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Trophic niches of macrobenthos: Latitudinal variation indicates climate change impact on ecosystem functioning

Marc J. Silberberger[1,2] ◉ | Katarzyna Koziorowska-Makuch[1] | Henning Reiss[3] |
Monika Kędra[1]

[1]Institute of Oceanology Polish Academy of Sciences, Sopot, Poland

[2]Department of Fisheries Oceanography and Marine Ecology, National Marine Fisheries Research Institute, Gdynia, Poland

[3]Faculty of Biosciences and Aquaculture, Nord University, Bodø, Norway

Correspondence
Marc J. Silberberger, Institute of Oceanology Polish Academy of Sciences, Powstańców Warszawy 55, Sopot 81-712, Poland.
Email: marc.silberberger@gmail.com

Abstract

Benthic food-web structure and organic matter (OM) utilization are important for marine ecosystem functioning. In response to environmental changes related to the ongoing climate change, however, many benthic species are shifting their ranges to colder regions, which may lead to altered community composition, but it remains largely unknown how it will affect ecosystem functioning. Here, stable isotope analysis was used to study benthic OM utilization and food-web structure and to assess whether their spatial patterns reflect today's community differentiation among biogeographic regions and depth zones. Benthic fauna and OM mixtures were collected from two depth zones (100–150 m vs. 200–250 m) within a temperate, two sub-Arctic, and an Arctic fjord along a latitudinal gradient (59–78°N) that was used as a space-for-time substitution to assess the impact of climate change. Our results showed that Arctic and temperate communities are functionally different. Arctic communities were characterized by a strong resource partitioning among different feeding types, irrespective of depth zone. In contrast, all feeding types in temperate communities seemed to rely on sedimentary OM. The sub-Arctic presented a transition zone. In the sub-Arctic, shallower communities resembled Arctic communities, suggesting a functional transition between temperate and sub-Arctic regions. Deeper sub-Arctic communities resembled temperate communities, suggesting a functional transition between the sub-Arctic and Arctic regions. This implies that the regions north of the current transitions (deep Arctic and shallow sub-Arctic) are most likely to experience functional changes related to an altered OM utilization in benthic food webs in response to climate change.

KEYWORDS
benthic macrofauna, depth, isotopic niche, marine food webs, space-for-time substitution, stable isotope analysis

1 | INTRODUCTION

Climate change affects primary production, vertical organic matter (OM) fluxes, and species distribution globally (Griffiths et al., 2017; Pinsky et al., 2020), and accordingly, profound changes in ecosystem functioning must be expected. Benthic food-web dynamics and trophic structure are among the marine ecosystem properties projected to change most drastically (Doney et al., 2012; Griffiths

et al., 2017). Benthic communities are an important component of marine ecosystems that plays a crucial role in determining the fate of OM, whether it is OM remineralization (Silberberger et al., 2022), its assimilation as biomass available to higher trophic levels (Hobson et al., 2002; Silberberger et al., 2018), or long-term storage in the sediment (Włodarska-Kowalczuk, Mazurkiewicz, et al., 2019).

Fjords have been identified as particularly important habitats regarding the marine carbon cycle globally, since 11% of the annual marine carbon burial occurs in fjords (Smith et al., 2015). While high carbon burial rates and long-term carbon storage are characteristic of all fjords due to their restrictive nature (Smeaton et al., 2016), the quantity and quality of sediment OM (SOM) vary between and within fjord systems. SOM in all inner fjord basins is typically dominated by terrestrial OM (Faust & Knies, 2019), and accordingly, SOM composition in inner basins is very fjord-specific, depending on the fjord's catchment. For example, glacial-influenced Arctic fjords receive large quantities of ancient OM (Kim et al., 2011), while sub-Arctic and temperate fjords with forested catchment areas receive a large quantity of terrestrial detritus (McGovern et al., 2020). In contrast, SOM in the outermost basins—the border between fjords and shelf—of the European Boreal-Arctic fjords is typically dominated by OM of marine origin (Faust & Knies, 2019). This marine OM is considered a suitable food source for the rich benthic communities in this part of the fjords (Włodarska-Kowalczuk et al., 2012). While this holds true for all outer fjord basins, distinct latitudinal differences in quantity and quality of SOM have been found in outer basins of fjords along the European Boreal-Arctic coast (Faust & Knies, 2019; Włodarska-Kowalczuk, Mazurkiewicz, et al., 2019). Sediments of temperate fjords were reported to have a particularly high OM content that is about twice the content of sub-Arctic or Arctic fjords (Włodarska-Kowalczuk, Mazurkiewicz, et al., 2019). Approximately one third of this OM has a terrestrial origin in the outer basins of temperate fjords (Włodarska-Kowalczuk, Mazurkiewicz, et al., 2019). In contrast, the contribution of terrestrial OM to SOM in the sub-Arctic is low, while Arctic fjords have a higher terrestrial OM load due to glacial erosion of ancient OM that can represent almost half the SOM in the outer basins of some Svalbard fjords (Faust & Knies, 2019; Włodarska-Kowalczuk, Mazurkiewicz, et al., 2019). Although these patterns of OM accumulation have been recognized, it has not been studied in detail how benthic communities utilize the OM and how this in turn affects benthic food-web structure and functioning.

Improving our current understanding of how OM properties are linked to benthic OM utilization is crucial, since northern Atlantic and Arctic fjords are located in a region most strongly impacted by the ongoing climate change (Hoegh-Guldberg & Bruno, 2010). Temperature increase, earlier snow melt, prolonged stratification, and productive period are occurring simultaneously in this region as a result of the climate change, with profound changes for marine ecosystems (Hoegh-Guldberg & Bruno, 2010; Ingvaldsen et al., 2021; Silva et al., 2021). Benthic food webs and ecosystem functioning will likely be affected by the poleward shift of species (Renaud, Sejr, et al., 2015; Węsławski et al., 2011) and an altered OM flux to the seafloor (Griffiths et al., 2017). Furthermore, temperature, benthic community structure, and the vertical flux of OM are also changing with depth (Jordà

Molina et al., 2019; Sen et al., 2022). In fjords from mainland Norway, a depth separation of benthic community structure has been identified that occurs at approximately 200m (Sen et al., 2022). While Sen et al. (2022) reported no significant differences in macrofaunal richness, abundance, or diversity among the different depth zones, they found that different species compositions were responsible for the separation in deep and shallow communities. It remains, however, unknown what environmental drivers are responsible for this separation, whether shallow and deep communities are functionally different, and whether climate change will affect benthic ecosystems functioning at different depths in the same way.

There are only a few studies that have looked into the trophic niches of benthic communities in sedimentary habitats in North Atlantic and Arctic fjords (Renaud, Løkken, et al., 2015; Włodarska-Kowalczuk, Aune, et al., 2019). The majority focused on shallow coastal environments characterized by abundant macroalgae (Bridier et al., 2021; Fredriksen, 2003; Kędra et al., 2012) or considered the benthic compartment primarily as a trophic pathway to higher trophic levels (Nilsen et al., 2008; Renaud et al., 2011; Silberberger et al., 2018). Nonetheless, these studies found that food webs in outer fjord regions resembled food webs on the open shelf (Renaud et al., 2011; Silberberger et al., 2018), while inner basins' food webs are distinctly different due to the local environmental conditions (e.g., terrestrial influence—Włodarska-Kowalczuk, Aune, et al., 2019).

