



Weak seasonality in benthic food web structure within an Arctic inflow shelf region

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ARTICLE INFO

Keywords:

Seasonality
Arctic
Food web structure
Stable isotopes
Benthos

ABSTRACT

The Arctic Ocean is characterized by pronounced seasonality in the quantity and quality of organic matter exported from the surface ocean. While it is well established that changes in food availability can alter the abundance, biomass and function of benthic organisms, the impact on food web structure is not well studied. We used bulk carbon and nitrogen stable isotope analysis to assess the quantity and quality of sediment organic matter and structure of the benthic food web in four seasons within the Northern Barents Sea (76°N – 82 °C). Despite a highly seasonal vertical flux, we found that the organic carbon and chlorophyll-*a* content of surface sediments was seasonally stable, suggesting a lack of seasonality in food availability at the seafloor. However, organic biomarkers indicate that the *quality* of sediment organic matter increased to a maximum in August and December, up to 6 months after the spring bloom. The seasonal stability of food quantity was mirrored in food-web structure (e.g., total isotopic range, number of trophic levels) which did not change significantly across sampling periods. We expected that suspension and deposit feeders would respond more readily to seasonal changes in food quality compared to predators. However, we observed no significant seasonal changes in the trophic levels or isotopic niche areas of benthic functional groups. The centroids of isotopic niches of all benthic functional groups shifted seasonally by <2 ‰ along the δ¹³C-axis, suggesting minimal shifts in carbon resource use. Because the northern Barents Sea experiences significant changes in seasonal sea ice cover, we expected that stable-isotope ratios of benthic organisms would show an increased consumption of sympagic-derived organic matter through less negative δ¹³C values in early spring and summer. However, only two taxa (the soft coral *Gersemia* spp. and bivalves in the family Yoldiidae) showed ¹³C-enrichment in spring or summer consistent with the assimilation of sympagic-derived organic matter, despite previous evidence suggesting widespread use of this carbon source. Overall, our results show that there is an apparent de-coupling in time between pelagic processes and benthic food-webs in which the accumulation and assimilation of high-quality organic matter occurs for benthos during the fall and early winter months when there is little to no fresh organic matter generated at the surface. This temporal mismatch highlights the importance of considering the timescales over which components of the marine ecosystem respond to short-term environmental changes and the methods employed to assess seasonality.

1. Introduction

Seasonal food pulses are a defining feature of polar ecosystems (Carmack and Wassmann, 2006; Clarke, 1988) and have been shown to modulate benthic abundance, biomass, the timing of reproduction, and processes like bioturbation and respiration (Campanyà-Llovet et al., 2017; Carroll et al., 2008; Gontikaki et al., 2011; Grebmeier and Barry,

1991; Grebmeier and McRoy, 1989; Hobson and Ambrose, 1995; Renaud et al., 2008). Polar benthic organisms are well adapted to a highly seasonal supply of food, and respond quickly to the deposition of fresh phytodetritus, including that of sympagic origin (McMahon et al., 2006; Renaud et al., 2007; Sun et al., 2006). However, omnivory is also a common feeding strategy of many polar benthic taxa which can utilize a wide range of other food sources including advected organic matter,

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<https://doi.org/10.1016/j.pocean.2023.103109>

Available online 23 August 2023

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large food falls, and chemosynthetic products (Arntz et al., 1994; Åström et al., 2022; Norkko et al., 2007). The ability of individual organisms to exploit varied food sources or exhibit different feeding strategies in response to changing food availability are useful adaptations to the seasonal food-limitation in polar regions. Seasonal feeding plasticity is best documented in zooplankton (Kohlbach et al., 2021; Olli et al., 2019; Tamelander et al., 2008), but has also been observed in some benthic organisms, notably through the increased consumption of sympagic-derived organic matter during early spring (Cautain et al., 2022; Peck et al., 2005; Søreide et al., 2013). In addition to individual changes in diet, changes in food availability have been shown to broadly alter food-web structure, including the overall trophic diversity, the number of trophic linkages per species, and the number of trophic levels in a food web (Kortsch et al., 2019; Rossi et al., 2019; Sporta Caputi et al., 2020). In coastal regions of the Antarctic, however, it was found that a relatively constant supply of high-quality components of algal detritus was available to benthic consumers year-round which reduced the seasonality observed in food web structure (Mincks et al., 2008, 2005; Norkko et al., 2007). Similarly, studies within two Arctic fjords (Kongsfjorden, Svalbard and Young Sound, Greenland) found that despite strong seasonality in local oceanographic conditions and food availability, food web structure was stable across seasons (Bridier et al., 2021; Kędra et al., 2013; Renaud et al., 2011) and sediment remineralization rates did not mirror the seasonality in overlying productivity or organic matter flux (Morata et al., 2020; Sørensen et al., 2015). These Arctic studies have been conducted in regions that are either heavily influenced by Atlantic Water (e.g., Fram Strait, the West Spitsbergen Current, Southern Barents Sea) or that are shallow and coastal (e.g., Svalbard fjords) and, hence, greatly influenced by glacial dynamics and terrestrial inputs of freshwater and carbon. Thus, it remains unknown whether a lack of seasonality in the benthic food web would also be observed in Arctic regions that are less impacted by Atlantic Water and removed from terrestrial or nearshore inputs. One such location of interest is the northern Barents Sea.

The seasonality of the Barents Sea ecosystem is largely controlled by the solar cycle and sea-ice cover which together limit the amount of light available in surface waters for photosynthesis. In general, phytoplankton biomass reaches a maximum between May and July (Goraguer et al., 2023; Hegseth, 1998) following the seasonal retreat of sea ice that is initiated in March or April (Arthun et al., 2012). However, the exact timing of sea-ice retreat and the start of the spring phytoplankton bloom varies by up to 3 months between the southern and northern Barents Sea (Leu et al., 2011). This is partly due to latitude because, regardless of sea-ice cover, the sun (hence, photosynthesis) returns after the Polar Night earlier in the south than in the north. Secondly, the distribution of water masses in the Barents Sea (especially that of warm Atlantic Water) causes a latitudinal gradient of sea-ice cover which increases northward. Atlantic Water enters the Barents Sea primarily from the southwest, and to a lesser degree from the north in the region east of Svalbard (Ingvaldsen et al., 2002, 2004; Lundesgaard et al., 2022) transporting heat that prevents sea-ice growth in the southern Barents Sea year-round, and melts sea ice in the north (Fig. 1) (Arthun and Schrum, 2010; Parkinson and Cavalieri, 1989; Ivanov and Repina, 2018). Thus, the combination of the annual solar cycle and sea-ice cover results in a latitudinal gradient in the timing of bloom initiation which progresses northward during the spring (Wassmann et al., 2020). After being produced in surface waters, organic matter is exported from the euphotic zone, and the vertical flux of this material ultimately provides the food for the benthos. The quantity and quality of organic matter that is exported from the euphotic zone to the seafloor is dependent on the phytoplankton biomass, the rate of passive sinking by algal cells, the composition of the algal community, bacterial degradation, and the rate of zooplankton grazing which both removes algal biomass and repackages it into fecal pellets (Lalande et al., 2016; Olli et al., 2002; Reigstad et al., 2008; Wakeham et al., 1997; Wassmann, 2001; Wexels Riser et al., 2008). During peak bloom conditions in the seasonally ice-

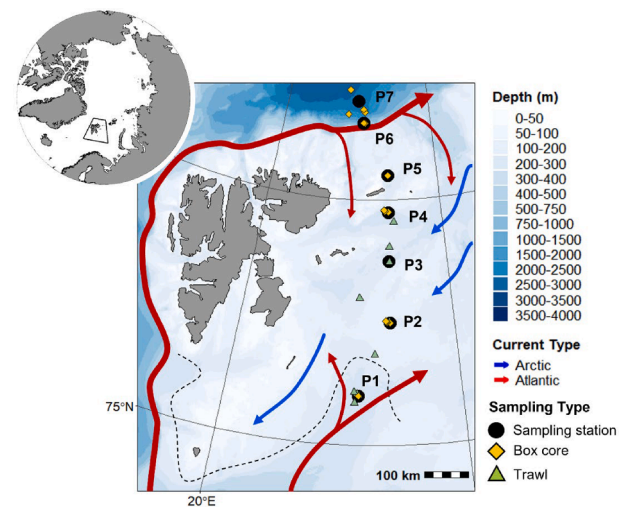


Fig. 1. Map of the study region in the northern Barents Sea. The general locations of the main sampling stations (P1-P7) are shown by the black circles. Individual boxcore deployment locations are shown as yellow diamonds and starting locations for benthic trawls as green triangles. Depth is given by the blue shading and elevations > 0 m (land or glacier) is shown in grey. Approximate locations of major currents of Atlantic (red) and Arctic (blue) Water origin are shown and an idealized position of the Polar Front where these waters meet given by the dashed line (Harris et al., 1998). This map was made using the ggOceanMaps package in R (Vihtakari, 2022) with bathymetric data from GEBCO 15-arc second grid 2021 and land shapefiles from Natural Earth Data (1:10 physical vectors with land and minor islands datasets combined). The inset shows the general location of the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

covered regions of the Barents Sea (>ca. 75°N, here referred to as 'northern Barents Sea'), high attenuation of sinking particulate organic carbon (POC) occurs in the upper 30–60 m (Reigstad et al., 2008) leaving little organic matter to be transported to the seafloor. However, at sites with weaker stratification and strong wind mixing, POC flux can be high, reaching 120–220 mg POC m⁻² d⁻¹ at 90–200 m depth (Reigstad et al., 2008). This suggests that a high proportion of food for benthic organisms can be delivered to the seabed during the short spring bloom period in the northern Barents Sea. Long-term sediment trap studies in the region northeast of Svalbard confirmed that POC flux increases after the onset of the spring bloom around May, to a maximum in late June to early July as the POC quality, indicated by a higher diatom cell flux and reduced fecal pellet carbon, concurrently increases (Dybwad et al., 2022). However, in the region northeast of Svalbard where the influence of Atlantic Water is reduced, there is less seasonal change in POC flux and quality (Dybwad et al., 2022). This regional difference suggests that there is a significant influence of Atlantic Water on the advection and vertical flux of organic matter, and that a dampened seasonality in food availability and quality may be expected within the northern Barents Sea where there is a mix of both Atlantic and Arctic Water.

Once at the seabed, the composition and quality of organic matter continues to change. Over days to months, heterotrophic grazers degrade the phytopigments in organic matter (such as chlorophyll-*a*) generating biproducts collectively referred to as phaeopigments (Mincks et al., 2005; Sun et al., 1993; Stephens et al., 1997; Bianchi et al., 1988; Helling and Baars, 1985; Shuman and Lorenzen, 1975; Welschmeyer and Lorenzen, 1985). In addition, the nitrogen in organic matter is utilized more rapidly relative to carbon thereby increasing the C:N ratio and δ¹⁵N value of the remaining organic matter (Sambrotto et al., 1993; Möbius, 2013). Thus, a higher chlorophyll-*a*/phaeopigment ratio, lower C:N ratio and lower δ¹⁵N value of organic matter indicate higher quality and freshness. In the open Barents Sea, the main food source for benthic

suspension and deposit feeders is detritus that is derived from either pelagic or sympagic autotrophs (Cautain et al., 2022). Because sympagic autotrophs grow in a CO₂-limited environment within the sea ice, their biomass has a higher $\delta^{13}\text{C}$ value compared to that of pelagic phytoplankton (Gleitz et al., 1996; Hobson and Ambrose, 1995; Mizutani and Wada, 1982; Rau et al., 1997). Overall, the composition and quality of organic matter influences benthic invertebrate nutrition and influences feeding selectivity (Levinton et al., 1984; Zinkann et al., 2021). These processes can influence invertebrate diet (and isotopic composition) as well as the efficiency with which energy is transferred between trophic levels, ultimately impacting the structure and stability of food webs (Bell et al., 2016; Rosenzweig, 1971). Therefore, it is important to consider the potential for seasonal changes in organic matter quality when investigating food web structure, especially when using bulk stable isotopes.

