**Biogeosciences
Discussions**

Interactive comment on "Interannual variation in the epibenthic megafauna at the shallowest station of the HAUSGARTEN observatory (79° N, 6° E)" *by* K. S. Meyer et al.

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We thank Anonymous Reviewer #2 for his or her comments on our manuscript. The comments are helpful and pertinent. Our response appears below.

The reviewer states that our study does not cut across disciplines, as stated in the journal objectives, but rather is a descriptive biodiversity study and requires major revision before publication in Biogeosciences. We agree that our study is primarily concerned with the biological community of our station; however, the documentation of changes in biogenic sediment compounds indicating food availability at the seafloor and benthic biomass – as well as the discussed correlation between these parameters and the

C8524

abundance and diversity of megafauna – make our study more than just a biodiversity study. Rather than merely reporting on the identity and abundance of megafauna found at our station, we discuss the interaction between biochemical conditions of the sediment and the megafaunal community over a 10-year timeframe. Discussion of this interaction broadens the significance of our study and fits well with the stated journal objectives. Megafaunal organisms and their activities alter the small-scale (centimetres to metres) habitat structure and biogeochemical regime. Therefore, a study describing changes in megafaunal densities, especially in biota that alter the sediment structure (e.g. sea cucumbers), also pertains to changes in biochemical properties (Quéric and Soltwedel, 2007; Soltwedel and Vopel, 2001; Hasemann and Soltwedel, 2011). We have changed some wording in the introduction and discussion sections of our revised manuscript to better emphasize the interaction between biotic environmental parameters and the benthic megafauna:

From section 1: "We focus on...the influence of food input to the seafloor, as indicated by biochemical condition of the sediment, on the epibenthic megafauna. Conversely, megafaunal organisms and their activities can alter the small-scale habitat structure and biochemical regime (Soltwedel and Vopel, 2001; Quéric and Soltwedel, 2007; Hasemann and Soltwedel, 2011)."

From section 4.2: "Our results indicate that benthic megafaunal dynamics are greatly influenced by biochemical condition of the sediment, which indicates food input to the seafloor. In the years leading up to 2007, food input to the seafloor decreased slightly, as indicated by sediment-bound pigments in the top sediments. This lower phytodetrital input could explain the lower overall faunal density, in particular that of the dominant deposit-feeding ophiuroid O. gracilis in 2007..."

Perhaps a weakness of the manuscript in its current state is the lengthy discussion of extraneous information which distracts from our key findings. See below for our specific responses to the reviewer's comments on sections 3.4, 4.1, and 4.6. The reviewer made a valid point in stating that section 3.6, which is concerned with sediment

C8525

biochemical parameters, is very short in comparison to other sections concerned with biological species. We would like to point out, however, that these results, though concise in their reporting, are discussed at greater length in sections 4.2 and 4.3.

To answer the reviewer's question, there is nothing special about the dates 2002, 2007, and 2012. Sampling dates were chosen to be at regular intervals over a time span long enough to potentially generate observable changes in benthic megafaunal abundance but not so long as to leave large gaps between sampling dates. The availability of ship time was also a consideration in choosing sampling dates. The fact that ground-truthing was not conducted in the same years as photographic sampling (except 2012) also reflects limitations on ship time. We would like to point out, however, that many studies on megafauna rely solely on camera observations with no physical samples at all. Also, one of the great advantages of using a camera system is that the method is not invasive. Even if we had the ship time available, we would not have wanted to trawl during every single campaign for the sole purpose of ground-truthing, as it damages the seafloor and changes its communities. The reason for the repeated trawling was the need for megafaunal tissue samples for other analyses (i.e. stable isotope/food web studies).

