Kiel, 29st of April 2020

Dear Tina Treude (editor),

please find below our revised manuscript (marked-up version).
Right after this cover letter we have added our point-by-point response to the reviews, including a listing of all relevant changes made in the manuscript.

In respect to this manuscript, we also have to inform you that my co-author and mentor Hans Tore Rapp has died unexpectedly during the review process (on the 7th of March 2020).
He had expressed his consent with the original manuscript version we submitted and we have added a sign next to his name to indicate that he is deceased.
We hope that this is according to the formal requirements of Biogeosciences. If we need to do anything else in this respect, please let us know so that we can take care of it.

Kind regards,
Kathrin Busch on behalf of the authors

2nd Response to Editor and Reviewer Comments on Manuscript bg-2020-15:

On giant shoulders: How a seamount affects the microbial community composition of seawater and sponges

Kathrin Busch, Ulrike Hanz, Furu Mienis, Benjamin Müller, Andre Franke, Emyr Martyn Roberts, Hans Tore Rapp, Ute Hentschel

To the editor and reviewer # 2,

We have followed your advice and revised again our submitted manuscript. In particular we have modified existing figures (Fig. 1, Fig. 4) and created a new figure (Supplementary Material S1). With the latter we aimed to facilitate a trace-back of potential temporal variations (which we argue are only minor in our study) and to provide a presentation of basic sampling information without the need to go to the PANGAEA repository. In addition we have modified the manuscript text following the reviewers suggestions. Our detailed point-to-point answers can be found below. We show the referee´s and editor´s comments in black text, while our responses are formatted in red. The line numbers and figure names in our responses refer to the new (marked-up) manuscript version.

With kind regards,

Kathrin Busch on behalf of the authors

Tina Treude, Editor (Comments to the author):

Associate Editor Decision: Reconsider after major revisions (22 Apr 2020)

Dear Kathrin and Co-Workers,

after the review of the revised manuscript, the reviewer has still some comments and requests that warrant a second major revision. However, my understanding is that the required modifications are mostly of technical nature and you should be able to implement them easily. The reviewer is generally very supportive of the study and has a high appreciation of the dataset. I advice you to take the suggestions seriously.

I have a few comments myself in response to the reviewer's suggestion:

- I agree that Fig S1 (map) should be included in the main manuscript. I am a little irritated, however, that instead of a single red dot marking the location of the study site there appear to be an accumulation of dots. Do these mark different locations? If so, please add a zoomed-in insert map to the main map that provides enough resolution to tell the dots apart. If not, then please reduce to just one dot.

Done. We have indicated the location of the seamount's summit in the map and moved Supplementary Material S1 (now Fig. 1) into the main manuscript.

(For clarification: The multiple points indicated in the previous version of the map were those sampling sites along Schulz Bank which are presented more closely in Fig. 3, just with very large circle sizes).

- The reviewer finds that referencing the interactive map provided on PANGAEA is not sufficient and requests to incorporate more details into the actual manuscript. I sympathize with this request. I advice you to extract the minimum amount of

information required from PANGAEA to understand the study and provide it in the manuscript. This does not have to be the entire map, just as much information that is required to follow and understand your study. Basically, someone should not be required to go to PANGAEA to follow your study. Data repositories along publications are mainly meant to provide details not required for your interpretations and to allow others to make use of the data in the future.
Done. We have created an additional figure (Supplementary Material S1A-B) accounting for this criticized aspect. Supplementary Material S1A shows which seawater samples were sampled in which year to clarify on the temporal aspect. Supplementary Material S1B depicts locations of sponge sampling in relation to seawater sampling positions.

- The reviewer suggest to move Figure 3 to the discussion, because no new (unpublished) data are presented. If that is the case, I agree with with this suggestion. If, however, new data were incorporated, I would be OK with leaving it in the results but please provide more details of the combination of new and existing datasets that went into the plot.
Done. Figure 3 (now named Fig. 7) has been moved to the discussion.

Let me know in case you have any questions.
Please provide a point-by-point response and a track-changes-version of your manuscript when you submit the revised manuscript.
All the best and stay safe!
Tina

Reviewer # 2 (Comments for the authors):

Evaluation of Busch et al: On giant shoulders: How a seamount affects the microbial community composition of seawater and sponges (bg-2020-15-manuscript-version3).

The authors improved the manuscript considerably, and the new figures are a welcome addition that make the text better comprehensible. But still, there are a couple of issues left, and the authors' rebuttal to the original comments are not always convincing. Particularly, missing information regarding methodological aspects and a discussion which considers only part of the results make a further revision necessary. I will try to explain my concerns in detail below.

Detailed comments:

(line numbers apply to the Response to Reviewer Comments in bg-2020-15-AC2-supplement.pdf).

L45: I am not sure about the policy of Biogeosciences, but I think this map is basic information that belongs into the paper proper, not into a supplement
Done. We have moved Supplementary Material S1 (now Fig. 1) into the main manuscript.

L64: This is not sufficient. As a reviewer of the paper, but also as a reader I do not want (and usually do not have the time) to delve into any data repositories to search for information which is essential for the interpretation of the data, and I see no reason why the authors do not provide this information here.
Agreed. We have created an additional figure (Supplementary Material S1 A-B) accounting for this criticized aspect. Supplementary Material S1A shows which seawater samples were sampled in which year and should help to clarify on the temporal aspect. As we find samples from different years within the same near-bed water cluster (consider for example different coloured points in BW4, Fig. S1A), we conclude that time is not the main driver of similarities or dissimilarities in microbial community compositions in our study. We have added an according statement into the revised manuscript (LL219-222). Supplementary Material S1B depicts the locations of sponge sampling in relation to seawater sampling positions.

L69: see comment above. And the information that seawater and sponges were sampled in close vicinity should be provided in the Methods section - this would be just one additional sentence.

Agreed. See comment above, we have added a new figure as Supplementary Material S1B. This figure shows the locations of sponge sampling in combination with the seawater sampling positions. We have added a sentence into the manuscript (LL 126-127) saying that seawater and sponges were sampled in close vicinity, but not exactly at the same position. This aspect, that sponges and seawater were not always sampled exactly at the same position (despite close spatial proximity) is also the main reason why we performed and want to stick to our machine learning approach (Fig. 3 and Supplementary Material S1). For those sponges that were not sampled exactly at the same position as seawater samples, the machine learning approach helped to define the sponge sampling location's cluster affiliation. An according sentence has been added into the manuscript (LL261-264).

L111 ff: I am still not happy with these extrapolations. It is far from clear which parameters go into this "machine-learning process". For example, how were (isolated) BW1 regions outside the data points discriminated from BW2 in the same area - just from depth, which is the only parameter available outside the sampling points? This extrapolation is particularly strange since only one BW1 data point exists, and a possible Taylor column which may be responsible for the BW1 cluster, is locally restricted. Currently, it is kind of a magic black box - something goes in (but the reader does not know what) and the predictions come out. Certainly it is not necessary to go into details, but some basic information of what's going on in the black box would be very useful. And the purpose of the extrapolations/predictions is still not clear: For the outcome of the study, they are not necessary, and they are in fact not used and interpreted in the paper.

Done. A sentence has been added to the manuscript specifying the input of the machine learning approach (LL 184-186). Geographic locations (coordinates) and cluster affiliations of the 114 seawater samples have been used as input. The cluster affiliations were predicted into space by using a k-Nearest-Neighbor-algorithm approach. The main purpose for conducting this machine learning approach has been to allow predictions of seawater cluster affiliation at any geographic point across Schulz Bank. In our case predictions at the geographic points of the sponge sampling locations were the most relevant output of this approach. Please consider also our argumentation above about the attribution of sponge samples to respective seawater near-bed clusters.

L126: I fully agree that Fig. 3 provides a very good conceptual model of how the various parameters around Schulz Bank may interact. But I still feel that this figure does not belong into the results section, because it does not present results, which have not been shown before. In the text of the results section Fig. 3 is mentioned only in connection with the temperature profiles (which obviously are not own results and are hardly discernible in the figure), and that these determine the water mass distribution. Because the limits of the water masses are not indicated, even this information cannot be deduced from the figure. Nethertheless, the figure is certainly useful for the interpretation of the results, and as such it is in fact used in the Discussion, where it should be placed.

Done. We have moved this figure (now Fig. 7) and the respective text from the Results to the Discussion (LL330-335).

L150: This has to be clarified. According to M&M, 19 stations were sampled, and exactly these 19 stations show up as dots in Fig. 2B, one of which is labelled BW1. Have there multiple (independent) microbial samples been taken per station? This is not mentioned in M&M, but is important information.

We have sampled 19 stations, each with 2 sampling depths (mid-water and near-bed water). At each station and at each depth we took 3 biological replicates (from different Niskin bottles) for analyses of the seawater microbial community composition. This sums up to 114 seawater samples in total. Please consider our modified description in L158-159.

L163: I am sorry if the authors feel that my comment criticises their sampling design. I am fully aware of the limitations of deep-sea sampling, and I acknowledge that the authors collected an impressive dataset. My comment aimed at the incomplete information provided in the text - one example is shown in the comment above.

We have addressed all comments above and elaborated further on the manuscript text as requested by the reviewer (see above).

L204: Again, I do not deny the value of the study, on the contrary. But, just looking at the data, some patterns are quite striking, and even if they cannot be tested statistically, they may be relevant and should be considered, e.g. the relative abundances in BW1 being very different from the other clusters.

In this point we disagree with the reviewer. We think it would not be appropriate to draw conclusions such as that relative abundances at the seamount summit (BW1) are very different from the other parts of the seamount, as this pattern is not constant across the different sponge species (consider for example S. rosea and L. complicata data in Fig.6). We think that an over-interpretation of our data is not helpful in this respect. We have already mentioned in the previous revision round that we are confident that our study provides valuable insights into the trends across clusters, but that we think we do not have appropriate data to go for pair-wise assessments.

L214 (and elsewhere in the text and figures): the F value in ANOVA is a ratio, and hence the dF comprise two values.

Yes, that is right. We have modified Fig.4 (plus its figure legend) and added the second values (df2) into all sub-plots. In addition we have added all df2 values into the manuscript text (LL216-217, LL241, LL247, L248).

L240: It is fully ok to discuss the presented data, but since the stations are not directly comparable due to the different distances between near-bottom and water column samples, some cautious statement about the limitations of the conclusion would be appropriate

Done. We have added several sentences into the revised manuscript mentioning the limitations of our study in this respect (LL319-324).

L244: I do not know where this knowledge comes from, but it is simply wrong. Given the same driving forces, anticyclonic Taylor caps/columns are generated also at seamounts in the southern hemisphere, but of course in counter-clockwise direction (anticyclonic = clockwise in northern hemisphere, counter-clockwise in southern hemisphere). Examples can be found, for instance, in Rogers et al. 2017, Pelagic communities of the South West Indian Ocean seamounts: R/V Dr Fridtjof Nansen Cruise 2009-410, DSR II Vol. 136

We have changed the respective sentence to: “This oceanographic phenomenon describes an isolated anti-cyclonic flow circulation pattern over a seamount and hence may promote temporary spatial isolation of a seamount ecosystem from adjacent waters.” (L327-329).

