



Megabenthic standing stocks and organic carbon demand in a warming Arctic

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ABSTRACT

Benthic megafauna (organisms large enough to be visible on seabed photographs) are regarded as important for carbon cycling in benthic habitats. They are a food source for many predators like fish and marine mammals and may stimulate carbon mineralization in sediment by bioturbation. However, few studies address these basic characteristics of megabenthos quantitatively. This study quantifies the spatial variability in standing stock (biomass) and functioning (secondary production, respiration and carbon demand) of benthic megafauna in fjords and on the continental shelf of Svalbard. Organisms were measured from sea bottom images to assess their biomass using length-weight relationships and volumetric methods, then respiration and production were estimated with empirical artificial neural network models. Significantly higher standing stock, secondary production, respiration, and carbon demand were found in fjords categorized as 'cold' (as defined by water temperature, prevailing water masses and ice-cover) than in the 'warm' ones. Cold fjords were dominated by Echinodermata, while in warm fjords Crustacea prevailed. All megafaunal community parameters were negatively correlated with bottom temperature. It was not possible to assess specific direct impacts of temperature, and indirect effects may be more relevant to our findings. These include temperature-driven changes in primary production, ice cover and ice-algae production or predation pressure from carnivores expanding their ranges northward. The progression of climate warming may affect megafaunal communities by reducing their biomass, production, and carbon demand and have profound effects on ecosystem functioning.

1. Introduction

Benthic communities in the Arctic are influenced by various environmental factors, which control spatial and temporal variability in species composition, biodiversity, and standing stocks. Among them, the most important are primary productivity, quality and quantity of food available on the seabed (usually controlled by depth and/or terrestrial inputs), substrate type, currents and water masses distribution, natural disturbances associated with glacial mineral sedimentation or river discharge, and iceberg bottom scouring (Bluhm et al., 2009; Kuklinski et al., 2006; Meyer et al., 2015; Morata et al., 2008; Roy et al., 2015, 2014; Włodarska-Kowalczyk et al., 2005). Importance of these factors

may differ depending on the investigated region (i.e. Mackenzie Shelf of the Beaufort Sea influenced mostly by Mackenzie River, or Barents Sea influenced by warm Atlantic water from south and Arctic water masses from north) and spatial scale of the study (Jørgensen et al., 2015; Roy et al., 2015, 2014). In addition, over the last few decades, the Arctic ecosystem has been influenced by climate change, more severely than other regions of the world. The Arctic is facing increasing temperatures, sea-ice loss, glacial retreat, and increased human activity (ACIA, 2005; IPCC, 2013). These stressors impact all groups of organisms, both terrestrial and marine. Simultaneously, biotic changes like changes in phenology, growth rates, or range extensions are affecting the functioning of the whole Arctic ecosystem (Wassmann et al., 2011). The

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number of new species spreading into the Arctic is increasing, and many of them could potentially outcompete local species or prey on them, significantly influencing food webs (CAFF, 2017; Jørgensen et al., 2019; Renaud et al., 2012). Despite increasing knowledge regarding recent changes in the Arctic ecosystem, there are still key ecosystem components that are understudied in this context.

Benthic megafauna can be operationally defined as organisms large enough to be visible on seabed photographs (usually exceeding 1 cm diameter) and to be caught by bottom trawls (Gage and Tyler, 1992; Grassle et al., 1975). They are regarded as important actors in the functioning of benthic habitats, especially in those with low food supply such as polar seas or deep-sea ecosystems, due to their substantial role in carbon cycling processes (Piepenburg and Schmid, 1997). Despite their relatively large sizes, they occupy a range of trophic positions, acting both as primary consumers (in some locations occurring in great numbers) and predators (Bergmann et al., 2009; Sswat et al., 2015). Many epifaunal organisms serve as food for upper trophic level predators like fish, birds, and marine mammals, linking benthic and pelagic food webs (Bluhm and Gradinger, 2008; Sakshaug et al., 2009). This relation may be very tight, species like walrus or sea ducks rely on dens aggregations of prey (e.g., hotspots of benthic biomass at Chukchi Sea) and utilize them for effective foraging during crucial stages of their life cycle (Grebmeier et al., 2015; Moore and Kuletz, 2019). Moreover, megafaunal organisms may significantly enhance ecological functioning of the ecosystem indirectly (Morris et al., 2016). By burrowing into sediments and creating pits or tracks, motile organisms like echinoderms, bivalves, and demersal fish increase heterogeneity of the environment, modify biogeochemical processes in the sediment–water boundary, and stimulate microbial metabolism (Norkko et al., 2013). Habitat-forming organisms like sponges, corals, and bryozoans build three-dimensional structures that may provide shelter or substrate for settlement for other organisms (Buhl-Mortensen and Mortensen, 2005; Kaiser et al., 1998). Arctic megafauna seem to be relatively well-studied in terms of taxonomic composition and biodiversity (CAFF, 2017). Yet, much of the data come from trawl surveys that do not allow exact quantitative comparisons (e.g., Jørgensen et al., 2015), since precise dredging area cannot be assessed (without additional gear like depth-finding sonar) and due to catch selectivity and low efficiency for some species (Eleftheriou, 2013; Reiss et al., 2006). Therefore data on standing stock or functioning of megafauna are rarely provided.

The world ocean is regarded as a carbon sink and a very important regulator of CO₂ concentrations in the atmosphere (IPCC, 2013). The process of organic carbon burial in ocean sediments allows for the sequestration of carbon and its exclusion from the global cycle. Some areas are regarded as hotspots of organic carbon burial e.g., shallow vegetated habitats, river deltas, and recently also fjords (Kennedy et al., 2010; Smith et al., 2015; Włodarska-Kowalczyk et al., 2019). Organic carbon may be supplied to the ocean from land, e.g., by river discharge, or may be produced from dissolved CO₂ by marine autotrophic organisms. Part of this organic carbon is consumed and mineralized through pelagic food webs, while the remaining organic material reaches the seafloor, supplying food for benthic fauna. Large benthic invertebrates play a special role in carbon remineralization, as they both consume organic matter and stimulate microbial communities through burrowing activity (Norkko et al., 2013). These processes depend on various environmental factors such as temperature, rates of primary production in the water column, quality of the organic matter, and biological parameters such as species composition and faunal community size structure (Grebmeier et al., 1989; Norkko et al., 2013; Włodarska-Kowalczyk et al., 2019). Partitioning of carbon consumption among size-fractions of the benthic community (i.e., meiofauna, macrofauna, etc.) may vary depending on environmental settings (Piepenburg et al., 1995). Available assessments attribute dominating role in total benthic carbon demand to infaunal organisms (mostly macrofauna), due to their high metabolic rates, also meiofauna and macrofauna has been studied more extensively than larger organisms. However in favourable

conditions the role of megafauna may be of great importance. The share of benthic megafauna in total benthic carbon demand varies across seabed habitats, being very small in deep-sea communities (2–3%) and substantial in shallow waters (up to 41%) (Piepenburg et al., 1995; Renaud et al., 2007a).

