organic matter and oxygen concentrations.

Similarly, a set of flow velocities and an effective diffusion coefficient is assigned to each water/organism grid cell. Please note that because the water flow is simulated by the marker and cell method, four velocities are assigned on the edges of each grid cell while one pressure is defined at the center of each grid cell (e.g., Hoffmann and Chiang, 2000).

Changes in manuscript (Page numbers/Line numbers):

We have added explanations of the calculations of water flow, organic matter and oxygen (as in our response above) to the revised manuscript (P5/L33-P6/L3, P7/L31-P8/L5, P8/L24-P9/L2).

Comment 3:

“Results: How robust are the findings, shown for example in Figure 7? What is the uncertainty in the stochastic default simulation? This is particularly important as results are shown in several panels relative to the default. For example, Fig11b shows an increase in D_b at depth relative to the default, at a depth where D_b is small. Is this consistently found for multiple realizations of the default simulation? If not, consider establishing uncertainty estimates. And is any of the patterns seen an effect of the boundaries (i.e. too small domain size)? On page 12, at the end of the first paragraph, it is stated that "When we remove the advective flow from the calculations, i.e., simulation (f), the resultant oxygen profiles, fluxes, burrow geometry and biodiffusion coefficient are generally similar to those with the default settings (panels (a) and (f) of Figs. 4, 5, 6, 7). Accordingly, with the assumptions adopted in the present study, advective water flow has only insignificant influences on bioturbation." If one follows the bioturbation definition of Kristensen et al. 2012, MEPS ("all transport processes carried out by animals that directly or indirectly affect sediment matrices.") I'd agree that at the low velocities resulting from with the movement of macrofauna, fluid flow is not important for solid phase distribution. However, there is ample observational evidence (documented in several of the papers cited) that shows the importance of bioadvective flow for solute distributions

(O₂ profiles) and fluxes.”

Response:

We ran 5 runs for each simulation to evaluate the contribution of stochastic processes to the bioturbation results in Section 3.

Increasing the size of calculation domain does not significantly change the results. Please note that the left and right boundaries adopt the periodic boundary condition (i.e., they are continuous) and also, if we increase the modeled sediment grid width (12 cm in the default setting) by a factor of 2, then the number of organisms must be increased by the same factor to maintain the same population density of organisms in the sediment. We conducted a simulation where the calculation domain is wider by a factor of 2 and populated by two organisms of the same properties and with otherwise default settings. The results using the wider calculation domain and correspondingly increased number of deposit feeders are not significantly different from those using the default settings.

We agree that with a pumping action (e.g., Meysman et al., 2005), advective flow caused by infauna can become more important. As in our response to Comment #1 by Anonymous Referee #1, we ran simulations with increased biologically induced water flow to implicitly account for pumping action in eLABS. According to these simulations, results from increasing the contribution of advection to oxygen mixing within sediment are similar to those using a high shear velocity. Nonetheless, further development of eLABS is necessary to explicitly simulate pumping action. Please also see our response to Comment 1 by Anonymous Referee #1.

Changes in manuscript (Page numbers/Line numbers):

We have added a description of stochastic effects in Section 3 (P9/L31-P10/L3, P13/L21-22, P14/L12-13). Where necessary, we also modified descriptions in Section 3 indicating the multiple results for each simulation (P12/L1-2, P12/L13-14, P12/L27-28, P13/L28, P14/L12, P15/L23-24).

We have added an appendix which shows results from 5 runs of the default simulation to illustrate the effects of stochastic animal behavior in eLABS (Appendix D, P18/L25-29) and another appendix which shows the results from a simulation where a wider calculation domain is assumed (Appendix B, P18/L1-6).

We have added still another appendix to show results from simulations where biologically induced water flows are increased (Appendix E, P19/L2-14). We also mention that simulations with a high contribution of advection to oxygen mixing yield similar bioturbation results to those from a simulation with a high shear velocity and refer to Appendix E (P12/L30-31). Please also see our changes in manuscript in response to Comment 1 by Anonymous Referee #1.

Comment 4:

“Summary: The summary/conclusions points to what is missing in the paper, namely a rigorous testing against data (page 15, line 16). Overall, I consider this an interesting paper and valuable expansion on an existing model. It clearly is a framework to test scientific hypotheses. The potential is undoubtedly there, but the feasibility of establishing the mechanistic explanations for empirical relationships largely remains to be demonstrated and will be a significant undertaking.”

Response:

We have addressed the issue of a more rigorous testing against data in our response to Comment 1 by Anonymous Referee #1.

Changes in manuscript:

Please see our changes in manuscript in response to Comment 1 by Anonymous Referee #1.