L293: I cannot follow this argumentation ("… would enormously inflate the discussion"), and I find it strange to leave the interpretation of results to the reader. If results of the other clades and sponges do not add to the discussion or are not relevant, they can be omitted. The authors now state that Chloroflexi in G. hentscheli are discussed as "representative example". For what is this example representative? Does it mean that the results are similar in the other phyla and clades? Then this has to be stated. But looking at the results, this is certainly not the case.

As stated above we see the main value of our study in the description of general trends in microbial diversity across the determined near-bed water clusters. With Fig. 6 (and the whole network analysis behind it) we were particularly interested to address the following two questions in respect to sponge microbiomes: (i) Are the same microbial phyla significantly enriched or depleted in all three sponge species? (Question A); and (ii) Are only low abundant microbial phyla significantly enriched or depleted in all three sponge species? (Question B).

To answer these two questions we need to show all microbial phyla, but we see no value in discussing each and every phylum in detail. We have submitted this paper to Biogeosciences and not to a microbiology journal. We therefore think that most of the readers will also not be interested in a lengthy discussion of each and every microbial phylum.

Further, we disagree with the reviewer in his statement that we “leave the interpretation of results to the reader”. Please consider our interpretation of the results in respect to Question A in LL425-428, and in respect to Question B in LL388-392.

However, we have realised just now thanks to the reviewer, that our formulation “representative example” is ambiguous. We have added a short explanation addressing this issue into the manuscript (LL414-418).

L324: see also my comment to L64 - the sampling design in relation to the three cruises is not comprehensible from the information given in the paper, and searching in Pangaea is not a reasonable option. And I still miss some convincing statement why interannual variability is no issue.

We have addressed this concern in our replies above. Briefly, we have added Supplementary Material S1 into the revised version of the manuscript. Further, we have modified parts of the manuscript text to accommodate for this request.

L330: This is exactly the point. If an influence (of biogeochemical factors) is suggested, the underlying assumption is a causal relationship, which my comment pointed at.

We agree with the reviewer that solely statistical correlations between biogeochemical parameters and microbial diversity, but no causal relationships can be established based on 16S data. We are fully aware that for causal relationships usage of other techniques, such as genomic inventories or stable isotope tracing, would be more appropriate. With this study we did not have the intention to describe causal relationships. As knowledge on deep-sea sponge microbiomes is very limited (less than a dozen studies have been published today), we have the opinion that statistical correlations provide an inevitable starting point before one can derive at causal relationships. We cannot deny that we had testing of a scientifically reasonable hypothesis (an assumption) in mind, when we set up this study.

Taking the reviewers remark seriously, we have modified the criticized sentence in the conclusion (LL433) to:

"Further, our correlation-based results suggest that the biogeochemistry of seawater which varies over depth (NO_3^- , SiO_4^-, and O_2 concentrations) has a detectable, but variable influence on the composition of sponge-associated microbiomes."

On giant shoulders: How a seamount affects the microbial community composition of seawater and sponges

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† deceased March 7, 2020

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Abstract. Seamounts represent ideal systems to study the influence and interdependency of environmental gradients at a single geographic location. These topographic features represent a prominent habitat for various forms of life, including microbiota and macrobiota, spanning benthic as well as pelagic organisms. While it is known that seamounts are globally abundant structures, it still remains unclear how and to which extent the complexity of the seafloor is intertwined with the local oceanographic mosaic, biogeochemistry and microbiology of a seamount ecosystem. Along these lines, the present study aimed to explore whether and to what extent seamounts can have an imprint on the microbial community composition of seawater and of sessile benthic invertebrates, sponges. For our high-resolution sampling approach of microbial diversity (16S rRNA gene amplicon sequencing) along with measurements of inorganic nutrients and other biogeochemical parameters, we focused on the Schulz Bank seamount ecosystem, a sponge ground ecosystem which is located on the Arctic Mid-Ocean Ridge. Seawater samples were collected at two sampling depths (mid-water: MW, and near-bed water: BW) from a total of 19 sampling sites. With a clustering approach we defined microbial micro-habitats within the pelagic realm at Schulz Bank, which were mapped onto the seamount's topography, and related to various environmental parameters (such as suspended particulate matter (SPM), dissolved inorganic carbon (DIC), silicate (SiO_4^-), phosphate (PO_4^{3-}), ammonia (NH_4^+), nitrate (NO_3^{2-}), nitrite (NO_2^-), depth, and dissolved oxygen (O_2)). The results of our study reveal a 'seamount effect' (sensu stricto) on the microbial mid-water pelagic community at least 200 m above the seafloor. Further, we observed a strong spatial heterogeneity in the pelagic microbial landscape across the seamount, with planktonic microbial communities reflecting oscillatory and circulatory water movements, as well as processes of bentho-pelagic coupling. Depth, NO_3^{2-}, SiO_4^-, and O_2 concentrations differed significantly between the determined pelagic microbial clusters close to the seafloor (BW), suggesting that these parameters were presumably linked to changes in microbial

community structures. Secondly, we assessed the associated microbial community compositions of three sponge species along a depth gradient of the seamount. While sponge-associated microbial communities were found to be mainly species-specific, we also detected significant intra-specific differences between individuals, depending on the pelagic near-bed cluster they originated from. The variable microbial phyla (i.e. phyla which showed significant differences across varying depth, NO_3^{2-}, SiO_4^-, O_2 concentrations and different from local seawater communities) were distinct for every sponge-species when considering average abundances per species. Variable microbial phyla included representatives of both those taxa traditionally counted to the variable community fraction, as well as taxa counted traditionally to the core community fraction. Microbial co-occurrence patterns for the three examined sponge species *Geodia hentscheli*, *Lissodendoryx complicata*, and *Schaudinnia rosea* were distinct from each other. Over all, this study shows that topographic structures such as the Schulz Bank seamount can have an imprint ('seamount effect' sensu lato) on both the microbial community composition of seawater and of sessile benthic invertebrates such as sponges by an interplay between the geology, physical oceanography, biogeochemistry and microbiology of seamounts.

1 Introduction

Seamounts and mid-ocean ridges are prominent geologic features that add to the complexity of the seafloor. In the traditional sense, seamounts are defined as isolated submarine volcanic features with a minimum height of 1.000 m from base to summit (Menard, 1964; Wessel et al., 2010). However, geologic features with a height of 50-100 m may also be considered as seamounts (Staudigel et al., 2010, Smith and Cann, 1992; Wessel et al., 2010). There may be up to 100.000 to > 25 million seamounts present in the oceans (IUCN, 2013), although the error rate associated with these estimations is high (IUCN, 2013). Despite the lack of accurate numbers, there is no doubt that with anestimated 10 million km² coverage, the area occupied by these habitats is globally significant. Elevated topographic features in the open ocean are often hotspots of biological diversity and productivity (IUCN, 2013; Morato et al., 2010). It appears that interaction of the topography with the hydrography creates a combination of amplified tidal flow, increased current speed, and the formation of internal waves, which strongly enhances vertical mixing around seamounts (Lavelle and Mohn, 2010; Van Haren et al., 2017; Roberts et al., 2018). Consequential upwelling of nutrient-rich deep waters stimulates primary productivity in this layer of enhanced mixing (IUCN, 2013). In addition to vertical mixing processes, also horizontal fluxes of organic matter may be affected by the presence of seamounts, as they may promote enclosed or semi-enclosed oceanographic circulation patterns, like Taylor caps or columns [(Chapman and Haidvogel, 1992; Roberts et al., 2018) and references therein], leading to a retention of organic and inorganic matter.

Above mentioned processes make seamounts important habitats for pelagic as well as benthic species (Morato et al., 2010; Rogers, 2018) due to beneficial prevailing conditions. Particularly areas with strong water flows (evoked by interactions of currents and tides with elevated topography), in combination with a steep and irregular hard substrate, represent suitable habitats for benthic suspension feeders, which indeed densely populate most seamounts (Genin et al.,

1986; IUCN, 2013). Sponges (Porifera (Grant, 1836)) often dominate these suspension feeder communities and are increasingly recognised as key components of shallow and deep marine ecosystems (DeGoeij et al., 2017; Maldonado et al., 2016). Due to their high filtering capacity and association with diverse microbial communities, sponges are considered to substantially influence the carbon, nitrogen, and silicate cycling in marine systems (Taylor et al., 2007; Maldonado et al., 2012; De Goeij et al., 2013; Rix et al., 2016a; Maldonado et al., 2019) and to contribute to benthopelagic coupling by actively removing particulate organic matter (POM) from the water column (Pile et al., 1997; Reiswig, 1971; Ribes et al., 1999). In addition to their influence on particulate organic matter pools, many sponges have been identified to primarily feed on dissolved organic matter (DOM) (De Goeij et al., 2008; Mueller et al., 2014; Hoer et al., 2018; Gantt et al., 2019). Energy and nutrients stored in this DOM are then transferred into particulate detritus, which fuels benthic food webs (De Goeij et al., 2013; Rix et al., 2016b).

Intimate sponge-microbe associations have been observed throughout diverse habitats, reaching from coastal shallow sites in tropical and temperate regions to the deep-sea and polar seas (Helber et al., 2019; Kennedy et al., 2014; Moitinho-Silva et al., 2014; Naim et al., 2014; Schmitt et al., 2012; Steinert et al., 2019; Thomas et al., 2016). According to their microbiome, sponges can be classified to either feature high microbial abundance (HMA) or low microbial abundance (LMA) (Hentschel et al., 2003; Moitinho-Silva et al., 2017; Weisz et al., 2008). The dichotomy between HMA and LMA sponges is considered a main driver of the microbial community structure associated with shallow water sponges (Moitinho-Silva et al., 2017). In comparison to shallow waters, comparably few studies have been conducted on the microbiology of deep-sea sponges (Borchert et al., 2017; Jackson et al., 2013; Kennedy et al., 2014; Reveillaud et al., 2014; Tian et al., 2016). However, for example for deep-sea sponges of the genus *Geodia* (*G. barretti, G. macandrewii, G. phlegraei, G. atlantica*), similar microbial phyla have been observed as in HMA shallow water sponges, such as Acidobacteria, Poribacteria and Chloroflexi (Luter et al., 2017; Radax et al., 2012; Schöttner et al., 2013). In addition to the HMA-LMA dichotomy, an important factor in structuring the microbiomes of shallow water sponges is host taxonomy, which is manifested in ubiquitous species-specific sponge microbiomes (Easson and Thacker, 2014; Steinert et al., 2017; Thomas et al., 2016). Systematic analyses of the influence of biogeochemical parameters (particularly dissolved inorganic substances) on sponge-associated microbial diversity and interactivity are still lacking, particularly in deep-sea sponges. Seamounts provide an ideal study system in this regard, as they offer the potential of examining steep environmental gradients over small spatial scales. Sponge ground ecosystems are areas harbouring high densities of structure-forming sponge individuals. The Arctic Schulz Bank seamount has been observed to host a rich and diverse community of sponges (Roberts et al., 2018; Meyer et al., 2019) and may be considered a sponge ground ecosystem harbouring a reservoir of yet unexamined microbial biodiversity.

