9 January 2020

Subject: Revision of MS No.: bg-2019-304

Dear Associate editor,

We would like to thank both reviewers for their thorough revision of the manuscript.

We addressed the main concerns regarding Figure 3 and Table A1 and elaborated on certain parts of the methodology. Figures were redone to make sure the same dataset was used and the text was corrected whenever necessary. We argument the use of the ind/100m metric due to the limitation of the data collection, which is explained in more detail below.

All our other detailed replies to the reviewers' and associate editor's queries, the changes made to the manuscript (with line references of the revised manuscript) and a marked-up manuscript version are enclosed,

Sincerely,

Daphne Cuvelier

Associate Editor Comments to the Author:
Dear authors,

2 reviewer comments have been received for your manuscript that you have both responded to. Both reviewers have made substantial comments that need to be addressed and incorporated during the revision of your manuscript. This should be possible considering your replies.

A few additional comments (in addition to the reviewer's comments) from my side are:
I agree with the reviewers that Figure S1 presents essential information on the size of seamounts, water depths and locations of the transects. Therefore it should be moved into the article. However, important information is not accessible from the current figure, because axes and color code labels are not readable (even if zooming into the PDF) due to too low resolution of the figure.

A: Figures are embedded in a pdf as requested when submitting a manuscript for Biogeosciences, which is why their resolution is not that high. We have increased the letter type so that the numbers are readable and increased the scales so that the size of the seamounts can be deduced. We will provide high resolution figures when the manuscript is accepted.

During the revision, please take care to significantly improve the quality of all figures (Fig.7 has a similar problem) that labels and annotations become readable.

A: See comment above. We reorganised figure7 to enhance its readability whilst embedded in the pdf.

It may be useful to add a table in the supplement containing specific information for each seamount raised by R#1 (i.e. size, summit and base depth, average slopes at sampling/video depths and average current direction/velocity (e.g. sampling site upstream or downstream), etc).
A: All this information can be found in the text and in the improved Fig 1. Slope can be calculated using the depth gradient and the length of the transect.

Sampling sites were all downstream – this is mentioned in L83-84 of the revised ms.

R#1, comment 3: The distance between the ROV laser spots on the videos (I believe it is 50 cm for the parallel beams, but please confirm with the ROV team of Kiel6000) should enable estimating the width of the visual field and hence allow providing an area for the transects, i.e. ind/m2. This would increase comparability.

A: This was considered previously and extensively, but lasers were not always visible during the entirety of the seamount dives. Changing camera pan and tilt and forward-looking view also introduce bias in any possible surface calculations (e.g. perspective view). Additionally, the non-constant travel speed, and changing ROV altitude complicates the surface calculations. In order to counter this, we considered subsampling images at a predefined distance interval (e.g. every 10 m) and extrapolate the surface covered. Nevertheless, as stated before, lasers were not visible/operational during the entire dive and would thus only increase over-or underestimation of the surface covered and therefore of the faunal densities. Overall, the ind/100m appears a more correct representation of the patterns observed and therefore the *in situ* reality and allowed for an in-detail comparison to the nodule field dives, which was one of the main objectives of this study.

R#1, comment L.288-295: This is an important point and I agree with the reviewer that more discussion on possible reasons would be helpful. For example, the seafloor POC flux in APEI3 seems to be reduced by ~30% compared to the investigated license areas (see biogeochemistry paper of Volz et al. (2018) Deep-Sea Research I 140).

A: We mitigated the overall statement that the nodule coverage would be the main driving factor and added more on possible other factors at play using the reference proposed. L329-331.

R#2, comment 3: Where is Fig. R1 you mention in your reply?
A: It was attached as a supplementary figure during the first review round and can be found in the "reply to reviewer 2" .pdf. We have inserted the figure in the appendix (Fig. A1) and referred to it in Section 3.2.

Reviewer 1:

R1: My main concern is that no environmental data are presented. In additon to missing hydrographical data, there is no detailed description of the sampling sites, particularly the seamounts, such as size, summit and base depth, inclination of slopes/general bathymetry, or current field. More important, no information is given on habitat types encountered along the transects. It is well known that substrate can vary considerably at short distances at seamounts, and of course megafaunal communities are strongly associated with substrate type. This is briefly mentioned in the discussion, but I do not understand why this information is not provided and analysed in the results. It should easily be available from the video footage.

A: Regarding the reviewer's comment on the description of the sampling sites: There was a supplementary figure (Fig. S1) from which the size of the seamount, the depth of the base and bathymetry can be deduced and which we now have incorporated into Figure 1 (as requested by the other reviewer and associate editor).

We have added information on the amount of hard substrata under the form of 3 categories: (1) Predominant soft substrata (<40% hard substrata), (2) mix or transition (between 40 and 60% hard substrata) and (3) predominant hard substrata (>60% hard substrata), annotated per 10m distance unit. This has been added to the methods section (L121-124). The amount of hard substrata was linked with faunal observations in higher taxonomic groups. No significant correlations between substratum type and faunal abundances were found for ROV02, ROV04 and ROV09. This is most likely due to the amount of hard/mix/soft substrata, which were almost equally distributed over the transects (varying between 16-39%, 30-51% and 15-38%, respectively). This highlights the need for a more in-detail assessment of substratum type, which is currently underway as the geomorphology of the seamount transects is being modelled (based on backscatter data) and investigated in detail, but this falls outside the scope of the current manuscript.

Based on the preliminary substratum results, a paragraph was added in section 3.1 L206-218

Concerning the hydrographical properties, a link with the POC-flux as known for the CCZ area was elaborated, also following the associate reviewer's suggestion (L328-332). Following the comments of the other reviewer, we have added the predominant current direction at the CCZ in the Methods section.

R1: There are also some methodological issues. The basic problem, as also admitted by the authors in the discussion, is that only a very limited number of rather short transects without replications are available and that transects at the seamounts and at the nodule fields were taken at different depths; in the case of Mann Borgese Smt the depth sampled was nearly 3000 m less than on the corresponding nodule field, and hence the data are hardly comparable. Although the depth difference at the other sites was much smaller, it may also limit the comparability of the data. This is mentioned in the discussion, but the consequences should be elaborated in more detail, and it makes the conclusion that "seamounts appear inadequate as refuge areas to help maintain nodule biodiversity" disputable.

A: In name of all the co-authors, I think we were very cautious in our conclusions, recognising the sampling shortcomings as well as the limited amount of data. We purposefully stated "*Based on our current knowledge*; seamounts appear inadequate as refuge areas to help maintain nodule biodiversity." And then urged on for more proper sampling to adequately corroborate or refute observations done here. We recognised the shortcomings throughout the manuscript. We think it is important to take a look at the entirety of the sentences written and to not take parts of them out of context.

Moreover, because of the unknown impacts and extent of mining, we could speculate that only the communities living outside a certain range in distance across the seafloor and upwards in the water column, will be protected from the mining plumes (and other impacts). Hence, it is relevant to also investigate "shallower" areas of the seamounts, as there is a possibility that recolonisation will start from these somewhat shallower areas.

R1: I am also not convinced that the quantification of the samples is correct. In section 2.1, the authors state that the altitude of the ROV was "kept constant whenever possible". Apart from not providing the information at which target altitude the ROV was kept, and whether this was the same at all transects, the authors inform in section 2.2 that, due to varying altitude as well as pan and tilt of the camera, "surface coverage" could not be used for standardisation and instead just transit length was used. However, since the field of view and thus the number of visible objects per unit transit section depend on the altitude and angle of the camera, the standardisation to 100 m transit sections, without taking into account the varying field of view, could strongly bias the results. Generally, the methods section has to be improved with much more detail.

A: Target altitude was 2m above seafloor and travel speed ~0.2m/s, though interrupted by sampling actions, instrument check-ups, exploration, object avoidance (in the case of the uphill seamount transects) etc. L100-102

Regarding the comment that ind/100m might not be a good metric, we would like to clarify that the length of the transects was calculated only taking into account the parts of the dive when the ROV was visualising the seafloor. The parts of the dives where the ROV was higher up in the water column (i.e. >10m altitude) and/or not visualising the seafloor (e.g. Transiting or checking ROV parts or instruments) whilst travelling forward, were omitted out of these calculations, thus granting a best estimative possible and allowing for comparison.

We agree with the reviewer's observation that changing altitude and angle of the camera bias the observations, but by excluding the parts of the transect that were too high up, it is the best approximation possible with the data at hand.

Throughout the paper, we acknowledge the importance of performing standardising video transects and recognise the shortcomings of our study to this respect. However, on seamounts we cannot fly straight all the time, it does not necessarily prevent comparisons between transects, because the bias is systematic across transects. Moreover, while this shortcoming may pose limitations to quantitative comparisons, it does not preclude qualitative comparison between habitats, which are the main objective of this study.

Information on ROV altitude and transects length calculations were added in the Methods section with the following paragraph:

"For the transect length calculation for each dive, we omitted all parts of the video footage in which the ROV was at an altitude of >10m, or sections where the ROV was not visualising the seafloor (e.g. during transiting or inspecting ROV parts or instruments). Visualisation of ancient disturbance tracks were omitted as well, as these fell out of the scope of the article." L128-132

R1: Further, it is not clear how the investigations made in this study relate to those by Vanreusel et al (2016) who also presented results for epifaunal communities in the CCZ, comparing APEI, BGR, GSR and others. Obviously the sampling was done on the same cruise using the same gear. Were the same nodule field transects analysed? If yes, this has to be justified, the additional value of this study as compared to Vanreusel et al (2016) has to be demonstrated (apart from the additional seamount transects) and any overlap and differences in the analysis indicated. If not, a thorough comparison between the results of both studies is necessary.

A: Vanreusel et al. was based on a subset of the BGR, GSR and APEI3 nodule field videotransects/dives analysed here (they investigated 2740 m of the 6100m nodule fields transects as presented here or 44% of our study**)**, and, as stated by the reviewer, they did not study the seamounts. Moreover, and most importantly, Vanreusel et al. did not identify individuals to morphospecies level but stayed at a higher taxonomical level such as Actiniaria, Echinoidea etc.

The following paragraph has been added in the ms for clarification purposes**,** in methods 2.2. L115-120

"A subset of the nodule field transects form BGR, GSR and APEI3 was presented by Vanreusel et al. (2016), and correspond to 44% of what we studied here and limited organism identification to a higher taxonomic level (Order (e.g. Alcyonacea) or Class (e.g. Ophiuroidea)). In our study, the entire transects (100%) were annotated to morphospecies level, allowing a more detailed comparison between seamounts and nodule fields."

Specific comments

R1: Use consequently "Ophiuroida, Asteroida" etc. instead of "ophiuroids, asteroids" etc.

A: Ok

R1: Abundances given in the text are not always consistent with those presented in Tab. A1. I did not check all entries, but two examples caught my eye: A total abundance of 89.2 ind/100 m is given for ROV10 in Tab. 1 and in the text, but summing up all observations in Tab. A1 results in ca. 67 ind/100 m. Another example: For Porifera, numbers given in the text match those in Tab. A1 for Rüppel and Senckenberg, but those presented for Heip and Mann Borgese are much lower than in the table (3 vs. 7.5 and 0.68 vs. 1.9, respectively). This has to be checked and resolved.

A: We carefully and meticulously checked all the densities, abundances and number of observations, to make sure they were correct and verified that the correct dataset was used for all figures and graphs.

R1: Line 42: Insert common definition for "seamount" and citation

A: We added the definition from the glossary of the International Seabed Authority: "*Seamounts are defined as isolated sub-surface topographic feature, usually of volcanic origin, of significant height above the seafloor (International Seabed Authority (ISA), 2019)*" on L42-43

https://www.isa.org.jm/scientific-glossary/

R1: 73: When did the sampling take place?

A: In 2015, this was added on L74

R1: 96: What is the difference between "exploration and opportunistic sampling"? More detail is needed.

A: The words chosen are rather self-explanatory. Explorative dives are dives when a site is visited for the first time and observations made during the dive are key to decide what happens during its course, e.g. sampling when the occasion presents itself or just imagery sampling. It was also mentioned in the text of the first submitted ms (L113-114) and now in L125-126.

R1: 98: What does "whenever possible" mean? 90 % of the transects? What was the target altitude of the ROV, and was it the same at all transects? How did panning and tilting affect the field of view? (see also general comments).

A: See answer above

R1: 94-99: Generally, much more information on the sampling mode is necessary, including sampling strategy (e.g., straight line, deviations for interesting objects etc.), ROV speed, target altitude, field of view etc.

A: See answer above

R1: 104: What is "ID's"? I guess it should be IDs, but "ID" is not defined in the text. Same in line 111.

A: ID from identification. This was altered.

R1: 114: Is there a reason that specimens collected were obviously not used for proper identification?

A: Samples were used for proper identification whenever possible. Multidisciplinary research cruises such as SO239 based on larger research projects (JPIO) tend to have a multitude of institutes involved, with different or overlapping interests. Samples taken during the cruise were distributed and divided over different institutes, each working towards their own objectives. The organisms sampled for which we received identifications were incorporated as such, e.g. Porifera identifications as included here. Though as stated in ms L280-282, even when organisms were sampled and identified, they were hard to extrapolate across the video imagery. Same reasoning applied for the Ophiuroidea where many species were revealed based on the samples, though impossible to annotate or differentiate based on the imagery footage (Christodoulou et al 2019). Hence, no information on its abundance, distribution or even presence in other areas than the one sampled can be included. There is no use of having a name for one (sampled) species from one single location if you cannot recognise it elsewhere.

R1: 118: Which statistical testing? Did the authors use tests other than nMDS? If yes, they have to be described here in detail

A: We have added information on the Kendall species Associations test carried out. L136-138

R1: 127: Here and throughout the text: two significant digits are sufficient, for example 7.6 instead of 7.59 or 89 vs. 89.23. The two decimals pretend a non-existing precision of the data.

A: Ok

R1: 151/152: Aren't Acrocirridae polychaetes as well? (". . . Acrocirridae were observed. . . as well."). Do you probably mean they were observed in high densities in some of the transects?

A: This was corrected.

R1: 189/190: This belongs into the discussion.

A: This is also mentioned in the discussion and it was mentioned here as well to recognise the limited sampling. This links back to the methodological issues as stated by the reviewer, which we fully recognise throughout the manuscript.

R1: 193: Insert ", respectively" after "Table A1"

A: Ok

R1: 195: "less linear" - how was this assessed? I cannot see any linear or non-linear relations in Fig. 4d, nor can I see any curves crossing.

A: Replaced linear by straightforward. Curves cross at smaller sample sizes (<100 individuals) for ROV13,08 and 10.

R1: 198: What does "small sample size" mean? I think the sample size in this study was always small.

A: Less than 100 individuals, this was added.

R1: 205: Should read "least overlap". Explain similarity between these findings and the results from the seamount: For both habitat types, the samples at APEI3 had least overlap with the other sites.

A: Ok

R1: 220ff: According to Fig. 3 (not Fig. 8!), the majority of ophiuroids on the nodule fields were unidentified

A: This was corrected to *"The majority of the very abundant Ophiuroidea observed at the CCZ seamounts were small and situated on hard substrata (morphospecies 5), while most of the Ophiuroidea at nodule fields (including morphospecies 6) were observed on the soft sediments. Morphospecies 6 was only rarely observed on the seamounts (Fig. 3)"* L253-256

R1: 244/245: This is not clear. Variation "along the video transects" was obviously not analysed and cannot be seen in Fig. 5. Probably the authors mean "between transects"?

A: This was corrected to "among the video transects of both seamounts and nodule fields"

R1: 251: Kendall's coefficient is not mentioned in methods section. See comment above.

A: This was added, see reply above

R1: 255-258: This makes no sense. If sampling depth differs between seamounts and NF, and nMDS distinguishes between seamount and NF groups, then the grouping must correspond also to depth sampled. Omit this paragraph (and Fig. 7b) and state in the discussion that differences between seamounts and NF could be a result of different depths sampled.

A: It was already stated in the discussion, but in our opinion it is a visual presentation of this statement, which is why we decided to keep it for now.

R1: 262: This is not quite clear. Rephrase: ". . . at different locations and additionally, for the seamounts, different depth ranges." Possible differences in substrate etc. should be mentioned here.

A: Change was carried out

R1: 269: Rephrase: ". . . since (mega)faunal communities could be very different even between adjacent seamounts . . .

A: Ok

R1: 270: Which parameters? Name examples for depth-dependent parameters which drive faunal composition

A: "parameters that vary with depth, such as temperature, oxygen concentration, substratum type, food availability, and pressure" This was added. L302-304

R1: 278: Why would "elevated topography (peaks)" favour Porifera and Anthipataria? Name possible mechanism(s). By the way: Seamounts are per definitionem elevated topography

A: Peaks are more exposed and appear thus more advantageous for filter feeders such as Porifera and Antipatharia. This is mentioned in the text. L311

R1: 288-295: Do the authors mean that faunal density is negatively correlated with nodule coverage? This is in contrast to Vanreusel et al 2016, who found higher abundances at higher nodule coverage. So obviously in this study, the driver for the differences in faunal density was not nodule coverage, but probably organic input.

A: We searched for a possible explanation as to why APEI3 stood out and found that this difference, besides their more northward location under more oligotrophic waters (mentioned in L328-332), corresponded to a difference in nodule coverage. The patterns by which nodule coverage or densities influence the ecological patterns are still poorly understood. The nodule coverage data as mentioned in our ms originate from Table S1-1 from Vanreusel et al. 2016, and indeed in the body of text these authors reported higher epifaunal densities in areas with dense nodule coverage, reporting >25 versus ≤10 in sessile individuals per 100 m2 for nodule rich and nodule free areas respectively. Nevertheless, if we compare the nodule coverage from Table S1 to figure 3 (both from Vanreusel et al. 2016) same patterns as those described in our study are observed, namely: Higher nodule coverage in APEI3 and lower densities both for sessile and mobile fauna. It is possible that Vanreusel et al. made their statement by looking at the license areas only and not included the APEI in this comparison. We chose to keep our statement, but elaborated on other possible reasons that could influence (e.g. POC) the patterns as observed (L328-331).

R1: 296: Grammar: neither - nor

A: Ok

R1: 319: Clearly distinguish between own data and data from literature by rephrasing, e.g. "Vanreusel et al. (2016) found that ophiuroids. . .."

A: Ok

R1: 322 : The available data cannot show a gradient, therefore it should read: ">50% less at seamounts compared to nodule fields"

A: This was corrected

R1: 331: ". . . studied here."

A: Ok

R1: 338: How can an uneven distribution (of holothuroids) affect composition?

A: Unevenly distributed organisms can give different perceptions in sampling. Organisms with a wide distribution range can, when unevenly distributed, be present/absent in adjacent sampling localities, thus resulting in different faunal composition for these sampling locality.

R1: 350: This is an isolated statement here - what does it imply?

A: We moved it to the beginning of the paragraph which now starts off as follows: “Stalked organisms, such as Crinoidea (Echinodermata) and Hexactinellida (except for Amphidiscophora, Porifera) rely on hard substrata for their attachment and are considered being among the most vulnerable organisms when mining is concerned.” L381-383

R1: 352: And what about nodule-covered areas - did they host these taxa in Vanreusel's or this study? This paragraph is a bit confusing and should be re-sorted, also clearly distinguishing between own results and those of others.

A: This paragraph was re-written (taking into account the comments of the other reviewer as well) to make the distinction between our results and those from literature more easily: L391-402

R1: 361: "communities"

A: Ok

R1: 362: ". . . were more abundant. . ." - compared to what?

A: "… more abundant than on seamounts". This was added.

R1: 370: ". . .they are known to . . ." Citation?

A: This statement was based on our personal observations. We have rephrased it and changed the structure of the paragraph as to convey our point more clearly: L411-417

R1: 372: Does the reference (Baco 2007) apply to both statements? I suggest to rephrase, e.g. "The exception. . .common on seamounts, as also reported in other studies (e.g., Baco. 2007)." Baco 2007 is not in the reference list!

A: Baco 2007 refers to the Scleractinia being common on seamounts. We have clarified this and added the reference for Baco 2007 to the reference list. L415-417

R1: 373: Insert: ". . . Enteropneusta which in this study were found only on seamounts, were. . ."

A: Ok

Figures

R1: Fig. 1: What does the "A" in the upper left corner mean?

A: Figure 1 underwent some change taking into account the comments from the other reviewer.

R1: Fig. 2: I suggest to add morphospecies "names" (as given in Fig. 3) to the examples.

A: Morphospecies names were added to the caption.

R1: Fig. 3: This figure should be simplified. Most of the morphospecies were observed in very low numbers, and in these cases differences between NF and seamounts are difficult to see in the figure and rather not relevant. I suggest to include in this figure only morphospecies and higher taxa with a substantial mean abundance (e.g., >0.5 ind./100 m per habitat type); other morphospecies could be summarised or omitted. By contrast, Table A1 should be extended and present the results for all morphospecies, not only higher taxa (see below).

A: Figure 3 was withheld because it was considered a key figure to show how different the presence/absence/abundance of the fauna varies between the two ecosystems, but the 3 parts were separated more clearly with different breaks at the X-axis, thus enhancing readability and interpretability. We also reorganised figure 3 to correspond to the order of A Table 1.

Table A1 now includes the morphospecies densities as well.

R1: Fig. 4: Axis labels are incomplete (units are missing). What does "exact" on the y-axis in panels a and c mean? And what is sample size (units?) in panels b and d? I guess that not sample size was used for the rarefaction curves, but accumulated number of observations. Caption is incomplete: What do the shaded areas in panels a and c and horizontal and vertical lines in panels b and D mean?

A: Sample size is the number of individuals observed (or number of observations as you will). Information was added to the caption and axis were renamed and/or clarified. Horizontal lines of the lower panels were omitted because they did not provide significant information for the interpretation of the figure.

R1: Fig. 5: What does "values are relative" mean? - percent (of what?)? This has to be explained.

A: Values are relative due to different transect lengths and differences in richness. This was changed to "Values are indicative rather than absolute due to different transect lengths and differences in richness."

R1: Fig. 6: y-axis incomplete, should include quantity and unit.

A: I am not sure what this is about, since the Y-axis is complete and has ind/100m as title.

R1: Fig. 7: Omit panel b).

A: See comment above

Tables

R1: Tab. 1: Be consistent with units: here, #obs/100 m is given, whereas throughout the text and in figures and in Tab. A1 the unit for density is ind/100 m.

A: The number (#) of observations is more of a methodological way to describe it, since it was used prior to the results. This could be changed.

