Ecological Indicators 154 (2023) 110487

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Macrofauna and meiofauna food-web structure from Arctic fjords to deep Arctic Ocean during spring: A stable isotope approach

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ARTICLE INFO

Keywords:
Benthos
Depth gradient
European Arctic Ocean
$\delta^{13}C$
$\delta^{15}N$
Organic matter mixtures

ABSTRACT

The knowledge on benthic trophic relations is particularly important for understanding the functioning of still pristine and less studied Arctic Ocean ecosystems. This study examines the benthic food-web structure in the European sector of the Arctic Ocean and assesses if and how it differs along depth gradients in the marginal sea-ice zone during spring. Samples of the sediment organic matter were collected in May/June 2015 and May 2016 at stations representing different sedimentary habitats (fjord, shelf, slope/basin), and stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ were used to determine macro- and meiofauna food-web structure. Our results show that the food-web structure differed both among the three studied habitat types and between macro- and meiofauna components of benthic communities, and that these differences were related to the quality and quantity of organic matter. Meiofauna in fjords and on the shelf mainly relied on the reworked sediment organic matter while macrofauna utilized more fresh organic matter, sedimenting to the sea floor. In fjords and on the shelf, benthos displayed a high degree of omnivory and non-selective feeding while on the slope and in deep basins feeding on higher trophic levels dominated. In the latter, benthos seemed also to have utilized highly reworked organic matter. As the organic matter quantity and quality were major drivers of trophic relations in all studied areas, the benthic food webs will likely face cascading effects following the modification of pelagic food webs due to climatic changes.

1. Introduction

Food web studies are crucial for understanding ecosystem functioning as they depict the organic matter (OM) and energy flow among organisms (Hobson et al., 2002; Post, 2002). The Arctic benthos is among the ultimate recipients of OM produced in the euphotic zone, within the water and/or the sea ice, and exported to the sea floor (Boetius et al., 2013; Wiedmann et al., 2020a). Macrobenthic communities (>500 μm) play important roles in Arctic marine ecosystems, and their food webs are essential in processes related to production, turnover rates, and OM remineralization (Grebmeier et al., 2015; Renaud et al., 2015a; Tessin et al., 2020). Similarly, the meiofauna – smaller sized (32 μm – 500 μm) but extremely abundant and diverse component of benthic communities - can make a significant contribution to OM processing (Van Oevelen et al., 2011). This group has higher turnover rates than macrobenthos due to its small body sizes and is an important link between detrital OM and higher trophic levels in benthic systems (Van Oevelen et al., 2011; van der Heijden et al., 2018), enhancing the rate of OM mineralization and consumption of detritus (Urban-Malinga and Moens, 2006; Schratzberger and Ingels, 2018).

One factor shaping the benthic communities, their food webs and thus their roles in the ecosystem is the quality and quantity of OM reaching and being available at the sea floor (Kędra et al., 2015; Wiedmann et al., 2020a). In the Arctic, the sea floor receives the largest pulses of fresh OM in connection with spring blooms. The quality and intensity of OM fluxes to the sea floor depend on the irradiance, sea ice, and available nutrients in the upper column, because these factors regulate the onset of primary production (PP), the composition of primary producers (e.g., diatoms vs. flagellates), and the timing between the PP and sympagic and pelagic grazers (Flores et al., 2019; Lalande et al., 2019; Wiedmann et al., 2020a; Dybwad et al., 2021; Nadaï et al., 2021). As a result, benthic communities at shallower depths may either receive high quality and little reworked OM, such as algae, or highly

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https://doi.org/10.1016/j.ecolind.2023.110487
Received 19 December 2022; Received in revised form 26 May 2023; Accepted 8 June 2023

reworked and low quality OM consisting of fecal pellets, dead zooplankton, marine snow and/or re-suspended and laterally advected OM (Iken et al., 2005; Boetius et al., 2013; Lalande et al., 2019; Wiedmann et al., 2020a). The latter is often the only source of OM for benthic communities dwelling at greater depths. Thus, the sediment contains a large pool of potentially available OM, mainly in form of highly reworked detritus, that has accumulated over time and persists in the sediments for months (Mincks et al., 2005).

Close to the shore, the OM comes from various sources, both marine and terrestrial (Kuliński et al., 2014; McGovern et al., 2020; Bridier et al., 2021), and is usually abundant. Fjords for example are strongly impacted by marine and terrestrial endmembers, and benthic communities are there shaped by specific local environmental conditions (e.g., influence of glaciers, ice cover) and may differ largely within one fjord or between fjords (Włodarska-Kowalczuk and Pearson, 2004; Renaud et al., 2015b; Zaborska et al., 2018). Despite these regional differences, the diversity of macro- and meiofaunal communities in fjords is usually lower than on the shelf, while the biomass and abundance of macro- and meiofauna can be very high (Włodarska-Kowalczuk et al., 2012; Grzelak et al., 2016). On shallow Arctic shelves, on the other hand, benthos is rich and diverse (e.g., Hunt Jr. et al., 2013; Kędra et al., 2013) due to tight pelagic-benthic coupling (e.g., Tamelander et al., 2008; Grebmeier et al., 2015).

Shelves and continental margins are characterized by relatively high rates of PP and large standing stocks of OM produced in situ and, to less extend, derived from land. Moving “down the slope” results in a steep gradient of decreasing, mainly marine, OM supply and the benthic communities in large follow this pattern (Bluhm et al., 2020). The deep-sea communities (slopes and basins) are usually impoverished and food-limited due to low amount of OM reaching the sea floor (Rex et al., 2006; Bluhm et al., 2015; Stasko et al., 2018; Wiedmann et al., 2020a). However, the decrease in standing stocks of benthic communities with depth is less rapid for smaller groups like meiofauna (Rex et al., 2006; Wei et al., 2011). With increasing depth, the role of smaller organisms, such as meiofauna, increases as they replace those of larger size classes, which are more affected by food limitations, in terms of their contribution to the total community biomass (Rex et al., 2006; Danovaro et al., 2008; Wei et al., 2011).

Above mentioned differences related to the depth gradient, i.e., in the OM supply, in the benthic communities’ diversity and structure, and in the balance between macro- and meiofauna’s functions, shape benthic food webs and thus OM cycling. Despite a clear relation between benthic standing stocks and water depth (Rex et al., 2006; Wei et al., 2011), it is still unclear how the quality and quantity of OM input shapes distinct components of Arctic benthic food webs. In this context, natural stable isotope analysis contributes to identifying and quantifying the interactions between different trophic levels, because the enrichment of ^{13}C and ^{15}N from resources to consumers is observed (ca. 1‰ of ^{13}C and 3-4‰ of ^{15}N per trophic level; Post, 2002). Dual isotopic analysis is commonly applied to benthic macrofauna (e.g., for Arctic macrobenthos: Renaud et al., 2015b; Roy et al., 2015; Zaborska et al., 2018; Kohlbach et al., 2019; Włodarska-Kowalczuk et al., 2019), but less so to meiofauna due to sampling challenges and their small body mass that causes difficulties in obtaining sufficient material for analysis (Majdi et al., 2020). Therefore, the importance of meiofauna is often overlooked in the investigations of benthic food webs and only few studies have so far been conducted in polar regions (Moens et al., 2007; Ingels et al., 2010; Veit-Köhler et al., 2013; Ehrlich et al., 2020, 2021). For macrofauna, relevant information regarding their trophic position and feeding habitats in the Arctic system is more available and our knowledge on trophic relations is continuously increasing, particularly on shelves (e.g., Iken et al., 2010; McGovern et al., 2018; Włodarska-Kowalczuk et al., 2019). Despite the increasing number of investigations, our understanding of deep-sea macro- and meiofauna trophic relations is still limited, particularly for Arctic regions (Iken et al., 2001; Bergmann et al., 2009; Bluhm et al., 2011; Van Oevelen et al., 2011; Zhulay et al., 2021).

The currently observed climate change will impact multiple ecological features including OM production and cycling, and thus food-web structure and functioning of Arctic marine ecosystems (Kędra et al., 2015). Future sea-ice cover decrease will change the temporal and spatial extent of pelagic PP and thus have an impact on primary energy pathways within and among pelagic and benthic food webs (Maiti et al., 2010; Renaud et al., 2015a; Al-Habahbeh et al., 2020; Morata et al., 2020). This change will be particularly visible during the spring when sea-ice algae and phytoplankton bloom pulses reach the sea floor and trigger benthic activities after the winter months (Morata et al., 2015, 2020; Oleszczuk et al., 2019). Changes in patterns of primary productivity and grazing in the overlying water column will have cascading effects on the benthic community structure and their food webs (Boetius et al., 2013). Hence, understanding the Arctic marine food-web structure, particularly ones that include a wider size range of benthic species (i.e., macro- and meiofauna) is crucial for revealing the relation between sympagic and pelagic PP, pelagic OM cycling, and benthic systems, and how these linkages may change in the future.

We addressed this issue in the present study and examined the benthic food-web structure in the European sector of the Arctic Ocean to assess if and how it differs among different habitats in the marginal sea-ice zone during spring. We used stable isotope analysis to determine trophic relationships in macro- and meiofauna from fjords, through the shelf, to the slope/basins. These three habitats differ in terms of prevailing water masses, diversity of OM sources, PP levels and reworking of OM. We specifically looked into the changes in OM characteristics among different habitats (determined by the depth gradient), in the isotopic niches of different feeding groups and between macro- and meiofauna.

2. Material and methods

2.1. Study area

The study area was located around the Svalbard Archipelago, specifically in the fjords, the western Barents Sea, and deep areas north off Svalbard. It includes two fjords on the west coast of Spitsbergen (Van Mijenfjord and Hornsund), an open fjord and polynya in the south-eastern coast of Spitsbergen (Storfjord), stations located on the western Barents Sea shelf (south of the polar front), and areas in the northern shelf and slope, the Nansen Basin (Sophia Basin) and the Yermak Plateau (Table 1, Fig. 1). The sea-ice cover at all sampling locations varies interannually but in general the thickness and duration of sea ice increases northwards: the southernmost Barents Sea is generally sea-ice free, while sea ice in fjords and the central Barents Sea occurs usually late in the winter (December/January) and lasts to early spring (April/May) (Cochrane et al., 2009). At the northernmost stations, especially above 80° N, sea ice occurs earlier and lasts longer (until June) (Krumpen et al., 2021).