The present study aimed to characterise the microbial community composition of seawater surrounding the Schulz Bank seamount ecosystem, located on the Arctic Mid-Ocean Ridge. Seawater samples were collected at two sampling depths from a total of 19 sampling sites and the corresponding microbiome data were mapped onto the topography of the Schulz Bank seamount ecosystem. Secondly, we assessed the associated microbial community compositions of three sponge species along a depth gradient of the seamount. Diversity metrics, as well as changes in the abundance of individual microbial taxa

were related with a set of biogeochemical parameters. This study explores whether topographic structures such as the Schulz Bank seamount, can have an imprint on both the microbial community composition of seawater and of sessile benthic invertebrates, sponges.

2 Methods

2.1 Description of the Schulz Bank seamount

Schulz Bank is located on the Arctic Mid-Ocean Ridge (73.8 °N; 7.5 °E) between the Greenland and Norwegian Seas (~~Supplementary Material S1~~Fig. 1). It is exposed to three main water masses: (i) the Norwegian Deep Water (NwDW) that is present at the base and flanks of the seamount, (ii) the intermediate water mass (NwArIW), which is most likely Norwegian Arctic Intermediate Water and occurs at the summit and shallower areas, and (iii) the warmer surface water mass (NwAtW) which is Norwegian Atlantic Water. Notably near-bed water masses at Schulz Bank's summit have unusually low temperatures of around 0 to -1 °C (Roberts et al., 2018). Estimations of the seamount's basal dimensions state conservative values of 10 x 4 km to 15 x 6 km (Roberts et al., 2018), may however also be larger as Schulz Bank belongs to a ridge system. The summit of the seamount is located at around 600 m below the water surface and the base depth is at more than 2500 m below the water surface. In a two-dimensional view, Schulz Bank has a broadly elliptical shape (Roberts et al., 2018). Bathymetry data presented in this study were derived from the Bathymetry Data Portal of the European Marine Observation and Data Network (EMODnet) and spatial analyses were performed in QGIS (version 3.4.4) as well as ArcGIS (version 10.6).

2.2 Sampling procedures

Three cruises were undertaken onboard RV *G.O. Sars* (campaign names 'GS2016109A', 'GS2017110', and 'GS2018108') during northern hemisphere's summer in the years 2016-2018. Seawater samples were collected with a rosette water sampler equipped with 12 x 10 L Niskin bottles combined with a CTD sensor system (SBE-9, Sea-Bird Electronics Inc., Washington, USA). In total, 19 CTD stations were covered, carried out along transects aligned with the seamounts' minor and major axes, and also with the 73.8 °N line of latitude. At each of the 19 stations, seawater samples for microbial analyses and biogeochemical parameters were collected at two water depths during the CTD upcast (Fig. 3C and PANGAEA for metadata): (i) 400 m below the seawater surface (mid-water) and (ii) correspondingly, at 10 m above the seafloor (near-bed water). Naturally, the near-bed depths varied along with seamount topography, and ranged from 575 to 2966 m. Sponges were sampled between 580 and 2184 m water depth, along the CTD transects (and therefore in close spatial vicinity to the seawater samples), by a remotely operated vehicle (ROV Ægir 6000, University of Bergen). A total of 36 sponge individuals representing the most abundant species were randomly selected from a larger collection effort. This subset included included 16 *Geodia hentscheli* (Cárdenas et al., 2010) (Demospongiae), 8 *Lissodendoryx complicata* (Hansen, 1885) (Demospongiae), and 12 *Schaudinnia rosea* (Fristedt, 1887) (Hexactinellida). The sponges were taxonomically identified by visual inspection

on-board the ship. In addition, whole specimens and additional sponge samples were fixed in 99 % EtOH for deposition in the collections of the University of Bergen.

2.3 Biogeochemical analyses and measurements of environmental parameters

The following nine environmental parameters were analysed: depth, suspended particulate matter (SPM), dissolved inorganic carbon (DIC), silicate (Si), phosphate (PO_4^{3-}), ammonia (NH_4^+), nitrate (NO_3^{2-}), nitrite (NO_2^-), and dissolved oxygen (O_2). Depth and dissolved O_2 data were recorded during in situ water column profiling. Depth (pressure) was recorded with the CTD sensor system mentioned above. O_2 concentrations were derived from a dissolved oxygen sensor (SBE-43, Sea-Bird Electronics Inc., Washington, USA) that was attached to the rosette water sampler. For the analysis of suspended particulate matter (SPM), 2 x 10 L of water were filtered over pre-weighed combusted GFF filters, which were rinsed with demineralised water to remove salts (47 mm Whatman™ GF/F filters pre-combusted at 450 °C, stored at - 20 °C). Filters were freeze-dried and weighed before further analysis. For the analysis of inorganic nutrients (ammonia (NH_4^+), phosphate (PO_4^{3-}), nitrate (NO_3^{2-}), nitrite (NO_2^-), and silicate (Si)), seawater samples were filtered over 0.2 µm filters. Water samples for NH_4^+, PO_4^{3-}, NO_x analysis were stored at - 20 °C and for Si analyses at 4 °C. Nutrients were measured with a QuAAtro Gas Segmented Continuous Flow Analyzer (Seal Analytical, Norderstedt, Germany). Measurements were made simultaneously on four channels for PO_4^{3-} (Murphy and Riley, 1962), NH_4^+ (Helder and de Vries, 1979) and NO_3^{2-} combined with NO_2^- (Grasshoff et al., 2009) and separately for Si (Strickland and Parsons, 1972). A freshly diluted mixed nutrient standard containing Si, PO_4^3, and NO_3^{2-} was added to each run. The cocktail served as a guide to monitor the performance of the standards. All measurements were calibrated with standards diluted in low nutrient seawater (LNSW). For the analysis of dissolved inorganic carbon (DIC), seawater samples were transferred into a glass vial containing 15 µL $HgCl_2$ (mercury chloride) and analysed on a TechniconTraacs800 auto-analyzer (Technicon Instruments Corporation, Tarrytown, USA) following the methodology of Stoll et al. (2001). Analyses of variance (ANOVAs) were performed to test for statistical differences in the biogeochemical and physical parameters between the determined microbial near-bed water clusters (see below). As numbers of samples per mid-water cluster and per near-bed water cluster were unequal, we calculated Type III sums of squares for ANOVAs (unbalanced ANOVAs). We further calculated Spearman's rank correlations between depth and those biogeochemical parameters which turned out to differ significantly across the determined near-bed water clusters in the ANOVA analyses (see below).

2.4 Amplicon sequencing

Seawater samples were collected in triplicates from different Niskin bottles, yielding a total of 114 samples from all stations (i.e. 19 stations * 2 sampling depths * 3 biological replicates per station and depth = 114 seawater samples in total). Two litres of seawater sample were filtered onto polyvinylidene fluoride (PVDF) filter membranes (Merck Millipore) with a pore size of 0.22 µm and a diameter of 47 mm and stored at - 80 °C. For sponge collection, cubes of approximately 1 cm^3 were cut from the mesohyl with a scalpel, rinsed (sterile seawater), flash-frozen in liquid nitrogen and stored at - 80 °C. DNA was

extracted from half a seawater filter or ~ 0.25 g of sponge tissue by using the DNeasy Power Soil Kit (Qiagen, Venlo, The Netherlands). The quality of the DNA extraction was assessed based on the 260/280 ratio using a NanoDrop spectrophotometer as well as by polymerase chain reaction with universal 16S primers and subsequent gel electrophoresis. The V3-V4 variable regions of the 16S rRNA gene were then amplified in a one-step PCR using the primer pair 341F-806R (dual-barcoding approach (Kozich et al., 2013); primer sequences: 5'-CCTACGGGAGGCAGCAG-3' & 5'-GGACTACHVGGGTWTCTAAT-3'). After verification of the presence of PCR-products by gel electrophoresis, normalisation (SequalPrep Normalisation Plate Kit; ThermoFisher Scientific, Waltham, USA) and equimolar pooling was performed. Sequencing was conducted on the MiSeq platform (MiSeqFGx; Illumina, San Diego, USA) with v3 chemistry. The settings for demultiplexing were 0 mismatches in the barcode sequences.

2.5 Bioinformatic analyses

For computation of microbial core-diversity metrics, sequences were processed within the QIIME2 environment (version 2018.11, (Bolyen et al., 2018)). Amplicon Sequence Variants (ASVs) were generated from forward reads (truncated to 270nt) with the DADA2 algorithm (Callahan et al., 2016). Phylogenetic trees were calculated based on resulting ASVs with the FastTree2 plugin. Representative ASVs were classified using the Silva 132 99 % OTUs 16S database (Quast et al., 2013) with the help of a primer-specific trained Naive Bayes taxonomic classifier. Alpha and beta diversity indices (e.g. Faith's Phylogenetic Diversity and weighted UniFrac distances, respectively) were calculated within QIIME2. To evaluate sample separation in ordination space, non-metric multidimensional scaling (NMDS) was performed on weighted UniFrac distances for seawater and sponge-associated microbiomes separately.

A machine learning approach was used to define microbial micro-habitats within the pelagic realm. Seawater microbiomes were clustered based on weighted UniFrac distances. The NbClust function was applied in R (version 3.0.2, (R Development Core Team, 2008)) to generate 30 indices to identify the best number of clusters based on the majority rule. A coordinate grid was set up as a basis for a georeferenced extrapolation of sampling points. In detail, we used the sampling coordinates and the determined cluster affiliation of our 114 in situ measured seawater samples as the input for our predictions of seawater microbial cluster affiliation in space. Clustering regions were set up with the help of the k-Nearest-Neighbor-algorithm. The machine learning approach was fine-tuned in several ways: (i) the algorithm was trained in a way that in situ measured data points always belong to the cluster actually determined based on the sequencing data; (ii) a normalisation was applied with the help of a distance-weighted function meaning that closer data points have a higher weight; (iii) the probability of class membership was calculated and plotted as indication of confidence. Permutational multivariate analyses of variance (PERMANOVAs) were performed with 999 permutations to determine whether microbiomes of selected clusters were statistically significantly different from each other. In detail, pair-wise tests across the determined clusters were conducted for the following samples separately: mid-water samples, near-bed water samples, *G. hentscheli*, *L. complicata*, and *S. rosea*. A significance level of α=0.05 was applied for all statistical analyses in this study.

