



Epibenthic food web structure across the Northeast Greenland seascape

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ABSTRACT

The Arctic is in a state of rapid transformation driven by climate change and other anthropogenic stressors, making it essential to establish reference values for diversity, including trophic structure and variability of stable isotope values. Here, we use stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) to characterize the trophic structure of epibenthic faunal communities across the Northeast Greenland seascape, covering coastal, shelf, shelf-break and upper-slope habitats in this under-explored region. We found that epifauna communities show wide occupancy (niches) in stable isotope space, with relatively high overlap among habitats. Among the studied seabed habitats, the differences in consumer $\delta^{13}\text{C}$ were relatively minor, and no dominance of terrestrial input (highly depleted values) was evident even at coastal sites. However, epifauna in coastal habitats (fjord and bay) showed higher $\delta^{15}\text{N}$ values, which may indicate a reliance on more degraded organic matter. We did not find consistent trajectories in stable isotope values across feeding groups along the inshore-to-offshore gradient, suggesting multiple parallel feeding strategies and realized diets of generalist consumers across the seascape. Continued research on the structure of marine food webs can provide an important understanding of the development of ecosystem functioning in a future Arctic.

1. Introduction

Environmental gradients, including multiple co-varying gradients in inshore-to-offshore areas or across different regions, influence the diversity and availability of organic matter within regional and local food webs, shaping their structure and function (Chouvelon et al., 2015; de la Vega et al., 2019). A spatial perspective is essential for understanding the structure and functioning of marine food webs. Space-based approaches can be especially valuable for regions with limited temporal data, which is predominantly the case in under-explored areas of the marine Arctic.

Marine food webs of Arctic shelves are generally characterized by tightly linked benthic and pelagic compartments, i.e., tight pelagic-benthic coupling (Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Iken et al., 2010). In contrast to lower-latitude areas, two blooms – one in sea ice and one in the water column – provide carbon to the pelagic and benthic food webs; both blooms occur during a narrow window in the spring with the brief yet concentrated ice algal bloom

typically preceding the longer phytoplankton bloom by several weeks (Hobson et al., 1995; Søreide et al., 2010). In coastal areas, additional sources of organic matter contribute to benthic food webs (McMeans et al., 2013). Previously, it was hypothesized that terrestrial organic matter (a diverse mix of dissolved and particulate organic matter, including vascular plant debris and soil, particularly prevalent on interior shelves; Williams and Carmack, 2015), did not play a significant role in Arctic marine food webs. However, recent studies are challenging this view (Divine et al., 2015; Bell et al., 2016; Harris et al., 2018; McMahon et al., 2021). For example, along the coast, shelf, and slope of the Beaufort Sea, terrestrial organic matter from riverine sources and coastal erosion has been observed as suspended particulate organic matter in the pelagic zone. Furthermore, it has been found to be assimilated by benthic consumers (Dunton et al., 2012; Bell et al., 2016). The relative importance of terrestrial organic matter has been found to decrease with increasing distance from river mouths (Bell et al., 2016; McGovern et al., 2020), suggesting that inshore-to-offshore gradients are transition areas in terms of available or utilized organic matter in the

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Arctic. Where sizeable rivers are largely absent, such as along the Greenland east coast, glacial melt-water input provides terrestrial carbon subsidies instead (Hood et al., 2015; Pain et al., 2020). An additional, and to some degree overlooked, carbon source is found in littoral macroalgal production. For near-shore food webs, as well as areas further out on the shelf, macroalgal detritus may constitute a considerable part of assimilated carbon (McMeans et al., 2013; Renaud et al., 2015). In a study focusing on the depth gradient of Isfjorden (Spitsbergen), brown macroalgal detritus was found to be readily used by diverse groups of benthic consumers, including grazers and suspension feeders, in both shallow and deep waters, suggesting advection of this resource (Renaud et al., 2015). Still, much is unclear regarding the contribution of terrestrial and littoral production to benthic food webs in the East Greenland seascape.

For a thorough understanding of species communities and their role in the ecosystem, it is central that we characterize the trophic structure of these communities and the main pathways through which energy and nutrients are transferred. By examining stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of primary producers and epibenthic invertebrate consumers, we describe benthic food web structure in a high-Arctic marine ecosystem. Using isotopes allows us to track the flow of energy and the hierarchical position of the components in the food web, essentially mapping the assemblages in stable isotope space (Nordström et al., 2009). Arctic terrestrial production is characterized by depleted $\delta^{13}\text{C}$ values (ranging from -24‰ to -32‰ , often between -26‰ and -28‰) compared to phytoplankton (around -24‰), and in particular to sympagic (sea-ice associated) production, which, although variable, is often much more isotopically enriched, with $\delta^{13}\text{C}$ values around -10 to -17‰ (Søreide et al., 2006b; Gradinger et al., 2009; Knies and Martinez, 2009; Gradinger and Bluhm, 2020; McMahon et al., 2021; Amiraux et al., 2026). Likewise, terrestrial organic matter generally exhibits low $\delta^{15}\text{N}$ values compared to marine organic matter. If terrestrial subsidies to the overall benthic food webs are significant in near-shore areas, we could expect shifts in the location in stable isotope space for the different consumer assemblages toward more depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, with corresponding changes in isotopic overlap among habitats. Finally, if terrestrial detrital input is significant, then longer food chains through subsidy of the microbial loop could be observed in inshore areas (Schloemer et al., 2023).

Our aim was to assess benthic trophic structure in under-explored Arctic areas, namely the complex Northeast Greenland seascape. Using stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), we determined the trophic structure (the quantitative, multi-dimensional representation of an ecosystem's food web based on the isotope composition of its organisms) of epifaunal invertebrate communities along an inshore-to-offshore gradient, including coastal sites (fjord and coastal bay stations), shelf sites (bank and trough stations), as well as shelf-break and upper-slope sites. In this work, we built on the characterization of epibenthic invertebrate communities in the Northeast Greenland seascape by Fredriksen et al. (2020) and Armitage et al. (2025), who reported >270 taxa forming distinct epibenthic communities in terms of taxonomic diversity and trait composition, respectively, in different habitats along the gradient. We described the stable isotope values of basal resources and explored spatial trends in the stable isotope values of invertebrate consumers to determine whether the documented taxonomic and functional gradients are translated into corresponding shifts in trophic structure. We describe the consumer assemblages across the inshore-to-offshore gradient and exemplify with dominant and/or commonly occurring consumer taxa. In particular, we asked the following questions: i) how do location and overlap of the consumer assemblage in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space vary across the gradient? ii) Are there distinct trajectories in the isotope values for different feeding groups (surface deposit feeders, suspension feeders, omnivores, benthic predators and hyperbenthic predators) along the gradient?

