Author’s response

We like to thank the editor Ph.D. Tina Treude for given us the opportunity to re-submit our manuscript entitled ‘Deep-sea benthic communities and oxygen fluxes in the Arctic Fram Strait controlled by sea-ice cover and water depth’ und for support during the submission process. We further like to thank the referees Paul Renaud and the second anonymous referee for their helpful comments, which improved a first manuscript version substantially. In the following, first the comments from a referee is given, second the author responses (which starts with the term ‘Reply’), and third the author's changes in manuscript (given in blue). Furthermore, a track changes version is included in the reply.

We first address the comments of the referee Paul Renaud and afterwards the comments of the anonymous reviewer.

Author’s response to referee Paul Renaud:

Specific comments:

1. Time scales of response. Direct (and only linear) correlations between environmental parameters and O2 flux may be misleading, or non-representative, depending on when the samples are taken (and when relative to the bloom/flux phenologies among different stations). Benthic biomass/density/structure likely respond to various factors (especially food-related parameters which are often covariates of depth) in a more seasonally (or up to decadally) integrated fashion, whereas O2 consumption/C remineralization are often more responsive to food inputs on a much shorter time scale (approx. weeks) (e.g. Renaud et al. 2008 DSR II). This must be considered in your interpretation.

Reply: We thank the reviewer for this important aspect. As spring bloom data in this region for the studied period (2014-2015) are not yet citable and the authors are no experts in satellite data acquisition and analyses, we refer to the results of Cherkasheva et al. 2014 (http://dx.doi.org/10.1016/j.jmarsys.2013.11.008) to provide information regarding the date of the spring bloom. Furthermore, we acknowledged that correlations do not necessarily prove causal relationships and that oxygen flux measurements only represent a temporal snapshot. As we did not perform measurements during or right after the bloom deposition, we might have missed the immediate and short-term reaction of the benthos to the fresh organic matter. Nevertheless, we can expect a lower influence of macrofauna on the measured oxygen fluxes, compared to the findings in Renaud et al. 2008 (DSR II), owing to the high contribution of microbial benthic mineralization to the total benthic mineralization in the deep sea (Donis et al., 2016, Sauter et al. 2001, Wenzhöfer and Glud,2002), which is also expressed by the mean DOU/TOU ratio of 0.79 presented in our results.

P5, L27: The onset of the spring bloom usually starts in Mai (Cherkasheva et al., 2014).

P17, L6: However, a PCA only shows correlations which does not necessarily prove causal relationships and does not test for the significance of these relationships.

2. As noted in the Methods, the difference between the eastern and western Fram Strait and potential consequences for benthic processes go beyond ice cover. Advected POC/PON/dissolved nutrients and

warmer temperatures on the eastern side are far greater than on the western side. Of course that is linked to why the ice is there, but in this case, ice is more of a covariate and perhaps less likely a causative factors. In addition, different zooplankton and microbial communities can well lead to different ’food’ deposition. This must be considered in detail if the two transects are to be comparable.

Reply: We agree with the reviewer on the differences in advective and vertical food input between the eastern and western Fram Strait. However, the origin of the food input to the benthos can be >3000 km away from the Fram Strait (Lalande et al., 2016, doi:10.1016/j.dsr.2016.04.014). Therefore, a reliable track back and a clear differentiation between the food origin of the eastern and western Fram Strait would be speculative.

P17, L17: Additionally, the origin of the primary production responsible for the benthic food supply is difficult to assess and can be located >3000 km from Fram Strait (Lalande et al., 2016). In turn, the complexity of advective and vertical pelagic food input influencing processes in the Fram Strait is not considered in the ecosystem snapshot.

Furthermore, we pointed out that we used the parameter ‘sea-ice cover’ as a proxy for primary production patterns. The sea-ice in the western Fram Strait represents a suppressed light availability and a reduced nutrient supply (owing to the main currents WSC and EGC). Both light availability and nutrient supply are the main drivers of primary production. This suits the findings of Pabi et al. (2008, doi:10.1029/2007JC004578), showing contrasting primary production quantities among the western and eastern Fram Strait.

P17, L21: To summarise, sea-ice cover in the Fram Strait is a proxy for light availability and nutrient supply and therefore represents primary production in Fram Strait. In addition, water depth represents a proceeding degradation state of settling organic material towards the sea floor (Belcher et al., 2016). Both processes are responsible for the food supply to the benthos. Therefore, the independent factors ‘sea-ice cover’ and ‘water depth’ were the most important abiotic factors in the Fram Strait as they controlled the benthic food supply.

3. Methods: it appears that most of the variables measured were only assessed from the top 1 cm of sediment. Can you provide a justification (data-based) for this? For meiofauna, it is often the top 2-3 cm that contains the majority of the fauna, and for macrofauna, at least the top 5 cm, even at deep-sea depths.

Reply: Indeed, microbial and meiofauna data were assessed from the top 1cm. Macrofauna data and the biogenic sediment compounds, however, were assessed from the top 5cm (MUC cores) and from even deeper sediments (benthic chamber sampled sediments). We improved the method section to clarify this.

P7, L19: For the determination of the meiofauna density and identification of meiofauna taxa, sediment subsamples were taken with modified syringes (3.14 cm² cross-sectional area) from MUC recovered sediment cores after oxygen flux measurements were performed and from benthic chambers. The first centimetre of each sample, usually holding the highest meiofauna density (Górska et al., 2014), was stored in borax buffered 4 % formaldehyde solution at 4 °C.

P7, L30: For macrofauna analyses, the 0–5 cm layer from MUC sediment cores and the entire remaining sediment from the benthic chambers was used, sieved over a 500 µm mesh and stored in borax buffered 4 % formaldehyde and stained with Rose Bengal (Heip et al., 1985).

Regarding the Meiofauna, we refer to Gorska et al. 2014 (http://dx.doi.org/10.1016/j.dsr.2014.05.010) and regarding microbial data, we refer to Quéric et al., 2004 (https://doi.org/10.1016/j.mimet.2004.02.005). Both studies show that most of the investigated organisms in the Hausgarten area occur in the top 1 cm.

4. Ice cover in the two ’regions’ is essentially 70-80% vs 1-10% (heavy ice/no ice). Except for EG V (and N5 which is often excluded from analysis), there is nothing in between. How might this affect your results/interpretation? Many of the results from N5 are more similar to the LSC than the HSC stations (see comment 2 above).

Reply: We acknowledged in our discussion, that comparing only two sites (heavy ice/no ice) does not allow us to estimate the actual relationship between ice cover and the response variables. We would like to point out that only station SV I was often excluded from analyses, owing to its exceptional shallow water depth, compared to all other stations. The introduction of a third category (intermediate ice) would only be based on two stations (EG IV and N5). As these two stations are from the same water depth, they would not include the potential impact of water depth, which was identified as important and therefore would weaken the outcome of this approach.

P17, L21: Furthermore, by comparing only two sites (HSC/LSC) a statistical investigation of the actual relationship between ice cover and the response variables is not possible.

5. Ice cover as the key factor. Related to comment 2 above, have you evaluated whether correlations/differences between benthic parameters and ice cover are the strongest relationships among your data? Primary productivity, vertical flux attenuation, and essentially food supply to the sediment surface may or may not be caused by sea ice in any way. Or it could be a feature of Arctic vs Atlantic water supply that causes a ’cascade of processes’ and sea ice cover may just be a covariate with limited or even no direct causative effect (hence a logic problem on p 15 l 23-25). Your discussion implies that ice is the overriding factor but I do not see where you tested for this, or if it is even possible to disentangle all these variables to isolate depth as the key factor. If you ran similar analyses but grouped stations based on water mass characteristics instead of ice cover you would find the same result.

Reply: We verified whether correlations/differences between benthic parameters and ice cover are the strongest relationships among your data by running the PCA. The eigenvalues indicated that ‘TOC’, ‘Chl a’ and ‘Macrofauna biomass’ were responsible for the gradient along the x-axis and ‘water depth’, organic matter’ and ‘sea-ice concentration’ for the gradient along the y-axis. However, ‘sea-ice’ is a proxy for light availability and nutrient supply in Fram Strait and therefore represents primary production, whereas water depth represents pelagic mineralization and therefore the loss of organic matter in the pelagic zone. Both process are responsible for the final ‘TOC’ and ‘Chl a’ concentrations at the seafloor. To make this clearer, we included the proxy characterization in the method section, added the eigenvalues of the PCA to the manuscript and integrated our argumentation in the discussion.

P14, L26: The PCA on station specific, ex situ obtained mean values (Fig. 5) revealed that water depth was positively correlated with median grain size and negatively correlated with the DOU, the TOU, bacterial density, and the BPc. Sea-ice concentration was negatively correlated with the porosity, Chl a, TOC, organic matter, and solute exchange. Similarly, macrofauna biomass was negatively correlated with, water depth, sea-ice concentration, and the median grain size. The stations of the WS and EG area both followed the water depth gradient and shallower stations showed the higher oxygen fluxes. However, stations of the EG area were strongly influenced by the sea-ice cover, contained less organic matter and Chl a, and macrofauna biomass, compared to the WS stations. The two dimensions of the plot explained 72 % of the total variability of the data (Fig. 5). The eigenvalues indicated that 'Chl a', 'TOC', and 'Macrofauna biomass' (-0.89, -0.88, -0.83, respectively) were responsible for the gradient along the x-axis and 'Bacterial density', 'water depth', organic matter' and 'sea-ice concentration' (0.59, -0.57, -0.54, respectively) for the gradient along the y-axis.

6. P 12 l 6: unclear what water column nutrients, presented as a snapshot without context of 'preformed' (winter) concentrations add here. Bloom phenology certainly is responsible for e.g. the lower nitrate in WS vs EG. Consider removing these data. The discussion on p 15-16 and then sec 4.2 is not really based on the data collected, but more of a general pattern documented in the literature. I agree some of this should be included, but wouldn't a more extended and balanced discussion of benthic process rates and the other factors (proximal) responsible for variation in these rates be appropriate here?

Reply: We agree with the reviewer and removed the nutrient data from the manuscript. Further, we discussed benthic mineralization and the other proximal factors responsible for variation in these rates as well as the relation between primary production and benthic mineralization in more detail. Changes were made throughout the entire sections.

7. Nutrient supply under the ice in EG is extremely low and not expected to increase with further melting of sea ice (e.g. Mauritzen et al. 2011 Prog Oceanogr). This casts serious doubt into any scenario where increased PP due to more light is invoked.

Reply: We revised the potential future scenario, include spatial limitations and point out that this scenario only holds true for areas, where sea-ice disappears and nutrient supply will increase.

P19, L20: Our scenario is only suitable if sea-ice disappears and nutrient supply increase, which will result in enhanced primary production The development of future Arctic Ocean primary production patterns and changes is still under debate (Wassmann, 2011, Arrigo et al., 2012; Nicolaus et al., 2012, Boetius et al., 2013). However, it is likely that the described scenario becomes true in the Chukchi Sea and the Beaufort Sea, owing to the predicted strengthening of the nutrient rich Pacific inflow (Harada, 2015). Furthermore, owing to an increased atlantification, an increased nutrient supply is also likely for the continental margin at the Barents Sea (Neukermans et al., 2018). In addition, nutrient inflow by glacial and permafrost soil melt is also predicted to increase (Vonk et al., 2015). However, this riverine load might only enhance primary production at the shelf areas and therefore is not relevant for the deep sea. An enhanced primary production in the western Fram Strait is unlikely even if the light availability will increase, as the required nutrient supply increase is not expected for this region (Mauritzen et al., 2011).

Technical corrections/details

1. P4 l6-9: unclear sentence. Perhaps just unnecessary (same for l 14-17 as it just repeats what you have just written)

Reply: The sentence was removed.

2. P4, l 24: controlling the benthic ecosystem? Be more specific, including what you mean by ’labile organic matter’ (different from benthic chlorophyll?)

Reply: The sentence was changed to:

P4, L28: However, the principal factor controlling microbial activity in their study was most likely the supply of labile organic matter such as chloroplastic pigment equivalents (CPE; Thiel, 1978), proteins and dissolved free amino acids.

3. P6 l 10: if the algorithm can estimate ice cover at over 100% then couldn’t values between 0 and 100 also be mismeasurements? Could there be some (automated) check to assure that adjacent pixels are ’similar’, or some other way of testing for mismeasurement in this range?

Reply: Whenever there was a mismeasurement, the algorithm output was “128”. So it is not the case that a sea-ice concentration of 101% or 105% or 112% and so on, could be measured. Therefore, the algorithm does not estimate ice cover over 100%. The sentence was improved to make this point clearer. Furthermore, we added information regarding the quantity of these mismeasurements.

P6, L14: Satellite mismeasurements, which were <0.5% of the long-term data, resulted in an algorithm output value of “128” and were omitted from the dataset.

4. Also, is an annual average (vs some other ice cover parameter) the most relevant measure of ice cover?

Reply: We provided some alternative sea-ice concentration periods (mean of 1-month before sampling, mean since first of May (assumed spring bloom onset) till sampling) for the reader. However, as pointed out by the reviewer, “benthic biomass/density/structure likely responds to various factors (especially food-related parameters which are often covariates of depth) in a more seasonally integrated fashion”. To acknowledge this, we used the annual sea-ice cover in the PCA.

5. P 6 l 25: frozen not frosted

Reply: We followed the suggestion of the reviewer and change “frosted” to “frozen”.

P6, L27: All other samples were shock frozen at -80°C and stored at -20°C until they were analysed at the home laboratory.

6. P 8 l 25ff: Was non-local mixing (i.e. non-linear profiles) observed? How was this accounted for in the O_2 flux calculation?

Reply: Non-local mixing was observed in some cases and therefore the reported DOUs for those cases are underestimations. However, only eight out of 81 ex situ obtained oxygen microprofiles at various stations and in one out of 34 in situ obtained oxygen microprofiles showed signs of non-local mixing. This information was added to the method section.

7. P 9 l 1-5: How much of the sediment mass could be attributed to salt from the drying process?

Reply: It was 4.5% ± 1.9 over all samples. We added this information to the method section.

P9, L11: Non-local mixing was observed in some microprofiles and therefore the reported DOUs for those cases are underestimations. However, only at eight out of 81 ex situ obtained oxygen microprofiles at various stations and at one out of 34 in situ obtained oxygen microprofiles signs of non-local mixing were observed.

8. P 10 l 5: consecutive not subsequent

Reply: We followed the reviewers' suggestions and change 'subsequent' to 'consecutive'

P10, L11: The analysed data were obtained during two consecutive years (Table 1).

9. P 10 l 14: 'x to zero mean and unit variance' is unclear

Reply: In most applications of a PCA (e.g. as a factor analysis technique), variables are often measured in different units. For such data, the data must be standardized to zero mean and unit variance, a common standardization procedure. If this is not done, high values (e.g. macrofauna biomass with values of ten thousands of mg m^{-2}) will get a greater importance than low values (e.g. DOU with values of max. 2.1 mmol O2 $m^{-2}d^{-1}$). Similar terms used for this procedure are 'data normalization' or 'z-scoring'. Though, as we followed the suggestions provided by Buttigieg and Ramette (2014), we decided to follow their term of 'standardization' (https://mb3is.megx.net/gustame/indirect-gradient-analysis/pca).

10. P 10 l 21: you must exclude EG II from the analysis. You cannot make the assumption and assign a value. It was fine to exclude the shallow station, and you should do the same with EG II

Reply: We agree with the reviewers' comment that the assumption of a solute exchange value for EG II is not a valid approach to deal with data gaps. However, as the other parameters included in the PCA from EG II were actually measured, we rather prefer to perform the PCA without the parameters of 'solute exchange' from all stations. With this suggestion, EG II would still be part of the central analysis of the paper. Furthermore, as 'solute exchange' is well correlated with other parameters such as macrofauna biomass, it will still be represented in the PCA.

11. P 10 l 30: You need to indicate whether there was a different depth relationship between the two regions and then say what you did if this was (or was not) the case.

Reply: We added the information, that the depth relationships in terms of the bottom slope were similar between the two regions to the method section ('study site'). Furthermore, we indicate whether there were different depth relationships of variables between the two regions. We discussed that the microbial mineralization is the main driver of benthic deep-sea mineralization (see reply to reviewers‘ specific comment no°1). We further added to the discussion that microbial density did not show differences between the HSC and LSC categories and therefore was not the biotic link which connected the food input pattern (Figure S4) with the mineralization pattern (Figure 4).

P5, L32: Thereby the stations in the EG area (namely EG I, EG II, EG III, EG IV and EG V) and in the HG area (namely SV I, HG I, SV IV, HG II, HG III, HG IV, and N5) form a bathymetric transect with a similar bottom slope of ~11°.

For changes made in discussion section, please see the track changes version of the manuscript in attachment.

12. P 12 l 6: unclear what water column nutrients, presented as a snapshot without context of ’preformed’ (winter) concentrations add here. Bloom phenology certainly is responsible for e.g. the lower nitrate in WS vs EG. Consider removing these data. The discussion on p 15-16 is not really based on the data collected, but more of a general pattern documented in the literature.

Reply: We followed the reviewers’ suggestion and removed the nutrient data from the manuscript.

13. P 12 l 10ff (and Fig 3). Please indicate any statistical results such that the figures correspond to what is written in the text regarding comparisons between the two regions. Only statistically significant results should be expressed as ’differences’ (e.g. solute exchange is likely NS but significance is implied). Also, please clarify how many stations (and depth profile) each bar represents. This has some bearing on your comments about variability between the two locations.

Reply: We improved the text and used the term ‘differences’ only in case of significant differences. Further, we indicated significant differences between the stations in the figure and add the number of observations for each bar.

As an example, the results of the sediment compounds read now ‘The mean DOU in the EG area ranged between 0.4 ± 0.1 mmol O_2 $m^{-2}d^{-1}$ (n=10) at EG V and 1.0 ± 0.1 mmol O_2 $m^{-2}d^{-1}$ (n=10) at EG II. In the WS area, DOUs at stations within the same water depth range as the EG stations ranged between 0.5 ± 0.2 mmol O_2 $m^{-2}d^{-1}$ (n=8) at HG IV and 2.1 ± 0.6 mmol O_2 $m^{-2}d^{-1}$ (n=8) at SV IV. At the shallow station SV I the DOU reached 3.0 ± 1.7 mmol O_2 $m^{-2}d^{-1}$ (n=6, Table 3). The mean TOU in the EG area ranged between 0.9 ± 0.3 mmol O_2 $m^{-2}d^{-1}$ (n=2) at EG I and 1.6 mmol O_2 $m^{-2}d^{-1}$ (n=1) at EG II. Similar mean TOU values were measured in the WS area, at stations within the same water depth range as the EG stations. TOU values ranged between 0.5 ± 0.2 mmol O_2 $m^{-2}d^{-1}$ (n=5) at HG IV Lander and 1.9 ± 0.6 mmol O_2 $m^{-2}d^{-1}$ (n=5) at HG I. At the shallow SV I station TOU reached 5.1 ± 0.3 mmol O_2 $m^{-2}d^{-1}$ (n=3, Table 3). DOU differed significantly between the WS and EG area, while TOU was similar among the areas (Fig. 3, Supplement Table S4).

14. P 12 l 18: 'pelagic food supply indicating parameter in the sediment' rephrase to clarify that these are sediment values and careful about how you define food quality. Not all organisms eat chlorophyll (in fact maybe few actually do). Bacteria themselves are likely food for many organisms, and phaeopigments and other OC may also be quite high quality food for others.

Reply: We followed the suggestion of the anonymous second reviewer, added ranges of values regarding benthic food supply representing parameters.

P12, L30: The sediment bound Chl a concentration ranged between 0.4 ± 0.3 µg ml-1 sediment-1 (n = 15) at EG III and 12.7 ± 3.1 µg ml-1 sediment-1 (n = 15) at SV I (Table 3) and differed significantly between the EG and WS area (Figure 3, Supplement Table S4). A similar pattern was found for sediment bound Phaeo concentrations and CPE concentration with over 4 –times higher median values in the WS area compared to the EG area (Figure 3). The Chl a/CPE and Chl a/Phaeo ratios did not differ between the EG and WS area (Supplement Table S4), which indicates that the benthic community in both areas fed on a similar food quality and received the spring bloom food supply at the same time, respectively. Sediment bound TOC ranged between 0.44 ± 0.04 % (n = 15) at EG II and 1.58 ± 0.27 % (n = 15) at SV I and differed between the EG and WS area, similar to organic matter, which ranged between 3.45 ± 0.6 % (n = 15) at EG II and 12.0 ± 4.2 % (n = 30) at HG III (Table 3, Figure 3, Supplement Table S4). Proteins, lipids and FDA also differed between the EG and WS area with 5.6 times, 2.3 times, and 1.8 times higher median values in the WS area, respectively (Figure 3, Supplement Table S4).