All these systems are under strong influence of Atlantic water masses which are also highly productive when compared to Arctic water masses (Athanase et al., 2020). The southern areas of the Barents Sea are under strong influence from Atlantic Water while in the central part, at the Polar Front, strong turbulences occur in areas where relatively warm Atlantic waters meet with Arctic waters flowing from the north (Slagstad and McClimans, 2005). The West Spitsbergen Current, that also impacts fjords, carries nutrient-rich, warm, saline Atlantic waters ($T \geq 2$ °C, $S \geq 34.88$) northwards through the eastern Fram Strait (Aagaard et al., 1985; Cokelet et al., 2008). Fjords are additionally influenced by glacial and riverine discharge (McGovern et al., 2020). The north of Svalbard region is situated at the entrance of the Arctic Ocean, where Atlantic water flows into the Central Arctic Basin (Meyer et al., 2017). Between 78° and 80° N, the West Spitsbergen Current splits. The main branch flows along the western and then northern continental margin of Spitsbergen and continuously decreases its temperature and salinity

Table 1
Sampling station information. Stations are listed according to the three different habitat types. Please note, station numbering is unique for the ARCEx and PS92 – TRANSSIZ cruises. Sea-ice cover refers to the time of sampling campaigns. VM - Van Mijenfjorden, HRN – Hornsund, S – Storfjorden, SBS - Southern Barents Sea, NBS - Northern Barents Sea, NB – Nansen Basin, YP – Yermak Plateau.

Area	Cruise	Station	Location	Date	Latitude (°N)	Longitude (°E)	Depth (m)	Sea-ice cover (%)
Fjord	ARCEx	1	VM	May 2016	77.83	16.47	59–121	0
		2	HRN		77.02	16.45		
Shelf	ARCEx	3	S	May 2016	77.94	20.22	96–471	0–90
		4	SBS		79.21	26.00		
		5	SBS		77.27	29.44		
		6	SBS		76.60	30.01		
	PS92	19	NBS	May/ June 2015	81.23	18.51		
		20	NBS		81.04	19.32		
		32	NBS		81.16	20.01		
Slope/Basin	PS92	27	NBS	June 2015	81.31	17.15	797–2168	90–100
		31	NB		81.47	18.17		
		39	YP		81.94	13.69		
		43–1	YP		82.21	7.63		
		43–2	YP		82.17	6.97		
		46	YP		81.84	9.74		
		47	NB		81.34	13.64		

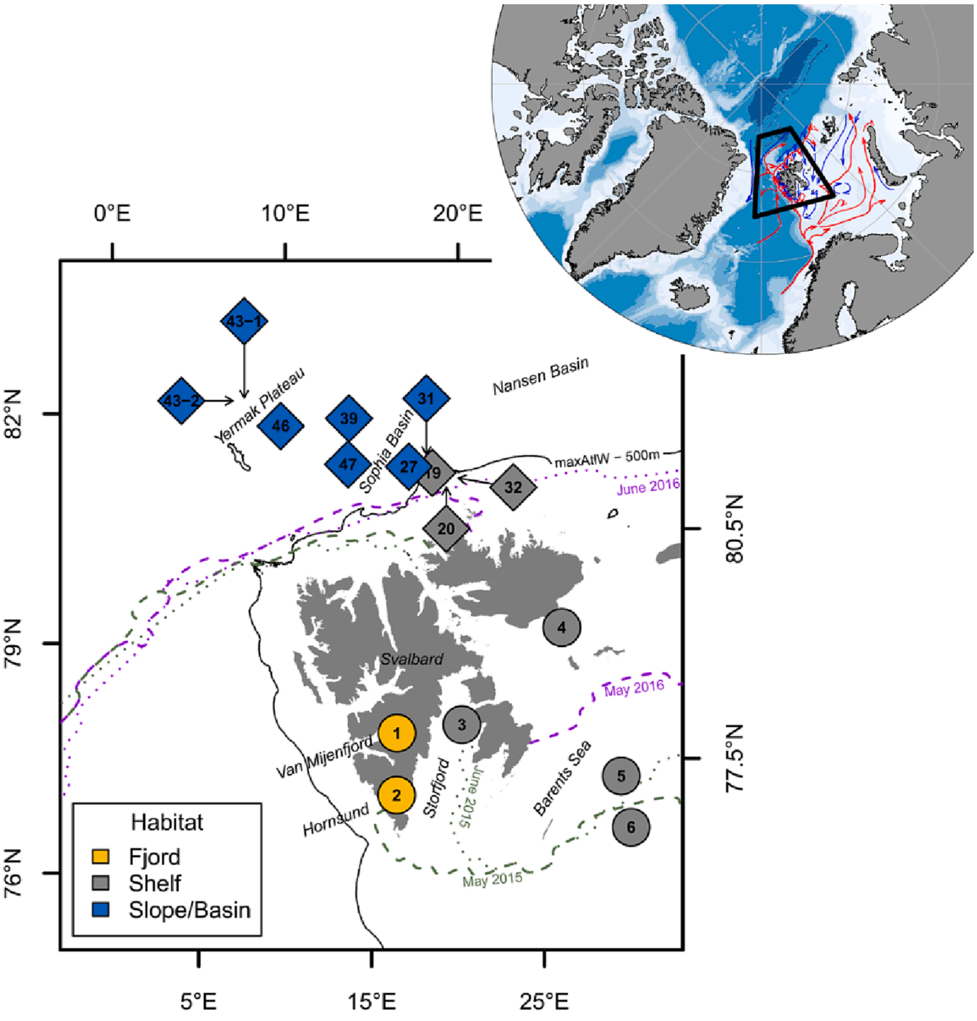

Fig. 1. Map of the study region with sampling locations. Colors indicate habitat type. Circle indicates stations sampled during ARCEx cruise and diamonds indicate stations sampled during TRANSSIZ cruise. The sea-ice extent for all sampling months is indicated: May and June 2015 in grey, and May and June 2016 in purple (data was smoothed; data from the National Snow and Ice Data Center, accessed July 1, 2021, www.nsidc.org). The 500 m isobath is emphasized as it indicates the maximum depth of Atlantic Water (data from the General Bathymetric Chart of the Ocean - GEBKO, accessed July 2, 2021, www.gebco.net). Top-right: Map of the Arctic with the study region indicated in black. Barents Sea ocean currents are indicated as given by Vihtakari et al. (2019). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Cokelet et al., 2008; Walczowski et al., 2017).

Among the sampled areas fjords, Barents Sea, shelve and slope regions are very productive (max. 150 g C m^{-2} y^{-1} on shelf and up to 180 g C m^{-2} y^{-1} in fjords) (Hop et al., 2002; Svendsen et al., 2002; Sakshaug, 2004; Slagstad et al., 2011). About 50% of the PP in the northern Barents Sea is likely advected there with the Atlantic waters (Vernet et al., 2019). The least productive regions of the present study are Yermak Plateau and the Nansen Basin with annual PP estimated at about 5–30 g C m^{-2} (Codispoti et al., 2013; Matrai et al., 2013; Vernet et al., 2019). The drop in the PP in the most northern stations in the study region is in large related to higher sea-ice concentrations, light limitation, and increased meltwater stratification, which hampers vertical mixing and thus replenishment of the nutrient concentrations in the upper water column (Tremblay et al., 2015). This limited sympagic and pelagic production also sets an upper limit to OM fluxes to the sea floor and impacts the benthic fauna (Bluhm et al., 2015; 2020).

2.2. Sampling

Sampling was carried out during two cruises: R/V Polarstern PS92 – TRANSSIZ (May/June 2015) and R/V Helmer Hanssen – ARCEx (May 2016). Samples were collected at 16 stations, representing three fundamentally different habitats: fjords (Van Mijenfjord and Hornsund, min. depth: 59 m), shelf (Storfjord polynya, Barents Sea shelf; stations with a max. depth of 500 m and not in a fjord), slope and deep basin [Barents Sea slope, Nansen Basin (Sophia Basin) and Yermak Plateau; all stations deeper than 500 m, max. depth: 2168 m; Fig. 1, Table 1].

A box corer (0.25 m^2 sampling area, TRANSSIZ cruise) or a Van Veen grab (0.1 m^2 sampling area, ARCEx cruise) were used to collect macrofauna at every station. Sediment samples for macrofauna were rinsed over a 0.5 mm mesh size sieve. Live animals were kept in filtered sea water at temperature and salinity corresponding to the ambient environmental situation for several hours to purge although no longer than 12 h after sampling. Later, macrofaunal organisms were picked up under a stereo microscope in the cold room onboard, cleaned of their epibionts and debris, identified to the lowest possible taxonomic level and frozen in −20 °C. Meiofauna samples were collected during the ARCEx cruise only, and were collected as three replicate sediment cores with an internal diameter of 3.6 cm, taken from the upper 5 cm of a box corer (0.25 m^2 sampling area) and stored in −20 °C until further analysis.

To determine the characteristics of the OM potentially available for the benthic fauna, samples were also taken in the water column of the respective benthic stations. The concentration of particulate organic matter (POM) was determined: 1) at the depth of the chlorophyll *a* maximum (Chl max), 2) in the bottom water, and 3) in sediment traps (deployed for 24 h, sampling depth 30 m, 60 m, 90 m, 120 m, and 200 m, except stations 3, 5, 20 and 43–2). Additionally, samples from the uppermost 2 cm of the sediment were collected to determine grain size, Chl *a* concentration in the sediment (Sed Chl *a*), Chl *a* and phaeopigments ratio (Sed Chl *a*/Phaeo; except station 5 where phytopigments were not collected), organic carbon (C_{org}), total nitrogen (N_{tot}), organic carbon and nitrogen ratio (C/N), as well as the δ^{13}C and δ^{15}N of the sediment. Details about sampling and sample preservation are provided by Dybwad et al. (2021) for the sediment traps deployed during the TRANSSIZ cruise, by Wiedmann et al. (2020b) for the sediment traps deployed during the ARCEx campaign, and by Oleszczuk et al. (2021) for all remaining sampling.

2.3. Sample processing

For isotopic analyses the whole dried and homogenized filters with POM (about 50 mg), and freeze-dried and homogenized sediment (30 mg) and macrobenthic organisms (about 1 mg) were weighed into silver capsules. In order to remove carbonates samples were acidified with 2 M HCl. Since Arctic benthos is typically low in lipids across multiple major taxa (Graeve et al., 1997; Iken et al., 2010), lipids were not extracted from the samples in order to avoid the negative impact of this process on nitrogen isotopes. The analyses were performed on an Elemental Analyzer Flash EA 1112 Series combined with an Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany) at the Institute of Oceanology Polish Academy of Sciences (Sopot, Poland) using high-temperature combustion (oxidation at 1020 °C, followed by reduction over copper at 680 °C). Measurements were performed according to the method described by Winogradow and Pempkowiak (2018).