R1: See also comment to Fig. 3. I suggest to list data for all distinguished morphospecies here and sums for higher taxa. It is irritating that densities for higher taxa (e.g., Holothuroidea) are given, but they do not include the identified morphospecies within that taxon. Not identified taxa should be clearly indicated, e.g. Holothuroidea indet., and they should sum up with the distinguished morphospecies to total Holothuroidea, etc. I also suggest to include absolute number of observations in addition to densities in this table. This would facilitate the evaluation whether, e.g., differences are based on a substantial number of individuals, or rely on just one or two specimens. The order of taxa in the table is not clear

A: Morphospecies densities (ind/100m) have been added to the table. We opted for densities to correspond to the data used in the manuscript. Absolute numbers are easy to deduce since the length of the transects are given in Table 1. The order of taxa in the table was reorganised

Reviewer 2:

Major comments

R2: 1) The appendix fig1 is a very important figure to place all the observations into context. I would move it from an appendix to a regular figure for the paper or as new panels in existing Fig. 1.

A: We have incorporated it as an extra panel in Figure 1.

R2: 2) The data presentation used to compare nodule transects to seamount transects should be refined. Right now figure 3 portrays averages of densities for fine taxa which, based on the finding of very low overlap between transects, means little - averaging a large number for one transect with low or zero numbers in other transects. Rather the data should be presented at broader taxonomic categories (as in Appendix table 1) with average (and standard deviation) densities and # of morphospecies. This would also follow the language in the results section better. Data on each fine morphospecies (level of taxonomy in Fig3) could be presented an an appendix and by transect.

A: We decided to add morphospecies to Table A1 (also taking into account the comments made by the other reviewer), which thus give information per transect, help to elucidate Fig. 3 and add the desired level of taxonomy. The order of morphospecies along the y-axis of figure 3 was also reorganised to correspond to that of Table A1. Figure 3 was thus withheld because it was considered a key figure to show how different the presence/absence/abundance of the fauna varies between the two ecosystems, but the 3 parts were separated more clearly and different breaks at the X-axis, thus enhancing readability and interpretability. This information was added in the figure caption as well.

R2: 3) Once data is pooled at higher taxa levels, statistical comparisons could be drawn to compare the average # morphospecies and average density between nodule and seamount transects.

A: There were no significant differences for the densities (T-tests for samples with unequal variance) per taxon (taxa pooled and tested: Actiniaria, Alcyonacea, Ceriantharia, Corallimorpharia, Antipatharia, Pennatulacea, Scleractinia, Zoantharia, Bryozoa, Asteroidea, Crinoidea, Echinoidea, Holothuroidea, Ophiuroidea, Porifera, Tunicata, Enteropneusta, Gastropoda. The pooled data were visualised as a histogram with st. dev. and added as an extra figure to this reply to the reviewer. We added the figure to the manuscript as Fig. A1 in the appendix and referred to it in Section 3.2.

The number of morphospecies per higher pooled taxon group proved more difficult, since often we know there are >1 or >2 morphospecies, but not the exact numbers. Using the minimum known number would be and under-estimation, which is why we chose not to test these pooled observations.

This comment was also taking into account for the overlapping morphospecies in Figure 6, for which standard deviation bars were added.

R2: 4) The authors conclude that the ratio of hard/soft habitat may explain some of the faunal trends they observe. Can’t this ratio be determined from the transects? If possible add this metric to help explain faunal communities along or between the transects.

A: We have added information on the amount of hard substrata under the form of 3 categories: (1) Predominant soft substrata (<40% hard substrata), (2) mix or transition (40-60% hard substrata) and (3) predominant hard substrata (>60% hard substrata), annotated over 10m distance units. Very few significant relationships were revealed (only for Mann Borgese ROV15), though backscatter data is currently being analysed to model the geomorphology along the transects in more detail and help reveal more details of fauna/substratum relationships, but it is out of the scope of this article.

The following paragraph was added in section 3.1 (also taking into account the other reviewer's suggestions): L205-2017

"About 57% of all sessile fauna was associated with predominantly hard substrata, followed by 31% on the mixed substrata. For the mobile taxa the pattern was less pronounced with 41 and 42% associated with predominantly hard and mixed soft/hard substrata respectively. The amount of predominantly hard and soft substrata were negatively correlated though, not significantly. This was due to the elevated amount of mixed hard/soft substrata featuring equal amounts 40-60%. Over all seamount transects pooled together, no taxa were significantly correlated with the amount of hard substrata, nor with soft substrata. When looking at the individual transects, no significant correlations were found between taxa and substrata for ROV02 or ROV04 or ROV09, most likely due to the equal distribution of the amount of hard/soft/mix substrata. In this perspective, ROV15 stood out, as it was dominated by predominantly hard substrata (56/%): For this transect, Pennatulacea were significantly negatively correlated with the amount of hard substrata and Zoantharia/Octocorralia were significantly and positively correlated with hard substrata, as were Ophiuroidea, Asteroidea, Crinoidea and Mollusca."

Specific comments

R2: line 82 - Explain why the north or northwestern flanks of the seamounts were chosen for the transects.

A: These flanks were chosen based on the positioning of the vessel and the predominant surface current in order to avoid the umbilical of the ROV to drift/being transported towards the vessel. Predominant currents in the CCZ are South-East oriented, allowing for an ROV positioning "downstream" of the vessel's location while visiting the north-northwestern seamount flanks. This was added in L81-84

R2: line - 97-99 - Provide the range of altitude, speed that were kept constant.

A: Target altitude was <2m above seafloor and travel speed ~0.2m/s, though interrupted by sampling actions, instrument check-ups, exploration, object avoidance (in the case of the uphill seamount transects) etc. This was added in the body of text. L99-102

R2: line 208-209 - this statement appears true when examining the higher taxa pooled data in appendix table 1. however in the cited fig 3, its hard to actually make this comparison because averages at finer taxonomic categories are highly variable due to lack of fine taxa overlap between transects.

A: This is amended by adding the morphospecies information in Table A1 and reorganising figure 3 to correspond to Table A1.

R2: line 267 - Start the sentence with, "Amongst the seamount transects,..."

A: Ok

R2: line 269 - The point of this sentence is not clear as it opposes the trend you find. Clarify.

A: This sentence was to point out that it could rather be depth influencing their similarity than their adjacent location. This part was changed (also taking into account the comments from the other reviewer) L298-303

R2: lines 296-306 - Nice to see a paragraph which lays out what future transecting should look like. The paragraph mentioned that wider depth ranges should be included and the data and literature certainly support that. Might it also be wise to have transects that move along countours so there are many replicate obsrevations at a given depth, instead of conducting uphill transects? Adding a sentence or two addressing across slope vs with slope transecting would be worthwhile.

A: This is a valid observation which was added in L340-342

R2: line 308 - The sentence should be slightly reworded based on the authros findings to "Seamounts were shown to share FEW fauna with surrounding habitats...."

A: Based on the literature, fauna from seamounts tend to occur in neighbouring habitats quite easily, but that is not the case here. We rephrased the sentence to clarify this. L345-347

R2: Line 316 - this topic sentence needs to be improved. Rather than simply reiterating the results section can this paragraph be rewritten and a topic sentence created that summarizes the functional differences between taxa on seamounts vs nodules?. See literature by Rowden etal that look at functional variation of taxa on seamounts and neighboring areas. E.g. Rowden et al 2010 Marine Ecology

A: We added in topic sentences for several paragraphs and cleaned up the remainder of the body of text as to not repeat the results. L353-409

On a side note, functional traits of seamount and nodule field fauna are being investigated in a broader framework, extending beyond the feeding group and including life history, mobility etc.

R2: Table 1 - Add "SM:" before Mann Borgese

A: This was added to the table.

R2: figure 3 - given that there is so little overlap in the morphospecies between each sampled transect. Figure 3 is a bit hard to interpret. Error bars would help. Its great that the taxonomic diversity is presented but this might be better in the appendix.

A: We changed the Y-axis of the different parts of the figure 3 graph to make them more easily interpretable. See reply above. We have uploaded an extra figure linked to this reply to the reviewers that was included in the appendix, pooling the densities into larger taxa and referred to in section 3.2.

R2: Instead, appendix table 1 which presents higher taxa and # morphospecies might be the better data to show in the main paper. Here densities at higher levels can be better compared. Averageing the abundances across the transects seems ill advised given the differences observed between each one.

A: We have added the morphospecies' densities to the appendix table, which also clarifies the taxonomy and figure 3.

R2: Figure 6 - It is not clear what data is being presented here. Are these only taxa present on both seamounts and nodules? Please clarify in the figure caption

A: Yes, indeed. We clarified the caption.

Are seamounts refuge areas for fauna from polymetallic nodule fields?

Daphne Cuvelier1*, Pedro A. Ribeiro1,2*, Sofia P. Ramalho1,3*, Daniel Kersken4,5, Pedro Martinez Arbizu5, Ana Colaço1

1 MARE – Marine and environmental sciences centre/IMAR – Instituto do Mar/Centro OKEANOS – Universidade dos Açores, Rua Prof. Dr. Frederico Machado 4, 9901-862 Horta, Portugal

2 Current address: Department of Biological Sciences and K.G. Jebsen Centre for Deep-Sea Research, University of Bergen, Bergen, Norway.

3 Current address: Departmento de Biologia & CESAM, Universidade de Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

4 Department of Marine Zoology, Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

5 German Centre for Marine Biodiversity Research (DZMB), Senckenberg am Meer, Südstrand 44, 26382 Wilhelmshaven, Germany

* Contributed equally to this work/Corresponding authors: Daphne Cuvelier (daphne.cuvelier@gmail.com), Pedro Ribeiro (Pedro.Ribeiro@uib.no) and Sofia Pinto Ramalho (sofia.pinto.ramalho@gmail.com)

Running title: Seamounts as refuge areas for nodule fauna

Six keywords: megafauna, seamounts, nodule fields, image analysis, deep sea, mining

Abstract

Seamounts are abundant and prominent features on the deep-sea floor and intersperse with the nodule fields of the Clarion-Clipperton Fracture Zone (CCZ). There is a particular interest in characterising the fauna inhabiting seamounts in the CCZ because they are the only other ecosystem in the region to provide hard substrata besides the abundant nodules on the soft sediment abyssal plains. It has been hypothesised that seamounts could provide refuge for organisms during deep-sea mining actions or that they could play a role in the (re-)colonisation of the disturbed nodule fields. This hypothesis is tested by analysing video transects in both ecosystems, assessing megafauna composition and abundance.

Nine video transects (ROV dives) from two different license areas and one Area of Particular Environmental Interest in the eastern CCZ were analysed. Four of these transects were carried out as exploratory dives on four different seamounts in order to gain first insights in megafauna composition. The five other dives were carried out in the neighbouring nodule fields in the same areas. Variation in community composition observed among and along the video transects was high, with little morphospecies overlap on intra-ecosystem transects. Despite the~~se~~ observation~~s~~ of considerable faunal variations within each ecosystem, differences between seamounts and nodule fields prevailed, showing significantly different species associations characterising them, thus questioning their use as a possible refuge area.

1. Introduction

Seamounts are abundant and prominent features on the deep-sea floor (Wessel et al., 2010). They are common in all the world's oceans, occurring in higher abundances around mid-ocean ridges, island-arc convergent areas, and above upwelling mantle plumes (Kitchingman et al., 2007). Seamounts are defined as isolated sub-surface topographic feature, usually of volcanic origin, of significant height above the seafloor (International Seabed Authority (ISA), 2019). They are generally isolated, typically cone shaped undersea mountains rising relatively steeply at least several hundred meters from the deep-sea floor. Seamounts comprise a unique deep-sea environment, characterised by substantially enhanced currents and a fauna that is dominated by suspension feeders, such as corals (Rogers, 2018). They represent hard substrata in the otherwise soft sediment deep sea and can thus be considered habitat islands (Beaulieu, 2001). Given the growing evidence that seamounts differ substantially across a range of spatial scales, the concept of seamounts as a single, relatively well-defined habitat type is outdated (Clark et al., 2012). Depth and substrate type are key elements in determining the composition and distribution of benthic fauna on seamounts, while location is likely the subsequent most important driver of faunal composition and distribution patterns (e.g. Tittensor et al., 2009). Connectivity varies substantially between seamounts, resulting in the presence of taxa with very localised to very wide distributions (Clark et al., 2010).

The Clarion-Clipperton Fracture Zone (CCZ), in the equatorial eastern Pacific Ocean, is most known for its extensive polymetallic nodule fields that will potentially be mined in the future. In this area, nodules represent the most common hard substrate on the soft-sediment abyssal plains, and many organisms rely on them for survival (Vanreusel et al., 2016). Removal of hard substrate through mining actions will impact all these organisms, which were estimated at about 50% of all megafaunal species in the CCZ (Amon et al., 2016). Nodule fields in the CCZ are interspersed by seamounts (Wedding et al., 2013), the only feature offering hard substrata besides the nodules. Based on this feature/characteristic, it has been hypothesised that seamounts could provide refuge for organisms during deep-sea mining activities or that seamounts could play a role in the (re-)colonisation of the disturbed nodule fields. Whether or not this is true may have important implications for management of the impacts of polymetallic nodule mining in the CCZ. However, knowledge on the biodiversity inhabiting seamounts in this region is currently lacking.

The objectives of the current study were twofold: (i) Provide first insights in seamount megafauna within the CCZ, (ii) Compare the benthic fauna inhabiting seamounts and nodule fields in the eastern CCZ. Since this is the first time the seamounts at the eastern CCZ were visited, a separate section is dedicated to describe these first insights.

2. Material and Methods

2.1. Study site and data

During the SO239 ECORESPONSE cruise in 2015 (Martinez Arbizu and Haeckel, 2015), four seamounts were visited for the first time within two different license areas and one area of particular environmental interest (APEI) within the Clarion-Clipperton Fracture zone (CCZ) (Table 1). Nodule fields within the same license areas were visited and sampled as well. Video imagery and faunal samples were collected by a Remotely Operated Vehicle (ROV Kiel 6000 (GEOMAR), equipped with a high definition Kongsberg OE14-500 camera).

Seamount transects were carried out uphill towards the summit resulting in a depth gradient along the transect~~, whilst nodule transects featured rather stable depth ranges~~ (Table 1). The four seamount transects were characterised by different depth ranges and lengths and, due to the vessel's positioning and the predominant South-East surface currents, ~~but~~ were all ~~situated~~ carried out downstream, on the north to north-western flanks of the seamounts (Table 1 and Fig. ~~S~~1). The names of the seamounts used here, Rüppel and Senckenberg (BGR, German License area), Heip (GSR, Belgian License area) and Mann Borgese (APEI3), are the ones agreed upon by the scientist during the ECORESPONSE cruise (Martinez Arbizu and Haeckel, 2015), pending incorporation of these names in the GEBCO gazetteer. The seamounts differed in shape and size with Senckenberg and Heip being a sea-mountain range, while Rüppel and Mann Borgese were more isolated, stand-alone seamounts (Fig. ~~S~~1). Nodule field dives were carried out on relatively flat surfaces (maximum depth range covered during a dive or transect was 30m difference, Table 1) and were referred to by the dive number and license area. The five nodule transects were all located between 4000-5000m depth and the transects differed in length between dives as well (Table 1). Within the same license area distance between different transects was 16 to 60km, while distance between license areas added up to several hundreds of kilometres (minimum ~700kms BGR – GSR, Fig. 1).

Investigated areas were restricted to the eastern part of the CCZ with APEI3 being the most north- and westward bound area. The optical resolution of the camera enabled reliable identification of organisms larger than 3 cm (Martinez Arbizu and Haeckel, 2015). The combination of exploration and opportunistic sampling restricted a systematic image collection. Target ROV travelling altitude was <2m and travelling~~,~~ speed was~0.2m/s ~~and camera zoom~~which, along with the camera zoom, were kept constant whenever possible~~,~~. Due to the explorative nature of the dives, ~~while~~the pan and tilt of the ROV camera were not kept constant.

2.2. Video analysis and statistics

All videos were annotated to the lowest taxonomic level possible. The number of morphospecies, defined as morphologically different organisms within the lowest taxonomic group identified, were assessed. Identifications were double checked with scientists working in the same area as well as taxonomic experts and comprise different taxonomic levels (e.g. Genus, Family). Those ~~ID's~~ identifications restricted to higher taxon groups (Family, Class, etc.) and for which it was impossible to attribute a morphospecies, are referred to as taxa and are likely to morphologically differ between transects. Xenophyophores, living on the soft sediment deep-sea floor, were less prominently present at seamounts than at nodule fields and were not quantified. Fish (Actinopterygii), ~~crustaceans~~ Crustacea (Nematocarcinidae, Aristeidae, Peracarida) and Polychaeta were quantified but left out of the comparing analysis due to their lack of representativity and possible attraction due to ROV lights. The same was done for jellyfish and other doubtful identification~~ID'~~s that could not be confidently assigned to a higher taxonomic group (Table A1). A subset of the nodule field transects form BGR, GSR and APEI3 was presented by Vanreusel et al. (2016), corresponding to 44% of what was studied here and limited organism identification to a higher taxonomic level (Order (e.g. Alcyonacea) or Class (e.g. Ophiuroidea)). In our study, the entire transects (100%) were annotated to morphospecies level, allowing a detailed comparison between seamounts and nodule fields.

Three categories of substratum types were distinguished: (1) Predominant soft substrata (<40% hard substrata), (2) mix or transition (between 40 and 60% hard substrata) and (3) predominant hard substrata (>60% hard substrata), were annotated per 10m distance units based on the video footage and tested for correlations with taxonomic abundances.

ROV transects on the seamounts were carried out as exploratory dives. Sampling strategy both at seamounts and nodule fields combined video and sampling or specimen collection. Due to varying altitude of the ROV and the use of camera pan, tilt and zoom, it was not possible to use surface coverage as a standardisation measure. We used video transect length instead. For the transect length calculation for each dive, we omitted all parts of the video footage in which the ROV was at an altitude of >10m, or sections where the ROV was not visualising the seafloor (e.g. during transiting or inspecting ROV parts or instruments). Visualisation of ancient disturbance tracks were omitted as well, as these fell out of the scope of the article. Faunal densities were calculated as the number of observations per 100m, in order to compensate for time spent collecting samples and differing transect lengths. Statistical testing was carried out in R (R core team, 2018) and the Non-metric multidimensional scaling analysis (NMDS) was based on Bray-Curtis dissimilarity and used the vegan package (Oksanen et al., 2018). The Kendall's coefficient of concordance (W) was calculated to identify significantly associated groups of species, based on correlations and permutations (Legendre, 2005).

3. Results

About 80% of all taxa observed across the two adjacent ecosystems, could be identified to a morphospecies level.~~A total of 252 taxa were observed across the two adjacent ecosystems, of which 207 (or 82%) could be identified to a morphospecies level.~~ At a first view, morphospecies revealed to be quite different between seamounts and nodule fields (Fig. 2). While the number of faunal observations at the seamount transects were within similar ranges (~~33.1-40.7~~34-42 ind./100m), those at the nodule transects featured both highest and lowest values (~~7.59~~6.3-~~89.23~~67.5 ind/100m) (Table 1). The lowest number of faunal observations were done at the two APEI3 nodule transects (ROV13 and 14) and highest at the GSR nodule transect ~~ROV08~~ROV10. What follows is a first description of eastern CCZ seamount megafauna (3.1.) and a detailed comparison with the neighbouring nodule fields (3.2.)

3.1. Insights in CCZ seamount megafauna

The most abundant and diverse (most morphospecies) taxa at the seamount transects comprised Echinodermata (Asteroidea, Crinoidea, Holothuroidea and Ophiuroidea), Anthozoa (Actiniaria, Alcyonacea, Pennatulacea, Scleractinia) and Porifera (Hexactinellida) (Table A1, Fig. 3). Keeping in mind the limitation of the video sampling, differences among the benthic seamount community composition are described here.

The transect at Mann Borgese (APEI3) was characterised by high densities of Antipatharia, more specifically Antipathidae (~~19~~18.~~1~~5~~1~~ ind./100m), and solitary Scleractinia (~~8.11~~7.9 ind./100m) (Table A1, Fig. 3). Antipathidae observations were mostly grouped at the end of the video transect, i.e. at the summit. Densities of both Antipatharia and Scleractinia were much lower on the other seamount transects (<~~≤0.2~~1 ind./100m) with Scleractinia being absent from Heip and Senckenberg transects. Alcyonacea corals were observed on all seamount transects. Isididae were found at Senckenberg and Heip transects, and one individual from Chrysogorgiidae was observed at the latter as well. Varying numbers of Primnoidae were observed on all transects (Table A1). High abundances of Pennatulacea were observed at Senckenberg (3.~~64~~8 ind./100m), representing about ~~26~~28% of sessile fauna annotations for this transect.

Enteropneusta were only observed on Rüppel and Senckenberg transects in the BGR area, represented by two different morphospecies, namely *Yoda* morphospecies (Torquaratoridae) at Rüppel and *Saxipendium* morphospecies (Harrimaniidae) at Senckenberg.

Highest Polychaeta densities were observed at Heip transect in the GSR area, which was mainly due to high densities of free-swimming Acrocirridae (4.2 ind./100m vs. 0. 2~~56 and 0.32~~ ind./100m in BGR ~~and 0.11 ind./100m in APEI3~~area~~). Free-swimming Acrocirridae were observed in very high densities as well (~~Table A1). Aphroditidae polychaetes were only present at the BGR transects (~~3~~ 0.2 ind./100m (corresponding to 3 indivuals along the transect) at Rüppel and 0.04 ind/100m (or 1 individual along the transect)~~1~~ at Senckenberg) (Table A1).

Porifera densities were highest at the Heip transect (~~3~~ 7.5 ind./100m), followed by Rüppel (3.5~~2.72~~ ind./100m), Senckenberg (1.9~~1.92~~ ind./100m) and lastly Mann Borgese (1.8~~0.68~~ ind./100m). Six Porifera families were annotated featuring >7 to >10 morphospecies (Fig. 3, Table A1). Cladorhizidae (two individuals) were only observed on Heip transect, and one *Poliopogon* sp. (Pheronematidae) was observed at Mann Borgese transect. Rossellidae gen. sp. nov. was present on three seamount transects, exception being Mann Borgese.

