

Review of: “Raised water temperature enhances benthopelagic links via intensified bioturbation and benthos-mediated nutrient cycling”

General review

The manuscript by Farrell et al. reports on a study where the bioturbation behavior and capacity to increase nutrient exchange between sediment and overlying water for four key species in the Wadden Sea was monitored in incubation experiments. As a variable of interest, two temperature regimes were used as treatments, representing the range of summer temperatures occurring in said area. The authors found clear differences between the different temperature regimes (and different species) for several of the dependent variables.

The manuscript is generally well written (see specific remarks/suggestions below), and the figures/tables are clear and contribute to the understanding of the results (though I recommend merging some). The experiment also appears to have been performed thoroughly and with an tested methodology, strengthening the observed results. I especially appreciate the work going into the large number of replicates for a study like this, and taking care of these organisms for a sufficiently long time. Overall, the results are a strong quantitative example of how shallow-water habitats function differently depending on the ambient temperature.

My main suggestion is to rewrite the manuscript in the context of (marine) heatwaves, occurring more frequently, instead of the more general “increasing temperatures”. The experiment is essentially that, since I expect that the 21.9 °C occurs mostly under these circumstances. Also I note that the difference in this experiment vs. reality is that likely the entire core was heated to 20 °C, since the fill core was surrounded by heated water. In reality, if the water temperature is 20 °C, the sediment column remains cooler in deeper layers. In prolonged heat waves, more of the sediment column is heated. By doing this, I believe you will be able to make more absolute statements about what the results mean for future scenarios in the discussion, instead of having to hypothesize regularly as is the case now.

This would also increase the novelty of the work. Though the experiment seems to have been performed well, the results that temperature increase faunal activity, and nutrient exchanges across the SWI have already been known for quite a while. Adding a novelty like marine heat waves could add a stronger context to frame the results.

Since this is quite some rewriting, I recommended major revisions.

Specific remarks / suggestions

Please check order of tables and figures (also supplement) so that they occur in the same order as in the text.

L34: Remove “important”, as all ecosystem functions are important.

L39: Please note that benthic nutrient fluxes / oxygen consumption are not ecosystem functions, rather “nutrient remineralization”.

L42: Peak -> highest.

L48: ...was enhanced with temperature... (something?).

L50: the Wadden Sea

L51: The sediment-water interface cannot be tightly coupled, the sediment and water-column can.

L53: However, in your incubations at 20 °C the *Arenicola* are doing just fine, no?

L55: both in terms of

L61: Aller 1980 ([https://doi.org/10.1016/0016-7037\(80\)90195-7](https://doi.org/10.1016/0016-7037(80)90195-7)), Aller 1986 ([https://doi.org/10.1016/0198-0149\(86\)90088-9](https://doi.org/10.1016/0198-0149(86)90088-9)), and Aller 1994 ([https://doi.org/10.1016/0009-2541\(94\)90062-0](https://doi.org/10.1016/0009-2541(94)90062-0)) as not so recent examples.

L71: have a profound influence

L91: enhances primary productivity in shallow water systems.

L92: Please reformulate this sentence, now not clear to me.

L97: Rephrase to either extreme temperatures, or normal regulation of organism metabolism which is T dependent, according to the references.

L102-103: already stated, please remove.

L124: draws porewater down or draws water column water down ?

L130: The 15 – 20 °C comes out of nowhere here in the introduction, and needs some more reasoning behind it. Are we expecting a sudden temperature increase of 5 °C ? Could it be possible to include a figure with average (and min-max) seawater temperatures for the sample areas throughout the year, or the summer period?

L140: How were these sediment characteristics measured?

L142: The words “contained” and “sediment” can be removed.

L143: The comma after “Station” can be removed.

L147: The word “experimental” can be removed.

L150: “at the location” can be removed.

L151: For this section in general, plural form “were sampled” may be more appropriate since multiple individuals of the species were collected.

L155-156: already stated previously (L148).

L164: Due to limited availability? Or a broader range so you picked individuals of varying sizes?

L170: Please remove surplus bracket after “2016”.

L175: What was the water temperature at the time of sampling? I am wondering whether the animals plunged into 20 °C water may have experienced a temperature shock. Is this 5 degree difference also what is more or less expected in terms of water temperature increase for the coming xxx years?

L187-188: The collected *H. diversicolor*

L197: suspension of luminophores was added

L202: How does the temperature of incoming Sylt water influence the fixed temperature in the tanks?

L244: Were the linear regressions tested for significance? Or was each regression line assumed to be significant?

L249: This correction was also to account for bacterial oxygen consumption, often the bulk of total oxygen consumption/scoc, correct?

