Response to Reviewer 2 Comments

Overall Response to Reviewer 2: We thank the reviewer for the constructive comments on the manuscript as well as the time taken to read through and give a thorough evaluation. Perhaps the largest change to our manuscript was the exclusion of the bio-mixing model results due, in large, to the feedback from the reviewer and further reflection on the topic. We realize that in these sediments, the reported D_B values is probably too simplistic to properly describe mixing due to the degree of non-local particle transport (facilitated by *L. conchilega*). These results were a late addition to the study and did not contribute greatly to the story and by removing it we also make our study more concise.

Reviewer 2 comments

General comments

This contribution presents results from an intense in situ experiment, investigating into trawling effects inflicted by different trawling gears on a shallow, 10 m water depth, sandy sediment inhabited by the polychaete Lanice conchilega, which locally forms dense tube "lawns", here termed biogenetic "reefs". The investigation encompasses physical impact on sediment structure, biological and biogeochemical effects thereof. It is well conducted and the data are by enlarge well interpreted; thus, this study is an important contribution to literature. The shallow water setting in particular, the different disciplines involved as well as a substantial data set on biogeochemical aspects of the impact, will make it a valuable publication.

It will contribute both to publications in Biogeosciences and in other journals on this growing body of evidence. I recommend the manuscript for publication subject to minor revisions.

Major points

1. **Reviewer comment:** Bioturbation results …

   Did you average D_B from different models? This would involve averaging D_B representative of different portions of the overall particle transport (D_B represents all of transport in model 2, however only parts of the overall transport in higher models)

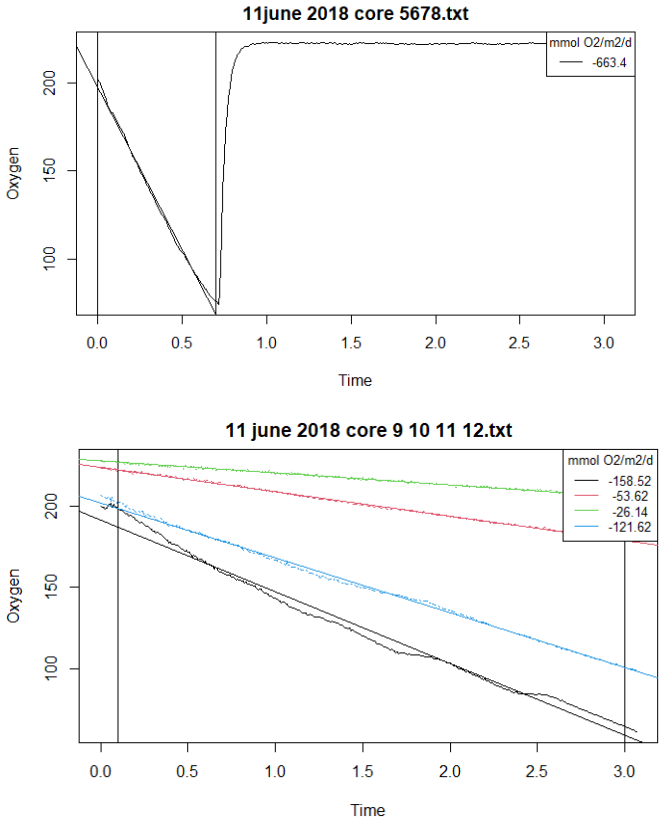
   Please comment on this and add information. This becomes particularly important in the context of results discussed in line 296, i.e. "physical trawling enhances D_B".
   Response: The reviewer highlights some important issues regarding the bio-mixing models used in this study. The reviewer is correct in that the D_B values were averaged from the best fitting models, however, as stated by the reviewer, particle transport as represented by the D_B value only describes some of the dynamics in the bio-mixing models for non-local exchange. *L. conchilega* often caused Chl-a to be injected in depth so non-local mixing models were often used to estimate sediment mixing. It may be too simplistic in this situation (with high non-local exchange) to generalize these D_B values in relation to trawling for this study. We also only have limited evidence (non-significant results) of trawling potentially increasing sediment mixing rates. This, and the fact that the reading of this study may be hindered by having too much information, has led us to remove the sections of the manuscript regarding sediment mixing as described by the bio-mixing models. We hope that this will streamline the reading and help readers focus on the main results of this manuscript.