Meiofauna specimens for isotopic analyses were isolated from frozen sediment. Samples were thawed, rinsed in 32-μm sieve and centrifuged in a solution of colloidal silica LUDOX HS to extract meiofauna organisms. LUDOX does not affect the isotope signal of the meiofauna (Guilini et al., 2010; Ingels et al., 2011). The extracted meiofauna was rinsed with Milli-Q water and sorted into Nematoda and Harpacticoida. At least 150 nematodes and 20 harpacticoids were handpicked randomly from each sample (or all organisms if the sediment contained a lower number of individuals), rinsed again in Milli-Q water to remove adhering particles and transferred to a drop of Milli-Q water in tin cups. Analysis was done following the protocol of Lebreton et al. (2012) and performed on an Elemental Analyzer Flash EA 1112, Thermo Scientific, combined with an Isotopic Ratio Mass Spectrometer Delta V Advantage with a Conflo IV interface (Thermo Scientific, Germany) at CNRS, Université de La Rochelle, France. To obtain sufficient biomass for a valid isotope analysis, large number of small-sized nematodes and harpacticoids were required. Due to the high generic diversity and the low availability of specimens in individual genera per sample, we did not separate individuals taken for the analysis into genera and/or feeding types. Therefore, the respective samples represent the nematode and harpacticoid community as a whole, which means that for some groups, nematodes in particular, different feeding modes were pooled together.

All results are given in the δ unit notation as a deviation from the international standards Vienna Pee Dee Belemnite and N_2 in air for δ^{13}C and δ^{15}N, respectively, following the formula: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively.

2.4. Statistical analysis

Non-parametric Kruskal-Wallis tests were conducted to test for differences in isotopic ratios of OM mixtures among habitats and among OM mixture types within habitat. If statistically significant (p-value threshold: 0.05), Dunn's test with Holm method for p-value correction was used for pairwise comparisons. The δ^{13}C and δ^{15}N of all macrofauna samples were used to build isotopic spaces for the three studied habitats (fjords, shelf and slope/basin). Standard ellipse area (SEA) based on the maximum likelihood of the isotopic representation (that contains 40% of the data) (Jackson et al., 2011) and the six Layman metrics (Layman et al., 2007) were calculated to identify differences in isotopic niche spaces between the benthic communities associated with the studied habitats. SEAs and the total areas of the convex hull can be used as a quantitative representation of isotopic niche space occupied by a community or community component. The other five Layman metrics are indicators of food chain length (δ^{15}N range), diversity of OM sources utilized by the community (δ^{13}C range), niche width (mean centroid distance – i.e., mean distance from each point to the centroid), and the taxa distribution within the occupied niche space (mean and standard deviation of nearest neighbor distance). To allow for statistical comparison between SEAs, a Bayesian approach was used. For pairwise comparisons of posterior distributions of feeding modes among habitats and among feeding modes within habitats Bhattacharyya's coefficients (BCs) were calculated (Bhattacharyya, 1943; Rauber et al., 2008). Silverman's rule of thumb was used to determine the bandwidths for the calculations of BCs (Silverman, 1986). BCs range from 0 (no overlap) to 1 (complete overlap). As threshold for statistical significance a $BC < 0.61$ was selected. This value was selected since the BC of two normal distributions has a value of 0.61 if the means of the two distributions is two standard deviations apart (Evin et al., 2018). The combination of SEAs and Layman metrics has been used in other studies to successfully describe the isotopic diversity of benthic communities in Arctic fjords and other coastal habitats that can be strongly influenced by terrestrial OM (Włodarska-Kowalczuk et al., 2019; Szczepanek et al., 2021).

The same analysis was used to compare isotopic niche spaces occupied by macro- and meiofauna collected during the ARCEx cruise at stations 1–6.

All macrofauna taxa were assigned to one of three feeding types: (1) suspension feeders, (2) deposit feeders, or (3) higher trophic levels (i.e., carnivores, omnivores, scavengers - COS). For comparisons between macro- and meiofauna, all taxa were assigned to one of two groups: primary consumers (i.e., suspension feeders and deposit feeders) vs. higher trophic levels. For meiofauna, all Harpacticoida were considered as primary consumers and all Nematoda as higher trophic levels.

All analysis were executed in R (R Development Core Team, 2019) using the SIBER package (Jackson et al., 2011).

3. Results

3.1. Organic matter properties

Stable isotope ratios of the collected OM mixtures varied strongly throughout this study (δ^{15}N range: 0.85‰ – 7.27‰; δ^{13}C range: −29.15‰ – −19.38‰; Fig. 2). The within group variation was small for sediment samples in comparison to all other OM samples (i.e., water column, sediment traps) that showed a strong variation of both studied isotopes (Fig. 2, Tables 2, 3, 4). Sediment samples and the material collected from sediment traps displayed stable δ^{15}N values across all habitat types of approximately 4.5‰ and 3.5‰, respectively (Fig. 2, Table 2). The habitats however differed considerably with regard to δ^{13}C. Fjord sediments were depleted in ^{13}C compared to shelf and slope/basin, however this difference was not significant, due to the low number of sediment samples from fjords (n = 2, Table 2). For OM collected in sediment traps, only the δ^{13}C of the shelf stations was elevated. Such an enrichment in ^{13}C was found for most OM samples from shelf stations, with the exception of bottom water samples (Fig. 2). No consistent relation between the stable isotope ratios of bottom water

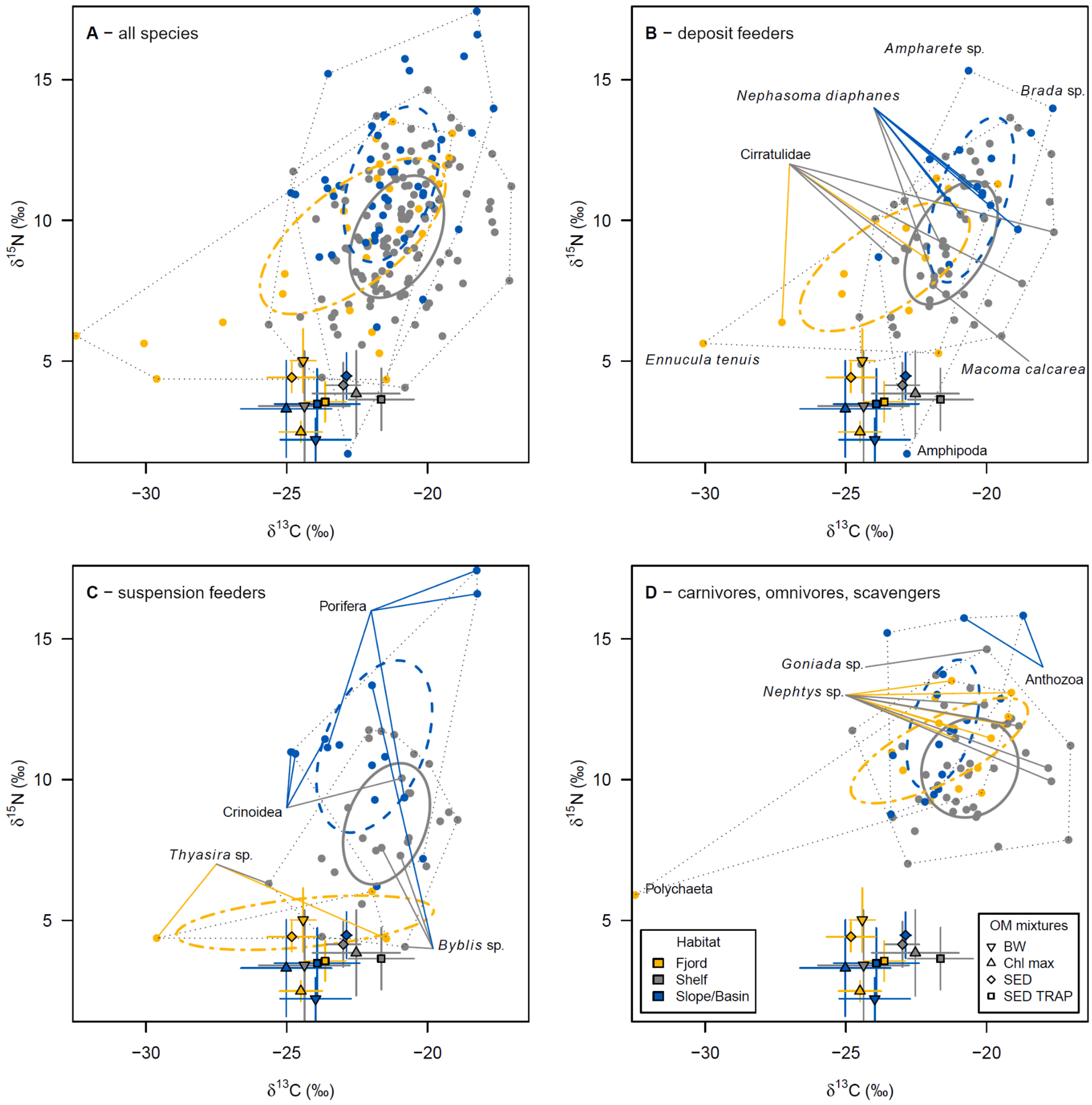

Fig. 2. Isotope biplot for macrofauna communities and organic matter (OM) mixtures. Standard ellipses (dot-dashed lines – fjord; full lines – shelf; dashed lines – slope/basin) and convex hulls (dotted lines) for (A) all species, (B) deposit feeders, (C) suspension feeders, (D) COS feeding group (i.e., carnivores, omnivores, scavengers). Sizes of standard ellipse areas (SEAs) and their pairwise overlaps are given in Table 4. Identity of selected samples is given. For all collected OM mixtures mean values for different OM types and habitats are given in each plot. Error bars indicate standard deviation and the following abbreviations are used: BW - bottom water, Chl max – depth of the subsurface chlorophyll *a* maximum, SED – sediment, SED TRAP – short-term sediment trap in the water column.

Table 2
Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values (mean ± SD) of particulate organic matter (POM) collected from Chl *a* maximum (Chl max), bottom water (BW), sediment traps (SED TRAP) and sediment (SED), in three regions (fjords, shelf, slope/basin). Significance (sig.) according to Kruskal-Wallis test and post-hoc Dunn's test is shown for each isotope among types of OM mixtures within habitats (lower case letters in italic) and for each type of OM mixture across habitats (upper case letters in bold). Lower case letters indicate groupings for each column (mixtures), while upper case groupings are given for each row (habitats) and isotope. Groups with the same letter are not significantly different while different letters mark significant differences. Number of replicates (n).

