Progress in Oceanography
September 2023, Volume 217 Pages 103105 (12p.)
https://doi.org/10.1016/j.pocean.2023.103105
https://archimer.ifremer.fr/doc/00850/96237/

Trophic ecology of epibenthic communities exposed to different sea-ice concentrations across the Canadian Arctic Ocean

Yunda-Guarin Gustavo [1, *], Michel Loïc [2], Roy Virginie [3], Friscourt Noémie [4], Gosselin Michel [5], Nozais Christian [6], Archambault Philippe [1]

[1] ArcticNet, Québec-Océan, Takuvik (UMI 3376), Université Laval, Québec, Québec, Canada
[2] Université de Brest, CNRS, Ifremer, UMR6197 Biologie et Écologie des Écosystèmes marins Profonds (BEEP), F-29280 Plouzané, France
[3] Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont-Joli, Québec, Canada
[4] Institute of Marine and Antarctic Studies, 20 Castray Esplanade, Tasmania 7004, Australia
[5] Québec-Océan and Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski, Rimouski, Québec, Canada
[6] Québec-Océan and Département de biologie, chimie et géographie, Université du Québec à Rimouski, Rimouski, Québec, Canada

* Corresponding author : Gustavo Yunda-Guarin, email address : gustavo-adolfo.guarin.1@ulaval.ca

Abstract :

Sea ice is one of the most critical environmental drivers shaping primary production and fluxes of organic inputs to benthic communities in the Arctic Ocean. Fluctuations in organic inputs influence ecological relationships, trophic cascades, and energy fluxes. However, changes in sea-ice concentration (SIC) induced by global warming could lead to significant shifts in trophic interactions, ultimately affecting the functioning of Arctic food webs. Despite the increasing concern over the need to understand benthic species and food web responses to rapid sea-ice loss, few studies have addressed this topic so far. Using multiple niche metrics based on stable isotopes, this research examined the trophic ecology of epibenthic communities in areas with different SIC across the Canadian Arctic Ocean. We found that trophic niches varied according to complex interactions between environmental conditions, resource supply, and biotic pressures such as predation and competition. Our results highlighted a lower isotopic richness (i.e., shorter food chain length and niche width) in low and high SIC areas, suggesting homogeneity of resources and a low diversity of food items ingested by individuals. In contrast, a higher isotopic richness (i.e., broad niche) was observed in the moderate SIC area, implying higher heterogeneity in basal food sources and consumers using individual trophic niches. Finally, our findings suggested a lower isotopic redundancy in areas with high SIC compared to low and moderate SIC. Overall, our results support the idea that sea ice is an important driver of benthic food web dynamics and reinforce the urgent need for further investigations of declining sea ice cover impacts on Arctic food web functioning.

Keywords : Benthic community, Food web, Stable isotopes, Sea ice, Arctic Ocean

1. Introduction

Arctic marine ecosystems are experiencing rapid and widespread changes due to increases in the average surface air temperature (Bhatt et al., 2014). As a result of this warming, the minimum multi-year sea-ice extent has been decreasing at a rate of 13.1% per decade, reaching its second-lowest minimum in September 2020 and its seventh-lowest maximum annual sea-ice extent in March 2020 (Perovich et al., 2020). In addition, there are trends toward an early onset period of sea-ice melt (2 days per decade) and delays in refreezing time (2.3 days per decade) (Post, 2017; Stroeve et al., 2014). Changes in the primary production of the Arctic Ocean are linked with decreases in sea ice (i.e., thickness and extent), alterations in sea-ice phenology, and changes in stratification intensity of the water column (Ardyna et al., 2020), which could yield to alterations in the timing, magnitude, and delivery of the produced organic matter across water depths in the coming decades (Lafond et al., 2019; Leu et al., 2011).

Benthic fauna is an important component of marine ecosystems. They play an essential role in key ecosystem processes such as fueling higher trophic levels, driving biogeochemical cycles, bioturbation and nutrient remineralization processes, organic carbon sequestration and providing biogenic habitats (Canuel et al., 2007; Ehrnsten et al., 2019). The distribution and taxonomic diversity of the benthos are significantly influenced by environmental gradients, including temperature, sea-ice dynamics, water masses, depth, currents, sediment type, silicate, and bottom topography (Kędra et al., 2013; Roy et al., 2014; Saeedi et al., 2022; Stasko et al., 2018a). Ecological and biological drivers also influence the benthic community structure at a geographic scale (Sokołowski et al., 2012). For instance, changes in primary production and delivery could lead to shifts in the composition and abundance of the benthic community, because benthic fauna relies largely upon the supply of ice-associated (i.e., sympagic) and water column (i.e., phytoplanktonic) production (Grebmeier and Barry, 1991; Roy et al., 2014). Thus, benthic communities are sensitive to changes in the timing, type, quality, or abundance of these organic carbon sources (Garf, 1989). Hence, fluctuations in the input of resources could control consumers' diets and the biomass of consumers at lower trophic levels, affecting the timing of species interactions across trophic levels (Post, 2017), and pelagic-sympagic-benthic coupling processes (Griffiths et al., 2017). Despite this, only a few studies have investigated the response of benthic species and marine food webs to changes in sea ice and organic carbon supply in the Arctic Ocean (e.g., Cautain et al., 2022; Koch et al., 2020; Post, 2017; Yunda-Guarin et al., 2020).

One of the biggest challenges in ecology is predicting the adaptive capacity of a system to maintain functional integrity when faced with various disturbances and understanding the consequences of environmental shifts toward ecosystem functioning and services (Frid and Caswell, 2016). To address this challenge, stable isotope analysis (SIA) is an essential tool used to understand species interactions and food web functioning. For example, stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) have been used extensively for the investigation of the trophic ecology of marine species (Middelburg, 2014), and to track carbon transfer pathways in food webs (Peterson and Fry, 1987). $\delta^{15}N$ ratios are typically used to estimate the trophic level (TL) of consumers in relation to food web baselines (Post, 2002), whereas $\delta^{13}C$ ratios are used to establish the relative contribution of basal food sources in the diet of consumers and energy pathways (Layman et al., 2007a). The nitrogen isotope ratio increases by about a range from 2 to 4‰ for each trophic level (McCutchan et al., 2003; Vander Zanden and Rasmussen, 2001), while the carbon isotope variation is ≤1‰ (DeNiro and Epstein, 1978; Fry and Sherr, 1984; McCutchan et al., 2003). Advances in SIA allowed community-wide measurements of the isotopic niche (i.e., the area occupied by individuals in a $\delta^{13}C$- $\delta^{15}N$ space), providing quantitative information on resources and habitat use that helps to characterize aspects of the ecological niche space (Jackson et al., 2011; Layman et al., 2007). New metrics in stable isotope ecology based on the approach of measuring multiple aspects of isotopic diversity might offer additional clues to understand the functioning of the food web (Cucherousset and Villéger, 2015).

The isotopic niche, an *n*-dimensional hypervolume of the "Hutchinsonian ecological niche" (Hutchinson, 1957), represents the consumer's isotopic distribution in a niche area (Martínez Del Rio et al., 2009; Newsome et al., 2007), and helps in the analysis of patterns of consumer-resource interactions (Shipley and Matich, 2020). The isotopic niche is a valuable approach to obtaining quantitative differences in trophic niches. For example, it is a useful conceptual tool to estimate variations in food web structure and trophic redundancy (degree of dietary overlap among taxa within a food web) of a community in response to environmental gradients (Layman et al., 2007a). The niche characteristics vary according to intrinsic and extrinsic factors (Costa-Pereira et al., 2017; Shipley and Matich, 2020). For example, in polar regions, the seasonal phenology in sea-ice concentration and ecosystem productivity have influenced isotopic-niche dimensions in benthic communities (e.g., Lesser et al., 2020; Michel et al., 2019; Yunda-Guarin et al., 2020). Inter-individual levels of dietary specialization and interspecific competition may also drive niche dynamics (e.g., Araújo et al., 2009; Evans et al., 2005; Semmens et al., 2009).