In this study, we focus on megafaunal communities in coastal waters off Svalbard, an archipelago located at the interface of Arctic and Atlantic water masses (Piechura and Walczowski, 2009; Walczowski and Piechura, 2006). We aim to quantify the spatial variability in standing stock (biomass) and functioning (secondary production, respiration and carbon demand) of benthic megafauna based on sea-bottom images from fjords and the continental shelf. Megafaunal standing stock and carbon consumption of the community have rarely been documented in Arctic seas. In this study, a set of environmental parameters (bottom water temperature, salinity and turbidity) is used to assess the impact of environmental features on the functioning of fauna and give clues about possible future changes due to climate change. This study was performed across locations differing in hydrographic conditions, i.e. classified as ‘cold’ (influenced by Arctic water masses and/or winter-cooled waters and with significant ice cover (Hop et al., 2019; Skogseth et al., 2020)) or ‘warm’ (more affected by Atlantic waters). In the Barents Sea, high megafauna biomass and secondary production were more common in Arctic water-influenced northern parts, contrary to warmer, Atlantic-influenced southern regions (Degen et al., 2016; Jørgensen et al., 2015). Therefore, we hypothesized that megafaunal standing stocks and carbon consumption in Svalbard coastal waters would be higher at ‘cold’ sites. By comparing estimated carbon consumption to that of other benthic size-fractions (as reported in the literature), we aim to evaluate the present and future role of megafauna in carbon cycling in the Arctic. The estimates of megafaunal carbon consumption fill an important knowledge gap that is critical for both regional (Arctic) and global carbon budget assessments (Ambrose et al., 2001; Sumida et al., 2014).

2. Materials and methods

2.1. Sampling and image analyses

Seafloor photographs were collected at 11 stations in five Svalbard fjords and on the continental shelf north of Svalbard, representing a depth range from 33 to 350 m (Fig. 1, Table 1). All stations had fine, homogenous sediments except station 7, where numerous large stones were recorded. The images were collected from the R/V *Helmer Hanssen* in September 2011 using a downward-facing digital drop camera (as described by Sweetman and Chapman (2011)). Along with the images, water temperature, salinity, and turbidity were recorded with a Seabird SBE9/11 + CTD equipped with turbidity sensor (Seapoint).

Images were analysed according to the methodology of Meyer et al. (2015). Fifteen images from each station were analysed. Images that were too dark, too turbid or were recorded at an anomalous altitude were considered ineligible and excluded from the analysis. Organisms that were clearly visible were enumerated and their body features were measured with ImageJ (National Institutes of Health, USA). Two parallel laser points, (spaced 26 cm apart, lasers were a part of the camera system) were used as a size scale. Each image was divided into a grid using the ImageJ grid tool. The grids were imposed and centred on each image (Fig. 2). Each grid represented 0.1 m². Only organisms from complete grid cells were analysed.

2.2. Assessment of organism biomass, production, respiration and carbon demand

The biomass of organisms was assessed according to published length-mass relationships (Berestovsky et al., 1989; Durden et al., 2016; Fey and Węśławski, 2017; Gundersen and Brodie, 1999; Orlov and Binohlan, 2009; Piepenburg, 2000). For taxa with no published size-mass relationship, the relationship for the most similar

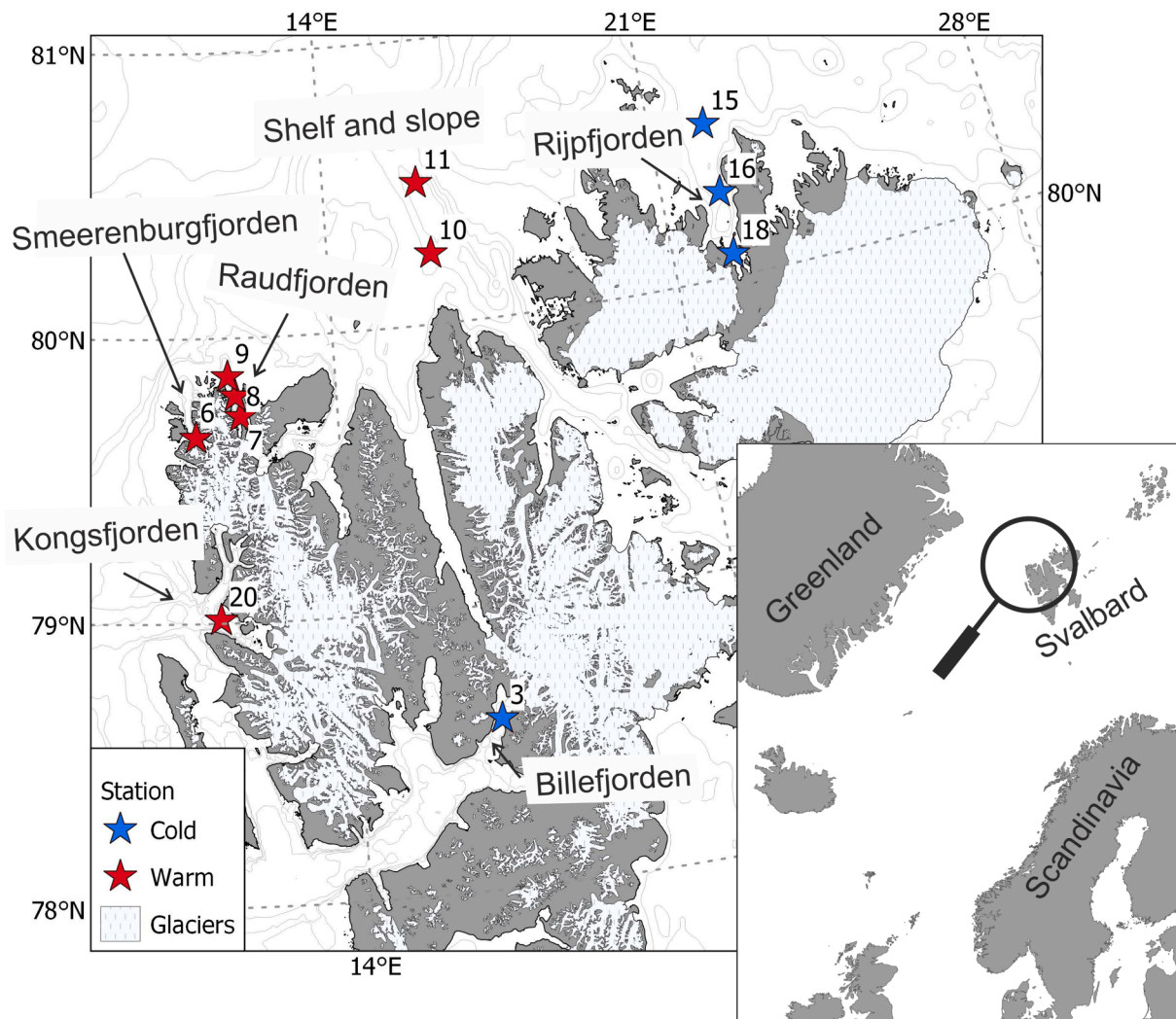


Fig. 1. Map of seafloor photography stations in Svalbard coastal waters.

