Community structure of macrofauna in the deep Fram Strait: A comparison between two bathymetric gradients in ice-covered and ice-free areas

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ABSTRACT

This study compares the macrofaunal communities along two bathymetric transects (1000 – 2500 m water depth) in predominantly ice-covered western (offshore Greenland) and generally ice-free eastern (offshore Svalbard) regions of the Fram Strait. Material was collected using an USNEL 0.25 m^2 box corer and all sediment samples were processed through a 500-μm sieve. A total of 1671 organisms from 169 species were found. Densities off Greenland were generally lower than those observed off Svalbard. On both sides of the Fram Strait, density, biomass and biodiversity generally decreased with increasing water depth. An exception was observed at the deepest station off Greenland (2500 m water depth), which was located within the Marginal Ice Zone. At this station, macrofaunal density was elevated (992 ± 281 ind. m^{-2}) compared to the adjacent shallower sampling areas off Greenland (272 ± 208 ind. m^{-2} to 787 ± 172 ind. m^{-2}) and the deeper stations (2000 and 2500 m water depth) off Svalbard (552 ± 155 ind. m^{-2} and 756 ± 182 ind. m^{-2}). The most abundant species along both transects was the polychaete *Galathowenia fragilis* (off Greenland: 288 ind. m^{-2}, off Svalbard: 740 ind. m^{-2}). Sea ice coverage and water depth, as well as the associated food availability at the seafloor, seem to be crucial factors driving the macrofaunal community patterns. A strong pelago-benthic coupling is observed to be typical in Arctic deep-sea ecosystems, and is also confirmed by our study.

1. Introduction

Arctic deep-sea ecosystems are characterized by low temperatures (Sverdrup et al., 1942; Gage and Tyler, 1991), high pressure, high oxygen saturation (Thistle, 2003) and frequently soft ooze seafloor sediments (Dietrich et al., 1975), as well as a seasonal light and sea ice regime given their high latitudes (Smith Jr and Sakshaug, 1990).

The occurrence, distribution, and thickness of sea ice are major factors influencing primary production across the Arctic Ocean (Wheeler et al., 1996), ultimately determining the light availability in the underlying water column (Arrigo et al., 2008), primary production in the upper waters and, therefore the quantity of particulate organic matter available for subsequent transport to the sea floor (Wohlers et al., 2009; Kortsch et al., 2012; Jones et al., 2014; Bourgeois et al., 2017). In areas of dense sea ice coverage such as the high Arctic,

primary production is comparably lower than at Arctic areas with less sea ice coverage (Wheeler et al., 1996). However, along Marginal Ice Zones (MIZs), where the sea ice covered region meets open water, primary production is far higher than further north (Smith Jr, 1987) due to stratification and nutrient enrichment within the euphotic zone during melting events (Sakshaug and Skjoldal, 1989).

At the deep seafloor the absence of light limits primary production to a few distinct locations, where microbial chemoautotrophic processes may occur, like at cold seeps and hydrothermal vents (Karl et al., 1980). For most areas of the World's oceans, benthic organisms rely on the particle input from the upper ecosystem compartments such as the water column and the sea ice in polar regions (Billett et al., 1983; McMahon et al., 2006; Soltwedel et al., 2018). Sea-ice algae blooms and degradation through the water column are major food sources for benthic communities in ice-covered areas (Boetius et al., 2013;

Fernández-Méndez et al., 2014). However, these inputs vary depending on season of the year, local depth and hydrographic characteristics (Renaud et al., 2008).

Benthic organisms of all sizes, including macrofauna, play important roles in biogeochemical processes at the sediment-water interface e.g., via bioturbation, ventilation and particle reworking, driving energy fluxes in the entire ecosystem, as detrivores, providing food sources for other animals and modifying the microtopography of the bottom (Hebbeln and Wefer, 1991; Romero-Wetzel and Gerlach, 1991; Graf, 1992; Huettel and Gust, 1992). As environmental conditions structure benthic communities, monitoring temporal and spatial changes in diversity, biomass and abundance of seafloor communities is of importance when attempting to understand these remote ecosystems, and to hypothesize their likely response to environmental changes.

Over the last decades, few studies have described depth-related changes in community structure of macrofauna in deep-sea sediments either off Svalbard (Wlodarska-Kowalczuk et al., 2004; Budaeva et al., 2008; Vedenin et al., 2016; Hoffmann et al., 2018) or off Greenland (Schnack, 1998; Brandt and Schnack, 1999; Seiler, 1999; Hoffmann et al., 2018). This study provides for the first time a comparison of macrofauna community structures on species level of Eastern Greenland deep seafloor communities with those found off Svalbard. Within this study the communities were compared along bathymetric transects, sampled at the same latitudes, from similar water depths, and within the same season and year. Based on studies of macrofaunal communities carried out in the same area (Hoffmann et al., 2018) as well as other ice-covered deep-sea areas such as the central Arctic Ocean (Kröncke, 1998; Kröncke et al., 2000) or offshore Greenland (Seiler, 1999), we assumed that macrofaunal abundance, biomass and diversity should be generally lower off Eastern Greenland than off Svalbard. Moreover, we expected that due to enhanced particle flux in the MIZ, macrofaunal communities should respond in some way to the increased food supply in these areas.