The studied areas, Baffin Bay (BB), Lancaster Sound (LS), and the Canadian Arctic Archipelago (CAA) (Figure 1) are characterized by significant interannual variations in primary productivity and sea-ice conditions (Stein and Macdonald, 2004). BB is partially covered by sea ice, excluding the completely ice-free months of August and September (Tang et al., 2004). Even if the ice breaks up in the spring, LS is never completely ice-free, as first-year and multi-year ice continue to move from west to east until the formation of new ice in September (Welch et al., 1992). In the CAA, sea ice component consists of a mixture of both first-year and multi-year ice (Kwok, 2006), multi-year ice is mostly located in Western CAA. It can represent more than 50% of the total ice-covered area before melting (Howell et al., 2013). Sea-ice conditions in the Beaufort Sea vary according to the season. In the Beaufort Sea, winter sea ice can be categorized into three regimes: the offshore pack ice (consisting of mobile annual and multi-year sea ice), the coastal landfast sea ice, and the Cape Bathurst polynya (Barber and Hanesiak, 2004). Polynyas are areas of reduced ice cover or open water enclosed by consolidated ice (Barber and Massom, 2007). Arctic polynyas exhibit a marked interannual variability in sea-ice dynamics, and the initial timing moment of formation, the persistence of open water, and the productivity vary considerably between polynyas (Arrigo and van Dijken, 2004; Grebmeier and Barry, 2007).

Using the isotopic niche as an approach to the food web structure, this study aimed at examining variations in the trophic niche of the epibenthic community associated with ice areas with different sea-ice concentrations (SIC) across the Canadian Arctic Ocean. The current study is one of the largest of its type and one of the few that uses a combination of different metrics to provide quantitative data to better understand how epibenthic food web structure responds to variations in sea-ice cover. We tested the following hypotheses: i) differences in SIC and the nature of the resources (e.g., ice algae vs. phytoplankton) will largely influence the isotopic composition of food sources and benthic epifauna, ii) the isotopic niche size will vary according to environmental and biological variables (i.e., SIC and seasonal primary production), in which a narrow niche size will be linked to ice cover areas with high SIC and more productive (g C m^{-2} y^{-1}) ecosystems (i.e., polynyas), and iii) higher trophic redundancy will be associated with more productive ecosystems, where greater resource availability may promote that benthic epifauna consumes prey over a narrow spectrum of trophic levels reducing isotopic variance.

2. Materials and Methods

2.1. Study area and sampling methods

Baffin Bay (BB) is a semi-enclosed ocean between Baffin Island and western Greenland (Tang et al., 2004). The Canadian Arctic Archipelago (CAA) comprises a larger number of islands and channels (Kwok, 2006). This area contains the four polynyas analyzed in this study (i.e., Cape Bathurst polynya (CB), Lancaster Sound-Bylot Island polynya (LS-BI), North Water polynya (NOW), and Viscount-Melville Sound polynya (VMS); Figure 1). The NOW is considered one of the largest and most biologically productive polynyas in the Arctic Ocean, where primary production reaches >250 g C m^{-2} y^{-1} (Klein et al., 2002; Stirling, 1997; Tremblay et al., 2006b). By comparison, primary production ranged from 23 to 49 g C m^{-2} y^{-1} in the Canadian Shelf between the Beaufort Sea and the Amundsen Gulf

(Forest et al., 2011; Lavoie et al., 2009; Martin et al., 2013), 90 to 175 g C m^{-2} y^{-1} in the Cape Bathurst polynya (Arrigo and van Dijken, 2004), and 56 g C m^{-2} y^{-1} in Lancaster Sound (Welch et al., 1992). The Canadian Beaufort Sea and the Amundsen Gulf are areas strongly influenced by terrigenous carbon inputs from different rivers, primarily by the Mackenzie River, which discharges approximately 340 km^3 y^{-1} of freshwater to the Arctic Ocean (Macdonald et al., 1999).

A total of 35 stations ranging in depth from 35 to 789 m were sampled between August 2011 and July 2016 during three different oceanographic campaigns: 2011 (Roy et al., 2015), 2014 (Friscourt, 2016), and 2016 (Yunda-Guarin et al., 2020; Figure 1). To study the isotopic composition of sources and benthic consumers, epibenthic specimens, surface sediments, and suspended particulate organic matter (SPOM) were collected at each station aboard the Canadian research icebreaker CCGS Amundsen. Epibenthic fauna was sampled using an Agassiz trawl with an opening of 1.5 m and a net mesh size of 40 mm, with a 5 mm cod-end liner. A box core (0.125 m^2) sampling was undertaken to collect surface sediment samples (upper 1 cm). For each box core, surface sediments (Sed-POM) were collected for pigment content (using 10 ml truncated syringes of an area of 1.5 cm^2) and stable isotopes analyses (using 60 ml truncated syringes of an area of 5 cm^2). In addition, pelagic-suspended particulate organic matter (i.e., POM) sources were collected at two depths, in the subsurface chlorophyll maximum (SCM-POM) and 10 meters above the seafloor (Bot-POM) using a CTD-Rosette with 12 L Niskin-type bottles. Water samples for SPOM were filtered onto 21 mm Whatman GF/F glass-fiber filters (nominal pore size 0.7 µm) pre-combusted at 450°C for five hours. Ice-POM isotope data were obtained from Beaufort Sea (Pineault et al., 2013), Baffin Bay (Yunda-Guarin et al., 2020), the NOW (Tremblay et al., 2006a), and Allen Bay/Resolute Passage (Roy et al., 2015). After collection, all samples, including filters, were immediately frozen at –20°C for further isotopic analyses. The quantification of surface sediment chlorophyll *a* (chl *a*) content was carried out at Université Laval (Quebec, Canada) following the modified protocol of Riaux-Gobin and Klein (1993) and Link et al. (2011).

To assess the possible effects of SIC on the trophic niche structure, sampled stations were grouped into three sea-ice condition categories: i) low SIC (< 10%) located within or in the vicinity of polynyas (15 stations); ii) moderate SIC (> 10 to 50%) situated in the CAA and BB (10 stations); and iii) high SIC (> 50%) located mainly in BB (11 stations) (Figure 1). Additional information about individual sampling stations can be found in Supplementary Table S1.

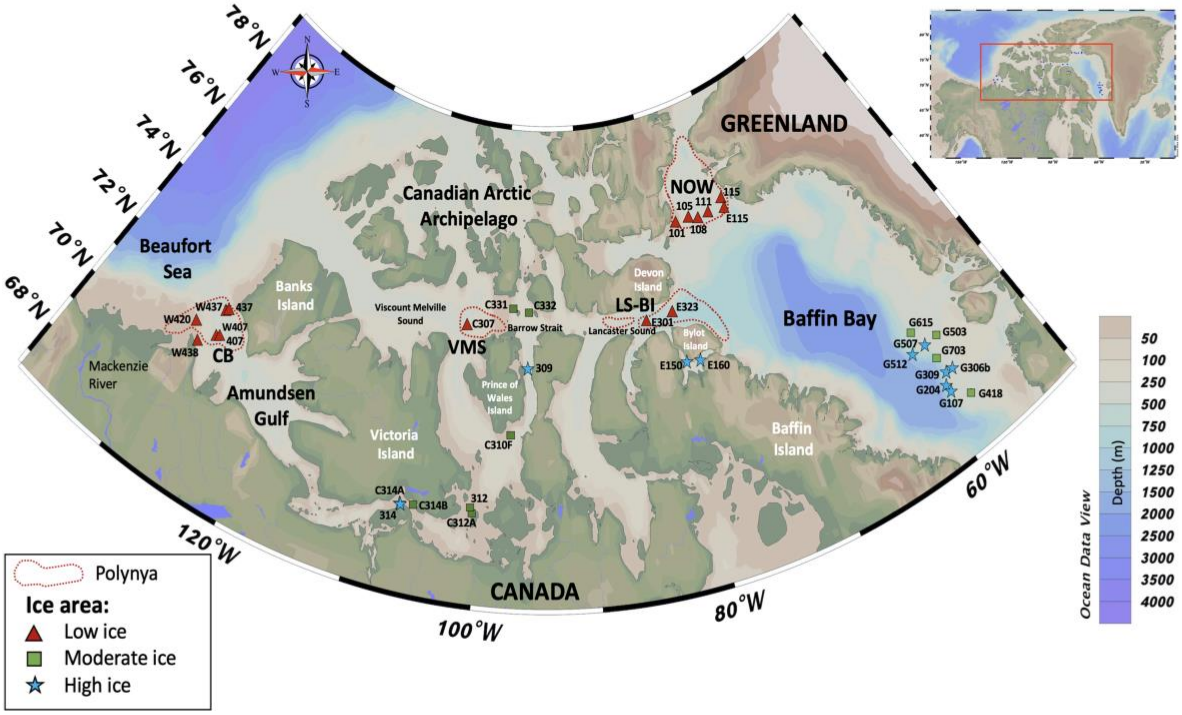

Figure 1. Location of sampling stations with seafloor bathymetry scale. Sampled stations were grouped into three ice areas according to the average sea-ice concentration (SIC) estimated over a 30-day period prior to sampling: low (red triangles, < 10% of SIC), moderate (green squares, > 10 to 50% of SIC), and high (blue stars, > 50% of SIC). Polynyas are represented by a red dotted line and their names are indicated by abbreviations in capital letters (CB: Cape Bathurst polynya, LS-BI: Lancaster Sound-Bylot Island polynya, NOW: North Water polynya, VMS: Viscount-Melville Sound polynya). The approximate location and delimitation areas of the polynyas were based on Barber and Massom (2007) and Roy et al. (2015).