(morphologically and taxonomically) taxon was applied. If no reasonable relationship could be found and matched, a volumetric approach was used: 1) biovolume of an organism was calculated using the formula for the volume of a sphere or cylinder (Hillebrand et al., 1999), 2) wet mass was calculated using the density factor 1.13 (Andrassy, 1956). Conversions from wet mass to shell free wet mass (in the case of bivalves and gastropods), wet to dry mass and from dry mass to energy content [J] and carbon content [g C_{org}] were performed using conversion factors obtained from Brey et al. (2010) for each taxon, using the lowest possible taxonomic level. In the case of ophiuroids with discs buried under sediments, their individual biomass was assigned as the mean biomass of all measurable ophiuroids in the image.

Biomass was not assessed for colonial and hard-bottom fauna (sponges, bryozoans, hydrozoans and ascidians) due to a lack of reliable methodology for calculating biovolume or biomass of these organisms from image measurements.

The ratio of annual secondary production to biomass (P/B) and respiration rates [J/J/d] for invertebrates were assessed using multi-parameter Artificial Neural Networks (ANN) models (Brey, 2012, 2010). For secondary production, the *BenthicPro* software package (Brey, 2012) was used, while respiration was calculated using an MS Excel macro sheet (Brey, 2010).

Prior to the calculations, a literature search was performed to assess appropriate model input parameters for every taxon including e.g., its feeding type or mobility. Both ANN models require mean annual

temperature, sampling depth, and annual mean body mass [J] of analysed taxa as inputs. As outputs, the models provide P/B and daily respiration ratios. The annual production of each taxon in each image was assessed by multiplying P/B by the total biomass of each taxon in each image. Annual respiration of each taxon was calculated by multiplying the daily respiration rate by 365 and by the total biomass of each taxon in each image.

The P/B and respiration rates [mg O₂ h⁻¹] for vertebrates - fish (Actinopterygii) - were obtained from literature (Ciannelli et al., 2004; Dupont-Prinet et al., 2013; Holeton, 1974; Raskhozheva and Karamushko, 2018; Zeller and Reinert, 2004). Annual respiration was calculated and converted to mg C_{org} by multiplying by 0.309 (Brey, 2010).

Annual carbon demand CD [g C_{org} m⁻² y⁻¹] was estimated according to Klages et al. (2004): $CD = (P + R)/0.608$, where P is annual secondary production, R is annual respiration and 0.608 is the ration between carbon assimilation and carbon demand.

2.3. Statistical analyses

Data analyses were performed in the R 4.0.2 computing environment (R Core Team, 2021). Averages of bottom temperature, salinity, and turbidity were calculated from data over the bottom 10 m of the water column. Based on the bottom water temperature (Table 1), study sites were divided into two groups: 1) cold (temperature lower than 0.5 °C) -

Table 1
Longitude [°E], latitude [°N], total analyzed seafloor area [m²], area per image [m²], depth [m], bottom temperature [°C], turbidity [FTU], salinity, total biomass [g C_{org} m⁻²], secondary production, respiration, and carbon demand [g C_{org} m⁻² y⁻¹] for each station. All ranges represent mean ± SD.

Location	Station	Longitude	Latitude	Total area	Area per image	Depth	Temperature	Turbidity	Salinity	Biomass	Secondary production	Respiration	Carbon demand
Billefjorden Rijpfjorden	3	16.513	78.600	40.6	2.71 ± 0.03	159	-1.83	0.434	34.62	1.52 ± 0.97	0.62 ± 0.40	2.07 ± 1.03	4.43 ± 2.32
	15	22.157	80.547	35.9	2.39 ± 0.03	241	0.50	0.438	34.71	1.28 ± 1.91	0.24 ± 0.14	1.31 ± 1.12	2.54 ± 2.05
	16	22.201	80.300	34.2	2.28 ± 0.32	245	-1.60	0.294	34.65	3.14 ± 2.31	0.92 ± 0.69	3.20 ± 2.30	6.77 ± 4.84
Kongsfjorden Smeerenburgfjorden	18	22.212	80.080	37.6	2.51 ± 0.27	170	-1.80	0.353	34.65	2.64 ± 2.03	0.84 ± 0.21	3.02 ± 0.91	6.34 ± 1.75
	20	11.627	79.012	12.8	0.85 ± 0.19	250	2.07	0.351	34.88	1.85 ± 0.97	0.50 ± 0.29	1.73 ± 0.86	3.67 ± 1.87
Raudfjorden	6	11.239	79.652	45.3	3.02 ± 0.39	146	2.55	0.822	34.68	1.55 ± 1.48	0.30 ± 0.29	1.50 ± 2.20	2.97 ± 4.08
	7	12.109	79.724	51.5	3.43 ± 0.45	78	4.50	1.745	33.72	0.90 ± 1.91	0.34 ± 0.75	0.83 ± 1.59	1.93 ± 3.80
shelf and slope	8	12.023	79.796	38.4	2.56 ± 0.20	190	2.95	0.798	34.45	2.30 ± 0.68	0.65 ± 0.22	2.80 ± 1.70	5.67 ± 3.10
	9	11.880	79.865	32.4	2.16 ± 0.50	166	4.22	0.692	33.90	0.15 ± 0.27	0.03 ± 0.04	0.12 ± 0.14	0.25 ± 0.29
	10	16.135	80.249	37.4	2.49 ± 0.19	286	3.96	0.169	35.05	0.73 ± 0.42	0.22 ± 0.10	0.96 ± 0.70	1.94 ± 1.31
	11	15.972	80.500	35.0	2.33 ± 0.23	350	2.92	0.302	35.00	0.84 ± 0.60	0.24 ± 0.20	1.10 ± 1.49	2.20 ± 2.76

Billefjorden and Rijpfjorden - and 2) warm (temperature higher than 2.1 °C) – Kongsfjorden, Smeerenburgfjorden, Raudfjorden, and the continental shelf.

Distributions of our data were visually inspected using histograms and QQ plots and indicated non-normal distributions. Therefore, all statistical tests used were non-parametric.

Differences among stations in total biomass, secondary production, respiration, and carbon demand (summed data for each image) were investigated with non-parametric Kruskal-Wallis tests. Differences between cold and warm locations were tested with non-parametric Mann-Whitney tests.

