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Biogeosciences Discussions

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 1

Dear Reviewer 1,

We would like to thank you sincerely for taking the time and effort in reviewing our manuscript. 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 you may receive the proposed

revision positively. Comment: The paper by Ingels & Vanreusel analyzes the spatial distribution of nematode diversity at different spatial scales in deep-sea ecosystems, in particular canyons and slope systems in two regions: Irish margin and Western Iberian margin. The dataset presented here is based on previously published data but analyze with a new approach. The paper suggests large efforts both for the field and laboratory activities to analyze nematode diversity (including functional diversity and standing stock). The paper is very interesting but needs a major revision before the final acceptance for publication. I find that some topics should be clarified to make the paper publishable.

Authors conclude that the main source of variability occurs at small scale but the analyses carried out do not consider the difference at larger spatial scale, the comparison between the two regions IM and WIM. In the introduction (lines 17-18): ": : :.. IM and WIM (ca 1550 km apart): : :" but this spatial scale has not been investigated. Authors should select their dataset to make available also this kind of comparison.

Response: The reviewer is quite right in saying that there is no direct statistical comparison between the Iberian Margin and the Irish Margin in the current version of the manuscript. The MDS plots can give an indication of similarity (or dissimilarity) between the two margins but no direct statistical value is given. The difficulty lies within the data (collection) itself, the depth ranges investigated in each of the Margins are different and do not allow direct comparison between the two within the framework of the PERMANOVA design that is used here (unfortunately, deep-sea sampling is often logistically arduous and brings many limitations). There is no way of comparing these two distant margins with the inclusion of all other factors. Any test performed that is out to test the significance of differences between margins will automatically have variability of other factors built in which cannot be extracted.

One option is to just compare the assemblages in a one-way comparison, disregarding the other factors. . . which would not be very useful given that these other factors cause significant differences as shown by our analyses. Another option is to perform a test

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whereby the factor area or canyon and the factor water depth are each nested in the factor margin in a three-way nested PERMANOVA test; hence leaving out the vertical profiles and the individual deployments as factors. We would opt to do this in the revision in response to the reviewer's request. The results of these tests do reveal a weak but significant difference between margins for structural diversity and community structure, but not for functional diversity and standing stocks. The significant margin results, however, may suffer from hidden variability due to differences between deployments (cores) and sediment depth (variability built in in the margin comparison), factors which cannot be separated in in this test. As shown with the original 4way PERMANOVA test, these small-scale factors have significant effects and the results for margin differences in the three-way test therefore have to be interpreted with caution. Any reference to whether margin differences are more important than regional or local differences could not be made with absolute accuracy using this approach and the text would be adapted accordingly.

So in response to the reviewer's request, we would add the results of a new three-way test in the text and mention that these results indicate limited margin differences, amongst other factor differences. We would, however, also mention the limited interpretability of the new results given that hidden variability may be contributing to the significant differences observed.

Comment: Moreover, I do not think that it is correct to compare a horizontal distribution with a vertical distribution of biodiversity. Please clarify this topic.

Response: The reviewer points to an interesting issue here, but to us it seems evident that horizontal and vertical spatial scales are included in an encompassing test. For instance, water depth has been considered in many studies as a factor influencing benthic assemblages but so is latitudinal variability. There is no methodological argument against including a vertical and a horizontal scale in a hierarchical model test to assess biodiversity differences (or any other descriptor difference for that matter); the only limitation is that of interpreting the results. There are studies which compare

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horizontal and vertical spatial scales (e.g. Danovaro et al, accepted in DSRI, Fonseca et al 2010 in Progress in Oceanography and Benedetti-Cecchi 2001 in Marine Ecology Progress Series) with enlightening results. In addition there are strong arguments to include both horizontal and vertical scales in spatial scale analyses since communities may differ along both spatial gradients; the sedimentary environment and the oceans are 3-dimensional systems. Excluding one does not mean that variability is explained by the other... both may be present. Of course, the meaning of the results lies in the interpretation of them and our understanding the mechanics behind the patterns. Does it make sense to compare vertical sediment layers and water depth and other, horizontal spatial scales? We strongly think that it does in the context of unravelling variability in different descriptors of benthic communities. In marine ecology there are a plethora of examples whereby different factors are tested against each other to explain communities and diversity. The methods used here are very powerful and allow the comparison of any factor that may be responsible of causing differences in communities, regardless of the measure and regardless of the scale. The present study tries to reveal which factor is causing the largest differences in nematode communities; does a nematode assemblage 100m away differ from an assemblage 1000m away or does a nematode assemblage 4 cm deeper differ more than an assemblage 1000m away are both valid questions. In the present study the vertical sediment differences were generally high and indicate that compared to a surface (0-1 cm) assemblage, conditions at 3cm depth may cause the community to be more different than a community 100m or 1000m or even 50km away! Perhaps it may seem trivial in larger spatial-scale analyses, but solute transfer variability and particle diversity on vertical scales (to name but two) are important in determining communities. By analysing different descriptors sets we attempted at clarifying which aspects of the nematode communities are affected by different spatial scales and to what extent.