Ecological theory predicts the partitioning of resources or diet specialization among consumers for coexistence in a seasonally resource-limited environment due to increased resource competition (Hutchinson, 1957; Tilman, 1980). The result is distinct resource use patterns by organisms, referred to as their ecological niche. Just as the ecological niche defines an organism's ecological role based on resource use, the isotopic niche defines an organism's trophic role based on assimilated food sources and trophic interactions (Newsome, 2007) which can be assessed using bulk stable-isotope analysis (e.g., Bearhop et al., 2004; Newsome, 2007). The isotopic niche can be used to compare resource use by species, functional groups, or entire populations within a robust, statistical framework (Jackson et al., 2011; Layman et al., 2007). Stable isotope analysis in trophic ecology traces chemical biomarkers of available food sources through trophic transfers among fauna to understand trophic relationships and the dietary contributions of different carbon sources. It is based on the predictable fractionation of elements (here, carbon and nitrogen) during reversible chemical reactions like photosynthesis and respiration (DeNiro and Epstein, 1981, 1978). The stepwise enrichment of the nitrogen isotope ratio of consumer tissues makes this element an ideal tracer for determining the trophic level of organisms (Minagawa and Wada, 1984). Conversely, the fractionation of carbon isotopes during trophic transfer is minimal, making the isotope ratio of carbon ideal for tracing the source of carbon assimilated by consumers (DeNiro and Epstein, 1978).

To test the hypothesis that seasonality in food availability and quality affects benthic food-web structure, we used bulk stable-isotope analysis of carbon and nitrogen to determine the trophic levels and isotopic niche areas of individual taxa and functional groups within the benthic community of the northern Barents Sea during four distinct seasons. We first tested whether sediment organic matter quantity (here measured as chlorophyll-*a* and total organic carbon content) and quality (measured by phytopigment content, elemental and isotopic composition) changed seasonally within our study region. We then compared measures of the isotopic niche of benthic fauna and relative trophic level seasonally to explore whether changes in food web structure matched the seasonality observed in food sources. Specifically, we expected the highest quantity and quality of sediment organic matter to occur around the time of the spring bloom (May) and to decrease through the fall and winter (December and March) as this organic matter is remineralized and consumed by benthic organisms. We also expected a decrease in trophic level and isotopic niche area during spring (May) when a large quantity of high-quality organic matter was expected to be present on the seafloor, given that typical particle settling velocities are 20–120 m d⁻¹ (Wekerle et al., 2018). Thus, a lag of <1 month was expected between the spring bloom and the arrival of fresh organic matter at the seafloor for the depth of the Barents Sea shelf. In winter, we expected organisms to have the broadest isotopic niche areas reflecting food limitation and increased resource use overlap among benthic taxa.

2. Methods

2.1. Sample collection

Four field sampling campaigns were conducted to the northern Barents Sea aboard the icebreaker *R/V Kronprins Haakon* in August 2019 (summer), December 2019 (fall), March 2021 (winter) and May 2021 (spring). March and May sampling were delayed by the COVID-19 pandemic such that seasons were not contiguous. Sampling locations focused on 7 stations (referred to as P1-P7 from south to north) which form a transect extending from approximately 76–81°N roughly along the 30°E longitude (Fig. 1). The study area covers the continental shelf south and north of the Polar Front (where Atlantic and Arctic water masses meet), and the continental slope and rise towards the Nansen Basin. Not all stations could be sampled in each season due to sea ice conditions and weather (see Table 1). At each station, sediments, benthic invertebrates (including epifauna and infauna) and demersal fish were collected using a boxcore (0.25 m²) and Campelen trawl. At least three replicate boxcores were collected at each station. Once boxcores were on board, the overlying water was carefully drained, and sub-cores were inserted to collect various samples. Sediments were collected using a 5-cm diameter sub-core which was sliced into 1-cm intervals and frozen at -20 °C until elemental and isotopic analysis (Ricardo de Freitas et al., 2022a, 2022b, 2022c, 2022d). Here, only surficial sediments (0–1 cm) are considered and data from replicate boxcores were pooled to the station level. The remaining 0–10 cm of the boxcore sample was removed and placed into buckets of cold seawater. The sediment was then gently sieved with a 500 µm sieve to collect all macrofauna. The collected material was placed back into a bucket of cold seawater, aerated, and stored in a cold room (0–4 °C) until further sorting and identification to the lowest taxonomic level possible could take place, within 48 h. When possible, soft tissue was sub-sampled from

Table 1

Approximate latitude and longitude (decimal degrees), and depth (m) of each station occupied during the four seasonal sampling campaigns to the northern Barents Sea. An 'x' indicates whether boxcore(s) or a trawl were conducted at the stations. Note that when multiple boxcores were conducted per station, only one approximate location is provided here for brevity.

Station	Latitude (°N)	Longitude (°E)	Depth (m)	Boxcore(s)	Trawl
August 2019					
P1	76.048	31.099	333	x	x
P2	77.499	34.001	188	x	x
P3	78.732	34.010	307		x
P4	79.746	34.017	334	x	x
P5	80.502	34.017	161	x	
P6	81.545	30.848	857	x	
P7	81.728	28.671	2649	x	
December 2019					
P1	76.085	30.846	327		x
P2	77.491	33.969	190	x	x
P4	79.739	34.004	338	x	
P6	81.547	30.863	870	x	
March 2021					
P1	76.000	31.220	325	x	x
P2	77.534	33.603	170	x	x
P4	79.771	33.612	327	x	
P6	81.547	30.852	869	x	
P7	81.728	28.671	2671	x	
May 2021					
P1	76.001	31.222	326	x	x
P2	77.500	34.002	190	x	
P4	79.755	33.994	330	x	x
P6	81.560	30.853	954	x	
P7	81.842	30.757	3103	x	

large individuals, but most individuals were frozen whole ($-20\text{ }^{\circ}\text{C}$) for further preparation and analysis ashore.

Trawl hauls were conducted at stations south of P6 using a Campelen trawl deployed to the seabed for approximately 15 min as the ship moved at a speed of about 3 knots, covering approximately 1.4 km of the seabed (The Nansen Legacy, 2022). Sea ice cover and great water depth prevented trawling at stations P6 and P7. Upon retrieval of the trawl, organisms were transferred to buckets of cold seawater and sorted to the lowest taxonomic level possible. Whole individuals or pieces containing soft tissue (e.g., asteroid arm) were then frozen ($-20\text{ }^{\circ}\text{C}$) for further processing ashore in a laboratory. In general, we aimed to collect a minimum of three replicates of each taxon at every station during each sampling campaign to capture some individual variability in isotopic composition.

2.2. Stable isotope and elemental analysis

In the laboratory, frozen faunal samples were thawed slightly to allow sub-sampling of soft tissue and removal of shells or other calcareous structures. For small organisms (e.g., infaunal polychaetes, etc.), many individuals were pooled together to ensure sufficient material for isotopic analysis. All samples were freeze dried for 48 h (Labconco model series 70020, 2.5 L capacity at $-50\text{ }^{\circ}\text{C}$) and ground using a mortar and pestle. For fauna containing calcium carbonate (e.g., echinoderms) a sub-sample of the dried and powdered sample was acidified using 1 M hydrochloric acid in a dropwise method, and re-dried in an oven ($60\text{ }^{\circ}\text{C}$) until all remaining liquid had evaporated (Jacob et al., 2005). Approximately 1 mg of all samples was weighed into tin capsules and analyzed at the CLIPT stable isotope biogeochemistry laboratory at the University of Oslo. Here, samples were analyzed for bulk stable isotopic and elemental composition of carbon and nitrogen using the Thermo Fischer Scientific EA IsoLink IRMS system comprised of a DeltaV Advantage Stable Isotope Mass Spectrometer coupled to a Flash Elemental Analyzer. The resulting isotope data were reported in delta notation: $\delta^n\text{X}$ (‰) = $[(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000$ where R is the ratio of heavy:light isotopes of the element X in our sample relative to the reference standards Vienna PeeDee Belemnite (VPDB, carbon, Craig, 1957) and air (nitrogen, Mariotti, 1983). During analysis, internal reference standards L-glutamic acid and glycine were calibrated to the International Atomic Energy Agency standards calcium carbonate (NBS19) and lithium carbonate (LSVEC) to normalize carbon isotope values to the $\delta^{13}\text{C}_{\text{VPDB}}$ -scale as well as to USGS40 and USGS41 to normalize nitrogen isotope values to the $\delta^{15}\text{N}_{\text{AIR}}$ -scale. The precision of isotope ratios was assessed by the standard deviation of repeat measurements of the quality assurance reference material, L-alanine, which was $\leq 0.11\text{ }‰$ for $\delta^{13}\text{C}$ and ≤ 0.10 for $\delta^{15}\text{N}$. Elemental composition was reported in weight percent and was used to calculate C:N ratios. It has been suggested that samples with C:N ratios > 3.5 (Post et al., 2007) should undergo a post-analysis correction to account for the $\delta^{13}\text{C}$ -depletion of lipids relative to other tissues. In this dataset, C:N ratios of organisms were weakly but significantly correlated with $\delta^{13}\text{C}$ values ($R^2 = 0.041$, Spearman rho = -0.27 , $p < 0.01$). However, a high standard error and spread of the data indicated that many samples with high C:N ratios were not depleted in ^{13}C relative to other samples. Elevated C:N ratios of infauna could be caused by analysis of whole individuals and structural components other than muscle tissue rather than reflecting elevated lipid content. Thus, we chose not to correct $\delta^{13}\text{C}$ values but discuss the potential impacts on the isotope-based metrics we present. The $\delta^{13}\text{C}$ values of acidified samples which were $> -15\text{ }‰$ were removed from further analysis ($n = 13$) as this was assumed to be caused by insufficient removal of inorganic carbon.

Trophic level for all taxa was calculated using the corresponding station and sampling period mean $\delta^{15}\text{N}$ values of sediment organic matter as the baseline according to the following equation:

$$\text{Trophic level} = \lambda + [\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}] / \Delta\text{N} \text{ (Post, 2002)}$$

In this equation, the constant λ is the trophic level corresponding to the producer or consumer used to determine the isotopic baseline ($\delta^{15}\text{N}_{\text{base}}$), $\delta^{15}\text{N}_{\text{consumer}}$ is the nitrogen isotope value of the consumer in question, and ΔN is the trophic discrimination factor. In this study, the isotopic baseline was sediment organic matter from the surface 0–1 cm where $\lambda = 1$ and we assumed a ΔN value of $3.4\text{ }‰$ (Post, 2002).