To evaluate co-occurrence patterns between microbial taxa across environmental gradients (i.e. determined near-bed water clusters**)**, networks were constructed separately for every sponge species and seawater. Mean relative abundances of microbial phyla were calculated for all biological replicates of each sample type and for the corresponding near-bed water cluster. Microbial phyla, which showed significantly different enrichment between clusters, were determined and ranked using the Linear Discriminant Analysis Effect Size (LEfSe) algorithm (Segata et al., 2011). A correlation matrix was established for those taxa that differed significantly between clusters, to assess co-occurrences. In particular, the direction and strength of correlations were characterised for any significant phylum with all other significant taxa (as well as the relations with depth).

3 Results

3.1 Structure and composition of seawater microbial communities

A NMDS plot on weighted UniFrac distances separated the microbial communities of mid-water and near-bed water samples in ordination space with few exceptions (Fig. 2). Cluster analysis based on weighted UniFrac distances revealed two distinct clusters in the mid-water samples of which one (MW1) was located precisely above the summit of Schulz Bank, while the other (MW2) covered the wider seamount region and vicinity (Fig. 3A). Four distinct microbiome clusters were detected in the near-bed water samples (BW1-4). In terms of similarity, cluster BW1 was most distinct from all other clusters while clusters BW2 and BW3 were most similar to each other (Fig.3B). Moreover, BW1 cluster samples separated in ordination space in that they grouped with mid-water rather than near-bed water samples (i.e. consider the few black dots grouping together with the white dots in Fig. 2). Plotting the clusters on a spatial map revealed that near-bed water cluster BW1 was located near the summit of Schulz Bank seamount (average depth = 575 m), while clusters BW2 and BW3 covered its flanks (average depth ± SE = 919 ± 106 m and 922 ± 142 m, respectively), and cluster BW4 represented the vicinity close to the seamount (average depth ± SE = 1836 ± 376 m) (Fig.3B). Statistical testing of the individual depth data points contributing to a given cluster revealed a significant difference in the depth parameter between the clusters (ANOVA, $p = 0.01$, $df1 = 3$; $df2 = 10$).

Fig. 3C shows the bathymetry highlighting the contour lines of Schulz Bank seamount and its vicinity (reference West and East) as well as the 19 sampling stations. As our samples originated from three different cruises, we also double-checked on the extent of temporal variability in our dataset. We observe frequently that seawater samples of different cruises belong to the same cluster (Supplementary Material S1A). From this we conclude that temporal variations are not the main driver of our observed similarities or dissimilarities in pelagic microbial community compositions. ~~In addition to this representation, a 3D visualization of the microbiome clusters at and around Schulz Bank seamount was created (Fig. 7). Here, a digital elevation model of Schulz Bank seamount is depicted in combination with the overlying water column structure and oceanographic context. Temperature profiles derived from whole water column sensing by CTD casts are plotted. Based on~~

these profiles the vertical distributions of the surface water (NwAtW), intermediate water (NwArIW), and Norwegian Deep Water (NwDW) were deduced in combination with the identified water masses as described in Roberts et al. (2018) (Fig. 7).

Microbial richness was overall slightly lower in the mid-water samples (mean Faith's Phylogenetic Diversity ± standard error = 45.5 ± 0.8) than in the near-bed water samples (54.4 ± 0.9) (Supplementary Material S2A). Near-bed water samples from the summit (BW1) displayed a slightly lower microbial richness than the other near-bed water samples (Supplementary Material S2B). The mid-water samples collected above Schulz summit showed also a slightly lower microbial richness than the other mid-water samples. Pairwise comparisons (PERMANOVA) revealed that the seawater microbial community clusters within the mid-water and near-bed water samples were significantly different from each other in terms of their microbial community composition (Supplementary Table S1). Furthermore, the pool of mid-water samples (MW1 - MW2) was significantly different from the pool of near-bed water samples (BW1 - BW4). Overall, the eight most dominant seawater microbial phyla, sorted in descending order of mean relative abundance, were: Proteobacteria (54 % of total community), Bacteroidetes (17 %), Verrucomicrobia (7 %), Marinimicrobia (SAR406 clade) (6 %), Actinobacteria (5 %), Chloroflexi (4 %), Acidobacteria (2 %), and Planctomycetes (1 %).

3.2 Seawater biogeochemistry at Schulz Bank seamount

When comparing the biogeochemical parameters of the mid-water clusters, only dissolved O_2 concentrations differed significantly (ANOVA, p = 0.02, df1 = 1; df2 = 17) with slightly higher concentrations in MW1 (6.90 ± 0.04 mL L^{-1}) compared to MW2 (6.75 ± 0.03 mL L^{-1}) (Supplementary Table S2). All other tested biogeochemical parameters (SPM (2.22 ± 1.39 mg L^{-1}), DIC (2269.07 ± 26.63 µmol L^{-1}), SiO_4^- (5.66 ± 0.06 µmol L^{-1}), PO_4^{3-} (0.86 ± 0.01 µmol L^{-1}), NH_4^+ (0.11 ± 0.03 µmol L^{-1}), NO_3^- (12.99 ± 0.08 µmol L^{-1}), and NO_2^- (0.02 ± 0.01 µmol L^{-1}) were not statistically different between MW1 and MW2. The values for mid-water samples are reported as average ± standard error.

Of the eight biogeochemical parameters tested, the following three differed significantly between the near-bed water clusters. These were NO_3^- (ANOVA, p = 0.04, df1 = 3; df2 = 10), SiO_4^- (ANOVA, p = 0.03, df1 = 3; df2 = 10), and dissolved O_2 (ANOVA, p = 0.01, df1 = 3; df2 = 15). Nitrate (range= 13.00-14.78 µmol L^{-1}) and SiO_4^- (range = 6.00-10.65 µmol L^{-1}) increased with depth, with lowest concentrations at the summit (BW1), intermediate concentrations at the flanks (BW2, BW3) and highest concentrations in the seamount vicinity (BW4) (Fig. 4). Dissolved oxygen (range= 6.48-6.99 mL L^{-1}) showed the reverse pattern in that its concentration was highest at the summit (BW1), intermediate at the flanks (BW2, BW3) and lowest in the seamount vicinity sites (BW4). Spearman's rank correlations calculated between depth and the three other significant parameters revealed indeed significant correlations in all cases (NO_3^- : rho= 0.77, $p<0.01$; SiO_4^- : rho= 0.85, $p<0.01$; dissolved O_2 : rho= -0.77, $p<0.01$) (Supplementary Material S3). The other biogeochemical parameters SPM (range= 0.49-1.87 mg L^{-1}), DIC (range= 2248.00-2265.67 µmol L^{-1}), PO_4^{3-} (range= 0.90-0.97 µmol L^{-1}), NH_4^+ (range= 0.10-0.17 µmol L^{-1}), and NO_2^- (range= 0-0.05 µmol L^{-1}) were not significantly different between the near-bed water clusters. At the summit, no pronounced differences in biogeochemical parameters were observed between the near-bed water (BW1) and mid-water samples (MW1) (Supplementary Table S2).

3.3 Structure and composition of sponge microbial communities

In order to analyze structure and microbial community composition of the sponges, we randomly selected at least four biological replicates per sponge species per BW cluster for statistical analysis. As sponges were sampled (in close vicinity but) not exactly at the same locations as seawater samples, BW cluster affiliations of the sponge sampling locations were determined based on spatial extrapolations of the seawater data as described before (see Supplementary Material S1B for exact sponge sampling locations). Overall, the three deep-sea sponge species *S. rosea*, *G. hentscheli*, and *L. complicata* showed host species-specific microbiomes, as indicated by a clear separation of their microbial communities in ordination space (Fig. 5). Sub-structuring based on near-bed water clusters in the non-metric multidimensional scaling plot as well as pairwise comparisons (PERMANOVA) revealed that the sponge microbial communities within each species differed significantly depending on the near-bed water clusters from which they were collected (Supplementary Table S1). The only exception was *S. rosea*, for which specimens from the flank (BW3) showed a microbial community composition that was intermediate between the summit (BW1) and the other flank cluster (BW2).

The dominant microbial phylum in *S. rosea* and *L. complicata* was Proteobacteria (Fig. 6A and Fig. 6B), whereas *G. hentscheli* microbiomes were dominated by Chloroflexi, Acidobacteria and Proteobacteria (Fig. 6C). Sponge microbiomes were more stable than seawater communities with less phyla exhibiting significant differences across the four near-bed water clusters or positively relating with depth (Fig. 6). For the hexactinellid *S. rosea*, the relative abundances of five bacterial phyla (Acidobacteria, Chlamydiae, Kirimatiellaota, Planctomyces and Proteobacteria) were significantly different between individuals that were sampled from different near-bed water clusters. Out of these five phyla, the Acidobacteria, Chlamydiae, Kirimatiellaota, and Planctomyces were positively related with depth while for the Proteobacteria neither a positive nor negative relation with depth was discernable. Consequently, the Proteobacteria showed a negative relation with the four other phyla in the network analysis. For the demosponge *L. complicata*, the relative abundances of the Bacteroidetes, Gemmatimonadetes, Nitrospinae, Planctomyces, Proteobacteria and Spirochaetes were significantly different between sponge individuals that were sampled from the different near-bed water clusters. For this sponge species, samples were only available from near-bed water clusters 1 and 2. Of the six phyla, the Planctomyces and Proteobacteria were positively related with depth, while the other four were negatively related with depth, which is also reflected in the network analysis. For the demosponge *G. hentscheli*, the relative abundances of eight phyla (Acidobacteria, Actinobacteria, Bacteoidetes, Chloroflexi, Dadabacteria, Entotheonellota, PAUC34f and Schekmanbacteria) were significantly different between sponge individuals sampled from the near-bed water clusters BW1-BW4. Of those, Chloroflexi and Schekmanbacteria were positively related with depth, while the others showed variable patterns over depth. The network analysis showed both positive and negative correlations between taxa for those increasing with depth as well as those displaying a variable response.

When analysing host-associated microbiomes, ambient seawater microbiomes are valuable references for comparison. In this study, a total of 21 microbial clades were identified in ambient seawater, whose relative abundances

varied significantly between the four near-bed water clusters. A total of nine taxa showed a positive relation with depth, one (Dadabacteria) showed a negative relation with depth, and the remaining 11 taxa showed a variable response to depth. For seawater more phyla varied between near-bed water clusters than for the sponge samples. Overall, more microbial taxa showed significant positive relations with depth, NO_3^-, SiO_4^- and negative relations with O_2 than vice versa. The microbial taxa showing a significant difference in relative abundance between the near-bed water clusters (as determined by LEfSe) were different between sponges and seawater also between sponge species. Further, significant differences in relative abundances were observed for both abundant and less abundant sponge symbiont lineages.