Pairwise Spearman rank correlations with a Bonferroni correction for multiple comparisons were calculated between biotic parameters (biomass, secondary production, respiration, and carbon demand (mean values for each station calculated from summed data for each image)) and environmental variables (depth, bottom salinity, bottom temperature, and bottom turbidity). Four multiple linear regression analyses were performed, where biotic data were treated as dependent variables and environmental data were used as predictors. Next, in order to find the most parsimonious model and the best set of predictors, a stepwise model selection procedure was performed based on an Akaike Information Criterion (AIC, Akaike, 1974).

3. Results

The total seafloor area investigated by image analysis differed among stations, spanning a range from 32.4 to 51.5 m² at most stations, except station 20, where it was much lower (12.8 m²). The average area investigated in one image varied among stations from 2.16 to 3.34 m² at most stations, except station 20, where it was much lower (0.85 m², Table 1).

Total biomass, secondary production, respiration and carbon demand varied among stations (Mann-Whitney test, $p < 0.001$). The range of values differed among stations by a factor of 21 (biomass) up to a factor of 31 (secondary production). The lowest values for all biotic parameters were noted in Raudfjorden (station 9), with the highest values in Rijpfjorden (station 16, Table 1). Total biomass and carbon demand ranged from 0.15 to 3.14 g C_{org} m⁻² and from 0.25 to 6.77 g C_{org} m⁻² y⁻¹, respectively. Total respiration was 2.4–5.5 × higher than total secondary production at all stations, making it the major contributor to carbon demand. The values of all biotic parameters were significantly higher at cold sites than at warm sites (Mann-Whitney test, $p < 0.001$; Fig. 3). The average total biomass was almost two times higher at cold than at warm sites (median = 1.5 and 0.8 g C_{org} m⁻², respectively), while average total carbon demand was more than three times higher (median = 4.4 and 1.7 g C_{org} m⁻² y⁻¹, respectively) at cold stations compared to warm stations.

Spearman rank correlations between biotic data and environmental variables showed significant (Bonferroni corrected $p < 0.05$) relationships between bottom temperature and average total respiration and carbon demand (Supplementary Table S1). In both cases, the correlation was strongly negative ($\rho = -0.77$).

A stepwise multiple regression analysis showed similar results to the correlation analysis. For all regressions, the best-fit relationship included only the bottom temperature as a predictor. Each model explained between 51 and 58% of the variation in biotic variables (Table 2). Each biotic variable decreased with increasing temperature (Fig. 4).

Thirty-three taxa belonging to 6 phyla (Annelida, Arthropoda, Chordata, Cnidaria, Echinodermata and Mollusca) and 10 classes were identified. Cold stations were dominated by Anthozoa (biomass 0.86–1.46 g C_{org} m⁻²), Asteroidea (high biomass only in stations 15 and 16; 0.55 and 0.66 g C_{org} m⁻², respectively) and Ophiuroidea (0.54–1.59 g C_{org} m⁻², except station 15, Fig. 5). Warm stations were more variable in terms of dominant taxa, though they had consistently higher (up to 80%) share of Malacostraca (in particular the northern prawn *Pandalus*

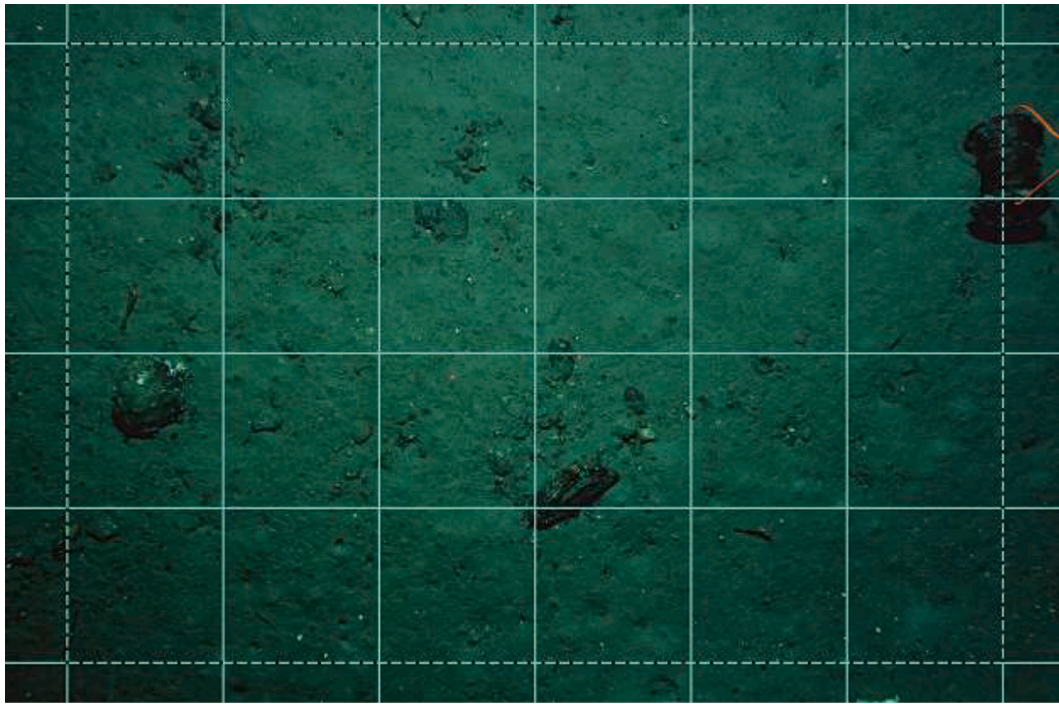


Fig. 2. Example of an image divided into grid cells. In this image, 2.4 m² was analyzed (area in dashed rectangle).