Overall Echinodermata densities were highest at Senckenberg seamount (~~17~~17~~.64~~ ind./100m), followed by Rüppel (~~12~~10~~.24~~ ind./100m) (Table A1, Fig. 3), both adding up to ~~60~~47% of all image annotations for these transects. The number of morphospecies for all echinoderm taxa (Asteroidea, Echinoidea, Holothuroidea and Crinoidea) was also highest at these 2 seamounts in the BGR area (Fig. 3). For comparison, echinoderms at Heip (~~11.68~~ 10 ind./100m) and Mann Borgese transects (3.~~08~~ 3 ind./100m) were responsible for ~~49~~32% and 8.~~8~~2% of observations respectively. Crinoidea densities were highest at Senckenberg (4.~~32~~2 ind./100m), while Holothuroidea were most abundant at Rüppel (~~5.2~~4.4 ind./100m). The holothuroid families of Elpidiidae and Laetmogonidae were only observed at Senckenberg and Rüppel (BGR). Psychropotid and synallactid holothuroids were observed on all seamounts, represented by different morphospecies. Deimatid holothuroids were not observed on Mann Borgese, but were present in the three other seamount transects, again with different morphospecies and densities. Velatid Asteroidea were only observed at Senckenberg and Rüppel (BGR), while Brisingida and Paxillosida were observed on all four seamounts. Aspidodiadematid echinoids were absent from the Heip transect and urechinid echinoids were absent from the Mann Borgese transect.

A species accumulation curve (Fig. 4a) confirmed the limitations of the restricted and exploratory nature of the sampling as no asymptote was reached. The rarefaction curves (Fig. 4b) showed that the transects with the most faunal observations, which corresponded here to the longer transects, were more diverse. However, at smaller sample sizes curves did not cross, thus maintaining the differences observed at higher sample sizes with the Senckenberg transect (ROV04) as most diverse followed by Rüppel (ROV02) (both BGR). The video transect carried out at Mann Borgese (ROV15, APEI3) was the least diverse.

A comparison of all morphospecies observed along the 4 transects was presented in a Venn diagram (Fig. 5a). Each seamount transect was characterised by a highest number of unique morphospecies, only observed on the transect in question and not elsewhere. Only ~~two~~ three morphospecies were present in all seamount transects, namely Ceriantharia msp. 2, a small red galatheid crab and a foliose sponge. Highest number of overlapping morphospecies (#~~14~~16) was observed between Rüppel and Senckenberg, both in the BGR area (Fig. 5a). Mann Borgese showed the smallest degree of overlap with the other transects (Fig. 5a).

About 57% of all sessile fauna was associated with predominantly hard substrata, followed by 31% on the mixed substrata. For the mobile taxa, the pattern was less pronounced with 41 and 42% associated with predominantly hard and mixed hard/soft substrata respectively. The amount of predominantly hard and soft substrata was negatively correlated, though not significantly. This was due to the equal amounts (40-60%) of mixed hard/soft substrata. Over all seamount transects pooled together, no taxa were significantly correlated with the amount of hard substrata, nor with soft substrata. When looking at the individual transects, no significant correlations were found between taxa and substrata for ROV02 or ROV04 or ROV09, most likely due to the equal distribution of the amount of hard/soft/mix substrata. In this perspective, ROV15 stood out, as it was dominated by predominantly hard substrata (56/%). For this transect, Pennatulacea were significantly negatively correlated with the amount of hard substrata and Zoantharia/Octocorralia were significantly and positively correlated with hard substrata, as were Ophiuroidea, Asteroidea, Crinoidea and Mollusca.

Due to the limited sample size, the representativity of the observed biological patterns remains to be corroborated by a more elaborate sampling strategy.

3.2. Comparison of seamount and nodule field faunal composition and variation

The faunal composition and richness (number of morphospecies in higher taxonomic groups) of the nodule transects can be consulted in Fig. 3 and Table A1, respectively. In concordance with the seamount transect, the species accumulation curve of the nodule transects did not reach an asymptote either (Fig. 4c). The rarefaction curves showed that the relations among transects were less ~~linear~~ straightforward for the nodule transects versus the seamount ones and did cross at smaller sample sizes (<100 individuals, Fig. 4d). ROV13 and ROV14 transects (both APEI3) were the longest in distance travelled (Table 1) but featured less faunal observations. At small sample sizes, the richness at ROV13 and 14 was highest. ROV08 and ROV10 (both GSR) showed parallel curves with ROV08 being more diverse (Fig. 4d).

A venn diagram showing the morphospecies overlap among the nodule transects showed a total of ~~5~~ 6 species re-occurring on all 5 transects (Fig. 5b). These were: Munnopsidae msp. 1 (Isopoda, Crustacea), Actiniaria msp.7 (Cnidaria), Ophiuroidea msp. 6 (Echinodermata), *Holascus* sp. and *Hyalonema* sp. (Hexactinellida, Porifera). There was a high number of unique morphospecies for each transect, though not as high as for the seamount transects (Fig. 5). ROV13 and 14 (both APEI3) showed ~~littlest~~ least overlap with the other transects, which is similar to what was observed at the seamounts.

Observations and quantifications of morphospecies confirmed the high degree of dissimilarity between the two neighbouring ecosystems. Porifera, Ophiuroidea (Echinodermata), Actiniaria and Alcyonacea (Cnidaria) were more abundant at nodule fields (Fig. 3). These taxonomic groups were also most diverse on nodule fields (i.e. highest number of morphospecies), exception being the Alcyonacea which featured more morphospecies on the seamounts (12 to 8 morphospecies for seamounts and nodule fields respectively) (Fig. 3). Of all Porifera, Cladhorizidae were more diverse at nodule fields than at seamounts (7 to 1 morphospecies, respectively).

There were only 21 morphospecies (10%) that were observed both on seamounts and nodule fields (Fig. 6). While this subset of morphospecies occurred in both ecosystems, they did so in very different densities, i.e. very abundant in one ecosystem and very low in abundance in the other~~, ~~: examples are Galatheidae small red msp. (Decapoda, Crustacea), *Synallactes* white msp. (Holothuroidea), Ophiuroidea msp. 5 and 6, Comatulida msp. 1 (Crinoidea), *Hyalonema* sp. and *Hyalostylus* sp. (both Hexactinellida, Porifera) (Fig. 6).

Three Ophiuroidea morphospecies were present at both seamounts and nodule fields (Fig. 2, ~~8~~3 and 6). The majority of the very abundant Ophiuroidea ~~ophiuroids~~ observed at the CCZ seamounts were small and situated on hard substrata (morphospecies 5~~). ~~), ~~While~~ while ~~the most~~ most of the Ophiuroidea at nodule fields (~~abundant morphospecies at nodule fields (~~including morphospecies 6) were~~as mostly~~ observed on the soft sediments~~ of the nodule transects~~. ~~This m~~Morphospecies 6 was only rarely observed on the seamounts (Fig. 3). Another easily recognisable morphospecies was found on Porifera, coral~~s~~ and animal stalks and was more abundant at seamounts than at nodule fields (morphospecies 4) (Fig. 2 and 3).

Crinoidea, Asteroidea (both Echinodermata) and Antipatharia (Cnidaria) were more abundant on the seamounts (Fig. A1). This coincided with a higher diversity for Asteroidea and Antipatharia on the seamounts as well. Crinoidea diversity was similar (5 to 4 morphospecies comparing seamounts to nodule fields). Holothuroidea occurred in similar densities in both ecosystems (Fig. A1, though they were characterised by different morphospecies (Fig. 3). Overall densities of Echinoidea were ~~highest~~ comparable between seamounts and~~at~~ nodule fields, though for the nodule fields this ~~this~~ was mostly due to one very abundant morphospecies, namely Aspidodiadematidae msp 1, which was absent at the seamounts (Fig. 3). Besides this~~ one very abundant morphospecies, which was only present at nodule fields~~, Echinoidea~~echinoids showed higher densities at seamounts and~~ were more diverse at seamounts (11 morphospecies vs. 5 at nodule fields).

There was no morphospecies overlap for Tunicata, Antipatharia, and Actiniaria. Alcyonacea, Ceriantharia, Corallimorphidae and Crinoidea only shared 1 morphospecies between seamounts and nodule fields, namely *Callozostron* cf. *bayeri*, Ceriantharia msp. 2, *Corallimorphus* msp. 2 and Comatulida msp. 1 respectively (Fig. 6).

There were no observations of Enteropneusta, Scleractinia and Zoantharia (Cnidaria), Aphroditidae (Polychaeta) or holothuroid Deimatidae at the nodule fields transects (Table A1, Fig. A1). While Actinopterygii were left out of the analysis, it should be noted that fish observations were more ~~abundant and~~ diverse at the seamounts than on the nodule fields ~~(Table A1)~~.

There was quite some faunal variation observed a~~l~~mong the video transects~~ carried out in the different license areas~~ of, both ~~for~~ seamounts and nodule fields (see fig. 5). The (dis)similarities were analysed by a nMDS analysis, which grouped the 9 different video transects based on their taxonomic composition. Despite the large intra-ecosystem variation, they pooled in two distinct groups separating the nodule fields from the seamounts (Fig. 7a). Within each group, BSR and GSR

Formatted: Font: (Default) +Body (Calibri), 11 pt transects were more similar to one another both for seamounts and nodule fields, whilst APEI3 transects stood out more.

The Kendall's coefficient of concordance (W, Legendre, 2005) corroborated the existence of two significantly different species associations, whose composition corresponded to the fauna characterising the nodule fields (W=0.20, p<0.001, after 999 permutations) and the seamounts (W=0.30, p<0.001, after 999 permutations).

Depth was fitted as a vector on top of the nMDS plot (Fig. 7b) and showed that the discrepancy in faunal composition between the two ecosystems also corresponded to a difference in depth, with the nodule transects all being situated below the 4000m isobath and the seamount transects ranging from 1650 to >3500m (Fig. 7b).

4. Discussion

4.1. Intra-ecosystem faunal variation

Community composition varied markedly within seamounts and nodule fields. The limited sampling (n=9 transects), ~~across~~ at different ~~localities~~ locations and additionally, for the seamounts, different depth ranges~~and for the seamounts different depth gradients~~, precluded any general conclusions on quantifications of biodiversity *per se*. However, taking this into account, it was also the first time seamounts were visited in the area, thus granting first insights in the fauna inhabiting these seamounts and allowing a first comparison with nodule faunal composition.

The two BGR seamount transects were most similar in faunal composition, followed by the Heip seamount transect (GSR). These seamount video transects were characterised by more similar depth ranges, and the two BGR transects were also geographically closest to each other. For seamounts, distance separating them might be a less determining factor than depth since (mega)faunal communities can be very different even between adjacent seamounts (Schlacher et al., 2014; Boschen et al., 2015). Overall, parameters that vary with depth, such as temperature, oxygen concentration, substratum type, food availability, and pressure are considered major drivers of species composition on seamounts (Clark et al., 2010; McClain et al., 2010). The quantification of the amount of hard and soft substrata was not distinctive enough to explain differences observed here. The difference in depth could also explain the higher dissimilarity with Mann Borgese (APEI3) who featured the shallowest transect and summit, which was dominated by Antipatharia.~~The two BGR seamount video transects were geographically closest to each other and were most similar in faunal composition but also in depth. For seamounts, distance separating them might be a less determining factor since adjacent seamounts were shown to be very different in inhabiting fauna (Schlacher et al., 2014; Boschen et al., 2015). Overall, parameters that vary with depth are considered major drivers of species composition on seamounts (Clark et al., 2010; McClain et al., 2010). Depth could be explanatory for the higher degree of similarity of these two BGR seamount transects and, to a lesser extent, the Heip seamount transect (GSR). Similarly, it could explain the higher dissimilarity with Mann Borgese (APEI3) who featured the shallowest transect and summit, which was dominated by Antipatharia.~~ Antipatharians were previously reported to be more dominant towards peaks as compared to mid-slopes at corresponding depths (Genin et al., 1986). Based on their filter-feeding strategy, Porifera (except carnivorous Cladorhizidae), were also thought to benefit from elevated topography (peaks) or exposed substrata in analogy to corals (Genin et al., 1986; Clark et al., 2010), though no such pattern was apparent here. Porifera are notoriously difficult to identify based on imagery. Although the sampled individuals allowed some identifications to genus or species level

(Kersken et al., 2018a and b), identifications remained hard to extrapolate across the different video transects. Generally, as in our study, seamount summits have been more intensively sampled (Stocks, 2009) although the little work done at seamount bases and deep slopes indicated that these areas support distinct assemblages (Baco, 2007).

Among the nodule transects a considerable amount of variation in faunal composition was observed (this study, Vanreusel et al., 2016). The two APEI3 nodule transects (ROV13 and 14) stood out in faunal composition, diversity and in low number of faunal observations.~~Among the nodule transects a considerable amount of variation in faunal composition was observed (this study, Vanreusel et al., 2016). The two APEI3 nodule transects (ROV13 and 14) stood out, both in the low number of faunal observations, faunal composition and diversity.~~ They were also the only two transects situated below the 4500m isobaths. But rather than depth, the nodule coverage ~~was thought to be more of a~~may be considered an important driving factor, since the density of nodule megafauna was shown to vary with nodule size and density/coverage (Stoyanova, 2012; Vanreusel et al., 2016, Simon-Llédo et al., 2019). Here as well, the APEI3 transects were characterised by a high nodule coverage (~40-88%, Vanreusel et al., 2016), whereas the BGR and GSR nodule transects (ROV3 and ROV 8 + 10, respectively) had a nodule coverage <30% and were also more similar in faunal composition (Vanreusel et al., 2016). Other factors that could be at play are ~~T~~the more oligotrophic surface waters of the northern CCZ ~~were proposed to be~~which could be the cause of the overall lower faunal densities at APEI3 nodule fields (Vanreusel et al., 2016). Volz et al. (2018) corroborated this, with the location of the APEI3 site in the proximity of the carbon-starved North Pacific gyre being characterised by a reduced POC-flux quantified to being 22-46% lower than the GSR and BGR areas respectively.

The species accumulation curves showed that no asymptote was reached ~~not~~ neither at seamounts, nor at nodule fields. Consequently, longer transect lengths might be necessary to representatively quantify and assess megafauna density and diversity (Simon-Lledó et al., 2019). In addition, for a first in-depth description and assessment of seamount fauna composition, one video transect is insufficient to describe the diversity and shifts in faunal assemblages of the surveyed seamounts. Rather, an ampler imaging strategy should be developed, with a minimum transect length exceeding 1000ms (Simon-Llédo et al., 2019) and replicate transects carried out on different faces of the seamount, on slopes with varying degree of exposure to currents and different substrate types. Wider depth ranges should be taken into account as well. Alternatively, across slope transects, following depth contours should be considered as these could provide observation replicates for a given depth. Despite its limitations, this study grants first insights in the seamount inhabiting megafauna of the eastern CCZ and an important first comparison with nodule fauna.

4.2. Faunal (dis)similarities between seamounts and nodule fields

In other areas, seamounts were shown to share fauna with surrounding habitats (Clark et al., 2010) and could thus potentially serve as source populations for neighbouring environments (McClain et al., 2009)~~Seamounts were shown to share fauna with surrounding habitats (Clark et al., 2010) and potentially serve as source populations for neighbouring environments (McClain et al., 2009)~~. While generally few species seemed restricted to seamounts only (Clark et al., 2010), in this study, morphospecies revealed to be quite different between seamounts and nodule fields with little overlap between both. Despite the high degree of variation observed among all the video transects, these grouped into two distinctly separate clusters, separating nodule from seamount transects. The few overlapping morphospecies did occur in different densities in each ecosystem, implying a different role or importance in the ecological community and its functioning.

Overall, nodule fields showed higher faunal densities than seamounts. Shifts in density patterns between nodule fields and seamounts were more evident in a number of taxa, where the variety of morphospecies and feeding strategy within each group was likely to be at play. An example of this are the Echinodermata, which include Asteroidea (predators and filter feeders (Brisingida)), Crinoidea (filter feeders), Echinoidea (deposit feeders), Holothuroidea (deposit feeders) and Ophiuroidea (omnivores).

~~-Taxa contributing to the differences between the two ecosystems are discussed here. Ophiuroids were more abundant on the nodule fields. Asteroids~~ Asteroidea were more abundant on seamounts and both Echinoidea and Asteroidea were more diverse in this ecosystem as well.~~and echinoids (with exception of one very abundant morphospecies at the nodule fields) were both more abundant and diverse on the seamounts~~ Ophiuroidea were most abundant on the nodule fields (ratio 7 to 1 when compared to seamounts).~~. Both ophiuroid and echinoids were shown to be present in both nodule-rich and -free areas, though their densities decreased more than 50% comparing the former to the latter (Vanreusel et al., 2016). Despite the abundance of hard substrata at seamounts, this was true for the ophiuroid densities observed here (>50% decrease form nodule fields to seamounts), but not for the echinoids, where differences in overall density between ecosystems were less pronounced. Ophiuroids did not show high levels of richness or endemism on seamounts (O'Hara, 2007).~~ Same ophiuroid morphospecies were present at seamounts and nodule fields but in very different abundances and they were observed on different substrata types~~showed preference for different substrata (at nodule fields on soft sediment (morphospecies 6), at seamounts on hard substrata (morphospecies 5))~~, which ~~appeared to correspond to~~indicates different lifestyles, feeding behaviour and corresponding dietary specialisations (Persons and Gage, 1984). Previously it was already demonstrated that Ophiuroidea did not show high levels of richness or endemism on seamounts (O'Hara, 2007). At nodule fields Ophiuroidea~~Ophiuroids~~ were often observed in association with xenophyophores ~~at nodule fields~~ (Amon et al., 2016, this study) and a similar observation was done at east Pacific seamounts off Mexico (Levin et al., 1986), though no such associations were observed on the seamounts studied here.

Holothuroidea densities were thought to possibly decrease when less soft sediment was available since they feed mainly on the upper layers of the soft-bottom sediment (Bluhm and Gebruk, 1999). No significant link was established between holothuroid densities and the amount of hard substrata in this study, but their community composition varied distinctly between nodule fields and seamounts with more families being observed at the latter. Additionally, at the seamounts, many holothurians were observed on top of rocks, possibly reflecting different feeding strategies and explaining the observations of different morphospecies. Geographical variations, different bottom topography, differences in nodule coverages and sizes and/or an uneven distribution of holothurians on the sea floor were thought to play a role in holothuroid community composition (Bluhm and Gebruk, 1999). On the other hand, variability in deep-sea holothuroid abundance was proposed to depend primarily on depth and distance from continents (see Billet, 1991 for a review).

~~Holothuroid composition varied distinctly between nodule fields and seamounts with more families being observed at the latter. Many holothurians feed on the upper layers of the soft-bottom~~

~~sediment (Bluhm and Gebruk, 1999), suggesting that their numbers would decrease when there is less sediment available. However, at the seamounts, many holothurians were observed on top of rocks, possibly reflecting different feeding strategies and explaining the observations of different morphospecies. Geographical variations, different bottom topography, differences in nodule coverages and sizes and/or an uneven distribution of holothurians on the sea floor were thought to play a role in holothuroid community composition (Bluhm and Gebruk, 1999). On the other hand, variability in deep-sea holothuroid abundance was proposed to depend primarily on depth and distance from continents (see Billet, 1991 for a review).~~

Stalked organisms, such as Crinoidea (Echinodermata) and Hexactinellida (except for Amphidiscophora, Porifera) rely on hard substrata for their attachment and are considered being among the most vulnerable organisms when mining is concerned. Crinoidea were ~~proportionally~~ more abundant on seamounts, possibly because hard substrata were less limiting than in the nodule fields. Porifera ~~proportions~~ densities (stalked and non-stalked) varied among all analysed transects, revealing no particular trends in abundance. However, the species composition of deep-sea glass sponge communities from seamounts and polymetallic nodule fields was distinctly different. Polymetallic nodule field communities were ~~pre~~dominated by widely-distributed genera such as *Caulophacus* and *Hyalonema*, whereas seamount communities seemed to have a rather unique composition represented by genera like *Saccocalyx*. ~~Stalked organisms are considered being among the most vulnerable organisms when mining is concerned.~~

Corals were generally considered to be more abundant on seamounts than adjacent areas, due to their ability to feed on a variety of planktonic or detritus sources suspended in the water column (Rowden et al., 2010). In this study, the Alcyonacea densities were lower on the seamounts than on the nodule transects. The majority of Alcyonacea morphospecies of the seamounts did not occur on the nodule fields and vice versa, with exception of *Callozostron* cf. *bayeri* which was also present at the nodule fields but in very low densities (1/10 of those observed at seamounts). The Antipatharia were most abundant at the Mann Borgese seamount (APEI3) compared to all other transects. The depth difference of more than 3000m between this particular seamount and the nodule fields could explain the abundance in Antipatharia which were shown to be more abundant at lower depths (Genin et al., 1986). Additional presence of Pennatulacea at seamounts, a taxon that was virtually absent from the nodule field transects and that appeared more linked to predominant soft substrata at seamounts, resulted in completely distinct coral communities for each ecosystem.

~~While alcyonacean and antipatharian corals were virtually absent from nodule-free areas (Vanreusel et al., 2016), this was not the case for the seamounts (although Alcyonacea densities were lower than on nodules). Depth difference added up to more than 3000m between Mann Borgese seamount (APEI3) and the nodule transects, which could explain the difference in Antipataria which were more abundant at lower depths (Genin et al., 1986). The antipatharian and alcyonacean morphospecies that were abundant on the seamounts did not occur on the nodule fields and vice versa, with exception of *Callozostron* cf. *bayeri* which was present at the nodule fields but in very low densities (1/10 of those observed at seamounts). Additional presence of Pennatulacea, which were virtually absent from the nodule field transects, resulted in a completely distinct coral community for both ecosystems.~~

Actiniaria were ~~more abundant on nodule fields. It was~~ denominated the second most common group at CCZ nodule fields, after the xenophyophores ~~(Kamenskaya et al., 2015).~~ (Kamenskaya et al., 2015) and, in our study, were also more abundant on nodule fields than on seamounts. Depending on the species and feeding strategy, the ratio hard/soft substrata and their preference for either one could play a role. Since morphospecies were distinct between seamounts and nodule fields, their role in the respective communities are likely to differ as well. Combinations of deposit feeding and predatory behaviour in Actiniaria have been observed, as well as burrowing activity, preference for attachment to hard substrata and exposure to currents (Durden et al., 2015a; Lampitt and Paterson, 1987; Riemann-Zürneck, 1998), all factors that could influence the differences in morphospecies observed.~~.~~

Some taxa were only observed on the seamounts in this study, while they occurred~~were also known to occur~~ on nodule fields elsewhere, be it in low densities. For instance, Enteropneusta, which in this study were found only on seamounts, were observed previously at CCZ nodule fields though observations were rather rare (Tilot, 2006). They appeared more abundant at the nodule fields of the Deep Peru Basin (DISCOL area), though a wide range in abundances was displayed there as well (Bluhm, 2001). The exception were the Scleractinia, which were ~~absent at nodule fields but~~ quite common on seamounts, as also reported in other studies (e.g.~~ this study,~~ Baco, 2007, Rowden et al., 2010), but~~.~~ distinctly absent at nodule fields.~~Contrastingly~~, ~~Enteropneusta were observed previously at CCZ nodule fields though observations were rather rare (Tilot, 2006). They appeared more abundant at the nodule fields of the Deep Peru Basin (DISCOL area), though a wide range in abundances was displayed there as well (Bluhm, 2001).~~

Explanation for the discrepancies ~~observed here~~ in faunal composition and the low degree of morphospecies overlap between seamount and nodule fields, as observed here, can be multiple. For one, nodules may not be considered a plain hard substratum, with their metal composition, microbial colonisation and the nodule/sediment interface influencing the epi-and associated megafaunal composition. The possibility of a specific deep-sea faunal community that tolerates or benefits from manganese substrata has been previously proposed (Mullineaux, 1988). The comparison between seamounts and nodule fields as two neighbouring hard-substrata ecosystems also entailed a comparison between depth gradients and possible thresholds (>4000m for nodule fields and 1500>x <4000m for seamounts). Related to this is the steepness of the seamount slope and its current exposure playing a role in the faunal colonisation (Genin et al., 1986; Rappaport et al., 1997). Other studies showed that habitat heterogeneity increased megafaunal diversity at seamounts (Raymore, 1982) and elsewhere, such as abyssal plains (Lapointe and Bourget, 1999; Durden et al., 2015b, Leitner et al., 2017, Simon-Llédo et al., 2019). Within this perspective the smaller-scale substratum heterogeneity transcending the ratio hard/soft substrata or amount of hard substrata ~~available~~ could play a role as well.