15. P13 l 21: 'which indicates bacterial activity and bacterial remineralisation as the major oxygen consumer' please indicate why you conclude this. Why would bacterial oxygen consumption not be reflected in DOU data. These are effectively two different techniques to measure the same thing, each with underlying assumptions. The conclusion you make regarding the ratio is not supported.

Reply: We rephrased the sentence to:

The mean DOU/TOU ratio, which describes the fraction of the total community mediated oxygen flux (TOU) covered by the microbial mediated oxygen flux (DOU, Glud, 2008,) across the entire Fram Strait was 0.79 ± 0.30, with 0.63 ± 0.22 in the EG area and 0.92 ± 0.30 in the WS area, indicating that the total oxygen uptake is mainly microbial mediated.

16. P 14 l 7-13: I would focus on the differences among EG and WS stations as revealed by PCA, and not individual variable correlations (which are NOT real correlations but instead are ordination-based relationships! If you want to look for correlation then run that analysis on the raw data).

Reply: We followed the suggestion of the reviewer and changed the paragraph to emphasize the differences among EG and WS stations.

P14, L29: The stations of the WS and EG area both followed the water depth gradient and shallower stations showed the higher oxygen fluxes. However, stations of the EG area were strongly influenced by the sea-ice cover, contained less organic matter and Chl a, and macrofauna biomass, compared to the WS stations.

However, the reason to perform the PCA was to reveal the relationships between the multiple parameters. Therefore, we performed a PCA in the scaling II mode, which emphasize the relationships between parameters (Buttigieg and Ramette, 2014, https://doi.org/10.1111/1574-6941.12437). We added this information to the method section. A performance on raw data as suggested by the reviewer is, however, not recommendable due to the reasons presented in the comment no°9. The correlation of single parameters with each other was already given in Table S2 and Figure S3. In addition, a PCA is a procedure that transforms a number of (possibly) correlated variables into a (smaller) number of uncorrelated variables called principal components. Thus a PCA eliminates redundant information. As it also gives the contribution of the single parameter (=strength of influence) to each principle component, the parameters most likely control the investigated area can be identified (Boetius and Damm, 1998, doi: https://doi.org/10.1016/S0967-0637(97)00052-6).

17. P 16 l 17: but macrofauna biomass has a similar relationship with depth between the two ice-cover systems

Reply: We rephrased the sentence to Continuing the cascade of dependencies, benthic community parameters should follow the same pattern as the sea ice at the surface and the benthic food supply parameters. Indeed, there were differences between the EG and WS area regarding meiofauna density and macrofauna density but not in the macrofauna biomass.

18. P 16 l 18-20. Repetitive

Reply: We followed the reviewers' suggestion and remove the repetitive content.

19. P 16 l 27: A CCA or RDA would find significant relationships.

Reply: We tested our data regarding the suitability of the usage of a CCA ('decorana'-command in R package vegan) with the outcome that our data showed linear correlations, so only a RDA would be a suitable approach. Usually, an RDA is used to correlate parameters of two information layers: environmental and biotic data, where the former influences the latter. However, from our point of view, we have three information layers: environmental, biotic, and flux data. It is common knowledge that environmental data influence biotic data and both are influencing the flux data. Therefore, we decided for an indirect ordination by a PCA as the direct approach of an RDA incorporates the measured parameters into the ordination, without considering the possible influence of other, unmeasured parameters.

20. Sec 4.3: first paragraph unnecessary.

Reply: We followed the reviewers' suggestion and remove the first paragraph.

21. P 19 l 4: neither citation is in the references. Are you sure the Kortsch ref is appropriate?

Reply: The reference of Jones et al., 2014 was added to the references, whereas Kortsch et al., 2012 was removed as suggested by the reviewer and we added the reference of Harada (2015) instead.

Authors response to second anonymous referee:

Specific comments:

1. The introduction will benefit from turning the lists of which factors depend on which other factors into a narrative explaining how they influence each other. This change would necessarily make the introduction a bit longer, but improve the logic, flow and justification for the study. Also, the authors would help the reader by providing a bit of background why they estimate remineralization of new production rather than calculating it because they can.

Reply: We followed the reviewers' suggestion and rewrote the introduction into a narrative explaining how factors influence each other by giving the information how single factors are correlated which each other. Further, we pointed out the link between the new production and the remineralization.

Benthic deep-sea remineralisation depends on primary production and is as such closely linked with primary production patterns, known as pelagic–benthic coupling (Graf, 1989). The relationship, however, includes many and partly inter-dependent factors. Benthic deep-sea remineralisation is positively correlated with surface primary production (Graf et al., 1995; Wenzhöfer and Glud, 2002; Smith et al., 2016), which is on its turn controlled by light availability and nutrient supply (Kirk, 2011; Cherkasheva et al., 2014; Fernández-Méndez et al., 2015). Though, only the annual new production leaves the euphotic zone (Platt et al., 1989) and can supply the benthos with organic carbon. Benthic remineralisation is negatively correlated to water depth (Jahnke et al, 1990; Jahnke, 1996; Wenzhöfer and Glud, 2002), as it represents a loss of organic carbon by pelagic remineralisation (Rullkötter, 2006; Belcher et al., 2016) and thereby a loss of benthic food. After organic carbon reached the seafloor, it is ingested and remineralised by the benthic community. Benthic community parameters, e.g. biomass, density, structure, and functions of different fauna size classes, are controlled by food supply (and thus by primary production) and water depth (Piepenburg et al., 1997; Flach et al., 2002; Smith et al., 2008) but also by sediment properties (Wheatcroft, 1992; Vanreusel et al., 1995). Benthic remineralisation rates also depend on benthic community biomass (Glud et al., 1994). Furthermore, benthic remineralisation is enhanced if the benthic community intensifies oxygenation of the seafloor (Glud, 2008) and thus also depends on the benthic community structure. Therefore, the ecosystem processes primary production, pelagic remineralisation and benthic remineralisation, as well as the components benthic community biomass, density, and structure are controlled by abiotic and biotic factors and additionally create a cascade of dependencies from the ocean's surface zone of primary production to and within the deep-sea benthos.

2. The discussion (especially 4.1 and 4.2) repeats the results to a large extent. Instead, it should place the results in the context of the extensive literature from the area and beyond. I recommend the authors summarize their findings more concisely and discuss their results in the context of, for example, the pan-Arctic scale Progress in Oceanography issue from 2015, primary productions model estimates covering the area, the series of three articles from Patrai – Codispoti 2013 etc.

Reply: Indeed, we repeated the results to a large extent, as we first needed to interpret our results before we could start to place the output in the context. However, we reduced the repetition where ever possible and thereby followed the reviewer's suggestion.

For example, the second paragraph of section 4.1 was changed to:

The results of Pabi et al. (2008) showed that the annual primary production pattern follows the general sea-ice concentration pattern in the Fram Strait and is up to 10-times larger in the WS area compared to the EG area. Thus, the sea-ice concentration represents the general primary production pattern in the Fram Strait. As the sampling was performed in Mid/End of June 2014 and July/August 2015, it is very likely that the spring bloom, which usually starts in May (Cherkasheva et al., 2014), had finished. This is indicated by lower nutrient concentrations in water depth ≤50 m compared to the nutrient concentrations between >50–300 m water depths (Graeve and Ludwichowski, 2017a, b). The N:P ratio in the upper 50 m during the expeditions was six and seven in the EG and WG area, respectively (Graeve and Ludwichowski, 2017a, b), indicating that primary production was nitrate limited, similar to the permanently sea-ice covered central Arctic Ocean (Tremblay et al., 2012, Fernández-Méndez et al., 2015). Furthermore, the timing of our sampling suggests that the increased carbon supply by the spring bloom had already reached the seafloor and enhanced the benthic remineralisation (Graf, 1989) in both areas. The pattern of contrasts between the EG and WS area continued in the benthic food supply, which was also found by Boetius and Damm (1998) for areas with contrasting sea-ice cover at the continental margin of the Laptev Sea.

We further integrated the results from the suggested articles.

3. Water depth and vertical flux are well-documented highly influential factors structuring benthic communities both in terms of biodiversity and biomass/abundance anywhere in the ocean, in addition to sea ice cover. While these factors are mentioned in the discussion (without much literature support actually), it should also be noted more prominently that eastern Fram Strait receives constant inflow of particle rich Atlantic water, and this advective input adds to the vertical flux (see for example Wassmann et al. 2015 PiO for a summary). It is indeed complex to separate out the effects of water mass properties including particle content, and ice cover – a fact that should be acknowledged.

Reply: We added information regarding the advective Atlantic input and acknowledge the complexity to track back the origin of organic matter resource (see reply no°2 to specific comments of first referee Paul Renaud). Indeed, there is quite some knowledge about the vertical carbon flux available. However, most of the data are from the more southerly and mainly sea-ice free locations in the Greenland Sea ("The Northern North Atlantic", edited by Schäfer, Schlüter and Thile). Owing to the complexity to separate out the effects of water mass properties, we only cited literature from very closed-by locations and thus, ensure a maximum of reliability of our comparison of remineralization data with the vertical carbon flux.

4. The authors said they struggled to find some relevant information (e.g. on primary production) for the western Fram Strait side, and therefore used values from the central Arctic. They might consider the results of the SFB313 that spent years investigating East Greenland including the slope, including carbon remineralization, primary production, benthic community structure etc., http://www.springer.com/us/book/9783540672319. Was the region never covered in any of the primary production models? Some additional useful information from eastern Fram Strait is also available, e.g. Wlodarska-K. et al. 2004 in DSRII.

Reply: We would like to excuse our unsuccessful literature research and thank the reviewer for the suggested literature. In the meantime, we found modeled primary production in the Arctic, which included estimates of primary production across Fram Strait. This source indicated the expected and contrasting primary productivity between the EG and WS area (Pabi et al, 2008, doi:10.1029/2007JC004578). The suggested study of Codespoti et al. (2013, http://dx.doi.org/10.1016/j.pocean.2012.11.006), which included values of new production, was used to give a more reliable insight into the relationship between primary production and benthic mineralization in the Fram Strait.

Small corrections/comments:

1. P4 l6 I would not call primary production and oxygen flux an ecosystem component, they are rate measurements of processes. The benthic community is an ecosystem component.

Reply: We followed the reviewers' suggestion, rewrote the introduction (see reply to anonymous reviewer 'specific comments' no°1) and thereby changed the term 'component' to 'process'.

2. P4 Delete l6-8 (redundant to previous sentence).

Reply: We deleted the redundant sentence in the rewritten introduction (see anonymous reviewers 'specific comments' no°1).

3. L4 l9 Rather 'nutrient concentrations' (or which property of nutrients?)

Reply: Following the suggestions of the reviewer Paul Renaud, all data regarding nutrients were removed from the manuscript. However, we added information regarding the nutrient state of the Fram Strait in the 'Study site' section and added the N:P ratio to the discussion.

P16, L19: This is indicated by lower nutrient concentrations at water depth ≤50 m compared to the nutrient concentrations between >50–300 m water depths (Graeve and Ludwichowski, 2017a, b). The N:P ratio in the upper 50 m during the expeditions was six and seven in the EG and WG area, respectively (Graeve and Ludwichowski, 2017a, b), indicating that primary production was nitrate limited, similar to the permanently sea-ice covered central Arctic Ocean (Tremblay et al., 2012; Fernández-Méndez et al., 2015).

4. P4l10 If this is to be general across the globe, add 'In general, benthic community ...'

Reply: We added the term 'In general,' to the sentence.

5. P4l14 and elsewhere. I was taught 'therefore' never starts a sentence.

Reply: We have to disagree with the reviewer and refer to the following websites:

http://grammarist.com/grammar/therefore/

https://www.iup.edu/writingcenter/writing-resources/grammar/common-problems-with-however,-therefore,-and-similar-words/

6. P4l20 ‘Western’ Arctic is a rather undefined term, since different nations use it in very different ways, rather give the region.

Reply: We followed the reviewers’ suggestion and change ‘western Arctic’ to ‘Chukchi and Beaufort Sea’.

7. P4l21-22 Unclear how the ‘better fit’ works when one doesn’t know what other factors were included.

Reply: We changed the sentence to ‘A pan-arctic benthic remineralisation model showed a better fit when water depth and benthic chlorophyll data (representing food supply from primary production) were taken into account, compared to a model using only water depth as controlling factor (Bourgeois et al., 2017). This indicates that surface primary production patterns and water depth are both relevant factors controlling benthic remineralisation in the Arctic Ocean.’.

8. P4l34 No need to repeat the three references for the same aspect since already given in l28 P5l17ff What time period is considered when talking about stable ice cover here? What time period is considered in the number of 0.6 years per decade? (And somewhere in the discussion the author talk about ice thinning, a bit of a contradiction.)

Reply: We removed the repetitive references. The cited references only mentioned ‘stable ice cover’ without data support. Therefore, the dataset presented in our manuscript actually describes the sea-ice conditions for the first time in reliable, satellite-based numbers. The time-period for the sea-ice rejuvenation was added. However, we have to disagree with the reviewer that a sea-ice rejuvenation is contradicting with a sea-ice thinning. Multi-year sea-ice is thicker than perennial, first-year sea-ice. Consequently, when sea-ice becomes younger, it is likely that it becomes thinner as well, which we pointed out in the introduction.

P5, L25: However, the sea-ice age becomes younger by 0.6 years per decade (2001–2012, Krumpen et al., 2015), which goes along with a decrease in the sea-ice thickness (Renner et al., 2014; Krumpen et al., 2015). The onset of the spring bloom usually starts in Mai (Cherkasheva et al., 2014).

9. P6l4 Why combine sea ice cover and nutrients under one sub-header? I suggest separating those sections.

Reply: As mentioned in the reviewers’ small corrections / comments no°3, data regarding nutrients were removed from the manuscript. Thereby, the identified issue was solved.

10. P5l6 rather ‘Study area and field sampling’ or ‘Study area and sample collection’. None of the sample preparation or processing is described here.

Reply: We followed the reviewers' suggestion and used the term 'Study area and field sampling'

11. P6l9 Although both 'data are' and 'data is' is allowed per some dictionaries, it really should be 'data are' (one datum, several data).

Reply: We changed the term to 'data are' throughout the entire manuscript.

12. P6l15 Provide a reference for the nutrient measurement method.

Reply: As mentioned in the reviewers' small corrections / comments no°3, data regarding nutrients were removed from the manuscript. However, we added information regarding the nutrient state of the Fram Strait (see reply to anonymous reviewer's small corrections / comments no°3).

13. P6l20 Which property of phospholipids and proteins and organic matter was measured – presumably concentrations?

Reply: We specify the measured property and change the sentence to 'Various biogenic sediment compounds including grain size, water content, chlorophyll a (Chl a) and phaeopigment concentrations (Phaeo), portion of total organic carbon (TOC), phospholipids concentrations, protein concentrations, portion of organic matter, and the bacterial enzymatic turnover rate (FDA) as bacterial activity proxy were determined from the sediments sampled by the MUC and chambers of the autonomous benthic lander system.'

14. P6 section 2.3 The methods description is extremely abbreviated, but it is an editor decision if this is sufficient.

Reply: We are aware of the intense use of abbreviations. However, all abbreviations are common and introduced before, as recommended by the manuscript guidelines of 'Biogeosciences'.

15. P7 2.4 What taxonomic resolution was aimed for?

Reply: We added the aimed taxonomic resolution, which was at least class level for macrofauna and order level for meiofauna.

16. P12l6 It would be appropriate to include the nutrient profiles (at least upper water column) into the MS figures rather than the supplement given that the nutrient inventories provide the basis to the level of primary production possible (although measured after the bloom was done presumably). At the very least some concentration ranges should be mentioned. Define 'surface'.

Reply: As mentioned in the reviewers' small corrections / comments no°3, data regarding nutrients were removed from the manuscript. However, we added information regarding the nutrient state of the Fram Strait (see reply to anonymous reviewer's small corrections / comments no°3).

17. P12l16 Why ‘indicates’? Later you test this!

Reply: We removed the sentence, as indeed we later test this.

18. P12l12 There are different opinions on this, but given that I would find at least a range of densities etc. presented (as is done in the next section 3.4). At the very least, table 2 should be referenced here so that the reader can find the results.

Reply: We followed the reviewers’ suggestion and present ranges for the parameter ‘median grain size’, ‘portion of grain size >63 µm’, ‘water content’ and ‘porosity’ in section 3.2. However, we deviated from the pattern used in section 3.4 for the parameter Chl *a*, Phaeo, CPE, Chl a/CPE ratio, Chl a/Phaeo ratio, TOC, organic matter, proteins, lipids, FDA, as it would lead to an absolutely illegible paragraph. Therefore, we presented the minimum and maximum values across the entire Fram Strait only for Chl *a*, TOC and organic matter and not distinguish between the EG and WS area. For the remaining parameter Phaeo, CPE, Chl a/CPE ratio, Chl a/Phaeo ratio, proteins, lipids, and FDA magnitudes were given. In addition, we refered the reader to Table 3 (former Table 2), Figure 3 and Supplement Table S4, which holds more detailed information.

The sediment bound Chl *a* concentration ranged between 0.4 ± 0.3 µg ml^{-1} $sediment^{-1}$ (n=15) at EG III and 12.7 ± 3.1 µg ml^{-1} $sediment^{-1}$ (n=15) at SV I (Table 3) and differed significantly between the EG and WS area (Figure 3, Supplement Table S4). A similar pattern was found for sediment bound Phaeo concentrations and CPE concentration with over 4 –times higher median values in the WS area compared to the EG area (Figure 3). The Chl *a*/CPE and Chl *a*/Phaeo ratios did not differ between the EG and WS area (Supplement Table S4), which indicates that the benthic community in both areas fed on a similar food quality and received the spring bloom food supply at the same time, respectively. Sediment bound TOC ranged between 0.44 ± 0.04 % (n=15) at EG II and 1.58 ± 0.27 % (n=15) at SV I and differed between the EG and WS area, similar to organic matter, which ranged between 3.45 ± 0.6 % (n=15) at EG II and 12.0 ± 4.2 % (n=30) at HG III (Table 3, Figure 3, Supplement Table S4). Proteins, lipids and FDA also differed between the EG and WS area with 5.6 –times, 2.3 –times and 1.8 –times higher median values in the WS area, respectively (Figure 3, Supplement Table S4).

19. P13l31-32 add ‘rather than an actual interannual difference’

Reply: We removed the entire sentence ‘These differences are probably a result of the different sampling periods (June in 2014 and end of July/beginning of August 2015), resulting in different Phaeo and CPE concentrations.’. For justification please look at small corrections / comments no°20.

20. P14l5 Just above you wrote the different is likely related to the months, while this line states it is a spatial difference. Both may be true, but as written the statements seem contradictory.

Reply: By removing the sentence in P13l31-32 (small corrections / comments no°19), the inconsistency identified by the reviewer was solved.

21. P14l26 Significant indeed, but the authors should mention that the global R values are rather low, same with the macrofauna results.

Reply: We agree with the reviewer that the global R values are low. We added this information to the text.

P15, L15: Regarding macrofauna communities based on density (Global R = 0.257, p = 0.007) and biomass (Global R = 0.238, p = 0.003), the ANOSIM revealed significant but weak differences between the HSC and LSC area. SIMPER routine results indicated dissimilarities of 56 % for the macrofauna density and 76 % for the macrofauna biomass between the HSC and LSC areas. The taxa which contributed most to the average similarity within and to the average dissimilarity between the HSC and LSC area are given in Supplement Table S10. The ANOSIM results for water depth groups showed that bathymetry could at least explain the dissimilarity in meiofauna communities based on density (Global R = 0.219; p = 0.01), even if the difference was weak. The SIMPER analysis, however, showed that the observed differences in meiofauna density regarding water depth were mainly due to the marked difference between the shallowest station (SV I at 275 m) and all other stations deeper than 1000 m (dissimilarity >50 %, Supplement Table S11). ANOSIM results for macrofauna communities based on density (Global R = 0.2, p = 0.008) and biomass (Global R = 0.346, p = 0.0001) revealed significant but also weak differences between water depth categories with >50 % dissimilarity between all water depth categories for macrofauna density (except between 1000 m and 1500 m) and macrofauna biomass (SIMPER, Supplement Table S11).