4 Discussion

Research records about seamount microbiology are sparse and comparably few studies have been conducted on deep-sea sponge microbiomes in general (Borchert et al., 2017; Jackson et al., 2013; Kennedy et al., 2014; Reveillaud et al., 2014). Our main aim was to assess whether and via which potential mechanisms a seamount can affect the community structure of pelagic and benthos (sponge)-associated microbial communities, using the Schulz Bank seamount as an exemplary field site. A total of 19 CTD sampling stations, each with two sampling depths, on and around Schulz Bank were analysed towards this goal, and combined with sponge-associated microbial data gained during additional ROV dives.

4.1 A seamount imprint on seawater microbial communities

In this study we observed a pronounced similarity between the microbial community composition of the mid-water cluster located precisely above Schulz Bank's summit (MW1) and the microbial community composition of the near-bed water cluster at the summit (BW1). This is evident in Fig. 2, where few black dots representing the BW1 cluster group with mid-water samples rather than near-bed water samples. In addition, the microbial community in the mid-water cluster above Schulz Bank's summit (MW1) was distinct from the community in the mid-water cluster covering the wider seamount region and vicinity (MW2), despite similar prevailing biogeochemical conditions in both mid-water clusters (MW1 vs MW2; exception = significant difference in O_2 concentrations between both clusters). From these two observations we conclude that the presence of a seamount can have an imprint on the microbial community structure in the overlying water column ('seamount effect' sensu stricto). In particular we suspect that topography-induced vertical mixing processes occur at Schulz Bank seamount, which reallocate microbial communities within the water column and in turn influence the pelagic microbial diversity as far as at least 200 m above the seamount's summit. In support of these interpretations, oscillating currents relating to the barotropic and baroclinic (internal) tide have been reported previously at the summit of the Schulz Bank seamount (Roberts et al., 2018) and other seamounts (Van Haren et al., 2017). Although these mentioned studies suggest that respective oceanographic processes are particularly pronounced at the summit part of seamounts, we cannot exclude the following two aspects based on our own study: (i) Since we only sampled one mid-water depth, vertical mixing of microbial communities could in theory extend far higher than 200 m above the seamount's summit. (ii) As the vertical distances

between the mid-water and the near-bed water samples were larger at other parts of the seamount compared to the summit, vertical mixing of microbial communities may in fact not only be restricted to the summit of Schulz Bank.

In addition to tide-induced vertical hydrodynamic processes, horizontal flow patterns can also help to explain the presence of seamount-specific microbial communities. Roberts et al. (2018) calculated that a Taylor cap or Taylor column may be (temporarily) present at Schulz Bank. This oceanographic phenomenon describes an isolated anti-cyclonic flow circulation pattern over a seamount ~~in the Northern hemisphere~~ and hence may promote temporary spatial isolation of a seamount ecosystem from adjacent waters. Our conceptual schematic overview of hydrodynamics at Schulz Bank seamount is shown in Fig. 7 (dashed lines). In this figure, a digital elevation model of Schulz Bank seamount is depicted in combination with the overlying water column structure and oceanographic context. Temperature profiles derived from whole water column sensing by CTD casts are plotted. Based on these profiles the vertical distributions of the surface water (NwAtW), intermediate water (NwArIW), and Norwegian Deep Water (NwDW) were deduced in combination with the identified water masses as described in Roberts et al. (2018) (Fig. 7). In addition to oceanographic insights, Fig. 7 includes a 3D visualization of our determined microbiome clusters at and around Schulz Bank seamount. This Figure recapitulates that similarities and dissimilarities in microbial signatures of seawater in this study (cluster dendrogram Fig.7) were consistent with the oscillatory water movements (i.e., due to internal tide-induced mixing) and possible circulatory flows (Taylor column) as predicted by Roberts et al. (2018).

Microbial richness was overall slightly lower at the summit of the seamount (BW1) than at the deeper locations (i.e. BW2-BW4). A similar trend was observed for the mid-water samples, where microbial richness was slightly lower for the microbial community above Schulz's summit in comparison to samples in its vicinity (MW1 vs MW2). On a macroscopic level, Morato et al. (2010) and others have described seamounts as hotspots of pelagic biodiversity, much less is however known about microbial diversity at seamounts. Our results of a lower microbial richness above the seamount summit might seem contradictory at first. However, Schulz Bank is a recognized sponge ground ecosystem, with a peak in sponge density and diversity at the seamount summit (Roberts et al., 2018; Meyer et al., 2019). Sponges are very efficient suspension feeders and are known for removing large amounts of particulate organic matter including prokaryotes and small eukaryotes from the water column (Leys et al., 2018). Benthic-pelagic coupling mediated by selective feeding of sponges on seawater microorganisms (McMurray et al., 2016; Van Oevelen et al., 2018) in combination with the discussed hydrodynamic patterns (vertical mixing) might explain the slightly reduced microbial richness of the water body residing directly above a sponge ground (BW1 and MW1). Sponge density and community composition changes along the topography of Schulz Bank seamount in that density is highest at the summit (Meyer et al., 2019; Roberts et al., 2018). This natural variation can further explain the observed differences in microbial community composition between the other near-bed water samples (BW2-4). For these samples, we observed distinct pelagic microbial communities at a finer resolution than can be explained by the pure water masses distribution (consider depth of intermediate (NwArIW) and deep water (NwDW) layers in Fig. 7). Particularly the near-bed clusters BW2 and BW3, originated from a similar depth range and both were located at the seamount's flanks. Besides ecologically rooted explanations (i.e. variable presence of benthic organisms that influence

biogeochemical cycles), also hydrodynamic processes (i.e. local flow direction linked to small scale topography and/or spatial orientation of the seamount's flanks) can explain the observation of distinct microbial community compositions within the near-bed water. We hence conclude that besides patterns related to water masses, we observe a much higher spatial heterogeneity of pelagic microbial communities than previously recognized. We call this kind of imprint on the pelagic microbial community composition, which is probably based on the topography combined with bentho-pelagic coupling processes and hydrodynamics, a 'seamount effect sensu lato'. These observations suggest that the presence of a seamount can have profound impacts on the distribution of microbial landscapes in the open ocean.

Seamounts are recognized as unique habitats in terms of ecosystem dynamics (Genin and Boehlert, 1985) and macroecology (Morato et al., 2010). The present study reveals that seamounts also have a unique microbial signature that extends hundreds of meters up into the overlying water column. In addition, we detected three distinct microbial clusters in seawater samples taken near the seabed directly above Schulz Bank which were distinctly different from those of seawater collected in the vicinity of the seamount (near-bed water clusters BW1-3 vs BW4). NO_3^-, SiO_4^-, and dissolved O_2 concentrations differed significantly between the four near-bed water clusters. The observation that the seamount is intersecting with different biogeochemical properties and microbial communities, is particularly interesting in regard to benthic organisms. In these lines, the Schulz Bank seamount provides a platform for sponges and their associated microbial communities to respond to topography-enabled environmental gradients (also a 'seamount effect sensu lato').

4.2 A seamount imprint on sponge-associated microbial communities

The investigated sponge species *S. rosea*, *G. hentscheli* and *L. complicata* were selected for this study as they represent key taxa of the sponge community at Schulz Bank. Microbiomes of these three species clustered clearly apart from each other in ordination space, indicating a dominant host species-effect on the associated microbial community structure. *S. rosea* and *L. complicata* showed characteristic microbial signatures of LMA sponges (as defined in Moitinho-Silva et al., 2017) that are being dominated by Proteobacteria. On the contrary, *G. hentscheli* displayed a microbial signature characteristic of HMA sponges with dominant clades such as Chloroflexi and Acidobacteria, which is consistent with previous reports on sponges of the genus *Geodia* (Luter et al., 2017; Radax et al., 2012; Schöttner et al., 2013).

When analysing each sponge species separately, sponge specimen microbiomes differed significantly between each other and depended on the near-bed water clusters to which they belonged. This finding suggests that an environmental signature is also detectable in sponge-associated microbial communities (seamount signature sensu lato). This observation is striking, as sponge-associated microbial communities are considered as highly stable associations (Cárdenas et al., 2014; Erwin et al., 2012, 2015; Pita et al., 2013; Steinert et al., 2016).

Previous studies have shown that abiotic factors (i.e. depth, geographical location) influence the microbial community structure in shallow-water sponges, but stated that the core community is shaped by the intimate interaction with the sponge host (Lurgi et al., 2019). Interestingly, in our study the major microbial players in terms of abundance, such as Chloroflexi in *G. hentscheli*, show significant enrichment/depletion patterns across the four clusters. Traditionally (shallow

water) sponge-associated microbes have been classified into core, variable and species-specific communities (Schmitt et al., 2012). The present study reveals that for the three investigated deep-sea sponges at Schulz Bank seamount the variable community overlaps with the core-community when considering high taxonomy ranks. In addition, network analyses showed both positive and negative correlations between taxa for those increasing with depth as well as those displaying a variable response. We suspect that primary responders to environmental parameters have cascading effects on microbial lineages that are not directly affected by water biogeochemistry.

In this study, silicate, oxygen and nitrate concentrations, as well as depth differed significantly between the four near-bed water clusters. While SiO_4^- and NO_3^- were positively correlated with depth, O_2 showed a negative relationship. An increase of nutrient concentrations with depth is consistent with our previous expectations [consider e.g. (Bristow et al., 2017)] and can be explained by remineralization processes of sinking marine snow within the deep water layers. Decreasing O_2 concentrations from the Intermediate Water (NwArIW) to the Deep Water (NwDW) are also consistent with our expectation based on physical oceanography, as water layers more recently oxygenated at the ocean surface at their site of formation, typically carry more oxygen (Jeansson et al., 2017). In general, the absolute differences in the concentrations of all three significant environmental parameters were comparably small (especially NO_3^- and O_2). However, as microbial communities were significantly different between the clusters, we posit that the observed biogeochemical differences, albeit small, should be considered as drivers of sponge microbial community composition. In support of our hypothesis, the process of denitrification is for example known to be highly sensitive to nanomolar concentrations of O_2 concentrations (Dalsgaard et al., 2013). In addition, a previous study on the sponge *Xestospongia muta* demonstrated that changing NOx concentrations over depth contribute to shaping the microbial community composition (Morrow et al., 2016). Furthermore, several studies have noted that depth is an important factor in structuring sponge-associated microbiomes (Indraningrat et al., 2019; Lesser et al., 2019; Steinert et al., 2016).