2.3. Sediment organic matter collection and analysis

Sediment was collected using 4.7 cm diameter cores taken from replicate box cores deployed at our sampling sites which were then sliced into 1-cm intervals, placed into whirl-pak bags wrapped in foil and stored at $-20\text{ }^{\circ}\text{C}$ until analysis. In the lab, the top 0–1 cm of sediments were thawed at $4\text{ }^{\circ}\text{C}$ in the dark and pigments were extracted with 100 % acetone for 24 h in the freezer (ca. $-20\text{ }^{\circ}\text{C}$). The extract was then analyzed via fluorometry following Holm-Hansen et al. (1965). To standardize fluorometric values, a calibration curve was generated by analyzing the concentration of a standard culture of *Anacystis nidulans* (obtained from Merck, product number C6144-1MG) using a spectrophotometer. The resulting pigment concentrations were then used to calculate area-standardized concentrations of chlorophyll-*a* and phaeopigments, as well as the chlorophyll-*a*/phaeopigment ratio (Akvaplan-niva, 2023a, 2023b, 2023c, 2023d). The concentration of chlorophyll-*a* was used as a proxy for the quantity of organic matter present in the surface sediments. The preparation and analysis of sediment samples for total organic carbon (TOC), total nitrogen (TN) and isotopic composition is detailed in Ricardo de Freitas et al. (this issue) and data are publicly available (Ricardo de Freitas et al., 2022a, 2022b, 2022c, 2022d). In brief, surface sediment samples (0–1 cm) were collected as described previously, then freeze dried, ground, and a sub-sample was acidified to remove inorganic carbon compounds using 1 M hydrochloric acid, rinsed with distilled water, and re-dried. Each sediment sample was then weighed (ca. 20 mg acidified and ca. 30 mg non-acidified) and sealed into analytical tin cups and analyzed for isotopic and elemental compositions of carbon and nitrogen (IsoAnalytical, UK) using a Europa Scientific Elemental Analyzer and Europa Scientific 20–20 Isotope Ratio Mass Spectrometer. During analysis, wheat flour, beet sugar and cane sugar (IA-R001, IA-R005, IA-R006) were used to calibrate $\delta^{13}\text{C}$ values against the international standard sucrose (IAEA-CH-6) while wheat flour and ammonium sulphate (IA-R001, IA-R045 and IA-R046) were used to calibrate $\delta^{15}\text{N}$ values against the international standard ammonium sulphate (IAEA-N-1). The precision of isotope ratios was determined from the standard deviation of repeat measurements of quality assurance reference materials and was $\leq 0.78\text{ }‰$ for $\delta^{13}\text{C}$ and $\leq 0.14\text{ }‰$ for $\delta^{15}\text{N}$. Total organic carbon (TOC) and total nitrogen (TN) were reported in weight percent and used to calculate the sediment C:N ratio while isotope values were reported in delta notation as described previously.

To test whether the quality of sediment organic matter varied seasonally, mean TOC content (%), C:N ratio, chlorophyll-*a* content (mg m^{-2}), chlorophyll-*a*/phaeopigment ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) of the sediment were statistically compared across each of the sampling periods. The data for each parameter were individually tested for normality of residuals and equal variances by Shapiro-Wilk tests and Levene's tests, respectively. For parameters that were both normally distributed and had equal variances across sampling periods (chlorophyll-*a*, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), means were then compared by a two-way analysis of variance (ANOVA) with "sampling period" and "station" factors. Post-hoc pairwise comparisons were conducted using Tukey's Honest-Significant-Difference test (Tukey's HSD). For parameters that did not meet ANOVA assumptions of normality and equal variances (chlorophyll-*a*/phaeopigment, TOC and C:N ratio), means were compared using a non-parametric Kruskal-Wallis rank sum test and post-hoc pairwise Wilcoxon rank sum tests with "sampling period" as a factor and all stations pooled. The Benjamini-Hochberg multiple testing correction was applied to all resulting p-values (Benjamini and

Hochberg, 1995). An additional Kruskal-Wallis rank sum test and post-hoc pairwise Wilcoxon rank sum tests were conducted for the same parameters using “station” as a factor to identify at which stations sediment parameters varied significantly. All statistical analyses were conducted in R version 4.2.0 (Team, 2022) and the level of significance used was 0.05.

2.4. Community- and functional group-level stable isotope metrics

Layman statistics (Layman et al., 2007) for all 1160 samples were calculated for each sampling period (all stations pooled by sampling period) using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al., 2011) including the total $\delta^{15}\text{N}$ range (NR), total $\delta^{13}\text{C}$ range (CR), mean distance to centroid (CD), the mean nearest neighbor distance (NND), the standard deviation of the mean nearest neighbor distance (SDNND), and the standard ellipse area corrected for small sample size (SEA_c). These metrics can provide ecologically relevant information regarding trophic relationships. NR the food web length (i.e., number of trophic levels), while CR provides the range of carbon resources assimilated by the organisms in the community. SEA_c describes the core isotopic niche area of a community, encompassing a standard 40 % of the data. The SEA_c shape is also described by the eccentricity (E) and angle of the major ellipse axis (θ), as well as its position in *iso*-space which is given by the position of the ellipse centroid (Reid et al., 2016). While NR, CR and SEA_c describe the isotopic breadth of the community, the spacing of individual samples in isotope space described by NND and SDNND provide information about trophic redundancy within a community. A community with a low NND and SDNND indicates an isotopically dense community with greater overlap in resource use and trophic redundancy, whereas a community with higher NND and SDNND is indicative of a community with greater trophic diversity and reduced redundancy among members of the community.

Different feeding guilds within the benthic food web may respond differently to seasonal changes in food quantity and quality. For example, suspension feeders intercept sinking organic matter before it is deposited on the seabed thereby reducing the amount of time it is exposed to remineralization processes by heterotrophic bacteria and grazers. As a result, the isotopic composition of suspension feeder tissues may provide a more sensitive indicator of benthic resource use and food web structure than, for example, a predator that consumes other fauna and indirectly reflects changes in organic matter. To robustly compare trophic niches of benthic functional groups between different sampling periods, a subset of the isotope dataset that included only taxa that were collected in all four sampling periods was selected for further analysis. This reduced any taxon-specific biases that could artificially alter our isotope-based metrics. The resulting dataset represented 641 samples from 24 taxa across 6 phyla. All benthic invertebrates and demersal fish were assigned to functional groups according to the highest fuzzy coding score of the feeding habit trait in the Arctic Traits Database (Degen and Faulwetter, 2019) and feeding habit information from FishBase (www.fishbase.org). Taxa that had fuzzy coding score ties for two or more feeding habits were assigned to the “generalist” functional group and “deposit feeder” encompasses both surface and sub-surface deposit feeders. Each benthic functional group contained at least 2 taxa but up to 10 (deposit feeders) in this dataset. Layman statistics were then calculated for each of the functional groups within each sampling period (all stations pooled by sampling period) as described previously. The overlap between seasonal SEA_c estimates for each functional group were calculated using the “splanx” package in R (Rowlingson and Diggle, 2022) and is presented as a relative index of seasonal variability in isotopic niche location in isotope space. A high degree of SEA_c overlap was considered an indicator of high resource use overlap and another metric of trophic redundancy, whereas a low degree of SEA_c overlap was interpreted as resource use divergence and trophic niche differentiation. To statistically compare the magnitude of the seasonal SEA_c estimates, we used a Bayesian approach to calculate the SEA (SEA_B) using SIBER

following Jackson et al. (2011) which quantifies the uncertainty of the SEA and does not require sample size corrections. Pairwise comparisons of the resulting posterior distributions of SEA_B for each sampling period and functional group were then made to test the likelihood that two SEA estimates statistically differed in size. Statistical significance was indicated by non-overlapping 95 % credible intervals of SEA_B , but non-significant results are also discussed.

2.5. The effect of depth on stable isotope values

Although we focused our analysis on seasonal patterns in food web structure, we also explored the impact of depth on the $\delta^{15}\text{N}$ values of benthic consumers. To test whether there was a significant ^{15}N -enrichment of sediment organic matter or fauna with depth, we conducted linear regressions between consumer $\delta^{15}\text{N}$ values at the community, functional, and species-level. We discuss the results of these analyses in the context of comparing food webs across a depth gradient using bulk stable isotope analysis.

3. Results

3.1. Measures of sediment organic matter quantity and quality

Seasonally, total organic carbon (TOC) content of surface sediments in the study region was consistent, with a mean of approximately 1.5 %, in all months sampled (Fig. 2a). Although there was significantly higher mean TOC content in surface sediments during August compared to all other months (Pairwise Wilcoxon rank sum test, $p = 0.034$ for all pairs with August, Fig. 2a), the total range of seasonal change was minimal, around only 0.2 %. There was no significant difference in the average surface sediment chlorophyll-*a* content (mg m^{-2}) among sampling periods (two-way ANOVA, $p = 0.367$, Fig. 2d) with values ranging from 2.67 to 3.35 mg m^{-2} . However, there was a marginally significant increase in the chlorophyll-*a*/phaeopigment ratio (Pairwise Wilcoxon Test, $p = 0.050$, Fig. 2b) and significant decrease in the C:N ratio (Pairwise Wilcoxon Test, $p < 0.001$, Fig. 2c) between March/May and August/December (Supplementary Table 1). The isotopic composition of surface sediment organic matter was seasonally rather stable; all samples occupied a narrow $\delta^{13}\text{C}$ range of only 1.3 ‰ and a $\delta^{15}\text{N}$ range of 2.2 ‰ (Fig. 3). Still, these small differences were statistically by sampling period and station (two-way ANOVA, $p = 0.0004$ and $p = 0.038$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively). The $\delta^{13}\text{C}$ value of surface sediment organic matter was on average approximately 0.2 ‰ enriched in ^{13}C in August and December relative to March (Tukey’s Honest Significant Difference test, Aug-Mar: $p = 0.00018$ and Dec-Mar: $p = 0.049$, Supplementary Table 2). Similarly, the $\delta^{15}\text{N}$ of surface sediments was on average 0.3 ‰ more enriched in ^{15}N during May relative to August ($p = 0.0032$, Supplementary Table 3).