Comment: Any role of the use of different sampling gear???

Response: The different gears are all very much similar in use and similar in the tech-

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nique with which the sediment is recovered. The sample surface differences are minimal (ca. 2.7cm2) and each sample (regardless of gear) was in effect a filled plexiglass core with a practically undisturbed sediment-water interface as it would have looked on the seabed. If the comparison was made between box corers or day grabs and multicorers, then indeed a test for sampling gear would be warranted but such gear differences are not present in this case. Setting up an appropriate test would also be very difficult since different locations are represented by different sampling gears. Consider the midicorers at the Irish Margin for instance. Two indications, however, that refute the effect of gear in the present study are found in the patterns shown by MDS plots 1) the close grouping of samples from the Nazare Canyon regardless of the gear used (push corer, midicorer or Megacorer) and 2) the vertical sediment depth pattern (dispersion away from 0-1 cm towards the deeper layers) is relatively consistent between different sampling gears. Nevertheless, we will mention these considerations in a revised version.

Comment: I would suggest to clearly explain that “their” small scale variability is referred to a vertical distribution.

Response: Good point; throughout the manuscript, we will be clearer about the type of scale we are referring to in the text, i.e. whether it is vertical or horizontal and try to avoid confusion between the two.

Comment: Sampling scale at “core level”. I have understood that core is a replicate (?) but is 1-200 m the spatial interval? This spatial interval is very large to be considered replicates from the same site.

Response: The reviewer has a good point here, and we agree that the reference to “replicate” should be avoided in this case. The gear is operated at great distance from the sea surface (700-4300m) and so the distance between the locations where the gear lands on the seafloor from different deployments can indeed be anywhere between 1 (e.g. ROV push cores with very accurate positioning) and 200m (tethered

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coring devices) apart. Calling these deployments replicates is standard in deep-sea research since non-ROV based operations can't be performed more accurately, even by very experienced deck crew and is dependent on the ability of the ship to maintain exact position and currents in the water masses below. Nevertheless, the independent deployments are still representative of the same location. In the present study independent deployments at one location (e.g. Nazare Canyon ca. 3400m) still represent samples typical for that location, but we have treated the distances between these independent deployments representative of a spatial scale in itself by assigning them to a factor. Therefore, independent deployments (cores) at a "station" represent a spatial scale. In many deep-sea studies these cores would be treated as true replicates for a location (since cores from a single deployment or several subsamples from a larger core or box are considered pseudoreplicates and are difficult to work with given that the often necessary statistical assumption of independence is violated. This is often a hurdle in the reviewing process of deep-sea papers, but there is ample evidence that pseudoreplication is not detrimental to the analysis perfomed, but that is a topic of discussion on its own and falls out of scope for the issue raised here by the reviewer), so by treating them as a spatial factor we are in fact not using them merely as replicates but as a spatial factor within a location. We will remove any reference to "replicates" in the revised version so not to confuse the reader and be more accurate. The changes will therefore be made according to the reviewer's suggestions.

Comment: It seems that there is also an important variation of depth among corers.

Response: Considering the depth differences between the classes of the factor water depth (It is quite obvious that 3520 m water depth falls in the 3400m class and not the 4300m class), the differences between cores are minor. Deep-sea sampling in a canyon environment with often steep sloped walls will inherently suffer from depth differences between different deployments but we believe these depth differences to be trivial. Nevertheless, we cannot exclude that a small part of the variability observed between cores is due to the small water depth differences whilst the main determinative

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factor is the horizontal variation and hence the variability observed at the core scale is perhaps a combination of both horizontal and vertical variability. We would therefore adapt the text accordingly to include this issue raised by the reviewer; by mentioning that differences between cores may include a small vertical explanatory component.