2. Material and methods

2.1. Study area

Our study area is part of the Northeast Greenland national park, which is the world's largest national park covering 972 000 km² of the interior and northeastern coast and marine shelf of Greenland. Our study was conducted during the TUNU-VI (August 2015) and TUNU-VII (September 2017) expeditions on the R/V *Helmer Hanssen*, UiT, as well as the TUNU-VIII (2022) expedition on the R/V *Kronprins Haakon* (see Table A1 in the Supplementary Information for details on the temporal and spatial structure of the sampling). TUNU (the Greenlandic word for East Greenland) is a long-term research program exploring fish and benthic communities of Northeast Greenland (Christiansen, 2012). During the three expeditions, sampling was conducted along the Northeast Greenland coast and shelf, with sites chosen to span inner fjord, coastal bay, shelf trough and bank, shelf-break sites, as well as stations on the upper slope (Fredriksen et al., 2020), between 74.55 and 79.27 °N, -21.72 and -5.22 °E, and between 65 and 1011 m depth (Fig. 1). Our study thereby includes habitats that differ in sea and glacial ice exposure, water properties (e.g., turbidity, temperature), and seabed morphology (Table 1). Key hydrographic features include the West Spitsbergen Current (WSC) that brings warmer, more saline water to the shelf break and slope, whereas the fjords and shelf receive cold water and sea ice from the Arctic basin as the Transpolar Drift converges with the East Greenland Current (EGC) (Gjelstrup et al., 2022). The fjords are further sites of high turbidity and sedimentation from glacial runoff, and overall low productivity (Bridier et al., 2021). Unlike other Greenlandic regions, such as Nuup Kangerlua and Young Sound, Northeast Greenland remains poorly studied from an ecological perspective. Our study contributes much-needed ecological information.

2.2. Sampling and analysis of stable isotopes

For the assessment of trophic structure using stable isotopes, we sampled food web basal resources (suspended particulate organic matter (POM), sediment organic matter, macroalgae, and leaves of terrestrial plants), as well as primary and secondary consumers (epifaunal invertebrates). POM was collected from the chlorophyll maximum layer (typically 30–50 m depth), using Niskin bottles attached to a CTD rosette. Corresponding water masses are described in Beroujon et al. (2022), with the chlorophyll maximum layer generally occurring in the upper water column and associated with Polar Surface Water. The water was filtered through pre-combusted filters (GF/F, volume filtered 300–900 ml). Sediments were collected using a box corer, and material from the top layer (1 cm) stored in a sterile bag. Macroalgal and terrestrial plant material, such as *Fucus* sp. and *Salix* sp., was collected when present in trawls targeting consumers or found in box cores. Some of the macroalgal material could not be consistently identified to species or genus level due to sample condition and was, therefore, categorized into broad morphological and taxonomical groups, namely filamentous (green and brown) algae and red algae. Observations were made of the genus *Desmarestia*.

Benthic epifaunal invertebrates were collected using a Campelen 1800 shrimp trawl and an Agassiz trawl. The Campelen trawl had an opening of 11.7 m, was rigged with a 35.6 m rock-hopper gear and had a mesh size of 80 mm in the wings and 40 mm in the cod end (Walsh and McCallum, 1997). Trawl duration varied between 10 and 29 min as recorded by a SCANMAR sensor attached to the trawl. The Agassiz trawl had a fixed frame (1.80 × 0.47 m) with a uniform net mesh size of 80 × 80 mm and bottom times lasting between 9 and 40 min (for details, see Fredriksen et al., 2020). The collected invertebrates were sorted and identified to the lowest possible taxonomic level. Some hyperbenthic and near-bottom pelagic taxa frequently occur in the benthic boundary layer and were included in the study when found (e.g., *Themisto libellula*, *Gonatus fabricii*) (here grouped as hyperbenthic species). A voucher collection was created

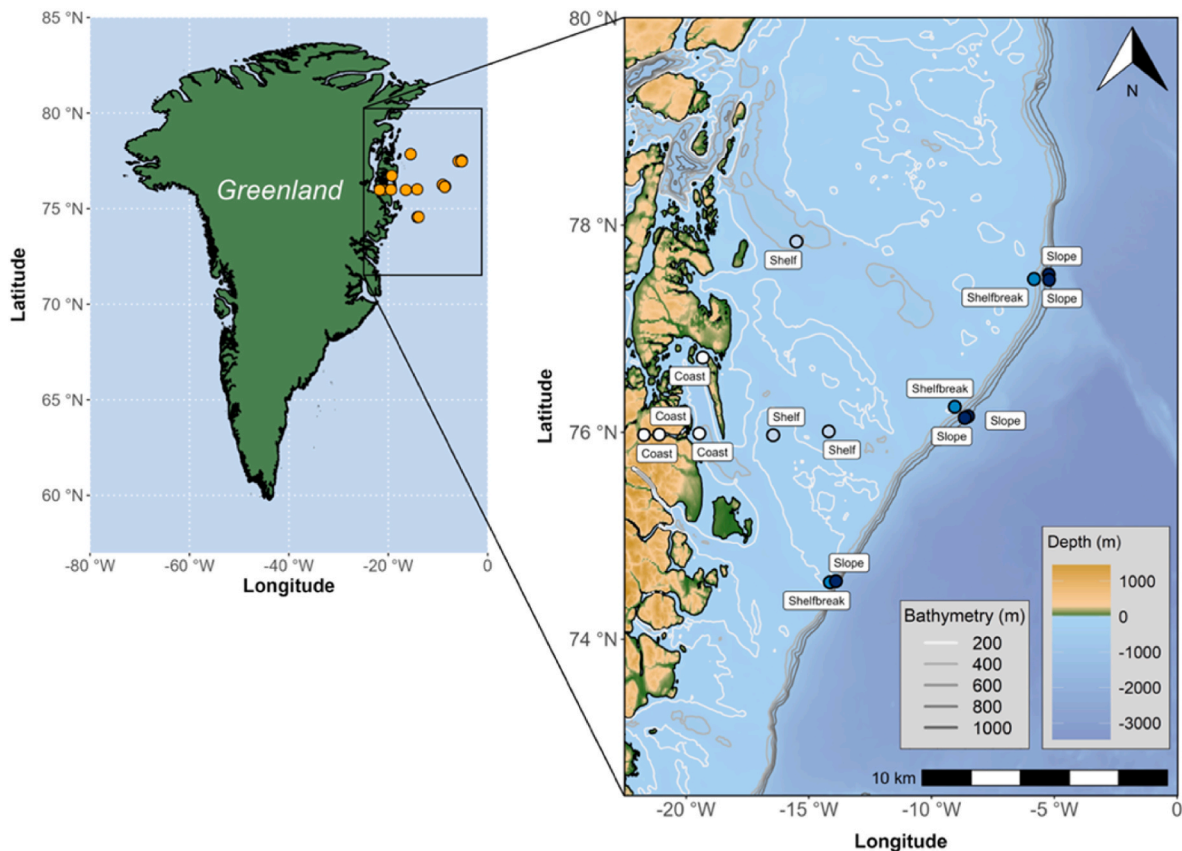


Fig. 1. Map over the study area showing stations visited. Station color denotes seascape habitat (coastal, shelf, shelf break and slope).