2.2. Sea-ice concentration data

Satellite sea-ice concentrations (SIC) data were derived from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data with polar stereographic projection at a grid cell size of 25 × 25 km and downloaded from the National Snow and Ice Data Center, NSIDC (Cavalieri et al., 1996). The average percentage SIC at each station was calculated for 30 days before sampling. This period was considered relevant in this study since isotopic values of invertebrates' tissues with Arctic distribution (e.g., *Alitta virens*, *Onisimus litoralis*, *Mytilus edulis*, *Nuculana radiata*, and *Macoma calcarea*) showed metabolic turnover rates of the organic matter assimilated by benthic consumers of approximately 30 days (Dubois et al., 2007; Kaufman et al., 2008; McMahon et al., 2006; Olive et al., 2003; Sun et al., 2006; Weems et al., 2012).

2.3. Carbon and nitrogen stable isotope analysis

Stable isotope ratios ($\delta^{13}C$ - $\delta^{15}N$) were measured in 136 epibenthic species with a total of 664 replicates analyzed among ice areas (276 in low ice, 205 in moderate ice, and 183 in high ice; Table S3). Benthos samples were freeze-dried at –50°C. Afterward, they were ground and homogenized to a fine powder with a mortar and pestle. Sediments and calcified benthic taxa were freeze-dried, acidified with an aqueous solution of 1M HCl until bubbling ceased, and dried at 60°C for 24h before the stable carbon isotopic ($\delta^{13}C$) analysis. Unacidified samples (filters, sediments, and not calcified benthic taxa) were used to assess the stable nitrogen isotopic ($\delta^{15}N$) composition. Multiple replicates were also performed on stable isotope analyses of POM sources between ice areas (Table S2). Filters for the analysis of SPOM isotopic signatures were freeze-dried for 48h, fumed with saturated HCl vapors for 24h, and dried at 60°C for 24h before conducting isotope analyses.

Stable carbon and nitrogen isotope ratios were measured in the Oceanography Laboratory at Laval University and the Marine Chemistry and Mass Spectrometry Laboratory of the University of Quebec at Rimouski (UQAR), Canada, with a continuous-flow isotope ratio mass spectrometry (CF-IRMS) in the continuous-flow mode (Thermo Electron ConFlo III) using an ECS 4010 Elemental Analyzer/ZeroBlank Autosampler (Costech Analytical Technologies). Replicate measurements of international standards (USGS40 and USGS41 from the International Atomic Energy Agency; B2151 from Elemental Microanalysis) established measurement errors ≤ 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$. Standards were calibrated against the international references Vienna PeeDee Belemnite (VPDB) for carbon and atmospheric air for nitrogen. Stable isotope ratios were expressed in delta (δ) units ($\delta^{13}C$; $\delta^{15}N$) as parts per mil (‰) differences from a standard reference material: $\delta X\,(‰) = \left[\frac{(\text{Rsample} - \text{Rstandard})}{\text{Rstandard}}\right] \times 1000$, where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

2.4. Statistical analyses

Mixed linear models were fit using the nlme package (v.3.1-140) in R (v3.6.1, R Studio v1.1.456) (Pinheiro et al., 2021). Models comprised only main effects and two-way interaction effects. $\delta^{13}C$ and $\delta^{15}N$ models were run against depth (quantitative), sea-ice concentration (quantitative), ice areas (three levels), and epibenthic consumer groups (three levels; GC: primary consumers, omnivores, and high consumers) as fixed factors and both region and sampling year as random factors to account for the variability they incurred. Nonsignificant two-way interaction effects were trimmed to increase model fit. Significant effects implicating categorical factors (ice areas and GC) were further analyzed with Tukey post-hoc using the emmeans package (v2.27-61) (Lenth and Lenth, 2018). The normality of residuals was tested by examining the characteristic Quantile-Quantile (QQ) plot (Zuur et al., 2007). If residual normality and homoscedasticity assumptions were not met, response variables were log-transformed.

2.5. Trophic position of benthic consumers

The trophic position (TP) for each epibenthic consumer was used as a proxy of relative assimilation and transfer of carbon across the benthic community. TP was computed using Equation 1:

$$\text{TP} = \frac{\delta^{15}\text{N consumer} - \delta^{15}\text{N base}}{\Delta^{\delta^{15}\text{N}}} + \lambda \qquad \text{Equation 1}$$

where $\delta^{15}N_{Consumer}$ is $\delta^{15}N$ of the benthic consumers; $\delta^{15}N_{base}$ is the nitrogen isotope ratio of surface sediment bulk organic matter for each ice area studied (Figure 1), namely the base of the food web; $\Delta^{15}N$ is the trophic enrichment factor between successive trophic levels – we assumed a constant enrichment factor (Δ) of 2.3‰ per trophic level in aquatic consumers (McCutchan et al., 2003); and $\lambda = 1$ is the trophic position of "baseline". Benthic epifauna was then categorized into three different groups: high TL consumers (including secondary, tertiary, or upper consumers as well as scavengers ($TP \geq 3$)), omnivores ($3 > TP > 2$), and primary TL consumers ($TP \leq 2$).

2.6. Trophic structure: community-wide metrics and isotopic diversity assessment

Using different approaches, we examined the potential effect of biological and environmental variables on the trophic niche structure of the epibenthic community between regions with contrasted sea-ice conditions. We used more than one metric in quantifying different aspects of the trophic niche to i) study differences in isotopic niche size among ice areas (hypothesis 2); and ii) include specific elements of the trophic niche, such as the isotopic redundancy (hypothesis 3). First, community-wide metrics (i.e., Bayesian ellipses) based on the relative position of individuals in bivariate isotopic space were used to describe different aspects of trophic ecology and food web structure according to the ecological niche approach. The core isotopic niche space occupied by the epibenthic community was calculated using the standard ellipse area in the 'SIBER' package in R (Jackson et al., 2011). Second, different facets of the isotopic diversity were measured using four different indices: isotopic dispersion (IDis), divergence (IDiv), evenness (IEve), and uniqueness (IUni) defined by Cucherousset and Villéger (2015). Isotopic diversity indices were measured in two-dimensional isotopic spaces providing data on multiple facets of isotopic diversity and redundancy of the benthic community (Cucherousset and Villéger, 2015). Briefly, IDiv index measures the amount of isotopic space occupied by an assemblage of species considering their distribution within the convex hull. IDis index estimates the variation or dispersion of a set of weighted values in iso-space and divides it by the distance to the gravity center. IEve index quantifies the regularity in the distribution of the species through the shortest spanning tree that connects all points in the isotopic space. IEve tended to 0 when most of the organisms are packed within a small area of the stable isotope space, while IEve tended to 1 when organisms are evenly distributed in the stable isotope space. Finally, IUni index measures the average distance of each species to the nearest neighbor. Therefore, it measures species' packing density in stable isotope space (for further description, see Cucherousset and Villéger, 2015). Before calculating the isotopic diversity indices, stable isotope values of consumers were homogenized in each ice area using the mean-correction method recommended by Le Bourg (2021). This method reduced the potential biases of isotope values between sampling stations caused by spatial and temporal differences in sample collection (for a review, see Le Bourg et al., 2021). It consists of taking the isotopic mean $\bar{X}$ ($\delta^{13}C$ or $\delta^{15}N$) of each individual i and subtracting it from the result of the subtraction between the station mean s for that isotopic value and the overall mean of all stations combined z. The result of the equation is the mean corrected value $\bar{X}c$ for the individual, Equation 2:

$$\bar{X}c = \bar{X}i - (\bar{X}s - \bar{X}z) \qquad \text{Equation 2}$$

Additionally, the multidimensional isotopic space ($\delta^{15}N$ and $\delta^{13}C$) was standardized (i.e., scaled between 0 and 1) to have equal importance in the index's calculation for each axis and to remove the potential scaling discrepancies present in δ-space across ice areas (Cucherousset and Villéger, 2015).