This is, to our knowledge, the first study that explores the impact of seawater biogeochemistry on deep-sea sponge microbiomes. We have used LEfSe analyses to identify sponge symbiont taxa whose relative abundance varies with depth, this being used as a proxy for selected biogeochemical parameters. We have further used co-occurrence networks to identify positively or negatively co-varying microbial clades. In the following we discuss one representative example of a sponge-(and seawater-) associated microbial phylum which was significantly enriched/depleted across the near-bed water clusters:~~.~~ *Chloroflexi* in *G. hentscheli*.~~:~~ ~~The relative abundance of~~ Chloroflexi (among several other phyla's) relative abundance differed significantly between the four near-bed water clusters for *G. hentscheli* and seawater, showing a positive relation with NO_3^-, SiO_4^-, and depth, and a negative relation with O_2. Members of the phylum Chloroflexi have been attributed to a relevant role in the degradation of organic matter, particularly in the deep ocean pelagic realm and within HMA-sponges (Bayer et al., 2018; Landry et al., 2017). High degradation rates of organic matter are often related with low O_2 and high nutrient concentrations, owing to biogeochemical feedbacks where nutrients enhance oxygen demand by increasing biological production and oxygen consumption during decomposition. Taken together, the differences in relative abundances of Chloroflexi in *G. hentscheli* and seawater could be driven by the NO_3^-, SiO_4^-, and O_2 concentrations in ambient seawater.

While sponge microbiomes are generally considered as being highly stable in time and space, we provide a first evidence that small differences in water biogeochemistry may affect sponge microbiome composition. However, no uniform shifts in relative abundances of microbial taxa were observed for *G. hentscheli*, *L. complicata*, and *S. rosea*, but rather an individual response of each host species related to biogeochemical parameters. One explanation is that biological interactions between the sponge host and its microbiome, or between the microbes themselves might have masking effects.

Conclusions

We provide insights into the variability of pelagic and benthic (sponge-associated) microbiomes at the Arctic Schulz Bank seamount based on the microbiome analyses of 114 seawater and 36 sponge samples. Interestingly, a 'seamount signature' is detected within the microbial community composition of samples originating as far as 200 m above the seamount summit. ~~We further show~~Further, our correlation-based results suggest that the biogeochemistry of seawater which varies over depth (NO_3^- , SiO_4^-, and O_2 concentrations) has a detectable, but variable influence on the composition of sponge-associated microbiomes. This study provides new perspectives on the influence of seamounts on the microbial diversity in their vicinity. We conclude that the geology, physical oceanography, biogeochemistry and microbiology of seamounts and similar structures are even more closely linked than currently appreciated.

Data availability

Sample metadata and biogeochemical data were deposited in the PANGAEA database: https://doi.pangaea.de/10.1594/PANGAEA.911304. Raw sequences were archived in the NCBI Sequence Read Archive under BioProject id: PRJNA600711.

Author contribution

KB, FM, BM, UHe designed the study. KB, UHa, FM, EMR, HTR participated in sampling. UHa, FM, KB focused on biogeochemical parameters. HTR conducted the sponge taxonomic analysis. UHe and KB were responsible for the microbial pipeline. AF was involved in sequencing. KB performed the data analysis (bioinformatics and visualisations). KB, UHe wrote the manuscript. BM, FM, EMR, UHa, HTR reviewed and edited the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

This work is dedicated to Hans Tore Rapp†, sponge taxonomist, deep-sea explorer, colleague and friend. Funding was provided by the European Union's Horizon 2020 research and innovation program under Grant Agreement No. 679849 (the SponGES project). This document reflects only the authors' view and the Executive Agency for Small and Medium-sized Enterprises (EASME) is not responsible for any use that may be made of the information it contains. Samples included in this study were collected in compliance with the Nagoya Protocol. We thank the crews and scientific parties of RV *G.O. Sars* cruises 'GS2016109A', 'GS2017110', and 'GS2018108' for great technical support while at sea. We are grateful for sponge sampling by Stig Vågenes and his ROV Ægir 6000-team (UiB), Christine Rooks (UiB) for sampling assistance on-board ship during 'GS2016109A', and Jasper de Goeij (UvA) for interesting discussions. We further acknowledge Ina Clefsen, Andrea Hethke, Ilona Urbach and Tonio Hauptmann (Kiel, Germany) for excellent laboratory support with the amplicon pipeline. Corinna Bang (IKMB, Kiel) provided valuable support with the sample sequencing and revised the manuscript before submission. We also thank two anonymous reviewers for their comments, which helped to improve this manuscript.

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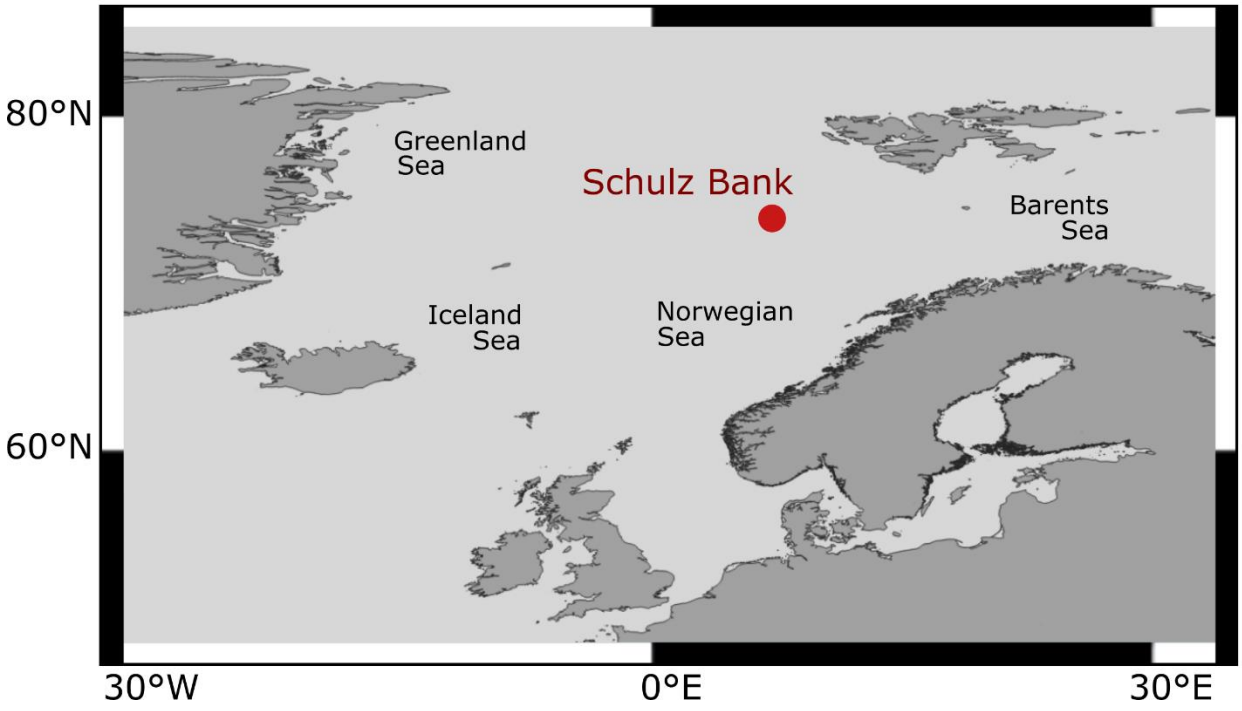

Figure 1: Overview map showing the location of the Schulz Bank seamount between the Greenland and Norwegian Seas.

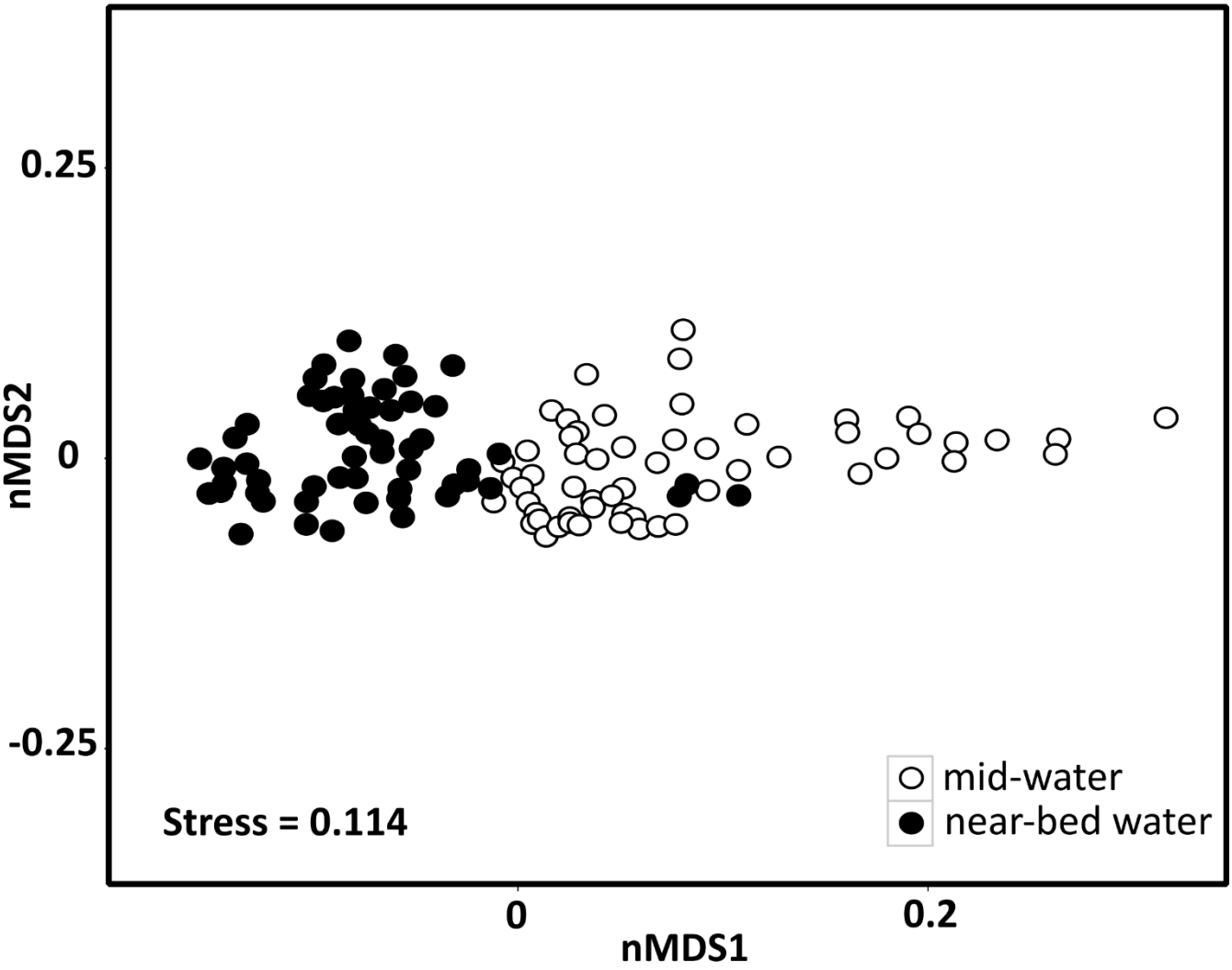

Figure 2: Seawater microbial community composition of mid-water and near-bed water samples visualised by a non-metric multidimensional scaling plot on weighted UniFrac distances. Each marker is one microbial community, with colors indicating the sample sub-type (i.e. mid-water or near-bed water).