Table 1

Abiotic and biotic characteristics for habitats in the NE Greenland seascape. Values represent minimum and maximum values recorded during sampling for near-bottom (NB) temperature, salinity, oxygen, and turbidity. Types of primary producers encountered during sampling, as well as the dominant consumer taxa by abundance and their feeding traits in the different habitats are given.^a Based on Fredriksen et al. (2020) and^b based on Armitage et al. (2025).

HABITAT	COAST		SHELF			SHELF BREAK	SLOPE
Location	Bessel fjord	Dove Bugt	76-N-Bank	S K Trough	Norske Trough	Multiple stations	Multiple stations
Depth (m)	235, 380	213, 487	65, 74	341, 350	401, 449	177, 385	937, 1011
Temperature (°C)	−1.8, −0.8	0.8, 1.3	−2.1, −1.9	0.9, 1.4	0.9, 1.2	1.0, 1.8	−0.2, −0.1
Salinity (PSU)	33.4, 33.5	34.7, 34.9	32.5	34.8	34.9	34.8, 35.0	34.9
Dissolved oxygen (ml L ^{−1})	6.8	6.0, 6.4	7.9	6.5	6.2	5.5, 6.4	5.7
Turbidity (FTU)	0.26, 0.49	0.18, 0.38	0.51	0.25	0.15	0.06, 0.15	0.06
Ice exposure	Fast and glacial	Fast and glacial	Sea and glacial	Sea and glacial	Sea and glacial	Open water	Open water
Littoral macroalgae encountered	Filamentous macroalgae	Filamentous & red macroalgae	Filamentous & red macroalgae, <i>Fucus</i> sp.	Filamentous macroalgae, <i>Fucus</i> sp.	Filamentous macroalgae, <i>Fucus</i> sp.	Filamentous macroalgae	Filamentous macroalgae
Terrestrial plant material encountered	<i>Salix</i> sp.	<i>Salix</i> sp.	None	<i>Salix</i> sp.	None	None	None
Dominant consumer taxa ^a	<i>Ophiopleura borealis</i> , <i>Lebbeus polaris</i> , <i>Themisto libellula</i> , <i>Styela</i> spp.		<i>L. polaris</i> , <i>O. borealis</i> , <i>Sabinea septemcarinata</i> , <i>Umbellula encrinus</i> , <i>Boreonymphon</i> sp., <i>Anonyx</i> sp., <i>Zoantharia</i> , <i>Nymphon hirtipes</i>			<i>Sclerocrangon ferox</i> , <i>L. polaris</i> , <i>Strongylocentrotus pallidus</i> , <i>O. borealis</i>	<i>Gonatus</i> sp., <i>Pasiphaea tarda</i>
Prevalent consumer feeding habits ^b	Deposit feeder: ~30% Suspension feeder: ~20% Opportunistic/Scavenger: ~20% Predator: ~30%		Deposit feeder: ~25% Suspension feeder: ~25% Opportunistic/Scavenger: ~20% Predator: ~30%			Deposit feeder: ~15% Suspension feeder: ~10% Opportunistic/Scavenger: ~35% Predator: ~40%	Deposit feeder: ~5% Suspension feeder: ~5% Opportunistic/Scavenger: ~20% Predator: ~70%

(see Fredriksen et al., 2020), and abundant taxa were selected for stable isotope analysis. Taxon names were standardized following the World Register of Marine Species (WoRMS Editorial Board, 2026). Feeding guild information was retrieved from available peer-reviewed literature (Bell

et al., 2016; Armitage et al., 2025) and databases, such as the Arctic Traits Database (Degen and Faulwetter, 2019).

Benthic invertebrates were sampled for muscle tissue or pieces of body wall. In the case of small species, such as amphipods, whole

specimens were used, and where possible, tissues with higher turnover rates (e.g., guts) were removed, so that samples consistently consisted of slow-turnover and mass-dominant tissue. Samples were stored at -20°C until further processing, when samples were dried at 60°C for 24 h. Material containing significant calcium carbonate structures (e.g., tissue samples of Echinodermata, Arthropoda, as well as sediments) was split into two subsamples; one acidified prior to analysis of $\delta^{13}\text{C}$ (Quillien et al., 2016) and one non-acidified for analysis of $\delta^{15}\text{N}$. The first subsamples were treated with 1 N HCl until bubbling stopped, after which the samples were washed with distilled H_2O and re-dried at 60°C . Filters were fumed with saturated HCl vapor for 24 h, and sediment samples were treated repeatedly with 1 N HCl and rinsed. No lipid extraction was performed since sample preparation (lipid extraction, carbonate removal), as well as composition (targeted tissues), may influence the comparability of stable isotope data among species and different studies (Søreide et al., 2006a; Mateo et al., 2008). Replication was on average 3 samples per species and station, but ranged from 1 to 4, depending on availability of material (see Table A1 in the Supplementary Information for the number of replicates at seascape level).

Samples were run on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer at the Alaska Stable Isotope Facility, the University of Alaska Fairbanks. Stable isotope ratios are expressed as conventional delta notation; $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where δ = the ratio of heavy to light isotopes (^{13}C : ^{12}C or ^{15}N : ^{14}N). Instrument precision for analysis was $<0.4\text{‰}$ and $<0.3\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, based on standard deviation of replicates of a peptone standard (run every 10 samples). Standards were Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ values, and atmospheric nitrogen for $\delta^{15}\text{N}$ values.