22. P15 l10 perhaps add ‘ marginally not significant’

Reply: We decided to omit the last part of the sentence. It now reads ‘Further, the two-way crossed PERMANOVA revealed that the sea-ice coverage (LSC and HSC) explains a significant (p = 0.008) portion of the macrofauna density variability.’ We reported that the result of the interaction effect of water depth and sea ice concentration on macrobenthic community biomass was significant. Therefore, it was pointless to look at the effects of the single factors, simply because the test just showed that their effect depends on the effect of the other factor.

23. P15l16 As phrased, this is not a question.

Reply: We rephrased the sentence to ‘The aim of this study was to link contrasting sea-ice conditions with…’

24. P15l23 Grammar. If there were a strong link ... we would expect .... (conditional)

Reply: We changed the sentence to ‘If there were a strong link between sea-ice conditions and deep-sea benthic oxygen fluxes, we would expect contrasting primary production, benthic food supply, benthic community parameters and benthic oxygen fluxes between the EG and the WS area.’

25. P16l14/15 This is not the right place to mention this point, move to figure caption or results text.

Reply: We removed the sentence, as the information is already implemented in the method description of the PCA.

26. P16l27 opposite to our expectations or in contrast to our expectations. The following PCA sentence is grammatically incorrect. The PCA only shows .. but does not test ...

Reply: We changed the sentences to ‘This is in contrast to our expectations and to findings of Boetius and Damm (1998). However, a PCA only shows correlations but does not test for the significances of these relationships.’

27. P19l4 The Kortsch paper is on shallow nearshore hard bottom communities, not quite the right reference here.

Reply: Indeed, Kortsch et al is not an appropriate reference, as it deals with benthic changes in a fjord system. The reference was removed and instead we added Harada (2015, doi: 10.1016/j.gloplacha.2015.11.005).

28. P19l10 In earlier sections the authors talk about ‘stable ice conditions’ in Fram Strait, while here they state that ice is thinning. Specifying by which metric the conditions are stable will relieve the contradiction.

Reply: We specified, that the term ‘stable conditions’ is used in terms of the general pattern of the sea-ice concentration in the Fram Strait (west: high concentration/east: low concentration).

P12, L14: This pattern also occurred in the other short-term datasets and in the long-term dataset. The latter indicated that the sea-ice cover in terms of sea-ice concentration was stable across the Fram Strait the last 15 years (Fig. 2, Supplement Table S3).

29. P19l14 My understanding of the Boetius et al. paper is that these authors discussed the high Melosira biomass to be generated on the shelf and maintained (but not produced) over the basin through constant resupply of –albeit low – nutrients during ice drift, not as a consequence of increasing algal biomass in the central Arctic. General: Someone should switch German to English comma rules throughout.

Reply: We are thankful for the additional perspective regarding the interpretation of the publication of Boetius et al. (2013). The aim of the sentence is to point out that the Fram Strait benthos did not receive any algae patches (as far as assessable), which would have had a dramatic impact on the microbial and therefore total remineralization and would indicate that our presented mineralization are underestimations. As this is not the case (no algae patches found), our results are reliable. However, in order to stress this, the sentence was changed to ‘However, fast sinking algae patches as reported by Boetius et al (2013) in the central Arctic, which would lead to increased benthic mineralization, were not observed during a video transect at EG IV in 2014 (pers. Comm. J. Taylor).’.

We applied English comma rules by using the free-ware version of gramma software grammaly.com. and we the manuscript was checked by a native speaker.

30. Table 2. Use same number of decimals within one parameter (e.g. days with sea ice has between zero and two decimals).

Reply: We adjusted the number of decimals to be consistent throughout one parameter.

31. Table 3. Spell out HSC and LSC.

Reply: We spelled out HSC and LSC in the table caption. It was changed to 'The table shows that there are differences in the macrofauna community between the highly sea-ice covered area (HSC) and the low sea-ice covered area (LSC), while this is not the case for the meiofauna community.'

32. Figure 1. Specify time frame for 'general summer sea ice extent', by month and period.

Reply: We specified the month and period for the 'general summer sea-ice extent', which is September 1981-2010 (http://nsidc.org)

33. Figure 3. Indicate if any of the differences between EG and WS were statistically significant. This and other figures explain abbreviations or say in caption where they are explained.

Reply: We indicated significant differences between the stations in the figure and add the number of observations for each bar according to the reviewer's suggestion and the suggestions of the reviewer Paul Renaud. Further, we explained the used abbreviations in the figure and table captions.

34. Figure 6. Typos: Arctic missing 'c'. Sauter et al. and Bourgeois et al. missing periods after al.

Reply: We corrected the typo's in figure 6.

In addition to the above mentioned changes, further changes were made in the manuscript either to increase readability (e.g. improved Fig. 1) or additional found flaws and typos were corrected. All changes that were made are trackable in the provide track-changes-version of the manuscript placed below.

Deep-sea benthic communities and oxygen fluxes in the Arctic Fram Strait controlled by sea-ice cover and water depth

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Abstract

Arctic Ocean surface sea-ice conditions are linked with the deep sea benthic oxygen fluxes via a cascade of dependencies across ecosystem components like primary production, food supply, the activity of the benthic community, and their functions. Additionally, each of the ecosystem components is influenced by abiotic factors ~~like~~ such as light availability, temperature, water depth, and ~~or~~ grain size structure. In this study, we investigated the coupling between surface sea-ice conditions and deep-sea benthic remineralis~~z~~ation processes through a cascade of dependencies in ~~the~~ Fram Strait. We measured sea-ice concentrations, a set of ~~nutrient profiles,~~ different sediment compounds, benthic community parameters, and oxygen fluxes at 12 stations ~~in~~ at the LTER HAUSGARTEN ~~area~~ observatory in ~~of the~~ Fram Strait ~~in~~ at water depth between 275–2500 m. Our investigations reveal that the Fram Strait is bisected in (I) a permanently and highly sea-ice covered area and (II) a seasonally and low sea-ice covered area, which both are long-lasting and stable. Within the Fram Strait ecosystem, sea-ice concentration and water depth are two independent abiotic factors, controlling the deep-sea benthos. Sea-ice concentration correlated ~~s well~~ with the available food~~,~~ while water depth with the oxygen flux, and both abiotic factors correlate with the macrofauna biomass. However, ~~in~~ at water depths >1500 m the influence of the surface sea-ice cover fades out and the water depth effect becomes more dominant. Benthic r~~R~~emineralisation across the Fram Strait on average is ~ 1 mmol C $m^{-2}d^{-1}$. ~~Owing to the contrasting primary production pattern, o~~Our data indicate that the portion of newly produced carbon that is remineralised by the benthos is 5~~–2.6~~ % in the seasonally low sea-ice covered eastern part of Fram Strait but can be 14~~>15~~ % in the permanently high sea-ice covered western part of Fram Strait. Furthermore, by comparing a permanently sea-ice covered area with a seasonally sea-ice covered area, we discuss a potential scenario for the deep-sea benthic ecosystem in the future Arctic Ocean, in which an increased surface primary production can lead to increasing benthic remineralisation ~~in~~ at water depths <1500 m.

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1 Introduction

Benthic deep-sea remineralisation depends on primary production and is as such closely linked with primary production patterns, known as pelagic–benthic coupling (Graf, 1989). The relationship, however, includes many and partly inter-dependent factors. Benthic deep-sea remineralisation is positively correlated with surface primary production (Graf et al., 1995; Wenzhöfer and Glud, 2002; Smith et al., 2016), which is on its turn controlled by light availability and nutrient supply (Kirk, 2011; Cherkasheva et al., 2014; Fernández-Méndez et al., 2015). Though, only the annual new production leaves the euphotic zone (Platt et al., 1989) and can supply the benthos with organic carbon. Benthic remineralisation is negatively correlated to water depth (Jahnke et al, 1990; Jahnke, 1996; Wenzhöfer and Glud, 2002), as it represents a loss of organic carbon by pelagic remineralisation (Rullkötter, 2006; Belcher et al., 2016) and thereby a loss of benthic food. After organic carbon reached the seafloor, it is ingested and remineralised by the benthic community. Benthic community parameters, e.g. biomass, density, structure, and functions of different fauna size classes, are controlled by food supply (and thus by primary production) and water depth (Piepenburg et al., 1997; Flach et al., 2002; Smith et al., 2008) but also by sediment properties (Wheatcroft, 1992; Vanreusel et al., 1995). Benthic remineralisation rates also depend on benthic community biomass (Glud et al., 1994). Furthermore, benthic remineralisation is enhanced if the benthic community intensifies oxygenation of the seafloor (Glud, 2008) and thus also depends on the benthic community structure. Therefore, the ecosystem processes primary production, pelagic remineralisation and benthic remineralisation, as well as the components benthic community biomass, density, and structure are controlled by abiotic and biotic factors and additionally create a cascade of dependencies from the ocean's surface zone of primary production to and within the deep-sea benthos.

In the Arctic Ocean, pelagic–benthic coupling is assumed to be stronger relative to temperate and tropical waters (Ambrose and Renaud, 1995; Graf et al., 1995; Grebmeier and Barry, 2007). A pan-arctic benthic remineralisation model showed a better fit when water depth and benthic chlorophyll data (representing food supply from primary production) were taken into account, compared to a model using only water depth as controlling factor (Bourgeois et al., 2017). This indicates that surface primary production patterns and water depth are both relevant factors controlling benthic remineralisation in the Arctic Ocean. The occurrence of sea ice in the Arctic Ocean, however, ultimately reduces the light availability and thereby suppresses primary production (Arrigo et al., 2008; Bourgeois et al., 2017). As a consequence, climate change induced alterations in the sea-ice cover influence biogeochemical cycles in the Chukchi and Beaufort Sea (Harada, 2015). Boetius and Damm (1998) also found a good correlation between sea-ice cover, benthic chlorophyll and benthic carbon remineralisation in the Laptev Sea. However, the principal factor controlling microbial activity in their study was most likely the supply of labile organic matter such as chloroplastic pigment equivalents (CPE; Thiel, 1978), proteins and dissolved free amino acids. Therefore, the strength of the relationship between sea-ice cover (controlling primary production) and benthic remineralisation, even if assumed as direct and strong, needs to be considered more carefully (Renaud et al., 2008).

~~The deep Arctic Ocean appears to have an enhanced coupling (relative to temperate and tropical waters) and therefore a strong linkage between surface waters and the benthos (Ambrose and Renaud, 1995; Graf et al., 1995; Grebmeier and~~

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~~Barry, 2007). For example, benthic deep sea oxygen fluxes, representing the benthic ecosystem activity and the benthic remineralisation of carbon (Thamdrup and Canfield, 2000; Wenzhöfer and Glud, 2002; Smith et al., 2013), mirror surface primary production patterns (Graf et al., 1995; Wenzhöfer and Glud, 2002). However, each ecosystem components (primary production, benthic community and its activity, and benthic oxygen flux) depend on each other in the order as they are mentioned here and are additionally influenced by further factors. Primary production is influenced by a combination of abiotic factors like light intensity and light availability, advection, water stratification, sea surface temperature and nutrients (Bourgeois et al., 2017 and references therein). Benthic community parameters, like biomass, density, structure and functions of different fauna size classes, are influenced by sediment properties (Wheatcroft, 1992; Vanreusel et al., 1995), water depth, water temperature and food supply (Piepenburg et al., 1997; Flach et al., 2002; Smith et al., 2008). Benthic oxygen fluxes are known to depend on water depth (Wenzhöfer and Glud, 2002), benthic community biomass (Glud et al., 1994), and benthic community functions (Braeckman et al., 2010). Therefore, the ecosystem components primary production, benthic food supply, benthic community biomass, density and structure, benthic community functions and benthic oxygen flux are influenced by abiotic factors and additionally create a cascade of dependencies from the ocean's surface to and within the deep-sea benthos.~~

~~The occurrence of sea ice is an additional factor influencing primary production across the Arctic Ocean, as it ultimately alters the light availability (Arrigo et al., 2008; Bourgeois et al., 2017). As a consequence, the climate change induced alteration in the sea-ice cover influence biogeochemical cycles in the western Arctic (Harada, 2016). Further, a pan-arctic benthic oxygen flux model by Bourgeois et al. (2017) showed a better fit when benthic chlorophyll data, indicating surface primary production patterns, were taken into account. Boetius and Damm (1998) also found a good correlation between sea-ice cover, benthic chlorophyll and benthic carbon remineralisation in the Laptev Sea. However, microbial biomass, microbial activity, and labile organic matter supply are reported to be the key parameters controlling the benthic ecosystem in the dataset of Boetius and Damm (1998). Therefore, the strength of the linkage between the sea ice cover and benthic remineralisation, even if often assumed as direct and strong, needs to be considered more carefully.~~

We were interested in the question, if we can link contrasting sea-ice conditions between the eastern and western Arctic Fram Strait (Soltwedel et al., 2005; Soltwedel et al., 2015; Spielhagen et al., 2015) with the deep-sea benthic oxygen ~~fluxes~~ consumption over ~~the~~ a cascade of dependencies. Benthic oxygen fluxes thereby represent benthic remineralisation rates of carbon (Thamdrup and Canfield, 2000; Wenzhöfer and Glud, 2002; Smith et al., 2013).~~ of abiotic factors, primary production, benthic food supply, the benthic community, its activity and its functions.~~ Our study provides sea-ice concentrations, sediment properties, biogenic sediment compounds, benthic community parameters, and benthic oxygen fluxes from 12 stations across the Arctic Fram Strait ~~in~~ at water depths from 275 m to 2500 m. We hypothesise that the contrasting sea-ice conditions in the eastern and western Fram Strait ~~(Soltwedel et al., 2005; Soltwedel et al., 2015; Spielhagen et al., 2015)~~ lead to differences between parameters representing the cascade of dependencies and result in contrasting benthic oxygen fluxes. Furthermore, our results allow us to estimate the portion of newly produced carbon that is remineralised by the benthic ecosystem. Furthermore, by comparing a permanently sea-ice covered area with a seasonally

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sea-ice covered area (western and eastern Fram Strait, respectively), we discuss a potential scenario for the deep-sea benthic ecosystem in the future Arctic Ocean.

2 Material and Methods

2.1 Study area and field sampling~~Study area and sample preparation~~

The Fram Strait is located in the northern Greenland Sea and forms a large passage (ca. 500 km wide) between northeast Greenland and the Svalbard archipelago (Fig. 1). It provides the only exchange route of intermediate and deep water masses between the Arctic and the Atlantic Ocean (Soltwedel et al., 2005; Forest et al., 2010). Two main currents influence the upper 300 m of Fram Strait waters (Manley, 1995): the East Greenland Current (EGC) and the West Spitsbergen Current (WSC). The EGC is located in the western Fram Strait and transports cold, less saline and nutrient poor (1 °C,~~;~~ ~~<~~≤34~~.4~~) Arctic waters southward (Manley, 1995; Mauritzen et al., 2011; Graeve and Ludwichowski, 2017a, b). In contrast, the WSC, located in the eastern Fram Strait, transports warmer, nutrient-rich Atlantic waters of higher salinity (>3 °C,~~;~~ >34~~5~~) northward (Manley, 1995; Mauritzen et al., 2011; Graeve and Ludwichowski, 2017a, b)~~(Manley, 1995)~~. About 22 % of the WSC is recirculated as the Return Atlantic Current (RAC). The remaining current bifurcates into the Svalbard Branch (SB; 33 %) and the Yermak Branch (YB; 45 %) following the Svalbard islands or flowing along the north-west flanks of the Yermak Plateau, respectively (Schauer, 2004). A high sea-ice cover is reported for the western Fram Strait and a low sea-ice cover for the eastern Fram Strait (Soltwedel et al., 2005; Soltwedel et al., 2015; Spielhagen et al., 2015). The sea-ice cover is relatively stable within the Fram Strait, even in ~~the~~ summer (Comiso et al., 2008; Soltwedel et al., 2015, https://www.pmel.noaa.gov/arctic-zone/detect/ice-seaice.shtml). However, the sea-ice age becomes younger by 0.6 years per decade (2001–2012, Krumpen et al., 2015), which goes along with a decrease in the sea-ice thickness (Renner et al., 2014; Krumpen et al., 2015). The onset of the spring bloom usually starts in Mai (Cherkasheva et al., 2014).

Two sampling campaigns were carried out at the long-term ecology research observatory HAUSGARTEN (Soltwedel et al., 2005) in the Fram Strait with RV *Polarstern*, expedition "PS85" from 6/6–3/7/2014 and expedition "PS93.2" from 22/7–15/8/2015. Samples were taken at five stations at the East Greenland continental slope (EG area) and at seven stations at the West Spitsbergen continental slope (WS area) at water depths between 275–2500 m (Fig. 1, Table 1). ~~Four stations in each area form a bathymetric transect roughly along the 79° latitude,~~ Thereby the stations in the EG area (namely EG I, EG II, EG III, ~~and~~ EG IV and EG V) and in the HG area ~~in the EG area and~~ (namely SV I, HG I, SV IV, HG II, HG III, ~~and~~ HG IV, and N5) form a bathymetric ~~in the WS area, both with water depths between 1000–2500 m (Fig. 1, Table 1). Further, four additional stations were sampled; "EG V" in the EG area and "N5", "SV IV" and "SV I" in the WS area. These stations are not located along the 79° latitude and were taken as they allow a deeper discussion of our hypothesis. The~~transect with a similar bottom slope of ~11°. The station EG IV includes two sites which are located <~~-~~2 km from each other (Table 1) and the stations HG I, HG II, HG III, and HG IV were sampled during both sampling years, 2014 and 2015.

Sediment sampling was performed by using a multiple corer (MUC) with eight tubes and autonomous benthic lander systems (Reimers, 1987; Glud et al., 1994) equipped with three benthic chambers and a sediment profiler with oxygen sensors (Donis et al., 2016). ~~Water sampling in different water depths was performed, using a SBE32 rosette water sampler equipped with 24 Niskin type sample bottles (12 L).~~ A detailed list of the number of used samples per station for the determination of different parameters is given in Supplement Table S1~~ in the supplements~~.

2.2 Sea ice data ~~and pelagic nutrient profiles~~

Daily sea ice concentrations for each of the analysed stations were obtained from the Center for Satellite Exploitation and Research (CERSAT) at the Institut Français de Recherche pour l’Exploitation de la Mer (IFREMER), France (Ezraty et al., 2007) and were previously published (Krumpen, 2017), except for station EG V. Sea-ice concentration was calculated based on the ARTIST Sea Ice (ASI) algorithm developed at the University of Bremen, Germany (Spreen et al., 2008). The data used ~~with~~in this study cover~~s~~ the period from 01/09/2001 till 31/08/2015 (long-term data) with a 12.5 x 12.5 km² spatial resolution around the station. Satellite mismeasurements, which were <0.5% of the long-term data, resulted in an algorithm output value of “128” and were omitted from the dataset. ~~Data points with a value of >100 % were omitted as such a value indicates a mismeasurement. A~~Three subsets for short-term examinations ~~was~~ were extracted~~,~~: ~~which includes~~ the ~~time period~~ a year before sampling, the period since the first of May till sampling, and one month before sampling. The period a year before sampling was~~This was the period~~ 01/07/2013–30/06/2014 for stations sampled in 2014 and 01/08/2014–31/07/2015 for stations sampled in 2015. From each dataset (long-term and short-term) the sea-ice cover and the percentage of days with sea-ice cover were extracted.