Here we study trophic niches (i.e., OM utilization) and food-web structure of macrobenthic communities along a latitudinal gradient (60–78° N) and in different depth zones (100–150m vs. 200–250m) in the outer part of European fjords. This large latitudinal gradient is used as a space-for-time substitution to study the possible impacts of climate change on OM utilization and ecosystem functioning. We expect deeper communities (200–250m) to rely primarily on sedimentary OM as a "food bank" across all climate zones (Smith et al., 2012) due to a high rate of OM processing in the water column and the majority of OM reaching the seafloor as low-quality food (Andreassen et al., 1999). In contrast, shallow communities (100–150m) are expected to differ between biogeographic sub-regions as they are well adapted to the location-specific seasonal succession of temperature, stratification depth, and OM flux and therefore are expected to utilize more abundant fresh OM reaching the seafloor at the shallower depths. Consequently, we hypothesize that the functioning of shallow communities is more vulnerable to climate change-related shifts in seasonality, while deep communities are more resilient toward this process.

2 | MATERIALS AND METHODS

2.1 | Study sites

Our study compares resource utilization and food-web structure in the outer part of four European fjords along a latitudinal gradient that includes three climate zones (Table 1, Figure 1). Selbjørnfjord is a cold temperate fjord in the northern North Sea on the western Norwegian coast. Saltfjord and Malangen are two sub-Arctic

TABLE 1 Study site characteristics and environmental data.

Fjord	Lat	Lon	Dep	Date	BW					SW	SED			
					Tem	Sal	Chl a	Chl a/phaeo	C_{org}	Chl a	MGS	Chl a	Chl a/phaeo	C_{org}
Isfjord	78.249	13.978	103	12.08.2021	0.8	34.5	0.04	0.40	0.092	0.32	193.9	8.60	0.36	1.63
	78.213	14.388	248	12.08.2021	1.3	34.8	0.04	0.27	0.168	0.80	139.9	9.68	0.65	2.13
	78.162[a]	14.174[a]	225[a]	12.08.2021										
Malangen	69.535	18.510	120	29.08.2021	8.2	34.8	0.17	0.76	0.329	0.75	376.3	0.34	0.15	0.31
	69.468	18.372	214	29.08.2021	6.8	35.2	0.03	0.29	0.135	1.08	107.8	1.96	0.16	1.42
Saltfjord	67.155	14.152	120	04.&05.08.2021	7.0	34.4	0.05	0.40	0.086	1.39	179.2	0.80	0.13	0.59
	67.175	14.130	255	04.&05.08.2021	7.3	35.0	0.02	0.30	0.106	0.93	118.8	0.86	0.16	0.97
Selbjørnfjord	59.995	5.234	140	04.09.2021	7.4	35.5	0.02	0.20	0.072	1.48	167.4	1.87	0.18	1.22
	59.986	5.246	220	04.09.2021	7.2	35.6	0.03	0.30	0.099	1.26	240.1	0.81	0.12	1.21

Note: Environmental data for bottom water (BW), surface water (SW), and sediment (SED) are given together with bottom depth and geographic location.

Abbreviations: Chl a/phaeo, Chlorophyll a/phaeophytin ratio; Chlorophyll a, Chl a (for water: μg L^{-1}; for sediment: μg g^{-1}); C_{org}, organic carbon (for water: mg L^{-1}; for sediment: %); Date, sampling date (dd. mm.yyyy); Dep, depth (m); Lat, latitude (°N); Lon, longitude (°E); MGS, mean grain size (μm); Sal, salinity (‰); Tem, temperature (°C).

[a]Second position in the deep zone in Isfjord, where two Van Veen grab samples were collected.
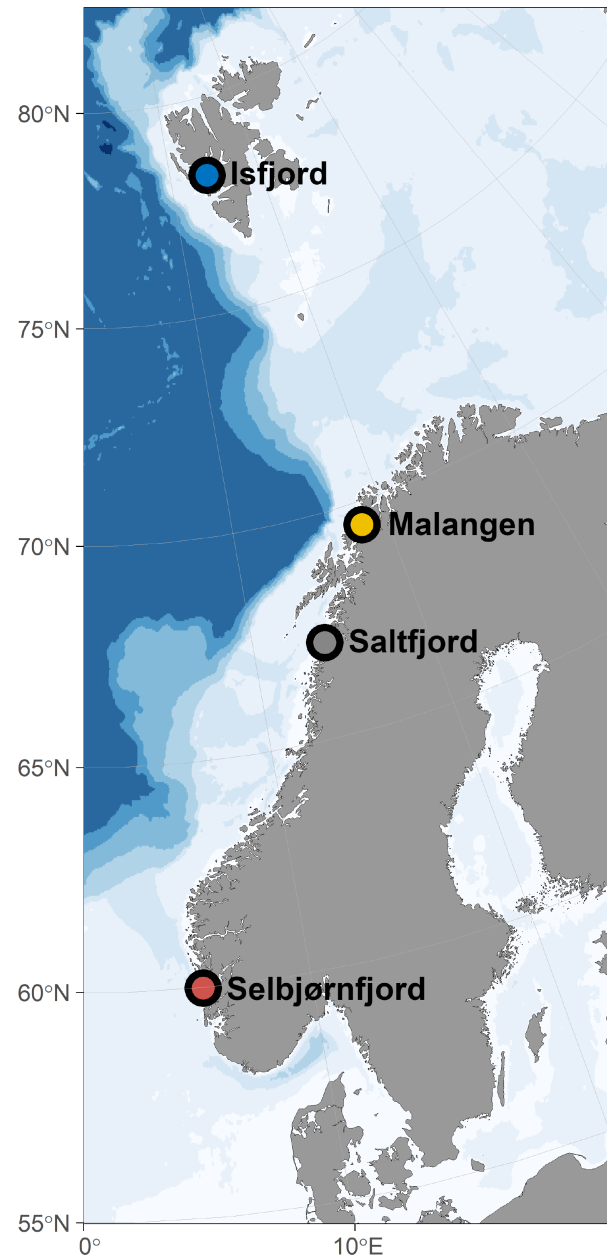

FIGURE 1 A map of the study area with the four studied fjords indicated.

fjords in the Norwegian Sea located south and north of the Lofoten-Vesterålen archipelago, respectively. Two locations in the sub-Arctic were chosen since the archipelago may form a physical barrier for population connectivity and because this is the region where the transition between the West Norwegian and Finnmark biogeographic subprovinces is located. Isfjord is a glacially influenced Arctic fjord on the west coast of Svalbard.

2.2 | Space-for-time substitution

The study locations were selected so that the latitudinal gradient can be used as a space-for-time substitution to study the possible

impacts of climate change. All studied fjords are strongly impacted by the Norwegian Atlantic current that transports warm and saline Atlantic water from the North Atlantic into the Arctic Ocean (Orvik & Niiler, 2002). The strength of this Atlantic water impact has increased due to climate change, causing multiple changes in the environment and ecosystems that have been collectively referred to as Atlantification (Csapó et al., 2021; Ingvaldsen et al., 2021; Jordà-Molina et al., 2023; Weydmann-Zwolicka et al., 2021). Accordingly, the gradient in our study represents multiple aspects of climate change that occur simultaneously. With regard to our study objective, two aspects are of particular importance: (i) northward range expansion of benthic taxa, and (ii) altered primary production and OM transformation.

2.2.1 | Northward range expansion

Northward range expansion due to climate change (mainly temperature-driven) is well documented in our study region (Brattegard, 2011; Kotwicki et al., 2021) and predicted to continue (Renaud, Sejr, et al., 2015; Węsławski et al., 2011). These range expansions are likely to exceed several 100 km, as already during a warm period in the previous century (1930–1950s), Atlantic benthic species were found to spread northward by approximately 500 km in our study region (Loeng & Drinkwater, 2007). Also, all our study locations are part of a larval drift continuum along the continental shelf (Descôteaux et al., 2022; Silberberger et al., 2016). Descôteaux et al. (2022) showed that a passively drifting particle released in Skagerrak can reach Svalbard within 1 year. Accordingly, all our study locations are effectively connected within a few generations, assuming a typical larval duration of 2–6 weeks for many infaunal taxa (Shanks, 2009).