2.3. Data analysis

Standard quantitative descriptors following a Bayesian approach (Jackson et al., 2011) were used to estimate community properties in isotope space for the different habitats. We assessed assemblage overlap based on 95% standard ellipse areas (‰^2) corrected for small sample sizes (SEAc) (Jackson et al., 2011). It should be noted that the communities differ in species richness as well as composition among habitats. The Jaccard coefficient of species similarity was used to quantify how similar the studied assemblages were in terms of taxa composition along the gradient. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the feeding groups were tested for differences across the inshore-to-offshore gradient, using a one-way ANOVA or a Kruskal-Wallis test if assumptions of normality and homoscedasticity were not met. To identify pairwise differences between locations, significant main tests were followed by post-hoc analysis corrected for multiple testing (Bonferroni). Analyses and data visualization were conducted in the programming environment R 4.0.2 (R Core Team, 2025) using custom code and packages ggplot2 (Wickham, 2016), patchwork (Pedersen, 2025), dplyr (Wickham et al., 2025), vegan (Oksanen et al., 2025) and RColorBrewer (Neuwirth, 2022). We acknowledge the confounding factor of time as different habitats were targeted during different sampling campaigns. Statistical analyses of temporal differences were not possible due to low or nonexistent replication.

Food web length was estimated through calculation of trophic position ($\text{TP}_{\text{consumer}}$) for each consumer taxon for each location. Trophic position for consumers was calculated as: $\text{TP}_{\text{consumer}} = \lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/\Delta_n$, where λ is the trophic level (TL) of the organism used to establish $\delta^{15}\text{N}_{\text{baseline}}$, $\delta^{15}\text{N}_{\text{consumer}}$ is measured directly, and Δ_n is the isotopic enrichment factor per trophic level. Individual trophic position was approximated relative to a common benthic baseline, specifically a primary consumer representing TL 2 (λ) to reduce uncertainty due to the variability of stable isotope values that is typical for taxa at primary producer level (Nordström et al., 2009). We used location-specific $\delta^{15}\text{N}$ values for the ophiuroid *Ophiopleura borealis* as baseline reference values ($\delta^{15}\text{N}_{\text{baseline}}$) as the species is found consistently across the sampled locations and assumed to integrate isotopic changes at temporal and

spatial scales relevant for the community of interest (Post, 2002). In our calculations, we assumed a $\delta^{15}\text{N}$ trophic enrichment factor (Δ_n) of 3.4‰ per trophic level (Post, 2002), in line with previous studies of food web structure on Arctic shelves (Iken et al., 2010; Dunton et al., 2012; Bell et al., 2016). We performed a two-factor analysis with consumer trophic position as the dependent variable and assessing the influence of feeding group and habitat as factors, as well as their interaction (following tests of normality and homoscedasticity).

3. Results

3.1. Primary producers and basal resources

Particulate organic matter (POM) was present in the water column at all habitats. In addition, other potential food sources were encountered along a gradient, with nearshore and shelf habitats supporting a greater diversity of basal resources and offshore habitats showing fewer available resources (Table 1). For example, terrestrial plant material (*Salix* sp.) was found at the coastal sites (Bessel Fjord and Dove Bugt), as well as at one shelf site (Store Koldewey Trough), but was absent at shelf-break and upper-slope sites. *Fucus* sp. macroalgae were found at Bessel Fjord and at three shelf sites (76-N-Bank, Norske Trough and Store Koldewey Trough). Red macroalgae were found at coastal (Dove Bugt) and shelf (76-N-Bank) sites, and brown and green filamentous macroalgae were found along the whole gradient, at coastal, shelf, shelf-break and upper-slope sites.

In terms of their stable isotope values, macroalgae spanned the full range of $\delta^{13}\text{C}$ values observed, with subtidal red algae showing the lowest mean value ($-37.5 \pm 0.8\text{‰}$) and *Fucus* sp. the highest ($-14.2 \pm 0.5\text{‰}$) across the habitats (Fig. 2). Filamentous macroalgae mean values ranged between $-26.4 \pm 0.9\text{‰}$ and $-22.2 \pm 0.4\text{‰}$. Leaves from the terrestrial plant *Salix* sp. were low in $\delta^{13}\text{C}$ ($-29.6 \pm 0.4\text{‰}$), representative for C-3 plants prevalent in the high Arctic. Sediment organic matter varied much less in $\delta^{13}\text{C}$, with a range from $-23.7 \pm 0.1\text{‰}$ to $-22.6 \pm 1.2\text{‰}$, whereas POM ranged from $-30.6 \pm 0.5\text{‰}$ to $-26.0 \pm 0.3\text{‰}$. For $\delta^{15}\text{N}$ values, red algae had means from $4.9 \pm 0.8\text{‰}$ to $5.8 \pm 0.1\text{‰}$. *Fucus* sp. $\delta^{15}\text{N}$ mean values varied between $2.9 \pm 0.7\text{‰}$ and $4.1 \pm 0.1\text{‰}$ between the coastal and shelf sites. Filamentous macroalgae ranged between $4.4 \pm 0.5\text{‰}$ and $5.4 \pm 1.2\text{‰}$, whereas *Salix* sp. ranged between $2.9 \pm 1.1\text{‰}$ and $3.9 \pm 0.2\text{‰}$. Sediment organic matter $\delta^{15}\text{N}$ ranged from $6.3 \pm 0.1\text{‰}$ to $11.7 \pm 0.7\text{‰}$ and for POM from $6.2 \pm 0.3\text{‰}$ to $12.5 \pm 1.4\text{‰}$.

Basal resource stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) varied along the inshore-to-offshore gradient without a consistent trend among the sources. POM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were relatively high at the shelf-break and upper slope sites ($\delta^{13}\text{C}$: $H_3 = 20.34$, $p < 0.001$; $\delta^{15}\text{N}$: $H_3 = 23.41$, $p < 0.001$), but the results from the pairwise comparisons were inconclusive. There was no significant difference in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ of *Salix* sp. leaves among habitats ($\delta^{13}\text{C}$: $F_{1,19} = 0.009$, $p = 0.933$; $\delta^{15}\text{N}$: $F_{1,17} = 0.088$, $p = 0.770$). For filamentous algae, the lowest $\delta^{13}\text{C}$ was found for the shelf sites (mean $-26.4 \pm 1.6\text{‰}$) ($F_{3,44} = 3.213$, $p = 0.032$), but showed high variation, potentially because the samples consisted of a variety of algal types (brown and green filamentous algae). Filamentous macroalgal $\delta^{15}\text{N}$ did not differ significantly along the gradient ($F_{3,44} = 0.285$, $p = 0.836$). Sediment $\delta^{13}\text{C}$ was the lowest at coastal sites ($H_3 = 9.130$, $p = 0.028$), and $\delta^{15}\text{N}$ was lower at coastal and shelf sites compared to shelf-break and slope sites ($H_3 = 23.017$, $p < 0.001$).