2. **Reviewer comment:** SCOC …

   Could you please comment on the unusually high absolute values (see also recent database by Stratmann et al. 2022)?

   SCOC of >400 mmol m^{-2} d^{-1} at ~500 g WW m^{-2} conchilega or ~700 mmol m^{-2} d^{-1} at ~1400 g WW m^{-2} seem at least questionable! My reasoning is as follows. The later biomass could be responsible for around 100 mmol oxygen m^{-2} d^{-1}, if biomass-specific respiration is around 2.5 mg O_2 g^{-1} h^{-1} as for smaller sized polychaetes (e.g. Bennett and Rakocinski 2020). However, who or which additional process in a lawn of Lanice conchilega could respire an additional 600 mmol m^{-2} d^{-1}?

Response:



We were also surprised at the very high SCOC values measured in this study. We are, however, quite confident in our methodology and measurements. Above you can see some of the raw data from a core which measured an O_2 flux of 663 mmol m^{-2} d^{-1} (the highest flux reported in this study) compared (underneath) to with varied oxygen flux estimates that represent more "normal" values. You can see in the first image that almost 100 mmol of oxygen was consumed within 30 minutes in a core with 15 cm of overlying water (the core was subsequently aerated). While this O_2 consumption is exceptionally high, biomass-specific respiration from *L. conchilega* is only one of several factors which can lead to the high consumption of oxygen in these sediments.

- High summer temperatures: During the experiments (and the week leading up to it), we experienced particularly warm temperatures (for early June in Belgium/Netherlands) with surface waters fluctuating between 16-17 degrees °C. This probably stimulated benthic metabolism and macrobenthos (and microbial) activity.
- Bioirrigation: fauna-mediated ventilation of the sediments is well known to enhance microbial respiration by greatly expanding the surface area available for microbial respiration and other oxidation processes (Kristensen and Kostka, 2013). The SPI images in our study provide evidence of strong bioirrigation with high levels of oxidized sediment when tubeworms were present.
- Microbial respiration, which can easily exceed 90 % of benthic O_2 uptake (Glud, 2008), is almost certainly significant factor in the high O_2 consumption found in our study.
- Anoxic mineralization: In addition to oxic respiration, O_2 is also taken up by the oxidation of previously reduced substances (Glud, 2008). Substances produced through anoxic mineralization diffuse towards the sediment surface and consume oxygen once reaching oxic conditions (Soetaert et al., 1996).
- Suboxic reactions: Oxygen is consumed with reactions from nitrification and iron reduction.

- Respiration and activity from other benthos: These sediments often contained high biomass from invertebrates other than *L. conchilega* and also contributed to oxygen consumption from direct respiration, bioirrigation and bioturbation (which can mix OM into deeper sediment layers and can enhance mineralization).
- High OM influx (Chl-a): Perhaps most importantly, these sediments exhibited very high Chl-a values. To put this in context, the average concentration of Chl-a in the T0 Tickler plots was 19 µg g^{-1} which was associated with an average O_2 consumption of 172 mmol m^{-2} d^{-1} while productive sandy mud habitats in the central North Sea can average 3 µg Chl-a g^{-1} linked with O_2 consumption values of 18 mmol m^{-2} d^{-2} (Tiano et al., 2019). The high input of fresh organic material (its degradation increasing the O_2 flux) coupled with high bioirrigation caused by *L. conchilega* is the most likely culprit causing the exceptionally high O_2 consumption from the experimental site.

De Smet et al., (2016) documented *L. conchilega* communities respiring, on average, 193 and 99 mmol C m^{-2} d^{-1} in two different intertidal locations in France (C and O_2 fluxes are comparable). This is within the range of the average O_2 consumption values from most of the samples within this study (Table 1 in the updated manuscript).