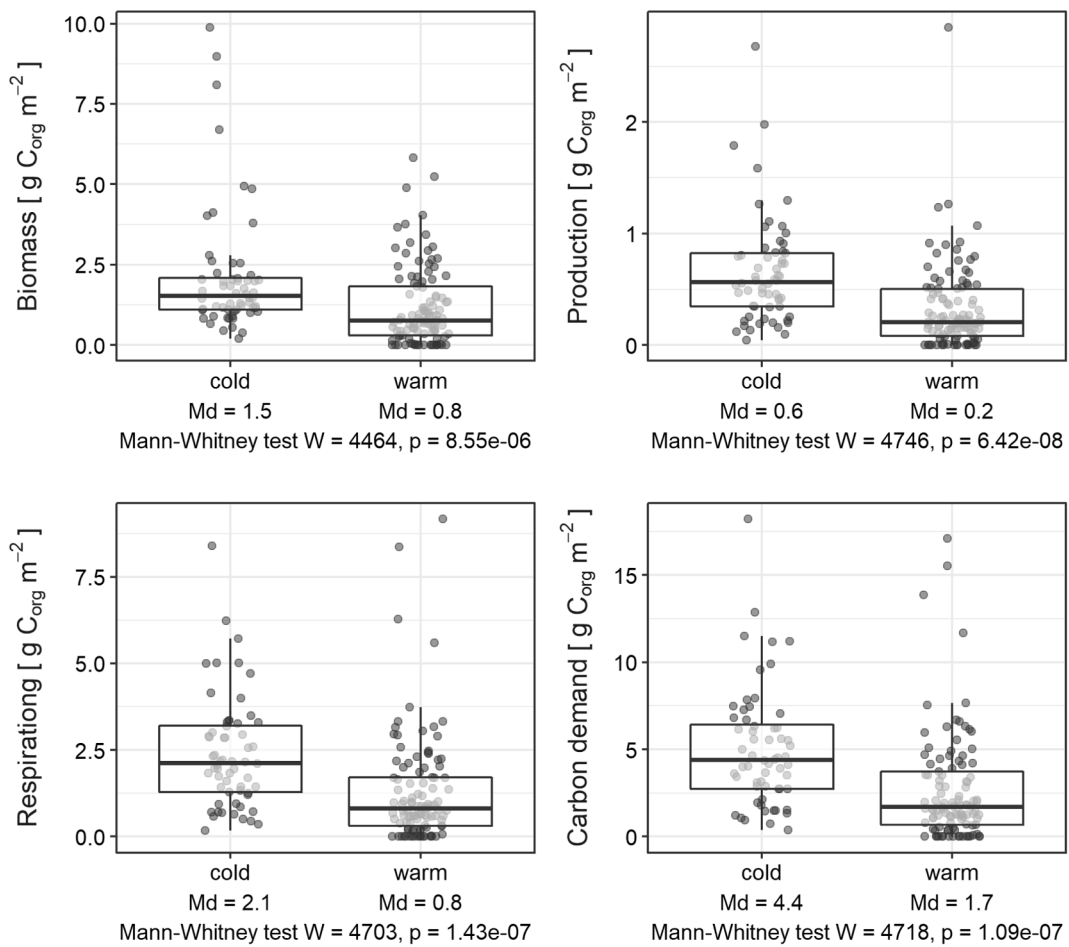


Fig. 3. Boxplots for biomass, secondary production, respiration and carbon demand at cold and warm stations. Md, median value. Box: 25th, median and 75th percentiles; lower whisker: 25th percentile – 1.5 interquartile range; upper whisker: 75th percentile + 1.5 interquartile range; dots: single observations (images).

Table 2
Ordinary least squares linear regression parameters for the best-fit relationships between biotic data and bottom water temperature.

	Intercept			Temperature (slope)			R ²
	Estimate ± SE	t statistic	p	Estimate ± SE	t statistic	p	
<u>Biomass</u>	1.97 ± 0.24	8.05	<0.01	-0.26 ± 0.08	-3.05	0.01	0.51
<u>Production</u>	0.59 ± 0.07	8.27	<0.01	-0.09 ± 0.02	-3.50	0.01	0.58
<u>Respiration</u>	2.20 ± 0.26	8.56	<0.01	-0.30 ± 0.09	-3.35	0.01	0.55
<u>Carbon demand</u>	4.58 ± 0.53	8.63	<0.01	-0.63 ± 0.18	-3.44	0.01	0.57

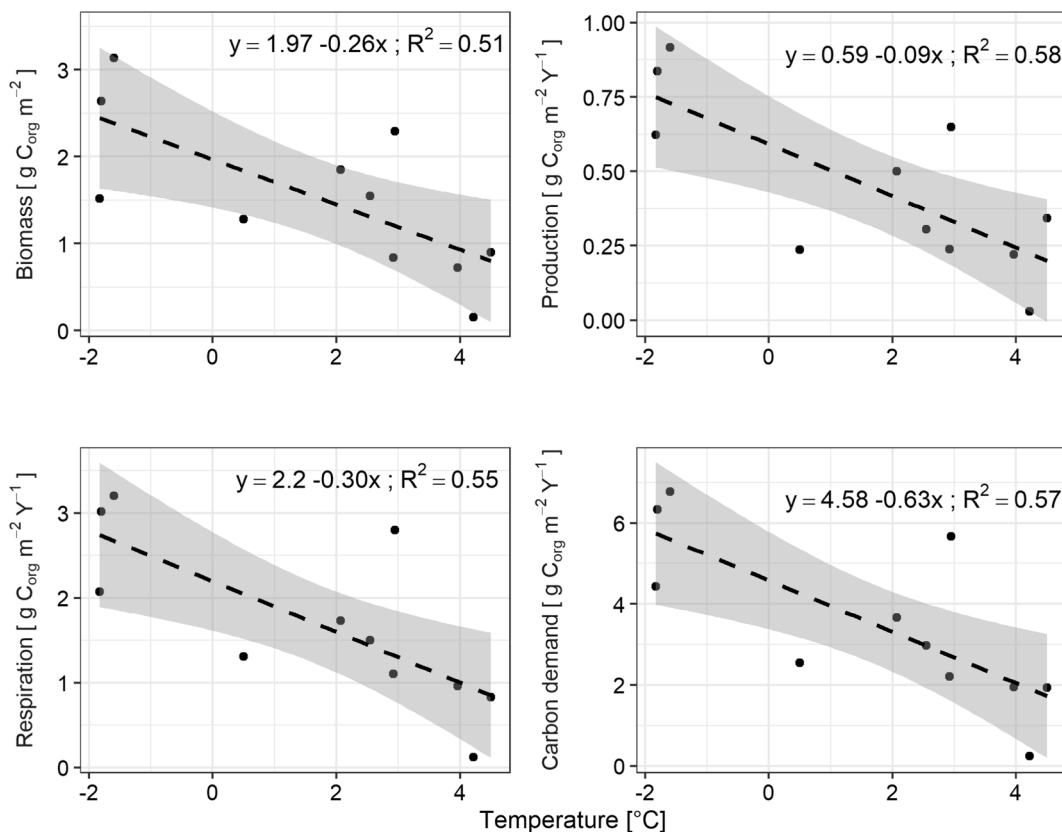


Fig. 4. Visualization of linear regressions between megabenthic community parameters and bottom water temperature. Dashed line, linear regression fit; grey area, 0.95 confidence interval of the regression.