5. Conclusions

Based on our current knowledge; seamounts appear inadequate as refuge areas to help maintain nodule biodiversity. In order to conclusively exclude seamount habitats as a refuge for nodule fauna, a more comprehensive sampling should be carried out. The sampling strategy wielded in this study lacked replicates, uniformity and was limited in sample size. Seamount bases should be taken into consideration as well as they can be characterised by distinctly different assemblages than the summits and they ~~occur at a~~feature depth ranges more similar to nodule fields.

While their role as refuge area for nodule field fauna is currently debatable, the possible uniqueness of the seamount habitat and its inhabiting fauna implies that seamounts need to be included in management plans for the conservation of the biodiversity and ecosystems of the CCZ.

Author Contributions

DC, PAR, SPR, DK analysed the images. DC analysed the data. PMA, PAR, AC conceptualised and carried out the sampling. All authors contributed to the redaction of the manuscript.

Data Availability

Data sets are made available through OSIS-Kiel data portal, BIIGLE and PANGAEA.

Competing interest

The authors declare that they have no conflict of interest

Acknowledgments

We thank the crew of SO239 and GEOMAR for their support in acquiring the images used in this article. The EcoResponse cruise with RV Sonne was financed by the German Ministry of Education and Science BMBF as a contribution to the European project JPI-Oceans “Ecological Aspects of Deep-Sea Mining”. This study had the support of PO AÇORES 2020 project Acores-01-0145-Feder-000054_RECO and of Fundação para a Ciência e Tecnologia (FCT), through the strategic projects UID/MAR/04292/2013 granted to MARE. The authors acknowledge funding from the JPI Oceans—Ecological Aspects of Deep Sea Mining project by Fundação para a Ciência e Tecnologia de Portugal (Mining2/0005/2017) and the European Union Seventh Framework Programme (FP7/2007–2013) under the MIDAS project, grant agreement n° 603418. DC is supported by a post-doctoral scholarship (SFRH/BPD/110278/2015) from FCT. PAR was funded by the Portuguese Foundation for Science and Technology (FCT), through a postdoctoral grant (ref. SFRH/BPD/69232/2010) funded through QREN and COMPETE. SPR is supported by FCT in the scope of the “CEEC Individual 2017” contract (CEECIND/00758/2017) and CESAM funds (UID/AMB/50017/2019) through FCT/MCTES. AC is supported by Program Investigador (IF/00029/2014/CP1230/CT0002) from FCT. PMA acknowledges funding from BMBF contract 03 F0707E. Pictures were provided by GEOMAR (Kiel).

References

Amon, D. J., Ziegler, A. F., Dahlgren, T. G., Glover, A. G., Goineau, A., Gooday, A. J., Wiklund, H., and Smith, C. R.: Insights into the abundance and diversity of abyssal megafauna in a polymetallic-nodule region in the eastern Clarion-Clipperton Zone. Sci. Rep., 6(1), 30492. https://doi.org/10.1038/srep30492, 2016

Baco, A.R. : Exploration for deep-sea corals on North Pacific seamounts and islands. Oceanography 20:109– 17, 2007

Beaulieu, S. E.: Colonization of habitat islands in the deep sea: Recruitment to glass sponge stalks. Deep-Sea Res Pt I, 48(4), 1121–1137. https://doi.org/10.1016/S0967-0637(00)00055-8, 2001

Bluhm, H.: Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor. Deep-Sea Res Pt II, 48(17–18), 3841–3868. https://doi.org/10.1016/S0967-0645(01)00070-4, 2001

Bluhm, H., and Gebruk, A. V.: Holothuroidea (Echinodermata) of the Peru basin - ecological and taxonomic remarks based on underwater images. Mar. Ecol., 20(2), 167–195. https://doi.org/10.1046/j.1439-0485.1999.00072.x, 1999

Boschen, R. E., Rowden, A. A., Clark, M. R., Barton, S., Pallentin, A., and Gardner, J.:Megabenthic assemblage structure on three New Zealand seamounts: implications for seafloor massive sulfide mining. Mar. Ecol. Prog. Ser., 523, 1–14. https://doi.org/10.3354/meps11239, 2015

Clark, M. R., Rowden, A. A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K. I., Rogers,A.D., O'Hara, T.D., White, M., Shank, T.M., and Hall-Spencer, J. M.: The Ecology of Seamounts: Structure, Function, and Human Impacts. Annu. Rev. Mar. Sci., 2(1), 253–278. https://doi.org/10.1146/annurev-marine-120308-081109, 2010

Clark, M.R., Schlacher, T.A., Rowden, A.A., K. Stocks, K.I., and Consalvey, M.: Science priorities for seamounts: research links to conservation and management. PLoS One 7(1): e29232., 2012

Durden, J. M., Bett, B. J., and Ruhl, H. A.: The hemisessile lifestyle and feeding strategies of *Iosactis vagabunda* (Actiniaria, Iosactiidae), a dominant megafaunal species of the Porcupine Abyssal Plain. Deep-Sea Res Pt I 102, 72–77. https://doi.org/10.1016/j.dsr.2015.04.010, 2015a

Durden, J. M., Bett, B. J., Jones, D. O. B., Huvenne, V. A. I., and Ruhl, H. A.: Abyssal hills - hidden source of increased habitat heterogeneity, benthic megafaunal biomass and diversity in the deep sea. Prog. Oceanogr., 137, 209–218, https://doi.org/10.1016/j.pocean.2015.06.006, 2015b

Genin, A., Dayton, P. K., Lonsdale, P., and Spiess, F. N.: Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. *Nature*, *322*, 59–61, 1986

International Seabed Authority (ISA): https://www.isa.org.jm/scientific-glossary/, last access: 29 October 2019

Kamenskaya, O. E., Gooday, A. J., Tendal, O. S., and Melnik, V. F.: Xenophyophores (Protista, Foraminifera) from the Clarion-Clipperton Fracture Zone with description of three new species. Mar. Biodivers., 45(3), 581–593. https://doi.org/10.1007/s12526-015-0330-z, 2015

Kersken, D., Janussen, D., and Martinez Arbizu, P.: Deep-sea glass sponges (Hexactinellida) from polymetallic nodule fields in the Clarion-Clipperton Fracture Zone (CCFZ), northeastern Pacific: Part I – Amphidiscophora. Mar. Biodivers. 48, 545–573.https://doi.org/10.1007/s10750-017-3498-3, 2018a

Kersken, D., Janussen, D., and Martinez Arbizu, P.: Deep-sea glass sponges (Hexactinellida) from polymetallic nodule fields in the Clarion-Clipperton Fracture Zone (CCFZ), northeastern Pacific: Part II—Hexasterophora. Mar. Biodivers. https://doi.org/https://doi.org/10.1007/s12526-018-0880-y, 2018b

Lampitt, R. S., and Paterson, G. L. J.: The feeding behaviour of an abyssal sea anemone from in situ time lapse photographs and trawl samples. Oceanol. Acta, 10(4), 455–461, 1987

Lapointe, L., and Bourget, E.: Influence of substratum heterogeneity scales and complexity on a temperate epibenthic marine community. Mar. Ecol. Prog. Ser., 189(2), 159–170. https://doi.org/10.3354/meps189159, 1999

Leitner, A. B., Neuheimer, A. B., Donlon, E., Smith, C. R., and Drazen, J. C.: Environmental and bathymetric influences on abyssal bait-attending communities of the Clarion Clipperton Zone. Deep-Sea Res Pt I, 125, 65–80. https://doi.org/10.1016/j.dsr.2017.04.017, 2017

Levin, L., DeMaster, D., McCann, L., and Thomas, C.: Effects of giant protozoans (class: Xenophyophorea) on deep-seamount benthos. Mar. Ecol. Prog. Ser., 29, 99–104. https://doi.org/10.3354/meps029099, 1986

McClain, C. R., Lundsten, L., Barry, J., and DeVogelaere, A.: Assemblage structure, but not diversity or density, change with depth on a northeast Pacific seamount. Mar. Ecol., 31, 14–25. https://doi.org/10.1111/j.1439-0485.2010.00367.x, 2010

McClain, C. R., Lundsten, L., Ream, M., Barry, J., and DeVogelaere, A.: Endemicity, biogeography, composition, and community structure on a Northeast Pacific seamount. PLoS ONE, 4(1). https://doi.org/10.1371/journal.pone.0004141, 2009

Mullineaux, L.S.: The role of settlement in structuring a hard-substratum community in the deep sea. J. Exp. Mar. Biol. Ecol. 120, 241-261, 1988

O'Hara, T. D.: Seamounts: Centres of endemism or species richness for ophiuroids? Glob. Ecol. Biogeogr., 16(6), 720–732. https://doi.org/10.1111/j.1466-8238.2007.00329.x, 2007

Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos. P., Stevens, M.H.H., Szoecs, E., and Wagner, H.: vegan: Community Ecology Package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan, 2018

Rappaport, Y., Naar, D. F., Barton, C. C., Liu, Z. J., and Hey, R. N.: Morphology and distribution of seamounts surrounding Easter Island. J. Geophys. Res., 102(B11), 24713. https://doi.org/10.1029/97JB01634, 1997

R Core Team: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/, 2018

Riemann-Zürneck, K.: How sessile are sea anemones? A review of free-living forms in the Actiniaria (Cnidaria: Anthozoa). Mar. Ecol., 19(4), 247–261. https://doi.org/10.1111/j.1439-0485.1998.tb00466.x, 1998

Rogers, A.D.: The Biology of Seamounts: 25 years on. Adv. Mar. Biol. 79, 137-224, https://doi.org/10.1016/bs.amb.2018.06.001, 2018

Rowden, A.A., Schlacher, T.A., Williams, A., Clark, M.R., Stewart, R., Althaus, F., Bowden, D.A., Consalvey, M., Robinson, W. and Dowdney, J.: A test of the seamount oasis hypothesis: seamounts support higher epibenthic megafaunal biomass than adjacent slopes. Mar Ecol, 31, 95-106, https://doi.org/10.1111/j.1439-0485.2010.00369.x, 2010

Simon-lledó, E., Bett, B. J., Huvenne, V. A. I., Schoening, T., Benoist, N. M. A., Je, R. M., Durden, J.M, and Jones, D. O. B.: Megafaunal variation in the abyssal landscape of the Clarion Clipperton Zone, Progr. Oceanogr. 170, 119–133. https://doi.org/10.1016/j.pocean.2018.11.003, 2019

Tilot, V., Ormond, R., Moreno Navas, J., and Catalá, T. S.: The Benthic Megafaunal Assemblages of the CCZ (Eastern Pacific) and an Approach to their Management in the Face of Threatened Anthropogenic Impacts. Front Mar Sci., 5, 1–25. https://doi.org/10.3389/fmars.2018.00007, 2018

Vanreusel, A., Hilario, A., Ribeiro, P. A., Menot, L., and Arbizu, P. M.: Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna. Sci. Rep., 6(1), 26808. https://doi.org/10.1038/srep26808, 2016

Wedding, L. M., Friedlander, A. M., Kittinger, J. N., Watling, L., Gaines, S. D., Bennett, M., Hardy, S.M., and Smith, C.R.: From principles to practice : a spatial approach to systematic conservation planning in the deep sea. Proc. R. Soc. B 280: 20131684. http://dx.doi.org/10.1098/rspb.2013.1684, 2013

Wessel, P., Sandwell, D., and Kim, S.-S.: The Global Seamount Census. Oceanography 23(1), 24–33, https://doi.org/10.5670/oceanog.2010.60, 2010

Tables

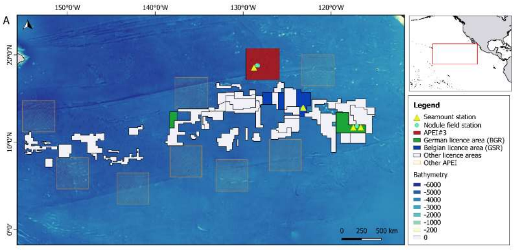
Table 1: Overview table on details of imagery transects analysed in the Clarion-Clipperton license areas. Video duration includes time spent sampling. Number of observations include undetermined organisms. Transect lengths do not include parts visualising ancient disturbance tracks or parts when the seafloor was not visualised or visible.

Station/Dive	**License Area**	**Seamount (SM) or Nodule field (NF)**	**Depth (m)**	**Video duration**	**Transect length**	**# obs/ dive**	**# obs /100m**
SO239_29_ROV02	BGR	SM: Rüppell	3000-2500	7h47	1250m	~~414~~429	~~33.1~~34.3
S0239_41_ROV03	BGR	NF	4080-4110	6h32	1590m	~~1023~~932	~~64.3~~58.6
SO239_54_ROV04	BGR	SM: Senckenberg	3350-2850	8h45	2500m	~~853~~890	~~34.1~~35.6
S0239_131_ROV08	GSR	NF	4470-4480	7h35	710m	~~486~~445	~~68.5~~62.8

Formatted: Font: 11 pt

SO239_135_ROV09	GSR	SM: Heip	3900-3550	7h35	1000m	~~365~~359	~~36.5~~35.9
S0239_141_ROV10	GSR	NF	4455-4480	7h35	520m	~~464~~351	~~89.2~~67.5
S0239_189_ROV13	APEI 3	NF	4890-4930	9h01	1790m	~~136~~113	~~7.6~~6.3
S0239_200_ROV14	APEI 3	NF	4650-4670	9h19	1490m	~~184~~179	~~12.2~~12.0
SO239_212_ROV15	APEI 3	SM: Mann Borgese	1850-1650	6h25	900m	~~366~~378	~~40.7~~42.0

Figures



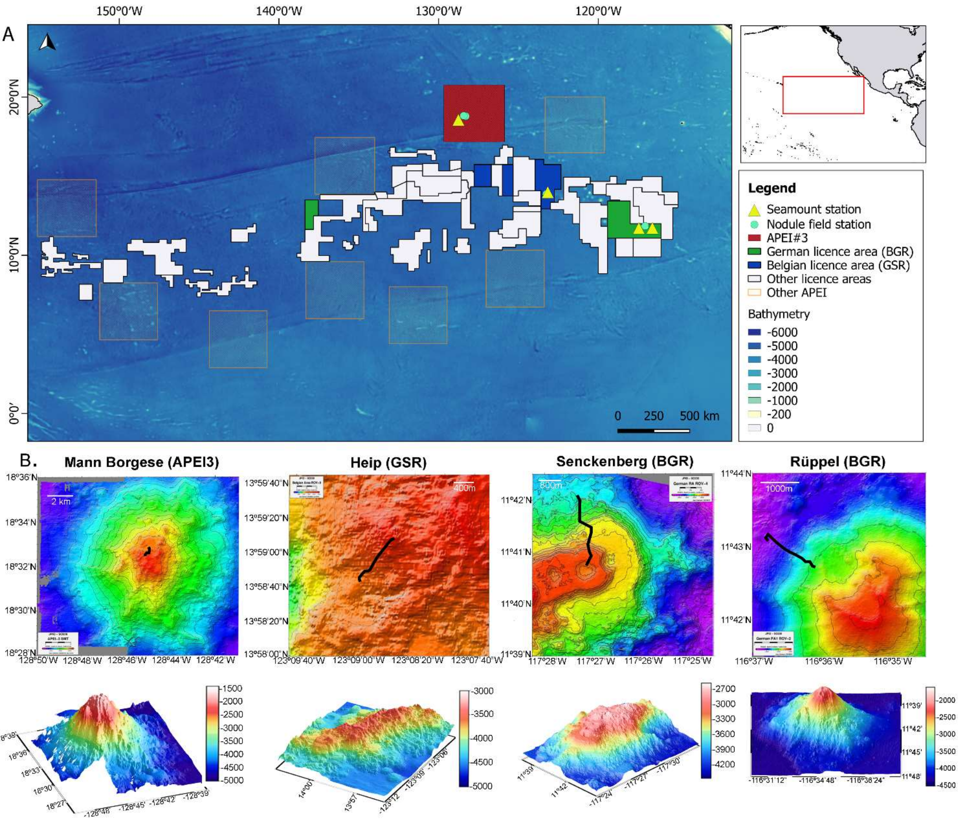


Fig. 1. (A). Location of the Clarion-Clipperton Fracture zone in the equatorial eastern Pacific Ocean featuring the contract areas from the International Seabed Authority (ISA) and the positions of the sampled areas (seamounts and nodule fields). Information on transect length and depth gradients can be found in Table 1. (B). Location of the seamount transects carried out towards the summit on the north –north-western flank and seamount profiles. Rüppel (BGR, ROV02) and Mann Borgese (APEI3, ROV15) are single seamounts, while Senckenberg (BGR, ROV04) and Heip (GSR, ROV09) are

sea-mountain ranges.

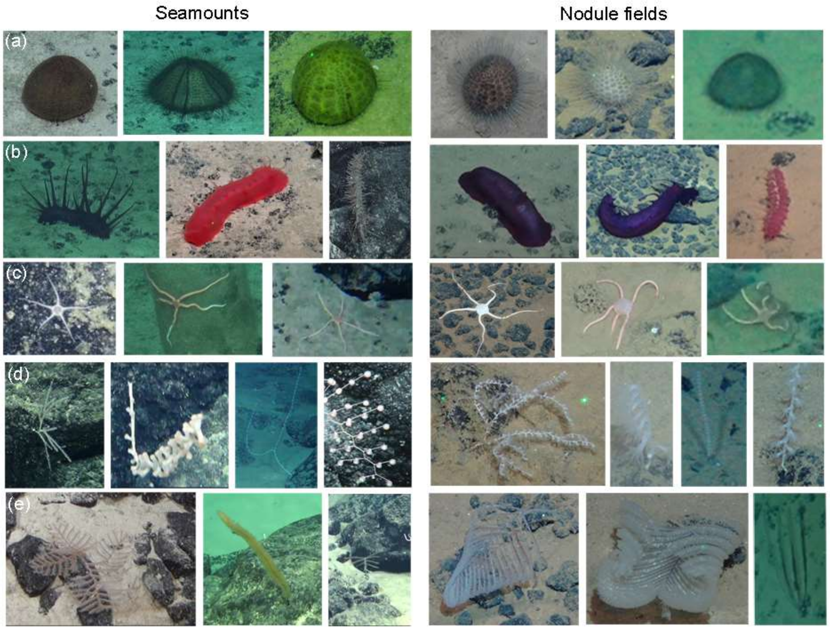


Fig. 2. Some examples of different morphospecies at seamounts and nodule fields in the CCZ. Selected taxa were (a) Echinoidea (from left to right, Urechinidae msp 4 (URC_019), Urechinidae msp 2 (URC_013), Urechinidae msp 3 (URC_009), Urechinidae msp. A (URC_020), Urechinidae msp. B (URC_021), Urechinidae msp. C (URC_005), (b) Holothuroidea (from left to right, Psychropotidae msp 1 (HOL_088~~-~~), *Benthodytes* red msp. (HOL_101), Deimatidae - irregular papillae msp. (HOL_070), *Psychropotes verrucosa* (HOL_045), Laetmogonidae (HOL_030), *Synallactes* msp 2 pink (HOL_008)(c) Ophiuroidea (from left to right, Ophiuroidea msp. 5 (OPH_003), Ophiuroidea msp. 4 (OPH_005), Ophiuroidea msp. 6 (OPH_006), Ophiuroidea msp. 6 (OPH_006), Ophiuroidea (OPH_012), Ophiuroidea msp. 4 (OPH_005)), (d) Alcyonacea (from left to right, *Callozostron* cf. *bayeri* (ALC_009), *Bathygorgia* aff. *profunda* 2 (ALC_005), *Keratoisis* aff. *flexibilis* msp 2 (ALC_029), *Chrysogorgia* cf. *pinnata*~~-~~, *Abyssoprimnoa* cf. *gemina* (ALC_008), *Bathygorgia* aff. *profunda* 1, *Calyptrophora* cf. *persephone* (ALC_007),~~-~~ *Bathygorgia* aff. *abyssicola* 1 (ALC_003), (e) Antipatharia (*Umbellapathes* aff. *helioanthes* (ANT_018), cf. *Parantipathes* morphotype 1 (ANT_017), *Bathypates* cf. *alternata* msp 1 (ANT_010), *Bathypathes* cf. *alternata* (ANT_006), *Abyssopathes* cf. lyra ~~-~~(ANT_022), *Bathypathes* sp. (ANT_003)). Codes refer to an ongoing collaboration in creating one species catalogue for the CCZ and align all morphospecies of different research groups. Copyright: SO239, ROV Kiel 6000, GEOMAR Helmholtz Centre for Ocean Research Kiel

Formatted: Font: (Default) +Body (Calibri), 11 pt

Formatted: Font: (Default) +Body (Calibri), 11 pt, Not Highlight

Formatted: Font: Italic

Formatted: Font: (Default) +Body (Calibri), 11 pt, Italic

Formatted: Font: Italic

Formatted: Font: (Default) +Body (Calibri), 11 pt

Formatted: Font: (Default) +Body (Calibri), 11 pt, Not Bold

Formatted: Font: (Default) +Body (Calibri), 11 pt

Formatted: Font: (Default) +Body (Calibri), 11 pt, Not Bold, Italic

Formatted: Font: (Default) +Body (Calibri), 11 pt, Not Bold, Italic

Formatted: Font: (Default) +Body (Calibri), 11 pt

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: (Default) +Body (Calibri), 11 pt, Italic