3. Results

3.1. Stable isotope composition of basal food sources and epibenthic trophic groups

Basal food sources displayed a wide range of isotope signatures among areas with contrasting ice conditions (Table S2; Figure 2). Overall, on average, the pelagic (mean SCM-POM ‰ ± SD = –25.9‰ ± 1.3, n = 32) and bottom water (mean Bot-POM ‰ ± SD = –25.8‰ ± 3.1, n = 21) sources were most ^{13}C-depleted across ice areas (Figure 2). In contrast, sediment-POM and Ice-POM were more ^{13}C-enriched than pelagic baseline sources (Figure 2). Linear models showed a significant effect of depth (p-value < 0.001) and significant interaction effects between depth and SIC (p-value < 0.001) on the $\delta^{13}C$ isotopic composition of Sed-POM (Table 1).

On average, the most ^{15}N-depleted values were found in Ice-POM sources in ice areas with high SIC (mean Ice-POM ‰ ± SD = 3.0‰ ± 0.6, n= 9), whereas Bot-POM had the most ^{15}N-enriched values in ice areas with low SIC (mean Bot-POM ‰ ± SD = 7.3‰ ± 2.2, n= 21). Based on linear models, a significant effect of both depth (p-value < 0.001) and SIC (p-value < 0.01) on the $\delta^{15}N$ isotopic composition of Sed-POM was detected, as well as a significant interaction effect between these two environmental variables (Table 1). Finally, linear models did not find a significant effect of depth or SIC on $\delta^{13}C$ and $\delta^{15}N$ isotopic values for the other basal food sources of SPOM between ice areas (Table 1).

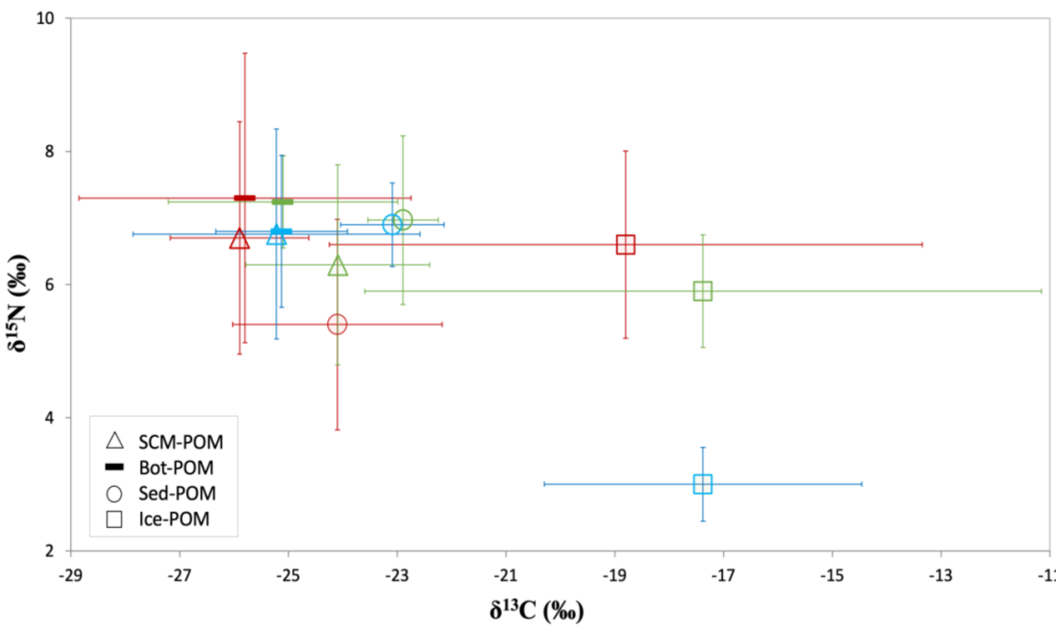

Figure 2. Biplot of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}C$) composition of basal food sources. Isotopic $\delta^{13}C$ and $\delta^{15}N$ composition (mean ± SD) of basal food sources in three ice areas: with low SIC (red); ice areas with moderate SIC (green), and ice areas with high SIC (blue) concentration. Basal food sources: subsurface chlorophyll maximum (triangle, SCM-POM), bottom water particulate organic matter (rectangle, Bot-POM), surface sediment particulate organic matter (circle, Sed-POM), and ice particulate organic matter (square, Ice-POM).

Table 1. Summary of the main effects of environmental variables on $\delta^{13}C$ and $\delta^{15}N$ values of baseline food sources from samples collected at different locations of the Canadian Arctic Ocean (n = 31 stations).

	Model $\delta^{13}C$				Model $\delta^{15}N$			
Main effects and significant interaction effects	Degree of freedom	F-value	p-value	Effect size (slope)	Degree of freedom	F-value	p-value	Effect size (slope)
SCM-POM[a]					SCM-POM			
Depth (bottom)	1	1.09	0.301		1	0.18	0.670	
SIC[b]	1	1.07	0.307		1	0.65	0.425	
Depth × SIC	1	6.85	0.012*		1	<0.01	0.976	
Bot-POM[a]					Bot-POM			
Depth	1	<0.01	0.970		1	1.52	0.228	
SIC	1	1.31	0.262		1	<0.01	0.973	
Depth × SIC	1	1.26	0.272		1	<0.01	0.924	
Sed-POM[a]					Sed-POM			
Depth	1	82.02	<0.001***	0.006	1	17.09	<0.001***	0.004
SIC	1	3.03	0.087	– 0.173	1	8.96	0.004**	4.937
Depth × SIC	1	15.01	<0.001***		1	8.12	0.006**	

[a] The baseline food sources: subsurface chlorophyll maximum particulate organic matter (SCM-POM), bottom water particulate organic matter (Bot-POM), and surface sediment particulate organic matter (Sed-POM).
[b] Sea-ice concentration (SIC).
The level of statistical significance: ***p < 0.001, **p < 0.01, *p < 0.05.

Benthic fauna under areas with contrasting ice conditions displayed a wider range of isotopic composition than the basal food sources (Figure 3; Table S3). The average benthic fauna $\delta^{13}C$ composition was –19.0 ± 1.7‰ (range from –24.1‰ to –14.7‰) in ice areas with low SIC, –18.4 ± 2.1‰ (range: –23.8‰ to –13.5‰) in ice areas with moderate SIC, and –18.1 ± 1.9‰ (range from –21.7‰ to –13.4‰) in ice areas with high SIC. Among the benthic fauna studied, the most ^{13}C-enriched values corresponded to the brittle star *Ophiacantha bidentata* (high TL consumer) in high SIC areas (–13.4‰), while the most depleted in ^{13}C were hydrozoans of the family Sertulariidae (omnivorous consumer) in low SIC areas (–24.1‰). Among benthic trophic groups, primary consumers in low SIC areas were the most depleted group in ^{13}C values (mean $\delta^{13}C$‰ ± SD = –20.3‰ ± 1.4, n= 34), whereas high consumers in high SIC areas were the most enriched in ^{13}C (mean $\delta^{13}C$‰ ± SD = –17.6‰ ± 1.7, n= 114). Besides, linear models showed a significant positive effect of SIC on the $\delta^{13}C$ isotopic composition of benthic consumers (p-value < 0.001). However, the effect of SIC on the $\delta^{13}C$ is more significant in high SIC areas (Table 2). No effect of bottom depth on $\delta^{13}C$ isotopic composition was detected (p-value = 0.42; Table 2).

The average $\delta^{15}N$ composition in benthic fauna was 12.8 ± 2.8‰ (range from 4.6‰ to 19.4‰) in ice areas with low SIC, 12.8 ± 3.2‰ (range of 5.4‰ to 21.3‰) in ice areas with moderate SIC, and 13.4 ± 2.8‰ (range from 6.4‰ to 20.5‰) in ice areas with high SIC. Among benthic species, the sea stars *Stephanasterias albula* and *Korethraster hispidus* (high TL consumers) were the most ^{15}N-enriched species in ice areas with high (21.3‰) and moderate (20.5‰) SIC, respectively. In contrast, the brittle star species, *Ophiocten sericeum* and *Ophiura robusta* (primary TL consumers) were the most ^{15}N-depleted in areas with low SIC with $\delta^{15}N$ of 4.6‰ and 5.9‰, respectively. Among benthic groups, primary consumers in low SIC areas were the most depleted group in ^{15}N values (mean $\delta^{15}N$‰ ± SD = 7.9‰ ± 1.0, n= 34), whereas high consumers in moderate SIC areas were the most enriched in ^{15}N (mean $\delta^{15}N$‰ ± SD = 15.4‰ ± 1.9, n= 106). Linear models indicated that bottom depth was an important variable affecting $\delta^{15}N$ isotopic composition for consumers (p-value < 0.001; Table 3).