	Fjord					Shelf					Slope/Basin				
	n	δ^{13}C (‰)	sig. δ^{13}C	δ^{15}N (‰)	sig. δ^{15}N	n	δ^{13}C (‰)	sig. δ^{13}C	δ^{15}N (‰)	sig. δ^{15}N	n	δ^{13}C (‰)	sig. δ^{13}C	δ^{15}N (‰)	sig. δ^{15}N
Chl max	5	−24.5 ± 0.8	*a* - **A**	2.5 ± 0.4	*a* - **A**	24	–22.5 ± 1.6	*a,c* -**B**	3.8 ± 1.5	*a* - **A**	24	−25.0 ± 1.6	*a* - **A**	3.3 ± 1.7	*a,b* - **A**
BW	5	−24.4 ± 0.5	*a* - **A**	5.0 ± 1.1	*b* - **A**	23	−24.4 ± 1.6	*b* - **A**	3.4 ± 2.0	*a* – **A,B**	18	−24.0 ± 1.3	*a,b* - **A**	2.2 ± 0.8	*a* - **B**
SED TRAP	23	–23.6 ± 0.7	*a* - **A**	3.6 ± 0.7	*c* - **A**	63	−21.6 ± 1.2	*c* - **B**	3.6 ± 1.1	*a* - **A**	59	–23.9 ± 1.5	*b* - **A**	3.5 ± 1.3	*b* - **A**
SED	2	−24.8 ± 0.9	*a* - **A**	4.4 ± 0.5	*b,c* - **A**	7	–23.0 ± 0.6	*a,b* - **A**	4.1 ± 0.8	*a* - **A**	7	–22.9 ± 0.2	*b* - **A**	4.5 ± 0.8	*b* - **A**

and the other OM mixtures was observed for the other habitat types. In the fjords the isotopic ratios of bottom water were similar to those found in sediment samples, but had a significantly higher δ^{15}N values than the ones in the Chl max. In contrast, isotopic ratios from bottom water, sediment trap and Chl max were more alike to each other than the isotopic ratio of sediment in the slope/basin stations.

3.2. Fauna characteristics and habitat specific niche space

The samples collected in this study represented a total of 84 macrofauna taxa with mainly mobile and deposit feeding organisms prevailing in all habitats (Table A1). The macrofaunal communities associated with the different habitat types occupied three distinct isotopic niche spaces. The δ^{15}N of macrofauna in fjords and shelf spanned similar ranges of 9.16‰ (from 4.35‰ for *Thyasira* sp. to 13.51‰ for the top predators in the fjord benthic food web, *Nephtys* sp.) and 10.57‰ (from 4.06‰ for *Byblis* sp. to 14.63‰ for the top predator in the shelf benthic food web, *Goniada* sp.), respectively (Fig. 2, Table A1). In comparison to fjord and shelf, the slope/basin macrofauna was enriched in δ^{15}N and occupied a considerably larger δ^{15}N range of 15.72‰ (from 1.71‰ for an unidentified Amphipoda to 17.43‰ for Porifera - the most ^{15}N enriched sample in the slope/basin benthic food web). Despite the overall enrichment of ^{15}N in slope/basin, the occupied δ^{15}N range by the slope/basin community overlapped completely with the fjord and shelf due to a single extremely depleted sample (unidentified Amphipoda) collected from station 47 (Fig. 2, Table 5a). This sample closely reflected the isotopic composition of a fine fluffy layer (δ^{13}C: –23.07 ± 0.27‰; δ^{15}N: 2.11 ± 0.08‰) that was collected by the box corer only at this station.

Taxa that were collected from shelf and slope/basin tended to be more ^{15}N enriched in the deeper habitat for deposit feeders and suspension feeders (Fig. 2). *Thyasira* sp. and Cirratulidae had on average a higher δ^{15}N on the shelf than individuals collected from the fjords. Similarly, *Nephasoma diaphanes*, *Byblis* sp. and Crinoidea were ^{15}N enriched in slope/basin in comparison to the shelf. For *Nephtys* sp., a member of the COS feeding group, the pattern was reversed and δ^{15}N was on average lower for individuals from the shelf than for individuals from the fjords (Fig. 2).

With regard to the δ^{13}C niche, the fjord macrofauna differed clearly from shelf and slope/basin. The δ^{13}C range for fjords was much larger than for other habitats (Table 5; Fig. 2). The δ^{13}C of fjord macrofauna spanned from –32.49‰ for an unidentified Polychaeta to −19.12‰ for a *Nephtys* sp. sample. With a minimum δ^{13}C of −25.64‰ (*Thyasira* sp.) and −24.85‰ (Crinoidea) and a maximum δ^{13}C of −17.02‰ (unidentified Polychaeta) and −17.65‰ (*Brada* sp.) on shelf and slope/basin, respectively, the occupied δ^{13}C-range of these two habitats was similar (Fig. 2, Table 5). Fjord fauna was generally depleted in ^{13}C in comparison to the other two habitats (Fig. 2). The δ^{13}C of shelf and slope/basin were overall very similar (Fig. 2), although the δ^{13}C range was slightly wider for shelf fauna (Table 5).

When different feeding types were analyzed separately, it became clear that the difference between habitat types was rooted in the lower

Table 3
Sediment characteristics for the three different regions (fjord, shelf and slope/basin): sorting, grain size, chlorophyll *a* (Sed Chl *a*), chlorophyll *a* and phaeopigments ratio (Sed Chl *a*/Phaeo), organic carbon (C_{org}), total nitrogen (N_{tot}), organic carbon and nitrogen ratio (C/N), stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes values (mean ± SD). Number of replicates (n).

	Fjord		Shelf		Slope/Basin	
	mean ± SD	n	mean ± SD	n	mean ± SD	n
Sorting (μm)	3.6 ± 1.3	2	5.2 ± 1.0	7	6.0 ± 1.1	7
Grain size (μm)	290.6 ± 195.9	2	124.5 ± 54.8	7	167.5 ± 107.2	7
Sed Chl *a* (μg/g)	1.8 ± 0.5	6	7.6 ± 6.9	16	0.7 ± 0.9	20
Sed Chl *a*/Phaeo	0.5 ± 0.1	6	0.9 ± 0.7	16	0.2 ± 0.2	20
Sed C_{org} (%)	2.1 ± 0.0	2	1.5 ± 0.8	7	1.2 ± 0.4	7
Sed N_{tot} (%)	0.2 ± 0.0	2	0.2 ± 0.1	7	0.2 ± 0.1	7
Sed C/N	15.4 ± 0.7	2	10.8 ± 2.1	7	9.0 ± 0.6	7
Sed δ^{13}C (‰)	−24.8 ± 0.9	2	–23.0 ± 0.6	7	–22.9 ± 0.2	7
Sed δ^{15}N (‰)	4.4 ± 0.5	2	4.1 ± 0.8	7	4.5 ± 0.8	7

Table 4
Sizes of standard ellipse areas (SEAs) shown in Fig. 2 and pairwise overlaps of the SEAs. Size of area and overlap are given in ‰^{2}. For overlaps, the proportion of the total area covered by the two compared ellipses is also given. COS - carnivores, omnivores, scavengers.

	SEAs			Overlap		
	Fjord	Shelf	Slope/Basin	Fjord v. Shelf	Fjord v. Slope/Basin	Shelf v. Slope/Basin
All species	22.3	10.7	13.8	8.0 (32.0%)	9.3 (34.5%)	5.7 (30.4%)
Deposit feeders	18.3	10.2	12.4	5.6 (24.5%)	3.5 (13.0%)	7.0 (44.8%)
Suspension feeders	24.8	10.3	19.4	0.0 (0.0%)	0.0 (0.0%)	3.9 (15.0%)
COS	13.2	9.8	8.9	5.1 (28.4%)	5.5 (32.7%)	3.0 (19.4%)

Table 5
Layman metrics for (a) macrofaunal communities associated with different habitat types collected during the TRANSSIZ and ARCEx cruises, and (b) the different size fractions of benthic fauna collected during the ARCEx cruise.

		$\delta^{15}N$ range	$\delta^{13}C$ range	Convex hull area	Centroid Distance	Nearest Neighbor Distance (NND)	Standard Deviation NND
a)	Fjord	9.16	13.37	67.18	3.56	0.80	0.52
	Shelf	10.57	8.62	65.01	2.40	0.41	0.37
	Slope/Basin	15.72	7.20	62.95	2.61	0.68	0.76
b)	Macrofauna	10.57	15.47	95.33	2.91	0.56	0.42
	Meiofauna	8.21	4.79	27.67	1.65	0.41	0.41

trophic levels (i.e., deposit feeders, suspension feeders). The isotopic niche space occupied by higher trophic levels (carnivores, omnivores, scavengers) was similar across all habitat types (Fig. 2D, 3). In contrast, the isotopic niche space occupied by lower trophic levels (deposit feeders, suspension feeders; Fig. 2B, C) differed considerably among the habitat types (Fig. 3). Deposit feeders from fjords were strongly depleted in ^{13}C in comparison to shelf and slope/basin fauna. For suspension feeders, the three habitat types displayed a continuum of ^{15}N enrichment with fjords being most depleted, shelf fauna intermediate, and slope/basin fauna most enriched (Fig. 2). This continuum is only weakly reflected in deposit feeders and virtually absent for the higher trophic levels.

3.3. Macrofauna and meiofauna comparison

Comparing the macro- and meiofauna isotopic niches highlights some fundamental differences (Fig. 4). The isotopic niche occupied by meiofaunal primary consumers (i.e., Harpacticoida) was also occupied by macrofaunal primary consumers (Fig. 4). Meiofauna, however, only occupied a small fraction of the macrofaunal niche space. This size difference of the isotopic niche space was confirmed by a significant difference between the standard ellipse areas (Fig. 5). Harpacticoida did not occupy the part of the macrofaunal niche space that was most depleted in ^{15}N, which was the part of the community that had also a wide range of $\delta^{13}C$ (Fig. 4, Table 5b).

Similar to the primary consumers, the macrofaunal niche space occupied by higher trophic levels was significantly larger than that of meiofauna (i.e., Nematoda) (Fig. 5). For the higher trophic levels, however, the overlap of the standard ellipses of the two community components was small (Fig. 4). Further, our analysis shows that the meiofauna was depleted in ^{13}C in comparison to the macrofauna, and that most of the meiofauna was enriched in ^{15}N compared to the macrofauna.

Further, there were some differences among the meiofauna group as well. Both $\delta^{15}N$ and $\delta^{13}C$ values for Nematoda (16 replicate samples) and Harpacticoida (7 replicate samples) did not differ much in the fjord ($\delta^{13}C$: –22.18 ± 0.83 and –22.45 ± 0.53, respectively; $\delta^{15}N$: 10.25 ± 1.75 and 11.92 ± 1.60, respectively). Also there were only minor differences between $\delta^{13}C$ values on the shelf: –22.94 ± 1.01 for 22 replicate samples of nematodes and –23.25 ± 1.61 for 5 replicate samples of harpacticoids. However, the shelf $\delta^{15}N$ values of these two groups differed more: 10.34 ± 3.31 for nematodes and 7.81 ± 1.32 for primary consumers - harpacticoids.