Spatially, there was a difference in surface sediment TOC content in which the southerly stations (closest to the Polar Front and Atlantic Water inflow) consistently exhibited higher sediment TOC than northerly stations (Pairwise Wilcoxon Rank Sum Test, $p < 0.05$ for all pairs, Supplementary Fig. 1 and Supplementary Table 4). Similarly, chlorophyll-*a* content was significantly higher at stations P1 and P2 compared to all other stations (Tukey’s HSD, $p < 0.01$ for all pairs vs P1 and P2, Supplementary Table 5) but did not vary significantly among stations from P4 northwards (Tukey’s HSD, $p \geq 0.87$ for all pairs, Supplementary Table 5). Finally, the surface sediment was significantly depleted in ^{15}N and enriched in ^{13}C at station P1 compared to the more northerly stations P4-P7 (Tukey’s HSD, $p < 0.0001$ and $p < 0.01$ all pairwise comparisons with P1 of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) but particularly compared to surface sediment at P2 which was highly enriched in ^{15}N and depleted in ^{13}C relative to all other stations (Fig. 3, Tukey’s HSD, $p < 0.0001$ for all pairwise comparisons with P2 of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, Supplementary Tables 2 and 3). This spatial pattern in sediment bulk stable isotope composition was seasonally conserved, hence the small

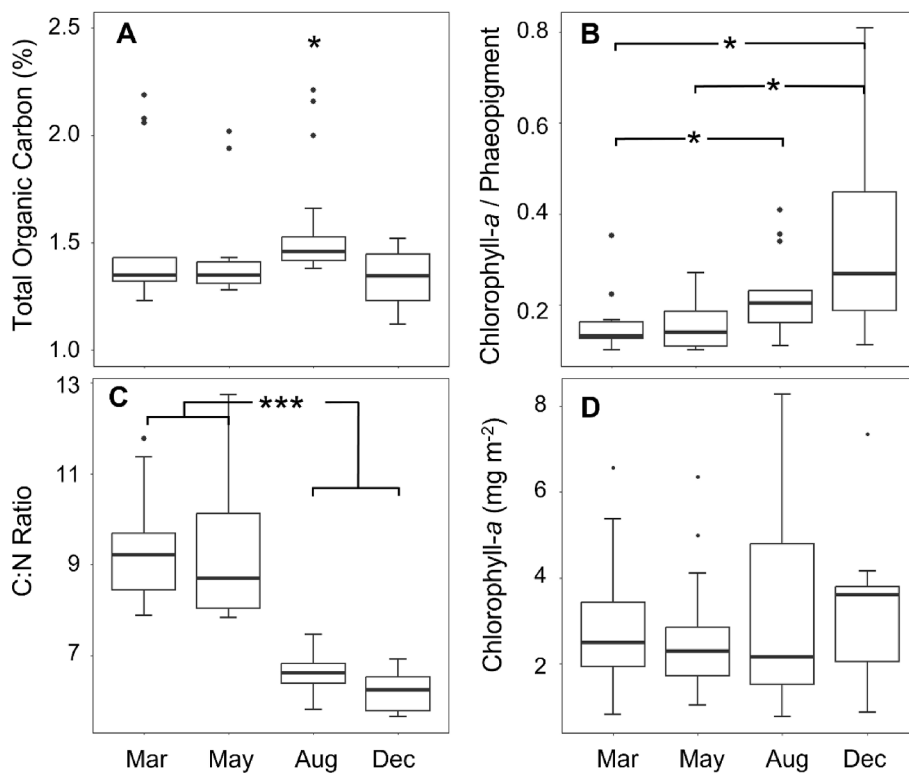


Fig. 2. Seasonal variability of measures of surface (0–1 cm) sediment organic matter quantity and quality in the different sampling periods (abbreviated as: Mar = March, May = May, Aug = August and Dec = December) in the northern Barents Sea. A) total carbon content (%) from Ricardo de Freitas et al. (2022 a-d) B) Chlorophyll-a/Phaeopigment ratio, C) C:N ratio and D) Chlorophyll-a + phaeopigment content (mg m^{-2}) from Akvaplan-niva (2023a-d). All boxplots represent the interquartile range (IQR) with whiskers representing $1.5 \times \text{IQR}$ and black points represent outliers ($>1.5 \times \text{IQR}$). Brackets and * show which pairwise comparisons yielded significant results: * = $p \leq 0.05$ and *** = $p \leq 0.001$.

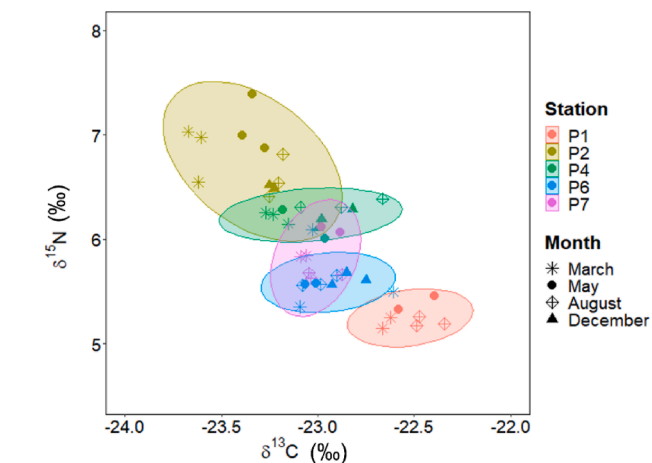


Fig. 3. The isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰) of sediment organic matter in the study region across seasons. Shapes correspond to the different sampling periods and colored ellipses encompass 95 % of the data within each sampling station, P1-P7.

observed difference in the average seasonal isotopic composition of surface sediments.

3.2. Isotope-based metrics of community-level food web structure

In total, 1160 samples of benthic fauna were analyzed representing 109 taxa from 11 phyla. The taxa with the largest sample sizes were *Ctenodiscus crispatus* ($n = 79$, phylum Echinodermata), Pycnogonida ($n = 43$, phylum Arthropoda), *Gersemia* spp. ($n = 41$, phylum Cnidaria), *Ophiacantha bidentata* ($n = 39$, phylum Echinodermata) and *Sabinea septemcarinata* ($n = 36$, phylum Arthropoda). The structure of the overall benthic community, based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, was similar across sampling periods (Fig. 4). In general, the trophic level of an organism

increases with increasing $\delta^{15}\text{N}$ relative to the $\delta^{15}\text{N}$ of the baseline. The highest trophic levels were occupied by predatory fish (*Hippoglossoides platessoides* and *Leptagonus decagonus*), decapod arthropods (*S. septemcarinata*, *Sclerocrangon ferox*) and echinoderms (e.g., the sea star *Icasterias panopla*) as well as suspension-feeding sponges and anemones (e.g., *Polymastia* sp. and *Allantactis parasitica*), the sub-surface deposit feeding sea cucumber *Molpadia* spp., and the sub-surface deposit-feeding sea star *C. crispatus*. The lowest trophic level consumers were bivalve molluscs (e.g., *Ciliatocardium ciliatum*, Yoldiidae), cumacean arthropods (e.g., *Diastylis* spp.), tunicates, and sea urchins (e.g., *Strongylocentrotus* spp.) (examples labelled as numbers in Fig. 4).

Layman statistics describing the stable-isotopic structure of the overall benthic community are given in Table 2. The NR for the entire benthic community was 10–11 ‰ in all sampling periods and organisms occupied approximately 4 trophic levels (3.9, 4.3, 4.0 and 4.1 for August, December, March, and May, respectively; Fig. 4). Overall, >50 % of all faunal samples were assigned to trophic levels 2–3, which represented >70 % of the taxa collected within each sampling period. Although the benthic community was under-sampled in December relative to all other sampling periods, SEA_c estimates were very similar for all sampling periods, occupying an area of approximately $10\text{--}11 \text{‰}^2$ and centered in a similar location in iso-space (Fig. 4).

Despite a lack of seasonality in community-level SEA_c , NR or the number of trophic levels, the community-level CR increased from December to May (8.5 to 11.8 ‰) suggesting a seasonal widening of carbon sources utilized by the benthic community (Table 2, Fig. 4). However, the apparent increase in CR between December and May was driven by the $\delta^{13}\text{C}$ -depletion of a single amphipod species (*Anonyx* sp.). Without the inclusion of this taxon, the CR in May was only 9.2 ‰ making the CR comparable to all other sampling periods. The community-level NND and SDNND were highest in December and March and the smallest in May and August (Table 2), suggesting that resource use by benthic fauna may be most similar in spring and summer and most divergent or variable in fall and winter months.

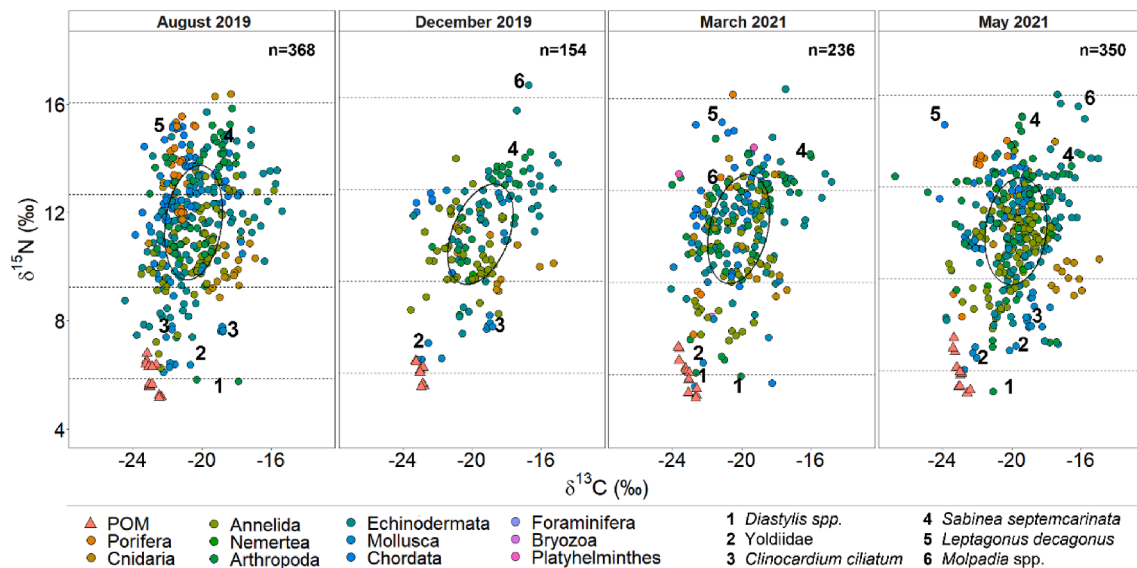


Fig. 4. Isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰) for benthic invertebrates and demersal fish in the study region in each sampling month colored according to phylum. POM indicates the sediment organic matter baseline (triangles) which was used to calculate trophic levels (TL) for each sampling period (indicated as dotted lines). The number of samples (n) analyzed is shown in the upper left corner and each circle represents an individual sample. Six taxa occupying the lowest (numbers 1–3) and highest (4–6) trophic levels of the entire benthic community are shown in iso-space with taxon names given in the legend. The black ellipse shows the Standard Ellipse Area corrected for small sample sizes (SEA_c) for the entire benthic community sampled during each sampling period.

Table 2

Isotope-based metrics (after Jackson et al., 2011; Layman et al., 2007) for the entire benthic community of the northern Barents Sea across seasons including invertebrates and demersal fish and separated by functional groups; SF = suspension feeders, DF = deposit feeders, GEN = generalists, PS = predator/scavengers. NR = $\delta^{15}\text{N}$ range (‰), CR = $\delta^{13}\text{C}$ range (‰), CD = mean Euclidian distance to centroid, NND = mean nearest neighbor distance, SDNND = standard deviation of the mean nearest neighbor distance, SEA_c = standard ellipse area corrected for small sample size (‰²), E = ellipse eccentricity of the SEA_c , θ = angle of SEA_c ellipse (°) with 0/360° horizontal and n = the number of samples.