Comment: The dataset is based on data already published, but the authors should show their data to make more easy the comprehension of the manuscript. These data could be included in the Table 1 or in a table in the supporting online 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 made by the scientific community.

Comment: Table 1 reports 0-5 cm: is the meaning 0-1, 1-2, 2-3, 3-4 and 4-5 cm? Please explain and indicate in which station the vertical distribution has been investigated.

Response: Our apologies for the confusion. The numbers in the table indicate to what depth the sample was investigated. Each 1 cm slice was investigated, so 0-5 cm in the table indicates that 0-1, 1-2, 2-3, 3-4 and 4-5 cm were investigated; we will make this clear in the table by adding a note at the bottom of the table saying that 0-5 means that all 1cm slices were investigated to a depth of 5cm.

Comment: Community structure or composition? Please explain

Response: Our apologies if there has been confusion in the text with the usage of composition vs. structure. There may have been instances where the two have been used interchangeably. Our understanding is that community composition holds the information on the constituents of the community; i.e. which genera are present. The structure

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can mean different things and includes evenness and possibly other measures. We will make sure that the two terms are not used interchangeably. The study here uses the relative abundance of the genera present and so holds information on the structure. We shall avoid reference to these terms where it is inappropriate and use the correct terms throughout the manuscript.

Comment: Most of the discussion is based on the trophic composition of the deep-sea sediments. Again the authors should summarize their environmental data and present in the supplemental material . Most of the discussion is referred to environmental and trophic conditions to explain the observed spatial variability. I think that the authors should utilize an appropriate statistical tool to support their discussion. I would suggest DISTML analyses to analyze the link between biodiversity and potential drivers at different spatial scales. Any role of the bathymetric, latitudinal and longitudinal gradient? Authors should clearly tested the potential role of these gradients that could influence the spatial distribution of biodiversity at large spatial scale.

Response: We think that some confusion may have arisen here. At no point in the manuscript have we presented environmental data from the stations we have sampled for the nematode communities. If there were sufficient environmental data representing the same spatial contrasts as presented by the biological data we would have pursued what the reviewer suggested, but this is unfortunately not the case. The environmental data we have in hand are too patchy and limited to make a sensible test that would give evidence of which parameters drive the variability shown in the nematode communities, and so we have chosen not to present a reduced and non-compatible version of it. The importance of the environmental data has been analysed and discussed in the original papers that use the different sets of nematode data and others that focus on the same regions/areas. The discussion in the present study is based on the biological data and the information given by various studies, not environmental data originating from the sediment samples obtained at the same time as the samples for the biological analyses. We appreciate the considerations made by the reviewer but the environmen-

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tal data is simply not sufficient enough to set up a spatial-hierarchical test similar to the one devised for the nematode descriptors. The importance of this study lies in the spatial patterns of the nematode communities and descriptors themselves, not the link with the patchy environmental data that exists. We hope that the reviewer can follow us in this logic.

Comment: Fig 3 and 4 show MDS outputs that are not very clear, I do not think that these figures show clear results.

Response: The MDS plots may not show clear separations between the different levels of each factor but that is because several interactions between factors occur and the variability between different levels of each factor (groups of samples) explain a proportion of total variability. An MDS plot (or a PCO/PCA plot) takes into account total variability between sample points and hence the picture that is painted on the plot is necessarily complex when considering multiple factors that may cause variability in multivariate space. Nevertheless, there are clear indications of the variability that is caused by the different groups. The differences between margins are relatively clear, and so are the divergent patterns between areas, water depths, stations and sediment depth. There is indeed overlap between the groups of data points, but that is exactly what the PERMANOVA tells us; i.e. that there are different factors that contribute in explaining total variability with certain factors contributing more than others.

The MDS plots may not give a clear separation between groups of one factor (spatial scale), but that is because we are looking at different spatial scales and differences between water depths for instance are relative to differences between, say, areas and sediment depth. Contrary to what the reviewer suggests here, we feel strongly that fig. 3 does illustrate the results well and removing it would be detrimental to the ability to interpret the results. The same goes for Fig. 4. Important is knowing how to interpret the MDS plots in light of the analyses performed. It is not merely about the visible separation of groups (that is not the underlying logic of an MDS), it is about the distances between data points (similar to how PERMANOVA uses distances of group data points

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to their centroids); the further they are apart, the more dissimilar they are, and vice versa. And MDS does this taking into account the total variability in multivariate space with a resemblance measure of choice.

