

Referee comments in black.

Author's responses in green.

The scientific methods are valid and up-to-date and the experiments and calculations are adequately described. The authors acknowledge related work and clearly discriminate their data from data obtained by others. In some cases, where they discuss their data (e.g., regarding winners and losers of the 'competition' of meio- and macro-fauna) in relation to that of others they should be more specific about the exact content of the cited data so the reader can better comprehend the authors' discussions and conclusions. The data presented are sufficient to reach conclusions part of which – and that is not criticizing the ambitious work behind this study – are pointing out gaps in knowledge. The paper is well structured and reads mostly fine – in some parts of the results the language may seem a bit repetitive (abundances and species numbers are presented with almost the same wording). The abstract provides a good summary. In the way it is currently presented, the first part of the discussion (about the relative success of meio and macrofauna in different deep-sea environments) should be either significantly reduced or more specific with a better and quantitative presentation of data on Meiofauna from the study area from other studies. I would vote for a reduction of that part as it seems to be a bit off the main focus anyway.

To me, the main shortcoming of the paper is, that the authors are very carefully when stating their conclusions and overcautious if it's about the consequences of their findings. As the work touches societal concerns and areas of strong debates the authors should address in more depth the implication of their work regarding procedures and management of nodule mining.

In our opinion, the main message of this study is that we don't know enough about species diversity and species ranges to be conclusive about the potential impact of nodule mining. We fully understand the need and eagerness to get answers to acute societal concerns, but we must be cautious of not over-interpreting the results of this study. Yet we agree that there are some questions that we can address and recommendations that can be made. In the following lines we will try to address the concerns where we can or explain why we can't.

e.g., can we decide on regional management based on the available knowledge and are the APEIs appropriate as they are?

The answer to these questions is 'No' but not for scientific reasons. The location of the APEIs has been initially defined based on available knowledge (see http://www.soest.hawaii.edu/oceanography/faculty/csmith/MPA_webpage/MPAindex.html) and then severely constrained by contractor areas and reserved areas. A comparison of Figure 3 in Wedding et al. 2013 with Figure 1 in Lodge et al. 2014 clearly shows the difference between recommendations and implementation.

This has been clarified in the Introduction (page 3 lines 17-28):

From 'Due to the paucity of biological data in the CCFZ, the spatial management plan was designed mainly based on nitrogen flux at 100 m depth (a proxy for trophic inputs to the seafloor), modeled nodule densities, the distribution of large seamounts and the dispersal distances of shallow water taxa (Wedding et al., 2013). The nine proposed 400 x 400 km managed (non-mining) areas were included in the regional management plan for the CCFZ and designated as APEIs (Lodge et al., 2014). Most of the CCFZ however has already been

preempted to current exploration contracts and areas reserved for future exploration. The distribution of APEIs at the periphery of the CCFZ thus deviates from an optimal design.'

To "Due to the paucity of biological data in the CCFZ, the recommendations issued by Wedding et al. (2013) for the design of a network of protected areas were mainly based on nitrogen flux at 100 m depth (a proxy for trophic inputs to the seafloor), modeled nodule densities, the distribution of large seamounts and the dispersal distances of shallow water taxa. One of the main assumptions underlying the management plan is that longitudinal and latitudinal productivity-driven gradients shape the community structure and species distribution of abyssal communities. As a result, Wedding et al. (2013) divided the spatial domain of the CCFZ into 3 x 3 subregions and suggested to create one large no-mining area in each subregion. The size of the no-mining areas was defined with the aim of maintaining viable population sizes for species potentially restricted to a subregion, taking into account the inferred dispersal distances of species and of the plumes created by nodule mining (Wedding et al., 2013). Those principles were implemented in the regional management plan for the CCFZ, which resulted in the designation of 9 APEIs (Lodge et al., 2014). Most of the CCFZ however had already been preempted to current exploration contracts and areas reserved for future exploration. Consequently, the APEIs were located at the periphery of the CCFZ thus deviating from an optimal design.

Are there any specific recommendations that can be provided, e.g., regarding the size or arrangement of mining patches?

It would be premature to provide specific recommendations, first because the level of confidence on our estimates of species ranges is too low, second because polychaetes may not have the smallest species ranges (see also below).

What should be the focus of future studies and what would be the expected effort needed to come to scientifically sound conclusions?

In an ideal world, a stratified random sampling at nested scales, from region down to seascapes, would provide the scales of species turn-over while intensive sampling of selected habitats up to the point where the number of singletons decreases with sample size would provide accurate estimates of species diversity.

The conclusions part is so far rather summarizing what has been stated already before and may be a good place to discuss these things. The fact, that those discussions are rather limited in the current version of the manuscript is the reason for my general proposition that the manuscript should undergo a major revision before publication.

Below some more detailed comments

MAJOR ISSUES – IMPLICATIONS FOR MINING / MINING REGULATION

Regarding the main shortcoming of the paper mentioned above I urge the authors to significantly extend the discussion of their results towards the implications of their work with regard to nodule mining and its regulation. This could be distributed in several parts of the discussion as well as in a separate section in the discussion or in the conclusions. This, of course, has to be done with some caution to not extend beyond the scope of the study and has to take into account that this is a scientific publication and not a policy paper. However, it is clear that the motivation of the study – and certainly of societies providing the funding for mining-related investigations these days – is to provide the basis for scientifically sound

procedures and decisions regarding deep-sea mineral exploration and exploitation. This should be better reflected in the text. This includes recommendations regarding the management and regulations - where the data of the study allow this - but also specific requests for future investigations where the results reveal significant gaps. Below I am providing some examples where I think the discussion needs to move beyond where it currently terminates.

Page 3, line 15/16 'The distribution of APEIs at the periphery of the CCFZ thus deviates from an optimal design.' Page 11, line 20-23 'The biogeochemical settings as well as the biological patterns of the three size groups of the benthic fauna thus converge to conclude that the structure and functioning of the benthic ecosystem in APEI#3 is not representative of any of the four exploration contract areas included in this study.' Page 12, line 26-29 'The influence of the fracture zones on the dispersal of the abyssal fauna remains to be better understood as the Clarion and Clipperton fractures may act as a barrier for species with low dispersal abilities such as infaunal brooders. If so, the representativeness of seven out of the nine APEIs, which are partly lying beyond the fractures, may be questionable.' If these statements hold true, the concept of APEIs and the regional management plan as a whole don't seem to be appropriate.

What is the advice of the authors to overcome this problem?

As for now, this is a hypothesis that needs to be further tested. Our main advice is to foster research in the APEIs and to support this research we propose the future Environmental Compensation Fund to be created by the regulations on exploitation of mineral resources in the Area. This recommendation has been added to the Conclusions:

Pages 16 lines 21-24:

In order to ascertain that the APEIs collectively meet their goal of preserving the biodiversity of the CCFZ an ambitious research agenda is needed, the funding of which could rely on the willingness of contractors and Sponsoring States but could also become a priority of the future Environmental Compensation Fund to be created by the regulations on exploitation of mineral resources in the Area (ISBA/25/C/WP.1).

What do we know about the other APEIs and how their environmental conditions and faunal communities compare to license areas?