~~Water samples were used to measure nitrate and phosphate concentrations. The measurement was performed with a standard photometric method using a Technicon TRAACS 800 continuous flow autoanalyser (Technicon Corporation). A daily calibration of the autoanalyser was executed using NIST standards (Merck, certified reference material: NMIJ CRM7602-a). The data were previously published by Graeve and Ludwichowski (2017).~~

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2.3 Sediment compounds and properties

Various biogenic sediment compounds including grain size, water content, chlorophyll a (Chl *a*) and phaeopigment concentrations (Phaeo), portion of total organic carbon (TOC), phospholipids concentrations, protein concentrations~~s~~, portion of organic matter, and the bacterial enzymatic turnover rate (FDA) as bacterial activity proxy were determined from the sediments sampled by the MUC and chambers of the autonomous benthic lander system. Generally, three pseudo-replicates from each MUC (sampled from different sediment cores, inner MUC tube diameter = 9.5 cm) were taken. Sediment samples of the 0–5 cm layer ~~uppermost five sediment centimetres~~ were taken by means of syringes with cut-off ends (1.17 / 3.14 cm² cross-sectional area). Samples for FDA, Chl *a*, and Phaeo were immediately analysed on board. All other samples were shock ~~frosted~~ frozen at -80°C and stored at -20°C until they were analysed at the home laboratory. Sediment samples, taken by the benthic chambers of the autonomous lander system, were treated similarly.

The grain size partitions were determined with a Malvern Mastersizer 2000G, hydro version 5.40. The Mastersizer utilizes a laser diffraction method and has a measuring range of 0.02–2000 µm. The water content of the sediment was determined by the difference in weight of the sediment before and after drying at 105°C. The bioavailability of phytodetritus at the seafloor was assessed by analysing sediment bound Chl *a* and Phaeopigments. Chloroplastic pigments were extracted in 90 % acetone and measured with a TURNER fluorometer (Shuman and Lorenzen, 1975). The bulk of pigments (Chl *a* plus Phaeo) are termed chloroplastic pigment equivalents (CPE) after Thiel (1978). Additionally, the ratios of Chl *a* to Phaeo, as an indicator of the relative age of the food, and the Chl *a* to CPE (% Chl *a*), a quality indicator of the labile organic matter, was calculated. The percentage of the TOC was measured by combustion using an ELTRA CS2000 with infrared cells. To indicate the quantity of cell wall material, phospholipids were measured following Findlay et al. (1989) with modifications after Boetius and Lochte (1994). Particulate proteins, defined as γ-globulin equivalents (Greiser and Faubel, 1988), were measured to differentiate between living organisms and detrital organic matter in the sediments. Hereafter, particulate proteins will be referred to only as proteins. The organic matter was determined as ash free dry weight after combustion (2 h, 500°C). Bacterial enzymatic turnover rates were calculated using the fluorogenic substrate fluorescein-di-acetate (FDA) as an indicator of the potential hydrolytic activity of bacteria (Köster et al., 1991).

2.4 Benthic community parameters

For the bacterial density determination, sediment subsamples were taken with modified syringes (1.17 cm² cross-sectional area) from MUC recovered sediment cores after oxygen flux measurements were performed and from benthic chambers. The first centimetre of each sample, generally holding the highest bacterial density (Quéric et al., 2004), was stored in a 2 % filtered formalin solution at 4 °C. The acridine orange direct count (AODC) method (Hobbie et al., 1977) was used to stain bacteria in the subsamples and subsequently bacteria were counted with a microscope (Axioskop 50, Zeiss) under UV–light (CQ-HXP-120, LEj, Germany).

For the determination of the meiofauna density and identification of meiofauna taxa, sediment subsamples were taken with modified syringes (3.14 cm² cross-sectional area) from MUC recovered sediment cores after oxygen flux measurements were performed and from benthic chambers. The first centimetre of each sample, usually holding the highest meiofauna density (Górska et al., 2014), was stored in borax buffered 4 % formaldehyde solution at 4 °C. The samples were sieved over a 1000 µm and 32 µm mesh. Both fractions were centrifuged three times in a colloidal silica solution (Ludox TM-50) with a density of 1.18 g/cm³ and stained with Rose Bengal (Heip et al., 1985). Afterwards, the taxa were identified and counted at order level. Foraminifera ~~are~~ were not considered, as the extraction efficiency of Ludox for different groups of foraminifera is insufficient for a quantitative assessment of the group. Therefore, only metazoan meiofauna is recorded and hereinafter ~~the use of~~ the term meiofauna refers only to metazoan meiofauna organisms.

After taking subsamples for bacteria and meiofauna densities, the remaining sediment from MUC recovered sediment cores and from the benthic chambers was used for macrofauna taxonomical identification, and density and biomass determination. For ~~these~~ macrofauna analyses, ~~only~~ the 0–5 cm ~~horizon~~ layer from MUC sediment cores and the entire remaining sediment from the benthic chambers was used, sieved over a 500 µm mesh and stored in borax buffered 4 % formaldehyde and stained with Rose Bengal (Heip et al., 1985). Afterward~~s~~, macrofauna taxa were identified to the highest taxonomic level (at least class level), counted and weighted (blotted wet weight).

From the macrofauna density (*Ai*) and biomass (*Bi*), together with a mobility score (*Mi*) and sediment reworking score (*Ri*) of each taxon, the community bioturbation potential (*BPc*) was calculated following Queirós et al. (2013, Eq. (5)):

$$BP_c = \sum_{i=1}^{n} \sqrt{B_i / A_i} \times A_i \times M_i \times R_i \qquad (5)$$

in which *i* displays the specific taxon in the sample. This index represents the bioturbation potential of the benthic macrofauna community.

2.5 Oxygen and bromide fluxes

Immediately after the retrieval of sediment cores by the MUC, a part of the overlying water was removed and stored separately for later purposes. At least 10 cm overlying water remained in the cores. The sediment of each core was carefully pushed upwards without disturbing the surface sediment layer until the sediment–water interface (SWI) was at a distance of around 10 cm from the upper edge of the core. A magnetic stirrer was added to the overlying water to assure a well-mixed overlaying water body. In this position, the sediment cores were stored in a water bath at in situ temperature (-0.75°C) until the start of the oxygen flux measurements.

For the determination of the ex situ diffusive oxygen uptake (DOU) at least two oxygen microprofiles per sediment core were measured simultaneously within 2 h after sampling with a vertical resolution of 100 µm. The profiling was performed by oxygen optical microsensors (OXR50, Pyroscience, Aachen, Germany) with a tip size of 50 µm in diameter, a response time of <2 s and an accuracy of ±0.02 %, calibrated with a two-point calibration using air saturated and anoxic waters (by adding sodium dithionite). The overlying water in the MUC cores was magnetically stirred and the water surface was gently streamed with a soft air stream during the profiling. The maximum penetration depth of the sensors during ex situ profiling was 42 mm. For in situ DOU determination autonomous landers were used (Reimers, 1987; Glud et al., 1994; Glud, 2008). The profiling unit was equipped with electrochemical oxygen microsensors (custom made after Revsbech (1989)) and calibrated with a two-point calibration. As the first calibration point, the bottom water oxygen concentration (water sample were taken by Niskin bottle), estimated by Winkler titration (Winkler, 1888), was used. As the second calibration point, the sensor signal in the anoxic zone of the sediment (when reached) or the sensor signal in an anoxic solution of sodium dithionite recorded on board was used. The measurements started three hours after the deployment of the autonomous lander, allowing resuspended sediment to settle on beforehand. Profiling was performed with a depth resolution of 100 µm. The maximum penetration depth of the sensors during in situ profiling was 180 mm. Running average smoothed oxygen profiles from ex situ and in situ approaches were used to calculate the DOU rates across the SWI using Fick's first law (Eq. (1)):

$$DOU = -D_s \times \left[\frac{\delta O_2}{\delta z}\right]_{z=0}, \qquad (1)$$

in which *Ds* is the molecular diffusion coefficient of oxygen in sediments at in situ temperature and salinity, and $\left[\frac{\delta O_2}{\delta z}\right]_{z=0}$ is the oxygen gradient at the SWI calculated by linear regression from the first alteration in the oxygen concentration profile across a maximum depth of 1 mm. *Ds* was calculated following Schulz (2006) as D/θ^2, with *D* as the molecular diffusion coefficient of oxygen in water after Li and Gregory (1974), and θ^2 as $1\text{-}ln(\varphi^2)$ (Boudreau, 1997). The sediment porosity φ was calculated following the equation of Burdige (2006, Eq. (2)):

$$\varphi = \frac{m_w/\rho_w}{m_w/\rho_w + (m_d - (S \times m_w))/\rho_s}, \qquad (2)$$

In this equation, *mw* is the mass of evaporated water, *ρw* is the density of the evaporated water, *md* is the mass of dried sediment plus salt, *S* is the salinity of the overlying water and *ρs* is the density of deep-sea sediment (2.66 g cm^{-3}, after Burdige, (2006)). To calculate *mw*, *ρw*, and *md*, the weight loss of wet sediment samples was measured by weighing wet samples, drying them overnight at 70 °C, weigh them again, dry the sample for 1 h at 70 °C and weigh them a second time. This procedure was repeated until the weights of the two dried samples differ not more than 0.05 %. Over all samples, 4.5 ± 1.9 % of the sediment mass was attributed to salt. Non-local mixing was observed in some microprofiles and therefore the reported DOUs for those cases are underestimations. However, only at eight out of 81 ex situ obtained oxygen microprofiles at various stations and at one out of 34 in situ obtained oxygen microprofiles signs of non-local mixing were observed.

For ex situ total oxygen uptake (TOU) measurements, sediment cores were used after oxygen microprofiling (see upper paragraph in this section). The sediment cores were closed airtight with no air bubbles in the overlying water. The distance between the SWI and the edge of the lid was measured for volume calculations of the overlying water. An optical oxygen microsensor (Pyroscience, Aachen, Germany) with a tip size diameter of 50 µm was ~~installed~~ mounted in the lid, allowing a continuous measurement of the oxygen concentration in the overlying water. The sediment cores were incubated in darkness for >40 h and the overlying water was kept homogenised by rotating magnets over that period. For in situ TOU measurements, benthic chambers (K/MT 110, KUM, Kiel, Germany) with an inner dimension of 20x20 cm were used. These chambers were pushed into the sediment and thereby enclosed a sediment volume of approximately 8 L and an overlying water volume of approximately 2–3 L. The oxygen concentration was measured in the overlying water continuously with an Aanderaa optode (4330, Aanderaa Instruments, Norway, two-point calibrated as described in the upper section) over an incubation period of 20–48 h. During the measurement, the overlying water was kept homogenised by a stirring cross at the inner top of the chamber. TOU from both ex situ sediment core and in situ benthic chamber incubations were calculated using Eq. (3):

$$TOU = \frac{\delta O_2 \times V}{\delta t \times A}, \qquad (3)$$

in which *δO2*, *δt*, *V* and *A* represent the difference in oxygen concentration, the difference in time, the volume of the overlying water and the enclosed surface area, respectively.

~~The~~ Both, the diffusive and total oxygen fluxes were converted to carbon equivalents (C-DOU and C-TOU) by applying the Redfield ratio (C:O = 106:138; Redfield (1934)) in order to compare them to the carbon fixed by primary production. Modifications, as suggested by Takahashi et al. (1985) and Anderson and Sarmiento (1994), would result only in minor changes of <10 % in the benthic carbon flux.

To assess the exchange of solutes across the SWI, which results from molecular diffusion, physical advection, and faunal ventilation activities, sodium bromide (NaBr) was added to the removed overlying water of the sediment cores to create a NaBr–solution of similar density as seawater (1028 g/L). The NaBr–solution was added to the sediment cores before the TOU incubation started. Three subsamples of water were taken during the incubation at three different times (t_0, t_1, t_2) and stored at 4 °C. Removed water volume of the subsampling at t_1 was replaced with the NaBr–seawater solution. The bromide concentrations were measured using ion chromatography. The dilution of the t_2–sample, due to the sampling procedure, was corrected by the known bromide concentration in the removed and the added water. The bromide exchange is represented by the bromide flux, calculated using the Eq. (4):

$$Bromide\ flux = \left(\frac{\delta Bromide\ concentration \times V}{\delta t \times A}\right), \tag{4}$$

in which $\delta Bromide\ concentration$, δt, V and A represent the difference in bromide concentration, the difference in time, the volume of the overlying water and the enclosed surface area, respectively.

2.6 Data analyses

The analysed data ~~sets~~ were obtained during two ~~subsequent~~ consecutive years (Table 1). To test whether there is a significant offset between sampling years, a principal component analysis (PCA) was performed on standardised (x to zero mean and unit variance) abiotic parameters (year, water depth, sea ice cover, percentage of days with sea ice cover, the portion of grain size >63 µm, median grain size) and all sediment compounds and property parameters from the 0-1cm sediment horizon, as it was the most complete data~~-~~set. Additionally, a non–parametric Wilcoxon signed rank sum test was performed on station specific mean values of both years on water content, TOC, organic matter, Chl *a*, Phaeo, protein, phospholipids, FDA, DOU and TOU following Cathalot et al. (2015). Both tests were performed only on data of stations that were sampled in both 2014 and 2015.

To reveal significant differences in measured parameters between the EG and the WS area, Students t-tests were performed. If t-test assumption of Gaussian distribution of the data (tested with a Shapiro–Wilk test) was not met, a non–parametric Wilcoxon signed rank sum test was performed. In case of heteroscedasticity (tested with a Levene's test) a Welch two sample t-test was carried out. The values from station SV I were excluded from the tests, due to its exceptional low water depth.

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To identify the most important parameters influencing the benthic Fram Strait ecosystem, a second PCA was performed in the scaling II mode on standardised (x to zero mean and unit variance) ex situ mean values of abiotic parameters (water depth, short-term sea-ice cover (year before sampling), the portion of grain size >63 µm, water content), biogenic compound parameters (Chl *a*, TOC, organic matter), oxygen fluxes (DOU, TOU), the benthic community (bacterial density, macrofauna biomass), and the ~~macrofauna mediated environmental functions (bromide exchange,~~ *BPc*~~)~~. All other parameters were excluded from the PCA as they correlated strongly (correlation >0.74, Pearson correlation, Supplement Table S2) with one of the mentioned parameters used for the PCA. This procedure results in a more resilient outcome of the PCA. Owing ~~For station EG II no bromide exchange value could be calculated because the residuals over the slope did not follow a Gaussian distribution. Nevertheless, in order to perform the PCA, the mean value of all EG stations and N5 was assumed to represent the bromide exchange at EG II. Furthermore, due~~ to its exceptional low water depth, the values from station SV I were also excluded from the PCA. For further insights and descriptions of the usage and interpretation of ~~a PCA~~a PCA ~~visualization~~, the reader is referred to Buttigieg and Ramette (2014).

Water depth and sea ice have a profound impact on benthic oxygen fluxes (Wenzhöfer and Glud, 2002; Harada, 2015~~6~~). To investigate the influence of water depth and sea ice in our data, the stations were merged into two sea-ice cover categories. First, a “high sea-ice concentration” area (HSC), which include stations with a short-term (a year before sampling) mean sea-ice concentrations of ≥ 30 %. Second, a “low sea-ice concentration” area (LSC), which include stations with a short-term (a year before sampling) mean sea-ice concentrations of <30 %. Regression analysis was used to test the water depth dependence of sediment compounds and property parameters, the benthic community parameters, the oxygen fluxes, and parameters of the macrofauna mediated environmental functions within the HSC and LSC categories. If the residuals over the slope did not follow the Gaussian distribution (tested with a Shapiro–Wilk test), values were transformed, either by square root or logarithmic transformation. Individual values that failed due to technical failure or mismeasurements were removed before statistical analyses. For all above mentioned statistical treatments, R Statistical Software (version 3.4.0) was used.

Analyses of the multivariate meio- and macrofauna community structure were based on square root transformed density and biomass data of sediment core replicates. Non–metric multidimensional scaling (MDS, (Kruskal, 1964)) and hierarchical cluster analysis with group average clustering were used to present the multivariate similarities between samples based on Bray–Curtis similarity. Significant multivariate differences between pre-defined group structures within the meio- and macrofaunal data were tested by the ANOSIM procedure (ANalysis Of SIMilarity) based on Clarke’s R statistic (Clarke and Warwick, 1994) with 9999 permutations. The SIMPER (SIMilarity PERcentage) routine was applied to determine the contribution of certain meio- and macrofauna taxa towards the discrimination between sea-ice cover categories and water depth categories. Differences ($p < 0.05$) between HSC, LSC and water depth regarding macrofauna density and macrofauna biomass were examined using a two-way crossed PERMANOVA (PERMANOVA+ for PRIMER; Anderson, 2005; Anderson et al., 2007) analysis with “site” (levels “HSC” and “LSC”) or “water depth” (levels:1000, 1500, 2000, 2500 m) as fixed factors. The significance level was set at 0.05. Significant main PERMANOVA tests were followed by pairwise PERMANOVA tests. Permutational P-values (PPERM) were interpreted when the number of unique permutations was >100; alternatively, Monte Carlo P-values (PMC) were considered. Bray–Curtis similarity was used to construct resemblance matrices. Data were standardised and fourth–root transformed (to down weigh the importance of the most dominant taxa) prior to the construction of resemblance matrices. The station SV I and the in situ stations HG I Lander and HG IV Lander were excluded from these test, owing to its shallow location (SV I) and different sampling device (benthic chambers ~~insteadt~~instead of MUC). All analyses of multivariate community structure were performed using the routines implemented in PRIMER vers. 6.1.15 (Clarke and Gorley, 2006; Anderson et al., 2007). Results are expressed as means ± standard deviation.

3 Results

3.1 Short- and long-term sea ice concentration comparison between the EG and WS area

~~Short~~Short-term and long-term data of the mean sea-ice concentrations and the percentage of sea-ice covered days were in a ~~comparable~~ similar range (Table 2~~), Supplement Table S3)~~. Both parameters ~~in both datasets~~ decreased from west to east with a sharp drop between N5 and HG IV in both the short and the long-term dataset (Table 2~~ for short-term data, Fig. 2 for long-term data~~). Therefore, the categorisation into a high sea-ice covered area (HSC) and a low sea-ice covered area (LSC) was introduced. The HSC includes all East Greenland stations (EG I–V) and the most northern West Spitzbergen station N5, while the LSC includes the remaining West Spitzbergen stations (HG I–IV, SV I, and SV IV).

As expected~~Generally~~, the east Greenland stations showed the highest sea ice concentration~~, as expected~~ due to the influence of the East Greenland current. The short-term sea-ice concentration ~~-~~in the EG area one year before sampling was highest at EG I with 82 ± 20 % (n = ~~n=~~364) and lowest at EG V with 56 ± 34 % (n = ~~n=~~364). In the WS area, sea-ice concentration was highest at N5 with 40 ± 31 % (n = ~~n=~~365) and lowest at SV IV with 0.1 ± 2 % (n = ~~n=~~365). The percentage of days, which showed sea-ice cover, during the short-term period in the EG area was highest at EG I, EG II and EG III (each with 100 %) and lowest at EG V (93 %). In the WS area the percentage of days, which showed sea-ice cover, during the short-term period was highest at N5 (82 %) and lowest at SV IV (>0.1%, Table 2). This~~ese~~ pattern~~s~~ ~~were also visible~~also occurred in the other short-term datasets and in the long-term dataset. This pattern also occurred in the other short-term datasets and in the long-term dataset. The latter indicated that the sea-ice cover in terms of sea-ice concentration was stable across the Fram Strait the last 15 years (Fig. 2, Supplement Table S3).

~~sea-ice concentration and the percentage of sea-ice covered days (Supplement Table S3).~~

3.2 ~~Water column nutrient profiles, s~~Sediment properties and benthic biogenic compounds in the EG and WS area

~~Nitrate and phosphate concentrations increased with increasing water depth. In general, both nutrients showed higher concentrations in the WS area than in the EG area. However, at the surface, nitrate concentrations were higher in the EG area (Supplement Fig. S1)~~

~~Values for all s~~Sediment properties and biogenic compound~~s~~ values at the deeper stations (>1500 m) in the EG and WS area were in the same range. In contrast, shallow stations (≤ 1500 m) of the WS area showed higher values compared to shallow stations of the EG area (Table 3~~2~~). This le~~a~~d~~s~~ to a higher ~~variances~~ variability in the WS area for most of the determined parameters (Fig. 3).