Maximum North Sea summer temperatures can typically peak around 18 °C in August (and only in southern coastal waters). We have added some information about the measured water temperatures in the results section describing water column conditions to describe the elevated (for June) temperatures:

"During the experimental period, the water column exhibited mixed thermal conditions with temperatures ranging between 15.8 – 17.0°C."

3. **Reviewer comment:** The reference stations are not ideal in that they represent extremes in some measures and do not represent an expected average background (high oxygen demand, high faunal density, intense bioturbation). It is necessary to address this issue for it obviously raises the questions if the trawling effects can be and are at all compared to the references, or if they are only compared between T0 and T1 on trawling plots. Does the statistical analyses take care of this? It is hard to see this easily.
Response: Both reviewers have highlighted the issue of reference stations not being completely representative of the trawled locations. Indeed, the spatial variability in the reference sites make it difficult to argue that they represent the same conditions in the trawled areas (which also have a high degree of spatial variability). Because of this, we have decided to move the information from the reference sites to the Table S5 in the supplement and have separated the results for each particular site (previously, R1 and R2 results were averaged). We have also included information on the 3rd reference area but specify that most of the information came during the T1 timestep (the end of the experimental period). The reference sites have been renamed the "untrawled adjacent sites" (AD1, AD2, AD3). These were not accounted for when statistically assessing trawl impacts, therefore, we removed BACI references in the text as our study only makes before-after statistical comparisons which are more appropriate in this situation. Upon close inspection, we also found an error in the reference/adjacent analysis and have some missing data for some grain size in the reference/adjacent T1 timestep and have corrected this this. If readers are curious about potential temporal effects or any other parameters in the untrawled adjacent areas, they can refer to Table S5 in the supplement.

Specific comments

4. **Reviewer comment:** L 41: "maximize" does not seem the right word here. Alterations of sediment structure implies changes of (possibly steady-state) diagenetic conditions. "Impairing biogeochemical processes"?
Response: This text refers mainly to Ferguson et al., (2020)'s results and discussion of trawling disrupting the suboxic areas in the sediment matrix where denitrification can be maximized. We have edited the text as suggested.

"Bottom fishing affects benthic carbon cycling by displacing bottom dwelling organisms (Hiddink et al., 2017; Sciberras et al., 2018), ~~removing~~ altering sediment structures ~~needed to maximize~~leading to the impairment of biogeochemical processes…"

5. **Reviewer comment:** L 61: the sentence would be more straightforward if it read: "With respect to sensitivity to direct impact and recovery potential, coarse sediment ecosystems characterized by high levels of natural disturbance typically display more resistance and resilience to bottom fishing …"
Response: We have taken the reviewers suggestion (and nicely worded sentence) and incorporated this into the text.

6. **Reviewer comment:** Fig 1: The insert dimensions are MUCH smaller (~1.8 km wide) than the square indicating the location on the left map in Figure 1 (~20 km wide). This is a bit misleading and could be changed by reducing the square's size.
Response: The square in the left part of the figure (large map) is now smaller to better describe the dimensions of the experimental area.

7. **Reviewer comment:** Tab 1: This table could easily move to supplements. It contains only background information that is not necessary for understanding the main text.
Response: This table has been moved to the supplementary material (now supplementary Table S1).

8. **Reviewer comment:** L 125: "wide" should be "width"
Response: This has been changed to "width".

9. **Reviewer comment:** L 154: The total number of 69 box cores cannot be understood without the information that at R3 only T1 was sampled! A total would be 72 (2 times 3 replicates at 9+3 plots/reference station, i.e. 6 x 12=72). Not sampling R3 for T0 reduces this number by 3. Right? Reword to include that R3 only T1 was sampled.
Response: The total number of box cores can be calculated by multiplying the treatment plots (9) and the first two adjacent stations by 3 replicates and 2 timesteps ((9 + 2) * 3 * 2 = 66). The three cores from the third adjacent site leads to 69 total box cores taken. The text has been edited to show the inclusion of AD3 (formerly R3) benthic samples only at the T1 timestep and AD3 has been added to the map figure.