Formatted: Font: (Default) +Body (Calibri), 11 pt

Formatted: Font: (Default) +Body (Calibri), 11 pt, Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: (Default) +Body (Calibri), 11 pt, Italic, English (United Kingdom)

Formatted: English (United Kingdom)

Formatted: English (United Kingdom)

Formatted: Font: (Default) +Body (Calibri), 11 pt, Italic, English (United Kingdom)

Formatted: English (United Kingdom)

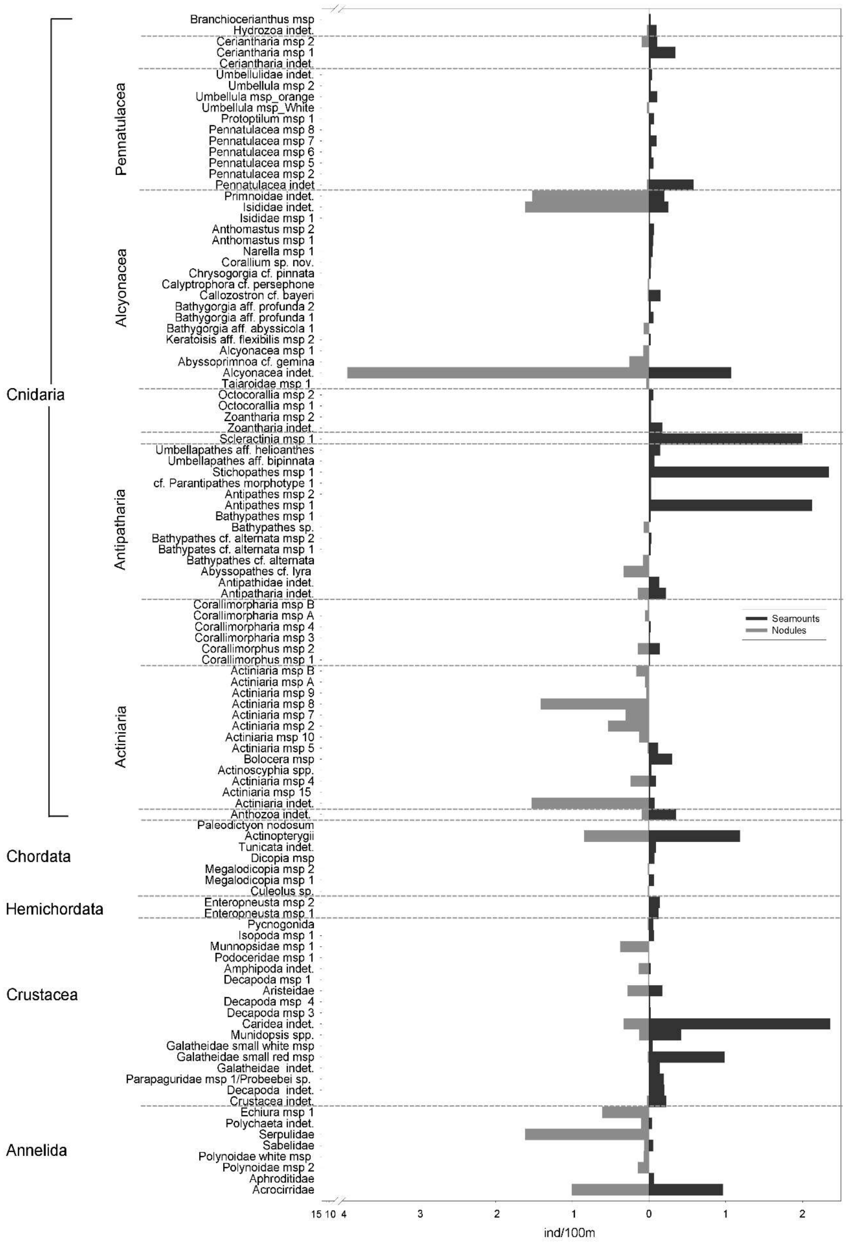
Formatted: Font: (Default) +Body (Calibri), 11 pt, English (United Kingdom)

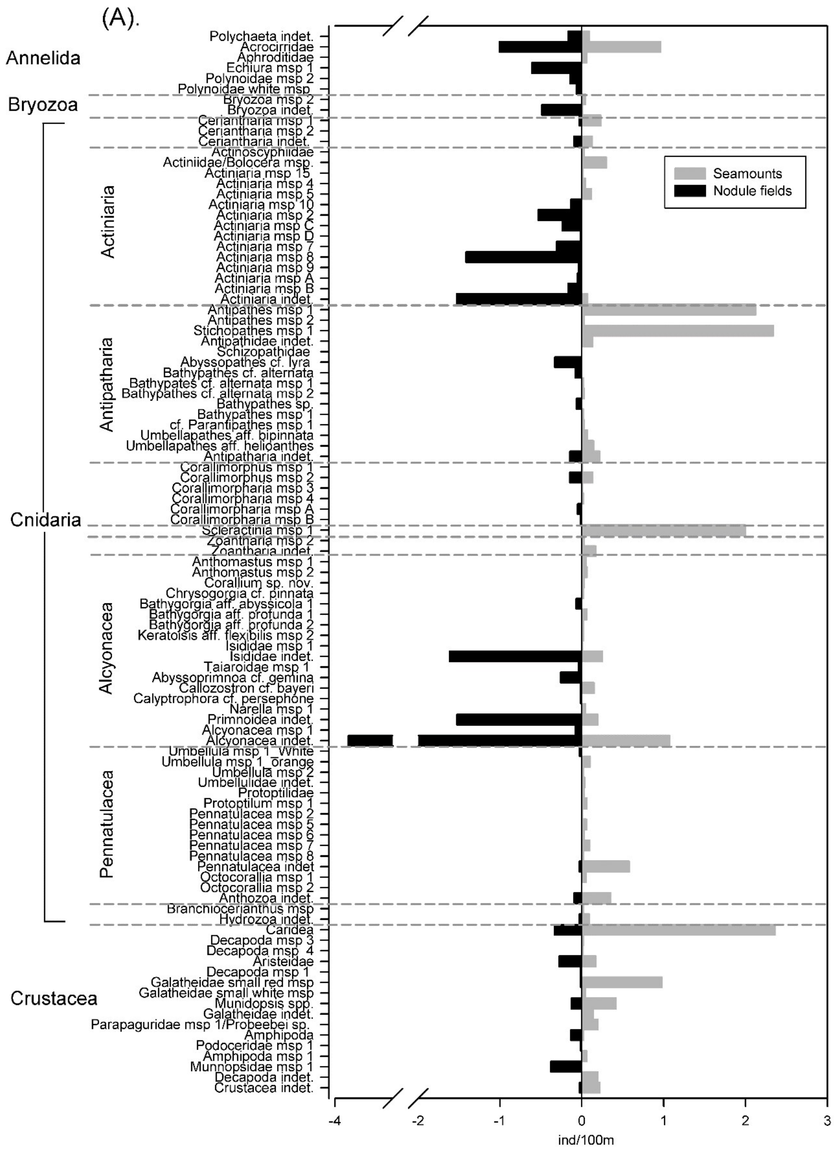
Formatted: Font: Italic

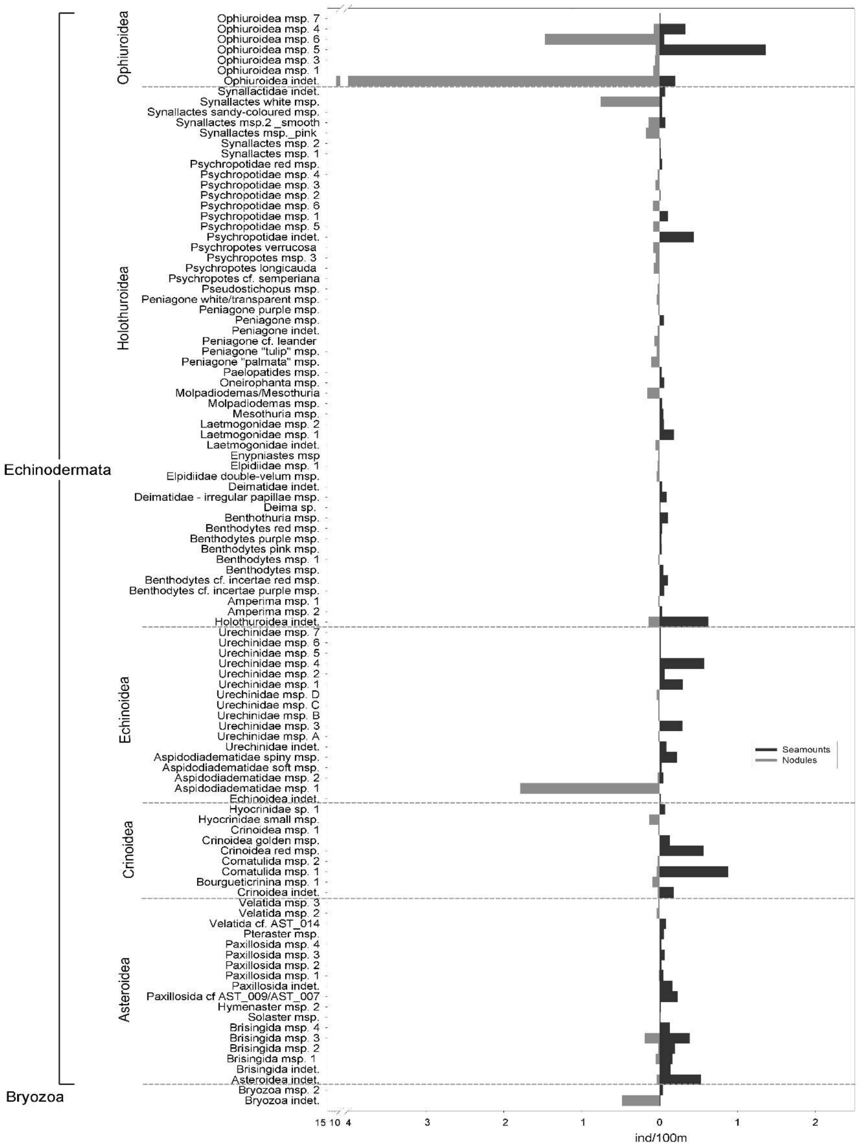
Formatted: Font: Italic

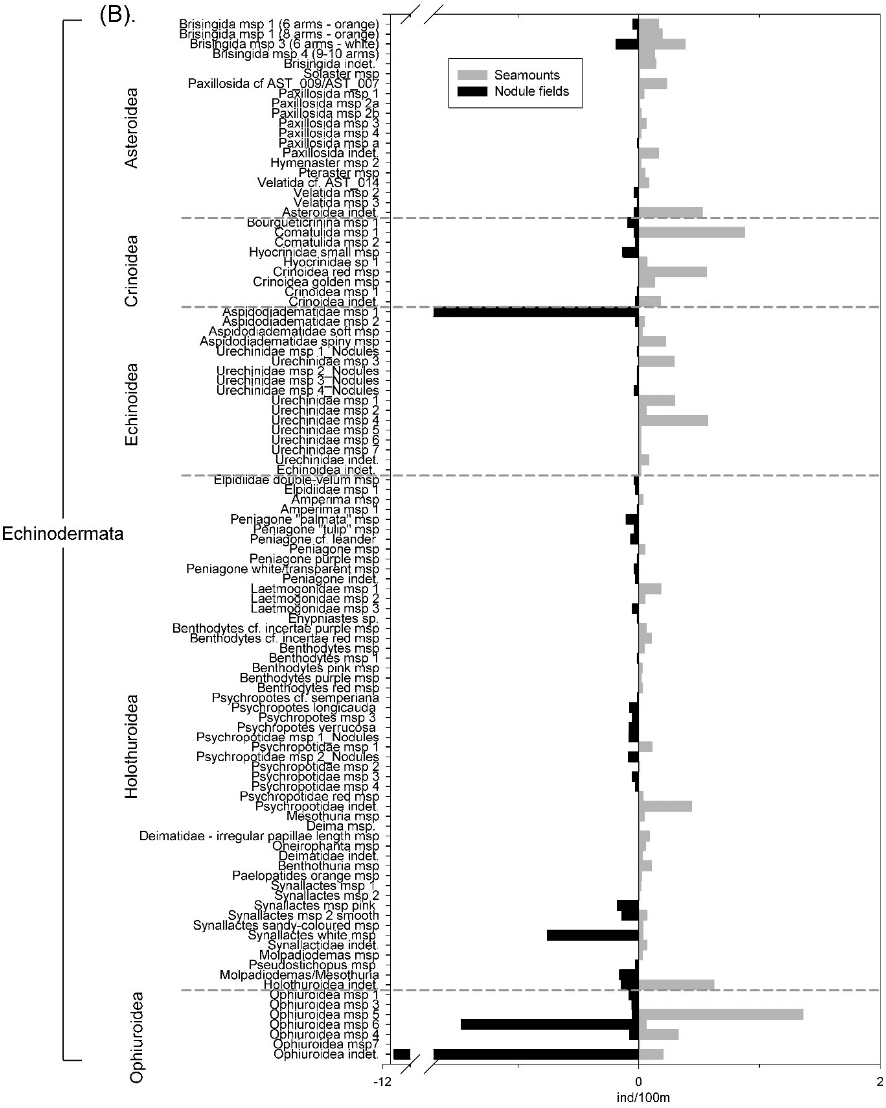
Formatted: Font: Italic

Formatted: Font: Italic


Cnidaria
Pennatulacea
Alcyonacea
Antipatharia
Actiniaria
Chordata
Hemichordata
Crustacea
Annelida
Branchioceriánthus msp
Hydrozoa indet.
Ceriantharia msp 2
Ceriantharia msp 1
Ceriantharia indet.
Umbellulidae indet.
Umbellula msp 2
Umbellula msp_orange
Umbellula msp_White
Protoptilum msp 1
Pennatulacea msp 8
Pennatulacea msp 7
Pennatulacea msp 6
Pennatulacea msp 5
Pennatulacea msp 2
Pennatulacea indet
Primnoidae indet.
Isididae indet.
Isididae msp 1
Anthomastus msp 2
Anthomastus msp 1
Narella msp 1
Corallium sp. nov.
Chrysogorgia cf. pinnata
Calyptrophora cf. persephone
Callozostron cf. bayeri
Bathygorgia aff. profunda 2
Bathygorgia aff. profunda 1
Bathygorgia aff. abyssicola 1
Keratoisis aff. flexibilis msp 2
Alcyonacea msp 1
Abyssoprimnoa cf. gemina
Alcyonacea indet.
Taiaroidae msp 1
Octocorallia msp 2
Octocorallia msp 1
Zoantharia msp 2
Zoantharia indet.
Scleractinia msp 1
Umbellapathes aff. helioanthes
Umbellapathes aff. bipinnata
Stichopathes msp 1
cf. Parantipathes morphotype 1
Antipathes msp 2
Antipathes msp 1
Bathypathes msp 1
Bathypathes sp.
Bathypathes cf. alternata msp 2
Bathypates cf. alternata msp 1
Bathypathes cf. alternata
Abyssopathes cf. lyra
Antipathidae indet.
Antipatharia indet.
Corallimorpharia msp B
Corallimorpharia msp A
Corallimorpharia msp 4
Corallimorpharia msp 3
Corallimorphus msp 2
Corallimorphus msp 1
Actiniaria msp B
Actiniaria msp A
Actiniaria msp 9
Actiniaria msp 8
Actiniaria msp 7
Actiniaria msp 2
Actiniaria msp 10
Actiniaria msp 5
Bolocera msp
Actinoscyphia spp.
Actiniaria msp 4
Actiniaria msp 15
Actiniaria indet.
Anthozoa indet.
Paleodictyon nodosum
Actinopterygii
Tunicata indet.
Dicopia msp
Megalodicopia msp 2
Megalodicopia msp 1
Culeolus sp.
Enteropneusta msp 2
Enteropneusta msp 1
Pycnogonida
Isopoda msp 1
Munnopsidae msp 1
Podoceridae msp 1
Amphipoda indet.
Decapoda msp 1
Aristeidae
Decapoda msp 4
Decapoda msp 3
Caridea indet.
Munidopsis spp.
Galatheidae small white msp
Galatheidae small red msp
Galatheidae indet.
Parapaguridae msp 1/Probeebei sp.
Decapoda indet.
Crustacea indet.
Echiura msp 1
Polychaeta indet.
Serpulidae
Sabelidae
Polynoidae white msp
Polynoidae msp 2
Aphroditidae
Acrocirridae
Seamounts
Nodules
15 10 4
3
2
1
0
1
2
ind/100m


(A).
Annelida
Bryozoa
Cnidaria
Crustacea
Actiniaria
Antipatharia
Alcyonacea
Pennatulacea
Polychaeta indet.
Acrocirridae
Aphroditidae
Echiura msp 1
Polynoidae msp 2
Polynoidae white msp
Bryozoa msp 2
Bryozoa indet.
Ceriantharia msp 1
Ceriantharia msp 2
Ceriantharia indet.
Actinoscyphiidae
Actiniidae/Bolocera msp.
Actiniaria msp 15
Actiniaria msp 4
Actiniaria msp 5
Actiniaria msp 10
Actiniaria msp 2
Actiniaria msp C
Actiniaria msp D
Actiniaria msp 7
Actiniaria msp 8
Actiniaria msp 9
Actiniaria msp A
Actiniaria msp B
Actiniaria indet.
Antipathes msp 1
Antipathes msp 2
Stichopathes msp 1
Antipathidae indet.
Schizopathidae
Abyssopathes cf. lyra
Bathypathes cf. alternata
Bathypates cf. alternata msp 1
Bathypathes cf. alternata msp 2
Bathypathes sp.
Bathypathes msp 1
cf. Parantipathes msp 1
Umbellapathes aff. bipinnata
Umbellapathes aff. helioanthes
Antipatharia indet.
Corallimorphus msp 1
Corallimorphus msp 2
Corallimorpharia msp 3
Corallimorpharia msp 4
Corallimorpharia msp A
Corallimorpharia msp B
Scleractinia msp 1
Zoantharia msp 2
Zoantharia indet.
Anthomastus msp 1
Anthomastus msp 2
Corallium sp. nov.
Chrysogorgia cf. pinnata
Bathygorgia aff. abyssicola 1
Bathygorgia aff. profunda 1
Bathygorgia aff. profunda 2
Keratoisis aff. flexibilis msp 2
Isididae msp 1
Isididae indet.
Taiaroidae msp 1
Abyssoprimnoa cf. gemina
Callozostron cf. bayeri
Calyptrophora cf. persephone
Narella msp 1
Primnoidea indet.
Alcyonacea msp 1
Alcyonacea indet.
Umbellula msp 1_White
Umbellula msp 1_orange
Umbellula msp 2
Umbellulidae indet.
Protoptilidae
Protoptilum msp 1
Pennatulacea msp 2
Pennatulacea msp 5
Pennatulacea msp 6
Pennatulacea msp 7
Pennatulacea msp 8
Pennatulacea indet
Octocorallia msp 1
Octocorallia msp 2
Anthozoa indet.
Branchioceríanthus msp
Hydrozoa indet.
Caridea
Decapoda msp 3
Decapoda msp 4
Aristeidae
Decapoda msp 1
Galatheidae small red msp
Galatheidae small white msp
Munidopsis spp.
Galatheidae indet.
Parapaguridae msp 1/Probeebei sp.
Amphipoda
Podoceridae msp 1
Amphipoda msp 1
Munnopsidae msp 1
Decapoda indet.
Crustacea indet.
Seamounts
Nodule fields
-4
-2
-1
0
1
2
3
ind/100m


Echinodermata
Bryozoa
Ophiuroidea
Holothuroidea
Echinoidea
Crinoidea
Asteroidea
Ophiuroidea msp. 7
Ophiuroidea msp. 4
Ophiuroidea msp. 6
Ophiuroidea msp. 5
Ophiuroidea msp. 3
Ophiuroidea msp. 1
Ophiuroidea indet.
Synallactidae indet.
Synallactes white msp.
Synallactes sandy-coloured msp.
Synallactes msp.2 _smooth
Synallactes msp._pink
Synallactes msp. 2
Synallactes msp. 1
Psychropotidae red msp.
Psychropotidae msp. 4
Psychropotidae msp. 3
Psychropotidae msp. 2
Psychropotidae msp. 6
Psychropotidae msp. 1
Psychropotidae msp. 5
Psychropotidae indet.
Psychropotes verrucosa
Psychropotes msp. 3
Psychropotes longicauda
Psychropotes cf. semperiana
Pseudostichopus msp.
Peniagone white/transparent msp.
Peniagone purple msp.
Peniagone msp.
Peniagone indet.
Peniagone cf. leander
Peniagone "tulip" msp.
Peniagone "palmata" msp.
Paelopatides msp.
Oneirophanta msp.
Molpadiodemas/Mesothuria
Molpadiodemas msp.
Mesothuria msp.
Laetmogonidae msp. 2
Laetmogonidae msp. 1
Laetmogonidae indet.
Enypniastes msp
Elpidiidae msp. 1
Elpidiidae double-velum msp.
Deimatidae indet.
Deimatidae - irregular papillae msp.
Deima sp.
Benthothuria msp.
Benthodytes red msp.
Benthodytes purple msp.
Benthodytes pink msp.
Benthodytes msp. 1
Benthodytes msp.
Benthodytes cf. incertae red msp.
Benthodytes cf. incertae purple msp.
Amperima msp. 1
Amperima msp. 2
Holothuroidea indet.
Urechinidae msp. 7
Urechinidae msp. 6
Urechinidae msp. 5
Urechinidae msp. 4
Urechinidae msp. 2
Urechinidae msp. 1
Urechinidae msp. D
Urechinidae msp. C
Urechinidae msp. B
Urechinidae msp. 3
Urechinidae msp. A
Urechinidae indet.
Aspidodiadematidae spiny msp.
Aspidodiadematidae soft msp.
Aspidodiadematidae msp. 2
Aspidodiadematidae msp. 1
Echinoidea indet.
Hyocrinidae sp. 1
Hyocrinidae small msp.
Crinoidea msp. 1
Crinoidea golden msp.
Crinoidea red msp.
Comatulida msp. 2
Comatulida msp. 1
Bourgueticrinina msp. 1
Crinoidea indet.
Velatida msp. 3
Velatida msp. 2
Velatida cf. AST_014
Pteraster msp.
Paxillosida msp. 4
Paxillosida msp. 3
Paxillosida msp. 2
Paxillosida msp. 1
Paxillosida indet.
Paxillosida cf AST_009/AST_007
Hymenaster msp. 2
Solaster msp.
Brisingida msp. 4
Brisingida msp. 3
Brisingida msp. 2
Brisingida msp. 1
Brisingida indet.
Asteroidea indet.
Bryozoa msp. 2
Bryozoa indet.
Seamounts
Nodules
15 10 4
3
2
1
0
1
2
ind/100m