Studies on other APEIs are ongoing but few results have been published yet. Simon-Lledó et al. (2019a, 2019b) recently described megafaunal community patterns as a function of seafloor heterogeneity and nodule density from imagery surveys. Comparisons with similar megafaunal surveys undertaken in contract areas is however difficult due to a current lack of standardization of methods, both for the surveys and the image-based taxonomy.

What would be an optimal APEI layout and how would you – from the results of your study – address the question whether an area is suited as APEI or not.

Our results suggest that the boundaries of the management area and sub-regions used by Wedding et al. (2013) could be improved but do not contradict the conceptual bases of the current management plan. Again, the implementation rather than the design of APEIs is problematic. APEIs had several conservation objectives, including the maintenance of sustainable and healthy populations of minimum viable sizes and a full range of habitat types. The topic of the representativeness of the APEIs is too broad to be addressed here.

Can we use some easily measured sedimentological (grainsize?) or biogeochemical measurement to assess the probability that an APEI will host similar faunal communities than a specific license area? Should the assessment of correlations of habitat characteristics and fauna in APEIs be a focus of future studies?

In our constrained multivariate analysis (RDA), the environmental factors that were available explained 13% of the local and regional variations in polychaete community composition. The explanatory power of the model is low and could certainly be improved to some extent by a better understanding of the physico-chemical niche of species. However, the main unknown is most likely about the biology and biotic interactions of species: how long do they live, how do they reproduce and disperse, do they interact and how are they interacting between others. These would be key questions to answer, although much more challenging than looking at correlations of abiotic factors and biological variables.

If you consider the lack of knowledge potentially only a few years before exploitation commences: Should the ISA setup a scheme by which contractors carry out or fund baseline studies in the APEIs?

There is not such funding mechanism in the mining code for exploration nor recommendations towards contractors to carry out baseline surveys beyond their contracted area and it's beyond our expertise to assess whether such a mechanism could be implemented in the framework of current exploration contracts. The draft regulations on exploitation of mineral resources in the Area provides for the establishment of an Environmental Compensation Fund (ISBA/25/C/WP.1). The purpose of the Fund does not include the promotion of baseline studies in the APEIs but this is a recommendation we can make.

The following lines were added in conclusion (page 16 lines 20-24):

'The sampling effort in both the contract areas and the APEI however remains quite limited. In order to ascertain that the APEIs collectively meet their goal of preserving the biodiversity of the CCFZ an ambitious research agenda is needed, the funding of which could rely on the willingness of contractors and Sponsoring States but could also become a priority of the future Environmental Compensation Fund to be created by the regulations on exploitation of mineral resources in the Area (ISBA/25/C/WP.1).'

One consideration that lead to the APEIs' current position outside the area covered by license areas was to allow for very large areas. In light of the fact that, according to the current planning, only part of the license areas will be used for nodule extraction and the seemingly low species' ranges: do we need APEIs to conserve biodiversity or would the areas inside the patch of license areas, that are not mined do the job? Or do we need APEIs somewhere else, e.g., smaller ones between license areas?

In the current draft regulations on exploitation of mineral resources in the Area, a plan of work in the case nodule mining shall not exceed 75000 km² (ISBA/25/C/WP.1), which is the size of the exploration contracts areas. Thus, in the current planning, the only area that won't be mined are Preservation Reference Zones (PRZ) and non-mineable areas (slopes, no-nodule, etc...). Since the PRZ haven't been clearly defined yet and since non-minable area do not represent the full range of habitats in the CCFZ, and especially not the most threatened habitats, we believe that APEIs are required.

In addition, APEIs are very large for two reasons: 1) To allow for the self-sustainability of populations within the APEI. An alternative would be to create a higher number of smaller inter-connected APEI but we lack data on dispersal range of species, which is different from the geographic range of species, to discuss this alternate design. 2) Avoid the impact of the sediment plume, again we don't have the data to discuss the relevance of this point.

Page 13, line 1-5 'However, based on the best knowledge we have, our study suggests that [. . .] nodule mining would affect each year an area that is equivalent to the average geographic range of a polychaete species.' Spatial ranges – especially if they are indeed that small – are highly relevant.

Can we use polychaetes as key species here or would we need to have similar data also for other size classes and other groups of macrofauna? What data are available already?

Polychaetes are the most abundant and most diverse among the macrofauna. Polychaete might however be less threatened than peracarids, which are brooders and show narrower species ranges on average. Polychaetes might also be less functionally important than nematodes, which dominate the metazoan biomass or foraminifera, off which we know very little. If the aim is to monitor and preserve all levels of biological diversity, from gene, to species, to functions then polychaetes are likely not enough. The good news is, numerous studies have recently been undertaken in the CCFZ and are still going on. Some have been published recently but there is still a lot come. Our knowledge of benthic biodiversity in the CCFZ is going to significantly increase in the years to come.

What are the implications of these results for mining operations and their regulation? Do we need more research to understand whether the estimated spatial range is really true or just mirrors the inappropriate sampling effort available scientific knowledge is based upon? Or do we 'know enough' and could provide specific suggestions as for how to spatially arrange mined patches? Taking this further: if we take the precautionary approach seriously: if we have an average species range of 20km (and, for some of the species obviously a smaller one) wouldn't we need to restrict the mining operations by contractors including secondary impacts by the plume to that size until it is proven, that the high turnover of beta diversity is an artifact of undersampling?

Indeed, if the species ranges are narrow AND if the environmental objectives are to avoid species extinction then the spatial footprint of mining impact would need to be severely restricted. This is the meaning of the sentence "If true, the risk of species extinction is very high because the environmental footprint of nodule mining would largely exceed the range of many species". "If true" in this sentence refers to the fact that we cannot yet exclude that the average species range that we have estimated is biased by singletons. Thus, with the data we have we can't provide specific suggestions regarding the spatial arrangement of mining. That's what we meant by "The assessment of potential risks and scales of biodiversity loss thus requires an appropriate inventory of species richness in the CCFZ."

We further underlined the uncertainty regarding species range in the conclusion, page 16 lines 31-32:

"non-parametric estimators of species richness suggest that total species richness across the five study areas does not exceed 498 species which likely implies a species range much larger than 25 km."

Page 15, line 27/28 'The assessment of potential risks and scales of biodiversity loss thus requires an appropriate inventory of species richness in the CCFZ.' While the conclusions are basically a summary up to this point, this is where the discussion in implications starts: How should this goal should be achieved?

As outlined above we can suggest 1) a stratified random sampling at nested scales, from region down to seascapes and 2) an intensive sampling of selected habitats up to the point where the number of singletons decreases with sample size. We agree that these general recommendations would need to be more specific. There is a need to carefully think the sampling design and sampling effort together with statisticians. This would be a topic for another paper.

We can already say is that it won't be cheap. And we can also paraphrase Coddington et al. (2009) here and share their hopes "we suggest that inventory analyses continue to assess undersampling bias in order to justify the budgets required to obtain adequate data. Funding sources and consumers of these essential data can scarcely argue that inadequate results are acceptable. If results continue to demonstrate that much greater sampling intensities are required, such will eventually become the norm, rather than the exception."