2.2.2 | Altered primary production and OM transformation

Overall, the duration of the annual productive period decreases from south to north in our study region. This is due to the longer duration of both spring and summer blooms, in the South, which decreases gradually with increasing latitude (Silva et al., 2021). Over the last decades, however, the bloom phenology in our study region has changed due to climate change (Silva et al., 2021). In the sub-Arctic and temperate regions, the summer bloom got delayed and the bloom duration increased (Silva et al., 2021). In the Arctic, an earlier spring bloom onset and longer duration have been found (Silva et al., 2021). Accordingly, the productive period throughout our study region is prolonging due to climate change, and the current gradient of the productive period duration from south to north can be interpreted as a space-for-time substitution in terms of the productive period duration.

Over the last decades, climate change has caused an earlier snow melt in the spring as well as increased rainfall and runoff in the autumn (Beldring et al., 2008), which in turn led to an earlier water column stratification and an overall longer duration of this stratification (Bianchi et al., 2020). This prolonged stratification has multiple effects on primary production, OM transformation in the water column, and OM export to the seafloor (Bianchi et al., 2020). On the one hand, prolonged stratification is a major driver of the above-described prolonged primary production duration (Silva et al., 2021). On the other hand, stratification can strongly reduce production once nutrients are depleted and the entire production is based on recycled nutrients (Silva et al., 2021). Furthermore, increased freshwater runoff results in a phenomenon termed coastal darkening (Aksnes et al., 2009; Konik et al., 2021; Szeligowska et al., 2021). This coastal darkening changes the underwater light climate, which has direct impacts on the primary production and performance of pelagic and benthic autotrophs (Striebel et al., 2023), restricting primary productivity to the upper few meters (Bianchi et al., 2020). Finally, stronger stratification in combination with altered primary production is also affecting the vertical export of OM (Henson et al., 2022). While the complexity of this OM export makes it difficult to model or measure it (Henson et al., 2022), it is certain that higher temperatures, together with stronger stratification, will result in stronger OM processing in the water column (Laufkötter et al., 2017). And therefore a higher fraction of low-quality OM reaches the seafloor in more stratified waters.

Taken together, our latitudinal gradient represents variation in benthic community composition, primary production patterns (duration and magnitude), as well as OM transformation and export that can be expected to gradually move northward with the progressing climate change. Considering that the above-described changes happened within a few decades, we assume that the studied latitudinal gradient reflects similar time scales among neighboring climate zones.

2.3 | Sampling

All sampling was conducted in August/September 2021 (Table 1). In each fjord's outer basin, samples were retrieved from two locations representing two depth zones: (i) 100–150 m bottom depth and (ii) 200–250 m bottom depth (Table 1), according to the separation of benthic community structure in Norwegian fjords that occurs at approximately 200 m (Sen et al., 2022). For each depth zone, a CTD profile of the entire water column was measured. Furthermore, water samples were collected with Niskin bottles from two depth layers: (i) bottom water—BW (~5 m above the seafloor) and (ii) surface water—SW (~20 m depth). The collected water was filtered through pre-combusted and pre-weighed Whatman GF/F filters (Ø 47 mm; pore size 0.7 μm) to collect suspended particulate organic matter (POM). Furthermore, water was filtered in the dark through Whatman GF/F filters (Ø 25 mm; pore size 0.7 μm) for pigments (chlorophyll *a* & phaeophytin). Five replicate filters were collected, each for POM (Ø 47 mm) and pigments (Ø 25 mm), and frozen immediately at −20°C and −80°C, respectively.

Five replicate Van Veen grabs were retrieved for each depth zone in each fjord to sample sediments and macrobenthos within (sampling depth >10 cm for all samples). Three subsamples were

collected from each replicate Van Veen grab: (i) granulometry, (ii) pigments (chlorophyll *a* & phaeophytin), and (iii) SOM. The subsamples were frozen until further laboratory analysis. The remaining content of each Van Veen grab was washed over a sieve (0.5 mm mesh size), and the fauna was kept alive in seawater for at least 12 h to allow for gut clearance. Macrofauna was identified to the lowest possible taxonomic level and frozen at −20°C. Names of all taxa follow the World Register of Marine Species (WoRMS Editorial Board, 2023). Depending on faunal body size, 1–25 individuals were pooled together for each sample. If possible, only soft tissue was collected for taxa with calcareous structures.

For the 200–250 m zone in Isfjord, repositioning of the ship was necessary during sediment sampling, and accordingly, sediment samples were collected from two positions (Table 1).

2.4 | Laboratory analysis

2.4.1 | Pigments

Chlorophyll *a* (chl *a*) and phaeophytin (phaeo) were analyzed with a fluorometer Trilogy® (Turner Designs Inc.) following the EPA 445.0 method (Arar & Collins, 1997) as described in Szczepanek et al. (2021).

2.4.2 | Granulometry

To determine the sediment grain size, samples were dried by lyophilization, homogenized with mortar and pestle, and sieved through a set of sieves (2000, 1000, 500, 250, 125, and 63 μm), and the weights of the size fractions were analyzed with the GRADISTAT software.

2.4.3 | Stable isotope analysis

Fauna and SOM samples were dehydrated by lyophilization. POM filters were oven-dried at 60°C. All samples were ground to a fine powder with a mortar and pestle and weighed into silver capsules. Samples were then repeatedly (×4) treated with 2 M HCl to remove carbonates. After each acid wash, samples were oven-dried at 60°C. Samples were analyzed for their organic carbon content (C_{org}), total nitrogen content (N_{tot}), as well as their stable isotopes (Sis—$\delta^{13}C$ and $\delta^{15}N$) with an Elemental Analyzer Flash EA 1112 Series interfaced to an Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany) as described in Silberberger et al. (2021) or Szczepanek et al. (2021). Quantitative measurements were calibrated against analyses of certified reference materials (Fluβsediment) provided by HEKAtech GmbH (Germany). Isotopic ratios, $\delta^{13}C$ and $\delta^{15}N$, were corrected against IAEA standards (CO-8 and USGS40 for $\delta^{13}C$ and N-1 and USGS40 for $\delta^{15}N$). Filters were analyzed entirely to allow for quantitative analysis of C_{org} and N_{tot} content, which is not possible if the organic layer is scraped from the filters prior to the analysis. To assure accurate SI measurements, the flow of carrier gas (helium) was constantly monitored to ensure that the transfer tubes were not clogged. SI measurements are reported in the commonly used delta (δ) notation in parts per thousand (‰) relative to the international standards Vienna Pee Dee Belemnite and atmospheric air for carbon and nitrogen, respectively.

2.5 | Data analysis

All statistical analyses were run in R version 4.2.1, with the packages SIBER (Jackson et al., 2011) and Vegan (Oksanen et al., 2018). Three permutational multivariate analyses of variance (PERMANOVA) (Anderson, 2001) were used to test for differences between the isotopic composition of the collected OM mixtures according to the factors: OM mixture (three levels: POM_{SW}, POM_{BW}, and Sediment), fjord (four levels: Isfjord, Malangen, Saltfjord, and Selbjørnfjord), and depth zone (two levels: 100–150 and 200–250 m).

Every taxon was assigned to one of four feeding types (suspension feeder, surface deposit feeder, sub-surface deposit feeder, or macrophages) according to scientific literature and online databases (Appendix S1: Table S1). The feeding type macrophages (i.e., animals that selectively feed on one food item at a time) compiled predators, scavengers, and omnivores, but no herbivores. Accordingly, taxa that were assigned to the feeding type macrophages are all able to feed on higher trophic levels but may also feed directly on the local OM pools (POM or SOM). The reason for merging predators, scavengers, and omnivores was the typical generalist feeding behavior of benthic invertebrates in this group (e.g., most predatory taxa are also known as scavengers). Furthermore, most benthic secondary consumers are known for their high degree of omnivory (Bridier et al., 2021).