~~-~~The median grain size in the EG area ranged between 13 ± 1 µm (n = 15) at EG I and 74 ± 30 µm (n = 15) at EG V and in the WS area between 10 ± 3 µm (n = 15) at N5 and 24 ± 5 µm (n = 30) at HG IV. The portion of sediment grain size >63 µm in the EG area ranged between 4 ± 2 % (n = 15) at EG I and 52 ± 7 % (n = 15) at EG V and in the WS area between 11 ± 6 % (n = 30) at HG I and 25 ± 5 % (n = 30) at HG IV.~~,~~ ~~median grain size,~~ The water content in the EG area ranged between 42 ± 6 % (n = 15) at EG V and 51 ± 7 % (n = 15) at EG I and in the WS area it ranged between 51 ± 14 % (n = 15) at SV I and 66 ± 5 % (n = 30) at HG I. The porosity in the EG area ranged between 0.77 ± 0.06 (n = 15) at EG I and 0.69 ± 0.06 % (n = 15) at EG V and in the WS area it ranged between 0.88 ± 0.04 % (n = 30) at HG II and 0.77 ± 0.06 % (n = 30) at HG I. Results of all stations are listed in Table 3. Median grain size, water content and porosity differed significantly between the WS and EG area, while the portion of sediment grain size >63 µm was similar (Supplement Table S4).

~~water content, and porosity showed a similar range of variances for the EG and the WS area and median values of the portion of sediment grain size >63 µm and the median grain size are highly comparable between both areas (Fig. 3.). Nevertheless, values of water content (59 ± 8 % in the WS area as opposed to 47 ± 9 % in the EG area) and porosity (0.83 ± 0.06 in the WS area as opposed to 0.73 ± 0.07 in the EG area) differ between the WS and EG area. It indicates sediment properties are a potentially important factor that maybe influence benthic oxygen fluxes.~~The sediment bound Chl *a* concentration ranged between 0.4 ± 0.3 µg ml^{-1} sediment^{-1} (n = 15) at EG III and 12.7 ± 3.1 µg ml^{-1} sediment^{-1} (n = 15) at SV I (Table 3) and differed significantly between the EG and WS area (Figure 3, Supplement Table S4). A similar pattern was found for sediment bound Phaeo concentrations and CPE concentration with over 4 –times higher median values in the WS area compared to the EG area (Figure 3). The Chl *a*/CPE and Chl *a*/Phaeo ratios did not differ between the EG and WS area (Supplement Table S4), which indicates that the benthic community in both areas fed on a similar food quality and received the spring bloom food supply at the same time, respectively. Sediment bound TOC ranged between 0.44 ± 0.04 % (n = 15) at EG II and 1.58 ± 0.27 % (n = 15) at SV I and differed between the EG and WS area, similar to organic matter, which ranged between 3.45 ± 0.6 % (n = 15) at EG II and 12.0 ± 4.2 % (n = 30) at HG III (Table 3, Figure 3, Supplement Table S4). Proteins, lipids and FDA also differed between the EG and WS area with 5.6 times, 2.3 times, and 1.8 times higher median values in the WS area, respectively (Figure 3, Supplement Table S4).~~. Median values for each pelagic food supply indicating parameter in the sediment (Chl *a*, Phaeo, and CPE) were four times higher and showed greater variances in the WS area than in the EG area. Values for parameters indicating food quality (Chl *a*: CPE ratio) and relative age of food (Chl *a*: Phaeo ratio) were in the same range for the EG and WS area. The WS area showed higher TOC, organic matter, protein and lipid contents than the EG area and as well had higher variances in the WS area compared to the EG area. However, the bacterial enzymatic activity (FDA) and its variances were similar between the EG and the WS area (Fig. 3). This indicates contrasting food supply quantities between the EG and the WS area, while the food quality is similar.~~

3.3 ~~Differences between b~~Benthic communities and community functions in the EG and WS area

Overall, 17 meiofauna taxa and 18 macrofauna taxa were identified (Supplement Tables S5~~4~~, S6~~5~~, S7~~6~~). The meiofauna density was dominated by nematodes (86 %), the only taxon present at each station. Crustaceans were the second most

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Formatiert: Schriftartfarbe: Automatisch dominant group with 4.5 % nauplii and 3.5 % Copepoda. The macrofauna density was dominated by polychaetes (40 %), followed by Copepoda (26 %), and Nematoda (12 %). Polychaetes (57 %) also dominated the macrofauna biomass, followed by Bivalvia (16 %) and Porifera (14 %). The mean values of the benthic faunal community parameters meiofauna density, macrofauna density and macrofauna biomass were 1.5 times, 4.6 times and 2.5 times higher in the WS area than in the EG area (Supplement Table S2), respectively, ~~and showed greater variances in the WS area~~and differed significantly from each other (Supplement Table S4). Contrasting, the bacterial density was ~~comparable~~ similar between the EG and WS area~~,~~ but showed a greater ~~variance~~ variability in the WS area (Supplement Table S4, Fig. 3).

The solute exchange across the SWI, represented by the bromide flux, did not differ between the EG and WS area (Supplement Table S4). The lack of difference might have methodological reasons. Bromide flux incubations were performed on 40 sediment cores but measurements from 13 sediment cores were omitted (seven from EG area, six from WS area), as either the calculations revealed a positive flux or the residuals were not homogenously distributed across the decreasing slope of the bromide concentration over time or slopes were not significantly different from zero. ~~and the community bioturbation potential, represented by t~~The community bioturbation potential, represented by the *BPc*, was also similar between the EG and WS area (Supplement Table S4) but the median *BPc* at the WS area was~~, were 1.2 times and~~ 2.9 times higher ~~in the WS area~~ than in the EG area~~, respectively, and showed higher variances in the WS area~~ (Fig. 3). This indicates that the benthic macrofauna community in the WS area is potentially able to rework the sediment stronger than the benthic macrofauna community in the EG area. ~~It needs to be mentioned that bromide flux incubations were performed on 40 sediment cores. Measurements from 13 sediment cores were omitted, as either the calculations revealed a positive flux or the residuals were not homogenously distributed across the decreasing slope of the bromide concentration over time or slopes were not significantly different from zero.~~

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3.4 Benthic ~~activity and~~ remineralisation

All oxygen microprofiles showed decreasing oxygen concentrations across the SWI (Supplement Fig. S1~~2~~) and steepness of oxygen gradients varied among microprofiles~~and varying steepnesses of oxygen gradients between profiles~~ and across various stations. Further, all sediment core incubations resulted in decreasing oxygen concentrations in the overlying water, with varying steepnesses ~~between~~ among sediment cores and across various stations. ~~In general, DOU and TOU values in the EG and WS area were in a similar range (Fig. 3).~~

The mean DOU in the EG area ranged between 0.4 ± 0.1 mmol O_2 $m^{-2}d^{-1}$ (n = ~~n=~~10) at EG V and 1.0 ± 0.1 ~~(n=10)~~ mmol O_2 $m^{-2}d^{-1}$ (n = 10) at EG II. In the WS area, DOUs at stations within the same water depth range as the EG stations ranged between 0.5 ± 0.2 mmol O_2 $m^{-2}d^{-1}$ (n = ~~n=~~8) at HG IV and 2.1 ± 0.6 ~~(n=8)~~ mmol O_2 $m^{-2}d^{-1}$ (n = 8) at SV IV. At the shallow station SV I the DOU reached 3.0 ± 1.7 mmol O_2 $m^{-2}d^{-1}$ (n = ~~n=~~6, Table 3~~2~~). The mean TOU in the EG area ranged between 0.9 ± 0.3 mmol O_2 $m^{-2}d^{-1}$ (n = ~~n=~~2) at EG I and 1.6 ~~(n=1)~~ mmol O_2 $m^{-2}d^{-1}$ (n = 1) at EG II. Similar mean TOU values were measured in the WS area, at stations within the same water depth range as the EG stations. TOU values ranged between 0.5 ± 0.2 mmol O_2 $m^{-2}d^{-1}$ (n = ~~n=~~5) at HG IV Lander and 1.9 ± 0.6~~ (n=5)~~ mmol O_2 $m^{-2}d^{-1}$ (n = 5) at HG I. At the shallow SV I station TOU reached 5.1 ± 0.3 mmol O_2 $m^{-2}d^{-1}$ (n = ~~n=~~3, Table 3~~2~~). DOU differed significantly between the WS and EG area, while TOU was similar among the areas (Fig. 3, Supplement Table S4). The mean DOU/TOU ratio, which describes the fraction of the total community mediated oxygen flux (TOU) covered by the microbial mediated oxygen flux (DOU, Glud, 2008,) across the entire Fram Strait was 0.8 ± 0.3, with 0.6 ± 0.2 in the EG area and 0.9 ± 0.3 in the WS area, indicating that the total oxygen uptake is mainly microbial mediated.~~The mean DOU/TOU ratio across the entire Fram Strait was 0.79 ± 0.30, with 0.63 ± 0.22 in the EG area and 0.92 ± 0.30 in the WS area which indicates bacterial activity and bacterial remineralisation as the major oxygen consumer.~~ In the EG area, DOU values showed no correlation with water depth, while in the WS area the correlation of DOU with water depth was significant (Fig. 4) and showed greater ~~variation~~ variability~~(Fig. 4)~~ (Fig 3). ~~Contrastingly~~In contrast, TOU values in the EG and in the WS areas showed no correlation with water depth (Supplement Fig. S3), but again, the ~~variations~~ variability of ~~the~~ TOU values ~~were~~ was higher in the WS area (Fig. 3)~~ (Fig. 4)~~. C-DOU and C-TOU followed the same trends as DOU and TOU, respectively, and are listed in Table 3.~~DOU and TOU values were converted into C-DOU and C-TOU and are listed in Table 2.~~

3.5 Relationships of the benthic remineralisation with the benthic community and environmental parameters

The PCA

~~3.5 Relations of the benthic community, its remineralisation activity, and environmental parameters~~

~~The PCA~~, which includes only abiotic parameters (year, water depth, sea ice cover, the percentage of days with sea ice cover, portion of grain size >63 µm, and median grain size) and biogenic compounds of the first sediment centimetre (Chl *a*, Phaeo, CPE, TOC, organic matter, lipids, and proteins), revealed differences between the sampling years 2014 and 2015 (Supplement Fig. S2~~S3~~). The difference occurred only in the second dimension, which explained~~s~~ 15.4 % of the variability and is mostly influenced by the parameters Phaeo and CPE (Supplement Table S8~~7~~). ~~These differences are probably a result of the different sampling periods (June in 2014 and end of July/beginning of August 2015), resulting in different Phaeo and CPE concentrations.~~ The non-parametric Wilcoxon signed rank sum test of the station specific mean values revealed no differences (p > 0.05) for any of the parameters between the sampling years. Furthermore, Henson et al. (2016) showed that it takes at least 15 years of continuous data to prove~~of~~ temporal trends in ocean biogeochemistry; and even longer in high latitudinal areas. Therefore, it is more likely that statistically revealed differences between sampling years ~~are presenting~~reflect spatial variability rather than time-related differences. ~~Therefore~~In turn, the data from stations sampled in 2014 and 2015 were merged and thus this study ~~to~~ focuses ~~on~~ solely on spatial patterns.

The PCA on station specific, ex situ obtained mean values (Fig. 5) revealed that water depth was positively correlated with median grain size and negatively correlated with the DOU, the TOU, bacterial density, and the *BPc*. Sea-ice concentration was negatively correlated with the porosity, Chl *a*, TOC, organic matter, and solute exchange. Similarly, macrofauna biomass was negatively correlated with~~ both~~, water depth, ~~and~~ sea-ice concentration, and the median grain size.

The stations of the WS and EG area both followed the water depth gradient and shallower stations showed the higher oxygen fluxes. However, stations of the EG area were strongly influenced by the sea-ice cover, contained less organic matter and

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Chl *a*, and macrofauna biomass, compared to the WS stations. ~~Additionally, EG I, EG II, and EG III were strongly influenced by the sea ice cover, while station EG IV was slightly more influenced by the factor water depth.~~ The two dimensions ~~in~~ of the plot ~~together~~ explained 72~~66.9~~ % of the total variability of the data (Fig. 5). The eigenvalues indicated that ‘Chl a’, ‘TOC’, and ‘Macrofauna biomass’ (-0.89, -0.88, -0.83, respectively) were responsible for the gradient along the x-axis and ‘Bacterial density’, ‘water depth’, organic matter’ and ‘sea-ice concentration’ (0.59, -0.57, -0.54, respectively) for the gradient along the y-axis.

Across the HSC area, DOU ~~(Fig. 4)~~ and TOU were not linearly dependent on water depth (Fig. 4, Supplement Fig. S3, Supplement Table S9~~8~~). The same was found for the water content, FDA, meiofauna and macrofauna densities, macrofauna biomass, and the solute exchange across the SWI. Otherwise, the fraction of sand in the sediment (% of grain size >63 µm), Phaeo, CPE, the Chl *a*–Phaeo ratio, the Chl *a*–CPE ratio, and lipids were positively linearly dependent on water depth across the HSC area and the BPc was negatively linearly dependent on water depth. Across the LSC area, the DOU was negatively linearly dependent on water depth, as well as sediment water content, Chl *a*, Phaeo, CPE, FDA, bacteria density and bioturbation potential. Contrastingly, TOU, Chl *a*–Phaeo ratio, protein, meio- and macrofauna densities, macrofauna biomass, and the solute exchange were not water depth dependent ~~across~~ in the LSC area. Within both sea-ice categories HSC and LSC, no linear water depth dependencies were found for median grain size, TOC, and organic matter as the residuals over the slopes did not follow the Gaussian distribution. This also applied for Chl *a*, protein, and bacteria density across the HSC area and for the portion of grain size >63 µm, the Chl *a*–CPE ratio, and lipids across the LSC area (Supplement Table S9~~8~~).

The ANOSIM (Global R = 0.122, p = 0.063) and SIMPER (33 % dissimilarity) routine revealed no differences between the HSC and LSC area regarding the meiofauna community based on density (Table 4~~3~~). Regarding macrofauna communities based on density (Global R = 0.257, p = 0.007) and biomass (Global R = 0.238, p = 0.003), the ANOSIM revealed significant but weak differences between the HSC and LSC area. SIMPER routine results indicated dissimilarities of 56 % for the macrofauna density and 76 % for the macrofauna biomass between the HSC and LSC areas. The taxa which contributed~~ing~~ most to the average similarity within and to the average dissimilarity between the HSC and LSC area are given in Supplement Table S10~~9~~. The ANOSIM results for water depth groups showed that bathymetry could at least explain ~~partly~~ the dissimilarity in meiofauna communities based on density (Global R = 0.219; p ~~P~~= 0.01), even if the difference was weak. The SIMPER analysis, however, showed that the observed differences in meiofauna density regarding water depth ~~are~~ were mainly due to the marked difference between the shallowest station (SV I at 275 m) and all other stations deeper than 1000 m (dissimilarity >~~-~~50 %, Supplement Table S11~~0~~). ANOSIM results for macrofauna communities based on density (Global R = 0.2, p = 0.008) and biomass (Global R = 0.346, p = 0.0001) revealed significant but also weak differences between water depth categories with >50 % dissimilarity between all water depth categories for macrofauna density (except between 1000 m and 1500 m) and macrofauna biomass (SIMPER, Supplement Table S11~~0~~). Further, the two-way crossed PERMANOVA revealed that the sea-ice coverage (LSC and HSC) explains a significant (p = 0.008) portion of the macrofauna density variability. ~~, while the portion explained by water depth (p = 0.06) and by the interaction of sea-ice cover~~

~~and water depth (p = 0.09) was not significant (Supplement Table S11). However, t~~The results of the pairwise test showed that only the neighbouring water depth classes 1000 m and 1500 m showed no significant differences (p = 0.45) while all other pairwise comparisons showed significant differences between water depths (Supplement Table S13~~2~~). For macrofauna biomass, the two-way crossed PERMANOVA revealed that the interaction of sea-ice cover and water depth explains a significant (p = 0.034) portion of the macrofauna biomass variability~~, while the portion explained by the sea-ice cover categories (p = 0.051) and by water depth (p = 0.058) was not significant (Supplement Table S11)~~. The results of the pairwise test showed that only the water depth classes 1000 m and 2500 m showed significant differences (p = 0.0187), while all other pairwise comparisons showed no significant differences between water depths (Supplement Table S13~~2~~).

4 Discussion

4.1 Linking contrasting sea-ice conditions with benthic oxygen fluxes

The main ~~question~~ aim of this study was to link ~~contrasting~~ sea-ice conditions within the Arctic Fram Strait ~~(Soltwedel et al., 2005; Soltwedel et al., 2015; Spielhagen et al., 2015)~~ with the deep-sea benthic oxygen fluxes over a cascade of dependencies. Our results documented two contrasting sea-ice concentration regimes in the Fram Strait with a high sea-ice concentration~~ver~~ in the western Fram Strait and a low sea-ice concentration ~~sea-ice cover~~ in the eastern Fram Strait (Table 2, Fig. 2). This is similar to sea-ice concentration snapshot observations by Schewe and Soltwedel (2003) and satellite observations of Krumpen et al. (2015). The observed pattern can be explained by the two major current systems present in the Fram Strait (Schauer, 2004), the EGC transporting cold, ~~-~~nutrient poor water and sea ice from the central Arctic Ocean southwards into the EG area and the WSC transporting warmer, nutrient richer and ~~-~~sea-ice free water from the Atlantic Ocean northwards into the WS area (Manley, 1995; Mauritzen et al., 2011; Graeve and Ludwichowski, 2017a, b). If there were a strong link between sea-ice conditions and deep-sea benthic oxygen fluxes, we would expect contrasting primary production, benthic food supply, benthic community parameters and benthic oxygen fluxes between the EG and the WS area.~~If there is a strong link between sea-ice conditions and deep-sea benthic oxygen fluxes, we expected contrasting primary production, benthic food supply, benthic community parameters and benthic oxygen fluxes between the EG and the WS area.~~

The results of Pabi et al. (2008) showed that in the Fram Strait the annual primary production pattern followed the general sea-ice concentration pattern and that the annual primary production was up to 10 times larger in the WS area compared to the EG area. Thus, the sea-ice concentration represents the general primary production pattern in the Fram Strait. ~~Our results indeed indicate a potentially higher primary production in the WS area, compared to the EG area. The general nutrient distribution differs between the EG and WS area, with higher nitrate and phosphate concentrations in the WS area. The nutrient distribution follows the sea-ice pattern and is also mainly influenced by the general current system in the Fram Strait, as the EGC transports water masses with lower nutrient concentrations and the WSC water masses with higher nutrient concentrations (Manley, 1995). Therefore, the initial conditions for primary production in the Fram Strait would support higher primary production in the WS area, as more light (owing less sea ice) and more nutrients are available.~~

As the sampling was performed in Mid/End of June 2014 and July/August 2015, it is very likely ~~that the season of new production~~that the spring bloom, which usually starts in May (Cherkasheva et al., 2014), had finished.~~, which usually starts in May (Cherkasheva et al., 2014), had already ended.~~ This is indicated by lower nutrient concentrations at water depth ≤50 m compared to the nutrient concentrations between >50–300 m water depths (Graeve and Ludwichowski, 2017a, b). ~~This explains the low nitrate concentration values within the first 20–40 m water depth in the EG and WS area (Supplement Fig. S1). Interestingly, higher phosphate concentration values were found in the EG area compared to the WS area w~~The N:P ratio in the upper 50 m during the expeditions was six and seven in the EG and WG area, respectively (Graeve and Ludwichowski, 2017a, b), ~~ithin the first 20–40 m water depth, which is contrary to the observed phosphate distribution pattern over the entire water depth. It indicates~~indicating that primary production ~~in the EG area is~~ was nitrate limited, similar to the permanently sea-ice covered central Arctic Ocean (Tremblay et al., 2012;~~,~~ Fernández-Méndez et al., 2015). Furthermore, the timing of our sampling suggests that the increased carbon supply by the spring bloom had already reached the seafloor and enhanced the benthic remineralisation (Graf, 1989) in both areas. The pattern of contrasts between the EG and WS area continued in the benthic food supply~~, with generally higher values of benthic food supply representing parameters in the WS area compared to the EG area (Fig. 3) and indicated by the negative correlation of the sea ice concentration with Chl *a*, TOC and organic matter (Fig. 5), ~~, which ~~also~~ was also found by Boetius and Damm (1998) for areas with contrasting sea-ice cover at the continental margin of the Laptev Sea.