The following lines were added in the Conclusions (page 17 lines 2-5):

In the framework of an ambitious and collective effort to inventory species richness in the CCFZ, a stratified random sampling at nested scales, from region down to seascapes, would provide the scales of species turn-over while intensive sampling of selected habitats up to the point where the number of singletons decreases with sample size would provide accurate estimates of species diversity.

How much of this work is, according to the knowledge of the authors, already done by baseline work of the different contractors and just needs metaanalysis of the pooled contractor's data (e.g., by an independent scientific consortium)? Or are samples and data lacking and more dedicated sampling campaigns needed? What effort would this take? Or - if that is too hard to estimate, how would you control if enough data are available (based on rarefaction curves? Based on biodiversity descriptors merging?)? If you compare this to what is found in the ISA regulations and guidelines: how does that compare?

This is a good point. Significant progress has been made during the last 5 years. Stratified random sampling has been carried out in the framework of the European project MIDAS (e.g. Simon-Lledo et al., 2019a, 2019b for megafaunal communities) and contractors are producing a large amount of data on macrofaunal communities in the Eastern CCFZ (e.g BGR: Janssen et al., 2015; GSR: De Smet et al., 2017; UKSR: Glover et al, 2016). A meta-analysis is going to be conducted that should provide insight onto species richness and species ranges (<https://www.isa.org.jm/news/deep-ccz-biodiversity-synthesis-workshop>). By the end of this Deep CCZ Biodiversity Synthesis we should be able to tell where we collectively stand in terms of what we know and what we don't know. In order to provide an accurate estimate of species richness, we would look for a decreasing trend in the accumulation curve of singletons.

What about the key-species concept? Could that become appropriated once the necessary knowledge was obtained or do you think we always have to cope with the full complexity when we want to address environmental impacts of deep-sea operations (assessment of the risks prior to operations, assessment of impacts happening during operations).

We must stress here that there is a difference between studies aiming at assessing the potential risks of mining and studies aiming at monitoring the impact of mining (i.e. Environmental Impact Assessment, EIA). The key species concept would apply to the EIA, which is beyond the scope of our study.

OTHER MAJOR ISSUES

Page line 3-27 The discussion of meiofauna in nodule areas comes as a bit of a surprise in the context of this paper, that does only provide data on macrofauna. If you want to leave this so prominent and detailed, you should first state what the data show. Does the Pape et al. study provides data from the same station so a quantitative comparison to other deep sea areas is possible? > In this case I would suggest to provide that quantitative information here. Otherwise consider reducing the discussion or move it to a less prominent part of the discussion. Maybe you could also connect it more to the paper, e.g. as an argument for focusing environmental impact studies on macro-fauna because they seem more relevant in terms of biomass and ecosystem function as in typical abyssal areas.

Page 11 lines 8-22. All meiofauna discussion has been reduced as suggested:

From 'Food supply, sediment grain size and the density of nodules are the three main environmental factors that seem to drive the structure and composition of polychaete assemblages in the CCFZ.

Nodules have antagonistic influences on different size groups of benthic communities. Meiofaunal assemblages are less abundant in nodule-rich than in nodule-free sediments (Miljutina et al., 2010; Pape et al., 2018). Nodules however increase habitat heterogeneity, providing hard substrate for sessile organisms and generally enhancing the standing stocks of both sessile and vagile megafauna (Amon et al., 2016; Vanreusel et al., 2016; Simon-Lledó et al., 2019). Similarly, nodules seem to enhance macrofaunal density (De Smet et al., 2017) and diversity (Yu et al., 2018). Our results support the reported positive and significant relationship between polychaete abundance and nodule density (De Smet et al. (2017). The macrofauna in nodule fields may benefit from increased food supply and the release from competition with meiofauna. Nodules increase seafloor roughness, thereby increasing friction (Sternberg, 1970; Boudreau and Scott, 1978) and potentially sediment deposition rates. The large sessile suspension feeders may similarly enhance biodeposition (Graf and Rosenberg, 1997). Both processes may stabilize sediments and increase organic carbon supply as tube lawns do, for example (Michael et al., 2000). An increase in food supply may explain the higher densities of polychaetes in nodule-rich areas. The divergent response of meiofauna to the presence of nodules further suggests some sort of competition between meiofauna and macrofauna. The contribution of meiofauna to benthic biomass generally increases along a bathymetric gradient to outweigh that of macrofauna at abyssal depths (Thiel, 1975; Rex et al., 2006; Wei et al., 2010). This pattern is assumed to reflect a selective advantage for small size at very low levels of food input (Thiel, 1975, 1979; Sebens, 1982, 1987; Rex and Etter, 1998). Sibuet et al. (1989) reported however a linear relationship between meiofaunal and macrofaunal biomass at abyssal sites. Both size classes indeed co-varied with organic carbon burial flux, which suggests the occurrence of a dynamic equilibrium between meiofauna and macrofauna at abyssal depths. Due to its small size, meiofauna is likely more efficient at exploiting the low level of food input, but this interstitial fauna may also be more sensitive to high nodule coverage because its ambit is largely limited to superficial sediments. The opposite effects of nodule coverage on meiofaunal and

macrofaunal densities may thus lie in a release from the advantage of being smaller in the abyss, inducing a shift in size-group equilibrium toward increased macrofaunal densities. These results suggest that nodule coverage have an influence on the functioning of the ecosystem, because it modifies biotic interactions and resource allocation among functional groups.'

To 'Food supply, sediment grain size and the density of nodules are the three main environmental factors that seem to drive the structure and composition of polychaete assemblages in the CCFZ.

The abundance and richness of polychaetes were positively correlated with nodule density, which is consistent with previous studies showing that nodules enhance macrofaunal densities and polychaete diversity (De Smet et al., 2017; Yu et al., 2018). Nodules may have antagonistic influences on different size groups of benthic communities. Meiofaunal assemblages are less abundant in nodule-rich than in nodule-free sediments, which may be due to the lower volume of sediment available in nodule areas (Miljutina et al., 2010; Hauquier et al. 2019). In our study, the volume and surface occupied by nodules were not quantified but the positive relationship between nodule density and polychaete abundance shows that space is not a limiting factor for polychaetes. Nodules also increase habitat heterogeneity, providing hard substrate for sessile organisms and generally enhancing the standing stocks of both sessile and vagile megafauna (Amon et al., 2016; Vanreusel et al., 2016; Simon-Lledó et al., 2019). Nodules increase seafloor roughness, thereby increasing friction (Sternberg, 1970; Boudreau and Scott, 1978) and potentially sediment deposition rates. The large sessile suspension feeders may similarly enhance biodeposition (Graf and Rosenberg, 1997). Both processes may decelerate water current, stabilizing sediments and, thus, increase organic carbon supply as polychaete tube lawns do, for example (Friedrichs et al., 2000). An increase in food supply may explain the higher densities of polychaetes in nodule-rich areas.'