To study the isotopic niches occupied by the sampled benthic communities, Bayesian standard ellipse areas (SEA_B) were used for each feeding type per studied community (i.e., the benthic fauna collected from one depth zone in one fjord) as a probabilistic measure of the occupied isotopic niche space (Jackson et al., 2011). The relative overlap of the SEA_B of the same feeding type within each fjord was calculated to identify similarities in the isotopic niche space between the two depth zones. Furthermore, to identify differences in resource utilization among feeding types, three Bayesian Layman metrics ($\delta^{13}C$-range, $\delta^{15}N$-range, CD—mean centroid distance) were calculated (Jackson et al., 2011; Layman et al., 2007). To do so, 2×10^4 posterior draws were made from each community. These draws represent the probability range of the population means for each feeding type. The Layman metrics were then calculated among the population means of the feeding types of each posterior draw (Jackson et al., 2011). In short, a low $\delta^{13}C$-range indicates that all feeding types rely on the same primary OM source. A low $\delta^{15}N$-range indicates that all feeding types feed on a similar trophic level, and a low CD indicates a high niche overlap of all feeding types. In contrast, high values for the Bayesian Layman metrics indicate that at least one feeding type differs in utilized basal resource ($\delta^{13}C$-range),

trophic position (δ^{15}N-range), or isotopic niche (CD). The above-described Bayesian analyses require at least five SI samples, representing each feeding type. Accordingly, feeding types represented by less than five SI samples at a specific sampling location were not included in the Bayesian analysis at this location.

Significant differences between probability distributions were identified using the Bhattacharyya coefficient (BC—Bhattacharyya (1943); Rauber et al., 2008). The BC is a measure of the amount of overlap between two statistical populations and ranges from 0 (no overlap) to 1 (complete overlap). A significance level of 0.61 was chosen since the BC for two normal distributions with their means two standard deviations apart is 0.61. The calculation of BCs requires a predefined bandwidth. To ensure the use of appropriate bandwidths for the tested probability distributions, Silverman's rule of thumb was used to determine the bandwidths for the calculations of BCs (Silverman, 1986).

Data were published and are freely available (Silberberger 2023a, 2023b, and 2023c).

3 | RESULTS

3.1 | Environment and organic matter mixtures

Bottom water temperature and salinity differed among sampling locations (Table 1). In general, salinity increased along the studied latitudinal gradient from north to south and within each fjord with depth. Temperature, however, distinguished the cold Arctic fjord from all three fjords on the Norwegian mainland; the latter were characterized by distinctly warmer bottom waters (Table 1). No overall trend in bottom water temperature between the depth zones was observed across all the studied fjords.

In terms of OM properties, the shallower depth zone in Malangen was distinct from all other locations. The shallow Malangen site was characterized by elevated C_{org}, Chl a, and Chl a/phaeo ratios in bottom water, while C_{org} and Chl a in the sediment were low. This distinction of the shallower depth zone in Malangen, however, was not apparent in the isotopic composition of the different OM mixtures (Figure 2). The depth zone had no significant effect on the SI ratios of the OM mixtures (Table 2). In contrast, the type of OM mixture, specifically SOM versus POM, was the factor most influential on the SI ratios (Table 2). The next significant factor was the fjord identity. A pairwise comparison, however, showed that the two sub-Arctic fjords did not differ significantly from each other in terms of OM mixture isotopic composition. Particularly, the δ^{13}C of SOM showed a strong latitudinal pattern with intermediate values in the temperate fjord, the highest values in the sub-Arctic fjords, and the lowest values in the Arctic fjord (Figure 2).

3.2 | Benthic fauna

A total of 390 fauna SI samples were collected, and they represent 118 taxa belonging to eight different phyla (Appendix S1: Table S1).

The total number of samples for the different locations ranged from 36 for the 200–250 m zone in Selbjørnfjord to 64 for the 100–150 m zone in Saltfjord.

In general, fauna was enriched in ^{13}C and ^{15}N in comparison to the collected OM mixtures (Figure 2). However, in both sub-Arctic fjords, some fauna samples had δ^{13}C values lower than SOM. Furthermore, three samples collected from Saltfjord had a particularly low δ^{15}N value (<5‰).

In the 100–150 m depth zone of the Arctic and both sub-Arctic fjords, suspension feeders were collected in high numbers with an overall low δ^{15}N values (2.89‰–9.56‰; Figure 2; Table 3). In contrast, only a few suspension feeders were collected in the 200–250 m depth zone in all fjords and in the 100–150 m depth zone in the temperate fjord ($n \leq 3$ in each community), and accordingly, suspension feeders from these locations could not be included in the Bayesian analysis. In these communities, all suspension feeders had high δ^{15}N values (8.86‰–15.11‰).

The measure of shared occupied isotopic niches of surface and sub-surface deposit feeders and the relative overlap of the SEA_B in the 100–150 and 200–250 m depth zones were low in the Arctic fjord and high in the temperate fjord (Figure 3). In the two sub-Arctic fjords, this relative overlap for both types of deposit feeders tended to be in between the low Arctic and high temperate overlap. However, the isotopic niches of sub-surface deposit feeders from shallow and deep habitat in Malangen were completely separated, and accordingly, this location departed from the general pattern for this feeding type (Figure 3). In contrast, the overlap for the SEA_B of macrophages showed no such latitudinal change. The size of SEA_B for both types of deposit feeders showed no clear pattern (Figure 4). For surface deposit feeders, it was almost constant across all studied communities. For sub-surface deposit feeders, the size of the SEA_B was more variable and particularly large for the 200–250 m zone in Saltfjord and the 100–150 m zone in Isfjord. Disregarding these two communities, the SEA_B size for sub-surface deposit feeders differed little. In contrast, the SEA_B for macrophages showed a significant increase in size in the sub-Arctic and the temperate 100–150 m zones. SEA_B sizes for suspension feeders were significantly larger in the 100–150 m zone of Saltfjord than in Isfjord and Malangen. The three calculated Bayesian Layman metrics showed similar spatial patterns. In general, the metrics were high in both depth zones in the Arctic fjord and low in both depth zones of the temperate fjord (Figure 5). In the two sub-Arctic fjords, however, the 100–150 m zone resembled the Arctic fjord more closely (i.e., high Bayesian Layman metrics), while the 200–250 m zone was more like the temperate fjord (i.e., low Bayesian Layman metrics).