In this study we therefore aimed to test the following hypotheses: (1) The macrofaunal density, biomass and biodiversity of seafloor communities off Eastern Greenland and off Svalbard differs, both according bathymetrical gradient and between areas. (2) The specific environmental conditions in the Arctic Ocean, i.e., variations in ice coverage, the associated difference in primary production rates and flux rates of particulate organic matter to the seafloor, have a stronger influence on macrofauna community composition than bathymetric patterns.

2. Material and methods

2.1. Sampling design

Sampling was conducted during RV *Polarstern* expedition PS99.2 in the boreal summer of 2016 at the LTER (Long-Term Ecological Research) observatory HAUSGARTEN (Soltwedel et al., 2005) using an USNEL-type box corer (sample area of $0.25 \, m^2$). Samples were taken along an east-west transect at approx. 79°N in the Fram Strait at four stations off Eastern Greenland (EG-I to EG-IV), and four stations taken off Svalbard (HG-I to HG-IV) at comparable water depths, i.e. ~1000 – ~2500 m (Fig. 1, Table 1). While the deepest station off Eastern Greenland was situated in the Marginal Ice Zone (MIZ) (Krumpen, 2017), all shallower sampling sites off Eastern Greenland were permanently covered by sea ice transported to the South by the East Greenland Current (Manley, 1995; Perner et al., 2015). Because of the warm West Spitsbergen Current flowing in a northerly direction (Manley, 1995; von Appen et al., 2015), the stations off Svalbard are predominantly ice-free through much of the year (Bauerfeind et al., 2009).
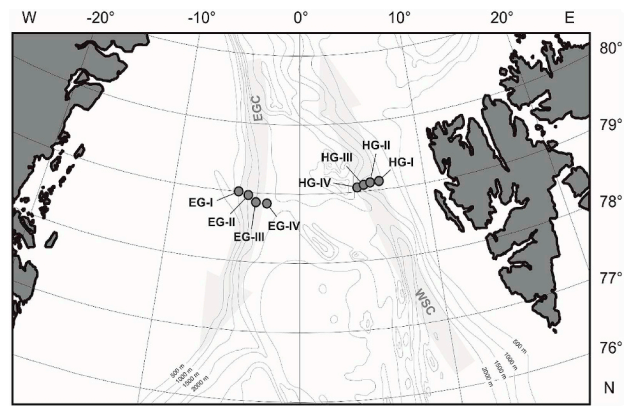

Fig. 1. Sampling area. Stations off Eastern Greenland (EG-I to EG-IV) and off Svalbard (HG-I to HG-IV) sampled during RV *Polarstern* expedition PS99.2 in 2016. West Spitsbergen Current (WSC) and East Greenland Current (EGC) highlighted in light grey.

Table 1
Sampled stations off Eastern Greenland and Svalbard during RV *Polarstern* expedition PS99.2.

Date	Station ID	Latitude	Longitude	Depth (m)
2016-07-02	EG-I	78.99 °N	5.43 °W	995
2016-07-01	EG-II	78.93 °N	4.64 °W	1548
2016-07-01	EG-III	78.85 °N	3.96 °W	1971
2016-06-30	EG-IV	78.82 °N	2.73 °W	2603
2016-07-10	HG-I	79.14 °N	6.08 °E	1282
2016-07-08	HG-II	79.14 °N	4.91 °E	1540
2016-07-11	HG-III	79.11 °N	4.60 °E	1887
2016-06-27	HG-IV	79.06 °N	4.18 °E	2462

2.2. Macrofauna sampling and sample processing

Sampling was restricted to one box corer deployment per station. As box corer subsampling owing to logistic constraints is a common approach in Arctic deep-sea research (see Kröncke, 1994), the sampled sediment from each box corer was divided into eight subsamples (pseudoreplicates) via foam core partition walls to allow to analyze distribution patterns on a small spatial scale. The uppermost 12 cm of these subsamples were analyzed to investigate the epibenthic and infaunal macrofauna. Each subsample of $3750 \, cm^3$ was processed through a 500-μm mesh size sieve. The particular area selected for the bathymetric transect off Svalbard, and the mesh size used for this study (500-μm) were chosen to complement and allow direct comparison with observations made from previous studies conducted in the same geographical region (Wlodarska-Kowalczuk et al., 2004; Budaeva et al., 2008; Vedenin et al., 2016). After sieving, residuals were fixed with 100% ethanol and stored at room temperature. Macrofaunal organisms were identified to the lowest possible taxonomical level, counted and extrapolated to an abundance estimation for 1 m²·Whenever identification to species level was not possible, the sample was identified to the next identifiable taxonomical category and assigned a putative species name (e.g., 'Hesionidae genus sp. 1', 'Hesionidae genus sp. 2'). Posterior fragments, exuviae, xenobionts, meiofauna taxa (Nematoda, Ostracoda, Harpacticoida) and empty tubes were excluded from the analysis.