4. Discussion

In this study we looked into the macro- and meiofauna food-web structure over a large depth gradient in the Arctic Ocean during spring. Our results suggest that in the European Arctic the properties (quality and quantity) of OM arriving to the sea floor are reflected in the food-web structure which was different in the fjords, on the shelf, and in the slope/basin habitat, and we suggest the OM quality and supply to cause this difference. We also showed that the macro- and meiofauna utilized OM differently with macrofauna mainly relying on fresher OM sedimenting to the sea floor and meiofauna utilizing reworked OM. Below we discuss our results for each of the study areas: 1) fjords, that are characterized by high PP and additional supply of terrestrial, so lower quality and more refractory OM (Hop et al., 2002; Svendsen et al., 2002; Sakshaug, 2004; Slagstad et al., 2011; Zaborska et al., 2018; Krajewska et al., 2020), 2) shelf, where fresh PP is abundant during spring in water column and available for the benthic fauna (Sakshaug, 2004; Slagstad et al., 2011; Vernet et al., 2019; Wiedmann et al., 2020a), and 3) slope and deep basin, where OM available at the sea floor is limited and mostly reworked and degraded (Codispoti et al., 2013; Matrai et al., 2013; Vernet et al., 2019; Wiedmann et al., 2020a). We also show that benthos in fjords and on the shelf displayed a high degree of omnivory and non-selective feeding while on the slope and in deep basins carnivores, omnivores and/or, scavengers dominated, and benthic communities rather relied on highly reworked OM. The habitats' characteristics and our findings on the benthic food webs are also summarized on Fig. 6.

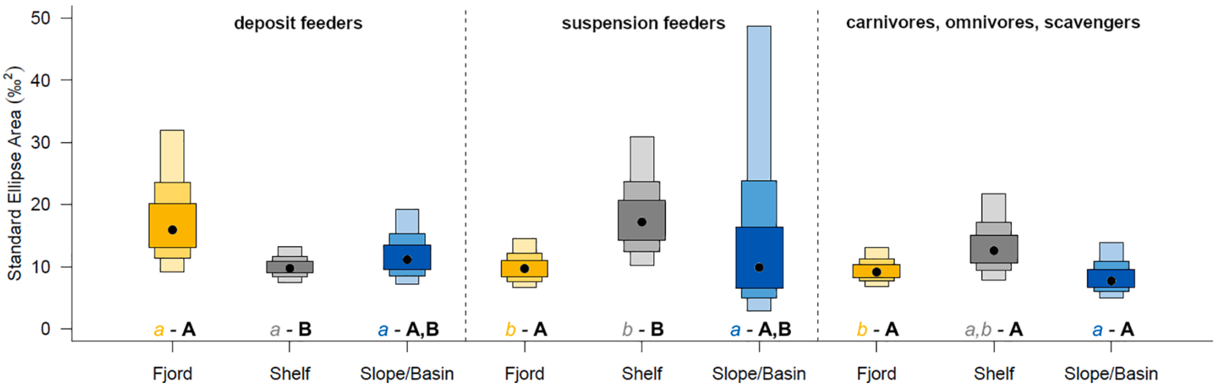

Fig. 3. Boxplot of the Bayesian standard ellipse area of three feeding types in three different community types. Dots are modes, and the boxes are 50%, 75%, and 95% credible intervals of the posterior probability distributions. Habitat type is indicated by color. Significance according to pairwise comparison by Bhattacharyya coefficient (significance level < 0.61) are given for different feeding types within one habitat (colored lower-case letters in italics) and for each feeding type across habitats (upper-case letters in bold). Groups with the same letter are not significantly different.

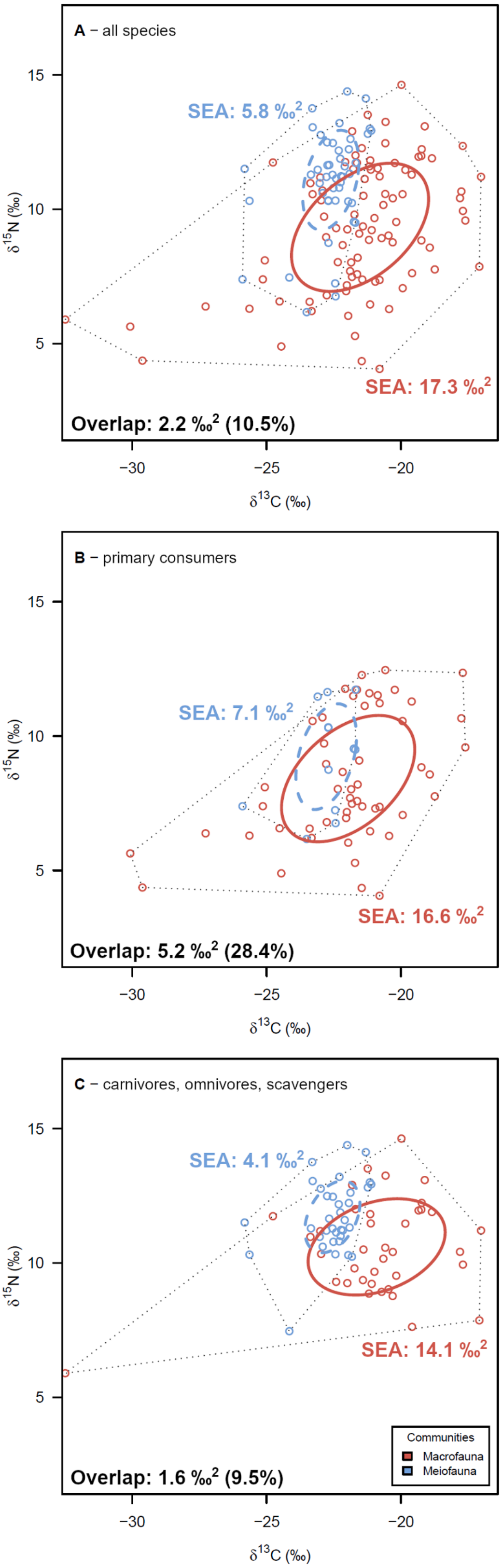

Fig. 4. Isotope biplot with standard ellipses (full lines) and convex hulls (dotted lines) for macro- and meiofauna collected during the ARCEx cruise (Table 1) for (A) all species, (B) primary consumers (i.e., deposit feeders, suspension feeders), (C) COS feeding group (i.e., carnivores, omnivores, scavengers). Sizes of standard ellipse areas (SEAs) and their pairwise overlaps are given.

4.1. Fjords

The mean δ^{13}C values of all OM samples collected in fjords during this study ranged between −24.62‰±0.74‰ and −23.6‰±0.74‰ which seem to be typical for many Arctic fjords (e.g., Sokołowski et al., 2014; Renaud et al., 2015b; Grzelak et al., 2016; McGovern et al., 2018; Zaborska et al., 2018). The concentration and isotopic composition of suspended POM in the water column give an indication of the current situation in the pelagic ecosystem, such as the stage and composition of the sympagic or pelagic spring bloom, the level of the OM degradation or the abundance of zooplankton grazers (Tamelander et al., 2006, 2009). Sediment OM mixtures, on the other hand, integrate sedimentary processes over a longer period. Sediments in the fjords studied here were depleted in ^{13}C (-24.8‰ ± 0.9) which suggests an influence of terrestrial and/or glacial runoff (Kuliński et al., 2014; Zaborska et al., 2018). As the terrestrial inflow in the inner parts of Hornsund and Van Mijenfjord can be high (Renaud et al., 2007; Zaborska et al., 2018; Włodarska-Kowalczuk et al., 2019), the OM of terrestrial origin is likely to occur throughout the whole fjords including our stations in the outer parts of the fjords.

Another potential source contributing to the low δ^{13}C values is macroalgae which often contribute to the sediment detritus and may alter the isotopic signal. For example, similar δ^{13}C values as found in our study were reported for brown algae, a possible food source for benthic communities in fjords (Renaud et al., 2015b; Buchholz and Wiencke, 2016; Silberberger et al., 2018; Buchholz et al., 2019). However, the algae's range of δ^{13}C values can also vary a lot depending on the sampling location and their age (Buchholz et al., 2019). Red algae are also a further possible source of strongly ^{13}C-depleted material (Renaud et al., 2015b) and their biomass may have contributed to the low δ^{13}C in the sediment.

Sediment OM in the fjords had elevated δ^{15}N values which suggests the presence of highly reworked OM. It is also likely that the elevated δ^{15}N values of POM, collected in sediment traps, bottom water, and sediments of the fjords may be a result of the presence of heterotrophic organisms, such as flagellates, ciliates, bacteria, as well as zooplankton fecal pellets in the pelagic system (Hirche et al., 2006; Kędra et al., 2012). In addition, the fjords' bottom water may have contained resuspended sediments, as the δ^{15}N value of the POM in the bottom water and the sediment OM was similar.

The elevated δ^{15}N values of collected OM mixtures were also reflected in δ^{15}N signature of deposit feeding macrofauna in the fjords but not for organisms with other feeding types. The fjord macrofauna community was also characterized by a low δ^{13}C signature, which reflects the low δ^{13}C of all collected OM mixtures at these locations (Fig. 2) and accordingly this suggests a predominant non-selective feeding in fjord communities. This is also in agreement with previous studies that found that in fjords and areas, where terrestrial OM, supplied by rivers and/or glaciers contributed to OM mixtures, the δ^{13}C values of benthic communities were lower than in areas where marine OM dominated (Włodarska-Kowalczuk et al., 2019; McGovern et al., 2020).

We also found extremely depleted values in three macrofauna individuals (δ^{13}C ~ -30‰), i.e., in the bivalves *Thyasira* sp. and *Ennucula tenuis*, and an unidentified Polychaeta. It is unlikely that their depleted δ^{13}C values resulted from selective feeding on terrestrial OM since the sediments at the sea floor contained mainly marine derived OM. Further, it is unlikely these organisms were feeding on red algae, because red algae are only directly utilized by very few specialized grazers, such as some gastropods (Fredriksen, 2003; Paar et al., 2019). Another possible OM source explaining the depleted ^{13}C signal of benthic fauna are free-living or symbiotic chemosynthetic bacteria (Zapata-Hernández et al., 2014). Though this signal was not reflected in our collected OM mixtures, we consider chemosynthetic derived OM as the most likely source of the extremely ^{13}C depleted fauna. Some suspension feeding bivalve species in the family Thyasiridae have chemoautotrophic sulfide-oxidizing bacteria as symbionts (Dufour, 2005). Previous studies have

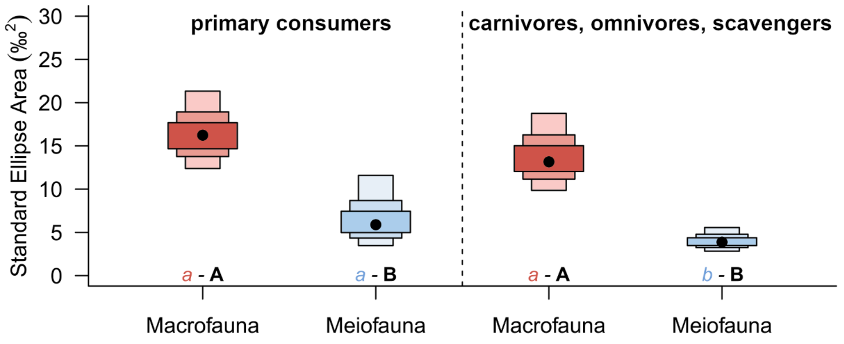

Fig. 5. Boxplot of the Bayesian standard ellipse area of two feeding types of macro- and meiofauna collected during the ARCEx cruise (Table 1). Dots are modes, and the boxes are 50%, 75%, and 95% credible intervals of the posterior probability distributions. Faunal community type is indicated by color. Significance according to pairwise comparison by Bhattacharyya coefficient (significance level < 0.61) are given for different feeding types within one habitat (colored lower-case letters in italics) and for each feeding type across community types (upper-case letters in bold). Groups with the same letter are not significantly different.