4 | DISCUSSION

Our results show a distinct difference in resource partitioning among benthic communities in the outer basins of the Arctic (Isfjord) and temperate fjords (Selbjørnfjord). The different feeding types collected in the Arctic fjord occupied separate isotopic niche spaces.
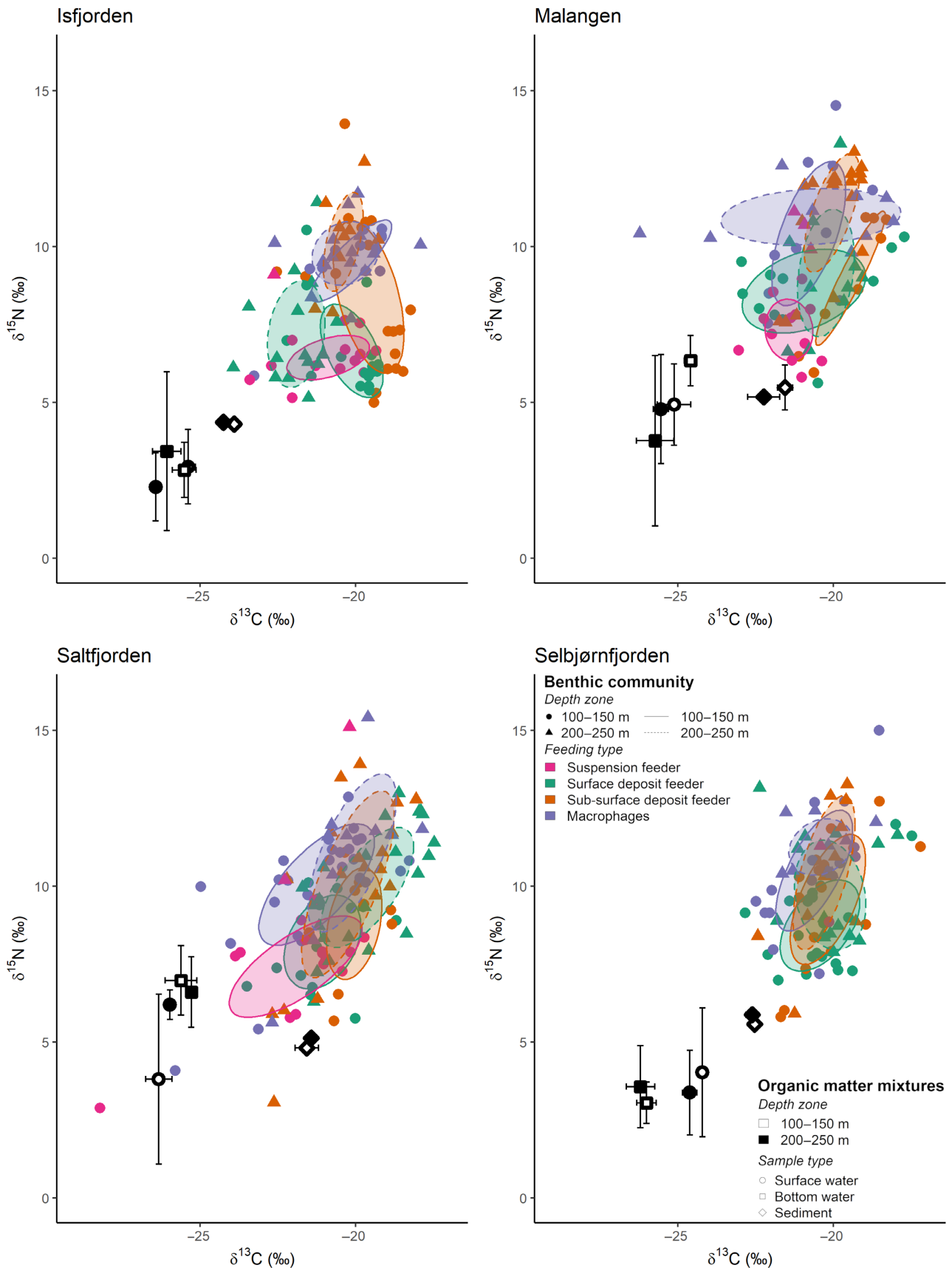
FIGURE 2 Isotope biplot for macrofauna communities and organic matter (OM) mixtures in each studied fjord. Every fauna sample is shown, and standard ellipses are drawn for each feeding type represented by at least five samples in the respective depth zone. For all collected OM mixtures, mean values and standard deviations are given.

TABLE 2 PERMANOVA results for the isotopic composition of the organic matter (OM) mixtures.

Factor	R^2	*p*-value
OM mixture type	0.39	<.001
Sediment versus surface water	0.48	**<.001**
Sediment versus bottom water	0.44	**<.001**
Surface water versus bottom water	0.02	.16
Depth zone	0.00	.34
Fjord	0.16	<.001
Isfjord versus Malangen	0.22	**<.001**
Isfjord versus Saltfjord	0.24	**<.001**
Isfjord versus Selbjørnfjord	0.11	**<.001**
Malangen versus Saltfjord	0.01	.19
Malangen versus Selbjørnfjord	0.04	**.02**
Saltfjord versus Selbjørnfjord	0.07	**<.001**

Note: Pairwise comparisons for significant factors are given in bold.

Furthermore, the isotopic niche of the same feeding type in the Arctic fjord differed between the two depth zones. In contrast, this differentiation of isotopic niches between feeding types and depth zones was not found in the temperate fjord. We identify the sub-Arctic as a transition zone between "temperate functioning" and "Arctic functioning". However, the region where this transition happens within the sub-Arctic differs between the studied depth zones (Figure 6).

4.1 | Latitudinal trends in resource partitioning

4.1.1 | Arctic functioning

The Arctic fjord was characterized by distinct isotopic niches occupied by the different feeding types. In both depth zones, the Bayesian δ^{15}N-range was around 3‰ (Figure 5), which is close to the typical ^{15}N enrichment that is expected for one trophic transfer. Due to a lack of species-specific ^{15}N trophic enrichment factors for benthos, a general enrichment of 3.4‰ per trophic transfer is often assumed for benthic invertebrate food webs across various habitats and climate zones (e.g., Post, 2002; Renaud, Løkken, et al., 2015; Szczepanek et al., 2022). Such an average ^{15}N enrichment was confirmed for the Arctic benthic food webs (Hoondert et al., 2021). Accordingly, the most ^{15}N-enriched feeding type (macrophages, Figure 2) in Isfjord occupied a trophic position that was approximately one level higher than that of the least ^{15}N-enriched feeding types (i.e., suspension feeder and surface deposit feeder). This reflects the pattern of different feeding types occupying different trophic levels as it has been described for other fjords in western Svalbard [Hornsund (Sokołowski et al., 2014); Kongsfjord (Renaud et al., 2011)].

The low relative overlap of the SEA among deposit feeders from the two depth zones in Isfjord (Figure 3) indicates different δ^{13}C

baselines for the two depth zones. Different δ^{13}C baselines for the two depth zones in Isfjord suggest that different major OM sources were utilized by deposit feeders in each depth zone, resulting in a minimal trophic niche overlap for surface and sub-surface deposit feeders among depth zones (Figure 3). We assume that the more enriched ^{13}C signal in deposit feeders in the 100–150 m zone is related to selective feeding on macroalgal detritus. Most macroalgae in Isfjord are ^{13}C enriched in comparison to other OM sources, and macroalgal detritus has previously been found to contribute significantly to benthic food webs in Isfjord (Renaud, Løkken, et al., 2015). Furthermore, macroalgal detritus was observed in our Van Veen grab samples in Isfjord (MJ Silberberger *personal observation*), and macroalgal detritus is a common contributor to sediment OM in Svalbard fjords (Zaborska et al., 2018).

4.1.2 | Temperate functioning

Within the temperate fjord, we found only very small differences in the isotopic niche of all feeding types. All three Bayesian Layman metrics were very low (Figure 5), indicating that all feeding types were utilizing similar OM pools (Layman et al., 2007). Such a benthic food-web structure was previously described for food-limited deep-sea food webs, where all fauna compete for very limited food resources [e.g., Porcupine Abyssal Plain (Iken et al., 2001)]. However, food limitation is a rather unlikely explanation for our observation in Selbjørnfjord since the sediments had an intermediate C_{org} content within our study (Table 1). We consider it more likely that the OM here is strongly recycled in the water column, making it less beneficial to select for scarce, high-quality food items, and that a generalist non-selective feeding on abundant but low-quality SOM is more effective under such conditions. Low Chl *a* in the bottom water (Table 1) despite high Chl *a* concentration in surface water in our study (1.47 and 1.26 µg L^{-1} at shallow and deep sampling locations, respectively) and a strong difference in δ^{13}C between surface and bottom water (Figure 2) suggest a strong transformation of OM before reaching the seafloor. Such a stronger transformation in the water column could be related to a longer and stronger stratification at lower latitudes that has an effect on the vertical export of OM (Henson et al., 2022). Particularly, the combination of stronger stratification with higher temperatures causes a longer residence of OM in the upper water column, while higher biological activities due to warmer temperatures result in a stronger OM processing in the water column (Laufkötter et al., 2017; Nydahl et al., 2013).