Biomass (blotted wet weight, ww) was determined by weighing each specimen and subsequently extrapolating all values to an area of $1 \, m^2$. Shelled organisms, such as mollusks, were weight in their shells. As biomass loss due to storage in ethanol is well-characterized, species-specific corrections were applied to accurately determine the weight of each specimen following the recommendations of Brotskaya and

Zenkevich (1939). Biomass data determined for station EG-IV had to be treated with caution as some individuals of the sponge species *Hymedesmia nummulus*, *Lissodendoryx complicate*, and *Forcepia topsenti* observed at this station could not be quantified as they were attached to stones and were excluded from the biomass analysis.

2.3. Environmental data

Samples for grain size analyses were already collected during RV *Polarstern* expedition PS85 in June/July 2014. Given that sedimentation rates in the Arctic Ocean are generally low (Hebbeln and Wefer, 1991) we assume no major change in grain size between 2014 and 2016. Other background parameters (water content, ash free dry weight (AFDW), chloroplastic pigment equivalents (CPE), chlorophyll *a* (Chl *a*), particulate proteins (PP)) were obtained from samples taken during RV *Polarstern* expedition PS99.2 in 2016 in parallel to the macrofauna sampling. Sediment sampling for environmental parameters was conducted, using a multiple corer (MUC) (Barnett et al., 1984). Sub-sampling was restricted to the uppermost 5 cm of the sediment using plastic syringes with cut-off ends and an inner diameter of 1.2 cm (CPE and PP) and 2.0 cm (AFDW and grain size), respectively.

Grain sizes were analyzed with a particle size analyzer (Mastersizer, 2000G, hydro version 5.40, Malvern instruments, UK). Classification of the grain size was done via the Udden-Wentworth scale (Wentworth, 1922). To determine the sediment water content, samples were dried at 70 °C in a drying cabinet. Subsequently, the dried sediment samples were incinerated in a muffle furnace to determine their ash free dry weight (AFDW). Food availability at the seafloor surface was estimated via sediment-bound chloroplastic pigment equivalents (CPE), i.e., the bulk of pigments containing chlorophyll *a* (Chl *a*) and its degradation product (phaeopigments) (Thiel, 1978). Concentrations of intact Chl *a* indicate the "freshness" of the phytodetrital matter at the sediment surface (Fonseca and Soltwedel, 2007). Chloroplastic pigments were extracted with 90% acetone in a cell mill. Pigment concentrations were measured using a fluorometer (Yentsch and Menzel, 1963; Holm-Hansen et al., 1965). Particulate proteins (PP) were analyzed to estimate the total biomass (small organisms and detrital matter) in the sediments following the procedure of Greiser and Faubel (1988). The sodium salt Coomassie Brilliant Blue stain was used to tag the protein fragments (Sedmak and Grossberg, 1977).

Sea ice concentration (see National Snow and Ice Data Center, 2008) data for all stations were provided by the Centre for Satellite Exploitation and Research (CERSAT) of the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), France. An area of 10×10 km surrounding the stations was used to calculate sea ice concentration at each station for the period 2011 to 2016. To reflect overall conditions in a representative way, we calculated the average sea ice concentration over the last five years.
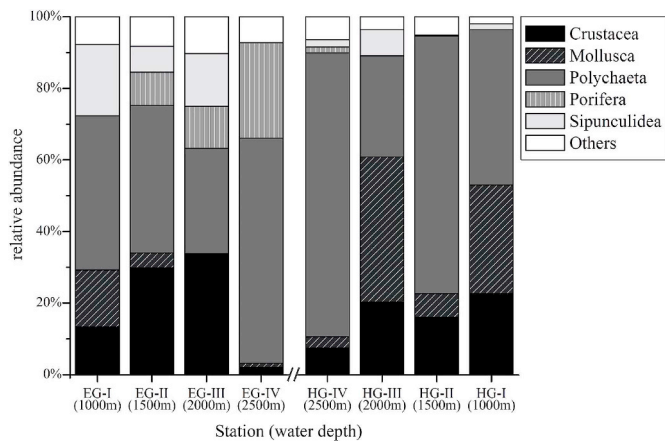
2.4. Statistical analysis

The Shannon index H'$_{(\log e)}$ (Shannon and Weaver, 1963), the Pielou evenness J' (Pielou, 1966) and the Hurlbert rarefaction ES$_{(n)}$ (Hurlbert, 1971) were determined for macrofaunal communities at each station. To describe the small scale aggregation the standardized Morisita dispersion index I$_p$ was used (Morisita, 1962; cf. Schroeder, 2005). Significantly aggregated occurrence of specimens are indicated by values > 0.5, whereas values < -0.5 can be interpreted as significantly even distributed (Krebs, 1999).