Continuing the cascade of dependencies, benthic community ~~biomass and density~~parameters should follow the same pattern as the sea ice at the surface and the benthic food supply parameters. Indeed, ~~T~~there ~~are~~ were differences between the EG and WS area regarding meiofauna density and~~,~~ macrofauna density but not in the macrofauna biomass. ~~and macrofauna biomass (Fig. 3). However, the comparable angles between the macrofauna–water depth arrow and the macrofauna–sea ice concentration arrow in figure 5 indicated that macrofauna biomass is also influenced by water depth and not only by the sea-ice cover. It needs to be mentioned that the term "macrofauna biomass" used in figure 5, also represents the macrofauna density, meiofauna biomass, and meiofauna density (Supplement Table S2) and therefore the entire benthic community.~~ In addition, also the macrofauna community structure differed between areas with high and low sea-ice cover. However, only when taking sea ice and water depth into account.~~Furthermore, when taking both abiotic factors (sea ice and water depth) into account, the contrasting water depth–macrofauna density relationship between high and low sea ice covered areas became visible (Supplement Fig. S4).~~ ~~Additionally, our data reveal significant differences in the macrofauna community structure based on sea ice cover categories (Table 3) and water depth (Supplement Table S10) and on macrofauna density and macrofauna biomass (Supplement Table S11 and S12). Thereby, The~~The performed PERMANOVA confirmed the influence of water depth on the macrofauna community and indicated that water depth is a considerable factor besides ~~the~~ sea-ice cover. Consequently, in the low sea-ice covered WS area macrofauna is mainly influenced by the abiotic factor water depth (Soltwedel et al., 2015), while in the highly sea-ice covered EG area the abiotic factor sea-ice cover co-acts or even replaces water depth as the most influencing abiotic factor.

Benthic remineralisation across the Fram Strait, represented by the oxygen consumption, was not correlated with sea-ice concentrations or benthic food supply, only with water depth (Fig. 5).~~Continuing the cascade of dependencies to the benthic activity, represented by the oxygen flux; we did not reveal a correlation of oxygen fluxes with sea-ice concentrations or benthic food supply, only with water depth (Fig. 5).~~ This is ~~contrasting~~ in contrast to our expectations and to findings of Boetius and Damm (1998). However, a PCA only shows correlations which does not necessarily prove causal relationships and ~~but~~ does~~o~~ not test for the significance~~s~~ of these relationships~~ within it~~. Therefore, we tested the significance of the correlation of water depth with DOU within the sea-ice concentration categories HSC and LSC, which reveals a slightly different pattern. The regression of the DOU on water depth is only significant in the LSC category, but not in the HSC (Fig. 4). Therefore, the bacterial benthic ~~activity~~remineralisation, which makes up ~ 80 % of the TOU~~ (Table 2)~~, depends on water depth in low sea-ice covered areas, but not in the highly sea-ice covered EG area. Bacterial density, however, did not show differences between the HSC and LSC categories and therefore was not the biotic link which connected the food input pattern (Supplement Fig. S3) with the remineralization pattern (Figure 4). Benthic bacterial biomasses and benthic bacterial community structures, factors which may explain the differences in the benthic mineralization patterns of high and low sea-ice covered areas, have been to date only investigated in the eastern Fram Strait (Jacob et al., 2013) but not in the western Fram Strait. ~~To~~ A test, if this pattern is also true for the macro- and meiofauna ~~activity~~remineralisation, represented by the fauna mediated oxygen uptake (= TOU minus DOU), ~~we~~ was assessed as not reliable owing a lower reproducibility of TOU values.

A PCA displays an ecosystem snapshot of factors which likely respond on different time scales. For example, benthic faunal biomass, density, and structure will respond to food-related parameters in a more seasonally to decadal fashion, while benthic remineralisation respond on short time scales such as days to weeks (Graf, 1989; Renaud et al., 2008). To acknowledge this, we decided to use the short-term dataset ‘year before sampling’ in the PCA. Additionally, the origin of the primary production responsible for the benthic food supply is difficult to assess and can be located >3000 km from Fram Strait (Lalande et al., 2016). In turn, the complexity of advective and vertical pelagic food input influencing processes in the Fram Strait is not considered in the ecosystem snapshot. Furthermore, by comparing only two sites (HSC/LSC) a statistical investigation of the actual relationship between ice cover and the response variables is not possible.

To summarise

~~In the Fram Strait, sea-ice cover and water depth are totally independent abiotic factors influencing the benthic ecosystem and thereby the cascade of dependencies between ecosystem components.~~ , ~~The~~ sea-ice cover in the Fram Strait is~~-~~ a proxy for light availability and nutrient supply and therefore represents primary production in Fram Strait. In addition, water depth represents a proceeding degradation state of settling organic material towards the sea floor (Belcher et al., 2016). Both processes are responsible for the food supply to the benthos. Therefore, the independent factors ‘sea-ice cover’ and ‘water depth’ were the most important abiotic factors in the Fram Strait as they controlled the benthic food supply. ~~directly linked to the primary production and to the benthic food supply. The deep-sea benthic community is influenced also by water depth, which represents a proceeding degradation state of settling organic material towards the sea floor (Belcher et al., 2016).~~ This fits ~~the~~ earlier findings, that labile organic matter is the most important factor determining Arctic deep-sea benthic communities (Grebmeier et al., 1988; Boetius and Damm; 1998; Klages et al., 2004). ~~Regarding the benthic activity~~Regarding benthic remineralisation, the Fram Strait is bisectional: water depth independent in the highly sea-ice covered western Fram Strait and water depth dependent in the low sea-ice covered eastern Fram Strait. However, the impact of sea-ice on the benthic remineralisation cannot be distinguished from the impact of water depth in water depth >1500 m.~~.~~

4.2 Primary production and benthic remineralisation in the Fram Strait

~~Our~~ The reported oxygen fluxes within the HSC and LSC categories are comparable to earlier findings within the Fram Strait ~~by (~~Sauter et al., ~~(~~2001;~~) and~~ Cathalot et al., ~~(~~2015)~~-~~ and ~~also by findings of Boetius and Damm (1998) for~~ the continental margin of the Laptev Sea (Boetius and Damm, 1998), but are slightly lower than ~~, but slightly lower than~~ the modelled results for the pan-Arctic region ~~by (~~Bourgeois et al., ~~(~~2017; ~~,~~ Fig. 6). In general, ~~T~~the total benthic carbon remineralisation across the entire Fram Strait on average is ~1 mmol C $m^{-2}d^{-1}$ ~~and mainly mediated by the bacterial community (DOU/TOU >80 %, Table 2).~~ .

The new primary production, the part of the total production which can fuel the benthos (Platt et al., 1989), ~~in the West Spitsbergen area~~ is ~~in the order of~~ 55 g C $m^{-2}yr^{-1}$ (Sakshaug, 2004, and references therein) in the West Spitsbergen area. This is equal to 38 mmol C $m^{-2}d^{-1}$, assuming a production period of 120 days ~~days as suggested by (~~Gradinger, ~~(~~2009)~~). This indicates that approximately 2.6 % of the new primary production in the WS area is remineralised by the benthic activity~~. Codispoti et al. (2013) reported net community production from nutrient depletion for the WS area of 27–32 g C m^{-2}. These values reflect the annual new production and thus can be converted to 19–22 mmol C $m^{-2}d^{-1}$ (under the same assumption of 120 days of production). This indicates that on average approximately 2.6–5.2 % of the new primary production in the WS area would be remineralised by the benthos. ~~However,~~ Lalande et al. (2016) reported from sediment trap studies ~~from particle trap measurements deployed at HG IV~~ that ~~only~~ 2.7 g C $m^{-2}yr^{-1}$ (= 1.9 mmol C $m^{-2}d^{-1}$ under the same assumption of 120 days of production, particle trap study at HG IV) and therefore ~~only~~ 5–14 % of the primary production reaches the seafloor. Taking these export fluxes into account, this indicates that ~~half~~ only 40 % of the organic material ~~, that~~ reac~~h~~eing~~s~~ the seafloor~~,~~ is remineralised by the benthos in the West Spitzbergen area in the eastern Fram Strait.

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The net primary production in the mainly sea-ice covered western Fram Strait is approximately 8 g C $m^{-2}yr^{-1}$ (Codispoti et al., 2013), which equals 5.6 mmol C $m^{-2}d^{-1}$ (under the same assumption of 120 days of production). This is similar to the similarly sea-ice covered central Arctic Ocean (Codispoti et al., 2013; Fernández-Méndez et al. 2015). ~~To our knowledge, there is no data on primary production for the eastern Fram Strait available. However, the EGC is fed by the Transpolar current. Therefore, we assume the same primary production conditions for the EG area as for the central Arctic Ocean. Sakshaug (2004, and references therein) reported a new primary production of <1 g C m⁻²yr⁻¹ (= 0.7 mmol C m⁻²d⁻¹ under the same assumption of 120 days of production) in the central Arctic Ocean. This would indicate that the benthos in the EG area is not only fed by ice- and under ice algae production because our oxygen consumption values are higher than~~

~~the new primary production.~~ Thus, 18 % of the new primary production in the EG area would be remineralised by the benthos. Annual POC flux values of 1–2.7 g C $m^{-2}yr^{-1}$ (= 0.7–1.9 mmol C $m^{-2}d^{-1}$, under the same assumption of 120 days of production) were reported for the ~~permanently~~ ice-covered ~~northwest water polynya~~regions at the Greenland shelf at 80 °N (Bauerfeind et al., 1997) and 1.6 g C $m^{-2}yr^{-1}$ (= 1.1 mmol C $m^{-2}d^{-1}$, under the same assumption of 120 days of production) at the Greenland s~~S~~helf at 74 °N ~~(~~(Bauerfeind et al., 2005). These values ~~-~~indicate that 13–34 % of the primary production reaches the seafloor, which is comparable to Arctic shallow shelf regions (Grebmeier et al., 1988; Renaud et al., 2007). It further suggests that 50 % to >100 % of the organic material, that reaches the seafloor, is remineralised by the benthic organisms at the East Greenland continental margin and that this area has to be supplied by organic carbon from other areas.~~support these findings. Current calculations of the new primary production in the central Arctic Ocean during the sea-ice minimum in 2012 by Fernández-Méndez et al. (2015), who estimated the carbon uptake since the winter water formation from nutrient, salinity and temperature profiles, found 9.4 g C $m^{-2}yr^{-1}$ (= 6.5 mmol C $m^{-2}d^{-1}$, assuming 120 days of production). This is roughly 10 times higher than the estimations done by Sakshaug (2004, and references therein). Transferring this value to the Fram Strait, >15 % of the surface primary production would be remineralised in the EG area, which is comparable to the Arctic shallow shelves (Grebmeier et al., 1988; Renaud et al., 2007).~~

~~However~~It has to be noted~~,~~ that these numbers have to be interpreted with caution, as a more reliable calculation of the primary production across the entire Fram Strait still remains difficult. Satellite-based chlorophyll measurements are only available in ice-free areas when there are no clouds or ~~and no~~ fog (Cherkasheva et al., 2014). Additionally, satellites only measure chlorophyll a in the upper water column. Therefore, to calculate the primary production, additional information about the mixed water depth, photosynthetically active radiation, water temperature, salinity, nutrient availability, the chlorophyll a to carbon ratio, growth rates of the different occurring algae (Sakshaug, 2004) and further parameters needed to be measured during the bloom period, which can be exclusively obtained by ship-based expeditions. The approach of Codespoti (2013) is preferable, when primary production and benthic remineralisation are compared. However, it relies on a good spatial resolution of nutrient profiles in the water column. Furthermore, ~~the~~ measurements of the benthic oxygen flux, crucial to evaluate the pelagic-benthic-coupling, remain only snapshots of remineralisation. The question, if the Arctic deep-sea benthic oxygen fluxes follow seasonal changes, has only been sparsely evaluated (Bourgeois et al., 2017). However, a pulsed supply of food and thus temporal response of the benthic community from other deep sea areas is known (e.g. Witte et al., 2008; Smith et al., 2016). A full annual cycle of benthic remineralisation in the Arctic is still missing and as such, a more reliable discussion of the pelagic-benthic-coupling and the carbon cycle remains difficult.

4.3 A future deep-sea benthic Arctic Ocean scenario

~~Atmospheric and ocean temperatures are increasing globally (IPCC, 2013) and this warming trend amplifies in polar areas (Manabe and Stouffer, 1980; Hassol, 2004). Generally, the warming trend causes a sea-ice thinning (Kwok and Rothrock, 2009), a diminishing sea-ice cover (Comiso et al., 2008), and a decrease of perennial sea-ice (Comiso, 2002). Furthermore, as the annual and the summer sea-ice extent decreases (IPCC 2013), the sea-ice edge is moving northwards. If these trends~~

~~continue, a sea-ice free Arctic Ocean is predicted for the second half of the century by the Intergovernmental Panel on Climate Change (IPCC 2013), while others (Arzel et al., 2006; Wang and Overland, 2012) predicted it to happen even earlier. Due to its stable sea-ice cover conditions, we can use the Fram Strait to discuss potential consequences for a future deep sea benthic Arctic Ocean. We compare different stations representing different states of the development from the former towards a predicted future Arctic Ocean. Within our comparison and owing to its specific regional characteristic sea-ice cover, the EG bathymetric transect represents the former Arctic Ocean, while the predicted, future Arctic Ocean is represented by the HG bathymetric transect. Furthermore, the station EG V represents a first transition step and station N5 a second transition step from former to the future Arctic Ocean.~~

Our results indicate that a development from a permanently sea-ice covered to a seasonally sea-ice covered Arctic Ocean will change the bentho–pelagic relationship from a ~~surface~~ sea-ice dependent towards a water depth dependent environment (Fig. 4). This may go along with a predicted compositional shift in the spring phytoplankton bloom from diatom dominated to coccolithophorid (Bauerfeind et al., 2009) or *Phaeocystis* sp. and nanoflagellates dominated bloom (Soltwedel et al., 2015). An altered algal composition will affect zooplankton communities (Caron and Hutchins, 2013) and partly organic particle fluxes (Wohlers et al., 2009). An additional predicted effect is an increasing annual matter flux towards the seafloor (Wassmann, 2011; Boetius et al., 2013, this study), while the labile detritus flux is predicted to decrease (Hop et al., 2006; van Oevelen et al., 2011). Therefore, the change in sea-ice cover in the Arctic Ocean may alter the quality and quantity of the organic matter flux to the seafloor, where it maybe affects benthic deep-sea communities ~~(Kortsch et al., 2012;~~ (Jones et al., 2014; Harada, 2015). However, the comparable DOU of the EG and HG site at water depth >1500 m (Fig. 4) indicates that the remineralisation ~~activity of~~ by the deep-sea benthos will possibly remain stable in the Arctic Ocean.

Our scenario is only suitable if sea-ice disappears and nutrient supply increase, which will result in enhanced primary production ~~in the Arctic Ocean would increase as the HG transect and especially N5, EG V and HG IV are located in the highly productive Marginal Ice Zone (Soltwedel et al. (2015). However, t~~The development of future Arctic Ocean primary production patterns and changes is still under debate (Wassmann, 2011;~~,~~ Arrigo et al., 2012; Nicolaus et al., 2012;~~,~~ Boetius et al., 2013). However, it is likely that the described scenario becomes true in the Chukchi Sea and the Beaufort Sea, owing to the predicted strengthening of the nutrient rich Pacific inflow (Harada, 2015). Furthermore, owing to an increased atlantification, an increased nutrient supply is also likely for the continental margin at the Barents Sea (Neukermans et al., 2018). In addition, nutrient inflow by glacial and permafrost soil melt is also predicted to increase (Vonk et al., 2015). However, this riverine load might only enhance primary production at the shelf areas and therefore is not relevant for the deep sea. An enhanced primary production in the western Fram Strait is unlikely even if the light availability will increase, as the required nutrient supply increase is not expected for this region (Mauritzen et al., 2011).

Additionally, the sea ice in the Fram Strait is already thinning (Krumpen et al., 2015). This may be led to more light in the upper water column and an already higher primary production in the EG area, which consequently may have resulted in a higher food supply to the deep-sea benthos in this area and thereby biases our former-Arctic-Ocean perspective. However, fast sinking algae patches as reported by Boetius et al (2013) in the central Arctic, which would lead to increased

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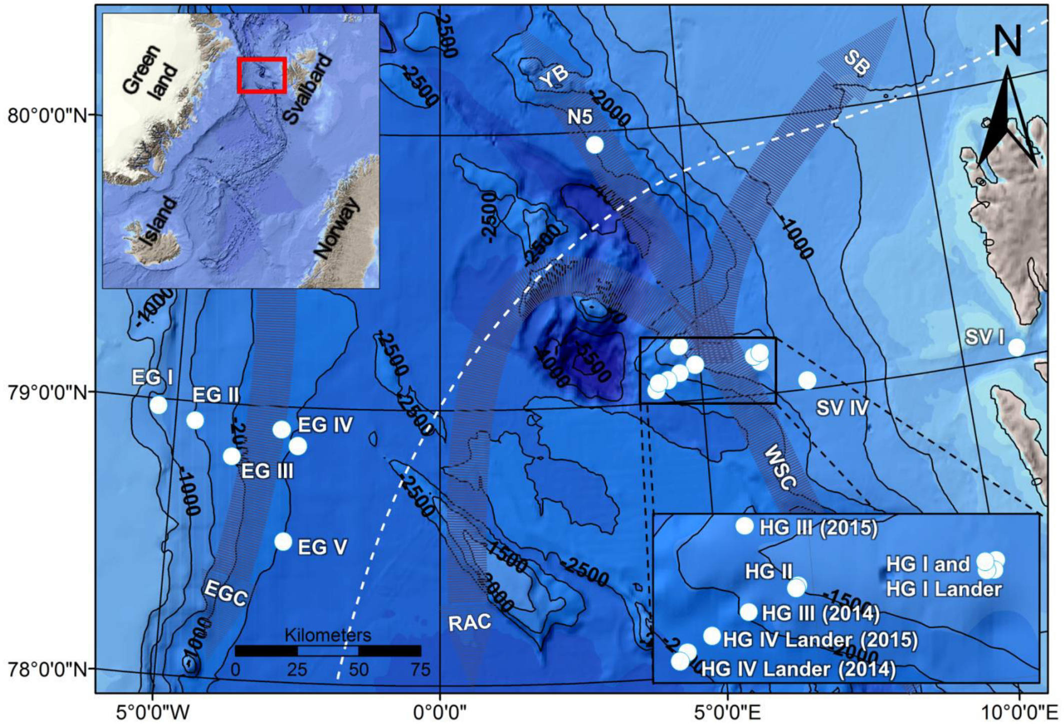
benthic remineralisation, were not observed during a video transect at EG IV in 2014 (pers. Comm. J. Taylor). ~~However, fast sinking algae patches as reported by Boetius et al (2013) in the central Arctic, indicative of a higher primary production by ice- and under ice algae due to changing sea ice conditions, were not observed during a video transect at EG IV in 2014 (pers. Comm. J. Taylor).~~ A further limitation of our scenario might be, that in contrast to the HG stations, there are no long-term data available about the benthic environment at the EG stations. Thus, an assessment of ongoing changes in the EG area, similar to the HG stations (Soltwedel et al., 2015), and ~~getting~~ insights into the natural variability of benthic changes remains difficult at the moment. Nevertheless, the ~~stable~~ general sea-~~-~~ice~~ conditions~~ concentration ~~-~~pattern in Fram Strait ~~across the eastern Fram Strait within~~ was stable over the last 14 years (Fig. 2)~~.~~. This indicates that at least the production period and therefore, the low ~~amount of~~ food supply at the EG stations was also stable within the last 14 years. In addition, the scenario is only valid for areas changing from permanent to very low sea-ice cover as our data does not allow to estimate a scenario for an intermediate (20–60 %) sea-ice cover.~~Besides the limitations of our scenario~~

Despite its uncertainties, observations are currently still the best method to create scenarios of future developments as consistent time series data from the entire Arctic Ocean, required to model reliable future predictions, are yet missing (Wassmann et al., 2011).~~, the lack of consistent time series data from the entire Arctic Ocean (Wassmann et al., 2011) to create reliable models for future predictions, observations are currently still the best and only method to create scenarios of future developments.~~ Thus, our comparative study provides new insights into the relationship between sea–ice cover at the surface and benthic oxygen fluxes in the Fram Strait via surface primary production, benthic food supply, benthic community and their functions. We hypothesis~~z~~e that if surface primary and secondary production will increase due to the retreating sea–ice cover, the deep-sea benthos of the Arctic Ocean may shift from a sea-ice dependent towards a water depth dependent environment. There might be a slightly increased food supply and an altered macrofauna community, but remineralisation at water depths greater than 1500 m seems to be hardly affected by these changes because it ~~is in any case~~remains food limited.