	NR (‰)	CR (‰)	CD (‰)	NND (‰)	SDNND (‰)	SEA_c (‰ ²)	E	θ (°)	n
March	10.98	9.26	2.37	0.25	0.24	10.79	0.70	55	236
May	10.98	11.83	2.14	0.21	0.22	11.01	0.55	61	350
August	10.62	9.09	2.40	0.21	0.19	10.86	0.69	69	368
December	10.14	8.51	2.34	0.29	0.24	10.05	0.77	43	154

4. Benthic functional group seasonality

4.1. Suspension feeders

The isotopic niche area of suspension feeders did not vary seasonally, yet the position of the isotopic niche in isotope space did (Fig. 5). SEA_c was smallest in March and May, a finding supported by a high proportion (>87 %) of the posterior SEA_B distributions in March and May being smaller than in August and December (Fig. 6). Seasonal variability in the isotopic niche area of suspension feeders was indicated by the small (<5.30 ‰²) overlap of all individual seasonal SEA_c estimates and the lowest proportional SEA_c overlap was between May and August (Supplementary Table 6). However, the 95 % credible intervals for SEA_B estimates of suspension feeders overlap substantially in all sampling periods indicating high variability in isotopic niche area and no statistically significant seasonal differences (Table 3, Fig. 6). The shape of the isotopic niche of suspension feeders varied seasonally. NR was narrowest in May and widest in August contrary to the CR which was at a maximum in May when the mean $\delta^{13}\text{C}$ was significantly enriched relative to the means of other sampling periods (Wilcoxon rank sum test, $p = 0.0032$). The eccentricity of SEA_c ellipses was also highest in March and May and was oriented nearly horizontal to the $\delta^{13}\text{C}$ -axis ($\theta > 333^\circ$) supporting the finding that isotopic variation during May and March was mainly in the $\delta^{13}\text{C}$ values.

The mean trophic level of suspension feeders was lowest and least variable during May (Fig. 7) though mean trophic levels were seasonally

very similar. Generally, taxa within this functional group occupied trophic level 2 with values ranging from 1.7 to 3.0, and $\delta^{15}\text{N}$ values were about 4.2 ‰ enriched relative to the sediment organic matter baseline. Suspension feeder SEA_c were consistently centered lower along the $\delta^{15}\text{N}$ axis relative to the centroids of the deposit feeders (by 0.67–1.05 ‰), suggesting a generally lower trophic level for suspension feeders.

A total of 16 taxa collected in this study were classified as suspension feeders, of which only two were collected during all four sampling campaigns: *Gersemia* spp. and *Astarte* spp. Both species exhibited trophic plasticity reflected by their occupation of distinctly separate isotope spaces (Fig. 8). Mean $\delta^{13}\text{C}$ values of *Gersemia* spp. and *Astarte* spp. were -17.9 ‰ and -21.7 ‰, respectively, and *Astarte* spp. individuals collected in August spanned > 4 ‰ in $\delta^{15}\text{N}$ (Fig. 8) with $\delta^{15}\text{N}$ values corresponding to trophic levels 1.8 to 3.0 (Fig. 9). Although the trophic level of *Gersemia* spp. did not vary significantly among sampling periods, there was a 2 ‰ enrichment in the tissue ^{13}C in May compared to March and August (pairwise Wilcoxon test, $p \leq 0.01$) suggesting a seasonal difference in carbon sources.

4.2. Deposit feeders

Deposit feeders were the least seasonally variable functional group in terms of isotopic niche area, shape, and relative position in isotope space (Fig. 5). Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were not significantly different among sampling periods (ANOVA, $p = 0.84$ and $p = 0.75$, respectively), and the overlap between all seasonal SEA_c estimates was greatest (7.77

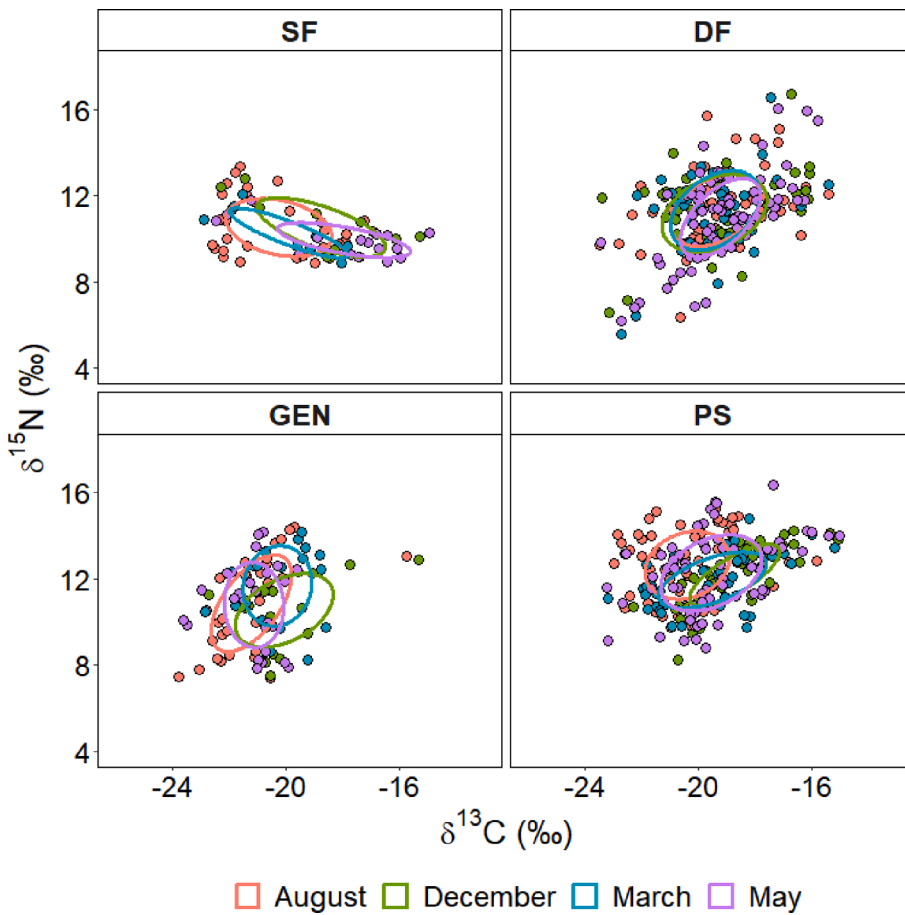


Fig. 5. Isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰) of the same invertebrates and demersal fish sampled during all four seasonal field campaigns in August (red), December (green), March (blue), and May (purple). Ellipses correspond to the Standard Ellipse Area corrected for small sample sizes (SEA_C , $\% \text{‰}^2$) computed using the SIBER package in R (Jackson et al., 2011) for each functional group abbreviated SF (suspension feeder), DF (deposit feeder), GEN (generalist) and PS (predator/scavenger). Each point represents an individual sample. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

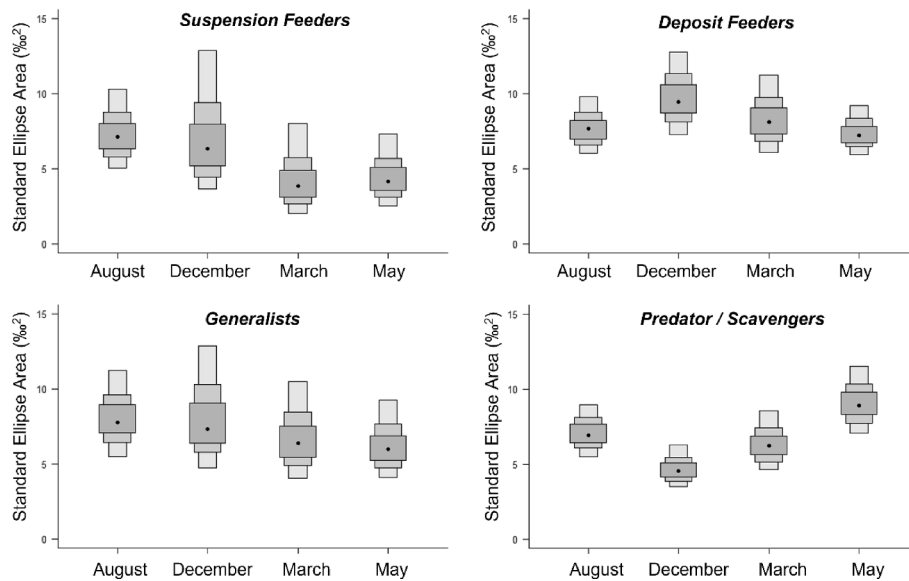


Fig. 6. Bayesian Standard Ellipse Area (SEA_B) estimates for each functional group during the four sampling periods. Black dots give the mode of the posterior distribution of SEA_B and boxes represent the 50 %, 95 % and 99 % credible intervals from dark grey to light grey, respectively.

$\% \text{‰}^2$) relative to other functional groups (Fig. 5). Seasonal SEA_C pairs overlapped by >65 % (Supplementary Table 6), and SEA_C centroids were consistently located in isotope space with < 0.4 ‰ differences in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value for all sampling periods. In addition, the shape of the ellipse (describing variation in consumer isotope values) was seasonally consistent indicated by little variation in eccentricity or angle (Table 3).

SEA_C in December appeared larger than in other sampling periods (Fig. 6), and in fact was larger than in May in 94 % of the SEA_B posterior distributions (Supplementary Table 7). However, 95 % credible intervals of SEA_B for all sampling periods overlapped indicating that there were no significant differences in isotopic niche areas between any of the sampling periods for this functional group (Table 3, Fig. 6).

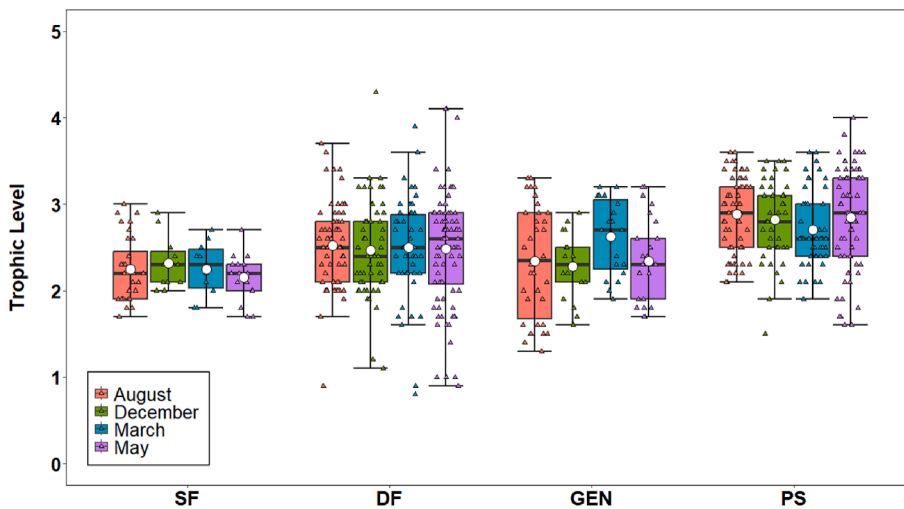


Fig. 7. Trophic level estimates for taxa in each functional group compared between sampling periods. Individual trophic level estimates are shown by the triangles and the data are summarized in box and whisker plots. The white point within each box plot represents the mean trophic level for that functional group. Abbreviations for functional groups are SF (suspension feeder), DF (deposit feeder), GEN (generalist) and PS (predator/scavenger). Colors represent the four sampling periods: August (red), December (green), March (blue) and May (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