(B).
Echinodermata
Asteroidea
Crinoidea
Echinoidea
Holothuroidea
Ophiuroidea
Brisingida msp 1 (6 arms - orange)
Brisingida msp 1 (8 arms - orange)
Brisingida msp 3 (6 arms - white)
Brisingida msp 4 (9-10 arms)
Brisingida indet.
Solaster msp
Paxillosida cf AST_009/AST_007
Paxillosida msp 1
Paxillosida msp 2a
Paxillosida msp 2b
Paxillosida msp 3
Paxillosida msp 4
Paxillosida msp a
Paxillosida indet.
Hymenaster msp 2
Pteraster msp
Velatida cf. AST_014
Velatida msp 2
Velatida msp 3
Asteroidea indet.
Bourgueticrinina msp 1
Comatulida msp 1
Comatulida msp 2
Hyocrinidae small msp
Hyocrinidae sp 1
Crinoidea red msp
Crinoidea golden msp
Crinoidea msp 1
Crinoidea indet.
Aspidodiadematidae msp 1
Aspidodiadematidae msp 2
Aspidodiadematidae soft msp
Aspidodiadematidae spiny msp
Urechinidae msp 1_Nodules
Urechinidae msp 3
Urechinidae msp 2_Nodules
Urechinidae msp 3_Nodules
Urechinidae msp 4_Nodules
Urechinidae msp 1
Urechinidae msp 2
Urechinidae msp 4
Urechinidae msp 5
Urechinidae msp 6
Urechinidae msp 7
Urechinidae indet.
Echinoidea indet.
Elpidiidae double-velum msp
Elpidiidae msp 1
Amperima msp
Amperima msp 1
Peniagone "palmata" msp
Peniagone "tulip" msp
Peniagone cf. leander
Peniagone msp
Peniagone purple msp
Peniagone white/transparent msp
Peniagone indet.
Laetmogonidae msp 1
Laetmogonidae msp 2
Laetmogonidae msp 3
Enypniastes sp.
Benthodytes cf. incertae purple msp
Benthodytes cf. incertae red msp
Benthodytes msp
Benthodytes msp 1
Benthodytes pink msp
Benthodytes purple msp
Benthodytes red msp
Psychropotes cf. semperiana
Psychropotes longicauda
Psychropotes msp 3
Psychropotes verrucosa
Psychropotidae msp 1_Nodules
Psychropotidae msp 1
Psychropotidae msp 2_Nodules
Psychropotidae msp 2
Psychropotidae msp 3
Psychropotidae msp 4
Psychropotidae red msp
Psychropotidae indet.
Mesothuria msp
Deima msp.
Deimatidae - irregular papillae length msp
Oneirophanta msp
Deimatidae indet.
Benthothuria msp
Paelopatides orange msp
Synallactes msp 1
Synallactes msp 2
Synallactes msp pink
Synallactes msp 2 smooth
Synallactes sandy-coloured msp
Synallactes white msp
Synallactidae indet.
Molpadiodemas msp
Pseudostichopus msp
Molpadiodemas/Mesothuria
Holothuroidea indet.
Ophiuroidea msp 1
Ophiuroidea msp 3
Ophiuroidea msp 5
Ophiuroidea msp 6
Ophiuroidea msp 4
Ophiuroidea msp7
Ophiuroidea indet.
Seamounts
Nodule fields
-12
0
2
ind/100m

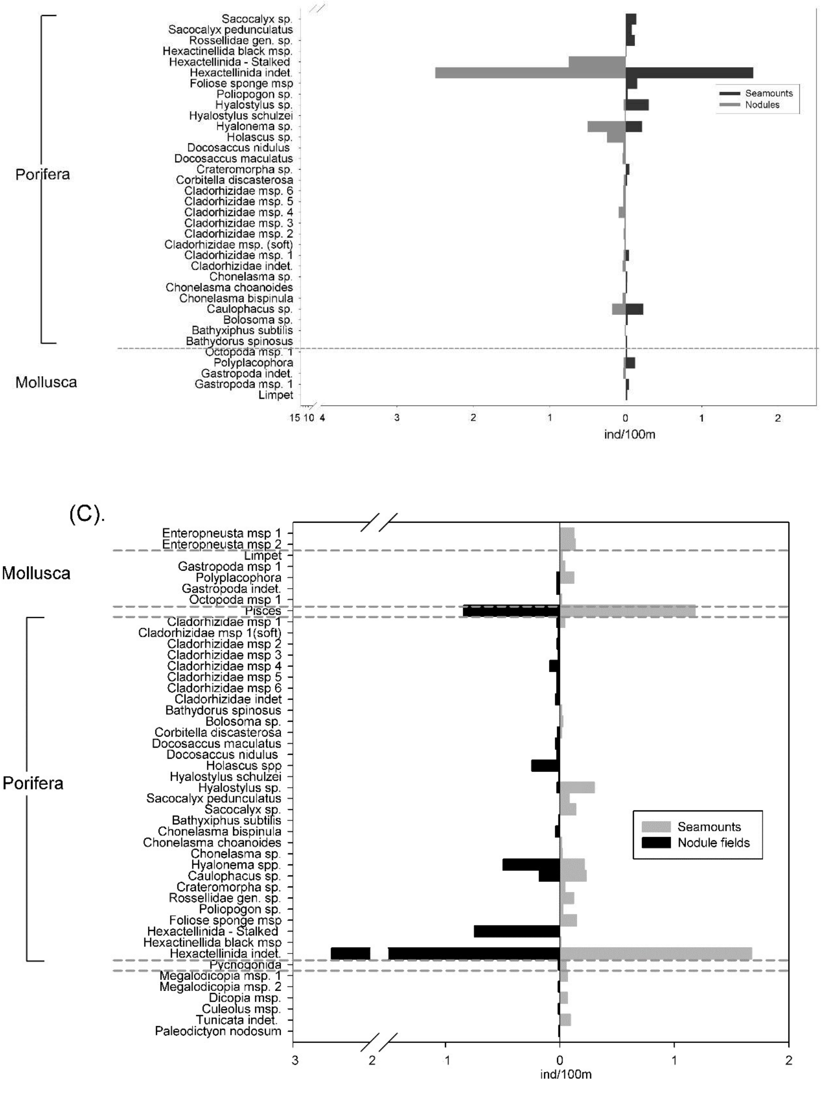
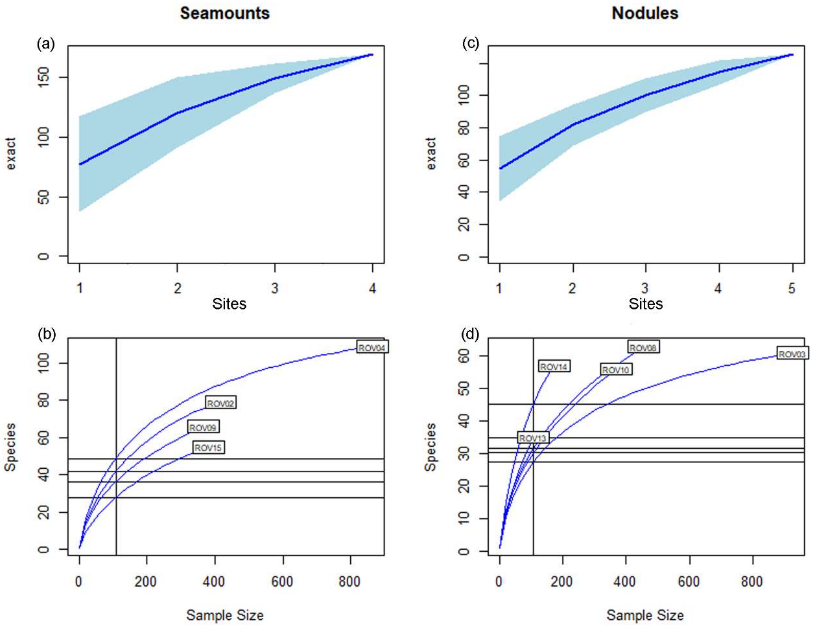


Fig. 3. Back-to-back histogram comparing average densities of morphospecies and taxa (ind/100m) for seamount (#4) and nodule field (#5) video transects. (a) Annelida, Bryozoa, Cnidaria and Crustacea, (B) Echinodermata and (C) Mollusca, Porifera, Hemichordata and Chordata (Tunicata).


Seamounts
Nodules
(a)
exact
0
50
100
150
1
2
3
4
Sites
(c)
exact
0
20
40
60
80
100
1
2
3
4
5
Sites
(b)
Species
0
20
40
60
80
100
0
200
400
600
800
Sample Size
ROV04
ROV02
ROV09
ROV15
(d)
Species
0
10
20
30
40
50
60
0
200
400
600
800
Sample Size
ROV14
ROV08
ROV10
ROV03
ROV13

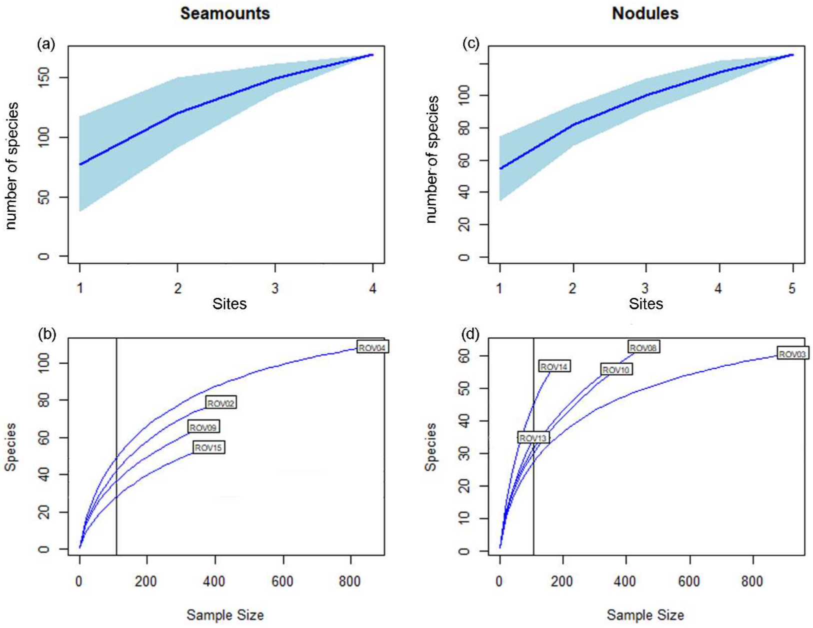
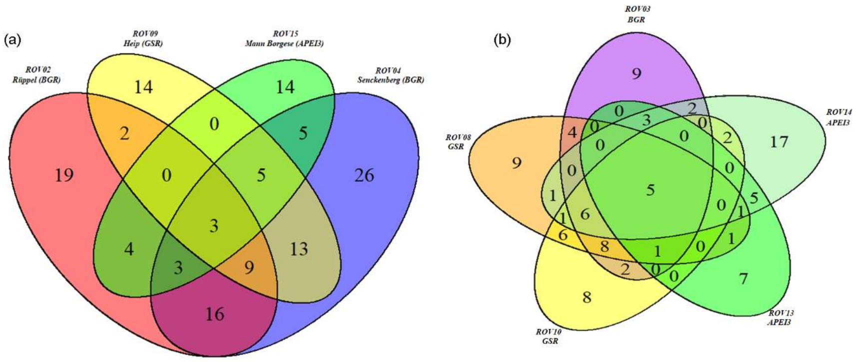


Fig. 4. Species accumulation (upper panel, a and c) and rarefaction curves (lower panel, b and d) for the seamount (#4) and nodule field (#5) transects. Seamount dives: ROV02= Rüppel (BGR), ROV04=Senckenberg (BGR), ROV09=Heip (GSR), ROV15=Mann Borgese (APEI3) in the lower left panel (b). Nodule field dives: ROV03 was carried out in the BGR area, ROV08 and 10 in the GSR area and ROV13 and 14 in the APEI3, presented in the lower right panel (d). Sample size is the number of individuals. Vertical line in the lower panel shows sample size=100.



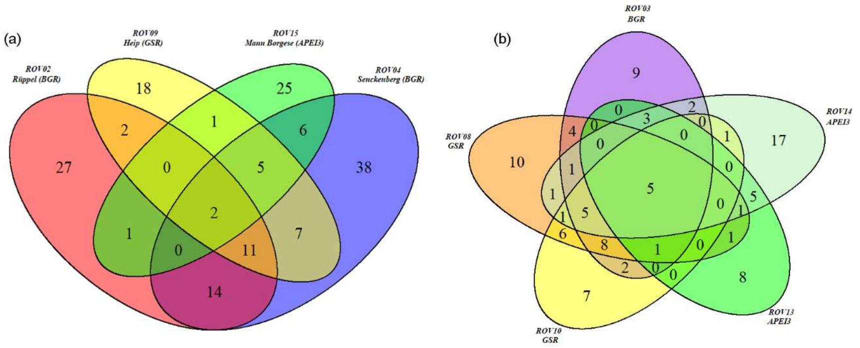
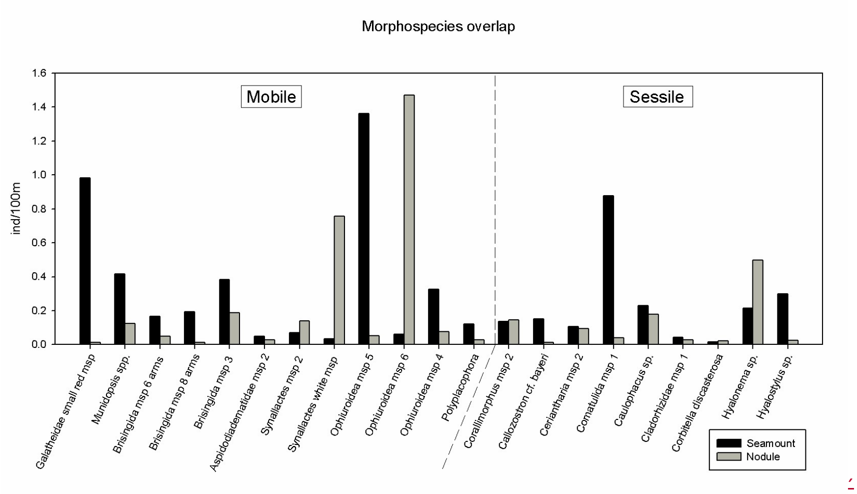


Fig. 5. A Venn diagram showing the unique and shared morphospecies among seamount video transects. Values are ~~relative~~ indicative rather than absolute due to different transect lengths and differences in richness. Left panel (a) features seamount transects and the right panel features the 5 nodule field transects. Colour codes were adapted among panels, with APEI3 nodule transects in green, related to Mann Borgese seamount transect. BGR (ROV03) transect was purple in correspondence to BGR seamount transects (red=Rüppel and blue=Senckenberg). GSR transects (ROV08 and 09) were shades of yellow.

Formatted: Portuguese (Portugal)



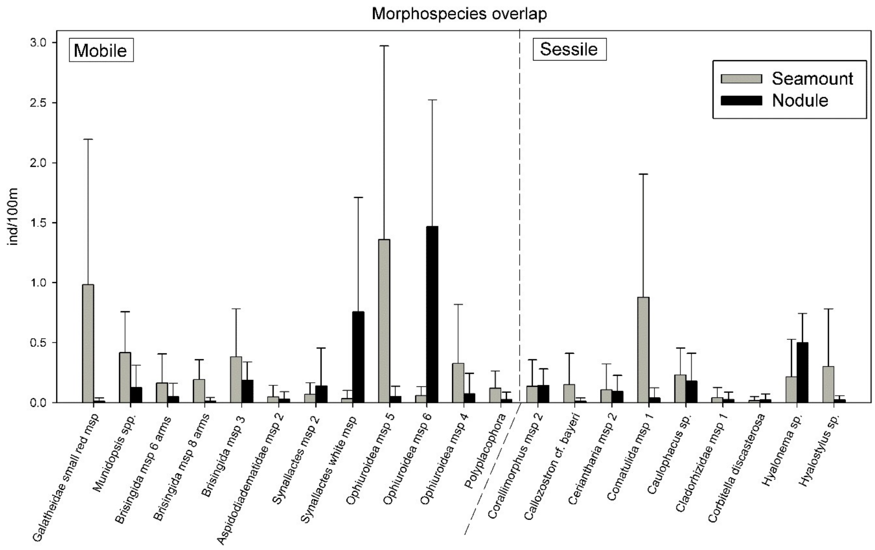
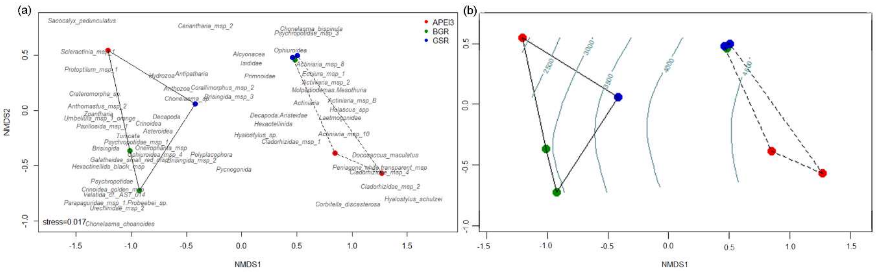


Fig. 6. Morphospecies present in both seamounts and nodule field transects ~~overlap~~ and their average density (ind/100m) and standard deviation per ecosystem. ~~between seamounts and nodule fields~~


(a)
Sacocalyx_pedunculatus
Ceriantharia_msp_2
Chonelasma_bispinula
Psychropotidae_msp_3
Scleractinia_msp_1
Alcyonacea
Ophiuroidea
Isididae
Protoptilum_msp_1
Hydrozoa
Antipatharia
Primnoidae
Actiniaria_msp_8
Echiura_msp_1
Actiniaria_msp_2
Anthozoa
Corallimorphus_msp_2
Molpadiodemas.Mesothuria
Crateromorpha_sp.
Chonelasma_sp.
Brisingida_msp_3
Actiniaria
Actiniaria_msp_B
Anthomastus_msp_2
Holascus_spp
Zoantharia
Umbellula_msp_1_orange
Decapoda
Decapoda.Aristeidae
Laetmogonidae
Crinoidea
Hexactellinida
Paxillosida_msp_1
Asteroidea
Tunicata
Hyalostylus_sp.
Actiniaria_msp_10
Psychropotidae_msp_1
Cladorhizidae_msp_1
Brisingida
Oneirophanta_msp
Ophiuroidea_msp_4
Polyplacophora
Docosaccus_maculatus
Galatheidae_small_red_msp
Brisingida_msp_2
Hexactinellida_black_msp
Pycnogonida
Peniagone_white_transparent_msp
Cladorhizidae_msp_4
Psychropotidae
Cladorhizidae_msp_2
Crinoidea_golden_msp
Velatida_cf._AST_014
Hyalostylus_schulzei
Parapagurdae_msp_1.Probeebei_sp.
Corbitella_discasterosa
Urechinidae_msp_2
stress=0.017
Chonelasma_choanoides
● APEI3
● BGR
● GSR
NMDS2
NMDS1
-1.0
-0.5
0.0
0.5
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
(b)
2500
3000
3500
4000
4500
0.5
0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
NMDS1

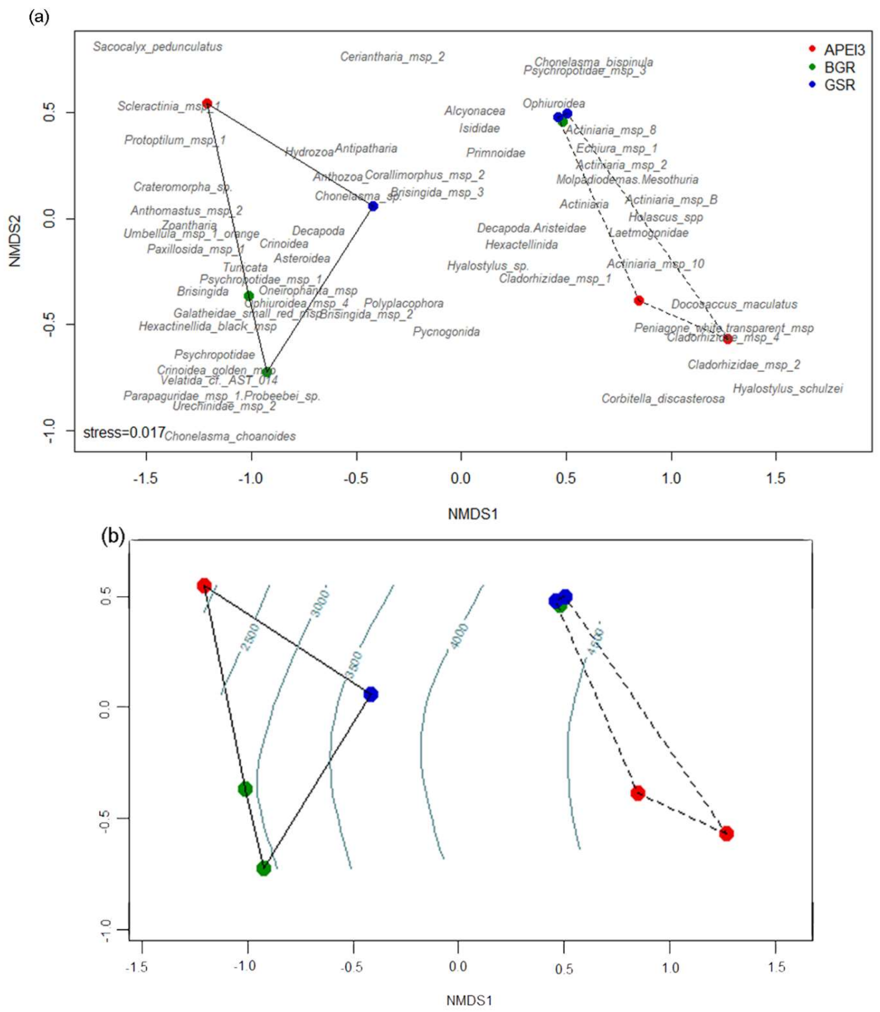


Fig. 7. nMDS-plot with faunal densities and Bray-Curtis distances. ~~Left~~ Upper panel (a) presents the grouping of the video transects based on their faunal composition and ~~right~~ lower panel (b) features the same plot but with depth as a vector fitting. Dotted lines group the nodule transects while the full line groups the seamount transects.