3.2. Invertebrate consumer communities

The occupancy of the epifaunal consumer communities in stable isotope space was wide, with carbon ranges spanning $7.9\text{--}14.8\text{‰}$. Across the inshore-to-offshore gradient, the degree of overlap in stable isotope space among the consumer communities varied from the coast towards shelf-break and upper-slope areas. The SEAc degree of overlap of

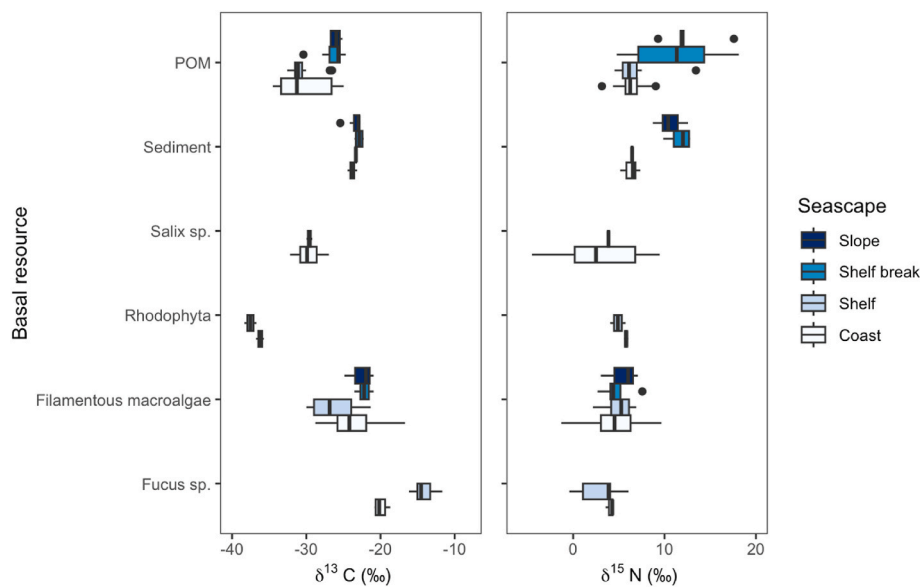


Fig. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ boxplots of basal resources in NE Greenland along inshore-offshore gradient. Station color denotes seascape habitat (coastal, shelf, shelf break and slope). Boxplots display the 25th percentile, median and 75th percentile, with whiskers extending to the minimum and maximum values and outliers shown in points. POM is particulate organic matter. (Note: Rhodophyta on shelf only had 2 replicates.).

adjacent habitats was 44% for coast and shelf habitats, 87% for shelf and shelf-break habitats, and 63% for shelf-break and upper-slope habitats (Fig. 3, Figure A1). The main difference between coastal and shelf habitats was due to higher $\delta^{15}\text{N}$ values of the fjord consumer assemblage. In contrast, the Jaccard coefficient of similarity for the taxonomic composition of the sample assemblages was 0.52 between coast and shelf, 0.46 between shelf and shelf-break, and 0.80 between shelf-break and slope habitats (Fig. A1), suggesting that community occupancy of stable isotope space is at least partially decoupled from species composition.

At the feeding-group level, consumer $\delta^{13}\text{C}$ values revealed group-specific, and some contrasting, trends along the inshore-to-offshore gradient (Fig. 4). For example, surface deposit feeders $\delta^{13}\text{C}$ values were higher at coastal and shelf habitats compared to shelf-break and slope sites ($F_{3,135} = 13.64$, $p < 0.001$), whereas omnivore $\delta^{13}\text{C}$ values were lower for coastal and shelf habitats than in the areas further offshore ($F_{3,33} = 23$, $p < 0.001$). Both suspension feeders and hyperbenthic predators showed elevated $\delta^{13}\text{C}$ at shelf-break habitats ($F_{3,100} = 6.418$, $p < 0.001$; $F_{3,113} = 4.466$, $p = 0.005$), whereas the spatial structure for benthic predator $\delta^{13}\text{C}$ indicated higher values at shelf-break locations but remained statistically inconclusive ($H_3 = 21.471$, $p < 0.001$, no significant differences obtained in pairwise comparisons).

Consumer $\delta^{15}\text{N}$ values showed a more consistent pattern along the inshore-to-offshore gradient, with relatively high values at the coastal sites. Surface deposit feeders showed higher $\delta^{15}\text{N}$ at the coast compared to all other habitats ($F_{3,135} = 56.77$, $p < 0.001$), whereas for suspension feeders, the difference was identified for coast vs. shelf and shelf break sites ($F_{3,100} = 9.757$, $p < 0.001$), for benthic predators between coast and shelf habitats ($H_3 = 35.121$, $p < 0.001$), and for hyperbenthic predators between coast and slope habitats ($F_{3,113} = 4.469$, $p = 0.005$). The spatial structure for omnivore $\delta^{15}\text{N}$ remains inconclusive ($H_3 = 25.627$, $p < 0.001$, no significant differences obtained in pairwise comparisons), but, visually, the data match those for benthic predators (Fig. 4). (For taxon-level $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plots, see [Supplementary Material Fig. A2.](#))

3.3. Consumer trophic positions

The benthic consumer assemblages spanned three trophic levels above the primary producers (Fig. 5). Trophic position was influenced

