

Interactive comment on “The importance of different spatial scales in determining structure and function of deep-sea infauna communities” by J. Ingels and A. Vanreusel

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Reply to reviewer 2

Dear Reviewer 2,

We would like to thank you sincerely for taking the time and effort in reviewing our manuscript and providing us with constructive comments. You have brought forward several issues that need clarification, some of which require changes in the manuscript. We have taken everything on board and hope that the changes we are suggesting are sufficient. In cases where we thought there may have been confusion of misinterpretation, we have clarified our point of view and have proposed a solution. We hope that

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you may receive the proposed revision positively.

General comments The paper by J. Ingels and A. Vanreusel is dedicated to analyze the effect of different spatial scales in driving the structural and functional biodiversity in the deep-sea benthic communities, giving a strong contribution in testing ecological hypothesis in the deep sea, one of the most remote environments on Earth. The authors presented a considerable and composite dataset, since samples were collected from two regions of European continental margins in the Atlantic ocean, from different habitats (canyon and open slope) in each region and from different stations at different water depth (from 700 to 4300 m water depth) in each habitat. So that, this paper is very suitable for the publication in Biogeosciences. The manuscript is quite well structured, written and clear. The experimental approach is rigorous and well described.

However, to my opinion, there are some considerations that authors should take into account, to make the paper more easily readable. Here below the detailed comments.

Comment:Title I am wondering if is appropriate to refer to “function of communities”. Indeed, to my opinion, the paper deals with the “functional diversity of the communities” and not to the function that such communities plays as a whole in the ecosystem. So that, maybe it should be better to refer to “: : in determining the structural and functional diversity of deep-sea infauna communities” in the title.

Response: The reviewer is correct in that “functional diversity” is probably a more accurate description of the measures we have used in this manuscript. We propose to change the title accordingly and use “functional diversity” rather than “function” throughout the manuscript.

Comment:Abstract

Comment:Pag. 196, Line 5 and Line 10. Again, maybe it could better to refer to “functional diversity of communities”, instead of “function of benthic communities”. The “ecosystem function of communities” is quite unclear. Again at Line 14, to my opinion

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the “function” is not a descriptor of the community as a whole (at least in this paper). On the contrary, different nematode species have different functions in the meiobenthic community.

Response: We agree with the reviewer and will change the text accordingly

Comment:Pag. 196, Line 7. Which “other ecosystem” the authors are referring to? Terrestrial? Marine, coastal?

Response: in this instance we meant terrestrial and we will change the text accordingly.

Comment:Pag. 196, Line 10-12. “Here, we used an extensive integrated dataset of free-living nematodes from deep-sea sediments to unravel which spatial scale is most important in determining benthic infauna communities.” To my opinion, there is not a spatial scale “most important” than another. First of all, it could be strictly dependent upon the analyzed world ecoregion, or habitat, water depth, etc. Then, more appropriately, maybe the authors should refer to different spatial scales in influencing in different way benthic infauna communities, through different drivers which act at different spatial scale.

Response: the reviewer is quite right and we will change the text to say that the study aims at investigating the importance of different spatial scales in determining benthic infauna communities through different drivers that act on different spatial scales. Reference to the “most important” scale will be avoided in the revised manuscript.

Comment:Introduction Pag. 197, Line 2. Which kind of variability? In abundance, standing stock, diversity?

Response: We meant “community composition, structure and diversity” in this particular instance. We will change the text accordingly.

Comment:Pag. 197, Line 5. Maybe it could be better to change Levin et al. 2001b as Levin et al. 2001a, since is the first article by Levin et al. cited in the text.

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Response: This was automatically performed by Endnote, our apologies – we will change it accordingly

Pag. 197, Line 9. “e.g.” could be eliminated.

Response: We will eliminate “e.g.”

Comment:Pag. 197, Lines 10-12. This paragraph could be better explained. “Geographical barriers” and “sediment grain size” are not “phenomena”, but environmental or topographic settings/characteristics. Moreover, they could be considered as “environmental drivers” which are cited in the following sentence. Maybe, it could be better to refer to biotic or abiotic factors acting at different spatial scale, from local to regional spatial scale.