An alternative that we have considered (cf. comment of reviewer 2) is performing a CAP test and visualisation but the resulting plots are severely distorted because of the constraints of the ordination; it just calculates the axes appropriate to maximize divergence between levels of 1 factor. In CAP, the axes are therefore defined to comprise maximum variability for 1 particular factor (e.g. areas, see figure attached with this response) and can't include multiple factors at the same time; all other factors are hidden away to the benefit of that one factor of interest.

Whilst this may be desirable when testing a particular hypothesis (in this case (see figure) for instance "is there a way of separating the different areas in multivariate space"), the CAP analysis does not really say anything that the PERMANOVA analysis doesn't. On the contrary, CAP actually gives less information since it doesn't give any insights into what variability the groups of different factors may explain taking the whole sample set into account and is therefore not desirable for the present study.

We sincerely hope that the reviewer can appreciate our point of view. We understand that there may be concerns regarding the clarity of the MDS plots to the non-experienced eye, but we have considered alternatives and MDS is just the appropriate tool to use. In addition, when interpreted correctly, the visible MDS patterns explain what the PERMANOVA is telling us; namely that different spatial scales cause different levels of variability for the different descriptor sets.

Comment: It seems that the comparison between sediment layers is between 0-1 and 4-5 cm. I think that the comparison should be carried out considering all sediment layers. Please explain.

Response: We think that the reviewer may have been confused here. The starting symbol and endsymbol represent 0-1 and 4-5cm, respectively, but there are of course

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the 1-2, 2-3 and 3-4 cm layers in between which have been integrated in the analysis and are connected by lines in the MDS plot. The places where there is change of direction in the line indicates the other layers; 0-1 is connected with 1-2, 1-2 with 2-3 and so on. The lines therefore represent the vertical profile. This is mentioned in the captions of the figures but we will make sure that this is more clearly mentioned in the caption of the figure to avoid confusion.

Interactive comment on Biogeosciences Discuss., 10, 195, 2013.

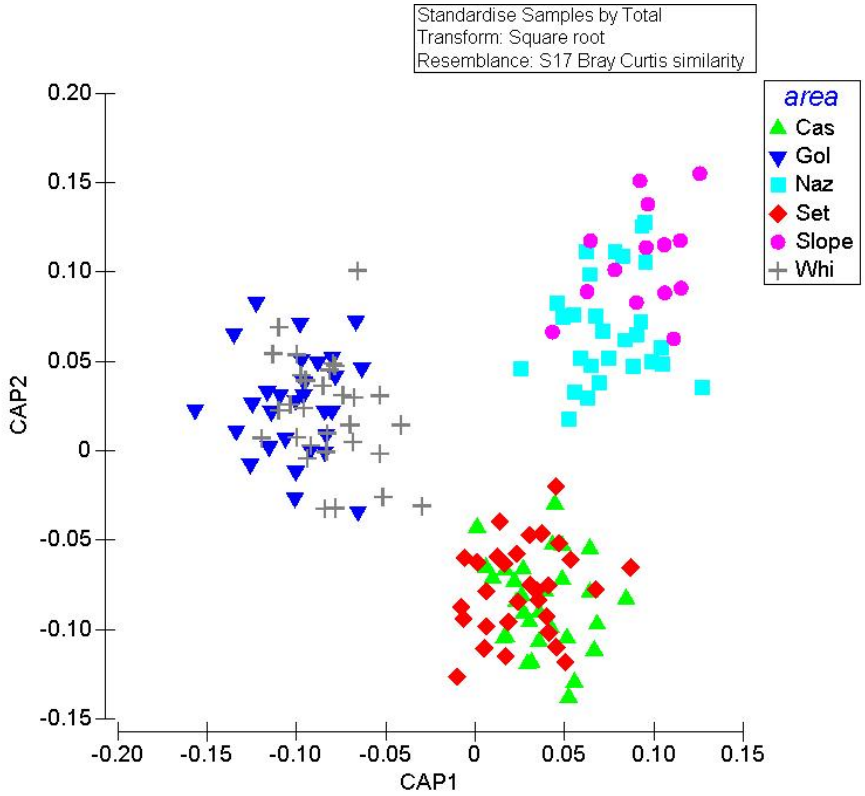

Fig. 1.

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