Multivariate analysis was carried out on fourth-root transformed abundance data to increase the influence of rare species and decrease the influence of highly dominant species on the results. Between-station similarities were calculated using the Bray-Curtis similarity index (Bray and Curtis, 1957). The resulting resemblance patterns of the macrofauna communities were visualized via non-metric multidimensional scaling (nMDS). An analysis of similarity (ANOSIM; Clarke, 1993) test was used to assess similarities between macrofaunal species composition and abundances off Eastern Greenland and Svalbard. Additionally, the Similarity Percentages routine (SIMPER; Clarke and Warwick, 1994) was implemented to calculate similarities within and between the different levels of the chosen factors and to differentiate which species explain these similarities. The relationships between multivariate community structure and abiotic variables were examined using the BEST BIO-ENV routine (Clarke and Warwick, 2001) to define suites of variables that best explain the community structure. Prior to multivariate analysis we checked all environmental variables for autocorrelation and excluded those parameters which showed such correlations (CPE and AFDW). After this, an exploratory BEST BIO-ENV routine was carried out to define which single variable and combination of variables "best explained" the benthic community structure. This exploratory test was followed by a second test with 9999 permutations to test for significant correlations. All multivariate statistical analyses were performed using the software PRIMER-v6 and v7 (Clarke and Gorley, 2006, 2015).

3. Results

3.1. Macrofaunal density and biomass

Integrating all stations, a total of 1671 organisms from 169 taxa were found. On average, lower macrofaunal densities were observed off Eastern Greenland (608 ± 208 ind. m^{-2}) than off Svalbard (1063 ± 247 ind. m^{-2}; Table 2). Along both transects macrofauna densities decreased with increasing water depth. However, at the deepest stations EG-IV and HG-IV at 2500 m depth, we observed higher densities than at EG-III and HG-III at 2000 m depth. The macrofaunal densities at the deepest station off Eastern Greenland (EG-IV: 992 ± 281 ind. m^{-2}) even exceeded those found at the shallowest station off Eastern Greenland (EG-I: 780 ± 172 ind. m^{-2}).

Table 2

Summary of the main community descriptors: number of individuals m^{-2} (N), total species richness per box corer (0.25 m^2; S), biomass in g wet weight m^{-2} (excluding *Mohnia mohni* at HG-IV), heterogeneity of the community structure H'$_{(\log e)}$, evenness J', number of species relative to the number of organisms ES$_{(50)}$ and dispersion of individuals I$_p$ for each station investigated during PS99.2.

	N		S	Biomass		H'$_{(\log e)}$	J'	ES$_{(50)}$	I$_p$
	ind. m^{-2}	SD		g ww m^{-2}	SD				
EG-I	780	± 172	55	1.62	± 0.06	3.37	0.84	26.14	0.07
EG-II	388	± 171	43	6.58	± 1.21	3.29	0.88	27.74	0.50
EG-III	272	± 208	29	4.21	± 0.78	2.84	0.84	23.52	0.52
EG-IV	992	± 281	39	2.63	± 0.46	2.82	0.77	18.14	0.50
HG-I	1448	± 405	62	12.09	± 1.08	3.43	0.83	24.87	0.50
HG-II	1496	± 245	71	5.68	± 0.91	3.40	0.80	24.48	0.10
HG-III	552	± 155	37	3.73	± 0.64	3.16	0.87	23.70	0.14
HG-IV	756	± 182	30	2.87	± 0.15	2.36	0.70	15.43	0.14

Fig. 2. Relative macrofaunal abundance among higher taxa. The group "others" comprise of the taxa Cnidaria, Echinoidea, Enteropneusta, Nemertea, Oligochaeta, Ophiuroidea, and Tunicata. Stations arranged following the longitudinal transect beginning with the westernmost sampling site offshore Eastern Greenland.

Macrofaunal biomass also tended to progressively decrease with increasing depth along both transects, except for EG-I at 1000 m depth, where the lowest biomass values (1.62 g ww m^{-2}) across all eight stations was observed (Table 2). When excluding one single observation of the large gastropod *Mohnia mohni* macrofaunal biomass off Svalbard was lowest at HG-IV (biomass HG-IV including *M. mohni*: 4.07 ± 0.42 g ww m^{-2}, biomass HG-IV excluding *M. mohni*: 2.87 ± 0.15 g ww m^{-2}).