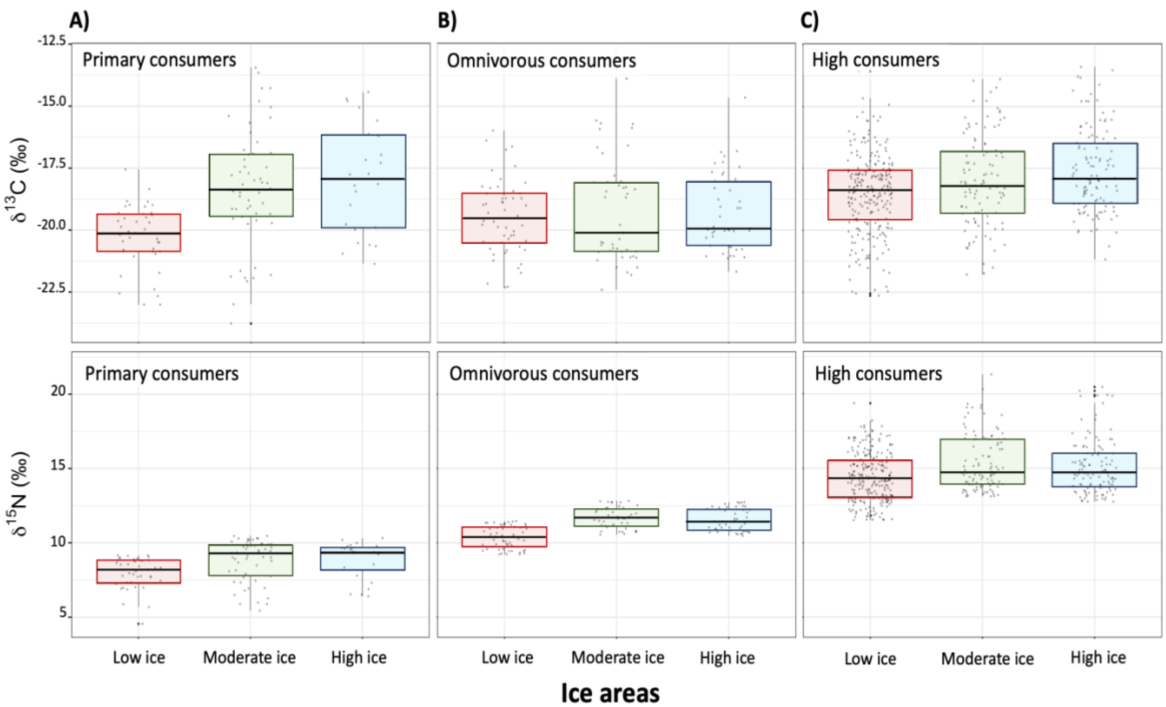

Figure 3. Boxplot showing the stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of epibenthic consumer groups under contrasted sea-ice conditions. Individual isotopic values of benthic consumers (black dots) are shown in three ice areas with different sea-ice concentrations (SIC): low ice (< 10% of SIC; red), moderate ice (> 10 to 50% of SIC; green), and high ice (> 50% of SIC; blue). Benthic taxa were divided into three groups: high TL consumers, omnivorous consumers, and primary TL consumers according to their trophic positions. The middle part of the box, or the "interquartile range," represents the middle quartiles (or the 75th minus the 25th percentile). The black line in the box represents the median. The minimum and maximum values of the data are indicated by the upper and lower lines of the box, respectively. Points beyond the lines represent outliers in the data set.

Table 2. Summary of main effects and significant two-way interaction effects of environmental variables on $\delta^{13}C$ values of epibenthic taxa collected at different locations in the Canadian Arctic Ocean.

Model					Post-hoc		
Main effects and significant interaction effects	Degrees of freedom	F-value	p-value	Effect size (slope)	Significant effect	p-value	Effect size
Depth (bottom)	1	0.65	0.421				
SIC[a]	1	11.20	<0.001***	2.525			
Ice area[b]	2	5.63	0.004**		Moderate > High	0.024*	1.597
GC[c]	2	23.84	<0.001***		High TL consumers > Primary TL consumers	0.013*	0.591
					Primary TL consumers > Omnivorous	0.019*	0.648
					High TL consumers > Omnivorous	<0.001***	1.239
Depth × Ice area	2	5.27	0.005**		($\delta^{13}C$ ~ Depth) Moderate > High	<0.001***	0.005
					($\delta^{13}C$ ~ Depth) Moderate > Low	0.021*	0.003
Depth × GC	2	4.59	0.011*		($\delta^{13}C$ ~ Depth) High TL consumers > Omnivorous	0.041*	0.002
SIC × Ice area	2	8.52	<0.001***		($\delta^{13}C$ ~ SIC) High > Moderate	<0.001***	7.960
Ice area × GC	4	3.26	0.012*		(High) High TL consumers > Omnivorous	<0.001***	1.467
					(Moderate) High TL consumers > Omnivorous	<0.001***	1.402
					(Moderate) Primary TL consumers > Omnivorous	0.002*	1.392

The level of statistical significance: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Table 3. Summary of main effects and significant two-way interaction effects of environmental variables on $\delta^{15}N$ values of epibenthic taxa collected at different locations in the Canadian Arctic Ocean.

Model					Post-hoc		
Main effects and significant interaction effects	Degrees of freedom	F-value	p-value	Effect size (slope)	Significant effect	p-value	Effect size
Depth	1	119.02	<0.001***	0.0023			
SIC[a]	1	6.32	0.012*	0.0408			
Ice area[b]	2	0.29	0.7476				
GC[c]	2	955.73	<0.001***		High TL consumers > Omnivorous	<0.001***	3.550
					Omnivorous > Primary TL consumers	<0.001***	3.040
					High TL consumers > Primary TL consumers	<0.001***	6.590
Depth × GC	2	16.61	<0.001***		($\delta^{15}N$ ~ Depth) High TL consumers > Primary TL consumers	<0.001***	0.003
					($\delta^{15}N$ ~ Depth) Omnivorous > Primary TL consumers	<0.001***	0.003

[a] Sea-ice concentration (SIC).
[b] Ice area: low ice (≤ 10% of SIC), moderate ice (> 10 to 50% of SIC), and high ice (> 50% of SIC).
[c] Consumer group (GC): Primary TL consumers, omnivorous consumers, and high TL consumers.
The level of statistical significance: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

3.2. Epibenthic food web structure based on community-wide metrics

Bayesian standard ellipse areas revealed differences in the trophic niche size of benthic communities among the three ice area categories (Figure 4A). In the whole benthic community, the largest niche width corresponded to the ice areas with moderate SIC, whereas the smallest niche width was related to the ice areas with high SIC. In addition, a shorter food web length in the epibenthic community was found in the ice areas with low SIC compared to ice areas with moderate and high SIC. Furthermore, ellipses showed differences in niche overlap of consumers in the low SIC area compared to the other ice areas, suggesting differences in the isotopic composition of resources (Figure 4). Among epibenthic trophic groups, bidimensional metrics showed a similar pattern in the trophic niche size, indicating that the broadest niche corresponded to high TL consumers in ice areas with low SIC, whereas omnivorous consumers in ice areas with high SIC showed the narrowest niche (Figure 4B; Supplementary Table S4).

3.3. Trophic and isotopic ecology of the whole epibenthic community based on isotopic diversity indices

Among the three ice areas, isotopic diversity indices denote variations in the distribution of the isotopic ratios of epibenthic consumers in the 2D iso-space (Supplementary Figure S1; Table 4). For example, under moderate ice conditions, the epibenthic community registered the highest values of isotopic divergence (IDiv = 0.721) and isotopic dispersion (IDis = 0.488), which indicate that isotopic values of organisms had a wide distribution, far from the center of gravity at the edges of the convex hulls. In turn, the lowest IDis values were recorded in both low and high SIC areas (IDis = 0.363 and 0.362, respectively), suggesting an approximation of the isotopic values of organisms to the centroid of the area of the convex hulls. Isotopic evenness (IEve) showed slight differences in IEve values between ice areas, displaying the highest value for the ice area with moderate SIC (IEve = 0.745), whereas the lowest value was found in the ice area with low SIC (IEve = 0.72).