Response: The reviewer has made a very valuable suggestion here, and we would rewrite these sentences accordingly. The two sentences would be changed to: “It is generally accepted that benthic distribution and diversity patterns can be related to abiotic factors such as geographical barriers, productivity gradients, current regimes, amongst others (e.g. Levin et al. 2001a, Levin et al. 2001b, Rex and Etter 2010). In turn, biotic factors may regulate deterministic processes including colonisation, competition for food resources, predation, etc. Both biotic and abiotic factors can act at different spatial scales, leading to the large and small spatial scale patterns in benthic fauna, but available data seems to suggest that particular attention should be paid to the scale of the organism and their interactions when investigating benthic processes (Jumars, 1976).”

Comment:At Line 12 and 21 the references are missing.

Response: at line 12 we would include the following references to support the statement made: Levin, L.A., Sibuet, M., Gooday, A.J., Smith, C.R., Vanreusel, A., 2010. The roles of habitat heterogeneity in generating and maintaining biodiversity on continental margins: an introduction. *Marine Ecology* 31 (1), 1-5. Rex, M.A., Etter, R.J.,

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2010. Deep-sea biodiversity: pattern and scale. Harvard Univ Pr. Gage, J.D., Tyler, P.A., 1992. Deep-Sea Biology: a Natural History of organisms at the Deep-Sea floor. Cambridge University Press, Cambridge. Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics* 32, 51-93.

At line 21, we would include the following reference: Russell, B.D., Harley, C.D.G., Wernberg, T., Mieszkowska, N., Widdicombe, S., Hall-Spencer, J.M., Connell, S.D., 2011. Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. *Biology Letters*.

Comment: The sentence at Lines 13-18 is too long.

Response: the sentence has been split in two parts and rewritten following the suggestions in the two previous comments by the reviewer.

Comment: Pag. 198, Line 2. Since this paper deals with standing stock and diversity, maybe it could be better to explicit which are the effects (on abundances, standing stocks, diversity?) of different drivers on communities.

Response: The reviewer has a good point, touching on this topic in the introduction would be relevant but we would opt to stay general in the introduction. Reasons for this are 1) that the study does not present any environmental data to support the understanding of mechanisms behind the benthic patterns; the suggestion of several drivers that may explain benthic patterns is liberally covered in the discussion section and the topic is so complex and detailed that explaining it in the introduction may harm the conciseness of it as it stands; 2) The comment was already made that the introduction is lengthy and so we have aimed at reducing the text in this section and an extra part on the possible drivers and effects would counteracting the request to shorten.

Nevertheless, we want to acknowledge the importance of introducing the different de-

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scriptors we have used in this study and will mention them in the introduction at an appropriate position as follows: "In addition to the complexity of the spatial scalability of the processes influencing benthic communities in the deep sea, we are also confronted with the complexity of characterising the benthic communities themselves. Important characteristics of benthic communities are composition, community structure, structural and functional diversity and standing stocks, and biotic and abiotic factors may influence these characteristics differently depending on the community descriptors used and the spatial scale of interest. "

We hope that the reviewer can follow us in our reasoning in this and be satisfied with this topic remaining in the discussion section.

Comment: Pag. 198, Line 21. Ingels et al. 2011b has not been cited, so far.

Response: We will check the references thoroughly and make sure that the order is correct and that the references in the text match the ones in the Reference section.

Comment: Pag. 199, Line 1. To better connect this paragraph with the previous ones, it could be better to refer the submarine canyons as deep-sea habitats. As suggestion: "Among the deepsea habitats, submarine canyons can perhaps be considered as the most heterogenic topographic systems". Moreover, it sounds too exaggerate the statement "Submarine canyons can perhaps be considered as the most heterogenic habitats in the marine realm", since there are other heterogenic habitats in the marine realm (tropical coral reefs, as just an example). Maybe it could be referred to deep-sea environments.

Response: we will change the sentence according to the reviewer's suggestion.

Pag.199, Line 9. References are missing.