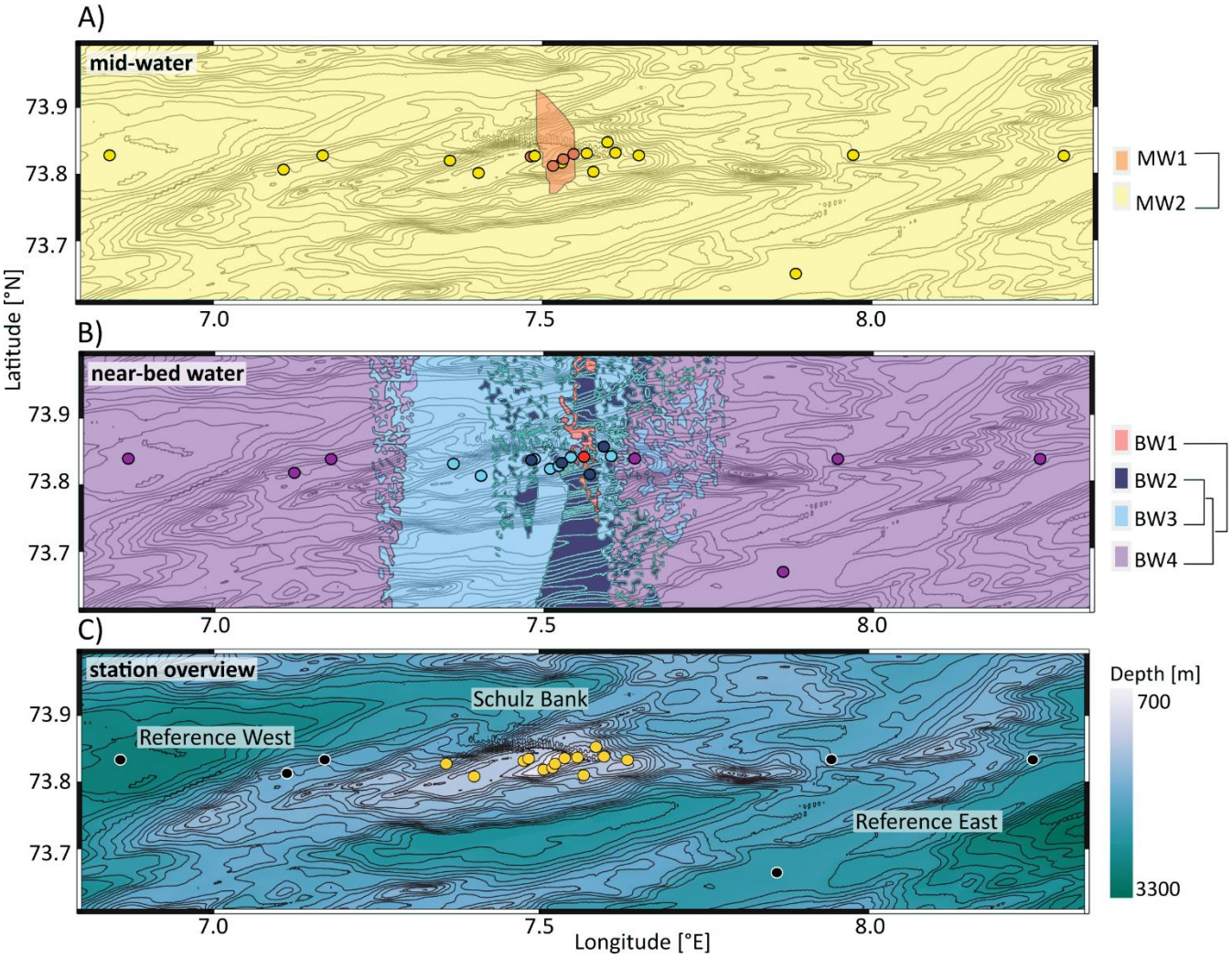

Figure 3: Seawater microbial community structure across Schulz Bank. Contour lines in all three subplots represent the underlying topography. Colors in A) and B) represent clusters based on weighted UniFrac distances, where colored dots indicate stations with in situ sampling and filled areas represent extrapolations based on machine learning. The further away predicted areas are from actual sample points, the higher is the associated uncertainty of these predictions. A) includes all mid-water samples derived during the CTD transects. B) includes all near-bed water samples. Here, the degree of cluster similarity can be deduced from the dendrogram to the right of the plot(s). C) provides an overview of the sampling area, showing the locations of all 19 CTD stations. Stations directly located on the Schulz Bank are coloured yellow, while reference stations (west and east of Schulz Bank) are indicated by black colours. Colouring in sub-plot C) was done according to depth.

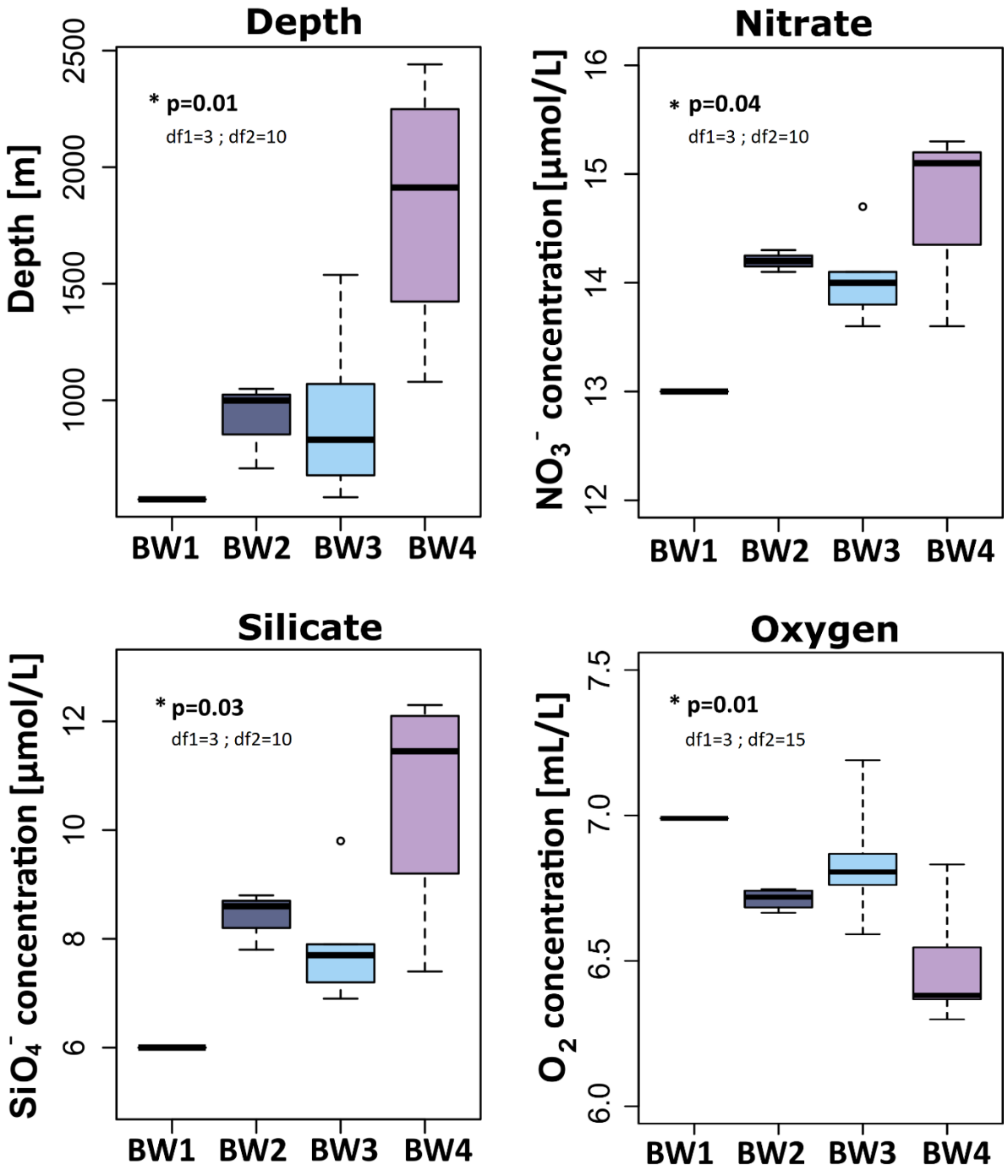

Figure 4: Concentrations and measurements of significant (ANOVA, α=0.05) biogeochemical parameters for near-bed water samples, across the determined near-bed water clusters. p-values as well as degrees of freedom (df1 and df2) for these parameters are written into the respective graphs. Coloring is the same as chosen for Fig. 2 and 3.