3.2. Macrofaunal community composition and diversity

In the overall study, a total of 169 species were identified belonging to 81 families and 128 genera. The most abundant taxa off Eastern Greenland was *Galathowenia fragilis* (family Owenidae, class Polychaeta), with an abundance of 288 ind. m^{-2} and comprising 12% of the total EG samples. The distribution pattern of macrofaunal species off Eastern Greenland changed with increasing water depth (Fig. 2). The sipunculid *Nephasoma (Nephasoma) diaphanes* was most abundant at EG-I (17%). The crustacean *Diastylis polaris* dominated at EG-II (16%) and at EG-III (24%). However, at EG-IV the polychaete species *Chaetozone* sp. as well as *G. fragilis* (both 17%) were the most dominant taxa.

Along the off Svalbard transect, the species *G. fragilis* was most abundant comprising 17% of the total HG samples (740 ind. m^{-2}). Bivalves were the most dominant species at stations HG-I and HG-III, where *Thyasira* sp. comprised 13% of the total macrofaunal abundance at HG-I and *Yoldiella annenkoave* comprised 17% at station HG-III. The polychaete *Aricidea abranchiata* and *G. fragilis* were the most abundant species at stations HG-II (each representing 14% of the abundance) and HG-IV (each representing 34%).

Heterogeneity of the macrofaunal community H'$_{(log\ e)}$ decreased along the bathymetric transects off Svalbard and Eastern Greenland. In contrast, evenness J' was highest at EG-II (1500 m) and HG-III (2000 m) but lowest at the deepest station on each transect (EG-IV and HG-IV, respectively). H'$_{(log\ e)}$ was generally higher off Svalbard than off Eastern Greenland, whereas ES$_{(50)}$ was lower at the communities off Svalbard compared to communities off Eastern Greenland. The standardized Morisita dispersion index (I$_p$) indicated a random spatial distribution pattern of macrofaunal organisms at the stations EG-I, HG-II, HG-III and HG-IV, while at all other stations the distribution was aggregated (Table 2).

The results of the nMDS (Fig. 3) showed that the communities off Eastern Greenland and Svalbard appear to be clearly different in their species compositions. Furthermore, a distinct depth separation within the two transects was observed. The one-way ANOSIM demonstrated
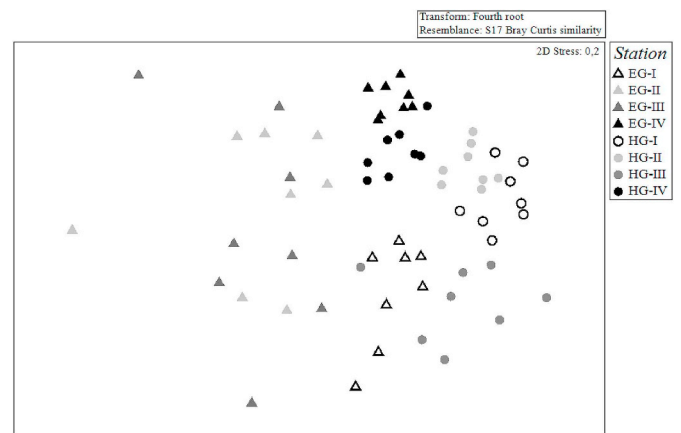
Fig. 3. Non-metric multidimensional scaling plot (nMDS) of the community structure of each station. The grey scale is following the bathymetric transect by withe being the shallowest stations (1000 m) and darkest the deepest (2500 m).

the apparent difference between transects to be statistically significant (Global R = 0.298, *p* < 0.001, 9999 permutations). Within the community off Eastern Greenland the separation between the depth groups was significant except for the stations of intermediate depth (ANOSIM pairwise R = 0.126, *p* = 0.063, 9999 permutations, Table S1). The community off Svalbard showed a separation between all stations (all ANOSIM pairwise R > 0.8, *p* < 0.001, Table S1). Further details on the results of the pairwise ANOSIM are provided in Table S1 of the supplementary material.

Results of the SIMPER routine showed an average dissimilarity of 82.6% between the macrofaunal communities off Eastern Greenland and Svalbard. In total five taxa contributed to the > 50% difference between transects (polychaetes: 31%, mollusks: 7%, crustaceans: 6%, poriferans: 4% and sipunculids: 3%). Within group average similarity was 19% off Eastern Greenland and 30% off Svalbard.

3.3. Environmental parameters

Median grain sizes at the stations off Eastern Greenland decreased with increasing water depth and ranged from fine silt (EG-I) to very fine sand (EG-IV) (Table 3). A similar trend was found for the stations along the bathymetric transect off Svalbard. However, along this transect all sediments were characterized as medium silt. The water content of the sediments was generally higher at stations off Svalbard compared to those at stations off Eastern Greenland (Table 3). There were minor differences between total organic matter content (AFDW) of the sediments along the two transects, but a tendency for higher values off Svalbard was observed (Table 3).