We now respond to more specific aspects of the manuscript which the reviewer addressed. The reviewer is mistaken in stating that the camera altitudes were different in 2002-2007 and 2012. During camera deployments in all sampling years, we aimed to take photographs at an altitude of 1.5 m above the sea floor. Of course, sea conditions and variations in bottom topography precluded us successfully hitting the ideal 1.5 m altitude in every image. Therefore, images in a narrow range of altitudes had to be used in the statistical analysis. In 2012, altitude was measured and recorded directly for each image, so we constructed a histogram of image altitudes and selected those images for statistical analysis which were in the most common range of altitudes, which in this case is 1.3-1.5 m. In 2002 and 2007, no mechanism was available to measure altitude directly. Instead, a forerunner weight was attached to a 1.5 m rope and hung from the

C8526

OFOS frame; the weight was visible in the camera viewfinder during deployments, so the winch operator could make the necessary adjustments to keep the weight as close to the sea floor as possible without contacting it and thus obtain images of our ideal altitude. Again, variations in sea state and bottom topography meant not every image was recorded at exactly 1.5 m altitude, so we needed to select a range of altitudes for the analysis. Since altitude was not measured directly, we used the surface area of each image as a proxy for altitude and selected images in the most common range of surface area values (3.3-4.1 mˆ2) for our statistical analysis. This range of surface areas corresponded to the images in which the forerunner weight was close to but not contacting the sea floor, approximating our ideal altitude of 1.5 m. We have added a clearer explanation of our methods in the revised manuscript:

From section 2.3: "The laser points present in each image were detected by a computer algorithm and used as a standard to calculate the surface area of each image, which could then be used to convert species abundances to densities. In 2002 and 2007 images, the surface area of each image was used as a proxy for altitude because altitude was not measured directly. Images that were within the most common surface area or altitude range (2002 and 2007: 3.3-4.1 mˆ2; 2012: 1.3-1.5 m altitude), were recorded automatically, and were not unusually bright or dark were eligible for analysis."

Pages 18047-18048. Kruskall-Wallis and Mann-Whitney tests were used because the data violated the assumptions of normality and homogeneity of variances. For those cases in which a log(x+1) transformation of the data ensured homogenous variances between years, an ANOVA test was used; however, this transformation was only successful in a limited number of cases. A similar explanation to that given here appears in section 2.5 of the manuscript:

From section 2.5: "Comparisons of species densities, habitat feature densities, and diversity indices between years were carried out using (non-) parametric analysis of variance in SPSS (IBM, USA). A Levene's test was used to test homogeneity of variance. In the instance that a log(x+1) transformation ensured equal variance, an ANOVA

C8527

test on log(x+1)-transformed data was used, and post-hoc Bonferroni tests showed differences between pairs of years. For cases of unequal variance, pairwise differences between the years were discerned using Mann-Whitney U-tests with a Bonferroni correction of p = 0.05/3 comparisons = 0.017."

Section 3.4. We believe the inclusion of this section is justified because, while the primary objective of the paper is to describe differences in densities of the most common members of the megafaunal community over time and what may have caused them, a secondary objective is to report on all megafauna present at station HG I in the Fram Strait. It is important to note the presence of species other than those included in statistics because they also affect the community. In particular, the three species which are discussed at some length (the sabellid polychaete, the isopod cf. Munnopsidae, and the bivalve Bathyarca frielei) are quite common in images from 2012, and thus may serve important ecological roles in the epibenthic megafaunal community. The uncertainty involved in their identification in images from 2002 and 2007 was due merely to lower resolution of the camera, and considering this, we believe the reader deserves to be aware of their presence. The reviewer asked us to discuss the limitations of our study, and we believe that pointing out which species were not included in analysis and why is a fitting and pertinent way of doing so.

Figure 6. Similarly, we find it important to include figures of species not included in the statistical analysis for these reasons: first, that the reader deserves to know what species were present in the images but not included in analysis; and secondly, making these figures widely available may assist in taxonomic identification of as-yet unidentified fauna. A major reason why species were not included in analysis was uncertainty of identification, and if this uncertainty can be eliminated, we find inclusion of the figure worthwhile.