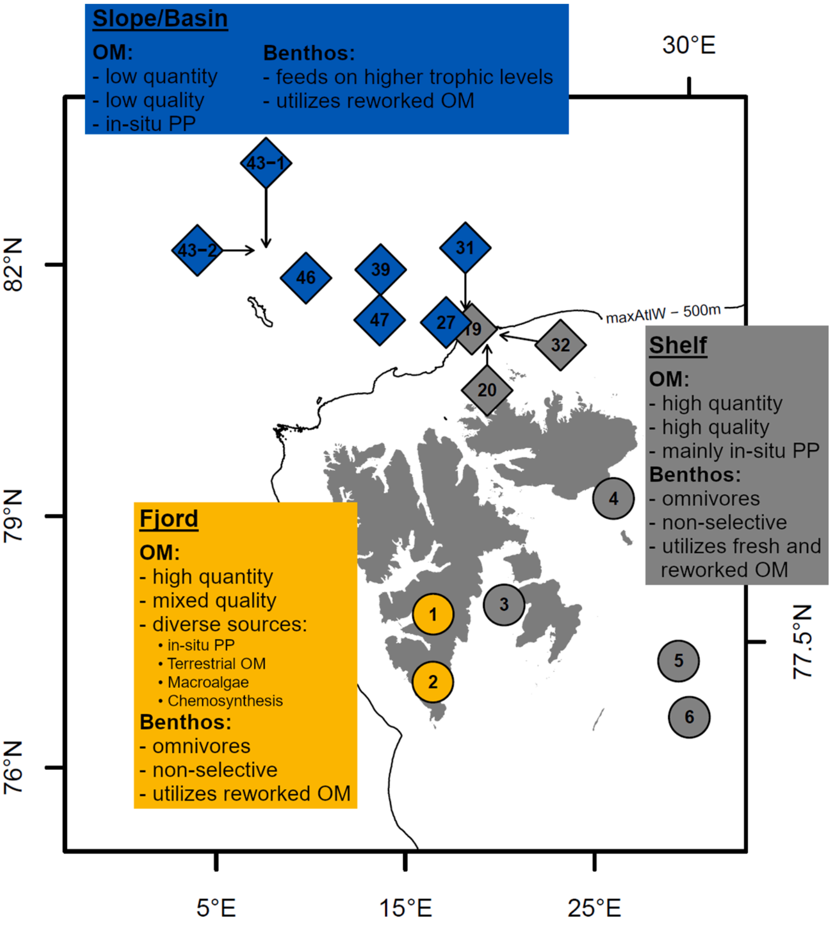

Fig. 6. Conceptual diagram showing three scenarios for benthic food webs in three different habitats: fjords, shelf, and slope/deep basin. Properties of Organic Matter (OM) supply (references provided in the text) is summarized along with benthic food-web response to the environmental and food characteristics. PP – primary production.

therefore attributed the ^{13}C depletion in Thyasiridae to chemosymbiotic bacteria (Rigolet et al., 2014; Silberberger et al., 2018) and we consider it likely that such symbionts are also the reason for the extremely ^{13}C depleted *Thyasira* sp. in our study. We also found another bivalve with a depleted ^{13}C, *E. tenuis*, which is a sub-surface deposit feeder with no chemosymbiotic bacteria. However, as bacteria are the major diet of *E. tenuis* (Kędra et al., 2021) we suggest that the isotopic signature of *E. tenuis* may be explained by sub-surface deposit feeding on free-living sulfide-oxidizing bacteria in small patches of H_2S rich sediment that may occur in the fjords (McLeod et al., 2010).

The meiofauna displayed a small δ^{13}C range in the fjords and occupied only a small fraction of the macrofaunal niche space. This, however, may have been caused by the analysis of the meiofauna samples, as it was necessary to pool large numbers of individuals to obtain sufficient material for the stable isotope analyses. Accordingly, the meiofauna samples rather represent the mean for this group while the macrofauna ones represent mainly individuals and are more likely to have outliers. Compared to macrofauna, the meiofauna signatures were depleted in ^{13}C, and mainly reflected the δ^{13}C values of the sediment OM. This suggests that meiofauna in fjords feeds exclusively on the sediment OM. Degraded OM, in form of detritus, is most likely available throughout the whole year, acting like a persistent food bank for benthic detritivores (Mincks et al., 2005). Arctic and Antarctic deep-sea nematodes have been shown to prefer bacteria over fresh phytoplankton as a carbon source (Moens et al., 2007; Ingels et al., 2010) and to feed mainly on degraded OM (Veit-Köhler et al., 2013), and this may also be the case in

Svalbard fjords. In contrast to the δ^{13}C values, meiofauna was enriched in ^{15}N compared to macrofauna in our study. This seems to further confirm that the meiofauna prefers bacterially reworked sediment OM, possibly in the form of detritus.

4.2. Shelf

The OM mixtures collected during this study on the shelf displayed a wider range of δ^{13}C values than in the other sampled habitats. The δ^{13}C signatures of POM collected from sediment traps were particularly high. In contrast, the range of δ^{15}N values was quite narrow. As the microalgae bloom was either starting or ongoing during our field campaigns and as most sampling stations (Table 1) were covered by sea ice, sea-ice algae should be considered as an additional source enriched in ^{13}C (Søreide et al., 2006). Another possible source of OM mixtures on the shelf are terrestrial OM and/or macroalgal biomass but we consider this less likely due to the location of the stations in considerable distance from the shore.

The macrobenthic food web on the shelf showed the typical structure of high latitude food webs relying on a single food source (e.g., Silberberger et al., 2018). The suspension feeders occupied an isotopic niche that suggests the consumption of OM from the bottom water. On average, suspension feeders at the shelf stations had a δ^{13}C of −21.5‰ and δ^{15}N of 8.4‰ (δ^{13}C range: −25.6 – −18.9; δ^{15}N range: 4.1 – 11.8), which were similar to the POM in the bottom water with an average δ^{13}C of −24.4‰ and δ^{15}N of 3.4‰ (δ^{13}C range: −27.7 – −22.1; δ^{15}N range: 1.2 – 7.3). Further, the δ^{13}C and δ^{15}N values of the suspension feeders indicate an average trophic enrichment of 2.9‰ and 5.0‰ for δ^{13}C and δ^{15}N, respectively. These enrichment factors fall close to the typical observed enrichment in marine Arctic food webs (Hobson et al., 1995; Renaud et al., 2015b) and are almost identical to the trophic fractionation ($\Delta^{13}C \approx 2.5$; $\Delta^{15}N \approx 5$) found on the sub-Arctic Lofoten-Vesterålen shelf during a spring bloom (Silberberger et al., 2018). In comparison to suspension feeders, the deposit feeders were slightly enriched in ^{13}C and ^{15}N. The isotopic enrichment was, however, not equally pronounced in all collected deposit feeders and as a result a more elongated standard ellipse was found (Fig. 2b). This extended isotopic niche is probably caused by the difference between surface and sub-surface deposit feeding. Surface deposit feeders are likely to ingest freshly settled OM with isotopic signatures similar to the bottom water, while sub-surface deposit feeders consume larger quantities of old, bacterially reworked OM. Consequently, the average isotopic ratios of surface deposit feeders were identical to suspension feeders (δ^{13}C = -21.5‰; δ^{15}N = 8.4‰), while the subsurface deposit feeders had on average elevated values (δ^{13}C = -21.0‰; δ^{15}N = 9.9‰). The COS (carnivores, omnivores, scavengers) group was even further enriched in both isotopes (δ^{13}C = -20.6‰; δ^{15}N = 10.4‰), which indicates the higher trophic level of organisms in this group. However, the difference between COS and the primary consumer groups falls short of the typical trophic enrichment for the trophic step from primary to secondary consumers ($\Delta^{13}C \leq 1$‰; $\Delta^{15}N \sim 3$‰) (Post, 2002; McCutchan et al., 2003). In addition, a considerable overlap among the isotopic niches of the three feeding types was observed which is indicative for a high degree of omnivory in shelf benthic food webs (Bridier et al., 2021). Włodarska-Kowalczuk et al. (2019) reported the same realized trophic niche for the same feeding groups fauna at the fjord-shelf boundary in Hornsund (Fig. 1). This similarity in food-web structure and functioning on the shelf and at the fjord mouth suggests that the transition from fjord food webs to shelf food webs is located within the fjord.

Some of the taxa collected in fjords and on shelf tended to have lower δ^{13}C values in the fjords. The δ^{13}C signatures of deposit feeding cirratulidae polychaetes most likely reflect lower δ^{13}C signatures of OM. A similar pattern of lower δ^{13}C signatures in the fjords was observed for *Nephtys* sp. This species most likely can switch to predatory feeding mode when diverse and abundant OM is available (and thus abundant benthic communities), like in the fjords. On the shelf, where food becomes more limited than in fjords, *Nephtys* most likely has to display more diverse diet including deposit feeding. A similar ability to switch diet from predatory to omnivory in certain habitats was reported from tidal flat sediments for *Nephtys hombergii* (Schubert and Reise, 1986). It is however possible that the switch in diet we observed is rather result of species specific diet preferences that we were not able to detect as we only identified our specimens to genus level. Such possibility was also discussed by Schubert and Reise (1986) who suggested that *N. hombergii* they studied was a species complex. Still, the diet switch seems to be more likely explanation as benthic species in the Arctic and in deep areas commonly exhibit a high degree of omnivory accompanied by multiple feeding behaviors and ability to change their diet temporally (Iken et al., 2010; Kędra et al., 2012, 2019). Such high plasticity of feeding behaviors allows benthic organisms to adapt to the accessibility and quality of the OM by switching the sources of OM and/or the feeding behavior (Stead and Thompson, 2006; Morata et al., 2015). Also, there are many indices that such diet switch is possible for some benthic species in the Arctic [e.g., bivalves *Macoma* sp., *Yoldia hyperborea*, polychaete *Praxillella praetermissa* (Kędra et al., 2019, 2021)] and in temperate areas [e.g., *Macoma balthica* (Törnroos et al., 2015; Silberberger et al., 2021; Szczepanek et al., 2021), polychaete *Hediste diversicolor* (Szczepanek et al., 2022)].