Connected to this: Page 10, line 16 'The contribution of meiofauna to benthic biomass generally increases along a bathymetric gradient [. . .] which suggests the occurrence of a dynamic equilibrium between meiofauna and macrofauna at abyssal depths.' Again - this is very detailed for a study that does not focus on size class comparisons. I assume the Sibuet paper focuses on non-nodule areas? I understand you want to put forward that macrofauna is particularly important in the CCZ / in nodule areas as they – different to what was previously reported - show but a relative increase as compared to Meiofauna (i.e., neither do they show a relative decrease at depth as compared to meiofauna nor do they scale with meiofauna). This really would need a quantitative basis, i.e., a comparison of macrofauna abundances (better biomass) to meiofauna abundances at your study sites relative to other areas. > consider adding more quantitative information

This has been deleted following previous comment.

Connected to this: Page 10, line 23 'Due to its small size, meiofauna is likely more efficient at exploiting the low level of food input, but this interstitial fauna may also be more sensitive to high nodule coverage because its ambit is largely limited to superficial sediments.' Do you mean, that the meiofauna is restricted to the top layer where the available sediment volume is limited by the presence of nodules? I think you dont show the data but I assume that also for polychaetes the top sediment layer is the one where most individuals are found. In any way you could strengthen this idea by comparing your abundance vs. depth

relationship with that of meiofauna in nodule areas. > please comment, explain and consider including this information in the manuscript

This has been deleted as previous comment.

Page 14, line 7/8 'Overall, the combination of high local diversity, unsaturated rarefaction curves, high levels of cryptic diversity and high rates of species turnover suggest that polychaete diversity in the CCFZ is large and vastly under-sampled.' It needs a discussion of the most appropriate technologies (sampling gear, analysis) and the expected effort it needs to raise our knowledge to a level appropriate to decide on mining (yes or no, spatial organization of operations and protected areas), and allow for scientifically sound impact assessment and management

Differences in sampling gear, type of preservation and how the diversity estimators consider the large presence of singletons were discussed along the Discussion. The expected efforts needed to reach an appropriate biodiversity assessment was suggested in the Conclusions with the following sentences:

Page 16 lines 20-24:

'The sampling effort in both the contract areas and the APEI however remains quite limited. In order to ascertain that the APEIs collectively meet their goal of preserving the biodiversity of the CCFZ an ambitious research agenda is needed, the funding of which could rely on the willingness of contractors and Sponsoring States but could also become a priority of the future Environmental Compensation Fund to be created by the regulations on exploitation of mineral resources in the Area (ISBA/25/C/WP.1).'

And page 17 line 2-5

'In the framework of an ambitious and collective effort to inventory species richness in the CCFZ, a stratified random sampling at nested scales, from region down to seascapes, would provide the scales of species turn-over while intensive sampling of selected habitats up to the point where the number of singletons decreases with sample size would provide accurate estimates of species diversity. Both strategies are needed to assess the potential risks and scales of biodiversity loss due to nodule mining in the CCFZ'.

Maybe in this context it should also be discussed, if (and why!) the authors believe, that polychaetes may serve as a model group for baseline and impact assessments. Or is this just the 'pet group' of the authors and any other group should be similarly addressed before taking decisions? > please extend discussions to include these points.

Polychaetes are the most abundant and most diverse among the macrofauna. Polychaete might however be less threatened than peracarids, which are brooders and show narrower species ranges on average. Polychaetes might also be less functionally important than nematodes, which dominate the metazoan biomass or foraminifera, off which we know very little. If the aim is to monitor and preserve all levels of biological diversity, from gene, to species, to functions then polychaetes are likely not enough.

The following text was added in aim explaining the relevance of studying polychaetes:

Page 4 line 6-10

'To tackle these issues [study aims], we focused on polychaete assemblages. Polychaetes are the dominant and most diverse group of the macrofauna; they can be quantitatively

sampled, and identify down to species level using a combination of morphological and molecular methods (Hessler and Jumars, 1974; Janssen et al., 2015; Wilson, 2017). Polychaetes also show a wide range of biological traits, from trophic behaviors to life history strategies, and play a major role in the functioning of benthic communities (Hutchings, 1998; Jumars et al., 2015).'

MINOR ISSUES

Page 1, line 1-3 Including the metaanalysis performed the study indeed addresses the entire CCZ. However, the stations of this study are all rather in the eastern part. > rephrase the title to not raise false expectations, e.g., by replacing 'across the nodule province of the Clarion-Clipperton Fracture Zone' with add 'across the nodule province of the eastern Clarion-Clipperton Fracture Zone'

Page 1 lines 1-3. Done as suggested.

Page 1, line 17 '. . .the SO239 cruise aimed at improving species inventories. . .'. Was this really the subject of the cruise as a whole or of this expedition? > consider rephrasing

*Page 1 line 17. This has been changed to '. . . the SO239 cruise **provided data to improve species inventories.**'*

Page 2, line 6 'Only about 1 % of abyssal plains have been explored to date'. In this context of this paper I would restrict the use of the term 'explore' / 'exploration' to deep-sea mining-related activities > consider rewording

*Page 2 line 8. This has been changed to 'Only about 1 % of abyssal plains have been **investigated to date...**'*

Page 2, line 7 'In particular' seems to connect to the previous sentence but in fact does not. > consider remove

Page 2 line 9. Done as suggested (removed).

Page 2, line 9 '. . .mainly manganese and iron, . . .' > I would also mention copper, nickel and cobalt right away here - than you don't have to repeat that in line 13/14.

*Page 2 lines 10-11. Done as suggested. It has been changed to '..., mainly manganese and iron **but also copper, nickel and cobalt ...**'*

The repeated words were removed.

Page 2, line 15/16 '. . .the International Seabed Authority [. . .] is in charge of protecting fauna against any pollution or other hazards...' Pollution is not the main concern in the context of nodule mining and expected impacts related to this study. > I would rephrase. Maybe just refer to harm (i.e., 'protecting fauna against harm')?

Page 2 line 19. Done as suggested.

*It has been changed to '. . .the International Seabed Authority [. . .] and is in charge of protecting fauna against any **harm...**'*

Page 2, line 25 I don't understand what is meant with 'scaling issue'. Is this referring to the uncertainties connected to effects of the full scale, long-term operations with large plumes as compared to single experimental tracks? > please rephrase / be more specific

Page 2, line 31. This has been changed from 'Beyond the scaling issue...' to 'Beyond the unpredictable effects of the full-scale mining...'

Page 2, line 27 > replace 'the high diversity' by 'a high diversity'

Page 3 line 1. Done.

Page 3, line 23 'test the hypotheses that support spatial conservation planning in the CCFZ'. I don't think that these hypotheses (that the authors think would serve as guidance or that form the basis of the current regional management plan are explicitly stated somewhere in the publication. > consider being more specific here or state them elsewhere in the paper

Page 3 lines 20-22. The following sentence was added in Introduction: "One of the main assumptions underlying the management plan is that longitudinal and latitudinal productivity-driven gradients shape the community structure and species distribution of abyssal communities."

Furthermore, we have reworded the aims (page 4 lines 3-6):

From "The structure and composition of polychaete assemblages were analyzed to describe and identify alpha and beta diversity patterns, test the hypotheses that support spatial conservation planning in the CCFZ, assess the representativeness of an APEI and potentially improve the assessment of potential risks to biodiversity due to nodule mining."