Section 3.5. Lebensspuren were marked by the same method as all other fauna and habitat features: they were marked on the images in BIIGLE. The length of Lebensspuren was unable to be determined due to technological limitations. Be-

cause of this limitation, we were cautious in making any interpretation of the extent of Lebensspuren from our data and rather commented on the abundance. We thank the reviewer for the suggested references and have included a citation to one in our revised manuscript:

From Section 4.7: Lebensspuren densities decreased between each pair of sampling years. Lower Lebensspuren density may be the result of decreased megafaunal movement or, conversely, increased megafaunal movement that lead to decreased Lebensspuren residence time (Bell et al. 2013). Unfortunately, we were unable to quantify the lengths of Lebensspuren.

Section 3.6. At the time of writing, values for measured biochemical parameters were not available for 2012. We chose to submit the manuscript without waiting and including these values in order to meet the submission deadline for the special issue "Deep-Sea Environments in European Waters" and because benthic biochemical parameters from 2012 are not especially pertinent, considering the well-established ∼1-year time lag between food input to the sea floor and changes in the abundances of benthic megafauna (Ruhl and Smith, 2004).

Section 4.1. Inclusion of the biogeographic ranges of the species found at HG I was meant to be informational for the reader and to assist in the discussion. Considering the length of the paper and the reviewer's opinion, we have removed this section.

Page 18055, lines 21-23. We state here that while we observed differences in phytodetritus input to the sea floor between the years 2002, 2007, and 2012, we are not able to determine the specific cause of the observed differences. Comparison to ice-cover and water temperature data yields no observable patterns, and we are unable to comment further. A discussion of the factors influencing phytodetritus input to the sea floor is outside the scope of our paper, and the reader is referred to the references cited in that paragraph.

Section 4.3, line 20. We made the suggested word change.

Section 4.4. The word "detrital" refers to phytodetrital flux to the seafloor, which was measured as chlorophyll a and phaeopigment content of the sediment. A slight decrease in both these parameters is readily visible from Figure 7. We have revised the wording in this passage to clearly indicate to the reader that phytodetritus input to the seafloor is being discussed:

From Section 4.4: "For deposit feeders and suspension feeders, the slight decrease in phytodetrital input to the seafloor observed in 2004-2005 (as measured by chlorophyll a and phaeopigment content of the sediment) may have caused increased mortality, decreased recruitment, or caused emigration to areas of higher food supplies that lead to lower observed population densities in 2007. Conversely, the increase in phytodetrital input to the seafloor in 2007-2011 may have caused elevated recruitment or migration of individuals from adjacent areas of lower food input."

Section 4.4, line 13. This is a typo. The text should properly read "9 of 11." We thank the reviewer for catching this mistake.

Section 4.5, line 20. The mentioned "7 of 11" species included Lycodonus flagellicauda, which only had a significant difference in density between one pair of tested years (2002-2007), and the p-value for this difference fell right on the cut-off for significance. L. flagellicauda was included in the sweeping general claim that the majority of species showed no significant differences in density between tested years. However, we agree with the reviewer that for clarity, this sentence should be edited to say "6 of 11" and have changed it accordingly.

Section 4.6. While not directly related to the objectives of the study, we found this section important to include because it builds on the discussion of why the observed changes in megafaunal density may have occurred. Six of the 11 species included in statistical analysis did not have significantly different densities between different years despite large observed changes in food input to the sea floor. Our goal in including a short discussion of the reproductive biology of the various species was to point out

that perhaps slow growth and long generation times could be important factors in the patterns we observed, and also to point out the need for further research in this area. Considering the length of the paper and the reviewer's opinion, we have removed this section and given instead only short mention to the idea that slow generation time could have contributed to stable populations.

Bell, J.B., Jones, D.O.B., and Alt, C.H.S.: Lebensspuren of the bathyal mid-Atlantic ridge. Deep Sea Res Pt II, In press, 2013.