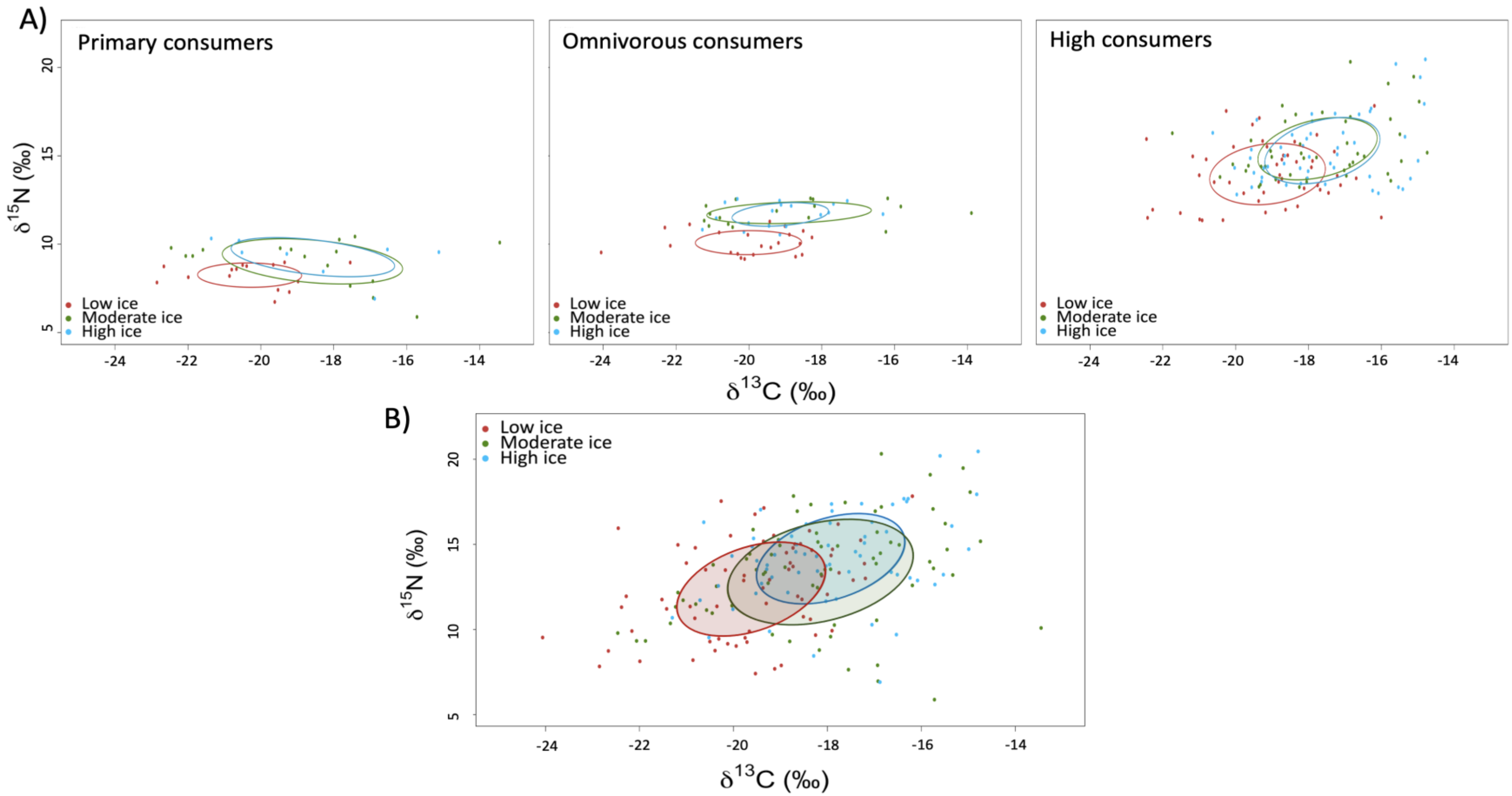

Figure 4. Biplot illustrating the isotopic niche structure of the epibenthic community under contrasting sea-ice conditions. The positions occupied by benthic fauna in the isotopic space are represented by dots in each $\delta^{13}C$ - $\delta^{15}N$ biplot. The representation of the ellipses (solid lines) encloses the size-corrected standard ellipse area (SEAc, fits 40% of the data) in (A) epibenthic groups (high TL consumers, omnivorous consumers, and primary TL consumers), and (B) the whole benthic community. Isotope data of benthic groups are shown in areas with different sea-ice concentrations (SIC): low ice (≤ 10% of SIC; red), moderate ice (> 10 to 50% of SIC; green), and high ice (> 50% of SIC; blue).

Finally, the isotopic uniqueness (IUni), used here as a proxy to estimate the redundancy of the benthic community between ice areas, exhibited the lowest value in the ice area with low SIC (IUni = 0.197), pointing to a higher overlap of isotopic values between organisms and suggesting a greater redundancy of the benthic community in this ice area (Table 4).

Table 4. Results of the isotopic diversity indices of the whole epibenthic community under contrasted sea-ice conditions. Different facets of the isotopic diversity were measured using four different indices: isotopic dispersion (IDis), divergence (IDiv), evenness (IEve), and uniqueness (IUni) defined by Cucherousset and Villéger (2015).

Metric	**Ice area category[a]**		
	Low ice	**Moderate ice**	**High ice**
Isotopic diversity index			
IDiv	0.667	0.721	0.677
IDis	0.363	0.488	0.362
IEve	0.720	0.745	0.739
IUni	0.197	0.291	0.302

[a] Sea-ice concentration (SIC) across ice areas: low ice (≤ 10% of SIC), moderate ice (> 10 to 50% of SIC), and high ice (> 50% of SIC).

4. Discussion

4.1. Sea ice influencing food resource availability and isotopic composition

Sea ice in polar regions is a critical environmental component that indirectly affects dietary patterns in consumers by controlling the timing, magnitude, and distribution of organic carbon that sustains benthic communities (Norkko et al., 2007). In this context, sea ice, together with other abiotic components such as temperature and seafloor depth, is perhaps one of the main abiotic drivers that indirectly influence the isotopic composition of benthic consumers. Our results indicated spatial variability in the $\delta^{13}C$ isotopic composition of food items and epibenthic consumers among three ice area categories (i.e., low, moderate, and high SIC areas). For example, in surface sediments, the most ^{13}C-depleted (less than –28.0‰) occurred in low SIC area in the Beaufort Sea, while the most ^{13}C-enriched (–21.4‰) were registered in moderate-to-high SIC areas in the Baffin Bay. The depletion in ^{13}C values observed in sediments from the Beaufort Sea suggested that the OM they contained was presumably more of terrestrial and/or phytoplanktonic origin rather than from other sources. Further, linear models indicated a significant effect of depth on the $\delta^{15}N$ isotopic composition of sediments and benthic fauna. In contrast, a significant effect of SIC on $\delta^{13}C$ values of consumers was observed, which partially supported the first hypothesis that predicted SIC as an important driver affecting the isotopic composition of both resources and consumers. However, it should be remembered that many interacting biogeochemical and physiological processes (such as temperature, metabolism and remineralization) might also affect changes in the isotopic composition of consumers (Davias et al., 2014).

Moreover, $\delta^{13}C$ values showed the occurrence of different trophic pathways, among which benthic fauna was sustained mainly by a mix of sea-ice algae and phytoplankton sources, where according to Stein and Macdonald (2004) the conbined $\delta^{13}C$ values of both sources commonly range from –19.0 to –24.0‰. Macroinvertebrate ^{13}C composition also revealed a wide range of isotopically different resources ingested by the benthos, suggesting fluctuations of benthic diets in response to prey availability. For example, as suggested for benthos in the Beaufort Sea by Bell et al. (2016), primary consumers in low SIC areas had the most ^{13}C-depleted average in isotopic composition, which implies that consumers primarily relied on phytoplankton or terrestrial sources. In contrast, primary consumers in high SIC areas had the most ^{13}C-enriched average in isotopic composition, suggesting a greater reliance on ice-derived carbon and/or the consumption of alternative sources, including reworked organic material by sedimentary microbial communities (Iken et al., 2005; Mäkelä et al., 2017). The diet of benthic fauna must also include additional OM contributions from other sources of which we have no records in the current study, particularly when these species were collected across environments with different characteristics (e.g., near the coast or rivers, offshore). For instance, in Arctic fjords and deep waters close to shore, macroalgal detritus ($\delta^{13}C$ values range from –13.6 to –28.0‰) have been shown to be a considerable input of OM supporting and influencing benthic communities and food web structure at different depths (Dunton and Schell, 1987; Renaud et al., 2015; Vilas et al., 2020). Our findings also highlighted that depth was the most important environmental driver influencing the $\delta^{15}N$ isotopic composition of both sediment and epibenthic consumers. These results align with previous studies that denoted a similar pattern of the influence of depth on $\delta^{15}N$ values, with tendencies of increasing ^{15}N in benthic fauna as a function of depth (e.g., Roy et al., 2015; Stasko et al., 2018b). However, with depth, some benthic species (e.g., *Ophiocten sericeum* and *Ophiura robusta*) showed ^{15}N-depleted values, suggesting that depletion in ^{15}N could also vary in function of prey $\delta^{13}C$ composition, microbial-driven factors, and turnover rates. Some limitations were detected in the present study. For example, using a single biomarker (i.e., SIA) in our analyses did not allow a high resolution in the interpretation of the results, such as changes in the faunal diet due to overlapping carbon isotope values (e.g., phytoplankton vs. ice algae) of resources. A combination of different biomarkers (e.g., fatty acids, highly branched isoprenoids) in future studies would be ideal to have better answers regarding the response of benthic fauna and food webs to changes in resource supply and environmental conditions.