To "The aims of our study were (a) **to test the hypotheses that support spatial conservation planning in the CCFZ, particularly the environmental drivers of alpha and beta diversity such as organic carbon fluxes to the seafloor and nodule density**; (b) to assess the representativeness of an APEI (i.e. APEI#3) and (c) to improve the assessment of potential risks of biodiversity loss due to nodule mining."

Page 4, line 1/2 > replace '...were located between 4000 and 5000 m depth. . .' by 'had water depths between 4000 and 5000m'

Page 4 lines 19-20. Done as suggested.

Page 4, line 12/13 '...all nodules picked up from the sediment surface, washed and individually measured and weighed. . .' It should be mentioned already here that the water that was used for washing the nodules was sieved after washing. Have the nodules themselves been inspected for small polychaetes, e.g, living in tubes attached to the nodules? > rephrase and make sure to mention somewhere in the paper, if the data also include nodule-associated polychaetes

Page 5 lines 8-10. This has been changed and the nodule-associated polychaetes clarified:

From 'The box core sample surface was photographed, and all nodules picked up from the sediment surface, washed and individually measured and weighed.'

To 'The box core sample surface was photographed, and all nodules picked up from the sediment surface, **washed with cold seawater over a 300 µm-mesh sieve and individually weighed. Sessile polychaetes, if present, remained attached to the nodules and were not considered in this study.**'

Page 4, line 18 '...The sieve residues from the overlying water and the washed nodules were combined with all layers for the community analysis...' Was the material combined (i.e., before analysis) or the data? > specify in the text

These layers (overlying water, the nodule washing water and the 0–3 cm layer) were combined after sieving, before sorting. It has been clarified in previous sentences (page 5 lines 13-14):

From ‘The overlying water residue and the 0–3 cm layer were immediately sieved in the cold room with cold seawater (4 °C) and then live-sorted.’

*To ‘The sieve residues from **the overlying water and nodule washing were added to the 0-3 cm layer and live-sorted.**’*

The correspondent lines (page 5 line 16) cited by Referee #2 were changed:

From ‘The sieve residues from the overlying water and the washed nodules were combined with all layers for the community analysis’

To ‘All layers were combined for the community analysis.’ making reference to all layers (overlying water and washed nodules added to 0-3 cm; 3-5 and 5-10 cm).

Page 4, line 20/21 ‘. . .(see Section 2.3 DNA extraction, amplification, sequencing, and alignment)’ No need to refer to a section that follows directly > remove

Done (removed).

Page 4, line 24/25 ‘. . .and 1600 bp of 18S genes. . .’ ? Are 18S data really used in this study (I could not find it later on)? If not: restrict M&M to 16S and COI or discuss why that approach was not successful or not included in the analyses.

This is correct, the 18S data is not considered in the present study. However, we will available them concomitantly with the other genes. Because this, the methods used to amplify them must figure in the manuscript.

We have added (page 9 lines 17-19) the following sentence in the Results section to clarify: ‘The 18S gene was sequenced for phylogenetic purposes on a restricted number of specimens. The 21 sequences of the 18S gene that have been obtained are mentioned here because they were archived concomitantly with COI and 16S sequences in GenBank and BOLD public datasets but they are not further considered in this study.’

Page 5, line 13 ‘To separate closely related species...’ [...] observed between intraspecific and interspecific variations’ What does ‘closely related species’ mean? Specimen that could not be discriminated based on morphology? > specify Page 5, line 13-17 To separate closely related species [...] observed between intraspecific and interspecific variations’ This section is describing the principle not what actually was done. This does not fully qualify for a Materials and Methods part > Move to another part of the study (introduction?) or rephrase.

Page 6 lines 11-12. This has been clarified with the addition of the suggested information and rephrasing:

From ‘To separate closely related species, the principle of phylogenetic species was used, [...] observed between intraspecific and interspecific variations’

*To ‘We separated closely related **species (specimens that could not be discriminated morphologically)** using the principle of phylogenetic species, whereby the genetic divergence among specimens belonging to the same species (intraspecific) is smaller than the divergence among specimens from different species (interspecific) (Hebert et al., 2003b)’*

Page 5, line 25 ‘. . .to calculate nodule density. . .’ Is nodule mean size or size distribution also considered in this study? If not, why was this not included as a parameter that may shape communities? > explain, consider adding explanation to the paper

The nodules were weighted but not sized.

Page 5 lines 8-9. It was corrected:

From ‘The box core sample surface was photographed, and all nodules picked up from the sediment surface, washed and individually measured and weighed.’

To ‘The box core sample surface was photographed, and all nodules picked up from the sediment surface, washed with cold seawater over a 300 µm-mesh sieve and individually weighed.’

Page 5, line 25-29 ‘Particulate organic carbon flux (POC, mg C m⁻² d⁻¹) at the seafloor for our study areas [. . .] applying the Suess algorithm (POC at the seafloor as a function of the net primary production scaled by depth; Suess, 1980; Table 2).’ How do POC fluxes estimated with different methods compare where they overlap (i.e. in the study area?) > consider adding that information to the paper.

Spearman correlation shows a significant correlation (rho 0.90, p < 0.05). This was included in the Figure 3.

Page 6, line 1 ‘2.6 Regional-scale data’ Also the Ocean Productivity-based POC fluxes in the previous section refer to the regional scale > choose another headline, e.g., ‘Regional scale polychaete community data’

Page 7 line 1. Done as suggested but also modified in order to clarify the range of the meta-analysis: ‘2.6 NE Pacific-scale polychaete community data’

Page 6, line 6 > add references for ES163 and bootstrap

References of the papers providing ES163 and bootstrap are given in the text (page 7 line 5) as well as in Table 2. Reference of the paper describing bootstrap are given in the text (page 7 line 19).

Furthermore, ES163 has been explained in the text with the addition of the following sentence:

Page 7 lines 14-15 ‘Based on these data the expected number of species was calculated for 12 individuals (ES12) and 163 individuals (ES163); as well as for three samples (S3).’

