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Interactive comment on "Stimulation of microbial nitrogen cycling in aquatic ecosystems by benthic macrofauna: mechanisms and environmental implications" *by* P. Stief

Anonymous Referee #2

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The manuscript by P. Stief reviews the impact of benthic macrofauna on sediment N cycling. It differentiates between ecosystem engineering, grazing and symbiotic interactions, for which the mechanisms of interactions are discussed. Subsequently, Stief compiles existing data to provide a first-order estimate of the impact of macrofauna on nitrification, denitrification and benthic exchange fluxes of nitrate and ammonium. Finally, the impact on N2O is highlighted.

This paper is a welcome addition to the literature, and nicely compiles the major ways in which benthic fauna impacts N transformations, and I recommend its publication after suitable revision.

The introduction provides an overview of the N processing. By addressing N cycling in many settings, the manuscript covers a very wide range of material and highlights the broad role of macrofauna in N cycling. However, due to the breadth of topics, there are some gaps. For example, there is little discussion of N uptake, either for heterotrophic metabolism or in primary production in shallow water environments with benthic photosynthesis where one may also expect a significant presence of macrofauna. I recommend expanding the manuscript to include that.

Ecosystem engineering: The paragraph on sediment infauna (2.1.1) is well developed, but not without challenges, because any attempt to find simple general patterns is hampered by the diversity (functional diversity in particular) of macrofauna. This is reflected e.g. in the discussion of the effect (or lack thereof) of organism density. I realize that not all existing literature can be reviewed, but I believe that the manuscript could benefit from mentioning studies such as the work by Gilbert et al. 2003 (J. Mar Res 61: 101-125) that attempt to target underlying mechanisms for the presence/absence of density effects, or that of Emmerson et al. 2001 (Nature 411: 73-77) which looks at the role of biodiversity on ammonium fluxes. The review mentions the importance of coral reefs, but then largely focuses on other sediment epifauna. To avoid leaving the impression that N cycling on reefs has not been studied much, I suggest to upfront (i.e. in section 2.1.2) reference some of the existing recent reviews related to N cycling in reefs, e.g. the chapter by O'Neil and Capone on N cycling in coral reef environments (O'Neil and Capone 2008. Nitrogen cycling in coral reef environments. in Capone, Bronk, Mulholland and Carpenter (eds): Nitrogen in the Marine environment, 2nd edition, Elsevier), or the review by Fiore et al. 2010 in Trends Microbiology, which is cited in section 2.3.3. In the section on ecosystem engineering, it might also be worthwhile pointing out the importance of the tertiary reef structure (as opposed to the effect of filter feeding mentioned here) for light conditions.

Balance: the review is clearly geared towards infauna, and the compilation of the observational data in section 3 is interesting. My main concern is that I don't get a clear sense of how robust these trends, and how comparable the different data really are. I suggest expanding figure 4, which is central to this paper, and provide more information that allows one to compare the studies cited (e.g., indicate in a separated column which are freshwater and which are marine studies, highlight the method used to quantify N cycling, add other indicators reflecting the environmental setting). Do you see the same patterns when you only compare data obtained similar methods (e.g. denitrification measured using acetylene vs. 15N label)? Do they change dramatically if one was not to focus on the highest densities in each study only? While I find the first order estimate of the impact on N cycling very useful, it is important to not only acknowledge a potential bias (p. 11801), but present some quantitative assessment. Along the same line, Table 1 presents standard deviations based on Fig 4, but this does not account for the variation within each study and one might expect the results to be less significant if accounting for that.

Conclusion: When reading the paper, I was presented with a lot of interesting material, but there was no overall synthesis that tied together the main findings, linked in N2O production as one climatically important aspect, or discussed the overall role of macrofauna in eutrophication (stimulation of ammonium fluxes, but also enhanced denitrification). In essence, the manuscript would benefit tremendously from a concise conclusion which is currently missing.

The figures could be improved as follows:

Figure 1 should contain arrows for ammonium and nitrate out of the sediment as well.

Figure 2 to me was of limited use - consider deleting it. Also, there is no pink in panels A and C (surely there is microbial activity round the burrow)

Figure 3: are the arrows indicating stimulation or how does this figure differ from figure 1? can it be deleted, or possibly integrated into figure 1?

Figure 4: would it be possible to add error estimates to the bars shown? And if using

reference numbers, they need to be added to the reference list

Minor points:

- how are 'N-cycle bacteria' defined (section 2.3)

- section 3.1, line 19: diffusion of nitrate into deeper anoxic layers implies vertical redox zonation. However, in a bioirrigated sediment, the zonation may be lateral, or conditions may change with time rather than space.

- can you give an estimate of the importance of N uptake and removal by birds, animals and humans?

- Table 1: state that stimulation factors were only calculated if the sign of the flux didn't change not just for nitrate, but for ammonium as well (or, if that is not so, explain what was done)

In summary, this is a nice and important paper, the main weaknesses being the lack of a proper conclusion section that brings the paper to a closure, and the lack of detail presented in the analysis of the effect of macrofauna on benthic DIN fluxes and rates of nitrification and denitrification.

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