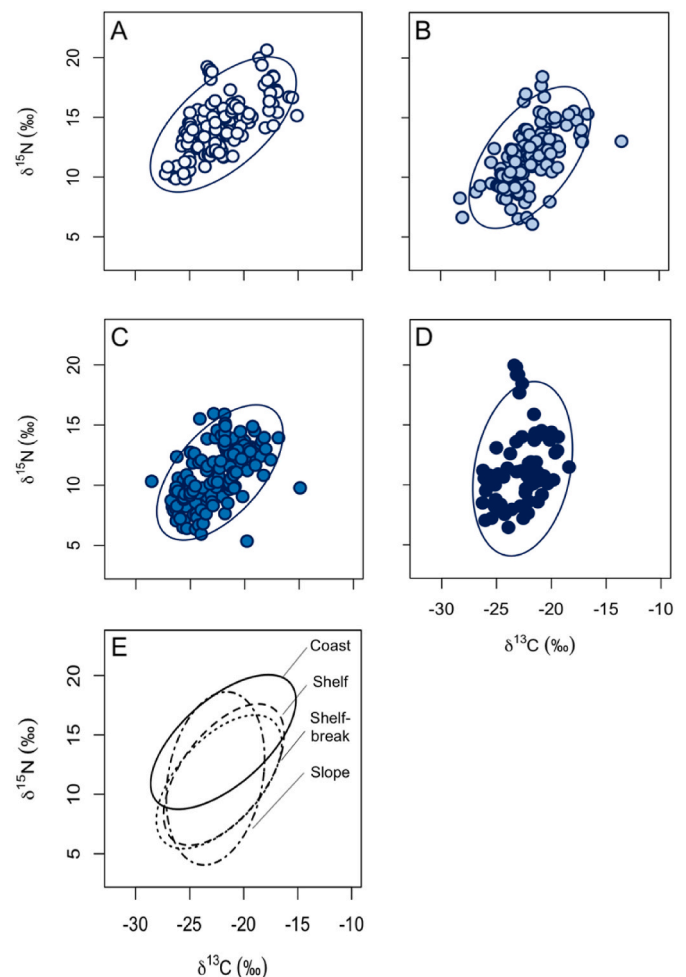


Fig. 3. Invertebrate consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) in the four habitats: coast (A), shelf (B), shelf break (C), and slope (D) locations. Each point shows one sample of a taxon and the ellipses show 95% standard ellipse areas (SEAc). Overlap of standard ellipses shown in E.

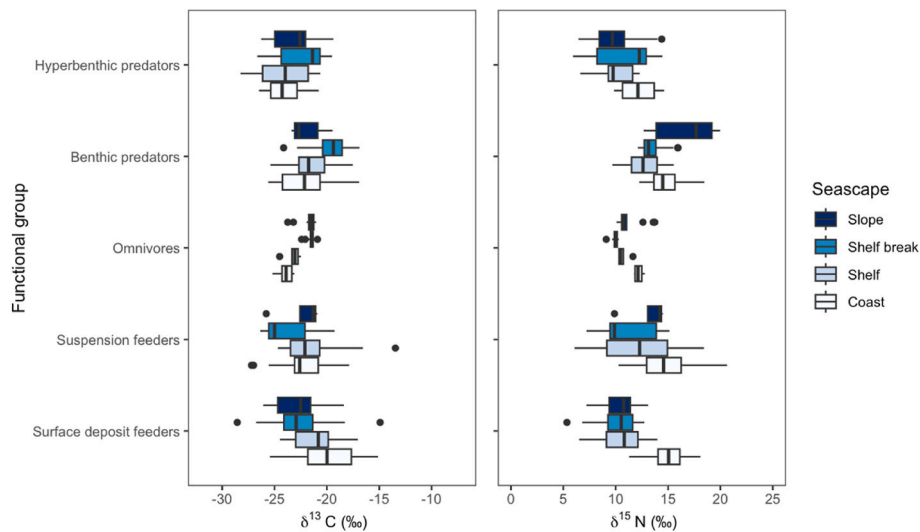


Fig. 4. Inshore-to-offshore gradient in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes for invertebrate surface deposit feeders, suspension feeders, omnivores, benthic predators and hyperbenthic predators in the NE Greenland seascape. Group color denotes seascape habitat (coastal, shelf, shelf break and slope). Boxplots display the 25th percentile, median and 75th percentile, with whiskers extending to the minimum and maximum values and outliers shown in points.

both by habitat and by feeding group ($F_{12, 487} = 6.54$, $p < 0.001$). The highest average trophic position was found for benthic predators at slope sites. Despite having generally higher $\delta^{15}\text{N}$ values, feeding groups at coastal locations (Bessel Fjord and Dove Bugt) had relatively lower trophic positions. The lowest average trophic positions were found for omnivores and hyperbenthic predators at coastal habitats. Hyperbenthic predators were generally positioned low in the food web compared to the baseline of benthic consumers, indicating distinct trophic pathways and resource partitioning between the pelagos and the benthos. Several feeding groups, such as the suspension feeders, showed wide range in trophic position.

4. Discussion

We set out to characterize epibenthic food webs of Northeast Greenland waters and describe the overall trophic structure along an inshore-to-offshore gradient of coast, shelf, shelf-break and upper-slope habitats. Our findings include relatively high overlap among consumer assemblages in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space, with shifts partly decoupled from species composition in the sampled communities, as well as largely variable and taxon-specific trajectories in the isotope values along the gradient. The feeding-group trajectories and the documented overlap in isotope space across the different habitats did not strongly indicate terrestrial input as a driving factor of the stable isotope trophic structure