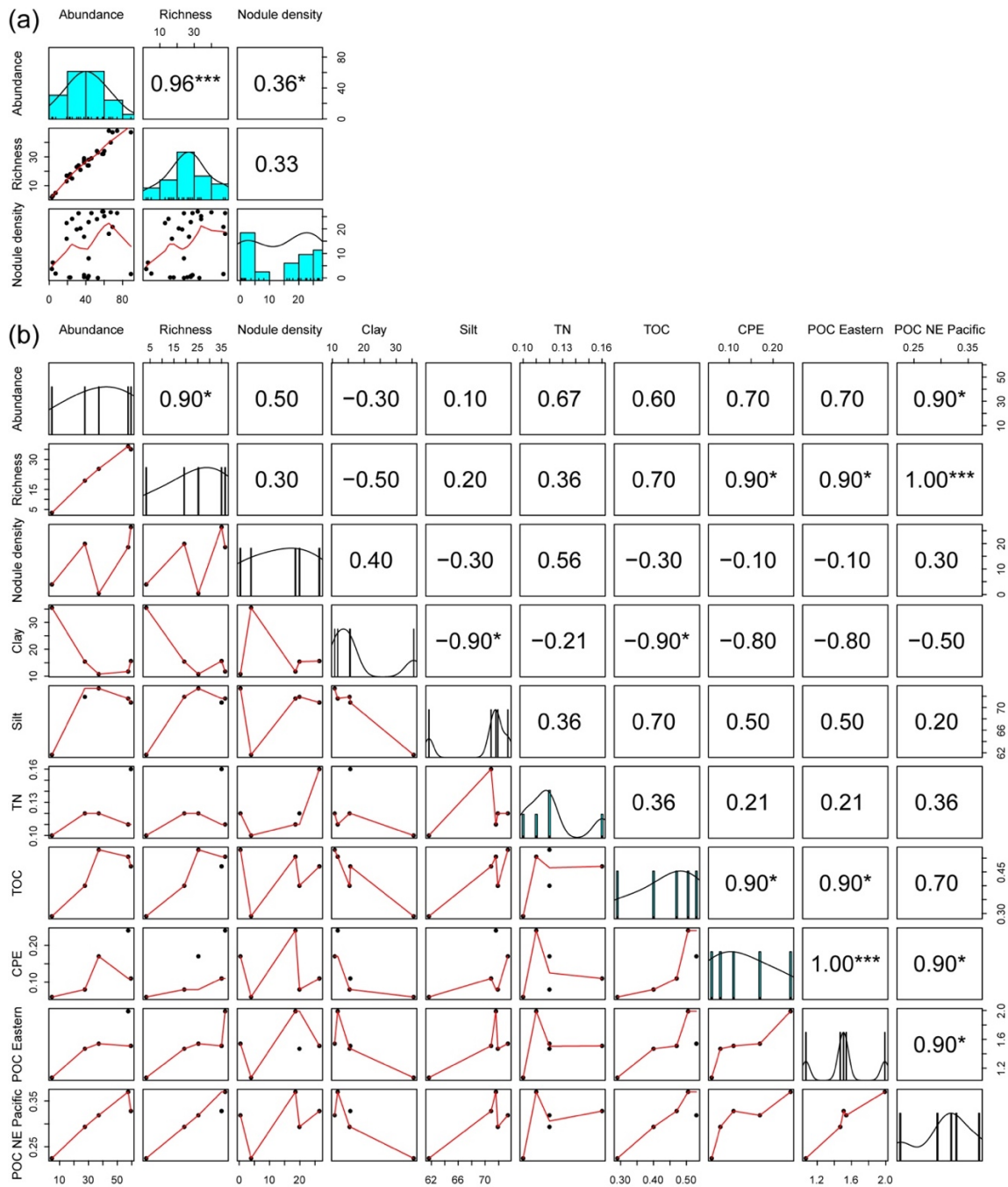
Page 6, line 20/21 ‘Spearman correlations were sought between biotic and abiotic variables, using data from the SO239 cruise in the CCFZ and data compiled from the literature.’ The data used for these correlations should match the data sources listed in section 2.5 > to avoid confusion I suggest to just refer to section 2.5. here. If the ‘biotic and abiotic variables’ include data not mentioned in section 2.5 add them there.

Figure 3 (below). The variables POC flux at seafloor from Volz et al. (2018) and the POC flux at seafloor estimated in the present study were included in the revised Figure 3 as POC Eastern and POC NE Pacific, respectively. The following sentence was added in the caption ‘POC Eastern values provided by Volz et al. (2018); POC NE Pacific values were estimated in the present study.’

Moreover, in order to be clear, the figure was separated in (a) when having data from each box-core sample such abundance, richness and nodule density (n=30); and (b) when having data averaged by area (n=5) such clay, silt, TN, TOC, CPE, POC Eastern and POC NE Pacific, and averaged abundance, richness and nodule density.

The corresponding caption was changed from 'Figure 3. Correlation matrix between biotic and abiotic variables from sampled areas within the eastern CCFZ. Diagonal panels show the distribution frequency of values for each variable. Below-the-diagonal panels show the correlation plot between pairs of variables. Above-the-diagonal panels show the Spearman coefficient correlations between pairs of variables. "*" indicates $p < 0.05$, "***" $p < 0.01$ and "****" $p < 0.001$.'

To 'Figure 3. Correlation matrix between biotic and abiotic variables from sampled areas within the eastern CCFZ. Diagonal panels show the distribution frequency of values for each variable. Below-the-diagonal panels show the correlation plot between pairs of variables. Above-the-diagonal panels show the Spearman coefficient correlations between pairs of variables. **Abundance, richness and nodule density per box-core (a) and average biotic and abiotic variables per area (b). POC Eastern values provided by Volz et al. (2018); POC NE Pacific values were estimated in the present study.** "*" indicates $p < 0.05$, "***" $p < 0.01$ and "****" $p < 0.001$.'



Page 6, line 23 to Page 7, line 14 Also in this section it should be described what has been done while a description of how the methods work does not seem appropriate for the M&M section (e.g., 'Low values of m give a high weight to dominant species, high values of m give a high weight to rare species.'). > Rephrase, possibly move parts to other sections

The NNESS and CNESS distances are not commonly used in community ecology although they have interesting properties, in particular to rationalize the weight given to abundant and rare species rather than the arbitrary choice of a data transformation (e.g square root, double square root...). For this reason we think that it is worth providing some information on the use of these metrics in the M&M section.

Page 7, line 21 '...tended to decrease from east to west with high spatial variation' 1. the main axes does not seem to go strictly longitudinal > replace 'east to west' by 'southeast to

northwest' 2. 'high spatial variation' would make more sense in a study design, that follows a clear geographical transect. > consider rephrasing, e.g., 'high variability between neighboring areas'.

Page 8 line 25-26. Done as suggested.

Page 8, line 2 'The relative contributions of trophic guilds also varied among the areas...' Is there an explanation found somewhere, how trophic guilds were determined? > If not, add description and references to M&M.

The trophic guilds were defined based on literature (Jumars et al., 2015).

The following phrase was included in the section 2.4 Operational taxonomic units (OTUs) (page 6 lines 19-20): 'Trophic guilds were determined following Jumars et al. (2015) at family level.'

Consequently, the section name (page 6, line 8) has been changed to '2.4 Taxonomic identification and feeding guilds classification'

The changing from "Operational taxonomic units (OTUs)..." to "Taxonomic identification..." followed a comment of Referee #4.

Page 8, line 6 'Off the 1223 polychaetes, 1118 specimens belonging to 78 possible genera within 40 families were identified down to Morphospecies. . .' What are 'possible genera'? > consider rewording, e.g., '. . .possibly belonging to 78 genera. . .?'

This makes reference to possible new genera. It was corrected to valid genera only. Also, we have corrected the number of sampled polychaetes which is 1233 instead of 1223.

*This was changed (page 9 line 11) to 'Off the **1233** polychaetes, 1118 specimens belonging to **62 genera** within 40 families were identified down to morphospecies.'*

Page 8, line 6/7 '1118 specimens [...] were identified down to morphospecies (see Section Data availability)' Not sure why you refer to that section here. > please provide explanation and consider including it in the text.

This has been removed.

Page 8, line 14 'The mean number of species tended to decrease from east to west with high spatial variation. . .' see comment above (regarding Page 7, line 21, second comment)

Page 9 lines 20-21. Done as suggested.