4.1.3 | Transition zone

We identified the sub-Arctic as the transition zone between "temperate functioning" and "Arctic functioning" (Figure 6). Moving from north to south, macrophages extended their isotopic niches (Figure 4) and occupied an isotopic niche that overlapped more with the isotopic niche of deposit feeders in the sub-Arctic (Figure 2). This

TABLE 3 Overview of the distribution of $\delta^{13}C$ and $\delta^{15}N$ ratios (both in ‰) for the different feeding types in all studied communities.

| Feeding type	n	$\delta^{13}C$			$\delta^{15}N$		
		Median	Min	Max	Median	Min	Max
Isfjord							
100–150m							
Suspension feeder	13	−20.35	−23.40	−19.34	6.34	5.15	7.63
Surface deposit feeder	16	−19.62	−22.62	−19.27	6.07	5.39	10.53
Sub-surface deposit feeder	19	−19.41	−22.53	−18.24	7.96	5.00	13.94
Macrophages	12	−19.71	−23.26	−19.16	9.91	5.85	10.56
200–250m							
Suspension feeder	1	−22.63			9.10		
Surface deposit feeder	15	−21.63	−23.93	−20.61	6.50	5.15	11.42
Sub-surface deposit feeder	9	−20.52	−21.31	−19.29	10.33	7.89	12.72
Macrophages	15	−20.17	−22.60	−17.92	9.77	7.69	11.70
Malangen							
100–150m							
Suspension feeder	12	−21.28	−23.04	−20.37	7.44	5.80	8.96
Surface deposit feeder	11	−21.64	−22.95	−17.73	8.89	5.62	10.31
Sub-surface deposit feeder	8	−19.09	−21.12	−18.30	9.44	5.96	10.93
Macrophages	11	−20.82	−22.11	−18.74	9.94	7.54	14.53
200–250m							
Suspension feeder	3	−20.93	−21.26	−20.73	10.70	9.91	11.21
Surface deposit feeder	10	−20.23	−21.47	−19.07	8.85	6.63	13.31
Sub-surface deposit feeder	19	−19.96	−21.74	−19.08	12.04	7.57	13.04
Macrophages	9	−19.43	−26.22	−18.08	10.81	9.81	12.60
Saltfjord							
100–150m							
Suspension feeder	15	−21.32	−28.21	−19.73	7.85	2.89	9.56
Surface deposit feeder	14	−21.23	−23.50	−18.70	8.48	5.76	10.12
Sub-surface deposit feeder	9	−20.03	−21.49	−18.84	9.24	5.68	11.08
Macrophages	26	−20.81	−25.79	−18.28	10.55	4.09	12.86
200–250m							
Suspension feeder	2	−21.24	−22.28	−20.20	12.66	10.20	15.11
Surface deposit feeder	23	−19.68	−21.71	−17.48	9.96	6.30	12.99
Sub-surface deposit feeder	18	−19.89	−22.68	−18.06	10.58	3.07	13.92
Macrophages	11	−20.29	−22.69	−17.86	11.64	5.63	15.42
Selbjørnfjord							
100–150m							
Suspension feeder	1	−20.14			8.86		
Surface deposit feeder	20	−20.61	−22.84	−17.49	8.62	6.98	11.99
Sub-surface deposit feeder	16	−20.43	−21.69	−17.21	10.14	5.81	12.73
Macrophages	16	−20.54	−22.49	−18.54	10.41	7.19	15.00
200–250m							
Suspension feeder	1	−20.42			11.30		
Surface deposit feeder	16	−20.06	−22.37	−17.95	8.82	7.89	13.16
Sub-surface deposit feeder	10	−20.03	−22.43	−19.29	10.64	5.92	13.27
Macrophages	9	−20.20	−21.65	−18.64	11.31	10.39	12.43
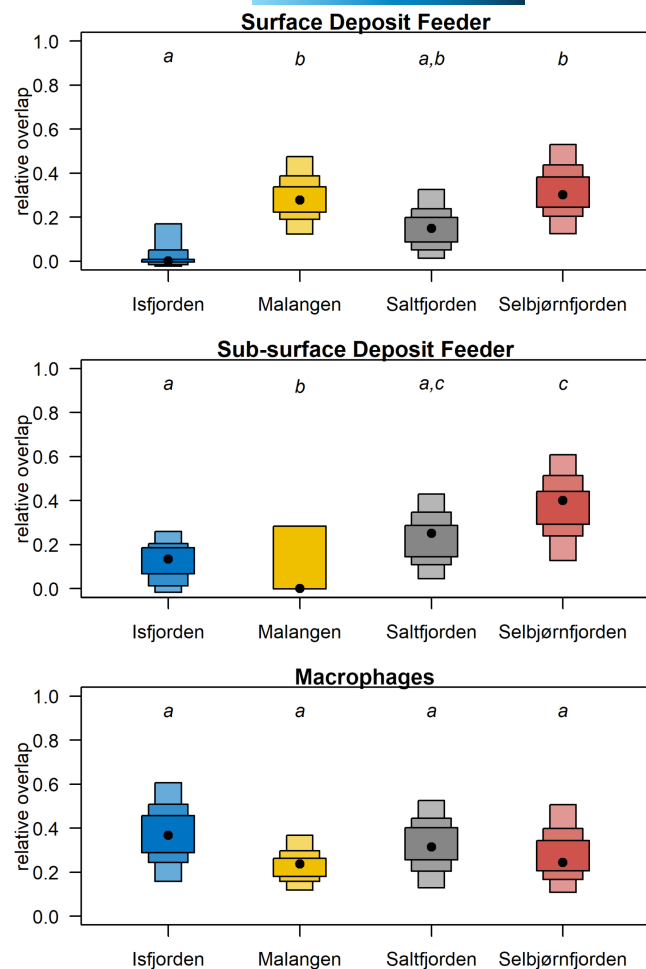
FIGURE 3 Density plots of the relative overlap of the Bayesian standard ellipse of the 100–150 and 200–250 m zones for surface deposit feeders, sub-surface deposit feeders, and macrophages. Colors indicate the different fjords, and significant differences between the overlaps for a specific feeding type among fjords are indicated by letters (fjords with the same letter are not significantly different). Black dots represent the mode, while the boxes indicate 50%, 75%, and 95% credible intervals.