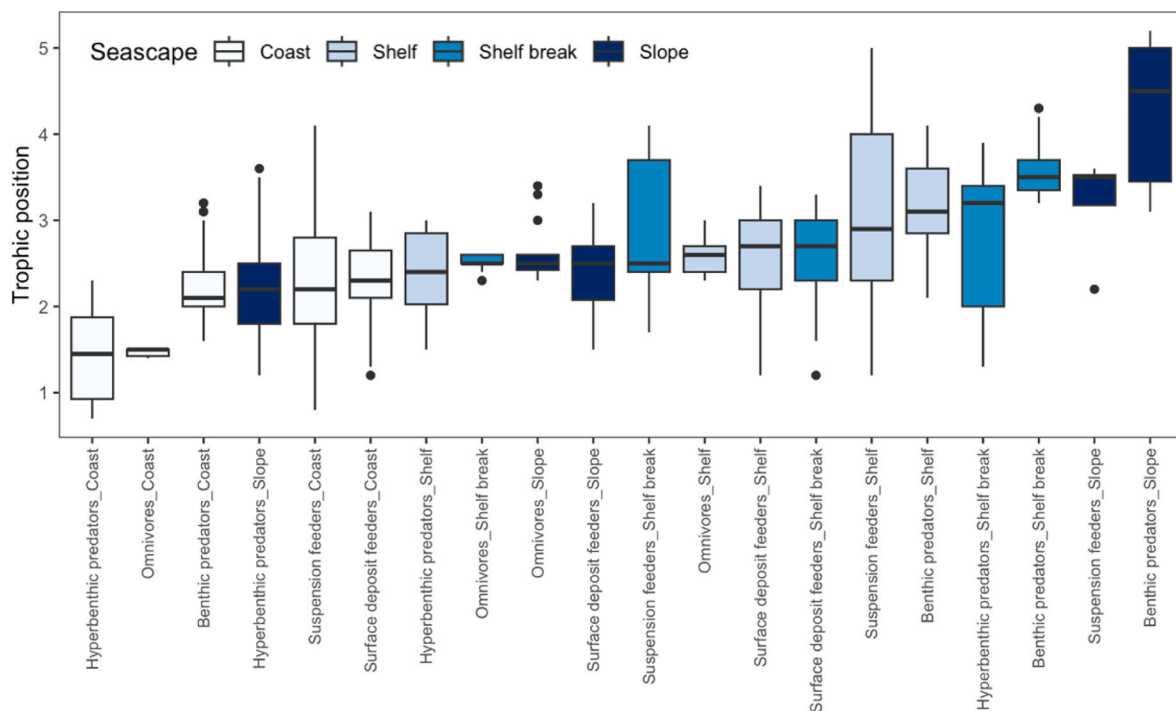


Fig. 5. Epifauna feeding groups ordered by median trophic position across the seascape of NE Greenland (colors denote coastal, shelf, shelf-break or slope habitats, shown in x-axis labels). Boxplots display the 25th percentile, median and 75th percentile, with whiskers extending to the minimum and maximum values and outliers shown in points.

at consumer assemblage level. There are multiple, co-occurring and non-exclusive mechanisms that may underlie this observation, including spatial-temporal dynamics in resource availability, in species composition and functional diversity of the consumer community, as well as spatial shifts in feeding preferences.

4.1. Resource availability and potential use

Environmental gradients across the seascape shape both the availability of resources and the relative importance of different food sources (Iken et al., 2010; Divine et al., 2015). In the study area, these gradients are reflected in the diversity of organic matter sources, from sea ice algae produced in early spring inside brine channels and phytoplankton in the water column produced over a broader time span in coastal Greenland (Hobson et al., 1995; Holding et al., 2019), to terrestrial material and glacial run-off from Greenland, macroalgae increasingly produced in Greenland's littoral zone (Krause-Jensen et al., 2012), as well as microphytobenthos (Attard et al., 2024). While the data of isotope signatures of the sampled organic matter sources partly overlap (Fig. 2) in our study, we capture some of the diversity of food sources described above, which provides a basis for interpreting trophic structure across the NE Greenland seascape.

Across the northeast Greenland seascape, habitats are characterized by different types of ice cover – fast ice and glacial ice in coastal habitats, pack ice from the outflow of the Central Arctic Ocean and glacial ice moved offshore from fjords across the shelf, and open water at the shelf break (Table 1), constituting gradients in ice-associated and pelagic primary production and vertical transport of particulate organic matter (Rysgaard and Sej, 2007; Holding et al., 2019). On the northeast Greenland outflow shelf, benthic food webs seem to be fueled mainly by sympagic production, based on findings from a study using highly branched isoprenoids as biomarkers to determine the relative importance of sympagic production to phytoplankton to benthic consumers. Reliance on sympagic production seemed particularly characteristic for fauna in coastal areas compared to those on the open shelf (Cautain et al., 2024). The higher $\delta^{13}\text{C}$ values of deposit feeders at the coastal sites in our study are consistent with that finding. Ice algae were not available at the time of sampling in our study, but they tend to be more enriched in $\delta^{13}\text{C}$ compared to phytoplankton, e.g., as seen in coastal fast ice off Alaska (Gradinger et al., 2009; Gradinger and Bluhm, 2020), and sink quickly to the seafloor, where they become available for benthic use (McMahon et al., 2021). A caveat is that the $\delta^{13}\text{C}$ values of the brown seaweed *Fucus* overlap with sea ice sources but given the findings by Cautain et al. (2024), we consider a role of ice algal carbon in benthic feeding highly likely. In the Barents Sea, sea ice duration strongly correlates with the relative importance of sympagic organic material to pelagic organic material assimilated in epibenthic fauna (Cautain et al., 2022). Such a trend was not found for NE Greenland, likely due to the much longer ice period resulting in a less pronounced gradient of ice cover duration in NE Greenland than in the Barents Sea (Cautain et al., 2024). In terms of net primary productivity in the marine Arctic, the contribution by sympagic production generally remains much lower (0–10%) than its pelagic counterpart (Gradinger et al., 2009), though proportions are undetermined in our study area to our knowledge. However, pelagic production is spatially variable across the Arctic and low on the Greenland outflow shelf (Arrigo and Van Dijken, 2015).

The approach Cautain et al. (2024) used, does not, however, allow for including terrestrial, seaweed or microphytobenthos carbon sources, although the latter two contribute considerably to primary production in the shallower parts of Greenland fjords (Attard et al., 2024; Krause-Jensen et al., 2012). Regarding the availability of terrestrial and littoral production, our observations of depleted POM $\delta^{13}\text{C}$ values at the time of sampling, together with catches of seaweeds far away from the coast, imply that marine epibenthic invertebrate consumers in the Greenland Sea coastal and shelf environments are likely to find some advected terrestrial and littoral organic matter available across the

seascape. Work in Svalbard's Kongsfjorden showed that macroalgae could at times contribute to the consumer communities in benthic environments way beyond the area of macroalgal production (Renaud et al., 2015). It is unclear to which degree littoral production in the form of advected macroalgal material currently contributes to benthic food webs far out on the Greenland Sea shelf, but both our catches of many kilograms of macroalgae in the trawl hauls very far from the coast at shelf stations, as well as recent model estimates (Filbee-Dexter et al., 2024) suggest inputs could be substantial. Based on eDNA samples, brown macroalgae were found to be the dominant contributors to carbon stocks in Arctic marine sediments, detected in both shallow and deep areas and as far as 350 km from the coastline (Ørberg et al., 2023). Exchanges between shelf and fjord are influenced by sill depth of a given fjord and occur, for example, as intermediary flows above sill depth (Straneo and Cenedese, 2015); conceivably sufficiently strong to transport organic matter out of a given fjord onto the shelf. Alternatively, seaweed material is buoyant enough to be transported out of fjords, where deep convection subsequently takes it to depth as was shown for SW Greenland fjords (Carlson et al., 2026). Glacial troughs may further enhance this connectivity by funneling particulate organic matter across the shelf through topographically steered currents and enhanced bottom transport, thereby facilitating the off-shelf export of both seaweed detritus and terrestrial material from coastal zones to shelf break, slope and deep ocean (Nittrouer and Wright, 1994; Krause-Jensen and Duarte, 2016; Kokubu et al., 2019).