Additional note 1:

“page 5/ line 20: avoiding oxygen depleted conditions does not necessarily translate into moving against the O₂ gradient. This seems to align with the statement on 14/34 that stresses the importance of food availability”

Response:

Agreed.

Changes in manuscript (Page numbers/Line numbers):

We have added ‘Note, however, that the stochastic behavior may occasionally lead organisms to unfavorable locations with respect to food and/or oxygen availability.’ (P5/L23-24).

Additional note 2:

“9/24: it says that the infaunal respiration flux = total O₂ consumption flux - O₂ flux by aerobic decomposition. I may be thrown off by the terminology (flux, rates), but what about non-steady state effects, and advective or diffusive transport?”

Response:

We use the term ‘flux’ to refer to a mass change in unit area per unit time (e.g., mol cm⁻² yr⁻¹), while the term ‘rate’ was used to refer to a mass change in unit volume per unit time (e.g., mol cm⁻³ yr⁻¹). Thus, depth integration of consumption rates within sediment provides the oxygen consumption flux.

In eLABS, oxygen fluxes caused by changes in the total amount of oxygen within the calculation domain, aerobic organic matter degradation, infaunal respiration, advection and effective

diffusion (i.e., molecular plus eddy diffusion) are calculated at each time step, as well as the residual oxygen flux as sum of the above fluxes to evaluate the calculation error (the residual flux must be close to zero if the mass of oxygen is conserved). The first flux, i.e., oxygen flux caused by changes in the total amount of oxygen within the calculation domain, represents the flux that is significant when the porewater chemistry is far from steady state. This non-steady-state flux can be recognized as a deviation of total oxygen supply (dominated by diffusive supply; orange curves in Figs. 5, 9 and 13) from the total oxygen consumption (black dotted curves), which is significant over dozens of model days from the start of simulations. After this initial period, the non-steady-state flux becomes relatively insignificant.

Changes in manuscript (Page numbers/Line numbers):

We have added a description similar to that above in the revised manuscript (P10/L18-19, P17/L11-26).

Additional note 3:

“10/18: it states that organic matter concentration is assumed to decrease with depth. However, on page 3, deterministic calculations of organic matter distributions are discussed. Please clarify”

Response:

A decrease of organic matter concentration with depth is adopted as the initial condition for organic matter. Changes in concentration of organic matter from this initial condition are deterministically calculated as explained in Section 2.3 of the previous manuscript.

Changes in manuscript (Page numbers/Line numbers):

We have modified descriptions in Section 2.3 to clarify the model calculation and assumption (P8/L24-26).

Additional note 4:

“11/11: how are permeability and porosity connected in the model? If this is explained in LABS papers cite the relevant publication.”

Response:

Porosity is assumed in eLABS, based on which sediment particles are randomly distributed. Permeability can be calculated by using the water flow calculation, solving the Navier-Stokes equation using sediment pore geometry that is determined by distributions of sediment particles (e.g., Manwart et al., 2002). Because the water flow calculation is one of the new features of eLABS, i.e.,

not included in LABS, there are no LABS papers which describe the relationships between permeability and porosity.

Changes in manuscript (Page numbers/Line numbers):

We added an appendix which explains that permeability can be calculated by solving the Navier-Stokes equation once the pore geometry (i.e., eLABS grid) is given (Appendix C, P18/L8-23).

Additional note 5:

“Consider discussing the role of predation on burrowing, in addition to the role of organic matter and oxygen”

Response:

The role of predation on burrowing (e.g., Posey, 1986, J. Exp. Mar. Bio. Ecol. 103, 143-161) cannot be explicitly discussed because LABS, on which eLABS was developed, does not include predation as an animal behavior. In ongoing developments to LABS, however, we have allowed changes in animal population as well as sizes of individual benthos based only on food supply [Kanzaki et al., in prep.]. Hence, we will be able to realize predation in future versions of LABS, but this is beyond the scope of our present study.

Changes in manuscript (Page numbers/Line numbers):

We have mentioned predation as a feature to be realized in eLABS in future developments in Section 4 (P16/L30).

Additional note 6:

“Is figure 3 necessary?”

Response:

We consider Fig. 3 necessary because the calculation of a water flow field based on animal behavior is a new feature of eLABS first presented in this study. Although advective water flow was found not to be significant when using the default setting for the present study, advective flow can become more important in simulations where biologically induced water flows are increased.

Changes in manuscript (Page numbers/Line numbers):

We have added an appendix which shows simulations where biologically induced water flows are increased (Appendix E, P19/L2-14). We mention that the conditions where the advective water flow

is important for oxygen mixing leads to similar bioturbation results compared to those in a simulation with high shear velocity (P12/L30-31).