10. **Reviewer comment:** L 171-177: Following these details describing the model "family" there is no information in lines 193 and thereafter as to why only D_B is reported.
Response: As detailed in the response to comment 1, we have removed the portions of the manuscript which refer to the bio-mixing model results.

    Was there no non-local effect visible in the modeling results? Maybe report (some) of these results as well in the supplement. And consider the information in D_B as mentioned in the major points above.
    Response: As described in the response to comment 1, there were many cores where non-local mixing was observed which complicated matters when trying to assess and compare trawl-induced sediment mixing with natural bioturbation. Ultimately, these results do not provide much robust insight (not statistically significant) on the effects of trawling on sediment mixing so decided to remove the sections of the manuscript where the bio-mixing models were used.

11. **Reviewer comment:** L 187: incubation on board or at land, how much time to settle after coring impact?
Response: This paragraph has been restructured and edited to describe the incubations occurring inside the research vessel after settling for ~ 6 hours.

12. **Reviewer comment:** 2.7.3. (SPI and benthic sample analysis) after reading this and not acquainted with the specific analyses, my impression is that this allows to separate effects of T0 or T1 and temperature at the same station for the mentioned parameters? Add some information explaining what the described procedure yields, please.
Response: This paragraph has been reworded to provide more clarity in our analysis and also why we chose this approach. This analysis just assesses statistical differences between T0-T1 while correcting for temperature and accounting for spatial variation between sample sites.

> "Linear mixed effects models (LMM) were used to investigate significant differences before and after fishing (T0 – T1) for: SPI ~~p~~measurements~~enetration depth~~, sediment parameters, porewater nutrient concentrations, biogeochemical fluxes, mass budget model results and ecological characteristics (~~individual~~ macrobenthos densities, biomass, species richness) using the *lmer*-function in the R package: "lme4" (Bates et al., 2015). For ~~each~~ a given ~~treatment~~variable and treatment (example: oxygen flux and tickler treatment), a ~~"~~full-model~~ a"~~ was ~~created to include~~specified using the "timestep" (T0 ~~or~~ T1) as a fixed effect variable, "temperature" as a co-variate, and "station" as a random effect variable~~ to minimize spatial autocorrelation between sample locations~~. A~~A~~ ~~"~~reduced-model~~model b"~~ was created to consider~~ed~~ only the random effect variable (station). The full ~~Model a~~ and reduced models~~model b~~ were tested against each other using a partial F test. This approach was

taken to assess the effect of fishing disturbance (timestep = before-after statistical comparison) in respect to temperature while minimizing spatial autocorrelation between stations."

13. **Reviewer comment:** Tables S1 and S2 have much too little information their respective legends. Please add.
Response: We have added text describing the results and statistics outside the legend for these tables. We think that this information will be better communicated this way instead of inside the legend (especially the descriptive results).

14. **Reviewer comment:** L 268-270: if all these statistical results are provided with reference to Figure 3, they should be shown there. I cannot find that statistical information in Fig 3!
Response: We originally reported corrected and uncorrected (Dunn test with a Benjamin-Hochberg correction) p-values to illustrate spatial differences in backscatter. This was not communicated very well and possibly takes away from the narrative so these sentences describing statistics between plots have been removed for readers to focus on the fishing effects. As we have now decided to only use Benjamin-Hochberg corrected p-values values (and only for fishing effects), this leaves no statistical differences in the plot to be reported. We also decided to move this plot into the supplementary material (Fig. S6) as the information does not contribute strongly to the story.

15. **Reviewer comment:** L 280 and thereafter: Some of the results reported here are somewhat superfluous for they display commonly known relations of sediment grain size and other sediment related parameters (coarser grain size is associated with less fines, more fine material usually correlates with more chlorophyll). Thus, the passage could be a bit shorter.
Response: We removed much of the superfluous text describing a significant increase towards larger grainsize as there is a text describing the decrease in silt fractions. We also removed text regarding the relationship between Chl-a and silt and have combined/shortened the sentences describing the particle size distribution curves (Fig. 4)

16. **Reviewer comment:** Figures 6 and 7: why is SCOC (fig.7) called oxygen consumption in Fig 6? Are those not the same values as in Fig 7?
Response: We thank the reviewer for pointing this out and have changed 'O_2 consumption' to 'SCOC' to remain.n consistent with the terminology.