was more strongly seen in Saltfjord, the more southern sub-Arctic fjord in our study. Moving further south, comparing sub-Arctic and temperate zones, the isotopic niche of macrophages decreased again. In the temperate fjord, however, the isotopic niche of macrophages was virtually indistinct from the isotopic niches of surface and sub-surface deposit feeders (Figure 2), suggesting that these feeding types rely on the same food source. In parallel, the isotopic niche size of deposit feeders remained unchanged between the Arctic, sub-Arctic, and temperate zones (Figure 4). This constancy in the isotopic niche of deposit feeders indicates that they do not alter their feeding behavior along the entire studied latitudinal gradient. Consequently, our results show that macrophages gradually change from predatory/scavenging feeding to detritus feeding when moving south along our study region. This means that benthic taxa that were assigned to macrophages according to literature are effectively carnivores in the Arctic, omnivores in the sub-Arctic, and detritivores

in the temperate fjord. While the above-described transition was identified for both studied depth zones, it was located further north in the 200–250 m zone than in the 100–150 m zone (Figure 6). This trend that different feeding types become isotopically less distinct in our sub-Arctic benthic food webs resembles the patterns reported in previous studies in this region that had a stronger focus on higher trophic levels (i.e., fish) but included benthic invertebrates (Nilsen et al., 2008; Silberberger et al., 2018).
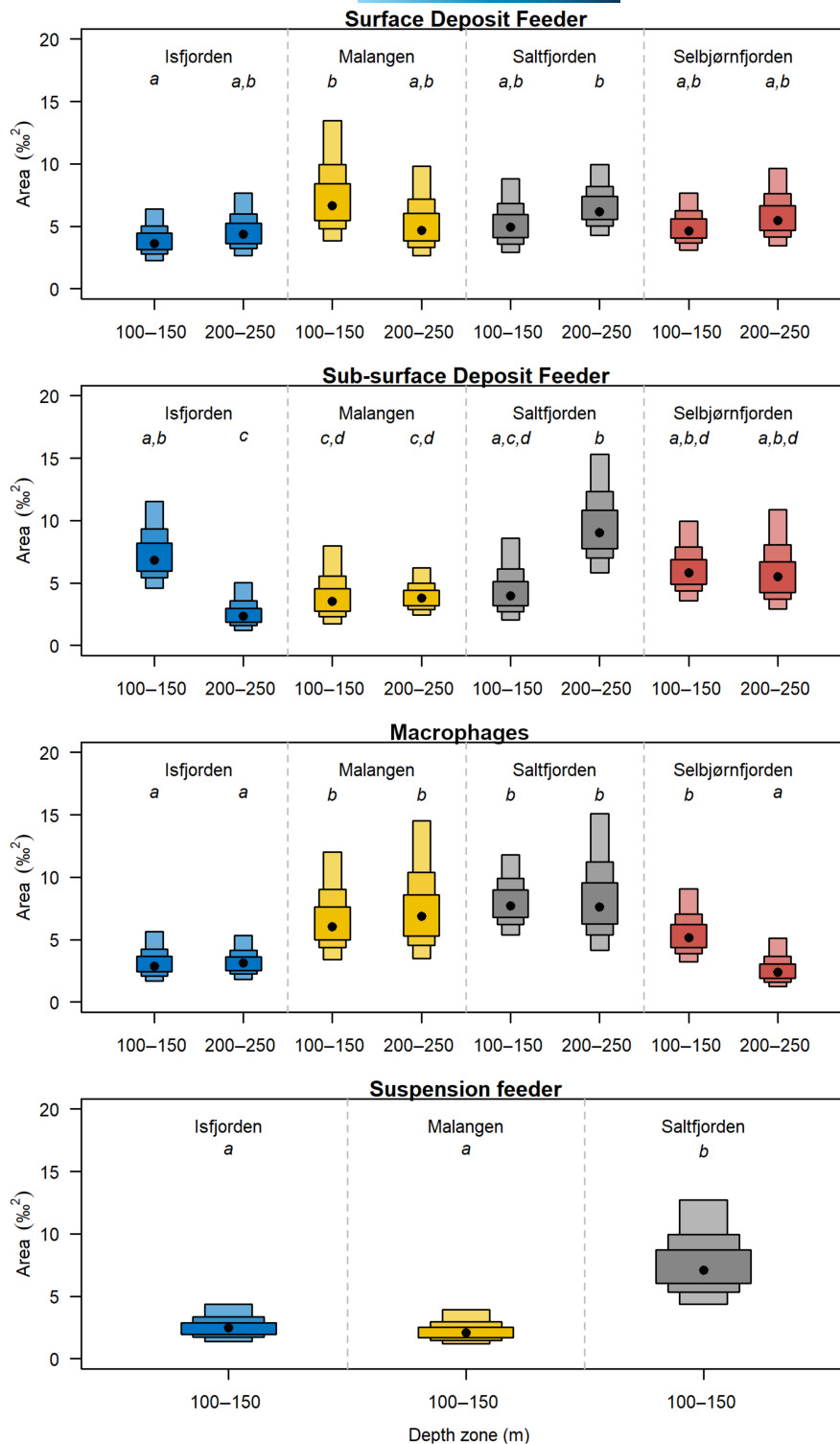
Accordingly, when we use our latitudinal gradient as a space-for-time surrogate to predict future climate change impact, we can hypothesize that refractory SOM may become more important for benthic food webs. The transition zone between temperate and Arctic functioning is expected to move gradually north, likely rendering the sub-Arctic toward the current temperate functioning. In the Arctic, the first changes are expected in the deeper communities since the transition zone at this depth is already located further north.

4.2 | Changing role of suspension feeders

Suspension feeders were almost absent from our samples in the 200–250 m zone in all fjords and from the 100–150 m zone in the temperate fjord. Although the sampling approach in our study gives no quantitative representation of the community composition at our study locations, this pattern was so strong (Table 3) that sole sampling bias is unlikely to explain it. Instead, the isotopic composition of suspension feeders suggests different resource utilization in the 100–150 m zone in Arctic and sub-Arctic fjords in comparison to all other sampling locations where suspension feeders were collected in low numbers. Similarly, the data presented by Renaud, Løkken, et al. (2015) showed different isotopic compositions of benthic primary consumers in Isfjord at depths from 120 to 200 m and from 210 to 270 m, including the suspension feeding bivalves *Ciliatocardium ciliatum*, *Bathyarca glacilis*, and *Similipecten greenlandicus* in the deeper zone. Interestingly, these three species in the 210–270 m zone were the most ^{15}N-enriched primary consumers in Isfjord (Renaud, Løkken, et al., 2015). This is similar to our results and the observation of high δ^{15}N in suspension feeders in communities where this feeding type is scarce. Such a ^{15}N enrichment in suspension feeders is likely related to strong microbial reworking of OM (Galloway et al., 2013). Our results suggest that this is the case in all communities below 200 m, but also that this situation extends to more shallow depth in the temperate fjord. It is likely that deposit feeders in deep communities are able to outcompete suspension feeders due to the unreliable and unpredictable sedimentation of fresh OM at such depth and the infrequent resuspension of SOM (Levinton, 1972), while the sediment serves as a more reliable, directly accessible food bank for deposit feeders. We expect that increased processing of OM in the water column before sedimentation to the seafloor (Turner, 2015) causes a similar disadvantage to suspension feeders in the temperate fjord in the 100–150 m zone.

Some signs of suspension feeders not exclusively feeding at the base of the food web were also observed in the southern sub-Arctic

fjord (Saltfjord). Here, the isotopic niche of suspension feeders was significantly larger than in Isfjord and Malangen because of some organisms that were enriched in ^{15}N. Similarly elevated δ^{15}N values of suspension feeders were previously found in the sub-Arctic Malnesfjord, a 160-m-deep fjord in the Lofoten-Vesterålen archipelago (Silberberger et al., 2018).