Several studies have identified shifts in consumer $\delta^{13}\text{C}$ values indicative of reliance on terrestrial production closer to the coast (and particularly in lagoons, e.g. McMahon et al., 2021; Harris et al., 2018), whereas little indication of that being the case was found in our study. However, without conducting any formal source-partitioning analyses, we are limited in the quantitative inference we can make. POM values were indeed overall indicative of terrestrial inputs (mean range -30.5 to -25.9‰), yet only very few observations (5.5%) were on consumer $\delta^{13}\text{C}$ values within that range, and these interestingly consisted mainly of the hyperbenthic/pelagic genus *Themisto*. In addition, we found that consumers at coastal sites showed higher values of $\delta^{15}\text{N}$, which could relate to baseline variation, trophic position differences, or nitrogen cycling processes. High $\delta^{15}\text{N}$ values could also suggest the use of more degradable material rather than refractory terrestrial organic matter, which is depleted in $\delta^{15}\text{N}$. Supporting this, the mean C:N ratio for coastal sediments (10.9) rather indicates mainly marine organic matter sources. Examining benthic communities in inner and outer fjord basins in Young Sound, Bridier et al. (2021) found spatial homogeneity of the food webs and also documented low-to-insignificant contribution by terrestrial organic matter to benthic primary consumers despite differing freshwater regimes at the two sites. The findings in the present study as well as those of Bridier et al. (2021) and Schloemer et al. (2023) of minor terrestrial influence on the benthic food web, are contrasting to ones from e.g. Arctic lagoons. A contributing factor to this may lie in the relatively lower vegetation cover in and around NE Greenland fjords compared to low-lying, highly vegetated areas with many rivers in North America and Siberia, which could influence the quality and quantity of terrestrial inputs in the region, and, hence, the strength of the terrestrial signal in the coastal food webs (Bridier et al., 2021). However, whether spatially heterogeneous contributions of terrestrial production to benthic communities are characteristic of fjords and coastal embayments in Northeast Greenland remains an area of uncertainty.

4.2. Community variability can influence spatial food web structure

There are documented taxonomic differences in the epifauna communities (Fredriksen et al., 2020) along the studied inshore-to-offshore gradient. The taxonomic dissimilarities further manifest as functional (trait) differences in the epifauna communities when moving from fjord to upper-slope habitats, including e.g. decreasing proportions of deposit feeders and increasing proportions of predators (Armitage et al., 2025).

Underlying shifts in species dominance are usually not accounted for in stable isotope assessments unless data are weighted by abundance or biomass of the different taxa (Quillien et al., 2016). A turnover in consumer identities may, however, contribute to differences between consumer assemblages in stable isotope space if different consumer taxa have different feeding preferences. If species turnover happens within a functional group, the result may not entail shifts in trophic function. Furthermore, the feeding preferences of consumer taxa may change, depending on the environmental setting or, for example, resource availability, as described above. The composition of our isotope sample assemblages also depended on seascape habitat (Fig. A1). However, there was no evident relationship between the Jaccard similarity of the sample assemblages and the overlap in stable isotope space of those same consumer communities.

Our study covers a large area and includes many habitats and diverse fauna. Across this seascape gradient, with distinct epibenthic communities and assumed gradients in carbon sources, food web structure (as here depicted in stable isotope space) is perhaps surprisingly stable, in particular with regard to assemblage $\delta^{13}\text{C}$ values. Examining intra-specific values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and trophic position revealed species-specific patterns and few consistent trajectories, e.g., among members of functional groups or feeding guilds. As such, these results may be suggestive of generalist feeding in the benthic assemblages. The ability to use multiple carbon pathways may be associated with an adaptive capacity that can function as a stabilizing mechanism in food webs, a hypothesis that warrants further investigation in these highly dynamic environments.

5. Future perspective

For the Arctic Ocean, an overall increase in primary production by 57% was documented for the period 1998–2018, likely related to decreased sea-ice extent and duration of ice cover, as well as increases in phytoplankton concentrations due to influx of nutrients (Arrigo and Van Dijken, 2015; Lewis et al., 2020). On outflow shelves like the East Greenland shelf, however, net primary production decreased or showed little change over the same period, although chlorophyll-*a* values can be spatially and temporally variable (Arrigo and Van Dijken, 2015). Climate-related changes in surface production influence the flux of particulate organic carbon and hence food quality and availability for deep-sea benthic organisms (Sweetman et al., 2017). Changes in primary production are also observed in coastal ecosystems, where subsidies in the form of littoral production transported to deeper waters are likely to increase in importance under ongoing climate change (Krause-Jensen et al., 2012). Already, substantial and persistent changes have been observed in the producer and consumer communities on shallow rocky shores in the Arctic, with increases in macroalgal cover. Along the Greenland coast, kelp depth extension and production are greater in southern (sub-Arctic) areas compared to more northern (Arctic) areas, which is related to water temperatures and the number of ice-free days, both of which increase towards the south (Krause-Jensen et al., 2012). These findings, as well as our observations of littoral and terrestrial organic matter along the explored spatial gradient, suggest that coastal primary production has the potential to increase in importance in coastal Arctic food webs, given a warming environment. Alongside prominent changes on primary producer level, shifts in the consumer communities are expected to occur. For example, significant impact on food web structure and resilience is anticipated from changes in consumer composition and relative abundances due to climate-related poleward shifts (Kortsch et al., 2015; Christiansen et al., 2016). In addition, coastal freshening may impact fjord food webs through changes in phytoplankton grazer communities, and through strengthening the halocline potentially creating adverse conditions for benthic organisms (Boone et al., 2018). In all, climate-driven regime shifts and borealization of ecosystems are expected to influence the structure, functioning and resilience of future Arctic food webs in a

complex manner (Degen et al., 2017; Husson et al., 2024). In this light, our study provides critical reference data for this data-poor area that facilitate evaluating changes in food web structure and carbon sourcing in future re-visits of the region. We suggest food web structure be integrated in long-term monitoring strategies such as in place via the Greenland Ecosystem Monitoring program and the pan-Arctic Distributed Biological Observatory.

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CRediT authorship contribution statement

M.C. Nordström: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **I. Zhulay:** Investigation, Writing – original draft, Writing – review & editing. **P.A. Armitage:** Data curation, Visualization, Writing – review & editing. **F. Norrbin:** Investigation, Writing – review & editing. **E. Bonsdorff:** Conceptualization, Funding acquisition, Investigation, Writing – review & editing. **J.S. Christiansen:** Funding acquisition, Investigation, Writing – review & editing. **B.A. Bluhm:** Conceptualization, Data curation, Funding acquisition, Investigation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2026.108295>.

Data availability

Data available at <https://doi.org/10.5281/zenodo.21511350>.

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