17. **Reviewer comment:** L 348: the passage "to physical, biogeochemical, and ecological characteristics" ios again mentioned in line 357 as "simultaneously investigates acute beam trawl impacts on biological (Rabaut et al., 2008), physical (Depestele et al., 2016) and biogeochemical dynamics". I suggest removing it in line 348.
Response: We have removed this sentence as suggested.

18. **Reviewer comment:** L 375 and thereafter: This is a lot of text for little change seen or measured! Can it be reduced?
Response: The text here has been edited to make it more concise.

19. **Reviewer comment:** L 396: Did D_B really increase? It may well be so, however, an increased burial with more random mixing of sediments is not always the case. Increased mineralization of labile material may counteract overall burial. A more cautious wording, such as "it may result in altered OM diagenesis and nutrient cycling", is warranted.
Response: As described in the response to comment 1, we have removed the bio-mixing results. These data were a late addition to the study and while we were initially excited to include them, we are less confident in these than the other results.

20. **Reviewer comment:** L 406: this is an unnecessary repletion of the bathymetry discussion above
Response: This sentence has been removed.

21. **Reviewer comment:** L 420: Lanice additionally extends its tubes up to 20 cm below the surface. Therefore the subsequent sentence (line 22) sentence should state "… to organisms without pronounced protruding sediment surface structures."
Response: We have restructured and edited the sentences as suggested.

"These results also suggest that areas with *L. conchilega* may be vulnerable to relatively shallow (~ 1 cm) seabed disturbances as their tubes extend from over 10 cm within the sediment to above the ~~sediment~~ seabed surface. Contrary to this, faunal-mediated biogeochemical functions in the Frisian Front are ~~more~~ relegated to organisms such as the burrowing mud shrimp, *Callianassa subterranea*, that do not exhibit any protruding sediment surface structures and reside~~ing~~ deeper within the ~~sediment~~ seabed (Amaro et al., 2007; Tiano et al.,

2020). ~~and~~ These organisms are probably less affected by trawling despite their habitats displaying ~~having~~ softer sediments which are prone to~~and~~ greater trawl penetration (Depestele et al., 2019; Tiano et al., 2019, 2020)."

22. **Reviewer comment:** L 464: This is a bit of discussion and maybe should not be in conclusions.
Response: We have removed the sentence discussing different results in the literature between pulse and beam trawls to keep the focus more on the conclusions of the manuscript.

23. **Reviewer comment:** L 479: "removal of sedimentary carbon"; this is why above there should be no statement of enhanced D'B' increasing burial!
Response: We think that the effects of trawling are more complicated than just the removal of carbon from the sediment surface. While this trawl induced erosion and resuspension of OM is something that we have observed several times in the field, trawling also mixes benthic sediments underneath the eroded surface layer (Depestele et al., 2018), and has been hypothesized to mix OM into deeper layers potentially resulting in increased carbon burial (Mayer et al., 1991). The net result of this is still a mystery as we do not yet know the extent of the trawl-induced mixing nor the fate of the resuspended carbon (how much is mineralized in the water column/how much is deposited in other areas). Either way, with the removal of the bio-mixing portion of the manuscript, our statement about enhanced burial has been removed.

Technical corrections

24. **Reviewer comment:** L 525 "(Blackburn 1988)" does not belong in this Breakman et al. 2010 citation
Response: We thank the reviewer for pointing out this typo and have corrected it.

Literature Cited

De Smet, B., Van Oevelen, D., Vincx, M., Vanaverbeke, J., & Soetaert, K. (2016). Lanice conchilega structures carbon flows in soft-bottom intertidal areas. *Marine Ecology Progress Series*, *552*(June), 47–60. https://doi.org/10.3354/meps11747

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Soetaert, K., Herman, P. M. J., & Middelburg, J. J. (1996). A model of early diagenetic processes from the shelf to abyssal depths. *Geochimica et Cosmochimica Acta*, *60*(6), 1019–1040.

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