Response: Following references will be added: Harris, P.T., Whiteway, T., 2011. Global distribution of large submarine canyons: Geomorphic differences between active and passive continental margins. *Marine Geology* 285 (1-4), 69-86. Kiriakoulakis, K.,

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Blackbird, S., Ingels, J., Vanreusel, A., Wolff, G.A., 2011. Organic geochemistry of submarine canyons: The Portuguese Margin. *Deep Sea Research Part II: Topical Studies in Oceanography* 58 (23-24), 2477-2488. Shepard, F.P., Dill, R.F., 1966. Submarine canyons and other sea valleys. Rand McNally, Chicago.

Comment:Pag. 199, Lines 11-13. To my opinion, the aim of this study was not to address the question “what is the most determinant scale for processes that regulate: :function of marine meiofauna”, but functional diversity of meiofauna.

Response: The sentence will be changed according to the reviewer’s suggestion

Comment:Pag. 199, Line 17. Maybe it could be useful for the authors to refer to different spatial scales as regional, macro-, meso- and micro-scale.

Response: We agree with the reviewer that such a classification is very useful. We will refer to the different spatial scales as interregional (between margins), regional (between areas within each region/margin), macroscale (stations within each area), mesoscale (deployments at each station), microscale (vertical sediment layers). For convenience and clarity however, the margin/area/station/core and sediment depth will also be referred to as these refer to the specific scales and are easily identifiable considering that these are also used for the PERMANOVA tests.

Comment:Pag. 199, Line 17. “Irish Margin and Western Iberian Margin” is not a spatial scale. Maybe authors should use a more proper term. Again, water depth (ca. 700, 1000, 3400 and 4300 m) is not a spatial scale. Maybe authors should refer only to a m or km distance among stations at different water depth.

Response: We have taken the reviewer’s comment into consideration and will refrain from saying that water depth or margins are spatial scales. It is in fact the distance between the levels of the factor that represents the spatial scale. We will make this clear throughout the manuscript. This is in line with one of the previous comments of the reviewer saying that it is perhaps better to use names for the scales investigated,

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i.e. interregional, regional, macro, meso, micro scale.

Comment:Materials and Methods

Comment: Pag. 201, Line 25. “2.2 Sampling design and sample processing”: the title of this paragraph refers to the description of the sampling design. However, the rigorous description of the sampling design is in the following paragraph (Pag. 204, Line 7). To my opinion, the titles of the paragraphs could be changed in something like “2.2 Sampling strategy (or collection) and processing” and “2.3 Sampling design and data treatment”.

Response: This is a very useful suggestion and we will change the sections in material and methods according to the reviewer’s comment. The titles will then reflect the content of these sections more accurately.

Comment:Pag. 203, Line 5. The authors did not explain what was the purpose of nematodes length and width measurements. I guess that it was for the estimation of the nematode biovolume then converted into biomass values.

Response: The reviewer is right; the purpose of the biomass measurements was to calculate biomass. We will add this information in this section and explain how we calculated biomass and add the relevant references as we have done in table 2. Table 2 mentions the method for calculating biomass but we will also refer to this in the text here.

Comment:Pag. 205, Line 1. Since the authors used the PRIMER v6 and PERMANOVA, I am wondering if it is better to use the output of CAP analysis (comprised in the PRIMER package) instead of the MDS (which has no statistical meaning) to visualize the data in a bidimensional plot.

Response: The reviewer makes the valuable suggestion to consider the use of CAP analysis to visualize the results, particularly accompanying the PERMANOVA results. We have considered the CAP approach before submitting the manuscript, but came to

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the conclusion that it is not suitable for several reasons. This is also partially explained in a comment by reviewer 1.

1) The results from the CAP permutation tests (after having found the axes that best separate the groups given at the start of the analysis) indicate what the PERMANOVA has told us but the plots have no additional value. On the contrary, we lose information because different factors are not considered simultaneously. CAP analysis just shows that the groups (significant in PERMANOVA) can be separated in multivariate space using the appropriate axes. MDS (or even PCA) gives an idea of the variability in multivariate space as a whole and if patterns arise between groups in such a plot, it means it is definitely there. If not, then one could still search for it with CAP, but PERMANOVA has done this for us already. Moreover, PERMANOVA is more powerful if there are multiple independent effects for each of a number of response variables. CAP is an alternative for PERMANOVA, but whilst CAP is designed to test a specific hypothesis and ask whether there is a specific axis in multivariate space that separates a priori groups for 1 factor, PERMANOVA asks whether between-group variation explains a significant proportion of the total variation in the system as a whole.