Sediment-bound chloroplast pigment equivalents (CPE) generally decreased with water depth at HG stations (122.14 ± 5.70 to 66.86 ± 12.60 μg/ml), whereas as for EG, the three stations EG-I to EG-III had similar values (21.13 ± 1.50 to 23.85 ± 6.50 μg/ml). Station EG-IV, however, exhibited the highest pigment concentrations off Eastern Greenland (45.48 ± 11.30 μg/ml), exceeding those at the shallower stations of this transect. Across both transects Chl *a* showed no clear bathymetric pattern in concentration. In general, pigment concentrations off Svalbard were two to six times higher than observed at the stations located off Eastern Greenland (Table 3). Furthermore, Chl *a* was up to eight times higher off Svalbard compared to sediments off Eastern Greenland. An exception was found at the deepest stations of the two transects, where the Chl *a* content was similar (Table 3). Benthic biomass, as indicated by the concentrations of sediment-bound particulate proteins (PP), also showed no clear bathymetric pattern. When comparing both transects overall, PP concentrations off Svalbard were almost twice as high as those measured off Eastern Greenland (Table 3).

Table 3
Environmental parameters (means ± SD): median grain size, Water content, AFWD: ash-free dry weight, CPE: chloroplastic pigment equivalents, Chl *a*: chlorophyll *a* and PP: particulate proteins.

	Median grain size μm	Water content %		AFDW mg/ml		CPE μg/ml		Chl *a* μg/ml		PP mg/ml	
EG-I	13.4 ± 1.2[a]	54	± 2	0.42	± 0.06	23.85	± 6.50	3.47	± 1.10	1.12	± 0.07
EG-II	15.1 ± 1.7[a]	46	± 1	0.48	± 0.05	21.13	± 1.50	2.23	± 1.30	0.78	± 0.06
EG-III	20.3 ± 3.9[a]	43	± 1	0.50	± 0.03	21.27	± 2.40	2.62	± 0.20	0.96	± 0.01
EG-IV	88.0 ± 47.7	43	± 1	0.49	± 0.03	45.48	± 11.30	6.70	± 1.40	1.33	± 0.07
HG-I	17.4 ± 1.2	66	± 1	0.58	± 0.05	122.14	± 5.70	16.81	± 0.40	2.94	± 0.14
HG-II	17.8 ± 2.9	62	± 2	0.63	± 0.07	96.48	± 13.00	14.52	± 1.60	3.19	± 0.23
HG-III	22.9 ± 1.9	52	± 3	0.50	± 0.04	90.47	± 15.60	16.10	± 6.70	2.45	± 0.26
HG-IV	26.3 ± 4.8	51	± 1	0.51	± 0.04	66.86	± 12.60	8.36	± 0.70	1.98	± 0.08

[a] cf. Hoffmann et al. (2018).
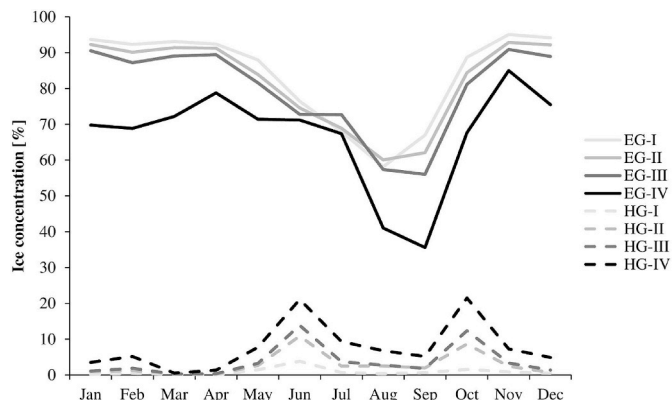
Fig. 4. Monthly sea ice concentration (%) at the sampled stations averaged over the years 2011 – 2016. Concentrations of stations located off Eastern Greenland are depicted in solid lines, stations off Svalbard in dotted lines.

Sea ice concentrations clearly differed off Eastern Greenland and off Svalbard. Sea ice concentration off Eastern Greenland ranged between 70 and 90% for most of the year, whereas sea ice concentration was generally well below 20% off Svalbard (Fig. 4). Station EG-IV in the MIZ off Eastern Greenland exhibited the lowest ice concentration off Eastern Greenland. The averaged minimum sea ice concentration of 36% occurred in the month September. Off Svalbard, ice concentrations were lowest at HG-I and highest at HG-IV, i.e., the average ice coverage increased with increasing distance from the coastline off Svalbard.

The explanatory BEST routine indicated that the top ten combinations of environmental variables explained between 61% and 68% of the macrofaunal variability (Table 4). A second BEST routine with 9999 permutations identified this correlation to be significant ($p = 0.013$). Water content, as single variable, was in the analysis indicated as the "best explanatory" variable in the analysis (Spearman correlation Rho = 0.453; $p = 0.011$). Water content in combination with grain size, Chl *a*, sea ice cover, and water depth were defined as the "best explanatory" combination of all variables included in this analysis (Spearman rank correlation Rho = 0.679; $p = 0.013$).