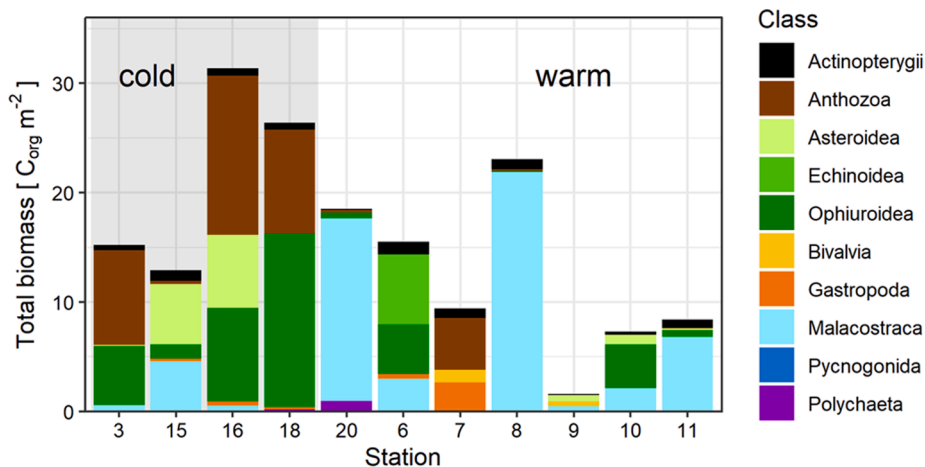


Fig. 5. Mean contributions of megafauna classes to total biomass at cold and warm stations.

borealis). The highest biomasses of Malacostraca were noted at station 20 (1.67 g C_{org} m⁻²), 8 (2.19 g C_{org} m⁻²), and 11 (0.68 g C_{org} m⁻²). At two stations (6 and 10), Echinoidea and Ophiuroidea constituted most of the biomass (>67%). The most unique community occurred at station 7, where the fauna were dominated by Anthozoa, Bivalvia and Gastropoda. The seafloor at this station was heterogeneous, with many rocks, which could favor hard-bottom fauna.

4. Discussion

4.1. Environmental drivers of megafaunal carbon demand

Megabenthic biomass, respiration, secondary production, and carbon demand calculated in this study were significantly higher at cold coastal sites in Svalbard, as predicted by our hypothesis. Except for secondary production, these biotic parameters were also significantly negatively correlated with bottom water temperature. The relationship between temperature and functioning of megabenthic communities has been demonstrated in other studies. Along with substrate type, depth, and current speed, temperature was reported to impact abundance and diversity of epibenthic megafauna on the West Greenland continental shelf (Yesson et al., 2015). In a study from Svalbard coastal waters, lower megafaunal diversity and lower functional trait diversity prevailed in locations characterized by higher bottom water temperatures and warm Atlantic water influence (Meyer et al., 2015). A large survey by Jørgensen et al. (2015) from the Barents Sea showed two main megafaunal assemblages: 1) northern – associated with cold Arctic waters and characterized by a high proportion of echinoderms and crustaceans, higher total abundance, and higher biomass and 2) southern – associated with warmer, Atlantic-influenced waters with high proportions of sponges, lower total abundance, and lower biomass. Moreover, parallel differences between these two regions, i.e. higher values in the Arctic-influenced north-east Barents Sea, were observed for megafaunal secondary production (Degen et al., 2016).

Certainly, water temperature is not the sole environmental factor influencing megabenthic communities. In fact, multiple abiotic and biotic factors are linked to temperature (Post et al., 2009), and the observed relationships may be a sign of indirect effects e.g., via temperature impacts on abiotic factors like ice cover, turbidity, and glacial sedimentation or biotic factors like productivity, species composition, size distributions of organisms, functional diversity, predation, and food-web structure (Coyle et al., 2007; Dossena et al., 2012; Renaud et al., 2008). Moreover, the influence of environmental drivers on megabenthic communities may be different depending on the spatial scale of the study, and inclusion of local phenomena in some cases is needed for a complete understanding of community-environment relationships (Roy et al., 2014).

At a global scale, megabenthic standing stock is highly positively correlated with the amount of organic matter, detritus, and zooplankton standing stock in the upper layer of the water column (Wei et al., 2010). On a regional scale limited to the Arctic, studies show that megabenthic species composition and biomass are strongly correlated to pelagic-benthic coupling and the amount of organic matter produced in pelagic and under-ice environments (Degen et al., 2016; Piepenburg et al., 1996; Piepenburg and Schmid, 1996a; Roy et al., 2014). The higher megafaunal standing stock and higher carbon demand observed in this study in cold fjords may be driven by the same processes. For instance, in Rijpfjorden, large amounts of sea ice transported to the fjord by ocean currents may be important vectors for organic matter entering the fjord ecosystem, which supplements organic matter produced in the pelagic zone to fuel the benthic community (Søreide et al., 2013).

Bottom water temperature and food availability usually decline with depth, and many studies also report a pronounced depth zonation of megafaunal communities. Piepenburg et al. (1996) noted three faunal zones defined by depth and food availability in a range between 190 and 2800 m around Svalbard. Roy et al. (2014) described six megafaunal

community types defined by depth and physical water properties in the Canadian Arctic (30 – 1000 m depth range). In our study, the depth range was relatively narrow (77–360 m), and we did not observe any pronounced bathymetric gradients of environmental conditions or relationships between depth and megafaunal characteristics. Grant et al. (2002) also found no depth dependence of benthic community oxygen consumption across a depth range of 247–680 m in Baffin Bay.

Rapidly changing temperatures in the Arctic may also reshape functioning of the whole ecosystem via e.g., decreasing ice cover or shifts in species distributions (Renaud et al. 2008, 2015). Recently, the Arctic has experienced an influx and establishment of boreal predators including demersal fish like Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) (Sswat et al., 2015), and crustaceans like snow crab (*Chionoecetes opilio*) and red king crab (*Paralithodes camtschaticus*), which may alter benthic communities (Jørgensen et al., 2019; Zakharov et al., 2020). According to Coyle et al. (2007), warming of the Bering Sea may increase predation of demersal fish on infaunal organisms and consequently reduce their biomass (similar phenomena may be also relevant for epifaunal organisms). It has a confirmation in the most recent studies. In a period between 2016 and 2019 a very small cold-pool extent was observed in the Bering Sea, what allowed subarctic benthivorous species like Pacific cod *Gadus macrocephalus*, adult walleye pollock *Gadus chalcogrammus* or arrowtooth flounder *Atherestes stomias* northward expansions what caused significant changes in local communities and trophic interactions (Grüss et al., 2021). Similarly, in coastal and fjord waters off Svalbard, in recent years, Atlantic cod and haddock have been frequently caught due to their northward range extensions (Olsen et al., 2010); however, they have not been observed in Rijpfjorden (a cold fjord in this study; Renaud et al., 2012). The diets of both species contain substantial proportions of epifaunal organisms, including echinoderms (Kohler and Fitzgerald, 1969; Mello and Rose, 2005). Therefore, lower megafaunal biomass observed in warm fjords could be a consequence of higher demersal fish predation. Cold Svalbard fjords were also observed to have lower densities of epifaunal scavengers and lower scavenging rates than warmer Svalbard fjords, which may reflect historical predation by boreal predators (Dunlop et al., 2020).