Hasemann, C., and Soltwedel, T.: Small-Scale Heterogeneity in Deep-Sea Nematode Communities around Biogenic Structures, PLoS ONE, 6, e29152, 10.1371/journal.pone.0029152, 2011.

Quéric, N. V., and Soltwedel, T.: Impact of small-scale biogenic sediment structures on bacterial distribution and activity in Arctic deep-sea sediments, Mar. Ecol., 28, 66-74, doi:10.1111/j.1439-0485.2007.00177.x, 2007.

Ruhl, H. A., and Smith, K.L., Jr.: Shifts in Deep-Sea Community Structure Linked to Climate and Food Supply, Science, 305, 513-515, doi: 10.1126/science.1099759, 2004.

Soltwedel, T., and Vopel, K.: Bacterial abundance and biomass in response to organism-generated habitat heterogeneity in deep-sea sediments, Mar. Ecol. Prog. Ser., 219, 291-298, 2001.

We thank Julian Gutt for his comments on our manuscript, and in particular for noting the uniqueness our results in the context of biodiversity responses to food limitation. We have incorporated this concept into a revised discussion:

From Section 4.3: "The deep sea is generally considered to be food-limited (Smith et al., 2008; Iken et al., 2001). The significantly higher faunal density, diversity and evenness we observed following years of elevated food input suggest that HG I is also food-limited. However, it is generally observed that food limitation in the deep sea

causes low abundance but high diversity of organisms, and when food input increases, whether by natural or artificial means, one or two opportunistic species come to dominate the fauna (Smith et al., 2008). For example, in response to increased detrital flux to the seafloor, the holothurian Amperima rosea underwent greatly elevated recruitment and came to dominate the fauna of the Porcupine Abyssal Plain (Billett et al., 2010). The fact that greater diversity and evenness were associated with greater food input to the seafloor in our study may indicate uniqueness of the megafauna at HG I and an exception to the commonly-accepted paradigm. In this case, continued future sampling is necessary to track patterns of change in faunal diversity with food input at HG I."

We have also incorporated Dr. Gutt's suggestions which pertain to specific points listed by page number in his review. One point warrants mention here:

Page 18049. We feel confident in making generalizations about the entire benthic megafaunal community at HG I based on the 11 species selected for analysis because these species comprise the vast majority of visible fauna in the images. In fact, only two megafaunal species of any significant density were excluded from the analysis, the sabellid polychaete and the bivalve Bathyarca freilei, because neither could be identified with certainty from 2002 and 2007 images. Below is an explanation we have added to our revised manuscript:

"Though our analysis included only those 11 species which were large enough to be reliably recognized in images, this group comprises the vast majority of the megafauna present at HG I and can be used to make generalizations about trophic structure. In fact, only two species of any significant density were excluded from analysis because they were only visible in images from 2012. These species include a sabellid polychaete and the bivalve Bathyarca freilei (see below). If both these species, which are suspension feeders, are included in the calculated proportions of fauna belonging to each trophic group in 2012, the results still indicate that the majority (63%) of fauna are deposit feeders. Another 31% are suspension feeders, and 4.6% are preda-

C8532

tor/scavengers. Unfortunately, it is impossible to comment on what changes there may be present between years if these species are included."

Billett, D. S. M., Bett, B. J., Reid, W. D. K., Boorman, B., and Priede, I. G.: Long-term change in the abyssal NE Atlantic: The 'Amperima Event' revisited, Deep-Sea Res Pt I, 57, 1406-1417, 2010.

Iken, K., Brey, T., Wand, U., Voigt, J., and Junghans, P.: Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis, Prog Oceanogr, 50, 383-405, 2001.

Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K., and Martinez Arbizu, P.: Abyssal food limitation, ecosystem structure, and climate change, Trends Ecol Evol, 23, 518-528, doi: 10.1016/j.tree.2008.05.002, 2008.

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