Appendix

Table A1. Overview of all ~~taxa~~ densities (ind./100m) ~~and number of morphospecies (msp.)~~ observed within each video transect. ~~Msp. numbers represent often minimum numbers and are indicative.~~ Higher taxa are in bold. * indicates taxa left out of the statistical analyses due to lack of representativity. Indets were organisms impossible to attribute to a lower taxonomic group. ROV02=Rüppel, ROV04=Senkcenberg, ROV09=Heip, ROV15=Mann Borgese

	~~**SEAMOUNTS**~~								~~**NODULE FIELDS**~~									
	~~ROV02 (BGR)~~		~~ROV04 (BGR)~~		~~ROV09 (GSR)~~		~~ROV15 (APEI3)~~		~~ROV03 (BGR)~~		~~ROV08 (GSR)~~		~~ROV10 (GSR)~~		~~ROV13 (APEI3)~~		~~ROV14~~	
-	~~ind/100m~~	# ~~msp~~	~~ind/100m~~	# ~~msp~~	~~ind/100m~~	# ~~msp~~	~~ind/100m~~	# ~~msp~~	~~ind/100m~~	# ~~msp~~	~~ind/100m~~	# ~~msp~~	~~ind/100m~~	# ~~msp~~	~~ind/100m~~	# ~~msp~~	~~ind/100m~~	# ~~msp~~
~~**Cnidaria**~~			~~0.04~~	~~1~~	~~0.1~~	~~1~~	~~0.22~~	~~>1~~										
~~Actiniaria~~	~~0.32~~	~~3~~	~~0.32~~	~~3~~			~~0.44~~	~~2~~	~~4.40~~	~~8~~	~~6.90~~	~~6~~	~~9.42~~	~~8~~	~~0.22~~	~~3~~	~~1.14~~	~~6~~
~~Actinoscyphiidae~~			~~0.12~~	~~1~~				-										
~~Actiniidae/*Bolocera* msp.~~	~~1.20~~	~~1~~	~~0.20~~	~~1~~				-										
~~Alcyonacea~~			~~0.16~~	~~>1~~	~~1.7~~	~~>1~~	~~2.78~~	~~>2~~	~~9.06~~	~~>2~~	~~6.62~~	~~>1~~	~~4.04~~	~~>1~~	~~0.11~~	~~1~~	~~0.20~~	~~>2~~
~~Alcyoniidae~~	~~0.24~~	~~1~~	~~0.04~~	~~1~~			~~0.11~~	~~1~~										
~~Chrysogorgiidae~~					~~0.1~~	~~1~~		-										
~~Isididae~~			~~0.20~~	~~2~~	~~1.2~~	~~>4~~		-	~~0.13~~	~~>1~~	~~5.77~~	~~>2~~	~~2.50~~	~~>2~~				
~~Taiaroidea~~								-					~~0.19~~	~~1~~				
~~Primnoidae~~	~~0.80~~	~~2~~	~~0.64~~	~~2~~	~~0.2~~	~~1~~	~~0.11~~	~~1~~	~~2.83~~	~~>3~~	~~4.08~~	~~>2~~	~~2.12~~	~~>2~~				
~~Coralliidae~~							~~0.11~~	~~1~~										
~~Ceriantharia~~	~~0.40~~	~~1~~	~~0.04~~	~~1~~	~~0.5~~	~~2~~	~~1.11~~	~~2~~			~~0.28~~	~~1~~	~~0.19~~	~~1~~				
~~Corallimorpharia/Corallimorphidae~~			~~0.64~~	~~4~~				-	~~0.38~~	~~3~~	~~0.28~~	~~1~~	~~0.38~~	~~2~~				
~~Antipatharia~~			~~0.08~~	~~1~~	~~0.2~~	~~1~~	~~0.67~~	~~>1~~	~~0.25~~	~~>1~~	~~0.28~~	~~>1~~	~~0.19~~	~~>1~~				
~~Antipathidae~~							~~19.11~~	~~2~~										
~~Schizopathidae~~			~~0.92~~	~~3~~	~~0.2~~	~~2~~	~~0.11~~	~~1~~	~~0.69~~	~~2~~	~~0.85~~	~~3~~	~~0.77~~	~~2~~			~~0.07~~	~~1~~
~~Pennatulacea~~	~~0.16~~	~~>1~~	~~3.04~~	~~>6~~			~~0.11~~	~~1~~										
~~Umbellulidae~~			~~0.56~~	~~>2~~			~~0.11~~	~~1~~									~~0.13~~	~~1~~
~~Protoptilidae~~			~~0.04~~	~~1~~			~~0.22~~	~~1~~										
~~Scleractinia~~	~~0.16~~	~~1~~					~~8.11~~	~~1~~										
~~Zoantharia~~			~~0.48~~	~~1~~			~~0.44~~	~~1~~										
~~Anthozoa~~	~~0.16~~	~~2~~	~~0.08~~	~~2~~	~~0.60~~	~~2~~	~~0.67~~	~~1~~	~~0.13~~	~~>1~~	~~0.14~~	~~>1~~	~~0.19~~	~~>1~~				
~~**Bryozoa**~~	-	-	~~0.04~~	~~1~~	~~0.2~~	~~1~~	-	-	~~0.44~~	~~>1~~	~~1.55~~	~~>1~~	~~0.19~~	~~>1~~	~~0.11~~	~~>1~~	~~0.13~~	~~>1~~
~~**Echinodermata**~~	~~0.16~~		~~0.16~~					-										
~~Asteroidea~~	~~0.32~~	~~>1~~	~~0.28~~	~~>1~~	~~1.3~~	~~>1~~	~~0.11~~	~~1~~	~~0.19~~	~~1.00~~								
~~Brisingida~~	~~0.64~~	~~5~~	~~1.44~~	~~7~~	~~2.0~~	~~4~~	~~0.44~~	~~2~~	~~0.44~~	~~2~~	~~0.42~~	~~1~~	~~0.19~~	~~1~~			~~0.20~~	~~2~~
~~Paxillosida~~	~~0.16~~	~~2~~	~~1.56~~	~~8~~	~~0.8~~	~~3~~	~~0.11~~	~~1~~							~~0.06~~	~~1~~		

~~Velatida~~	~~0.64~~	~~3~~	~~0.24~~	~~2~~				-					~~0.19~~	~~1~~			~~0.07~~	~~1~~
~~Crinoidea~~	~~2.80~~	~~4~~	~~4.32~~	~~6~~	~~0.2~~	~~2~~	~~0.56~~	~~≥2~~	~~0.69~~	~~2~~	~~0.42~~	~~2~~	~~0.19~~	~~1~~			~~0.34~~	~~3~~
~~Echinoidea~~								-										
~~Aspidodiadematidae~~	~~0.16~~	~~1~~	~~0.20~~	~~1~~			~~0.89~~	~~2~~	~~3.96~~	~~1~~	~~2.82~~	~~2~~	~~2.31~~	~~1~~				
~~Urechinidae~~	~~1.76~~	~~5~~	~~2.40~~	~~5~~	~~2.0~~	~~4~~		-	~~0.06~~	~~1~~					~~0.06~~	~~1~~	~~0.27~~	~~3~~
~~Holothuroidea~~	~~1.60~~		~~0.84~~		~~0.3~~		~~0.22~~	-	~~0.38~~	~~2~~	~~0.56~~	~~3~~	~~0.58~~	~~2~~			~~0.13~~	~~1~~
~~Deimatidae~~	~~0.08~~	~~1~~	~~0.36~~	~~3~~	~~0.4~~	~~3~~		-										
~~Elpidiidae~~	~~0.32~~	~~2~~	~~0.08~~	~~1~~				-										
~~Laetmogonidae~~	~~0.56~~	~~2~~	~~0.48~~	~~1~~				-					~~0.19~~	~~1~~			~~0.07~~	~~1~~
~~Mesothuriidae~~			~~0.12~~	~~1~~				-										
~~Molpadiodemidae~~			~~0.12~~	~~1~~				-										
~~Psychropotidae~~	~~1.60~~	~~>3~~	~~1.64~~	~~>6~~	~~0.4~~	~~4~~	~~0.22~~	~~2~~	~~0.50~~	~~4~~	~~0.99~~	~~5~~	~~0.77~~	~~3~~	~~0.06~~	~~1~~	~~0.07~~	~~1~~
~~Synallactidae~~	~~1.04~~	~~3~~	~~0.16~~	~~3~~			~~0.44~~	~~1~~	~~2.45~~	~~2~~	~~1.69~~	~~3~~	~~1.15~~	~~2~~			~~0.07~~	~~1~~
~~Ophiuroidea~~	~~0.48~~	~~2~~	~~3.40~~	~~5~~	~~4.4~~	~~3~~	~~0.44~~	~~1~~	~~20.44~~	~~4~~	~~18.45~~	~~4~~	~~25.96~~	~~3~~	~~0.39~~	~~2~~	~~1.34~~	~~3~~
~~**Crustacea***~~	~~0.07~~	-	~~0.31~~	-	~~0.51~~	-	-	-	-	-	-	-	-	-	-	-	~~0.13~~	-
~~Decapoda~~	~~4.42~~	~~4~~	~~3.15~~	~~5~~	~~4.41~~	~~3~~	~~0.75~~	~~2~~	~~0.25~~	~~2~~	~~0.99~~	~~2~~	~~1.73~~	~~2~~	~~0.28~~	~~3~~	~~0.47~~	~~3~~
~~Galatheidae~~	~~4.48~~	~~3~~	~~1.28~~	~~5~~	~~1.0~~	~~2~~	~~0.56~~	~~1~~	~~0.06~~	~~1~~								
~~Parapaguridae~~	~~0.64~~	~~>1~~	~~0.24~~	~~2~~				-										
~~Peracarida~~	-	-	~~0.08~~	~~1~~	~~0.25~~	~~2~~	-	-	~~0.63~~	~~2~~	~~0.70~~	~~2~~	~~0.19~~	~~1~~	~~0.28~~	~~3~~	~~0.81~~	~~2~~
~~**Enteropneusta**~~	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
~~*Yoda* msp.~~	~~0.64~~	~~1~~																
~~*Saxipendum* msp.~~	-	-	~~0.52~~	~~1~~	-	-	-	-	-	-	-	-	-	-	-	-	-	-
~~**Mollusca**~~								-										
~~Gastropoda~~			~~0.08~~	~~2~~	~~0.3~~	~~2~~		-			~~0.14~~	~~1~~						
~~Polyplacophora~~	~~0.32~~	~~1~~	~~0.52~~	~~1~~			~~0.22~~	~~1~~									~~0.13~~	~~1~~
~~Cephalopoda~~	~~0.08~~	~~1~~	-	-	-	-	-	-										
~~**Pisces***~~	~~2.96~~	~~9~~	~~1.44~~	~~10~~	~~0.6~~	~~5~~	~~0.33~~	~~3~~	~~1.57~~	~~4~~	~~0.42~~	~~2~~	~~1.54~~	~~3~~	~~0.34~~	~~3~~	~~0.34~~	~~2~~
~~**Annelida/Polychaeta** *~~	~~0.16~~	~~1~~	~~0.12~~	~~>2~~	-	-	~~0.11~~	~~1~~	~~0.13~~	-	-	-	~~0.38~~	-	-	-	-	-
~~Acrocirridae~~	~~0.16~~	~~1~~	~~0.16~~	~~1~~	~~4.2~~	~~1~~		-	~~0.57~~	~~1~~	~~0.14~~	~~1~~	~~0.58~~	~~1~~	~~1.79~~	~~1~~	~~1.95~~	~~1~~
~~Aphroditidae~~	~~0.24~~	~~1~~	~~0.04~~	~~1~~				-										

~~Echiura~~								-	~~0.57~~	~~1~~	~~1.13~~	~~1~~	~~1.15~~	~~1~~			~~0.20~~	~~1~~
~~Polynoidea~~	-	-	-	-	-	-	-	-	-	-	~~0.28~~	~~2~~	~~0.58~~	~~1~~	~~0.06~~	~~1~~	~~0.13~~	~~1~~
~~**Porifera**~~	~~0.08~~	~~1~~	~~0.04~~	~~1~~	~~0.6~~	~~>1~~		-										
~~Hexactellinida~~	~~1.76~~	~~>2~~	~~1.16~~	~~>3~~	~~3.7~~	~~>2~~	~~1.00~~	~~>2~~	~~5.79~~	~~>2~~	~~5.21~~	~~>2~~	~~8.27~~	~~>2~~	~~1.68~~	~~>1~~	~~2.08~~	~~>1~~
~~-Euplectellidae~~	~~0.47~~	~~3~~	~~0.20~~	~~2~~	~~1.4~~	~~2~~	~~0.44~~	~~2~~	~~1~~	~~1~~	~~1~~	~~3~~	~~0~~	~~1~~	~~0.34~~	~~5~~	~~0.13~~	~~2~~
~~-Euretidae~~	~~0.08~~	~~1~~			~~0.1~~	~~1~~		-					~~0.19~~	~~1~~	~~0.06~~	~~1~~		
~~-Hyalonematidae~~			~~0.08~~	~~>1~~	~~0.8~~	~~>2~~	~~0.11~~	~~1~~	~~0.38~~	~~>1~~	~~0.70~~	~~>1~~	~~0.77~~	~~>1~~	~~0.17~~	~~>1~~	~~0.47~~	~~>1~~
~~-Rosselidae~~	~~0.32~~	~~1~~	~~0.44~~	~~3~~	~~0.7~~	~~2~~	~~0.22~~	~~2~~	~~0.57~~	~~1~~	~~0.14~~	~~1~~	~~0.19~~	~~1~~	~~0.00~~	~~0~~	~~0.00~~	~~0~~
~~-Pheronematidae~~							~~0.11~~	~~1~~										
~~Cladorhizidae~~					~~0.2~~	~~1~~		-	~~0~~	~~1~~	~~0~~	~~2~~			~~0~~	~~3~~	~~1~~	~~>6~~
~~**Pycnogonida**~~	~~0.16~~	~~1~~	-	-	~~0.1~~	~~1~~	-	-	-	-	-	-	-	-	-	-	~~0.07~~	~~1~~
~~**Tunicata**~~	~~0.08~~	~~1~~	-	-	~~0.1~~	~~1~~	-	-										
~~*Megalodicopia* msp.~~	~~0.16~~	~~1~~	~~0.04~~	~~1~~	~~0.1~~	~~1~~		-									~~0.07~~	~~1~~
~~*Culeolus* msp.~~								-									~~0.07~~	~~1~~
~~*Dicopia* msp.~~	~~0.4~~	~~1~~	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
~~*Paleodictyon nodosum**~~								-							~~0.06~~	~~1~~		
~~**Indets**~~	~~0.88~~	~~>1~~	~~0.28~~	~~>1~~	-	-	~~0.22~~	~~>1~~	-	-	-	-	-	-	-	-	-	-

	SEAMOUNTS				NODULE FIELDS				
	ROV2	ROV4	ROV9	ROV15	ROV3	ROV8	ROV10	ROV13	ROV14
	ind/100m	ind/100m	ind/100m	ind/100m	ind/100m	ind/100m	ind/100m	ind/100m	ind/100m
Annelida*									
Polychaeta indet. * (No Serpulidae)	0.14	0.12	-	0.11	0.31	-	0.38	0.06	0.07
Acrocirridae	0.14	0.16	3.56	-	0.57	0.14	0.58	1.79	1.95
Aphroditidae	0.20	0.04	-	-		-		-	-
Echiura msp 1		-	-	-	0.57	1.13	1.15	-	0.20
Polynoidea		-	-	-		-		-	-
Polynoidae msp 2		-	-	-		0.14	0.58	-	-
Polynoidae white msp		-	-	-		0.14		0.06	0.13

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Bryozoa									
Bryozoa msp 2		-	0.17	-	-	-	-	-	-
Bryozoa indet.		0.038	-	-	0.44	1.55	0.19	0.11	0.13
Cnidaria									
Anthozoa									
Ceriantharia	-	-	-	-	-	-	-	-	-
Ceriantharia msp 1	0.34	0.04	0.34	0.22	-		-	-	-
Ceriantharia msp 2	-	-	-	0.43	-	0.28	0.19	-	-
Ceriantharia indet.	-	-	0.08		-			-	-
Hexacorralia									
Actiniaria									
Actinoscyphiidae	-	0.12	-	-	-	-	-	-	-
Actiniidae/*Bolocera* msp.	1.02	0.19	-	-	-	-	-	-	-
Actiniaria msp 15	0.07	-	-	-	-	-	-	-	-
Actiniaria msp 4	-	0.08	-	0.11	-	-	-	-	-
Actiniaria msp 5	0.07	0.08	-	0.32	-	-	-	-	-
Actiniaria msp 10	-	-	-	-	0.31	-	-	-	0.34
Actiniaria msp 2	-	-	-	-	1.07	1.13	0.19	-	0.27
Actiniaria msp C	-	-	-	-	0.38	0.42	0.38	-	-
Actiniaria msp D	-	-	-	-	0.06	-	-	-	-
Actiniaria msp 7	-	-	-	-	0.63	0.14	0.58	0.06	0.13
Actiniaria msp 8	-	-	-	-	0.13	3.66	3.08	-	0.20
Actiniaria msp 9	-	-	-	-	-	-	0.19	-	-
Actiniaria msp A	-	-	-	-	-	-	0.19	-	0.07
Actiniaria msp B	-	-	-	-	0.25	0.14	0.38	0.06	-
Actiniaria indet.	0.14	0.15	-	-	1.57	1.41	4.42	0.11	0.13
Antipatharia									

Formatted: Font: 11 pt
Formatted Table
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted Table
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted Table
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted: Font: 11 pt
Formatted Table

Antipathidae										
Antipathes msp 1	-	-	-	8.49	-	-	-	-	-	
Antipathes msp 2	-	-	-	0.11	-	-	-	-	-	
Stichopathes msp 1	-	-	-	9.35	-	-	-	-	-	
Antipathidae indet.	-	-	-	0.54	-	-	-	-	-	
Schizopathidae										
Abyssopathes cf. *lyra*	-	-	-	-	0.50	0.56	0.58	-	-	
Bathypathes cf. *alternata*	-	-	-	-	-	0.14	0.19	-	0.07	
Bathypates cf. *alternata* msp 1	-	-	0.08	-	-	-	-	-	-	
Bathypathes cf. *alternata* msp 2	-	0.12	-	-	-	-	-	-	-	
Bathypathes sp.	-	-	-	-	0.19	0.14	-	-	-	
Bathypathes msp 1	-	-	0.08	-	-	-	-	-	-	
cf. *Parantipathes* msp 1	-	-	0.11	-	-	-	-	-	-	
Umbellapathes aff. *bipinnata*	-	0.19	0.08	-	-	-	-	-	-	
Umbellapathes aff. *helioanthes*	-	0.58	-	-	-	-	-	-	-	
Antipatharia indet.	0.07	0.08	0.08	0.65	0.25	0.28	0.19	-	-	
Corallimorpharia/Corallimorphidae	-	-	-	-	-	-	-	-	-	
Corallimorphus msp 1	-	0.04	0.00	-	-	-	-	-	-	
Corallimorphus msp 2	-	0.46	0.08	-	0.25	0.28	0.19	-	-	
Corallimorpharia msp 3	-	0.04	-	-	-	-	-	-	-	
Corallimorpharia msp 4	-	-	0.08	-	-	-	-	-	-	
Corallimorpharia msp A	-	-	-	-	0.06	-	0.19	-	-	
Corallimorpharia msp B	-	-	-	-	0.06	-	-	-	-	
Scleractinia										
Scleractinia msp 1	0.14	-	-	7.85	-	-	-	-	-	
Zoantharia										
Zoantharia msp 2	-	-	-	0.11	-	-	-	-	-	
Zoantharia indet.	-	0.46	-	0.22	-	-	-	-	-	
Octocorrallia										

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Alcyonacea									
Alcyoniidae									
Anthomastus msp 1	0.20	-	-	-	-	-	-	-	-
Anthomastus msp 2	0.00	0.15	-	0.11	-	-	-	-	-
Coralliidae									
Corallium sp. nov.	-	-	-	0.11	-	-	-	-	-
Chrysogorgiidae									
Chrysogorgia cf. *pinnata*	-	-	0.08	-	-	-	-	-	-
Isididae									
Bathygorgia aff. *abyssicola* 1	-	-	-	-	-	0.14	0.19	-	-
Bathygorgia aff. *profunda* 1	-	0.15	0.08	-	-	-	-	-	-
Bathygorgia aff. *profunda* 2	-	-	0.08	-	-	-	-	-	-
Keratoisis aff. *flexibilis* msp 2	-	-	0.08	-	-	-	-	-	-
Isididae msp 1	-	0.04	-	-	-	-	-	-	-
Isididae indet.	0.14	-	0.76	0.11	0.13	5.63	2.31	-	-
Taiaroidea									
Taiaroidae msp 1	-	-	-	-	-	-	0.19	-	-
Primnoidae									
Abyssoprimnoa cf. *gemina*	-	-	-	-	-	0.70	0.58	-	-
Callozostron cf. *bayeri*	0.07	0.54	-	-	0.06	-	-	-	-
Calyptrophora cf. *persephone*	-	-	-	-	0.06	-	-	-	-
Narella msp 1	-	0.08	-	0.11	-	-	-	-	-
Primnoidea indet.	0.61	-	0.17	-	2.70	3.38	1.54	-	-
Alcyonacea msp 1	-	-	-	-	0.13	-	-	0.11	0.13
Alcyonacea indet.	-	0.15	1.44	2.69	8.93	6.62	4.04	-	0.07
Pennatulacea									
Umbellulidae									
Umbellula msp 1 White	-	-	-	-	-	-	-	-	0.13
Umbellula msp 1 orange	-	0.31	-	0.11	-	-	-	-	-

