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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

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Author: I would like to thank the two referees for their insightful comments and suggestions that helped improving the manuscript. Below I provide a point-by-point response to the referees' comments and indicate how and where I modified the manuscript or explain why I declined to do so. I hope that the present version of the manuscript meets the quality criteria of Biogeosciences and look forward to your further correspondence.

Referee #1 (A. Dale): I) Section 3.1 deals exclusively with processes occurring in sediments and solute exchange across the sediment water interface. This text and Fig. 3 provide no new information to what has been given already in section 2. The theo-

retical considerations should either provide more balance toward the 4 animal-microbe interactions in Fig. 2, or be removed altogether. In my opinion, section 3.1 and Fig. 3 are superfluous and detract from the flow of the paper. Fig. 3 is anyhow uninformative and recycles information already contained in Figs 1 and 2.

Author: I deleted both Section 3.1 and Fig. 3. The first paragraph of former Section 3.1 was partially moved to the Introduction because there it strengthens the points (i) that the effects of benthic macrofauna on the aquatic N-cycle are often studied in the context of excess fixed nitrogen in aquatic ecosystems, (ii) that many of these studies suggestively link the stimulation of benthic nitrogen cycling by macrofauna to fixed nitrogen removal at the ecosystem level, and (iii) that stimulation of nitrous oxide emissions by benthic macrofauna has only recently been discovered.

Referee #1: II) Section 3.2.1. More information is needed on the procedures used to perform the laboratory experiments and how the laboratory controls were performed (i.e. defaunation). It would be great to include in Fig. 4 the water depth where the sediments were sampled. Significant differences in sediment reactivity (e.g. ammonium production rates) between experiments on the same class of organisms (Fig. 4) could bias the interpretation of the fluxes and the inferred impact of the organisms on fluxes. This caveat should be mentioned more clearly and, if possible, normalized. I would also like to see Fig. 4 modified to better indicate the animal-microbe interactions in Fig. 2. This should be straightforward to do.

Author: Both referees ask for additional information to be included in Fig. 3 (formerly Fig. 4). Since I believe that Fig. 3 is already pretty much replete with information, I decided to source out the requested information into a new table (Tab. 2). This table summarizes environmental and experimental settings that might be of importance for the interpretation of the process rates and solute fluxes compiled in Fig. 3, amongst others "water depth" and "sediment integrity". Tab. 2 is rather extensive and one consideration it might be to present it as Supplementary Information. The robustness of the stimulation factors was tested in the light of differences in sediment reactivity (water

depth, ammonium efflux) and experimental manipulations (nitrate addition, incubation temperature). It was tested whether the stimulation factors are correlated with any of these four variables and/or whether they are affected by factors like freshwater vs. marine ecosystem, method of N-analysis, and sediment integrity (i.e., intact vs. sieved sediment); the overall outcome of this analysis was that the stimulation factors are quite robust; these results are presented in Figs. S1 and S2 and discussed in the text (Section 3.1.3). Additionally, the data were normalized to ammonium efflux, nitrate concentration, and temperature and the results are presented and compared to the non-normalized data in Tab. S1 and are also discussed in the text (Section 3.1.3). I agree that it would be nice to indicate the type of animal-microbe interaction involved in the stimulation of process rates and/or solute fluxes in Fig. 3. However, 38 out of the 39 studies exclusively mention "ecosystem engineering" as the only or at least the dominant mechanism of stimulating benthic N-cycling (often without using the expression "ecosystem engineering" though). In only 8 studies, "grazing" or "symbiosis" are mentioned as additional explanations for the observed stimulation effects. Thus, studies on the stimulation of N-cycling by benthic macrofauna are clearly biased towards "ecosystem engineering by sediment infauna", possibly because the experiments necessary to demonstrate this mechanism are straight-forward and often produce clear results. Therefore, I think that Fig. 3 will not benefit from, e.g., a color code that indicates the type of animal-microbe interaction at play. Instead, I now discuss the just mentioned bias in the text (Sections 3.1.1 and 3.1.3 and Conclusions and perspectives).

Referee #1: III) Section 4 is not well integrated into the manuscript. Why is nitrous oxide given its own subsection? What is the justification? Are nitrous oxide fluxes of comparable magnitude to ammonium? Please provide numbers. More effort is needed to integrate this section into the rest of the manuscript since at the moment is seems a bit orphaned in its current position.

Author: In the course of making some other changes, I completely restructured Section 3. There are now two main subsections: 3.1 Fixed nitrogen removal and 3.2 Nitrous

oxide emission, thereby enhancing the status of former Section 4. The rather novel aspect of macrofauna effects on nitrous oxide emission is now to be read directly in the context of the more classical aspect of fixed nitrogen removal. Aside from this, I think that "nitrous oxide emission" is fairly well represented in the Abstract and Introduction. In the new Conclusions and perspectives, the aspect of nitrous oxide emission is picked up again. The new Section 3.2 is now spiked with way more flux estimates than before and in most cases they are directly compared with areal nitrification and denitrification rates.