Page 10, line 13/14 'Both processes [i.e., increased friction and sediment deposition / biodeposition rates] may stabilize sediments and increase organic carbon supply as tube lawns do' I dont see the connection to sediment stability. > please explain better what your idea is here

It has been showed (Graf and Rosenberg, 1997; Friedrichs et al., 2000) that biological structures in the sediment-water interface favored the biodeposition and avoid erosion (e.g. polychaete tube lawns) by deceleration of water flow leading to a possible increase in food supply.

*Page 11 lines 20-21. It has been rephrased to 'Both processes **may decelerate water current stabilizing sediments and, thus, increase organic carbon supply as polychaete tube lawns do**'.*

Also, the correspondent reference was incorrectly written (names in the place of surnames), we have changed to 'Friedrichs et al., 2000'

Page 10, line 15/16 'The divergent response of meiofauna to the presence of nodules further suggests some sort of competition between meiofauna and macrofauna.' I can see that - if nodules increase food supply but meiofauna abundances are relatively small, meiofauna may be unable to make full use of the additional food. What I don't understand is why the reason does need to involve competition with macrofauna (see also my major comment on the meiofauna discussion above). > please provide explanation and consider including it in the text.

This has been deleted as suggested.

Page 11, line 34/35 'No significant correlation was however found between alpha diversity and productivity, neither at the NE Pacific scale nor at the scale of the whole CCFZ.' Do the authors have a hypothesis why this can be the case? Could it be related to the fact that most of the tested areas lie within more or less similar mesotrophic conditions and that this 'biased' data set is not fully appropriate to address this question? > please consider discussing the reason for the missing significant correlation of diversity and productivity on larger scales.

Sorry but the sentence was not completely right. We have changed (page 12 lines 30-31) to:

"Species richness and productivity were significantly correlated at Eastern CCFZ scale, but no significant correlation was found between alpha diversity and productivity in the meta-analysis at the scale of the NE Pacific".

Furthermore, we believe that the missing significant correlation between diversity estimators and productivity at whole CCFZ scale is mostly due the differences in methods, in particular integrative vs. morphological taxonomy.

The following phrase was added (page 12 lines 31-32):

"The reason diversity and productivity were not correlated in the meta-analysis that included data from the literature could be mainly methodological. In particular, the use of integrative taxonomy in this study versus morphological taxonomy in previous works might hinder comparisons of diversity metrics."

Page 12, line 5/6 'The fact that the APEI#3 lies mostly north of the Clarion Fracture Zone may however also contribute to its dissimilarity with the areas located in the CCFZ per se.' This statement reads quite vague as the idea of geographical barriers is not mentioned and elaborated before the next section > please consider adding (see next section) after the statement.

This has been deleted because was vague and the next section will better discuss it.

Page 12, line 12/13 '...characterized by a peak and through ...' Typo > change 'through' to 'trough'

Page 13 line 14. Done as suggested.

Page 12, line 24-26 'However, species identification was based on morphology only, although cryptic species are common among scavenging amphipods, even in abyssal lineages (Melo, 2004; Havermans et al., 2013)' Another reason is, of course, that scavenging

amphipods are typically highly motile. > consider adding mobility as an argument why scavenging amphipode distribution is not limited by fracture zones.

Page 12 lines 27-28. It has been changed:

From 'In the abyssal Pacific, the CCFZ and the Peru Basin share nine species of scavenging amphipods (Patel et al. (2018), which thus potentially cross the Clipperton and Galapagos Fracture Zones'

*To 'In the abyssal Pacific, the CCFZ and the Peru Basin share nine species of scavenging amphipods (Patel et al. (2018), which are **highly motile** and thus potentially cross the Clipperton and Galapagos Fracture Zones'*

Page 13, line 5 'In other words, nodule mining would affect each year an area that is equivalent to the average geographic range of a polychaete species.' This sounds like one mining operation would lead to the extinction of one polychaete ('only' - as some may argue). > consider removing 'a', i.e., write 'equivalent to the average geographic range of polychaete species...'

Page 14 line 8-10. Done as suggested.

Page 13, line 27/28 '...suggesting that such extreme environmental conditions...' I don't share the view that the deep sea is per se an extreme environment. > replace 'such extreme' with 'the specific' or explain what specifically is considered extreme

Page 14 lines 31-32. Done as suggested.

Page 14, line 1/2 'This highlights a shortcoming of COI-based barcoding because success rates for COI sequencing are generally low...' ? Are current molecular approaches appropriate if only a relatively small proportion could be identified based on 16S and COI and even less with both? Where is the problem and can it be overcome? If there are new promising methods that base on other regions of the genome: how can we safeguard comparability of the full data set including new and older data?

The current molecular approach using COI and 16S genes has proved to be appropriate in delineating species (e.g., Carr et al., 2011), but the sequencing success, especially for COI, is low. The reasons for failure can be numerous from bad DNA preservation to inappropriate DNA primers, annealing temperatures, etc...To some point, the only way to overcome the problem is to invest more time and efforts to get DNA sequences out of reluctant samples. For now, the most parsimonious method in our opinion is to associate morphology and DNA.

Page 15 lines 5-7. It has been changed:

From 'This highlights a shortcoming of COI-based barcoding because success rates for COI sequencing are generally low and a combination of several genetic markers plus morphology is essential to accurately assess species diversity.'

*To 'This highlights a shortcoming of COI-based barcoding because success rates for COI sequencing are generally low. A combination of **several genetic markers associated to formal morphological descriptions are thus essential** to accurately assess species diversity.'*

Page 15, line 2-4 'The latter estimate assumes that we have sampled 0.1 % of the polychaete species in the CCFZ and that these species have narrow geographical ranges about the size of a yearly mined area.' If I understand right, this refers to the expected annual area exploited as part of one mining operation – not the total annually mined area >