The δ^{13}C values of both meiofauna groups (harpacticoids and nematodes) well reflected the δ^{13}C values of shelf sediment OM. This indicates that, similarly to the fjords, meiofauna on the shelf relied mainly on the sediment OM. With regard to the δ^{15}N values, the meiofauna on the shelf mainly differed with regard to their δ^{15}N values: harpacticoids had low δ^{15}N values, and though this was also true for nematodes, the range of nematode δ^{15}N values was there much larger. The difference between δ^{15}N values of harpacticoids and nematodes points to their feeding preferences and trophic levels. Nematodes are either deposit feeders, omnivores or predators (Moens and Vincx, 2009; Soltwedel et al., 2018) and their isotopic signatures show that they most likely fed on bacterially reworked OM (Figs. 4, 5). Harpacticoida, although less abundant than nematodes in marine sediments, are important grazers on PP including microalgae such as diatoms but also often select bacteria as their main food source or choose detritus (De Troch et al., 2006; Wyckmans et al., 2007; Cnudde et al., 2015). As the stations located on the shelf were mostly sampled in the early or mid-bloom condition (Dybwad et al., 2021) the fresh algal biomass sinking from the water column was expected in the sediments and the sampled harpacticoids probably grazed fresh phytoplankton biomass. This is corroborated by the large input of fresh OM caused by the ballasting of gypsum in this area during the 2015 campaign (Wollenburg et al., 2018). Ballasting of gypsum seems to be a re-occurring feature in the Atlantic water influenced first year ice of the Arctic Ocean (Wollenburg et al., 2020) allowing patchy input of fresh OM to the benthos.

4.3. Slope and deep-sea basin

The characteristics of the sediment OM in the deep areas (>500 m) suggest the predominance of marine, reworked OM. The amount of fresh OM in these sediments was low, as indicated by the low Chl *a* concentration and low Chl *a*/Phaeo ratio in the sediments (Table 3). Compared to the sediment OM, the POM in the water column (Chl max, sediment traps and in bottom water) was depleted in ^{15}N and ^{13}C. This suggests mostly pre-bloom conditions in the water column and a weak pelagic-benthic coupling particularly around the Yermak Plateau, as also found by Dybwad et al. (2021). The macrobenthic food web at the deeper sampling stations on the slope and in the basin was quite different from the fjords and shelves. The δ^{15}N was elevated for all feeding modes and the isotopic niches occupied by the different feeding groups overlapped to a large extent (Fig. 2). As mentioned above, a large niche overlap typically indicates a high level of omnivory, but this conclusion cannot be drawn for our deep stations. The particularly large difference between δ^{15}N of benthic fauna and the OM sources (Fig. 2) suggest an almost complete absence of any primary consumers from the deep stations and a predominant COS feeding mode for all macrofauna. While the latter is certainly true for some species (e.g., two apparently carnivorous sponges with $\delta^{15}N > 16‰$ among the suspension feeders; Fig. 2C), we propose three different mechanisms that likely caused the observed isotopic composition in the three feeding types and large niche overlap.

First, the deposit feeders are potential secondary consumers of sediment OM, as they may receive (parts of) their nutrition from microbial communities in their guts (Romero-Romero et al., 2021). Romero-Romero et al. (2021) demonstrated that abyssal deposit feeding echinoderms are secondary consumers of their own gut bacteria. Through this trophic interaction, the bulk isotopic composition of the echinoderms increased by 2-4‰ and 4-7‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. As we observed a similar difference (about 2.5‰ and 6.8‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively) between deposit feeders and sediment at the slope/ basin stations, we presume that a similar trophic link via gut bacteria may have been taken place also in other deposit feeders than echinoderms.

Second, suspension feeders in deep habitats are unlikely to rely on sediment OM alone because resuspension of sediments is usually limited at the sea floor in deep regions. Trophic fractionation via gut bacteria as described above is here however unlikely as the suspension feeders from the deep stations had a considerably lower $\delta^{13}C$ than the deposit feeders. Since the bottom water, the second possible OM source at the slope and in the basin, was more depleted in ^{15}N than the sediment, OM from this source would suggest an even higher trophic level for suspension feeder. It is however possible that OM with an isotopic signature similar to the one in the bottom water reached the sea floor shortly before our sample collection and that the suspension feeders did not reflect this isotopic signature due to a longer turnover time. A similar observation has been made during an ongoing spring bloom on the Vesterålen shelf in Northern Norway. There only suspension feeders reflected the spring bloom isotopic signal, while all other fauna reflected the winter isotopic baseline that was 3.1‰ higher for $\delta^{15}N$ than in the spring bloom (Silberberger et al., 2018). Among the suspension feeders in this study, a Bryozoan ($\delta^{15}N = 8.9‰$) and a Polychaete (*Euchone analis*; $\delta^{15}N = 7.2‰$) showed signs of a potential feeding relation to the OM in the bottom water (Fig. 2C). Since the ice cover was close to 100% at all deep stations (Table 1), and at most stations characterized by early or even pre-bloom conditions (Dybwad et al., 2021), a very limited spring isotopic signal may have been present in the OM sources, though not (yet) reflected in any fauna.

Third, the similarity in the $\delta^{15}N$ of all feeding modes found on the slope and in the basin suggests that the COS feeding group seems not to feed on other macrofauna. We suggest two alternative potential trophic pathways that may sustain the deep-sea COS feeding group: (1) The COS group may feed on foraminifera and meiofauna that may respond faster to seasonal pulses of OM in the deep sea (Nomaki et al., 2005); (2) The COS feeding group may rely on secondary production from shallow waters that reaches the sea floor in the form of dead zooplankton (Daase et al., 2021), large food falls like fish or whales (Klages et al., 2001), unsuccessful settling meroplankton (Ershova et al., 2019; Silberberger et al., 2021), or transport of OM via nepheloid layers (Thomsen et al., 2001).

Unfortunately, we do not have data for meiofauna food webs in the slope/deep basin area but other studies suggest that deep-sea meiofauna in polar regions feeds on reworked material and/or bacteria and prefers it over fresh OM (Moens et al., 2007; Ingels et al., 2010; Veit-Köhler et al., 2013). Nematodes were also reported to be able to exploit older and more refractory organic compounds (Rudnick, 1989; Iken et al., 2001). At the same time, the reported meiofauna uptake of OM in the deep sea is low (Moens et al., 2007; Ingels et al., 2010) although their contribution to total (macro- and meiofauna) biomass and production increases with increasing depth (Górska et al., 2020; Oleszczuk et al., 2021).

4.4. Comparison of benthic communities along the fjord – shelf – slope/deep basin gradient

Along the fjord – shelf – slope/basin gradient we found different macrofaunal communities. The fjord macrobenthic food webs differed from open shelf food webs because in fjords: 1) terrestrial derived OM is utilized (non-selective), 2) diversity of suspension feeders in sedimentary habitats is low, and 3) some specialized taxa that utilize additional OM sources (e.g., chemosynthesis, macroalgae) are present. Our results suggest that on a regional scale (Svalbard - northern Barents Sea region) there was overall similar benthic food web structure for fjords and shelves, but these shallow parts varied mainly dependent on how much terrestrial and/or glacial impacts they received (Kuliński et al., 2014; Zaborska et al., 2018). Both new and old OM are directly consumed by macrofauna which shows signs of high omnivory. However, the new OM is mainly utilized by suspension and surface deposit feeders while the old OM is rather consumed by subsurface deposit feeders. So far, this similarity between fjord and shelf food webs was only identified in single fjords and their directly adjacent shelf (Renaud et al., 2011; Silberberger et al., 2018) and our study illustrates that this seems to be a more general pattern in the European Arctic.

The meiofauna seems to display similar feeding patterns in fjords and on the shelf though it is likely that on the shelf primary consumers take advantage of fresh primary biomass when available (Wiedmann et al., 2020b; Dybwad et al., 2021). The primary consumers and omnivore nematode showed similar $\delta^{13}C$ patterns on the shelf and in the fjords, however, the latter displayed a much larger range of $\delta^{15}N$ which is likely a result of their unlike feeding preferences and the different trophic levels they occupy. We do not have results for deep-sea meiofauna but other studies show that in the deep-sea meiofauna mainly relies on reworked OM (Moens et al., 2007; Ingels et al., 2010; Veit-Köhler et al., 2013).

The main differences between shallow (<500 m depth) regions and deeper ones (>500 m) were likely related to the differences in the OM quality and quantity (Bluhm et al., 2020; Dybwad et al., 2021). Our data however show that the sediment OM in the areas below 500 m were similar to the one collected on the shelf with regard to the quality characteristics such as $\delta^{15}N$ and $\delta^{13}C$ values, and the C/N ratio, but that the amount of fresh sediment OM in the deeper areas was much lower compared to shelf as indicated by the sediment Chl *a* concentrations. This resulted in distinct and specific trophic relations of deep-sea fauna with no primary consumers and a predominant COS feeding mode for the macrofauna. The limited access to high-quality food with increasing depth results in decreasing standing stocks and production of macrofauna (Oleszczuk et al., 2021). Meiofauna seem to be much less limited due to its ability to utilize OM that is unavailable to macrofauna (McLachlan and Brown, 2006). As a result, the nematode production might be several times higher than the macrofauna production (Oleszczuk et al., 2021) which suggests that the role of meiofauna is particularly important in the deep-sea food webs where the available OM is scare and often highly reworked. Moreover, our results propose that at least some of the sampled macrofauna species could feed on meiofauna and this makes meiofauna an important link between bacterial OM and higher trophic levels.

5. Summary

In this study, we determined the macro- and meiofauna food-web structure over a large depth gradient (fjords, shelf, slope/Arctic Ocean basin) during spring. Our study revealed differences between the benthic food webs in the three studied habitat types and between the macro- and meiofauna components of benthic communities. We showed that the meiofauna, which was only sampled in fjords and on the west southern Barents Sea shelf, mainly relied on the bacterially reworked OM in the sediments, most likely in form of detritus. Macrofauna on the other hand, relied more on fresh OM arriving through the water column to the sea floor. Moreover, our results suggest that the food webs in the fjords utilize more diverse OM sources in comparison to shelf and deeper areas (Fig. 6). A distinct functional difference between fjord, shelf, and slope/basin benthic food webs was also observed. Benthic food webs were overall similar in the fjords and on the shelf displaying a high degree of omnivory and non-selective feeding – the latter particularly in the fjords where benthos utilized terrestrial OM in addition to marine sources (Fig. 6). On the slope and in the deep basin macrobenthos seems to utilize highly reworked OM and the dominant feeding type is COS (Fig. 6). Our results show that the benthic food web isotopic characteristics rely on the quality and quantity of OM flux to the sea floor and have implications for further studies related to climate change induced shifts in the OM production. As the OM quantity and quality are major drivers of trophic relations across the depths gradients the benthic food webs will face cascading effects following the modification of the pelagic food webs due to climatic changes. At the same time this systemic change may be mitigated by high feeding plasticity of feeding behaviors of benthic species (e.g., Kędra et al., 2019; 2021; Szczepanek et al., 2021).