Figures


Green land
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EG I
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EGC
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HG III (2015)
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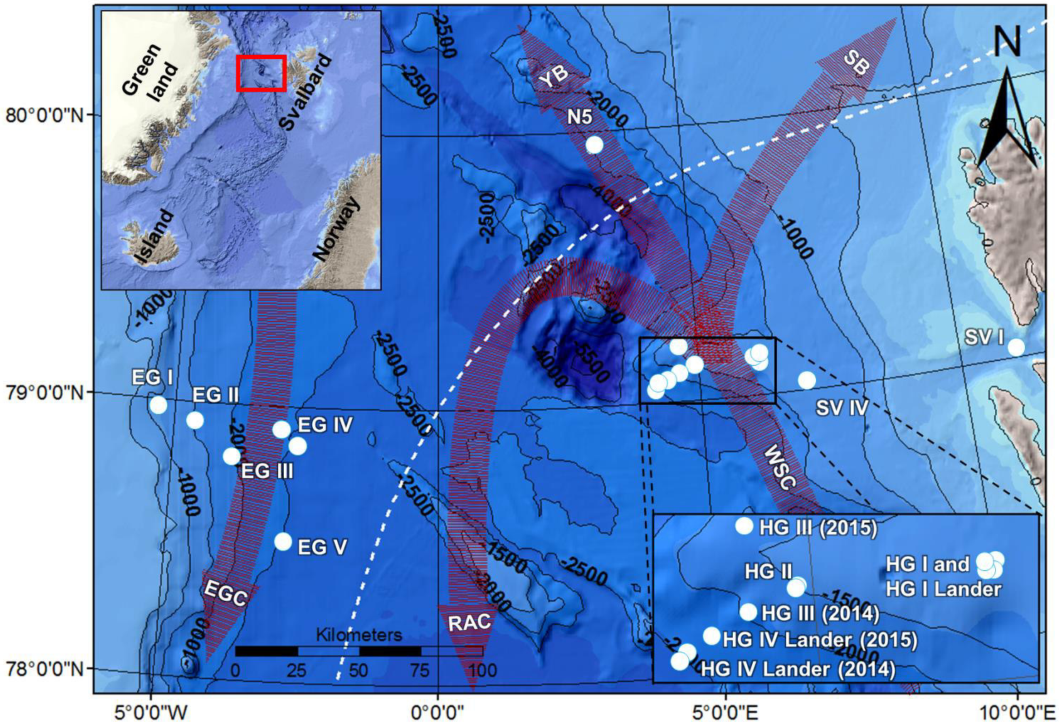

Figure 1. Location of the sampled stations in the Arctic Fram Strait. White dashed line = ~~General~~ mean summer sea-ice extent in September (1981-2010, (http://nsidc.org))~~: white dashed line~~. Red arrows = ~~G~~general current system~~: grey arrows~~. EGC = East Greenland Current, WSC = West Spitsbergen Current, SB = Svalbard branch, YB = Yermak branch, RAC = ~~Recirculating~~ Return Atlantic current. White dots = stations with station names~~-~~. More station-specific details are given in Table 1.

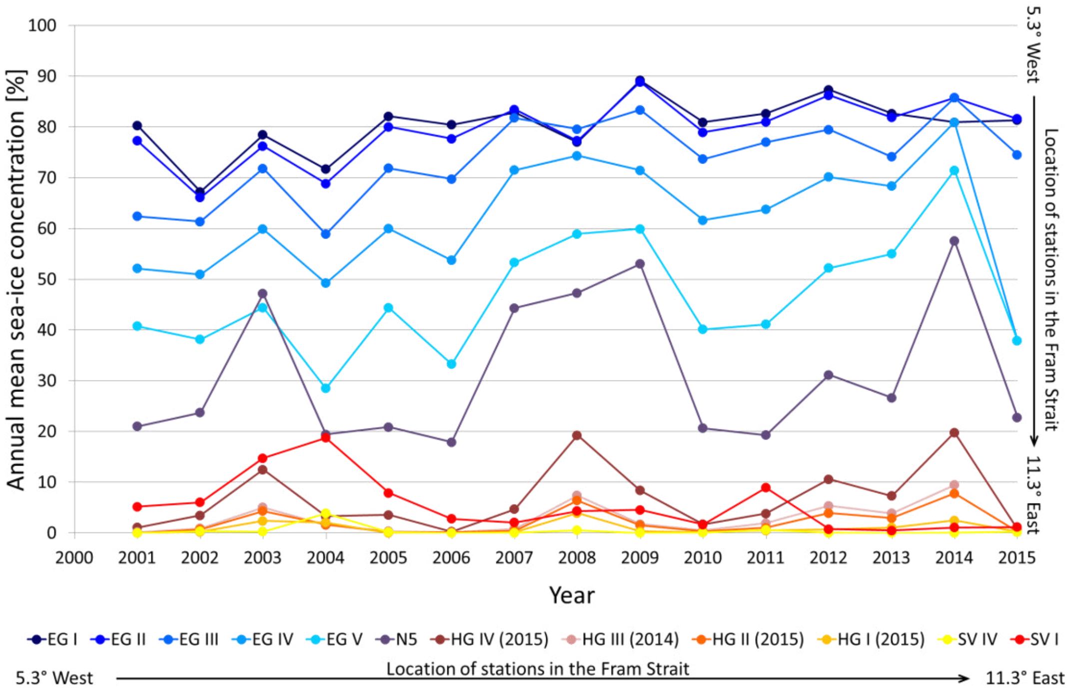

Figure 2. Annual mean sea-ice concentrations from 2001 to 2015 of a subset of ~~the~~ sampled stations. The sampling year at the HG stations is given, as HG stations where sampled in 2014 and 2015 and therefore, the given sampling year refers to the exact position from which the sea ice data were obtained.

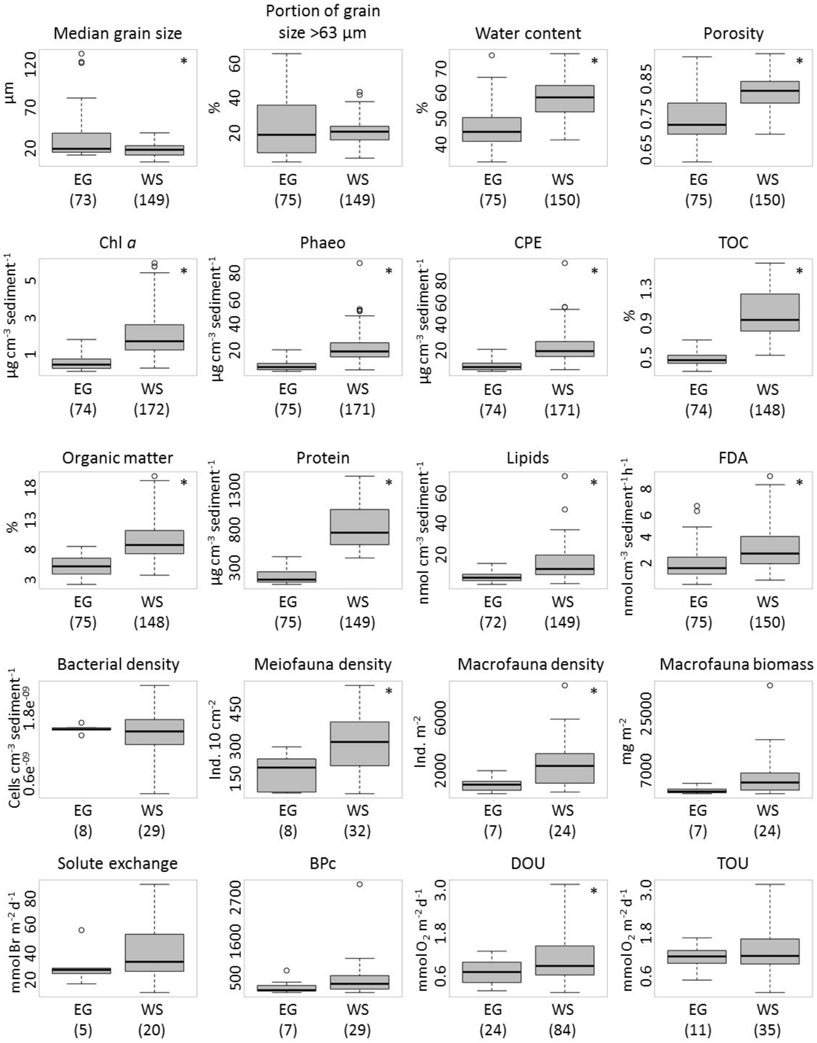

Figure 3. Boxplots of sediment properties, biogenic compound values (Chl *a* = chlorophyll a, Phaeo = phaeophytin, CPE = chloroplastic pigment equivalents, TOC = total organic carbon, FDA = bacterial enzymatic turnover rates calculated using the fluorogenic substrate fluorescein-di-acetate), benthic community data and function (BPc = bioturbation potential), and oxygen fluxes (DOU = diffusive oxygen flux, TOU = total oxygen flux), ~~from oxygen fluxes conversed carbon fluxes~~ of the East Greenland (EG) and West Spitsbergen (WS) area. For a detailed description of which stations were included at which site, see section 2.1. The number of observations is given in brackets below the area. Parameters showing significant differences between areas are marked with an asterisk. For comparability, the WS site does not contain values from SV I station.

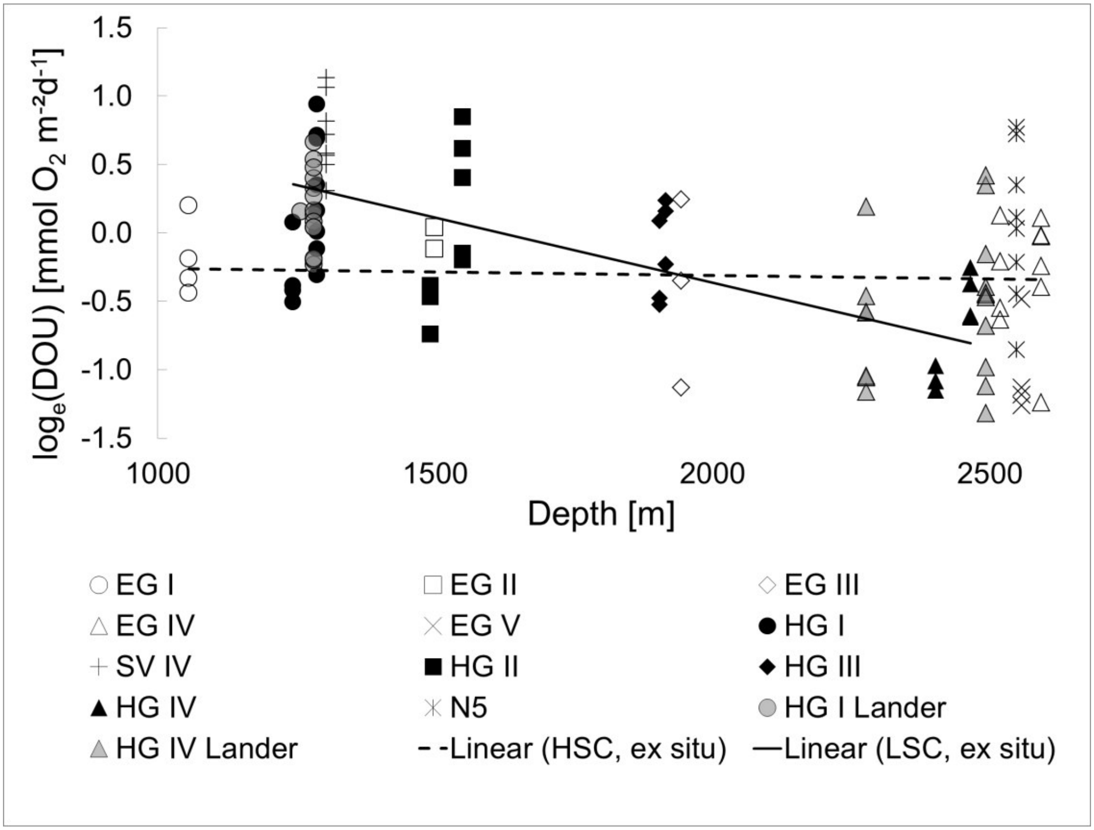

Figure 4. Log-transformed DOU data as a function of water depth at each station and linear regressions in the HSC and LSC categories (from ex situ values). The full line indicates a significant decrease of DOU with water depth in the LSC area, while the dashed line indicates that the slope did~~oes~~ not differ significantly from zero.

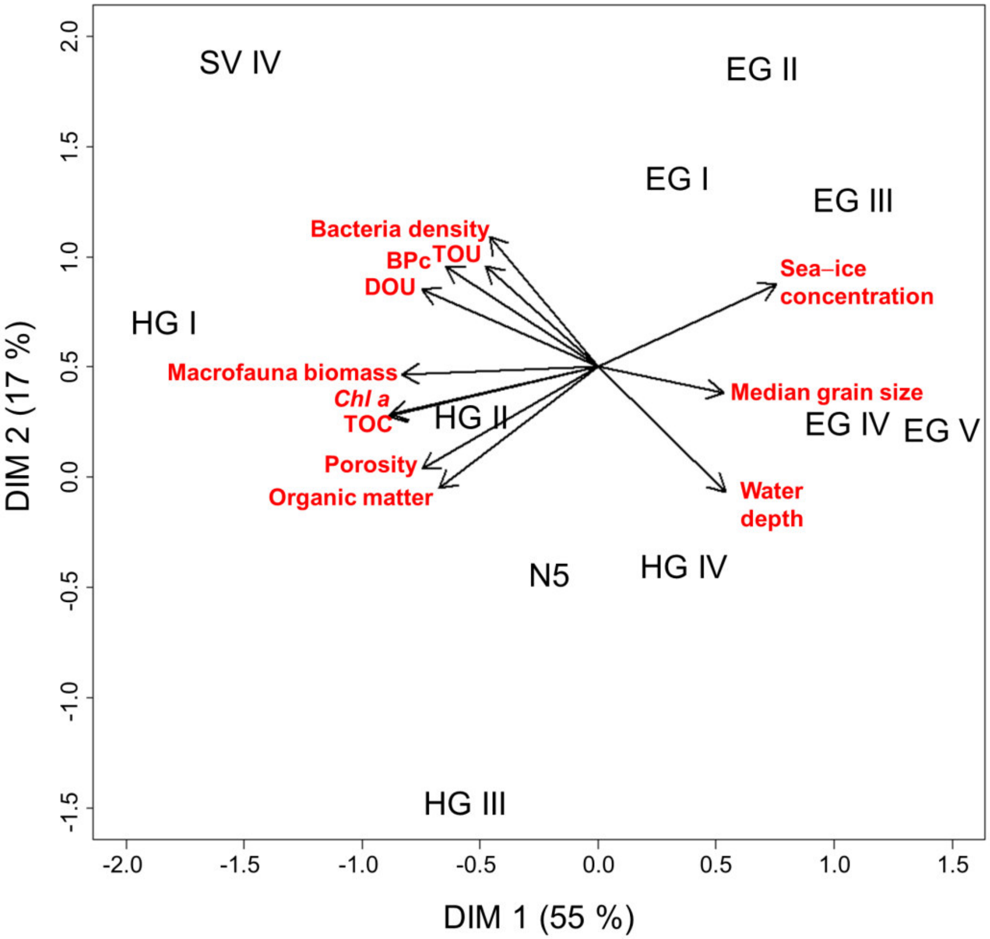

Figure 5. Visualisation of PCA results on standardised ex situ mean values of abiotic parameters (water depth, sea-ice concentration, median grain size, porosity), biogenic compound parameters (Chl *a*, TOC, organic matter), benthic community parameters (bacterial density, macrofauna biomass), ~~macrofauna mediated environmental functions (Solute exchange, BPc)~~bioturbation potential (BPc), and oxygen fluxes (DOU, TOU). All other parameters were excluded from the PCA as they correlated strongly with one of the mentioned parameters (correlation >0.74, Pearson correlation, Supplement Table S2). For comparability, Station SV I was excluded from the PCA. Therefore, the figure reflects ~~dependencies~~ relations of different parameters in the Fram Strait ~~for~~ in water depths ~~between~~ of 1000–2500 m.

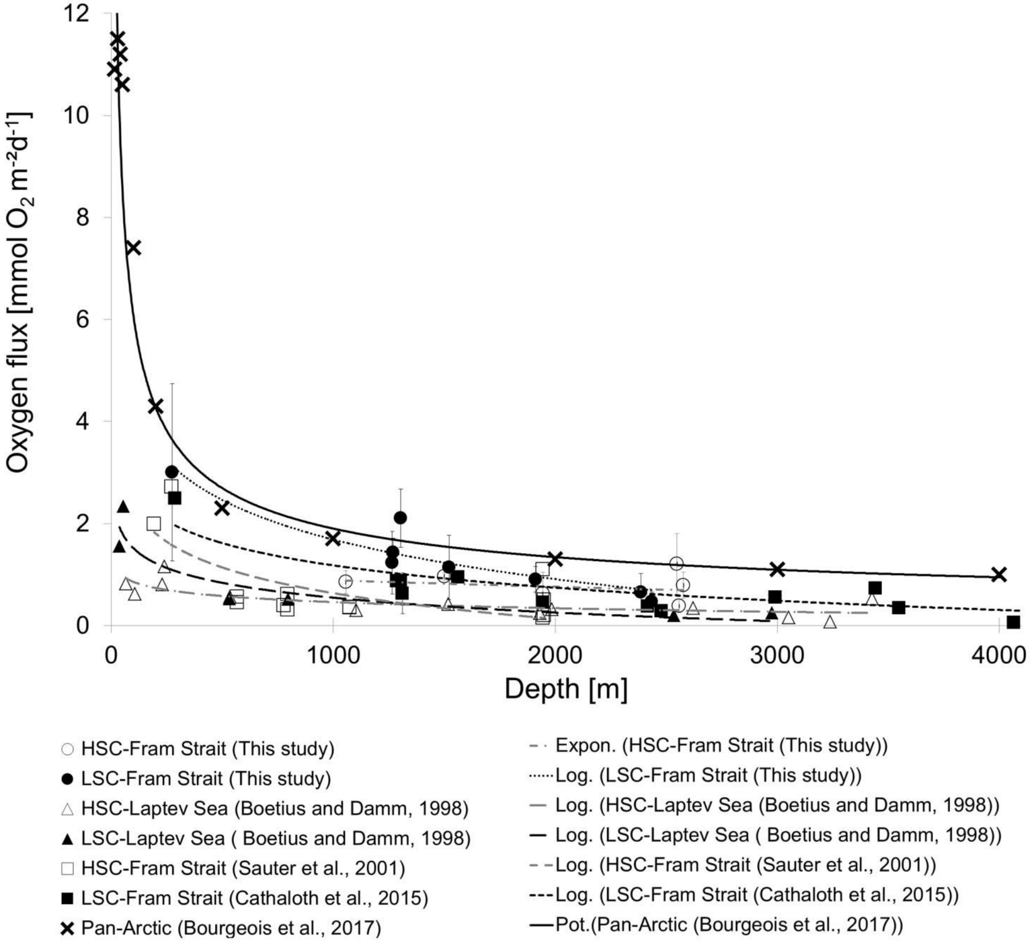

Figure 6. Sediment oxygen uptakes in different water depths (15 ~~m~~– 4000 m) for HSC and LSC sea-ice categories from this study and from literature data for the Laptev Sea, Fram Strait, and Pan-Arctic region and related regressions. HSC regression from this study: y=-0.124ln(x)+1.7388 (R^2=0.0255); LSC regression from this study: y=-1.119ln(x)+9.4144 (R^2=0.8695); HSC regression from Sauter et al. (2001): y=-0.727ln(x)+5.6587 (R^2=0.5026); LSC regression from Cathalot et al. (2015): y=-0.63ln(x)+5.534 (R^2=0.7013); HSC regression from Boetius and Damm (1998): y=-0.172ln(x)+1.6496 (R^2=0.6074); LSC regression from Boetius and Damm (1998): y=-0.421ln(x)+3.4515 (R^2=0.8428); Pan-Arctic regression from Bourgeois et al (2017): y=7.1338e$^{-6E-04x}$ (R^2=0.7288). Regression types were chosen based on best fit (R^2). The model of Bourgeois et al. (2017) included DOU and TOU values, while all other references refer only to DOU values.