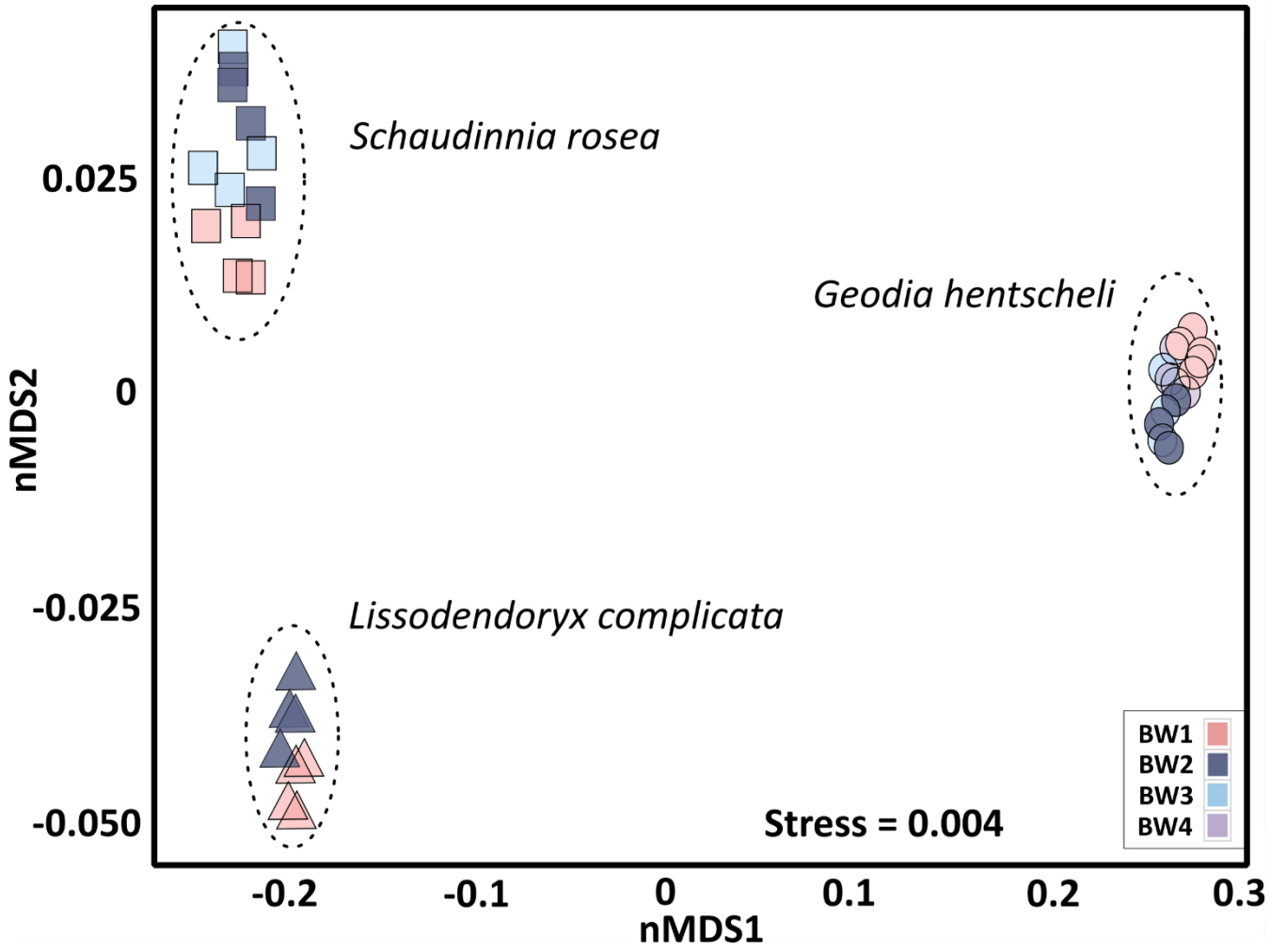

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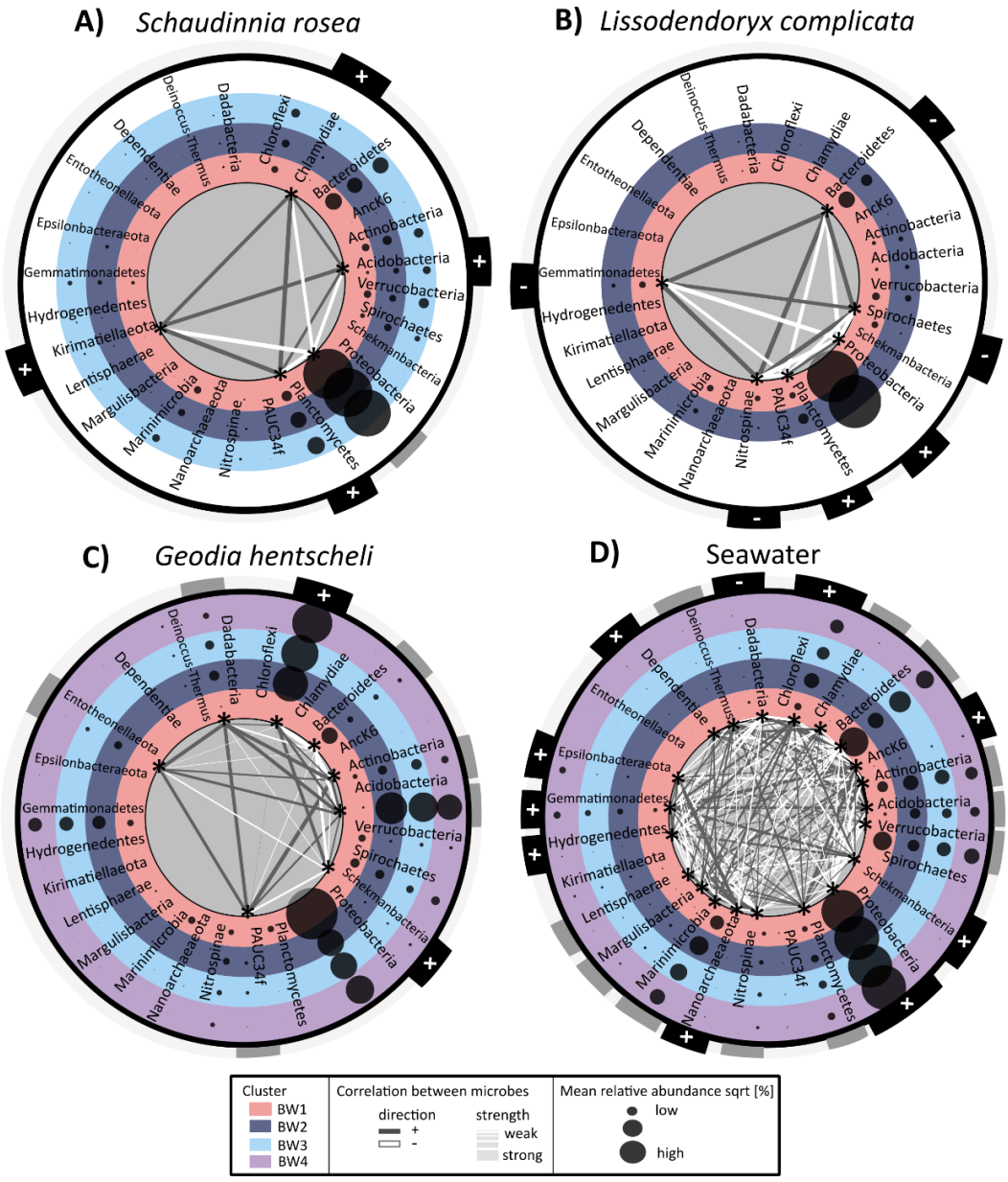
Figure 5: Sponge microbial community composition visualised by a non-metric multidimensional scaling plot on weighted UniFrac distances. Each marker is one microbial community, with symbols representing the sample sub-type (i.e. sponge species) and colors indicating the near-bed water cluster present at the respective sponge sampling location.



695 **Figure 6: Co-occurrence network and differential abundance of microbial phyla across the four determined near-bed water clusters. Sub-plots A-C) show sponge data, with plot A) showing average *Schaudinnia rosea* data, B) presenting average *Lissodendoryx complicata* data and C) illustrating *Geodia hentscheli* data. Sub-plot D) contains seawater data. Near-bed water clusters are represented by differently colored rings. Each ring contains a list with microbial phyla which are alphabetically sorted. Average relative abundances of each of the respective phyla for the samples within a given cluster are indicated by bubble**
700 **sizes. Those microbial phyla which are statistically significantly enriched or depleted across the four clusters (LEfSe analysis), are marked with an asterisk inside the inner most ring. Only for those taxa where the difference is significant, correlation strength (indicated by size of connecting lines) and direction (represented by color of connecting lines: white = negative correlation, dark grey = positive correlation) with all other significant taxa are plotted. For all microbial phyla relation with depth is indicated in the outer ring of each plot by + (meaning significant positive relation) or - (meaning significant negative relation).**

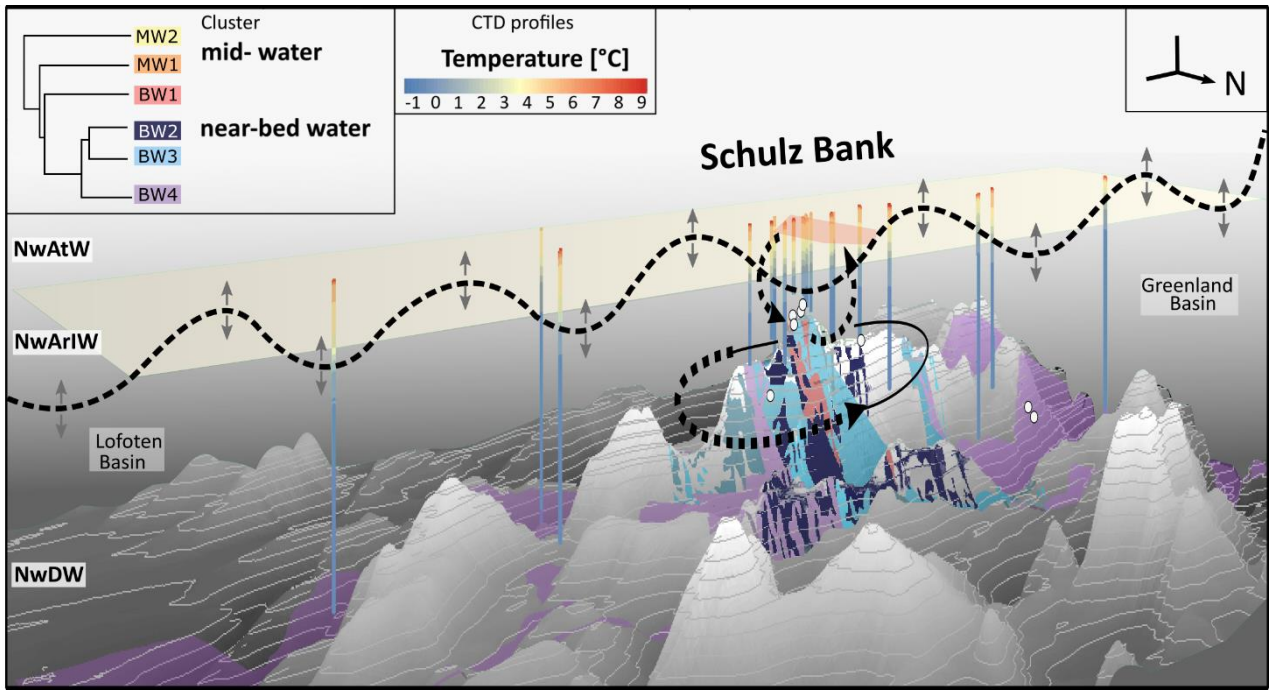


Figure 7: Conceptual overview and vertical 3D section showing spatial distribution of microbial clusters and oceanographic patterns on the Schulz Bank seamount. Extrapolated seawater microbial clusters are indicated by colored polygons: mid-water clusters are marked in orange (MW1) and yellow (MW2), while near-bed water clusters are marked in red (BW1), dark blue (BW2), light blue (BW3), and purple (BW4). The degree of cluster similarity can be deduced from the dendrogram in the left corner of the plot. Whole water column CTD profiles are indicated, showing the measured temperature values from surface to bottom at the respective sampling locations. Sponge sampling locations visible on this side of the seamount are indicated by white balls. Vertical positions of major watermasses: Norwegian Atlantic Water (NwAtW), Norwegian Arctic Intermediate Water (NwArIW), and Norwegian Deep Water (NwDW) are indicated. To give a broad orientation in space, a north arrow is depicted, as well as the major geologic features (Lofoten Basin and Greenland Basin). For Schulz Bank, water flows, such as a potential Taylor column circulating around the seamount, mixing between summit and pelagic realm, as well as tidally-driven internal motions (black horizontal line with bidirectional arrows) are indicated by dashed arrows and lines.