L253: I don't fully understand – this is the first time I see this methodology applied. What is the difference with the previous control using the control cores? These also only have diffusive transport, no? Also, if it is strongly remineralized in the sediment, does it not flow out into the water column?

L264-268: Not necessary if Wrede et al. (2019b) is cited in above paragraph.

L292: How can this layer be 0.94 cm if only 4g / 15 mL of luminophores were added to the core?

L296-298: can be removed.

L302: all predominantly carry out surficial sediment modification

L306: “this” can be removed.

L311: So to calculate this, the Crank model from above is first applied on log-transformed luminophore data, from which Dblog is produced?

L311: concentrations

L393: species' can be removed.

L396: Figures 3-5, possibly 6 can all be combined into one multi-panel figure, or at least figures 3 and 4 should be combined. This is all information with the same x-axis and same colour codes, and would give an immediate full overview of most results.

L436-443: Is there any way that the pure oxygen demand of the organisms themselves can be separated from their presumed effect on microbial processes in the sediment through their activities? Now, indeed sedimentary oxygen uptake is increased, but this might just as well be the oxygen demand of the organisms themselves, without any effect on microbial processes through bioturbation activities.

L448: furthered -> increased (?)

L453: “a small trend” is not very subjective. Please consider removing this.

L456: Please add labels to the sub-panels of the figure and refer to this in the text to help the reader.

L455-...: Again, I don't fully understand what this second normalization achieves on top of having control cores with only diffusive transport. Please try to clarify this in materials and methods or consider removing it.

L461: Is it not the opposite? To me it seems that in panel B, the points for *L. conchilega* and *C. edule* derive most from this line, indicating more P-efflux than expected.

L465: Why is the panel about normalized oxygen consumption not discussed? Also, what is the redfield ratio between O₂ and Si ?

L466-: Are you not multiplying by a constant here (the biomass from Baird et al., 2004), and is this result then not the same as the results of figure 7? Or is there a difference?

L475-: "it's" -> "its"

L479: This seems contradictory, if it is in anaerobic metabolism, should you not expect much less oxygen consumption? Were the *Arenicola* "hyperventilating" before shutting down, you presume?

L487: But in summer this area can reach temperatures of 21.7 degrees, do these organisms stop functioning then at that point? Also, if they can do this for 10 days apparently, what would make them stop after this time?

L474-487: I think it might make sense to consider this from a heatwave approach (see general remarks), which might help explaining the behavior of *Arenicola* observed in the experiment.

L491: Isn't the solubility and dissolution of all the biogeochemical compounds increased with temperature elevation?

L495: heightened -> increased (?).

L506: Please note the previously measured values here.

L521-523: How do the findings here emphasize this? In the experiment the *Hediste* appeared to be doing just fine, expect for consuming more oxygen as expected under increasing temperatures?

L525: Again, it looks like the opposite to me judging on P-removal from figure 8 B. Please clarify where I am wrong.

L535: Would be nice to see those previously measured *Db* for easier comparison. Were the rates that are being compared measured in the field, or also experimentally derived?

L550: Perhaps the constant irrigation is the reason for lower fluxes, as it are often oscillating redox conditions that stimulate sediment processes such as coupled nitrification-denitrification.

L551: I'm not convinced that this is correct, for the reason you have mentioned previously: organic matter mixing to deeper layers, the source for all mineralization processes.

L554-557: I don't get the message here, please try to rephrase this.

L565-567: Please rephrase this sentence, I don't understand "values are much likely on a larger scale".

L569-570: What is meant with: "gives gravity to pivotal role" ?

L579: For more context: is 20 °C rather the exception than the norm?

L586: Is there a chance that the organisms will be able to adapt?

L593: However, in the experiment, the *A. marina* looked like it was doing reasonably well, but just breathing faster (As were the other organisms)? It also does not have the highest Q10, *Hediste* has, though for this species higher temperature optima have been found as was stated.

L597-600: Something wrong with structure of this sentence.

L610-612, L629-631: I think these statements may be reasons to look at this experiment from a heatwave perspective. A 10 day experiment is too short to look at physiological adaptations to a sustained elevated seawater temperature in a future climate scenario, especially when organisms are immediately subjected to this elevated temperature, coming from a temperature

of xx degrees. What you can say, is how animals behave during heatwaves, periods of increased temperature that occur quite suddenly, and will also be more common in the future.

L625: "by some measure" sounds very vague.

L626-628: The bioturbation was not concretely linked to nutrient fluxes, rather both were measured side-by-side, and assumptions were made that one has an effect on the other. A more concrete link would have been possible by also incubating organisms on their own to check their individual respiration and nutrient release, to separate this from bioturbation-induced bacterial mineralization in the sediment.

Figure 7: gAFDM requires a superscript -1.