Referee #1: 1) P11787, L14-18: suggest rephrase to: Thus, benthic mineralization of PON and microbial nitrogen conversions eventually produce either dissolved inorganic nitrogen (DIN) that partially diffuses back into the water column where it fuels primary production or dinitrogen that is biologically unavailable to most organisms and is thus lost to the overlying water.

Author: This rather long sentence was split into two sentences, which hopefully improved its readability. Additionally, the aspect of PON burial was made clearer.

Referee #1: 2) P11787, L19: nitrification is also a recycling reaction, since it converts ammonium to nitrite to nitrate. Coupled nitrification-denitrification is, however, a DIN sink.

Author: I re-phrased the sentence to make this point clearer.

Referee #1: 3) L28: Compounds toxic to which organisms? Certainly not microorganisms.

Author: It is now mentioned that nitrite and ammonia are toxic to fish.

Referee #1: 4) P11790, L8: Clarify here the meaning of 'density-driven'.

Author: An explanation of "density-dependent" is now included in the sentence.

Referee #1: 5) The two sentences on L13-16 appear to be contradictory. Density-

dependent stimulation of N cycling is stated in both examples.

Author: I agree that the position of the sentence starting in L13 was not well chosen. I moved this sentence to the end of the paragraph and now explain in more detail why density dependence may be more frequently observed in microcosm experiments than under in situ conditions.

Referee #1: 6) L24: Clarify how CO2 stimulates nitrification, since N and O2 are typically limiting the rate of nitrification. Has this been shown experimentally?

Author: It is indeed not widely accepted that nitrification is stimulated by elevated CO2 levels (but see Posso-Blandon (2005)). I removed CO2 from the list of factors stimulating nitrification in the burrow environment because I could not find any experimental evidence for this in the literature.

Referee #1: 7) P11791, L11-13: The rate of solute exchange is arguably the most important factor.

Author: Maybe this is a misunderstanding. Here, I am not discussing the relative importance of stimulated rates vs. stimulated solute exchange, but rather the possible net outcome of ventilation-enhanced solute exchange, which will depend on the ratio between rates of several processes. Hopefully, my re-phrasing of the sentence makes this point clearer.

Referee #1: 8) P11792, L20. The bivalve are not used in shellfish farming, they are the cultivated species.

Author: Sentence was rephrased.

Referee #1: 9) P11803: suggest changing 'Essence' to 'Synthesis'.

Author: Change made.

Referee #1: 10) Table 1: If the stimulation factor for nitrate was only calculated for cases in which the nitrate flux was directed into the sediment, why is the maximum

absolute change positive?

Author: Right, this stimulation factor was exclusively calculated for cases in which the net uptake of nitrate by the sediment was enhanced in the presence of macrofauna. This calculation would not make sense, if it would be applied to the enhancement of the net release of nitrate from the sediment or whenever the solute exchange changes sign in the presence of macrofauna. The latter two scenarios, however, were indeed observed in a number of studies. To account for all of these possible scenarios, the average absolute change of the nitrate flux was calculated for all studies in which the nitrate flux was determined in the presence and absence of macrofauna. It is then no surprise that the maximum value is positive because in some cases the presence of macrofauna caused the release of nitrate from the sediment to increase or the uptake of nitrate by the sediment to revert into a nitrate release. In Tab. 1, I added a second footnote in which it is explained that the fluxes under the header "Absolute change of flux" were calculated from all studies, in contrast to the stimulation factor that was only calculated from a subset of the studies considered here.

Referee #1: 11) Fig. 1. All solutes can potentially be transported up and down by diffusion/bioturbation and irrigation, not just nitrate and nitrogen.

Author: For the sake of clarity, this scheme has to focus on the predominant transport routes of particles and solutes between water and sediment. In the figure legend, I now state that the scheme is valid for aquatic ecosystems with nitrate present in the water column. Additionally, I clarify that the black arrows indicate the "predominant routes of net transport", thereby implying (i) that the exchange processes include transport in both directions, i.e., into and out of the sediment and (ii) that there is also transport of minor compounds like for instance NO. In the figure, I added two more transport routes that are of importance for this review: net transport of both NH4 and N2O from the sediment into the water column.

Referee #1: 12) Fig. 4. The reference list is not indicated by numbers. The units should

be written as μmol m-2 h-1.

Author: Unfortunately, it is journal style that references are given without numbers in the reference list; so my original numbering was erased during the editing process. Since I now include Tab. 2 which provides additional information for Fig. 3 (formerly Fig. 4), I decided to number only those references that appear in Tab. 2 and use these numbers in Fig. 3 too. The units were changed according to your suggestion throughout the manuscript.

Please also note the supplement to this comment:
http://www.biogeosciences-discuss.net/10/C6130/2013/bgd-10-C6130-2013-supplement.pdf

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