4.2. Epibenthic food web characteristics across ice areas categories

Sea ice has also been documented as an important component of the Arctic Ocean, influencing degrees of connectivity between the benthic and the pelagic habitats, trophic interactions, nutrient cascades, and, therefore, food web structure (Post, 2017; Post et al., 2000). Likewise, sea ice dynamics may be closely related to the seasonality and availability of prey resources, which may influence the degrees of competition and variability in dietary and foraging patterns of specialization among species (Araújo et al., 2011; Costa-Pereira et al., 2019). In agreement with our second hypothesis, community-wide niche metrics showed bidimensional niche variation of the benthic community across ice areas. A broader niche was interestingly associated with moderate SIC areas, whereas a reduction in niche breadth was linked to low and high SIC areas (Figure 4). Our results agree with previous studies highlighting a similar pattern in benthic food web structure linked to differences in sea-ice cover in the Arctic (Yunda-Guarin et al., 2020) and the Southern Ocean (e.g., Michel et al., 2019; Norkko et al., 2007). These studies suggested that a greater reliance of benthic invertebrates on sympagic algae in regions with high ice cover might result in a reduction of the trophic niche size of benthic communities. In this context, a limited $\delta^{13}C$ dispersion suggested homogeneity of resources and/or the use of a narrow range of OM sources by consumers. In contrast, a broad $\delta^{13}C$ dispersion indicated a higher heterogeneity in basal food sources and/or the use of food items with a greater difference in $\delta^{13}C$ isotopic composition (Wang et al., 2020). Similarly, when comparing the isotopic niche structure across epibenthic groups, primary TL consumers and omnivores showed a similar trend to those observed for the entire community, exhibiting narrow $\delta^{13}C$ ranges associated with ice areas with low and high SIC (Figure 4). Hence, reductions in isotopic niche width observed in systems with less diversity of prey could be related to high feeding selectivity or low dietary evenness of consumers over time (Bearhop et al., 2004; Costa-Pereira et al., 2019; Yunda-Guarin et al., 2022). Instead, a broader niche width observed in systems with a greater diversity of prey suggested an increase in the number of species with intraspecific inclinations toward a broad spectrum of diets or foraging behaviours (Bearhop et al., 2004; Yunda-Guarin et al., 2022).

Niche metrics also showed variations in the food web length, highlighting a broader $\delta^{15}N$ dispersion associated with ice areas with moderate SIC and a shorter food web (i.e., shorter chain length) linked to ice areas with low and high SIC (Figure 4). Previous studies suggested that food web lengths are influenced mainly by the amount of energy exchanges between trophic levels, which are controlled by ecosystem size (i.e., ecosystem dimensions in area or volume), productivity, biotic interactions, and disturbance events such as trawling (Post et al., 2000; Post, 2007; Takimoto et al., 2012; Ward and McCann, 2017). Hence, in natural communities of the Arctic Ocean, dynamics in the flux of energy and matter may differ in space and time, influencing the benthic food web topology (Post, 2017). Thus, in response to the availability of resources, weak energy fluxes induced longer food webs, while strong energy fluxes favoured shorter food webs (Ward and McCann, 2017). However, according to differences in organic matter input, benthic groups were affected differently by the effect of energy cascades through the trophic levels, with omnivorous and high consumers showing a reduction in the width of their isotopic niche (Table 4; Figure 4). Likewise variations in the food web length of the benthic community may also reflect changes in the isotopic composition of resources related to alterations in the biochemical characteristics of the organic matter due to abiotic degradation processes (Rontani et al., 2016). As a result, distinct stages of degradation of sinking OM particles should occur based on the origin of the resources (e.g., ice algae vs. phytoplankton), residence period time in the water column, and potential ingestion-excretion by zooplankton.

4.3. Ecosystem productivity variability and changes in the isotopic niche size

Based on Hutchinson's original conceptualization of the 'fundamental niche' (Hutchinson, 1957), a novel approach supported the idea that high ecosystem productivity is correlated to small niche size and limited niche overlap (Lesser et al., 2020). On this basis, we hypothesized a similar trend in the isotopic ecology of the benthic community, predicting small niches associated with highly productive areas (i.e., polynyas with low SIC). We also examined variations in the isotopic niche size between polynya's ecosystems, predicting the narrowest niche associated with the most productive polynya (i.e., NOW). Standard ellipse areas supported our second hypothesis, highlighting a reduction in the isotopic niche size of the benthic community associated with ecosystems with high primary production. However, these metrics also revealed a narrow niche associated with ice areas with high SIC (Figure 4), despite being less productive than the polynyas (primary production in BB range from 60 to 120 g C m^{-2} y^{-1}; Stein and Macdonald, 2004). Our results suggested that changes in the availability and diversity of resources (i.e., isotopically distinct prey items available for consumption) might be an important factor influencing the strength of species interactions, feeding strategies, species-specific dietary specialization, and thus isotopic niche sizes. Previous research suggested that productive regions might result in numerous species feeding on a specific seasonal carbon source, causing an increase in herbivorous behaviours of benthic omnivores (Evans et al., 2005; Michel et al., 2019). Hence, narrow niches linked with productive ice areas in this study could be connected to an increase in the number of species with comparable feeding strategies that use a limited range of resources. On the contrary in less productive regions, a greater breadth of the niche could be related to an increase in the predation pressure across trophic levels, the consumption of a broader range of prey items, or a high degree of species-specific dietary specialization (Robinson and Strauss, 2020; Yunda-Guarin et al., 2022). The observed variation in niche size of benthic communities among ice areas partly supports the interpretation that seasonal ecosystem productivity and species interactions are main drivers of niche structure in the present study. However, we could not accurately establish the role of species interactions (e.g., predation pressure, competition) on the trophic niche characteristics.

Regarding the polynyas, our results denoted niche reductions along a west-to-east gradient, exhibiting broader niches associated with CB and VMS-LS-BI polynyas, and a narrow niche associated with NOW (Supplementary Figure S2). Our results are compatible with Mäkelä et al. (2017) who, while studying variations in the benthic food web structure in two polynyas (i.e., NOW and LS), highlighted a shorter food web length associated with the more productive polynya. Variations in the isotopic niche of the polynyas may reflect a seasonal relationship between productivity, pelagic-benthic coupling strength, environmental changes, and fluctuations in the use of resources by consumers (Kędra et al., 2012). For example, the broad niche size in CB polynya could be linked to differences in the use of terrestrial and marine organic resources by consumers along a geographic/depth gradient that affected $\delta^{13}C$ and $\delta^{15}N$ composition in consumers and thus, the trophic niche structure (Bell et al., 2016; Divine et al., 2015; Dunton et al., 1989). Similarly, a broad isotopic niche in the deep LS polynya (789 m) was connected with a greater consumption of reworked organic material by invertebrates that was depleted in ^{13}C (Mäkelä et al., 2017). These results highlighted that niche architecture is extremely dynamic across the Canadian Arctic, varying geographically, with depth and seasonally due to a connection of intrinsic and extrinsic mechanisms that influence the isotopic composition, trophic interactions, and energy fluxes.