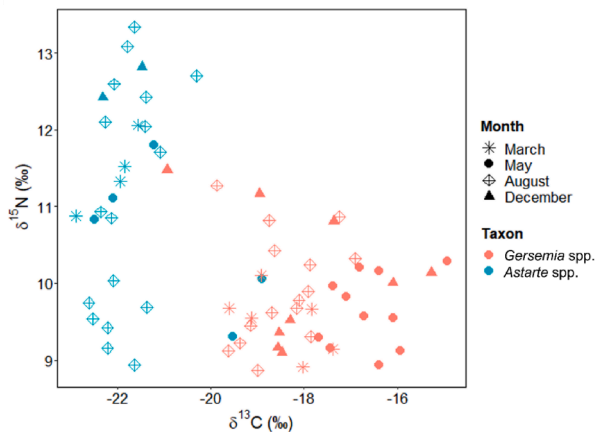


Fig. 8. Seasonal variation of isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰) of the suspension feeding soft coral *Gersemia* spp. (pink) and bivalve *Astarte* spp. (blue) collected in all four sampling periods (shapes). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The isotopic position of the deposit feeder functional group was, on average, about 5.0 ‰ enriched in $\delta^{15}\text{N}$ relative to the seasonal sediment organic matter baseline during all sampling periods. The mean trophic level was approximately 2.5, although the range in trophic level for deposit feeders was 0.8 to 4.3 (Fig. 7) with *Molpadia* spp. occupying the highest trophic level of this functional group (mean 3.4 ± 0.6 , range 2.2–4.3). At the species level, however, trophic levels were seasonally consistent for most taxa (Supplementary Fig. 2). Bivalves in the family Yoldiidae occupied the lowest trophic level in every sampling season (≤ 1.5 , Fig. 9), but at the deep basin station (P7) this taxon occupied a much higher trophic level (2.3). Yoldiidae had higher mean $\delta^{13}\text{C}$ values in August relative to other months (by > 2 ‰), though low sample size limited any robust statistical comparison. While most deposit feeders did not show any seasonal variation in trophic level, *Ctenodiscus crispatus* occupied a significantly lower trophic level in May compared to other seasons, particularly for individuals sampled at station P2 (Supplementary Fig. 3b).

4.3. Generalists

The generalist functional group had consistent isotopic niche sizes across seasons, but nearly all other niche metrics calculated for the

generalist community were highest in August (Table 3). The NR was highest in May and August indicating variability along the $\delta^{15}\text{N}$ -axis which was confirmed by higher eccentricity of these ellipses (Table 3), but the SEA_c for March was centered at a $\delta^{15}\text{N}$ value nearly 1 ‰ higher than all other sampling periods. While the SEA_c estimates for August and December were similar in magnitude, the centroid of the SEA_c was positioned along the $\delta^{13}\text{C}$ axis 1.2 ‰ higher compared to August. The most often sampled taxon in the generalist functional group, *Ophiacantha bidentata*, had significantly less negative $\delta^{13}\text{C}$ values in December and March compared to May and August (Pairwise Wilcoxon rank sum test, $p < 0.05$ for pairs). Despite this shift in isotope space, SEA_c for August and May overlapped by $> 68\%$ (Supplementary Table 6). In 80–98 % of the posterior distributions of SEA_B , the isotopic niche areas in December and August were larger than in May (Supplementary Table 7) but overlapping 95 % credible intervals indicate that these differences were not significant (Table 3).

Generalists were 4.4–5.5 ‰ enriched in ^{15}N relative to the sediment organic matter baseline indicative of approximately trophic level 2.5. Some taxa, however, like the urchin *Strongylocentrotus* spp. occupied a trophic level as low as 1.3 (Fig. 9) with a significantly lower trophic level in August compared to all other months (Tukey's HSD, $p < 0.05$ for all pairs).

4.4. Predator/Scavengers

The predator/scavenger functional group had the least seasonally consistent isotopic niche area of all functional groups. Seasonal SEA_c estimates overlapped in isotope space the least ($< 20\%$) between August and December (Fig. 5, Supplementary Table 6) which was because of a significant enrichment in ^{13}C in December compared to August (Pairwise Wilcoxon rank sum test, $p < 0.01$) which separated the ellipses along the $\delta^{13}\text{C}$ axis. A change in ellipse shape between August and December is also confirmed by a large increase in eccentricity (elongating the ellipse) while the angle indicates elongation along the $\delta^{13}\text{C}$ -axis. SEA_c was significantly smaller in December than in May indicated by non-overlapping 95 % credible intervals of SEA_B (Fig. 6, Table 3). Although not statistically significant, the SEA_c in December was smaller than all other sampling periods in $> 91.7\%$ of the posterior distributions of SEA_B (Supplementary Table 7). In general, taxa from this functional group occupied some of the highest trophic levels (4.0) and were about 6 ‰ enriched in ^{15}N relative to the sediment organic matter baseline. The unusually low trophic level of the typically predatory phylum, Nemertea, is noteworthy.

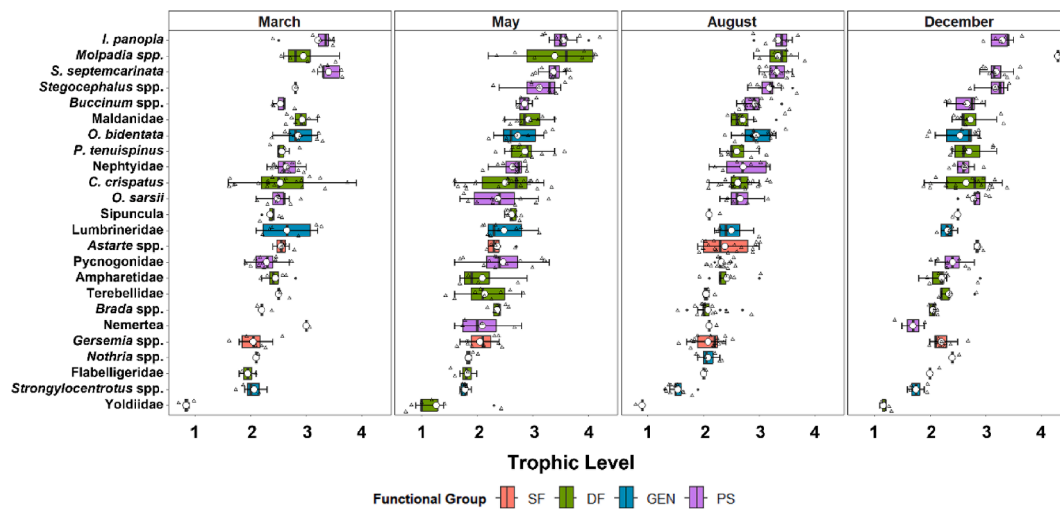


Fig. 9. Trophic level of invertebrate and fish taxa collected in all four sampling seasons (triangles) shown in box and whisker plots and colored according to functional group: Red = suspension feeders (SF), Green = deposit feeders (DF), Blue = generalists (GEN), and Purple = predator/scavengers (PS). The white points represent the mean trophic level of each taxon. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Isotope-based metrics for benthic taxa present in all four seasonal sampling periods within four functional groups, suspension feeders (SF), deposit feeders (DF), generalist (GEN), and predator/scavengers (PS). NR = $\delta^{15}\text{N}$ range (‰), CR = $\delta^{13}\text{C}$ range (‰), CD = mean Euclidian distance to centroid (‰), NND = mean nearest neighbor distance (‰), SDNND = standard deviation of the mean nearest neighbor distance (‰), SEAc = standard ellipse area corrected for small sample size (‰²), E = SEAc eccentricity, θ = SEAc angle (°) with 0/360° horizontal, SEAB = mode of the Bayesian SEA estimate, SEAB 95 % CI (‰) = [lower limit, upper limit] of the 95 % credible interval on the Bayesian standard ellipse area, and n = the number of samples.

	NR (‰)	CR (‰)	CD (‰)	NND (‰)	SDNND (‰)	SEAc (‰ ²)	E	θ (°)	SEAB (‰ ²)	SEAB 95 % CI (‰)	n
<i>Suspension Feeders (SF)</i>											
March	3.15	5.51	2.01	0.56	0.24	3.76	0.98	333	3.85	[2.05, 7.68]	10
May	2.87	7.56	1.96	0.58	0.33	4.57	0.97	346	4.17	[2.57, 7.27]	16
August	4.47	5.70	2.16	0.44	0.25	7.55	0.77	339	7.21	[4.98, 10.14]	32
December	3.72	7.04	2.13	0.80	0.57	7.23	0.93	334	6.47	[3.25, 12.50]	11
<i>Deposit Feeders (DF)</i>											
March	10.98	7.35	1.91	0.58	0.50	8.49	0.76	56	8.29	[6.08, 11.12]	44
May	9.84	7.70	2.08	0.35	0.31	7.42	0.89	57	7.36	[5.84, 9.17]	79
August	9.33	8.14	1.99	0.45	0.43	7.77	0.74	48	7.57	[5.93, 9.74]	65
December	10.14	7.31	2.21	0.50	0.54	9.88	0.71	42	9.61	[7.22, 12.68]	50
<i>Generalists (GEN)</i>											
March	5.97	4.28	1.99	0.70	0.40	7.09	0.76	84	6.38	[3.99, 10.47]	19
May	6.34	4.03	1.95	0.40	0.25	6.52	0.85	272	6.09	[4.03, 9.11]	25
August	7.00	8.04	2.32	0.51	0.71	8.17	0.90	65	7.69	[5.51, 11.18]	33
December	5.35	7.42	1.99	0.72	0.62	8.42	0.77	44	7.71	[4.60, 12.70]	17
<i>Predator / Scavengers (PS)</i>											
March	5.06	8.02	2.00	0.34	0.31	6.42	0.88	28	6.26	[4.58, 8.45]	44
May	7.58	8.24	2.23	0.36	0.35	9.22	0.73	44	8.94	[7.05, 11.59]	67
August	5.46	7.18	1.98	0.36	0.26	7.21	0.59	53	6.94	[5.48, 9.10]	64
December	6.00	7.27	1.84	0.37	0.29	4.67	0.93	41	4.61	[3.41, 6.25]	45

4.5. The effect of depth on consumer $\delta^{15}\text{N}$ values

There was a marginally significant negative relationship between $\delta^{15}\text{N}$ of sediment organic matter and sampling depth in our study (Fig. 10a, Supplementary Table 8), but no significant relationship between consumer $\delta^{15}\text{N}$ values and depth at the community level (Fig. 10b and Supplementary Table 9). Of the 24 taxa included in our functional group level assessment of isotopic niches, only six were collected at the deep stations (5 DFs and 1 GEN). We found no significant trend in $\delta^{15}\text{N}$ values with depth for the deposit feeder or generalist functional groups (Supplementary Fig. 4, Supplementary Table 10), but slopes varied by taxon. Lumbrineridae and Maldanidae had a significant positive

relationship between $\delta^{15}\text{N}$ and depth, while Sipuncula $\delta^{15}\text{N}$ values were negatively related to depth, and no significant trend identified for Ampharetidae, Terebellidae, or Yoldiidae (Supplementary Fig. 5 and Supplementary Table 11).