2) It is very important to look at the unconstrained (MDS, let the data do the talking) as well as the constrained plot (CAP, decide what you want the data to show), but in this case the constrained plot is superfluous and does not add anything valuable.

3) CAP only allows separating for one factor at a time and hence does not give any result on the variability caused by different factors (spatial scales) at the same time. See also our reply to a similar comment made by reviewer 1. In essence, CAP hides all the factors you want visualised and that is not desirable in this case. CAP is ideal for hypothesis testing but not to display various factor effects on the plot.

4) After careful deliberation, it seemed to make most sense to use the MDS plot since they contained most information and did not merely represent a (less accurate) repetition of the PERMANOVA results.

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Comment:Results

Comment:To my opinion, it could be better for the readers to have a table with the raw data used for the analysis (also in the Supplementary material).

Response: The original data has been published online and is open access through www.pangaea.de. We will include the appropriate DOI and website references to the datasets in table 1 so that the readers can access the data freely for their own perusal. In today's scientific community open access data and sharing policies are indeed important to stimulate scientific discussion and peer-review processes and we are happy to contribute to these efforts.

Comment:Overall, the Results section appears sometimes difficult to read. To make the section easier for the readers, the suggestion is to present the data following the description of sampling design, according to the different spatial scales (from the widest to the smallest, for instance), instead of following the investigated variables. This scheme was applied in the Discussion section, which results more clear than the Results one.

Response: We agree with the reviewer and will try to present the results section following a similar scheme as the discussion section. The spatial scales will serve as a guide through the results, rather than treating the different descriptors separately.

Comment:Discussion

Comment:I suggest to avoid acronyms, to make this section easier to be read.

Response: The acronyms were chosen to reduce the length of the manuscript and make it easier to go through the text. However, we understand the concerns of the reviewer and we will avoid the use of acronyms in the discussion section and instead refer to the actual spatial scales. E.g. "sediment depth" instead of SD and "water depth" instead of WD. Similarly, the interactions will be written as, for instance, "water depth x sediment depth" instead of "WD x SD".

Comment:The authors should be more precautionary, since they are just hypothesiz-

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ing the relation between their results and the environmental/trophic variables, without demonstrating them.

Response: this is indeed true and we will try and smoothen our statements accordingly.

Comment:Pag. 209, Line 13. I cannot understand how the sampling design may affect the analysis of latitudinal pattern. Maybe authors meant the sampling strategy or collection, which are very difficult in particular in deep-sea environments.

Response: We see how our statement may have been confusing. It actually refers to what has been said in the previous sentence of that paragraph, namely that the water depths investigated were different at the different margins and hence the water depth variability will be included in water depth differences. We will leave "sampling design" out of the sentence since this effects has been mentioned in the previous sentence. In any case, the addition of an extra PERMANOVA test that includes the comparison of margins (following the recommendation of Reviewer 1) will likely change how this paragraph is written. This will give us statistical results to support the statements made rather than deducing patterns from the MDS plots.

Comment:Pag. 209, Line 13. Which patterns? In abundance, standing stocks, biodiversity?

Response: we mean "descriptor patterns" and will change this in the revised version. As mentioned for the previous comment. This section will change according to the test performed to detect margin differences.

Comment:References

Comment:Please, double check the References. Gallucci et al. 2009 is cited in the text but is missing in the References, while Kiriakoulakis et al. 2011 is cited in the References but is missing in the text.

Response: thank you for pointing out the mistakes in the references. We will make sure that all the references in the text and in the References section are carefully checked

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and corrected

Comment:Tables

Comment:Table 1. Please, explicit the Unit for Sediment surface, and the meaning of MUC (multiple corer?) and PC (ISIS) (push core from ROV ISIS?).

Response: agreed, we will add the necessary information to the table

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