Data availability

Data are available via the PANGAEA data archive. https://www.pangaea.de/

Authors contribution

RH, UB, and FW designed this study; RH and UB were responsible for the measurements and calculations of the oxygen fluxes. Additionally, UB was responsible for the measurement of the grain size parameters and bromide concentrations, and pre-processing and identification of the meio- and macrofauna densities and macrofauna biomasses. CH was responsible for the measurements of the water content and the biogenic compounds. RH was responsible for the calculation of the porosity, the solute exchange, and the BPc and performed all statistical analyses within “R”. CH was responsible for the statistical analyses in PRIMER. RH prepared the manuscript with contributions from all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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Tables

Table 1. General station information regarding water depth, sampling date, location and station ID in the data archive Pangaea. Order of stations for each area follows the water depth gradient.

Area	Station name	Water depth (m)	Sampling date	Latitude (ddd.ddd °N)	Longitude [dd.ddd °E]	Pangaea Station ID
EG	EG I	1056.3	17/06/2014	78.973	-5.290	PS85/0436-1
	EG II	1499.7	18/06/2014	78.933	-4.650	PS85/0441-1
	EG III	1943.8	19/06/2014	78.803	-3.875	PS85/0445-1
	EG IV	2592	31/07/2015	78.862	-2.710	PS93/0058-12
		2518.5		78.914	-2.961	PS93/0058-17
	EG V	2557.7	20/06/2014	78.505	-2.817	PS85/0454-3
WS	SV I	275	06/08/2015	79.028	11.087	PS93/0066-2
	HG I	1244.2	24/06/2014	79.133	6.1065	PS85/0470-3
		1287.7	10/08/2015	79.138	6.0835	PS93/0080-9
	HG I Lander	1257.6	26/06/2014	79.142	6.124	PS85/0476-1
		1282.2	10/08/2015	79.134	6.092	PS93/0080-8
	SV IV	1304	08/08/2015	79.029	6.999	PS93/0074-3
	HG II	1492.3	24/06/2014	79.132	4.906	PS85/0469-2
		1550.2	09/08/2015	79.130	4.902	PS93/0078-2
	HG III	1904.8	24/06/2014	79.106	4.585	PS85/0468-1
		1916	08/08/2015	79.208	4.600	PS93/0077-2
	HG IV	2402.6	22/06/2014	79.065	4.183	PS85/0460-4
		2465.2	27/07/2015	79.065	4.179	PS93/0050-19
	HG IV Lander	2492.6	24/06/2014	79.052	4.138	PS85/0466-1
		2277.5	27/07/2015	79.083	4.337	PS93/0050-18
	N5	2548.2	03/08/2015	79.938	3.193	PS93/0060-10

Table 2. Sea-ice cover (%) and % of days with sea-ice cover on different time scales across the Fram Strait. The values are given in mean values ± standard deviation and number of samples in brackets. Sea-ice data a year before sampling are mean values for the period 01.07.2013–30.06.2014 for stations only sampled in 2014 and 01.08.2014–31.07.2015 for stations only sampled in 2015. For stations sampled in both years, data of both periods were combined. The date of sampling is given in Table 1.

Station name		EG I	EG II	EG III	EG IV	EG V	SV I	HG I	HG I Lander	SV IV	HG II	HG III	HG IV	HG IV Lander	N5
2001–2015	Sea-ice coverage (%)	80 ± 24 (5101)	79 ± 24 (5101)	74 ± 26 (5102)	64 ± 31 (5102)	47 ± 33 (5102)	5 ± 16 (5102)	1 ± 6 (5101)	1 ± 6 (5101)	0 ± 4 (5101)	2 ± 3 (5101)	4 ± 13 (5102)	7 ± 18 (5102)	6 ± 17 (5102)	32 ± 33 (5102)
	Days with sea-ice coverage within a year before sampling (%)	97	97	95	92	84	15	4	4	2	8	11	18	17	66
Year before sampling	Sea-ice coverage [%]	82 ± 20 (364)	80 ± 21 (364)	75 ± 27 (364)	72 ± 24 (365)	56 ± 34 (364)	1 ± 5 (365)	1 ± 7 (729)	1 ± 7 (729)	0.1 ± 2 (365)	4 ± 12 (729)	5 ± 14 (729)	10 ± 21 (729)	9 ± 19 (729)	40 ± 31 (365)
	Days with sea-ice coverage within a year before sampling (%)	100	100	100	98	93	6	4	4	0	13	16	25	24	82
Since 01.05. till sampling	Sea-ice coverage [%]	79 ± 15 (48)	77 ± 16 (49)	81 ± 13 (50)	56 ± 24 (90)	67 ± 22 (51)	1 ± 4 (96)	5 ± 9 (77)	15± 9 (78)	0 (98)	10 ± 12 (77)	10 ± 12 (77)	19 ± 15 (71)	19 ± 16 (71)	35 ± 23 (94)
	Days with sea-ice coverage within a year before sampling (%)	100	100	100	99	100	10	18	17	0	32	34	45	45	89
Month before sampling	Sea-ice coverage [%]	76 ± 16 (31)	73 ± 17 (31)	84 ± 10 (31)	57 ± 22 (31)	74 ± 19 (31)	1 ± 4 (30)	9 ± 11 (31)	8 ± 11 (31)	0 (30)	16 ± 12 (31)	15 ± 12 (31)	22 ± 17 (31)	23 ± 18 (31)	25 ± 21 (31)
	Days with sea-ice coverage within a year before sampling (%)	100	100	100	100	100	7	28	24	0	41	41	52	52	74

Table 3~~2~~. Mean values ± standard deviation and number of samples in brackets for each measured parameter at each station. The CPE is the chloroplastic pigment equivalent and the sum of Chl *a* and Phaeo. Chl *a*–CPE ratio indicates the available labile carbon source, while the Chl *a*–Phaeo ratio indicates the relative age of the carbon source. No value could be calculated for solute exchange across the sea-water-interface at EG II. ~~But in order to perform a PCA on the shown data, the solute exchange value at EG II is the mean value of all EG and the N5 stations.~~

Parameter category	Parameter	Station													
		EG I	EG II	EG III	EG IV	EG V	SV I	HG I	HG I Lander	SV IV	HG II	HG III	HG IV	HG IV Lander	N5
Sediment property	Median grain size (µm)	13.4 ± 1.2 (15)	15.1 ± 1.7 (15)	20.3 ±3.9 (15)	31.6 ± 7.3 (15)	74.2 ± 29.3 (13)	12.3 ± 2.7 (15)	12.7 ± 6.0 (30)	NA	20.4 ± 6.4 (15)	12.7 ± 5.8 (30)	19.3 ± 5.3 (29)	23.8 ± 5.3 (30)	NA	10.4 ± 2.9 (15)
	Portion of grain size >63 µm (%)	3.5 ± 1.5 (15)	8.6 ± 2.9 (15)	18.6 ± 6.0 (15)	29.5 ± 6.8 (15)	52.2 ± 6.7 (15)	17.7 ± 2.2 (15)	11.4 ± 5.7 (30)	NA	24.4 ± 5.6 (15)	12.6 ± 6.0 (30)	20.1 ± 4.2 (29)	24.5 ± 5.3 (30)	NA	20.7 ± 2.6 (15)
	Water content (%)	51 ± 7 (15)	48 ± 7 (15)	46 ± 9 (15)	48 ± 10 (15)	42 ± 6 (15)	51 ± 14 (15)	66 ± 5 (30)	NA	55 ± 5 (15)	62 ± 4 (30)	55 ± 5 (30)	51 ± 8 (30)	NA	60 ± 5 (15)
	Porosity	0.76 ± 0.06 (15)	0.73 ± 0.06 (15)	0.71 ± 0.08 (15)	0.73 ± 0.08 (15)	0.68 ± 0.06 (15)	0.75 ± 0.14 (15)	0.88 ± 0.03 (30)	NA	0.80 ± 0.04 (15)	0.85 ± 0.03 (30)	0.80 ± 0.04 (30)	0.77 ± 0.06 (30)	NA	0.84 ± 0.03 (15)
Food availability	Chl a (µg ml^{-1} sediment $^{-1}$)	0.5 ± 0.4 (15)	0.5 ± 0.3 (15)	0.4 ± 0.3 (15)	0.6 ± 0.5 (15)	0.63 ± 0.4 (14)	12.7 ± 3 (15)	3 ± 1 (29)	2.5 ± 1.5 (10)	2.2 ± 1.1 (14)	2.0 ± 1.2 (30)	2.1 ± 0.8 (30)	1.3 ± 0.6 (30)	1.1 ± 0.6 (15)	1.2 ± 0.4 (14)
	Phaeo (µg ml^{-1} sediment $^{-1}$)	4.2 ± 2.2 (15)	3.7 ± 2.4 (15)	3.0 ± 2.2 (15)	7.2 ± 5.6 (15)	6.7 ± 3.6 (15)	67.3 ± 10.8 (15)	30.9 ± 8.8 (30)	16.4 ± 8.6 (10)	24.4 ± 20 (14)	18.5 ± 8.6 (29)	20.0 ± 6.2 (30)	12.4 ± 6.2 (30)	9.8 ± 5.7 (15)	14.8 ± 3.8 (13)
	CPE (µg ml^{-1} sediment^{-1})	4.7 ± 2.6 (15)	4.2 ± 2.7 (15)	3.4 ± 2.5 (15)	7.8 ± 6.1 (15)	7.4 ± 4.2 (15)	80.0 ± 13.1 (15)	34.0 ± 9.7 (30)	18.9 ± 9.9 (10)	26.7 ± 21.3 (14)	20.4 ± 9.6 (29)	22.1 ± 6.7 (30)	13.6 ± 6.7 (30)	10.7 ± 6.2 (15)	16.0 ± 4.2 (13)
	Chl *a*–CPE ratio	0.10 ± 0.02 (15)	0.11 ± 0.02 (15)	0.10 ± 0.02 (15)	0.08 ± 0.01 (14)	0.09 ± 0.02 (15)	0.16 ± 0.02 (15)	0.09 ± 0.02 (30)	0.13 ± 0.03 (10)	0.09 ± 0.01 (15)	0.09 ± 0.02 (30)	0.10 ± 0.02 (30)	0.10 ± 0.02 (30)	0.10 ± 0.02 (15)	0.07 ± 0.02 (15)
	Chl *a*–Phaeo ratio	0.11 ± 0.03 (15)	0.13 ± 0.02 (15)	0.11 ± 0.03 (15)	0.08 ± 0.02 (14)	0.10 ± 0.02 (15)	0.19 ± 0.03 (15)	0.10 ± 0.03 (30)	0.16 ± 0.04 (10)	0.10 ± 0.02 (15)	0.10 ± 0.02 (30)	0.11 ± 0.03 (30)	0.11 ± 0.02 (30)	0.12 ± 0.03 (15)	0.08 ± 0.02 (15)
Other biogenic compounds	TOC (%)	0.55 ± 0.05 (14)	0.44 ± 0.04 (15)	0.45 ± 0.04 (15)	0.51 ± 0.11 (15)	0.53 ± 0.09 (15)	1.58 ± 0.27 (15)	1.37 ± 0.08 (28)	NA	0.98 ± 0.13 (15)	1.05 ± 0.19 (30)	0.92 ± 0.11 (30)	0.69 ± 0.07 (30)	NA	0.88 ± 0.03 (15)
	Organic matter (%)	7.1 ± 1.0 (15)	3.5 ± 0.6 (15)	3.5 ± 0.6 (15)	6.6 ± 0.7 (15)	5.0 ± 0.9 (15)	8.0 ± 2.2 (15)	9.1 ± 2.9 (30)	NA	8.0 ± 1.0 (15)	10.6 ± 1.3 (29)	11.4 ± 3.8 (28)	6.5 ± 0.9 (29)	NA	8.4 ± 0.4 (15)
	Proteins (µg ml^{-1} sediment^{-1})	100 ± 20 (15)	122 ± 22 (15)	120 ± 22 (15)	337 ± 80 (15)	259 ± 43 (15)	3253 ± 475 (15)	998 ± 314 (30)	NA	686 ± 85 (14)	1053 ± 95 (30)	1004 ± 313 (30)	530 ± 64 (30)	NA	748 ± 76 (15)
	Lipids (nmol ml^{-1} sediment^{-1})	2.9 ± 1.1 (15)	5.2 ± 2.1 (14)	4.2 ± 2.4 (14)	5.3 ± 2.2 (14)	8.4 ± 2.8 (15)	49.7 ± 21.0 (15)	10.4 ± 7.1 (30)	NA	22.3 ± 10.9 (15)	16.4 ± 8.5 (30)	13.7 ± 5.5 (29)	16.6 ± 16.3 (30)	NA	8.5 ± 3.4 (15)
	FDA (nmol ml^{-1} sediment^{-1} h^{-1})	1.9 ± 0.7 (15)	1.1 ± 0.8 (15)	1.3 ± 0.8 (15)	2.6 ± 2.1 (15)	2.1 ± 1.1 (15)	31.3 ± 12.2 (15)	4.7 ± 1.5 (30)	NA	1.7 ± 0.6 (15)	3.3 ± 2.1 (30)	3.0 ± 1.3 (30)	2.8 ± 1.7 (30)	NA	2.2 ± 0.6 (15)

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Benthic community	Bacteria density (Cells 10^9 ml^{-1} sediment)	1.60 (1)	1.57 (1)	1.55 (1)	1.57 ± 0.09 (4)	1.56 (1)	NA	1.79 ± 0.13 (4)	1.14 ± 0.20 (3)	1.83 ± 0.43 (3)	1.81 ± 0.08 (4)	1.29 ± 0.19 (4)	1.49 ± 0.07 (4)	9.28 ± 0.35 (4)	1.54 ± 0.04 (3)
	Meiofauna density (ind. $10cm^{-2}$)	229 (1)	83 (1)	86 (1)	192 ± 79 (4)	245 (1)~~.0~~	1150 ± 159 (3)	333 ± 134 (3)	357 ± 151 (5)	402 ± 123 (3)	277 ± 75 (4)	273 ± 83 (4)	352 ± 141 (4)	293 ± 202 (6)	268 ± 98 (3)
	Macrofauna biomass (mg m^{-2})	3524 (1)	1971 (1)	1301 (1)	433 ± 287 (3)	450 (1)	45370 ± 25609 (3)	12196 ± 13652 (4)	6929 (1)	8733 ± 1671 (3)	1325 ± 479 (4)	6186 ± 6137 (4)	2784 ± 1578 (4)	836 (1)	8166 ± 7364 (3)
	Macrofauna density (ind. m^{-2})	1414 (1)	991 (1)	284 (1)	1058 ± 722 (3)	1064 (1)	4945 ± 6286 (3)	2860 ± 1206 (4)	942 (1)	4143 ± 2817 (3)	2471 ± 612 (4)	4343 ± 2818 (4)	1148 ± 542 (4)	417 (1)	2023 ± 409 (3)
Community functions	Solute exchange (mmol Br $m^{-2}d^{-1}$)	29.3 (1)	~~25.3 (1)~~NA	57.7 (1)	17.7 (1)	28.1 (1)	38.8 ± 1.8 (3)	51.3 ± 14.1 (4)	NA	39.9 ± 6.3 (3)	38.9 ± 13.0 (5)	53.2 ± 27.3 (3)	50.8 ± 39.3 (2)	NA	15.0 ± 3.1 (3)
	BPc	644~~43.7~~ (1)	318~~87.5~~ (1)	93~~32.8~~ (1)	55~~54.8~~ ± 25~~.3~~ (3)	132~~.4~~ (1)	1586~~.1~~ ± 1042~~1.8~~ (3)	556~~.2~~ ± 266~~.1~~ (4)	397~~.1~~ (1)	909~~.2~~ ± 852~~1.6~~ (8)	199~~8.7~~ ± 51~~0.9~~ (4)	391~~.2~~ ± 90~~89.8~~ (4)	74 ± 40~~.3~~ (4)	70~~.0~~ (1)	106~~5.5~~ ± 39~~.4~~ (3)
Oxygen flux	DOU (mmol O_2 $m^{-2}d^{-1}$)	0.9 ± 0.2 (4)	1.0 ± 0.1 (2)	0.6 ± 0.4 (4)	0.8 ± 0.3 (4)	0.4 ± 0.1 (10)	3.0 ± 1.7 (6)	1.2 ± 0.6 (12)	1.2 ± 0.3 (15)	2.1 ± 0.6 (8)	1.1 ± 0.6 (8)	0.9 ± 0.3 (7)	0.5 ± 0.2 (8)	0.7 ± 0.4 (18)	1.2 ± 0.6 (8)
	TOU (mmol O_2 $m^{-2}d^{-1}$)	0.9 ± 0.3 (2)	1.6 (1)	1.5 ± 0.1 (2)	1.1 ± 0.1 (2)	1.0 ± 0.2 (4)	5.1 ± 0.2 (3)	1.9 ± 0.6 (5)	1.3 ± 0.2 (4)	1.8 ± 0.2 (3)	1.1 ± 0.2 (5)	1.0 ± 0.2 (5)	1.5 ± 0.5 (5)	0.5 ± 0.2 (5)	1.2 ± 0.3 (3)
	DOU/TOU	1.00	0.63	0.40	0.73	0.40	0.59	0.63	0.92	1.17	1.00	0.90	0.33	1.40	1.00
Carbon flux equivalent	C-DOU (mmol C $m^{-2}d^{-1}$)	0.7 ± 0.2 (4)	0.7 ± 0.2 (2)	0.5 ± 0.3 (4)	0.6 ± 0.2 (10)	0.4 ± 0.1 (4)	2.3 ± 1.3 (6)	1.0 ± 0.5 (12)	0.9 ± 0.3 (15)	1.6 ± 0.4 (8)	1.1 ± 0.7 (8)	0.7 ± 0.2 (7)	0.4 ± 0.1 (8)	0.5 ± 0.3 (18)	0.9 ± 0.5 (8)
	C-TOU (mmol C $m^{-2}d^{-1}$)	0.7 ± 0.3 (2)	1.3 (1)	1.1 ± 0.1 (2)	0.8 ± 0.1 (4)	1.0 ± 0.2 (2)	3.9 ± 0.2 (3)	1.5 ± 0.5 (5)	1.0 ± 0.1 (4)	1.4 ± 0.2 (3)	0.8 ± 0.2 (5)	0.8 ± 0.2 (5)	1.1 ± 0.4 (5)	0.4 ± 0.2 (5)	1.0 ± 0.2 (3)

Table 4~~3~~. ANOSIM and SIMPER results of the meio- and macrofauna community within sea-ice categories. The table shows that there are differences in the macrofauna community between the highly sea-ice covered area (HSC) and the low sea-ice covered area (LSC)~~ area~~, while this is not the case for the meiofauna community. The most contributing taxa regarding the in-group similarity within the sea-ice categories and the dissimilarity between the sea-ice categories are given in Supplement Table 8.

		Meiofauna density		Macrofauna density		Macrofauna biomass	
ANOSIM	Global R	0.143		0.266		0.227	
	p-value	0.036		0.005		0.004	
SIMPER		HSC	LSC	HSC	LSC	HSC	LSC
		In−group similarity	In−group similarity	In−group similarity	In−group similarity	In−group similarity	In−group similarity
		66.0 %	72.5 %	35.4 %	56.1 %	27.4 %	32.0 %
		Dissimilarity between groups		Dissimilarity between groups		Dissimilarity between groups	
		32.1 %		55.9 %		75.3 %	