CRediT authorship contribution statement

Barbara Oleszczuk: Conceptualization, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing – original draft. **Marc J. Silberberger:** Conceptualization, Formal analysis, Methodology, Visualization, Writing – review & editing. **Katarzyna Grzelak:** Investigation, Methodology, Resources. **Aleksandra Winogradow:** Investigation. **Christine Dybwad:** Investigation. **Ilka Peeken:** Investigation. **Ingrid Wiedmann:** Investigation. **Monika Kędra:** Conceptualization, Funding acquisition, Investigation, Project administration, 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.

Data availability

Data will be made available on request.

Acknowledgements

The presented material was collected during the R/V Polarstern TRANSSIZ cruise (ARK XXIX/1; PS92), carried out under grant number AWI_PS92_00 and organized by Arctic in Rapid Transition (ART), and during the R/V Helmer Hanssen ARCEx cruise 2016 (ARCEx - The Research Center for Arctic Petroleum Exploration), funded by the Research Council of Norway (project no. 228107), together with 10 academic and 8 industry partners. The study was completed with funding provided by the National Science Centre, Poland (grant no. 2015/19/B/NZ8/03945 to MK and partly by 2016/20/S/NZ8/00432 to KG). We would like to thank the Leading National Research Centre (KNOW) received by the Centre for Polar Studies for the financial support to BO. MJS was further supported by the National Science Centre, Poland grant no 2019/35/D/NZ8/01282 (CLIMB), MK and IW received additional funding from the European Union's Horizon 2020 research and innovation programme under Grant Agreement No. 869383 (ECOTIP), and IP was funded by the PoF IV program "Changing Earth - Sustaining our Future" Topic 6.3 of the German Helmholtz Association.

Appendix

Table A1

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values (mean ± SD) for macrofauna collected in three different regions (fjord, shelf, slope/basin). Number of replicates (n) is given for more than one replicate. Mobility and food type are marked by symbols: mobility type (D-Discretely motile - organisms capable of moving from place to place but remains sessile while feeding, M−Mobile - organisms able to freely move, S-Sessile - attached organisms that cannot move freely) and feeding type (sur-surface deposit feeder, sub-subsurface deposit feeder, sus-suspension feeder, car-carnivore, omn-omnivore, sca-scavenger). Samples for which only one isotope was analyzed were not included in the statistical analysis.

Taxonomic group/taxon	Mobility/ Food type	Fjord			Shelf			Slope/Basin		
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	n
Annelida										
Aglaophamus malmgreni	Mcar	−21.43 ± 2.08	11.74 ± 0.67	3						
Ampharete sp.	Dsur				−21.55	9.27		−20.25 ± 0.55	12.93 ± 3.38	2
Aphalochaeta sp.	Dsur	–22.17	8.67							
Axiothella catenata	Dsub				–23.19	5.94				
Brada sp.	Dsur							−17.65	13.98	
Bylgides sp.	Mcar				−20.47	9.02				
Capitella capitatta	Dsub	−21.71	5.28		−20.06	11.29				
Chirimia biceps	Dsub				−19.93 ± 0.79	12.14 ± 1.87	3			
Cirratulidae	Dsur	−27.27	6.38		−19.86 ± 2.98	8.64 ± 0.91	3			
Cirrophorus sp.	Dsur				–22.48	9.40				
Dodecaceria sp.	Dsur				–22.91	9.01				
Enipo sp.	Mcar				−20.70 ± 0.55	9.00 ± 0.32	2			
Ephesia gracilis	Msur							–22.02	12.17	
Eteone longa	Momn				–22.80	7.01				
Euchone analis	Ssus				–22.82	9.00		−20.16	7.19	
Gattyana sp.	Mcar				−20.72	8.93				
Goniada sp.	Mcar				−19.99	14.63				
Harmothoe sp.	Mcar				−18.61	10.95				
Laphania boecki	Dsur							−20.96	12.50	
Lumbrineris mixochaeta	Mcar	−20.65 ± 0.48	10.04 ± 0.52	2	−19.12	12.17				
Lumbrineris sp.	Mcar	−21.58 ± 1.97	9.93 ± 0.57	2						
Maldane sarsi	Dsub				−20.94 ± 1.18	11.21 ± 0.84	6	−20.33	11.20	
Maldanidae	Dsub				−20.87	11.52		−19.83	12.20	
Myriochele heeri	Dsur				−21.44	9.04		–23.84	8.70	
Naineris sp.	Msub				−19.47	5.89				

(continued on next page)

Table A1 (*continued*)

Taxonomic group/taxon	Mobility/ Food type	Fjord			Shelf			Slope/Basin		
		δ^{13}C (‰)	δ^{15}N (‰)	n	δ^{13}C (‰)	δ^{15}N (‰)	n	δ^{13}C (‰)	δ^{15}N (‰)	n
Nephtys sp.	Mcar	−20.30 ± 0.98	12.22 ± 0.87	6	−18.74 ± 1.00	11.38 ± 1.15	5			
Nicomache lumbricalis	Dsub				−18.88	13.29				
Notoproctus oculatus	Dsub				−20.40	12.11				
Oligochaeta	Msub				−21.35	8.10				
Orbiniidae	Msub				−17.70	12.36				
Pectinaria hyperborea	Dsub				–22.20 ± 0.83	8.58 ± 0.54	2			
Polychaeta	Momn	–32.49	5.90		−18.37 ± 1.90	11.57 ± 0.51	2			
Polycirrus arcticus	Dsur	–22.11 ± 1.07	10.43 ± 0.99	2						
Polydora sp.	Dsur				−17.76	10.66		−21.33	8.43	
Praxillella sp.	Dsub				−21.46	12.27				
Praxillella praetermissa	Dsub				−19.59	10.73				
Protula tubularia	Ssus				−20.48	10.91				
Scoletoma sp.	Mcar	−21.82	12.90		−20.58	13.25				
Sphaerodoridium sp.	Momn				–23.00	11.18				
Syllis sp.	Mcar				−21.11	11.46				
Terebellides stroemii	Ssur				–22.92	10.70				
Arthropoda										
Byblis sp.	Dsus				−21.13 ± 0.44	6.32 ± 1.96	3	−21.97	13.35	
Corophium sp.	Dsus				−22.08	11.47				
Crustacea	Dsur				−20.93 ± 0.57	7.58 ± 1.41	3	−21.47 ± 1.92	5.93 ± 5.96	2
Eudorella emarginata	Msur				–22.67 ± 0.93	6.69 ± 0.68	2			
Harpinia sp.	Momn				−20.92	10.40				
Lyssianasidae	Msca				–23.09 ± 2.37	10.55 ± 1.68	2			
Orchomene sp.	Msca	–22.00	9.25							
Tanaidacea	Dsur				−20.93	10.20				
Bryozoa										
Bryozoa	Ssus				−20.47 ± 0.37	7.54 ± 0.55	3	–22.27 ± 0.75	8.91 ± 2.53	3
Cnidaria										
Actinaria	Mcar				−21.80	13.71				
Anthozoa	Mcar				−21.40	10.50		−19.75 ± 1.48	15.79 ± 0.07	2
Echinodermata										
Amphiura sp.	Dsus				−19.94	10.56				
Asteroidea	Mcar							−19.50	12.87	
Crinoidea	Ssus				−20.91	10.05		−24.40 ± 0.66	11.12 ± 0.28	3
Ophiophalis aculeata	Dsus				−21.41 ± 0.33	11.66 ± 0.09	2			
Ophiura sarsi	Mcar				−21.00 ± 1.10	9.49 ± 1.14	5			
Ophiura sp.	Momn				–23.34	8.66		−21.98 ± 0.90	11.30 ± 1.90	13
Ophiuroidea	Momn				−20.76 ± 1.26	9.75 ± 0.94	3			
Fluffy sediment										
Fluff	–							–23.07 ± 0.27	2.11 ± 0.08	2
Mollusca										
Astarte borealis	Dsus				–22.08	11.76				
Axinopsida serricata	Dsus	−21.97	6.03							
Axinopsida sp.	Dsus				−22.33	5.58				
Bathyarca glacialis	Dsus				−20.64 ± 0.04	9.52 ± 0.00	2	−21.74 ± 0.32	10.66 ± 0.21	2
Bathyarca sp.	Dsus				−23.76	7.20				
Chaetoderma sp.	Msub				−24.52	6.57				
Chlamys islandica	Dsus				–23.53 ± 0.32	5.56 ± 1.61	2			
Ciliatocardium ciliatum	Dsus				−21.83	7.48				
Cuspidaria sp.	Dcar				−21.56 ± 0.96	10.35 ± 2.24	3			
Ennucula tenuis	Msub	−30.07	5.63		−23.93 ± 0.75	5.73 ± 1.18	2			
Euspira palida	Mcar				−21.19	8.86				
Frigidoalvania sp.	Msur				−23.96	10.05				
Gastropoda	Msur				−22.35	8.03				
Liocyma fluctuosa	Dsus				−19.24	8.84				
Macoma calcarea	Dsur				−21.90	7.70				
Menestho truncatula	Dsur	−20.69 ± 1.54	11.39 ± 0.15	2						
Musculus discors	Dsus				−18.93	8.57				
Nuculana pernula	Dsur				−21.68 ± 0.47	7.14 ± 0.80	3			
Nuculana radiata	Dsur				−21.44	7.38				
Oenopota sp.	Mcar				−17.09	7.86				
Thyasira gouldi	Dsus	−25.54 ± 5.77	4.36 ± 0.01	2	−25.64	6.30				
Yoldia hyperborea	Dsub	–23.92 ± 1.63	7.45 ± 0.92	2	−21.04 ± 1.55	8.07 ± 1.43	2			
Yoldiella lenticula	Dsub	−25.14	7.39							
Porifera										
Porifera	Ssus				−20.92 ± 1.95	8.22 ± 0.42	2	−20.21 ± 2.54	13.63 ± 3.98	4
Sipuncula										
Nephasoma diaphanes diaphanes	Dsur				−21.65 ± 0.28	8.32 ± 0.66	2	−20.31 ± 0.95	10.50 ± 0.54	5

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