4. Discussion

Our study revealed a general trend of decreasing macrofaunal densities and biomasses with increasing water depth off Eastern Greenland and off Svalbard. Furthermore, macrofaunal densities at the deepest site off Eastern Greenland from this study were high in comparison to a similar study by Kröncke (1994). The general trend of decreasing densities and biomass with increasing depth agrees with patterns previously observed in non-Arctic regions (e.g. Rex et al., 2006) and Arctic deep-sea regions across similar depth ranges (Kröncke, 1994; Schnack, 1998; Deubel, 2000; Hoffmann et al., 2018; Vedenin et al., 2018), including cold seeps (Åström et al., 2018), and the Chukchi slope in the Canadian Arctic (MacDonald et al., 2010; Degen et al., 2015). The significance of depth gradients on benthic biomass can be attributed to the generally decreasing food/energy availability with increasing water depth, which was reflected in lower CPE and PP values observed at greater depths in our study. At greater water depths, particles spend a longer duration in the water column before reaching the seafloor and benthic communities, when compared to particles reaching the seafloor on shallower depths (Stein and MacDonald, 2004). Due to this increased residence time of particulate organic matter in the water column, these particles are more likely to be consumed and degraded by pelagic organisms before reaching the seafloor, reducing the quantity and quality (freshness) of this potential benthic food source (Stein and MacDonald, 2004).

Our results showed marked community differences between the heavily ice-covered sampling area off Eastern Greenland and the mainly ice-free area off Svalbard. Considering that the BEST BIO-ENV routine displayed that ice concentration was one of the explanatory values with most influence on the macrofaunal density and biomass in our study area, the regional differences in macrofauna densities and biomasses with generally higher values in eastern parts of the Fram Strait can be explained by the contrasting sea ice regimes found at each transect site (e.g. Degen et al., 2015; Gutt et al., 2016). The three shallower stations off Eastern Greenland (EG-I, EG-II, EG-III) are characterized by permanent sea-ice cover, resulting in reduced primary production and, subsequently, reduced input of organic matter to the sea floor. This low production was reflected by comparatively low CPE and PP concentrations in surface sediments. In contrast, in the mostly ice-free region off Svalbard, overall higher pigment and protein concentrations in

Table 4
Results of the BEST routine (BIO-ENV, 9999 permutations, $p = 0.013$) showing the five combinations of environmental parameters best explaining the community structure.

Number of variables	Spearman rank correlation	Explanatory environmental parameters
5	0.679	Grain size, water content, Chl *a*, ice concentration, depth
4	0.658	Grain size, Chl *a*, PP, depth
4	0.642	Grain size, water content, Chl *a*, ice concentration
4	0.640	Grain size, water content, Chl *a*, depth
5	0.637	Grain size, Chl *a*, PP, ice concentration, depth

the sediments off Svalbard indicated a generally higher primary production and particulate organic matter sedimentation. This strong pelago-benthic coupling resulting in different macrobenthic communities in the deep Fram Strait is distinctive in the area of the LTER observatory HAUSGARTEN (Hoffmann et al., 2018).

Exhibiting a comparably high macrofaunal standing stock, the station EG-IV off Eastern Greenland indicated that the macrofaunal community differed from the general depth and regional patterns. The relatively high macrofauna density at EG-IV can be explained by its location in the transition zone between permanently ice-covered and ice-free areas off Eastern Greenland, the Marginal Ice Zone (MIZ). These areas are known as productive zones with subsequently enhanced particle flux from surface production to the sea floor (Heimdal, 1983). Ice algae produced in the MIZ are probably the most important food source for local benthic communities (McMahon et al., 2006). Even though this food source occurs only for a limited time period (Michel et al., 1996), it can still result in locally increased faunal abundance, diversity and biomass (Piepenburg, 2005; Boetius et al., 2013). Still, although macrofaunal densities at EG-IV were comparably high, biomass values determined for this station were lower than observed at the adjacent EG stations. While benthos at EG-IV appears to receive higher quantity of food (Table 3), this material has a long residence time in the water column, which might lead to lower quality of food for benthos (Stein and MacDonald, 2004). This low food quality could cause smaller body size and explain the high abundance but low biomass at EG-IV. Our assumption on food quality can be partly supported by the study of Zhang and Wirtz (2017) which observed food quality to be more important to explain benthic characteristics than food quantity. However, to further prove our assumption of benthic biomass to be lower due to poorer food quality, we would need more detailed data on food quality, which is unavailable at the time. Additionally, sponges generally represent a large proportion of benthic biomass in polar regions (Gerdes et al., 1992; Barthel and Tendal, 1993). Biomass of sponges attached to stones was unaccounted for, and this could further contribute to the high abundance, but low biomass found at EG-IV.