Such a loss of suspension feeders and increased reliance of benthic communities on SOM has the potential to alter carbon

sequestration in fjords. Suspension feeders are actively capturing suspended OM from the water column and immobilizing part of it as biomass (Kahn et al., 2015), which can later be buried in sediments or eaten by other organisms. In contrast, the biomass of deposit feeders is based on settled and temporarily immobilized OM in the sediment. In addition, deposit feeders (as well as mobile macrophages) stimulate microbial production and OM remineralization in the sediment through bioturbation and priming (Aller & Cochran, 2019; Lopez &
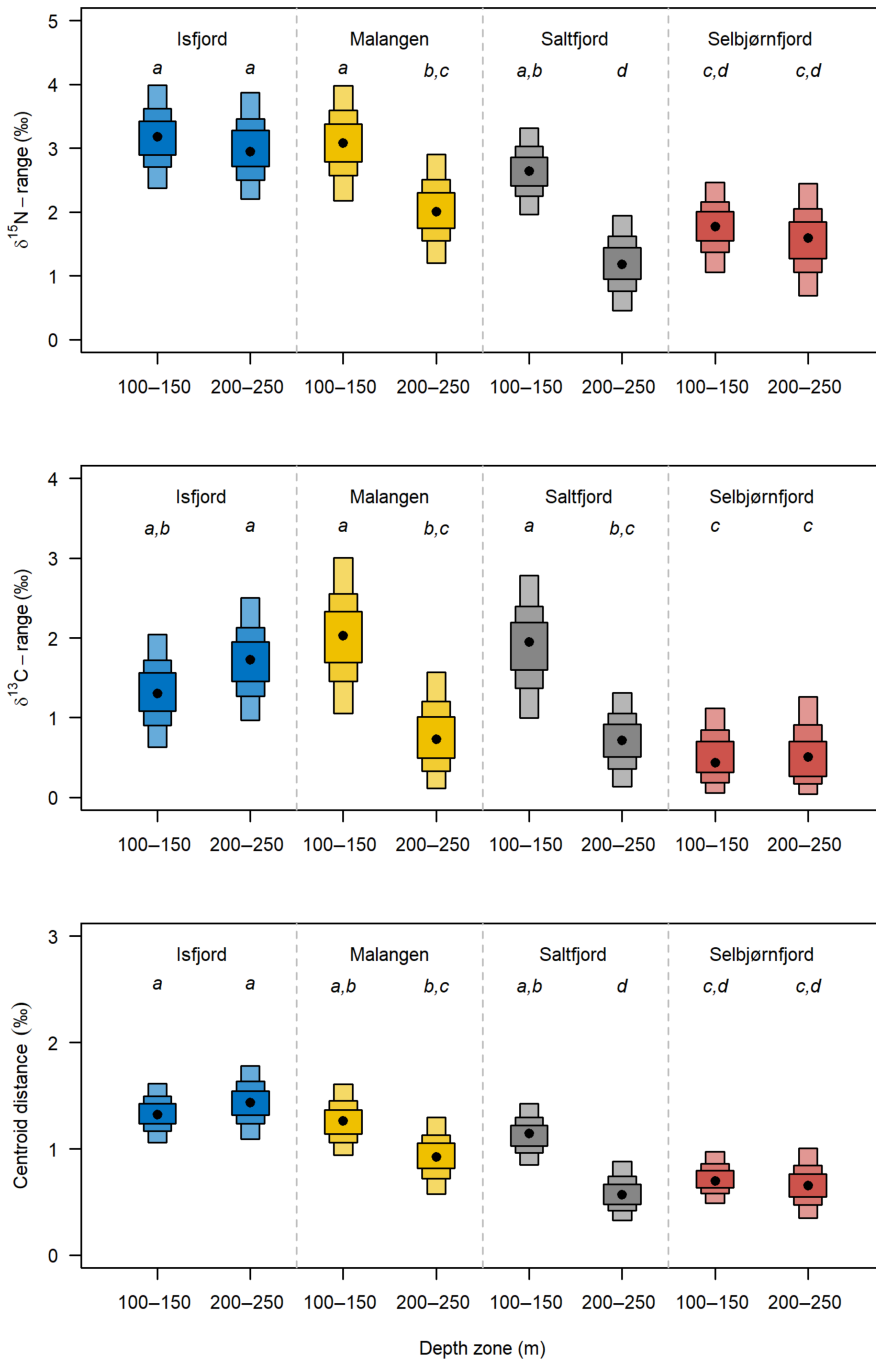
FIGURE 5 Density plots of Bayesian Layman metrics ($\delta^{15}N$-range, $\delta^{13}C$-range, mean centroid distance—CD) for different depth zones in the studied fjords. Significant differences for each metric are indicated by letters (boxes with the same letter are not significantly different). Black dots represent the mode, while the boxes indicate 50%, 75%, and 95% credible intervals.

Levinton, 2011). Although we are not able to quantify the impact of macrofauna on the remobilization of SOM, the replacement of suspension feeders by deposit feeders at the base of the food web has the potential to reduce carbon sequestration in fjord sediments, since it will reduce active OM capture by macrofauna and increase remineralization of immobile SOM.

5 | CONCLUSION

Taken together, our study indicates two benthic community types that are most likely to experience functional changes along with

progressing climate change: (i) shallow (100–150 m) sub-Arctic communities and (ii) deeper (200–250 m) Arctic communities.

Using the studied latitudinal gradient as a space-for-time substitution, we assume that with the progressing climate change, all feeding types will increasingly rely on SOM in the 100–150 m zone in the sub-Arctic. Furthermore, a loss of the suspension feeders as the base of the food web is possible, similar to the current situation in temperate fjords. These changes in the shallower communities may result in a functional homogenization of sub-Arctic fjords across different depth zones. In the Arctic, a reduction in resource partitioning is likely to occur first in the deeper regions of fjords. Furthermore, a gradual shift in the feeding of macrophages from carnivore to

Arctic Functioning:
- Resource partitioning among feeding types
- Isotopic niche differs between shallow and deep habitat
- Different feeding types occupy multiple trophic levels
- Multiple important food sources

Temperate Functioning:
- No resource partitioning among feeding types
- Isotopic niches in shallow and deep habitat indistinct
- Different feeding types occupy the same trophic level
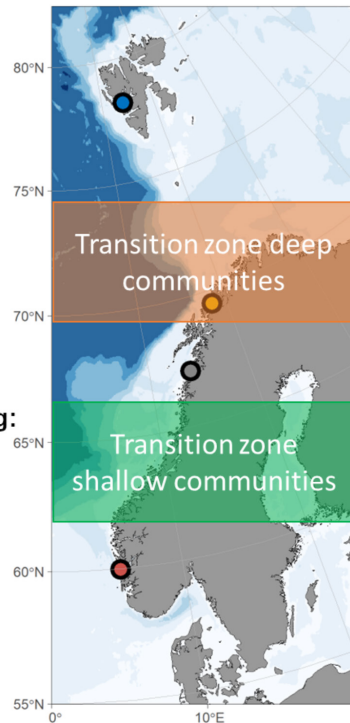- Sediment organic matter is main food source

FIGURE 6 Conceptual figure showing the functional differences between Arctic and temperate benthic food webs. The geographic location of the transition zones for shallow (100–150 m) and deep (200–250 m) communities is indicated.

omnivore and further to detritivore is possible, as observed along the entire latitudinal gradient in our study. Accordingly, we reject our original hypothesis and conclude that the functioning of benthic communities in both studied depth zones is vulnerable to climate change-related environmental changes. However, the regions where the most severe functional changes may be expected differ for the depth zones. According to the above-described spatial differences, we recommend increased efforts in monitoring of potentially altered resource utilization in deeper Arctic (200–250 m) and shallower sub-Arctic (100–150 m) fjord benthic communities as an indicator of the progressing climate change that is likely to foreshadow drastic changes in marine food webs, marine ecosystem functioning, as well as carbon sequestration in fjordic sediments.

AUTHOR CONTRIBUTIONS

Marc J. Silberberger: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing – original draft; writing – review and editing. **Katarzyna Koziorowska-Makuch:** Investigation; writing – review and editing. **Henning Reiss:** Writing – review and editing. **Monika Kędra:** Writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available for Organic carbon, nitrogen and stable isotopes, Pigments, and Granulometry.

ORCID

Marc J. Silberberger https://orcid.org/0000-0001-8819-4388

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