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Umbellula msp 2	-	0.08	-	-	-	-	-	-	-
Umbellulidae indet.	-	0.15	-	-	-	-	-	-	-
Protoptilidae	-	-	-	0.11	-	-	-	-	-
Protoptilum msp 1	-	0.04	-	0.22	-	-	-	-	-
Pennatulacea msp 2	-	0.04	-	-	-	-	-	-	-
Pennatulacea msp 5	-	0.23	-	-	-	-	-	-	-
Pennatulacea msp 6	-	0.12	-	-	-	-	-	-	-
Pennatulacea msp 7	-	0.38	-	-	-	-	-	-	-
Pennatulacea msp 8	-	0.08	-	-	-	-	-	-	-
Pennatulacea indet	0.14	2.08	-	0.11	-	0.14	-	-	-
Octocorallia msp 1	-	-	-	0.22	-	-	-	-	-
Octocorallia msp 2	-	-	-	-	-	-	-	-	-
Anthozoa indet.	0.14	0.12	0.51	0.65	0.13	0.14	0.19	-	-
Hydrozoa									
Branchiocerianthus msp	-	0.08	-	-	-	-	-	-	-
Hydrozoa indet.	-	0.08	0.08	0.22	-	0.14	-	-	-
Crustacea*									
Decapoda									
Caridea	3.47	2.54	3.22	0.22	0.19	-	1.15	0.11	0.20
Decapoda msp 3	-	0.08	-	-	-	-	-	-	-
Decapoda msp 4	0.07	-	-	-	-	-	-	-	-
Decapoda/Aristeidae	0.07	0.08	-	0.54	0.06	0.56	0.58	0.11	0.07
Decapoda msp 1	-	-	-	-	-	-	-	0.06	-
Galatheidae									
Galatheidae small red msp	2.79	0.54	0.17	0.43	0.06	-	-	-	-
Galatheidae small white msp	0.07	0.12	-	-	-	-	-	-	-
Munidopsis spp.	0.82	0.35	0.51	-	-	0.42	-	-	0.20
Galatheidae indet.	0.14	0.15	0.17	0.11	-	-	-	-	-

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Parapaguridae									
Parapaguridae msp 1/*Probeebei* sp.	0.54	0.23	-	-	-	-	-	-	-
Peracarida									
Amphipoda	-	-	0.08	-	0.06	0.28	-	0.06	0.27
Podoceridae msp 1	-	-	-	-	-	-	-	0.06	-
Amphipoda msp 1	-	0.08	0.17	-	-	-	-	-	-
Isopoda									
Munnopsidae msp 1	-	-	-	-	0.57	0.42	0.19	0.17	0.54
Decapoda indet.	-	0.12	0.68	-	-	-	-	-	-
Crustacea indet.	0.07	0.31	0.51	-	-	-	-	-	0.13
Echinodermata									
Asteroidea									
Brisingida									
Brisingida msp 1 (6 arms - orange)	-	0.15	0.51	-	0.25	-	-	-	-
Brisingida msp 1 (8 arms - orange)	0.14	0.38	0.25	-	-	-	-	-	0.07
Brisingida msp 3 (6 arms - white)	-	0.38	0.93	0.22	0.19	0.42	0.19	-	0.13
Brisingida msp 4 (9-10 arms)	0.14	0.38	-	-	-	-	-	-	-
Brisingida indet.	0.27	0.08	-	0.22	-	-	-	-	-
Paxillosida									
Solaster msp	-	0.04	-	-	-	-	-	-	-
Paxillosida cf AST_009/AST_007	-	0.50	0.42	-	-	-	-	-	-
Paxillosida msp 1	0.07	-	-	0.11	-	-	-	-	-
Paxillosida msp 2a	-	0.04	-	-	-	-	-	-	-
Paxillosida msp 2b	-	-	0.08	-	-	-	-	-	-
Paxillosida msp 3	-	0.08	0.17	-	-	-	-	-	-
Paxillosida msp 4	-	0.08	-	-	-	-	-	-	-
Paxillosida msp 1	-	-	-	-	-	-	-	0.06	-
Paxillosida indet.	-	0.65	-	-	-	-	-	-	-

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted Table

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Velatida									
Pterasteridae									
Hymenaster msp 2	0.07	-	-	-	-	-	-	-	-
Pteraster msp	0.20	-	-	-	-	-	-	-	-
Velatida cf. AST_014	0.14	0.19	-	-	-	-	-	-	-
Velatida msp 2	-	-	-	-	-	-	0.19	-	-
Velatida msp 3	-	-	-	-	-	-	-	-	0.07
Asteroidea indet.	0.48	0.42	1.10	0.11	0.19	-	-	-	-
Crinoidea									
Comatulida									
Bourgueticrinina msp 1	-	-	-	-	0.31	-	-	-	0.13
Comatulida msp 1	1.97	1.54	-	-	-	-	0.19	-	-
Comatulida msp 2	-	-	-	-	-	-	-	-	0.13
Hyocrinida									
Hyocrinidae small msp	-	-	-	-	0.38	0.28	-	-	-
Hyocrinidae sp 1	-	0.19	0.08	0.00	-	-	-	-	-
Crinoidea red msp	0.20	1.62	-	0.43	-	-	-	-	-
Crinoidea golden msp	0.14	0.38	-	-	-	-	-	-	-
Crinoidea msp 1	-	-	-	-	-	-	-	-	0.07
Crinoidea indet.	0.07	0.46	0.08	0.11	-	0.14	-	-	-
Echinoidea									
Aspidodiadematidae									
Aspidodiadematidae msp 1	-	-	-	-	3.96	2.68	2.31	-	-
Aspidodiadematidae msp 2	-	0.19	-	-	-	0.14	-	-	-
Aspidodiadematidae soft msp	-	-	-	0.11	-	-	-	-	-
Aspidodiadematidae spiny msp	0.14	-	-	0.75	-	-	-	-	-
Urechinidae									
Urechinidae msp 1_Nodules	-	-	-	-	-	-	-	-	0.07
Urechinidae msp 3	0.20	0.04	0.93	-	-	-	-	-	-

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Urechinidae msp 2 Nodules	-	-	-	-	-	-	-	-	0.07
Urechinidae msp 3 Nodules	-	-	-	-	0.06	-	-	-	-
Urechinidae msp 4 Nodules	-	-	-	-	-	-	-	0.06	0.13
Urechinidae msp 1	0.20	0.73	0.25	-	-	-	-	-	-
Urechinidae msp 2	0.20	0.04	-	-	-	-	-	-	-
Urechinidae msp 4	0.48	1.38	0.42	-	-	-	-	-	-
Urechinidae msp 5	0.07	-	-	-	-	-	-	-	-
Urechinidae msp 6	0.07	-	-	-	-	-	-	-	-
Urechinidae msp 7	0.07	-	-	-	-	-	-	-	-
Urechinidae indet.	0.14	0.12	0.08	-	-	-	-	-	-
Echinoidea indet.	0.07	-	-	-	-	-	-	-	-
Holothuroidea									
Elasipodida									
Elpidiidae									
Elpidiidae double-velum msp	-	-	-	-	-	-	0.19	-	-
Elpidiidae msp 1	-	-	-	-	-	-	-	0.06	0.07
Amperima msp	0.14	-	-	-	-	-	-	-	-
Amperima msp 1	-	-	-	-	0.06	-	-	-	-
Peniagone "palmata" msp	-	-	-	-	-	0.14	0.38	-	-
Peniagone "tulip" msp	-	-	-	-	-	-	0.19	-	-
Peniagone cf. *leander*	-	-	-	-	-	0.14	0.19	-	-
Peniagone msp	0.14	0.08	-	-	-	-	-	-	-
Peniagone purple msp	-	-	-	-	-	-	-	-	0.07
Peniagone white/transparent msp	-	-	-	-	0.06	-	-	0.06	0.07
Peniagone indet.	-	-	-	-	0.13	-	-	-	-
Laetmogonidae									
Laetmogonidae msp 1	0.27	0.46	-	-	-	-	-	-	-
Laetmogonidae msp 2	0.20	-	-	-	-	-	-	-	-
Laetmogonidae msp 3	-	-	-	-	-	-	0.19	-	0.07

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Pelagothuriidae									
Enypniastes sp.	-	-	-	-	-	-	-	-	0.07
Psychropotidae									
Benthodytes cf. *incertae* purple msp	-	0.15	0.08	-	-	-	-	-	-
Benthodytes cf. *incertae* red msp	-	0.42	-	-	-	-	-	-	-
Benthodytes msp	-	0.19	-	-	-	-	-	-	-
Benthodytes msp 1	-	-	-	-	-	-	-	-	0.07
Benthodytes pink msp	-	-	-	0.11	-	-	-	-	-
Benthodytes purple msp	-	-	0.08	-	-	-	-	-	-
Benthodytes red msp	-	0.04	0.08	-	-	-	-	-	-
Psychropotes cf. *semperiana*	-	-	-	-	-	-	-	0.06	-
Psychropotes longicauda	-	-	-	-	-	-	0.38	-	-
Psychropotes msp 3	-	-	-	-	0.06	-	0.19	-	-
Psychropotes verrucosa	-	-	-	-	0.25	0.14	-	-	-
Psychropotidae msp 1 Nodules	-	-	-	-	0.06	0.14	0.19	-	-
Psychropotidae msp 1	-	0.35	0.08	-	-	-	-	-	-
Psychropotidae msp 2 Nodules	-	-	-	-	-	0.42	-	-	-
Psychropotidae msp 2	-	0.04	-	-	-	-	-	-	-
Psychropotidae msp 3	-	-	-	-	0.13	0.14	-	-	-
Psychropotidae msp 4	-	-	-	-	-	0.14	-	-	-
Psychropotidae red msp	0.14	-	-	-	-	-	-	-	-
Psychropotidae indet.	1.22	0.42	-	0.11	-	-	-	-	-
Holothuriida									
Mesothuriidae									
Mesothuria msp	0.07	0.12	-	-	-	-	-	-	-
Synallactida									
Deimatidae									
Deima msp.	-	0.04	-	-	-	-	-	-	-
Deimatidae - irregular papillae length msp	-	0.27	0.08	-	-	-	-	-	-

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Oneirophanta msp	0.07	-	0.17	-	-	-	-	-	-
Deimatidae indet.	-	0.04	0.08	-	-	-	-	-	-
Synallactidae									
Benthothuria msp	-	-	-	0.43	-	-	-	-	-
Paelopatides “orange“ msp	0.07	0.04	-	-	-	-	-	-	-
Synallactes msp 1 (Synallactidae purple msp)	0.07	-	-	-	-	-	-	-	-
Synallactes msp 2	-	0.04	-	-	-	-	-	-	-
Synallactes msp 2 pink	-	-	-	-	0.13	0.56	0.19	-	-
Synallactes msp 2 pink (smooth)	0.20	0.08	-	-	-	0.70	-	-	-
Synallactes sandy-coloured msp	0.14	-	-	-	-	-	-	-	-
Synallactes white msp	0.14	-	-	-	2.33	0.42	0.96	-	0.07
Synallactidae indet.	0.27	-	-	-	-	-	-	-	-
Persiculida									
Molpadiodemidae									
Molpadiodemas msp	-	0.12	-	-	-	-	-	-	-
Pseudostichopodidae									
Pseudostichopus msp	-	-	-	-	-	0.14	-	-	-
Molpadiodemas/Mesothuria	-	-	-	-	0.19	0.28	0.19	-	0.13
Holothuroidea indet.	1.29	0.73	0.25	0.22	0.19	0.14	0.38	-	-
Ophiuroidea									
Ophiuroidea msp 1	-	-	-	-	0.06	0.14	0.19	-	-
Ophiuroidea msp 3	-	-	-	-	-	0.28	-	-	-
Ophiuroidea msp 5	0.14	1.92	3.39	-	-	-	-	0.06	0.20
Ophiuroidea msp 6	-	0.15	0.08	-	1.07	2.96	2.12	0.34	0.87
Ophiuroidea msp 4	0.27	1.04	-	-	0.38	-	-	-	-
Ophiuroidea msp7	-	0.04	-	-	-	-	-	-	-
Ophiuroidea indet.	-	0.12	0.25	0.43	18.93	15.07	23.65	-	0.27
				-					-
Enteropneusta									

Formatted ... [1]
Formatted ... [2]
Formatted ... [3]
Formatted Table ... [4]
Formatted ... [5]
Formatted ... [6]
Formatted ... [7]
Formatted ... [8]
Formatted ... [9]
Formatted ... [10]
Formatted ... [11]
Formatted ... [12]
Formatted ... [13]
Formatted Table ... [14]
Formatted ... [15]
Formatted ... [16]
Formatted ... [17]
Formatted Table ... [18]
Formatted ... [19]
Formatted ... [20]
Formatted ... [21]
Formatted ... [22]
Formatted Table ... [23]
Formatted ... [24]
Formatted ... [25]
Formatted ... [26]
Formatted ... [27]
Formatted ... [28]
Formatted ... [29]
Formatted ... [30]
Formatted ... [31]
Formatted ... [32]
Formatted Table ... [33]

Enteropneusta msp 1 cf. *Yoda*	-	0.50		-	-	-	-	-	-
Enteropneusta msp 2 cf. *Saxipendum* msp.	0.54	-		-	-	-	-	-	-
Mollusca									
Gastropoda									
Limpet	-	-	0.08	-	-	-	-	-	-
Gastropoda msp 1	-	-	0.17	-	-	-	-	-	-
Polyplacophora	0.27	-	-	0.22	-	-	-	-	0.13
Gastropoda indet.	-	-	-	-	-	0.14	-	-	-
Cephalopoda									
Octopoda msp 1	0.07	-	-	-	-	-	-	-	-
				-					-
Pisces*	2.52	1.38	0.51	0.32	1.57	0.42	1.54	0.34	0.34
Porifera									
Demospongiae									
Cladorhizidae									
Cladorhizidae msp 1		-	0.17	-	-	-	-	-	0.13
Cladorhizidae msp 1(soft)	-	-	-	-	-	-	-	-	0.07
Cladorhizidae msp 2	-	-	-	-	-	-	-	0.06	0.07
Cladorhizidae msp 3	-	-	-	-	-	-	-	-	0.07
Cladorhizidae msp 4	-	-	-	-	0.06	-	-	0.11	0.27
Cladorhizidae msp 5	-	-	-	-	-	0.14	-	-	-
Cladorhizidae msp 6	-	-	-	-	-	0.14	-	-	-
Cladorhizidae indet	-	-	-	-	-	-	-	0.06	0.13
Hexactellinida									
Euplectellidae									
Bathydorus spinosus	0.07	-	-	-	-	-	-	-	-
Bolosoma sp.	-	-	-	0.11	-	-	-	-	-

Formatted: Font: 11 pt

Formatted: Font: 11 pt, Portuguese (Portugal)

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Corbitella discasterosa	0.07	-	-	-	-	-	-	0.11	-
Docosaccus maculatus	-	-	-	-	-	0.14	-	0.06	-
Docosaccus nidulus	-	-	-	-	-	0.14	-	-	-
Holascusspp	-	-	-	-	0.63	0.28	0.19	0.06	0.07
Hyalostylus schulzei	-	-	-	-	-	-	-	0.06	-
Hyalostylus sp.	-	0.08	1.02	0.11	-	-	-	0.06	0.07
Sacocalyx pedunculatus	-	-	-	0.32	-	-	-	-	-
Sacocalyx sp.	0.27	0.12	0.17	-	-	-	-	-	-
Euretidae									
Bathyxiphus subtilis	-	-	-	-	-	-	-	0.06	-
Chonelasma bispinula	-	-	-	-	-	-	0.19	-	-
Chonelasma choanoides	0.07	-	-	-	-	-	-	-	-
Chonelasma sp.	-	-	0.08	-	-	-	-	-	-
Hyalonematidae									
Hyalonema spp.	-	0.08	0.68	0.11	0.38	0.70	0.77	0.17	0.47
Rosselidae									
Caulophacus sp.	-	0.31	0.51	0.11	0.57	0.14	0.19	-	-
Crateromorpha sp.	-	0.08	-	0.11	-	-	-	-	-
Rossellidae gen. sp.	0.27	0.04	0.17	-	-	-	-	-	-
Pheronematidae									
Poliopogon sp.	-	-	-	0.11	-	-	-	-	-
Hexactellinida/foliose sponge msp	0.07	0.12	0.08	0.32	-	-	-	-	-
Hexactellinida - Stalked	-	-	-	-	0.88	1.13	1.73	-	-
Hexactinellida black msp	-	0.04	-	-	-	-	-	-	-
Hexactellinida indet.	1.50	1.00	3.56	0.65	3.27	2.39	5.19	0.89	0.74
Pycnogonida	0.14	0.00	0.08	0.00					0.07
Tunicata									

Formatted ... [34]
Formatted ... [35]
Formatted ... [36]
Formatted ... [37]
Formatted ... [38]
Formatted ... [39]
Formatted ... [40]
Formatted ... [41]
Formatted ... [42]
Formatted Table ... [43]
Formatted ... [44]
Formatted ... [45]
Formatted ... [46]
Formatted ... [47]
Formatted ... [48]
Formatted Table ... [49]
Formatted ... [50]
Formatted Table ... [51]
Formatted ... [52]
Formatted ... [53]
Formatted ... [54]
Formatted ... [55]
Formatted Table ... [56]
Formatted ... [57]
Formatted ... [58]
Formatted ... [59]
Formatted ... [60]
Formatted ... [61]
Formatted ... [62]
Formatted Table ... [63]
Formatted ... [64]
Formatted ... [65]
Formatted ... [66]

Octacnemidae									
Megalodicopia msp. 1	0.14	0.04	0.08	-	-	-	-	-	-
Megalodicopia msp. 2	-	-	-	-	-	-	-	-	0.07
Dicopia msp.	0.27	-	-	-	-	-	-	-	-
Pyuridae									
Culeolus msp.	-	-	-	-	-	-	-	-	0.07
Tunicata indet.	0.14	0.04	0.08	0.11	-	-	-	-	-
Paleodictyon nodosum		-	-	-	-	-	-	0.06	-

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted: Font: 11 pt

Formatted Table

Formatted: Font: 11 pt

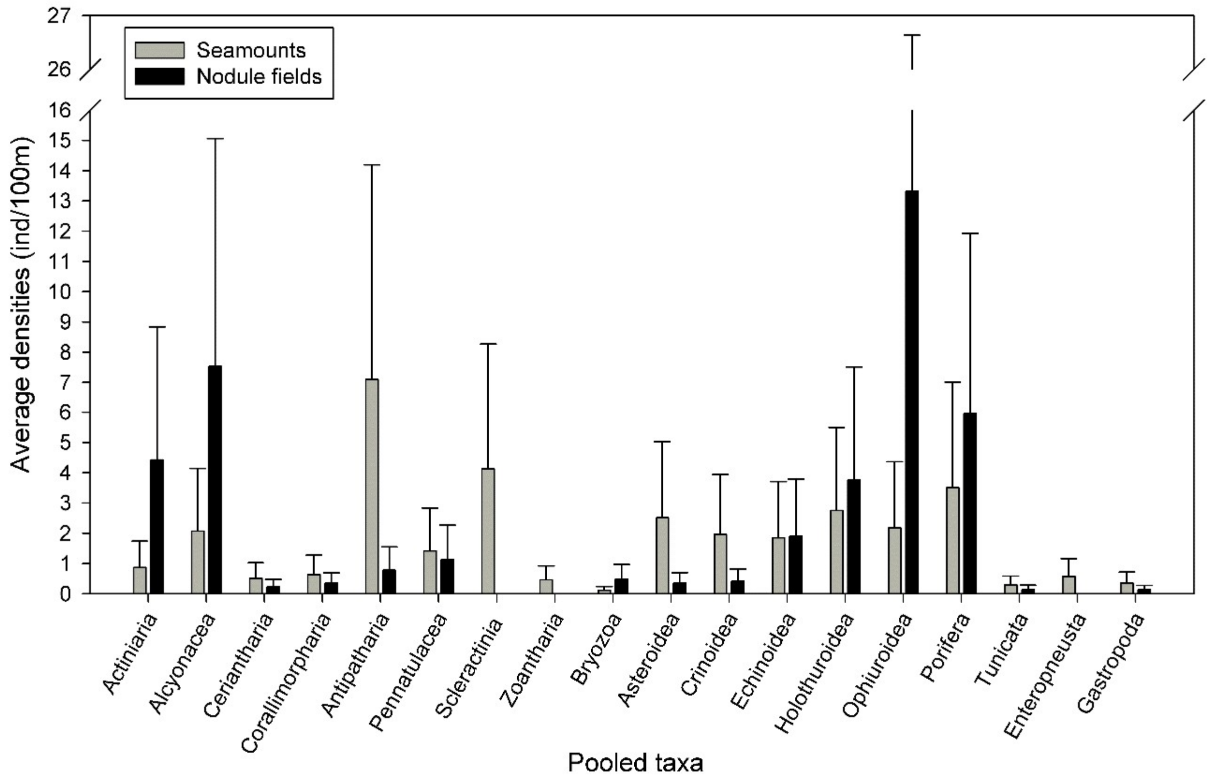


Fig. A1. Average densities at higher taxa level per ecosystem and standard deviation.

Formatted: Left: 3 cm, Right: 3 cm, Top: 2.5 cm, Bottom: 1.5 cm, Width: 21 cm, Height: 35 cm

Page 57: [1] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [2] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [3] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [4] Formatted Table	Daphne Cuvelier	16/12/2019 15:30:00

Formatted Table

Page 57: [5] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [6] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [7] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [8] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [9] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [10] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [11] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [12] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [13] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [14] Formatted Table	Daphne Cuvelier	16/12/2019 15:30:00

Formatted Table

Page 57: [15] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [16] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 57: [17] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [18] Formatted Table Daphne Cuvelier 16/12/2019 15:30:00

Formatted Table

Page 57: [19] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [20] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [21] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [22] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [23] Formatted Table Daphne Cuvelier 16/12/2019 15:30:00

Formatted Table

Page 57: [24] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [25] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [26] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [27] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [28] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [29] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [30] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [31] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [32] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 57: [33] Formatted Table Daphne Cuvelier 16/12/2019 15:30:00

Formatted Table

Page 59: [34] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [35] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [36] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [37] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [38] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [39] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [40] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [41] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [42] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [43] Formatted Table Daphne Cuvelier 16/12/2019 15:33:00

Formatted Table

Page 59: [44] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [45] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [46] Formatted Daphne Cuvelier 16/12/2019 15:03:00

Font: 11 pt

Page 59: [47] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [48] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [49] Formatted Table **Daphne Cuvelier** **16/12/2019 15:33:00**

Formatted Table

Page 59: [50] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [51] Formatted Table **Daphne Cuvelier** **16/12/2019 15:33:00**

Formatted Table

Page 59: [52] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [53] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [54] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [55] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [56] Formatted Table **Daphne Cuvelier** **16/12/2019 15:33:00**

Formatted Table

Page 59: [57] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [58] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [59] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [60] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [61] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [62] Formatted **Daphne Cuvelier** **16/12/2019 15:03:00**

Font: 11 pt

Page 59: [63] Formatted Table	Daphne Cuvelier	16/12/2019 15:33:00

Formatted Table

Page 59: [64] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 59: [65] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt

Page 59: [66] Formatted	Daphne Cuvelier	16/12/2019 15:03:00

Font: 11 pt