Density, biomass and macrofaunal diversity showed a decreasing tendency with increasing water depth along both transects. Furthermore, we also found significant differences between the two transects (one-way ANOSIM, $p < 0.001$), with higher species richness and diversity off Svalbard, and higher evenness off Eastern Greenland. Despite these differences, polychaetes, mollusks and crustaceans represented the dominant taxa at most stations along both transects, a pattern which has been described as typical for Arctic macrofauna communities (e.g. Vedenin et al., 2016; Mäkelä et al., 2017; Åström et al., 2018), primarily those inhabiting soft sediments (Piepenburg, 2005). Nonetheless, we found no endemic species within any of the station transects. It is assumed that Arctic deep-sea fauna is a rather youngcommunity, as the glaciation in the Pleistocene led to local extinction of many species or even all of them (Clarke, 2003). Arctic deep basins have been relatively recently recolonized by the deep-sea benthos (Dahl et al., 1976) and boreal-Arctic species are therefore common in the Arctic (Piepenburg, 2005).

Based on the ANOSIM results we distinguished three depth groups of macrofauna off Eastern Greenland and four depth groups off Svalbard. This depth-related decline in macrofaunal diversity is similar to that described in the Canadian Basin (MacDonald et al., 2010). While the pattern found off Eastern Greenland agrees with results obtained in a recent Arctic study (Vedenin et al., 2018), we could further divide the "1991–3054 m" cluster (sensu Vedenin et al., 2018) off Svalbard into two separate groups at 2000 and 2500 m water depth. Species evenness J′ of the present study corresponds as expected with values found at the Svyatogor Ridge in the Fram Strait (Åström et al., 2018). The Fram Strait and other polar deep-sea regions are proposed to have a vast occurrence of singletons and doubletons (Schwabe et al., 2007; Brandt

et al., 2015; Ghiglione et al., 2017), which could explain the relatively high evenness J′ (Åström et al., 2018) which was also found in this study.

Diversity itself is a rather complex community descriptor and has been discussed in various concepts for deep-sea community analysis (e.g. Sanders, 1968; Dayton and Hessler, 1972). In accordance with the diversity-productivity theory which indicates the relationship between water depth and diversity (Rex and Etter, 2010), we assume decreasing diversity with increasing depth is directly related to reduced food supply. Therefore, only certain taxa which can make more efficient use of lower food quality and quantity can be found at the deeper stations. We further assume that the spatial heterogeneity in community patterns found off Eastern Greenland and off Svalbard is related to a patchy food supply, which is characteristic for deep sea benthic communities (Grassle, 1989). These assumptions could explain the higher species richness and diversity found along the almost year-round ice-free stations off Svalbard, where the food supply is hypothesized to be less variable throughout the year compared to off Eastern Greenland with highly variable sea ice coverage. This variability is also reflected in the less aggregated communities found off Svalbard (see standardized Morisita dispersion index I_p). Contrastingly, the poorer food supply related to heavy sea ice conditions, could explain the highly aggregated fauna distribution patterns observed for most stations off Eastern Greenland, which matches the increased occurrence of sessile sponges along this transect, and could thus demonstrate the role sponges have as providers of substrate to other benthic organisms, thus increasing aggregation. Matts of sponge spicules are known to work as sediment traps and to provide habitat for other benthic species in deep-sea habitats (Barthel and Tendal, 1993) and polar habitats (Barthel, 1992; McClintock et al., 2005). Furthermore, particularities in food supply may also explain the rather high species richness found at station EG-IV. This site is located in the MIZ off Eastern Greenland, where production of sea-ice algae is enhanced during the ice thinning in Arctic spring followed by blooming of phytoplankton and subsequently increased organic matter/energy flux to the seafloor (Engelsen et al., 2002; Wassmann and Reigstad, 2011). The seasonal elevated quantity and quality of food is hypothesized to be sufficient to support more species than the shallower, permanently ice-covered EG stations.

To summarize, this study presents a unique data set for the Arctic deep-sea, as the macrofaunal data from two fundamentally contrasting Arctic marine regions were collected in the same season and year, from comparable water depths across bathymetric transects. A direct comparison of the selected transects was therefore possible without any of the temporal concerns posed when comparing data collected from differing years or seasons.

Based on our data set we observed and thereby confirmed our first hypothesis, that generally lower macrofaunal densities and biomasses of benthic deep sea macrofauna communities are found in ice-covered areas. A change in community composition along a bathymetrical gradient was observed in both, ice-covered and ice-free areas of the Fram Strait. We could confirm also our second hypothesis, finding that independent from the station depth, macrofaunal communities situated in MIZs can exhibit deviations from the general trend of decreasing density, biomass and biodiversity values with increasing depth. An increased regional primary production (e.g. as reflected in the MIZ) and subsequently increased food availability to the benthic communities can lead to local deviations in common community-depth relationships.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2019.103102.

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