4.2. Megafaunal taxonomic composition, standing stock, and carbon demand

Megabenthic epifauna include a variety of taxa representing most marine phyla; however, in previous reports from the Arctic soft bottom habitats, the majority of the megabenthic standing stock were comprised of echinoderms, mostly brittle stars (Degen et al., 2016; Meyer et al., 2015; Piepenburg and Schmid, 1996a). Other prominent taxa included mollusks (gastropods and bivalves) crustaceans (mostly northern shrimp *Pandalus borealis*) and sponges (Jørgensen et al., 2015; Klages et al., 2004; Piepenburg et al., 1996; Piepenburg and Schmid, 1996a; Piepenburg and Schmid, 1997). Our results also showed that echinoderms were dominant (in terms of biomass) at cold stations (Rijpfjorden and Billefjorden), while at warmer stations influenced by Atlantic water, echinoderm standing stocks were much lower and other groups (mostly crustaceans) had a higher share in the total biomass (Fig. 5). Moreover, at cold stations, we also noted a high contribution of cerianthid anemones, accounting for up to 57% of total biomass at some stations. This seems to be uncommon based on a literature search (Supplementary Table S2) and may arise from specific fjordic environmental conditions (high sedimentation rates, glaciomarine deposits) that are may be favorable for them (Hargrave et al., 2004; Jørgensen et al., 1999; Starmans et al., 1999).

The megafaunal biomass documented in this study (0.15–3.14 g C_{org} m⁻²) is comparable to values reported in other Arctic studies (usually a few grams C_{org} m⁻², see Supplementary Table S2). Piepenburg and Schmid (1996b) noted the highest biomass of *Ophiocten sericeum*, a dominant brittle star in the Barents Sea, reaching 5 g ash-free dry weight m⁻² (around 2.28 g C_{org} m⁻² assuming a conversion factor of 0.456

(Brey et al., 2010)). In the Laptev Sea, the maximum total biomass of megabenthic brittle stars was reported as $1.8 \text{ g C}_{\text{org}} \text{ m}^{-2}$ (Piepenburg and Schmid, 1997). On the shelf bank of Northeast Greenland, total biomass of epibenthic megafauna ranged from 1.8 to $10.5 \text{ g ash-free dry weight m}^{-2}$ (around $0.8 - 4.8 \text{ g C}_{\text{org}} \text{ m}^{-2}$, (Piepenburg and Schmid, 1996a)). Much higher megafaunal standing stocks were noted at open water sites characterized by high inputs of organic matter. In the Canadian Arctic, local megafaunal hotspots were characterized by biomass $> 300 \text{ g wet mass m}^{-2}$ (around $25 \text{ g C}_{\text{org}} \text{ m}^{-2}$), which was driven by strong advection of suspended matter by ocean currents or by terrestrial carbon inflows from the Mackenzie River (Roy et al., 2014). On Svalbard Bank in the Barents Sea, high megafaunal biomass ($12-90 \text{ g C}_{\text{org}} \text{ m}^{-2}$) was reported and linked to organic matter advection and high local primary productivity (Kędra et al., 2013).

Megafaunal carbon demand in Svalbard coastal waters ranged between 0.25 and $6.77 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$. This is comparable with many Arctic megafaunal studies, which report average values $< 10 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ (Supplementary Table S2). However, much higher values for carbon demand have been observed on local scales and – similar to studies reporting locally elevated megabenthic biomass - attributed to favorable food conditions. In a study from Beaufort Sea, Renaud et al. (2007a) noted megafauna carbon demand between 6.6 and $17.0 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ at three stations (compared to $0.01-0.75 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ at 9 other stations) and explained these high values by citing strong local pelagic-benthic coupling. On shallow banks of the Barents Sea, at stations characterized by high inflow of organic matter on ocean currents, megafaunal carbon demand was estimated to be even up to $70 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ (Kędra et al., 2013). In Kobbefjord (Greenland), carbon demand of about $31 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ for the dominant sea urchin *Strongylocentrotus droebachiensis* was attributed to locally high primary production in the fjord (Blicher et al., 2009).

4.3. Carbon demand in cold and warm conditions

The proportion of total benthic carbon demand attributed to megafauna may be different depending on thermal conditions. A very rough comparison of available data for Kongsfjorden (one of the warm fjord in our study) and Rijpfjorden (one of the cold fjords) indicates lower total carbon demand in colder Rijpfjorden, with a higher contribution attributed to megafauna. Sediment carbon demand (estimated based on respiration experiments, including microbial metabolism) was reported to be higher in Kongsfjorden (from $34 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ (Hulth et al., 1994) up to $86 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ (Kotwicki et al., 2018)), than in Rijpfjorden ($15-55 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ (Morata et al., 2013)). Combined meiofaunal and macrofaunal carbon demand (estimated from biomass as in the current study) was two times higher in Kongsfjorden ($50 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$) than in Rijpfjorden ($25 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$, Włodarska-Kowalczyk et al. 2019). When we include data on megafaunal carbon demand from this study, the total benthic (bacteria, meiofauna, macrofauna, megafauna) carbon demand in Kongsfjorden varies from 88 to $140 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ with a 3–4% contribution of megafauna, while in Rijpfjorden it varies between 45 and 85 with 6–12% contribution of megafauna. That suggests that megafaunal contributions to benthic carbon mineralization are relatively low in warm fjord but higher in the colder fjord, which is characterized by dominance of winter-cooled waters, longer ice cover (Hop et al., 2019) and a higher share of ice-algae in primary productivity (Leu et al., 2011; Søreide et al., 2013).

The observed higher total carbon demand (or respiration) in warmer fjord (Kongsfjorden) could be simply explained by the fact that the metabolic rate of ectotherms grows exponential with temperature (Clarke and Fraser, 2004), however it does not elucidate the shift in partitioning among different groups of organisms. We can consider the fact that in lower temperatures organisms tend to grow larger (Bergmann's rule, temperature-size rule; (Atkinson, 1994; Bergmann, 1847)) - than could explain both higher carbon demand of megafaunal organisms and their higher contribution to total community carbon demand in

colder fjord (Rijpfjorden). Mazurkiewicz et al. (2020) found that the distribution of biomass among meiofaunal and macrofaunal size classes remained consistent in fjordic communities between 60 and 81°N , despite changes in water temperature, food availability, species composition and total biomass. However they noticed that larger size classes (larger organisms) were present in colder localities but absent in warmer ones. Therefore, it is possible that in colder localities, environmental conditions support presence of large organisms (megafauna). As many of megafaunal organisms utilize the same (limited) resources as infaunal organisms (Bergmann et al., 2009), if present they outcompete and reduce available resources for smaller organisms, lowering their share in biomass or total carbon demand.