5. Discussion

5.1. Seasonality in food availability, food quality, and benthic consumer resource use

The quantity of food at the seafloor was seasonally constant despite a decrease in POC flux of more than one order of magnitude between May

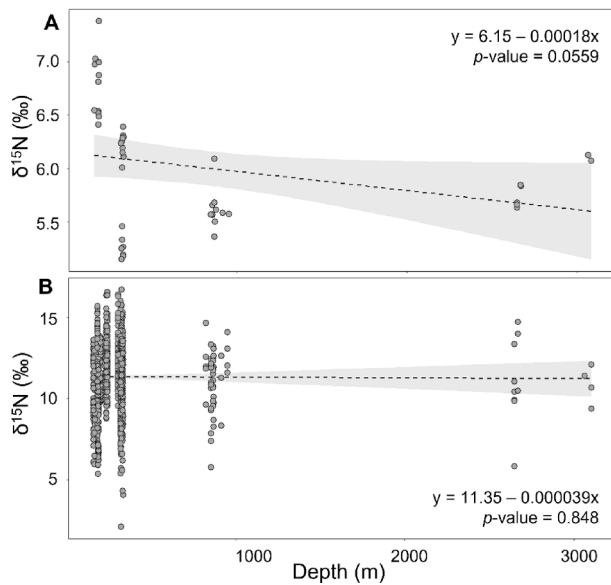


Fig. 10. The relationship between $\delta^{15}\text{N}$ (‰) and bottom depth (m) of **A)** sediment organic matter and **B)** all benthic fauna collected in this study. In both plots, points represent individual samples, the dashed line shows a linear regression model for the respective samples with the standard error of the estimate shaded in grey. The regression equations and p -values testing whether the slope significantly varied from 0 are given in each plot. Significance was evaluated at a level of 0.05.

and December (Bodur et al., this issue). The quality of this sinking organic matter varied seasonally, as expected, with the highest quality measured in May as evidenced by high chlorophyll-*a*/phaeopigment ratios, low C:N ratios, and the lowest $\delta^{15}\text{N}$ values (Bodur et al., this issue). At the seabed, however, the quality of sediment organic matter was highest *after* the spring bloom, namely, in August and December, indicated by high chlorophyll-*a*/phaeopigment and low C:N ratios. Interestingly, surface sediments had an overall lower $\delta^{15}\text{N}$ range and less clear seasonal ^{15}N -enrichment compared to sinking organic matter captured in the water column (Bodur et al., this issue) which could indicate that near-bottom sediment resuspension or redistribution changes the isotopic composition of organic matter in the region (discussed more below). Despite significant seasonal differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of surface sediments in this study, the variation (<0.3 ‰) was within ranges of error and our measurements are unlikely to represent a systematic difference in processes (e.g., remineralization), organic matter quality, or organic matter origin among sampling periods. The delayed accumulation of high-quality sediment organic matter has been documented for the northern Barents Sea (Morata et al., 2020; Morata and Renaud, 2008) suggesting that this may be a defining characteristic of this ecosystem. Overall, the seasonal pattern of organic matter quality appears to be delayed by up to 6 months at the seafloor relative to the water column, suggesting a temporal mismatch or decoupling between local primary production, export flux, and the accumulation of organic matter at the seafloor in the northern Barents Sea.

We found that the relatively constant quantity of detrital organic carbon available to the benthic community in the Barents Sea dampens the overall benthic community trophic response to seasonality of environmental conditions. There was little evidence of seasonality in the diversity of food sources utilized by benthos in the northern Barents Sea, and no significant seasonal changes in mean trophic level of benthic functional groups to suggest widespread significant seasonal shifts in resource use. A dampened trophic response to seasonality has also been documented in a similar inflow shelf region on the Antarctic Peninsula (Mincks et al., 2008) and in shallow coastal regions within the Arctic (Bridier et al., 2021; Kędra et al., 2013; Renaud et al., 2011). Mincks

et al. (2005) suggested that the low temperature of Antarctic shelf bottom waters (which is similar in the northern Barents Sea, Jørgensen et al., 2015; Mincks et al., 2005) reduced the remineralization and degradation rates of organic matter thereby maintaining a consistent sediment organic carbon content year-round. Resuspension of bottom sediments in the Barents Sea (Gardner et al., 2022) could make degraded organic matter available year-round as a food source which might otherwise be buried and inaccessible to benthic organisms. This hypothesis is supported by the lack of seasonal change in deposit feeder isotopic niche area, shape, or position in *iso*-space, and a lack of long-term variation (i.e., decadal) observed in organic carbon accumulation rates (Ricardo de Freitas et al., this issue). This suggests that the inventory of organic carbon available to deposit-feeding and deep-burrowing benthos is temporally stable in the northern Barents Sea.

Despite an overall muted expression of seasonality in resource use by benthic consumers, there was evidence of efficient coupling between pelagic and benthic ecosystem compartments by some taxa. For example, deposit-feeding bivalves in the family Yoldiidae had consistently low trophic level estimates across all seasons suggesting the direct consumption and rapid assimilation of fresh organic matter. Biomarker analyses of megafauna in deep sea communities have shown that deposit feeders can rapidly assimilate fresh algal-derived lipids during periods of high productivity supporting this finding (Jeffreys et al., 2009). Regardless of the functional group considered, multiple measures of food availability should be assessed in future studies as individual measures may be insufficient to document short term changes. For example, significant seasonal increases in benthic oxygen consumption were observed in the Beaufort Sea with no indication of increased sediment chlorophyll-*a* concentrations nor an increase in organic carbon or nitrogen content, despite sediment traps indicating the rapid sedimentation of fresh algal material (Renaud et al., 2007).

A lack of seasonal change in resource use or trophic level of benthic consumers is somewhat counterintuitive because it is reasonable to expect that benthic organisms seasonally utilize detritus originating from different and isotopically distinct food sources. For example, seasonal variation in the use of sympagic algal detritus has been documented for several benthic taxa across different functional groups in the Barents Sea using lipid biomarkers (Cautain et al., 2022). A recent study (Koch et al., 2023), however, found that benthos from multiple functional groups assimilated biomarkers derived from sympagic autotrophs year-round, suggesting the widespread utilization of this food source across all seasons. Using our bulk stable isotope approach, we observed very limited evidence of widespread seasonal assimilation of sympagic-derived carbon, apart from the ^{13}C -enrichment of *Gersemia* spp. tissues in spring and Yoldiidae in summer. The deposition of sympagic-derived organic matter to the seabed is episodic and patchy, which might have limited the assimilation of this food source by more individuals within the communities we sampled. Because many Arctic benthos are detritivores or omnivores, ^{13}C -enrichment of consumer tissue could have also been due to feeding on degraded organic matter rather than from consuming sympagic-derived carbon (Iken et al., 2005; McTigue et al., 2015). To use bulk stable isotope analysis to reliably identify the source of carbon assimilated by an organism, this method requires a clear differentiation between $\delta^{13}\text{C}$ values of individual carbon sources (Phillips and Gregg, 2003; Vander Zanden and Rasmussen, 2001). Sea ice conditions (e.g., thickness, crystal structure, etc.) affect the degree of CO_2 - and nutrient-limitation experienced by sympagic autotrophs, thereby affecting the degree to which their biomass is enriched in ^{13}C (Pineault et al., 2013). Thus, $\delta^{13}\text{C}$ values of sympagic autotrophs can effectively overlap those of pelagic phytoplankton limiting isotopic differentiation (Tamelander et al., 2009). Organic matter collected from sea ice cores during the same seasonal sampling campaigns presented here, was (atypically) more ^{13}C -depleted than surface sediments (A. Ziegler, unpublished data). Thus, we inferred that sympagic carbon contributed minimally to the detrital carbon pool available to benthos. However, it also indicated that particulate organic matter from sea ice cores would

represent an end member for sympagic autotrophs that was indistinguishable from sediment organic matter in this study. Surface sediment carbon isotope values exhibited little spatial or seasonal variation (<1.5 ‰) and were at the lower limit of previously reported values of sympagic autotrophs within the Barents Sea ($\delta^{13}\text{C}$ values of -20.0 ± 3.8 ‰ in Tاملander et al., 2008). Therefore, we lacked a robust isotopic end member for sympagic-derived carbon to use for estimating the contribution of sympagic carbon to benthic consumer diets. Complementing our bulk stable isotope analysis with fatty acid or compound-specific stable isotope analyses could have provided more sensitive measures of the quality and origin of benthic consumer food sources (e.g., Budge et al., 2007; Kelly and Scheibling, 2012).

5.2. Feeding ecology of Arctic benthos

Some of our results suggest feeding ecology of taxa that diverge from literature categorizations. For example, the two species in our seasonal analysis, *Astarte* spp. and *Gersemia* spp., were both *a priori* considered to be suspension feeders (Degen and Faulwetter, 2019). *Astarte* spp. samples, however, likely represented at least two species with different feeding affinities based on diverging isotope values and trophic level estimates. One group of samples had consistently lower trophic level estimates indeed suggesting a suspension feeding strategy. The second group had relatively elevated trophic level estimates suggesting detritivory. Dietary plasticity of at least two species of *Astarte* in the Arctic has been documented, which suggest suspension feeding on both fresh microalgae and other sedimentary detritus (De Cesare et al., 2017; Gaillard et al., 2017). Similarly, there is evidence that individuals in the genus *Gersemia* can not only suspension feed consuming sinking organic matter and zooplankton but can also deposit feed on lower quality detritus (Slattery et al., 1997) and assimilate carbon originating from kelp (Dunton and Schell, 1987). However, our data showed no clear sign of detritivory by *Gersemia* spp. compared to *Astarte* spp., though *Gersemia* spp. had consistently higher than expected $\delta^{15}\text{N}$ values and, therefore, trophic level.

Other taxa in this study showed surprising trophic relationships. Nematodes, for example, had low trophic level estimates for a typically predatory phylum. This result suggests either the very efficient transfer of energy from primary producers to top predators in this ecosystem, or that these organisms are more omnivorous than expected in order for individuals to have achieved such low trophic level values. Sea urchins in the genus *Strongylocentrotus* were classified in this analysis as a generalist which can deposit feed or graze on macroalgal detritus. However, the low trophic level found in this study suggests mainly grazing as a feeding strategy for the individuals collected in the northern Barents Sea. As consistently observed in trophic studies (Bell et al., 2016; Bergmann et al., 2009; Iken et al., 2005), the cumacean *Diastylis* spp., was depleted in ^{15}N relative to the sediment organic matter baseline indicating that this taxon may have consumed un-grazed, un-remineralized organic matter relative to all other taxa. This suggests that *Diastylis* spp. is a selective feeder able to exploit small patches of freshly deposited organic matter at the seafloor. However, the low $\delta^{15}\text{N}$ values may also be due to the high amount of exoskeleton relative to muscle in these small crustaceans (Søreide et al., 2006 and references therein). Assigning individual taxa to benthic functional groups is challenging and may have been limited by low taxonomic resolution of many samples in our study. Additionally, to maintain sample sizes sufficient for statistical comparisons, we limited the number of benthic functional groups assigned which may not have fully captured the feeding plasticity that many benthic organisms in the Arctic exhibit.