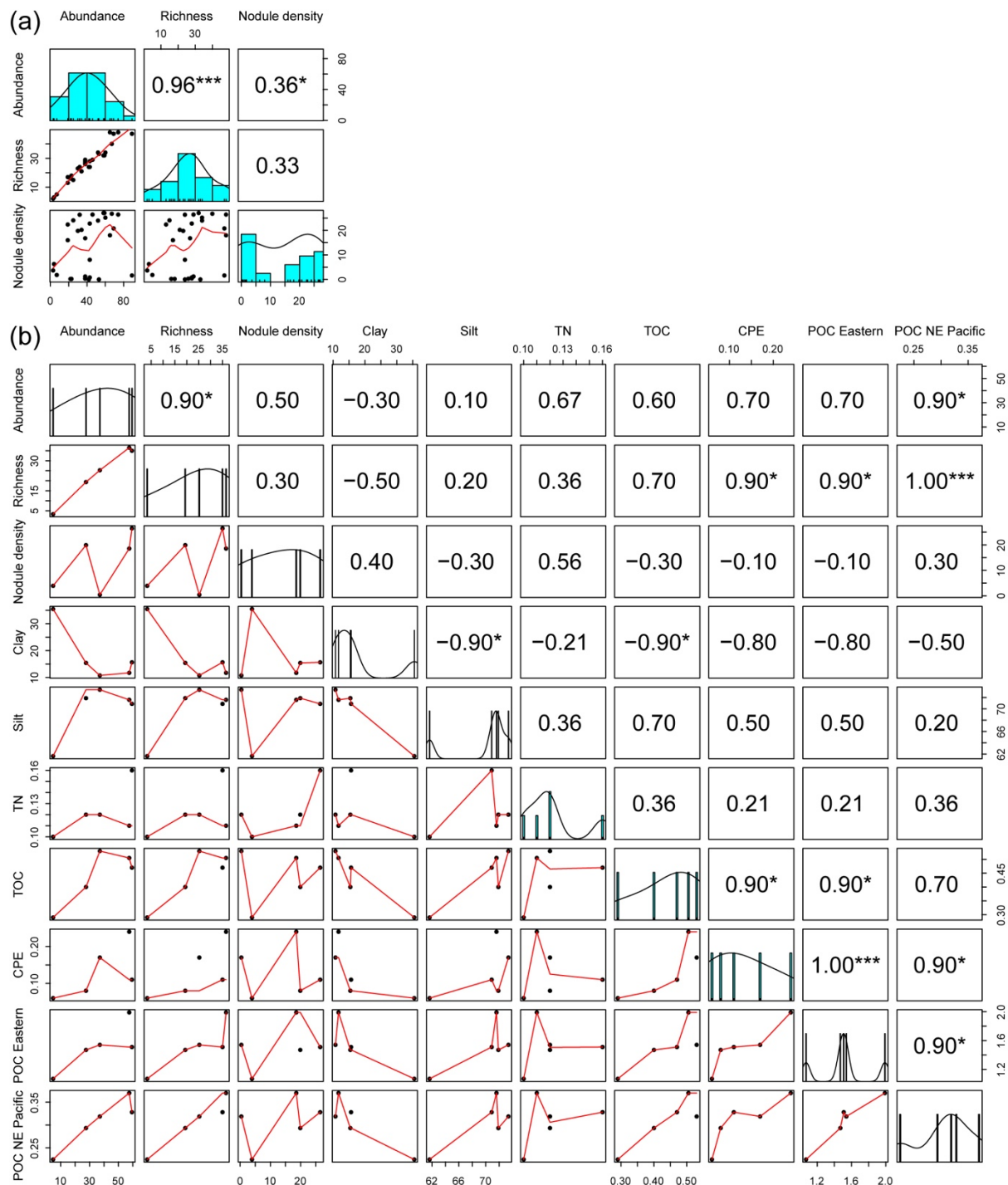
replace 'a yearly mined area' with 'the area that will presumably mined in one year by a single mining operation'.

Page 16 line 9. This has been changed.

Page 31, Fig. 3 Irrespective of the fact that the variables are provided in the diagonal panels I would prefer if to the side of the plot the variables would be indicated like in

<https://images.app.goo.gl/oFQRE6xD7fvFwxJR6>

Done as suggested, please see the revised figure 3 below:



Page 32, Fig. 4 '...in relation to the 2002–2018 average particulate organic carbon (POC) concentration at the seafloor along the CCFZ. The background map shows average POC flux

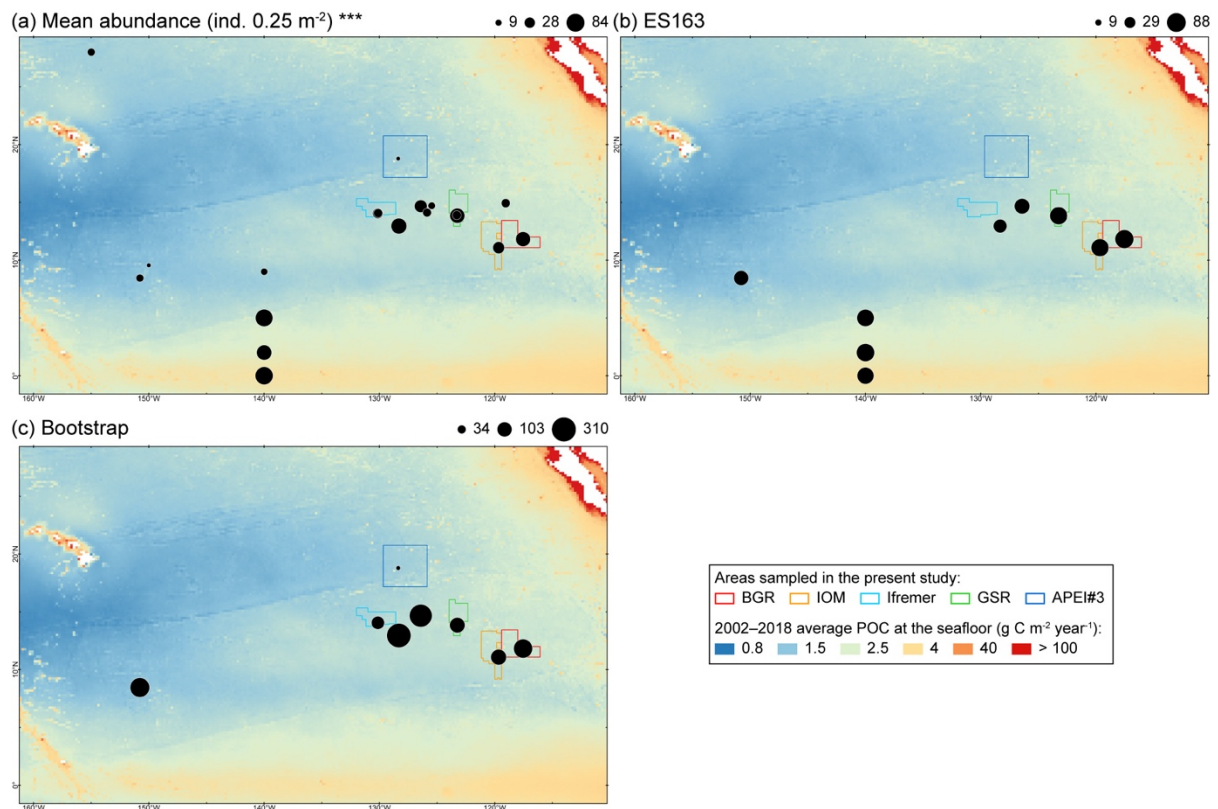
at the seafloor during the 2002–2018 period.’ How can the maps show relations to POC concentration and flux at the same time? > consider rephrasing the caption. The caption should also state that this shows / includes data from published studies and refer to section 2.6

Page 38 Figure 4. This has been rephrased:

From ‘Figure 4. Map of mean abundance (a) and diversity estimators, ES163 (b) and bootstrap (c), from the Northeast Pacific in relation to the 2002–2018 average particulate organic carbon (POC) concentration at the seafloor along the CCFZ. The background map shows average POC flux at the seafloor during the 2002–2018 period.’

To ‘Figure 4. Plot of mean abundance (a) and diversity estimators, ES163 (b) and bootstrap (c), from previous and the present study (Table 2) in relation to the 2002–2018 average particulate organic carbon (POC) flux at the seafloor along the CCFZ (background). “***” indicates significant ($p < 0.001$) Spearman correlation.’

Furthermore, an asterisk was included in Figure 4a in order to highlight that the relation between abundance and POC at seafloor was significant (figure below):



References cited in the authors answers:

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