4.4. Megafauna vs. other groups

On a global scale, megafaunal standing stocks are low compared to other groups of marine organisms. According to simulations by Wei et al. (2010), only 5% of benthic living carbon is stored in megafaunal organisms, as the majority of benthic carbon is constituted by macrofauna and bacteria (51 and 31%, respectively). In the Arctic, megafaunal biomass (usually up to few grams $\text{C}_{\text{org}} \text{ m}^{-2}$) seems to be up to one order of magnitude lower than that of macrofauna. For instance, macrofaunal biomass was reported to be between 5 and $24 \text{ g C}_{\text{org}} \text{ m}^{-2}$ in the Bering and Chukchi Seas (Grebmeier et al., 1988), between 1 and $24 \text{ g C}_{\text{org}} \text{ m}^{-2}$ (assuming a conversion factor carbon/wet mass = 0.084 (Brey et al., 2010)) in the Barents Sea (Kędra et al., 2013; Piepenburg et al., 1995), and from 5 to $15 \text{ g C}_{\text{org}} \text{ m}^{-2}$ in Svalbard fjords (Włodarska-Kowalczyk et al., 2019).

Most of the carbon demand in benthic communities is attributed to infaunal organisms (bacteria, meiofauna and macrofauna), due to their high metabolic rates (Piepenburg et al., 1995; Schwinghamer et al., 1986; Włodarska-Kowalczyk et al., 2019). However, some studies report high shares of megafauna in carbon demand. These studies concern localities with specific environmental conditions like high organic carbon supply, tight pelagic-benthic coupling, and strong bottom currents. Examples include the steep Beaufort Sea shelf, where megafauna carbon demand reached 41% of total carbon demand (Renaud et al., 2007a), and the Chukchi Sea shelf under the Alaskan Coastal Current, where megafauna were responsible for 26% of benthic carbon demand (Ambrose et al., 2001). As mentioned above, megafaunal carbon demand is usually below $10 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$. For comparison, combined macrofaunal and meiofaunal carbon demand has been reported to be up to $92 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ (Włodarska-Kowalczyk et al., 2019), and in many studies varies between 10 and $70 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ (Supplementary Table 2). Very high carbon demand values have been noted for sediments based on sediment cores incubations, driven mostly by bacteria and small-bodied infaunal organisms e.g., $34-60 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ in Svalbard fjords (Jørgensen et al., 2005) and $32-71 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ in the Bering and Chukchi Seas (Grebmeier and McRoy, 1989). The average carbon demand on Arctic continental shelves is estimated to be $39 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$ (based on sediment oxygen demand, (Bourgeois et al., 2017)).

4.5. Limitations of methodological approaches

Megafauna community biomass assessment is a challenging task, mostly due to the large sizes of the organisms and the large area of the seafloor that must be surveyed to give a reliable estimate. Two main methodological approaches can be used, but both have several biases that can influence the results. Dredging provides only semi-quantitative data, as the sampled area of the seafloor can be only approximated and may result in underestimation of organism density and biomass (Elftheriou, 2013). The advantage of this method is that specimens are collected, and this enables precise taxonomic identification and direct mass determination (Hughes and Gage, 2004; Nybakken et al., 1998). Sea bottom photography is a more quantitative method but requires application of indirect methods for biomass assessment, which may

introduce some uncertainties in the estimated data. An additional advantage of this method is that it is non-destructive.

Biomass can be estimated based on length – weight relationships or using volumetric methods. We used a formula from the literature, which was obtained by measuring and weighing individual specimens. The goodness-of-fit for several published formulas (as indicated by the coefficient of determination, R^2) was very high (e.g. 0.98 for the formula used to calculate dry weight of *Ophiura sarsi* or 0.86 for *Ophiacantha bidentata*; Piepenburg, 2000). However, in the case of some formulas (e.g. Berestovsky et al., 1989), the R^2 was not provided, so the accuracy is unknown. When length-weight relationships were not available, we estimated biomass using a volumetric approach that required geometric approximation of an organism's shape, which might be inaccurate in the case of geometrically complex organisms (Hillebrand et al., 1999). This method is also limited by the availability of features that can be measured e.g., in the case of anthozoans, we were able to measure their diameter only; therefore, we assumed their volume as a sphere, while their actual shape is rather ellipsoidal or cylindrical. Furthermore, a series of taxon-specific conversion factors from volume to biomass (Brey et al., 2010) were used to calculate carbon content and biotic parameters (production, respiration and carbon consumption), increasing the risk of inaccuracy at each step of the calculations. Still, for many taxa, this was the only available approach, and indirect methods are unavoidable when assessing quantitative characteristics of megafauna at the community level.

In our estimations, we were not able to include seasonal changes in respiration rates. Some studies report that the supply of organic matter from ice algae or after the phytoplankton bloom in spring can increase (short-term) oxygen demand of arctic benthic fauna, even by an order of magnitude (Morata et al., 2013; Renaud et al., 2007b). Therefore, our annual estimations (extrapolation of daily respiration rate to 365 days) may be slightly underestimated, as they do not take into account this spring period of the highest benthic activity. However, this may not be true for every location, since a recent study by Morata et al. (2020) shows that in fjords with a high contribution of detrital organic matter, the sediment community respiration rates does not vary during the year.

5. Conclusions

Climate change may have various consequences for benthic fauna in the Arctic, including changes in biodiversity, standing stocks, or productivity. Our results suggest that warming may affect functioning of coastal megafaunal communities (and probably entire benthic communities) through changes in the community structure and reduction in carbon demand. These changes may be attributed not only to increases in temperature (which should cause higher carbon demand) but rather to a number of indirect effects of warming, like decline of ice extent and ice algae production, predation pressure from boreal predators expanding into the Arctic, and weaker pelagic-benthic coupling (Paar et al., 2016; Renaud et al., 2015; Søreide et al., 2013; Wassmann et al., 2011; Zakharov et al., 2020). Yool et al. (2017) modeled the global change in benthic biomass in 100 years and, under the IPCC emissions climate warming scenario RCP 8.5, observed a decline in benthic biomass by 0.8% in 100–200 m depth range and 7.3% in 200–500 m depth range. Our study shows that the relative roles of different size-fractions of the benthic community in ecosystem functioning may also be altered, e.g., by a decreased contribution of megafauna to the total benthic carbon metabolism.

CRedit authorship contribution statement

Mikołaj Mazurkiewicz: Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization. **Kirstin Meyer-Kaiser:** Conceptualization, Resources, Writing - review & editing. **Andrew K. Sweetman:** Methodology, Resources, Supervision, Funding acquisition. **Paul E. Renaud:** Writing - review & editing,

Supervision, Funding acquisition. **Maria Włodarska-Kowalczyk:** Conceptualization, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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