5.3. The impact of spatial variability on seasonality in the northern Barents Sea

The spatial variability of POC flux (Bodur et al., this issue), bottom-water temperature (Koenig et al., this issue), and sea-ice cover in the

Barents Sea (Jordà Molina et al., this issue; Kohlbach et al., 2023) complicated the detection of seasonal trends in our data. Previous work has documented variability in benthic abundance, biomass and community structure at locations near the Polar Front which has been attributed to the influence of Atlantic and Arctic water masses (Carroll et al., 2008; Jørgensen et al., 2022). Similarly, Jordà Molina et al. (this issue) only observed seasonal differences in macrofaunal community composition and biomass at a single station, P2, which was characterized by particularly high seasonality in environmental conditions and is seasonally influenced by Atlantic Water. In the present study, sediment organic matter from our sampling stations was isotopically distinct at P2, where it was most enriched in ^{15}N , even compared to deep sampling locations on the slope and Nansen Basin. This suggests that factors other than depth affect the organic matter quality at this site. We also observed the highest yet most variable chlorophyll-*a*/phaeopigment ratios at the seafloor at station P2. In terms of the benthic food web, this site had the greatest variability in trophic level and bulk stable isotope values of the common deposit-feeding asteroid, *Ctenodiscus crispatus* (Supplementary Fig. 3b). and the lowest trophic level estimates of the infaunal polychaete family Maldanidae occurred at station P2 during May (Supplementary Fig. 3a), despite very low vertical flux present at that time (Bodur et al., this issue). These results all suggest that the seasonal distribution of Atlantic Water and heterogeneity in sediment deposition and resuspension within the northern Barents Sea affects the seasonality of the benthic community.

Spatial variability in environmental conditions within the Barents Sea is greatest during the spring (ca. May) as the spring bloom is initiated first in the south and propagates northward (Leu et al., 2011; Wassmann et al., 2020). This variability was reflected in the amount and composition of sinking organic matter (Bodur et al., this issue), the quality of sedimentary organic matter, and trophic relationships. Considering the relatively shallow (≤ 350 m) water depth of the Barents Sea, strong coupling between pelagic and benthic processes was expected. Our study, however, suggests that the benthic food web (and particularly deposit feeders) is temporally de-coupled from pelagic processes including the vertical flux of organic matter. The inflow of Atlantic Water is typically strongest in fall and winter months (Ingvaldsen et al., 2004) which could import advected organic matter of higher quality relative to locally generated POC, explaining the surprisingly high sediment organic matter quality we measured during fall. It also may explain how the suspension-feeding soft coral, *Gersemia* spp., occupied a lower trophic level in winter compared to spring or summer months. It is also possible that autumn phytoplankton blooms contributed fresh organic matter to the benthos late in the growing season which would increase the sediment organic matter quality well after the spring bloom has occurred locally. Autumnal blooms have been observed in the Barents Sea Marginal Ice Zone previously (Hegseth, 1997; Strass and Nöthig, 1996) and have increased in frequency within Arctic shelf seas in the past decades (Ardyna et al., 2014; Orkney et al., 2022). Although no direct evidence of an autumnal bloom was observed during our field sampling, it is possible that this phenomenon could affect the quantity and quality of food available to benthos within the northern Barents Sea over multi-annual timescales.

5.4. The effect of depth on isotope values

While we acknowledge the key role that high-quality organic matter plays in providing energy to Arctic benthos, most components of the benthic food web may in fact be supported by comparatively low- to moderate-quality organic matter. The sediment chlorophyll-*a*/phaeopigment ratios measured in this study (0.1–0.8 at < 350 m) were much lower than those in the shallow (ca. 45 m) Chukchi Sea where ratios as high as 8 were measured (McTigue et al., 2015) demonstrating the very rapid sedimentation of fresh organic matter there. The ratios we measured in the northern Barents Sea were more comparable to ratios measured in the less productive Canadian Beaufort Sea shelf, and even to

those measured in the deeper (even less productive) areas of the Beaufort Sea (Stasko et al., 2018) where organic matter quality is expected to be low due to great water depth and remineralization exposure during sedimentation. Thus, the quality of sediment organic matter in the northern Barents Sea may be relatively poor or at least of poorer quality than in the Pacific inflow shelf region. Nonetheless, seasonal differences in sediment organic quality were most pronounced at the deep stations (780–3300 m) in our study, suggesting that at some times of the year, relatively fresh and high-quality organic matter arrives at the seabed here through rapid sedimentation (Wollenburg et al., 2018), supporting previous observations in other parts of the Arctic Ocean (e.g., Boetius et al., 2013).

The effect of water depth on $\delta^{15}\text{N}$ values of organic matter has long been recognized as a challenge for comparing food webs across depth gradients (Bell et al., 2016; Bergmann et al., 2009; Mintenbeck et al., 2007). Generally, the $\delta^{15}\text{N}$ value of organic matter increases with increasing water depth (Bell et al., 2016) and subsequently increases the $\delta^{15}\text{N}$ values of benthic fauna. However, the degree to which benthic consumer isotope values are affected by depth depends on the feeding ecology of the consumer, with the greatest ^{15}N -enrichment typically observed in suspension feeders (Bergmann et al., 2009; Mintenbeck et al., 2007). The sampling sites in this study covered a large depth range with two sites (P6 and P7) occupying water depths of ca. 800–3100 m compared stations on the shelf (P1–P5) which were at ≤ 350 m water depth. However, there was only a marginally significant *negative* relationship between $\delta^{15}\text{N}$ of sediment organic matter and depth which we attributed to advection. Atlantic Water could transport fresher algal material (with lower $\delta^{15}\text{N}$) from more southerly locations where primary productivity is higher, to the deeper stations in the north prior to it settling on the seafloor and becoming available to benthic consumers. This hypothesis is supported by short-term sediment trap deployments which found that sinking organic matter at stations P6 and P7 was not enriched in ^{15}N relative to the shallow shelf stations and sinking organic matter at P6 had low $\delta^{15}\text{N}$ values in May comparable to that of the southernmost station P1 (Bodur et al., this issue). Our community-level analysis of isotopic niche and trophic level was not affected by any potential $\delta^{15}\text{N}$ dependence because there was no significant trend in faunal $\delta^{15}\text{N}$ values with depth, and trophic levels were calculated relative to site- and season-specific baseline $\delta^{15}\text{N}$ values. In addition, the number of samples from the deep stations included in the analysis was low relative to the number of samples from on the shelf (shelf: $n = 1098$, slope/basin: $n = 62$), and $\delta^{15}\text{N}$ values of the fauna collected at the deep stations did not represent isotopic end-members of the community but rather were encompassed by the range of isotope values already defined by shelf fauna ($\delta^{13}\text{C}$ range deep: -23.37 to -17.88 ‰, $\delta^{13}\text{C}$ range shelf: -26.76 to -14.82 ‰, $\delta^{15}\text{N}$ range deep: 5.76 to 14.73 ‰, $\delta^{15}\text{N}$ range shelf: 2.09 to 16.72 ‰). Despite there being significant depth-dependence in the $\delta^{15}\text{N}$ values of some consumers (e.g., Lumbrineridae, Maldanidae and Sipuncula), the direction of the relationship was not consistent across all taxa, and sample sizes were very low, often with only 1 individual analyzed from the deepest station. Regardless, our approach of grouping taxa into functional groups should reduce the influence of variability in isotope values of individual taxa on isotopic niche measures since each functional group was defined by multiple taxa. In addition, any depth-dependence would have affected $\delta^{15}\text{N}$ values consistently between seasons thereby not confounding our seasonal comparison of isotopic niches within functional groups. Thus, we are confident that depth did not affect the overall conclusions of the analyses we present here. Nonetheless, we echo cautions from other authors that depth-stratified approaches to comparing food web structure should be used whenever possible to avoid confounding results due to a depth effect on nitrogen isotope values.

5.5. Benthic resilience to short-term change

Understanding the response of benthic fauna to seasonal changes in

food quantity and quality could be used to infer trophic relationships and functioning under future conditions in the Arctic. It is observed and predicted that the timing and magnitude of overlying primary productivity in the Barents Sea will increase due to reduced sea-ice cover (Ardyna and Arrigo, 2020; Mousing et al., 2023; Sandø et al., 2021), but the impact this will have on sediment organic carbon content remains unclear (Faust et al., 2020). Our results suggest that benthic food-web structure in the Barents Sea may not be significantly altered by short-term changes in food availability. The weak signs of seasonality we observed in benthic food web structure may be the result of a food subsidy from organic matter supplied via the inflow of Atlantic Water. However, the continued role of this food subsidy and its regional variability remains unknown as the transport of Atlantic Water into the southern Barents Sea is predicted to decrease in the future (Årthun et al., 2019). Renaud et al. (2008) highlighted the need to consider the time-scales integrated by benthic standing stocks and processes when assessing pelagic-benthic coupling and seasonality. For instance, while feeding and respiration rate exhibit a rapid (days) response to increased food availability (e.g., Renaud et al., 2008; Renaud et al., 2007; Sun et al., 2007), community structure and biomass integrate multi-annual changes in food availability. In this study, we assume that our data represent the assimilation of food resources by benthos over moderate time scales of weeks to months. This assumption is based on the turnover rate of the elements within organisms' tissues (reviewed in Boecklen et al., 2011). Uncertainty in species- and tissue-specific isotopic turnover rates, especially of Arctic benthos, limits our ability to refine the temporal resolution of our method. Few isotopic turnover studies of Arctic benthos have been conducted with resulting turnover times (measured as half-life) ranging from two weeks to nearly four months (Barton et al., 2019; Kaufman et al., 2008; McMahon et al., 2006; Weems et al., 2012; Ziegler et al., 2023). Based on these turnover time estimates, we expect that the isotopic compositions of fauna we measured in this study could represent the diet and assimilated elements integrated over weeks to months preceding the sampling periods. In addition, the seasonal evaluation presented here was restricted to only one seasonal cycle but divided across years with contrasting winter sea-ice conditions (Kohlbach et al., 2023). This could limit how representative these sampling periods were of environmental conditions which we attribute to seasonality. Despite these challenges, our study suggests a resilience of the benthic food web to seasonal changes in food availability and quality and highlights the need to consider the temporal scale that different measurements integrate within the benthic ecosystem.

CRedit authorship contribution statement

Amanda F. Ziegler: Conceptualization, Formal analysis, Data curation, Visualization, Writing – original draft. **Bodil A. Bluhm:** Conceptualization, Supervision, Project administration, Writing – review & editing. **Paul E. Renaud:** Writing – review & editing. **Lis L. Jørgensen:** Conceptualization, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

The data are published and publicly available via the Norwegian Marine Data Center and GBIF (<https://www.doi.org/10.21335/NMDC-2139630788>).

Acknowledgments

This work was financially supported by the Research Council of

Norway [The Nansen Legacy, grant number 276730]. Collection of samples was made possible by all participants of the seasonal Nansen Legacy cruises. We sincerely thank the CLIPT laboratory at the University of Oslo (funded by the Research Council of Norway Centers of Excellence #223373) and IsoAnalytical (United Kingdom) for isotopic and elemental analytical services, especially Bill Hagopian for additional consulting on sample preparation, analysis, and quality control of the data. We acknowledge Liova Idahl (University of Düsseldorf) and Katrin Bluhm (Akvaplan-niva, AS) for sediment phytopigment analyses, as well as Johanna Hovinen (University of Tromsø) and Thaise Ricardo de Freitas (University of Oslo) for assisting in the preparation of stable isotope samples.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2023.103109>.

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