4.4. Isotopic diversity and epibenthic niche redundancy

Isotopic diversity indices (IDis, IDiv, and IEve) varied among ice areas (Supplementary Figure S1). IDis and IDiv denoted that the epibenthic community had a wider isotopic dispersion in moderate SIC areas suggesting a diversified use of the ecological niche by epibenthic consumers. However, slight differences in IDis and IDiv values in low and high SIC areas indicated that consumers in these areas have comparable ecological habits. Among ice areas, IEve showed a uniform distribution in the δ-space of consumers, indicating balance within benthic assemblages (i.e., the presence of both herbivores and predators with no tendency for one of these groups to dominate the benthic community). Regardless of seasonal changes in resource availability, a balance in the distribution of consumers in δ-space could highlight the ability of benthos to adapt diets among ice areas and seasons. On this basis, fluctuations in food availability and diversity of prey items could translate into changes in interspecific plasticity in foraging behaviors and a high degree of inter-individual dietary flexibility as a strategy to reduce competition and share available resources efficiently (Yunda-Guarin et al., 2022).

Isotopic uniqueness (IUni) suggested differences in isotopic redundancy of the epibenthic community, highlighting a gradual increase in ecological redundancy from high to low SIC areas. Variations in IUni revealed that the isotopic redundancy of the epibenthic community may fluctuate spatiotemporally even during periods of high seasonal ecosystem productivity. For example, in polynyas, the great availability but low diversity of resources could induce benthic consumers to feed on a narrow spectrum of $\delta^{13}C$ sources, reducing predation and intra- and interspecific competition, promoting the co-occurrence of species and increasing redundancy in the community (Brind'Amour and Dubois, 2013). However, in less productive ecosystems, higher predation and competition may diminish the possibility that benthic fauna specialize in ingesting a narrow range of resources (Comte et al., 2016), thereby reducing the isotopic redundancy. Based on this, changes in prey consumption patterns in response to variations in their abundance and diversity stood out as one of the possible main drivers of isotopic redundancy.

5. Summary

The responses of food webs to extrinsic and intrinsic drivers are still poorly understood for epibenthic communities in the Arctic Ocean. In this study, results highlighted that those variations in food web structure were substantially related to changes in environmental gradients (i.e., SIC and depth), ecosystem productivity, and diversity of food sources (as conceptually summarized in Figure 5). Thus, differences in trophic niche sizes suggested that both isotopic composition and niche architecture could be highly dynamic in the Arctic Ocean. In this sense, our results showed that greater ecosystem productivity may promote niche size reductions by inducing the exploitation of a low range of resources. On the contrary, an increase in niche size and food web length was found in less productive ecosystems that had, however, high diversity of resources. Likewise, the trophic niche characteristics varied as a function of SIC gradients, where an increase in niche size was related to moderate ice areas and a reduction of niche size was associated with low and high ice areas. These results suggested that sea ice is an important environmental component driving food web structure by influencing the abundance, diversity, and availability of resources. Our results also indicated spatial differences in the isotopic redundancy of the epibenthic community among ice areas, underlying a gradual increase in the isotopic redundancy from high to low SIC areas. Differences in isotopic redundancy also reflected that the degree of dietary overlap among taxa has a marked response to variations in environmental characteristics and food inputs. From the perspective of a longer ice-free season in the Arctic Ocean, our results showed a trend of increases in the ecological niche size of epibenthic communities, mainly induced by changes in the availability of some resources (e.g., sympagic carbon). More studies using multiple approaches are necessary to conclude more precisely how changes in biological and environmental drivers and their interactions may affect trophic interactions and food web structure.

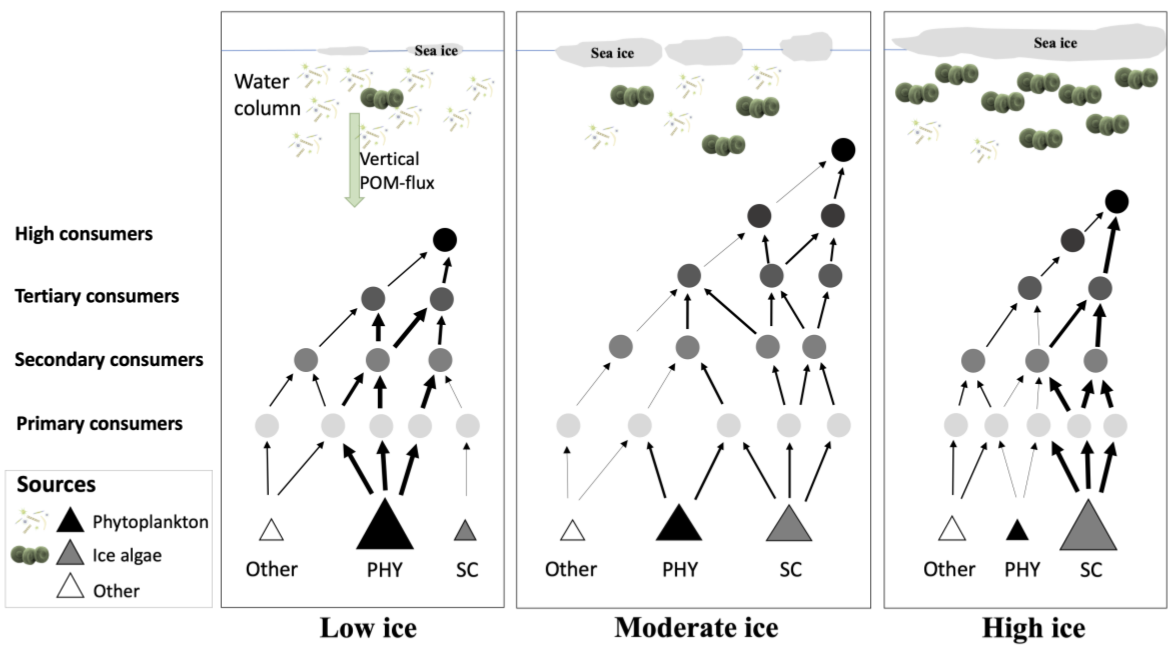

Figure 5. Schematic illustration of the influence of sea-ice concentration (SIC) and organic carbon sources on the food web structure of epibenthic communities. The thickness of the arrows indicates differences in the relative transfer to the next trophic level of each organic resource. The resources: ice-derived algae (sympagic carbon; SC), phytoplankton (PHY), and others (e.g., terrestrial, macroalgal, and microbial) are represented by triangles. The sizes of the triangles represent the relative contribution of SC and PHY sources in sediment and

benthic samples from areas with different SIC (based on Cautain et al., 2022; Koch et al., 2020; Yunda-Guarin et al., 2020). Epibenthic consumers are represented by circles and each gray shade represents a different trophic level.

Acknowledgments

We are grateful to ArcticNet, Natural Sciences and Engineering Research Council of Canada, and the Green Edge project (http://www.greenedgeproject.info) for providing us with the financial resources to make this research possible. We also thank Sentinel North and Québec-Océan for providing financial resources for training purposes. We want to thank the officers and the crew of the Canadian research icebreaker CCGS Amundsen for affording the support and facilities during the oceanographic campaigns of 2011, 2014, and 2016 in the Arctic. We also express our gratitude to Cindy Grant and the sampling team for their great work in the field campaign. Likewise, we thank the research professionals Laure de Montety, Lisa Treau de Coeli, and Caroline Guillemette for the help with the benthos; Geochemistry lab, and Jonathan Gagnon for his help in measuring stable isotope ratios. We are thankful to Université Laval, Takuvik, ArcticNet, and Québec-Océan for their contribution in terms of coordination, equipment, and facilities. The lead author expresses gratitude to Sergio Cortez Ghio for his help and valuable comments about the statistical analyses carried out throughout this investigation. The lead author expresses gratitude to the Institut français de recherche pour l'exploitation de la mer (Ifremer), Bretagne, France, for providing their facilities during the time of the internship in the institute. Finally, the authors would like to thank the reviewers for their fruitful comments on the manuscript.

Competing interests

Authors declare no competing interests.

Author contributions

Contributed to conception and design: GY-G, CN, PA.

Identification and separation of samples: GY-G.

Stable isotope data analyses: GY-G and LNM.

Figures: GY-G.

Writing original draft: GY-G.

Drafted and/or revised this article: GY-G, LNM, VR, NF, MG, CN, PA.

Approved the submitted version for publication: GY-G, LNM, VR, NF, MG, CN, PA.

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Appendices

Supporting Information for “Trophic ecology of epibenthic communities exposed to different sea-ice concentrations across the Canadian Arctic Ocean”

Authors: Gustavo Yunda-Guarin, Loïc N. Michel, Virginie Roy, Noémie Friscourt, Michel Gosselin, Christian Nozais, Philippe Archambault

Supporting Figures

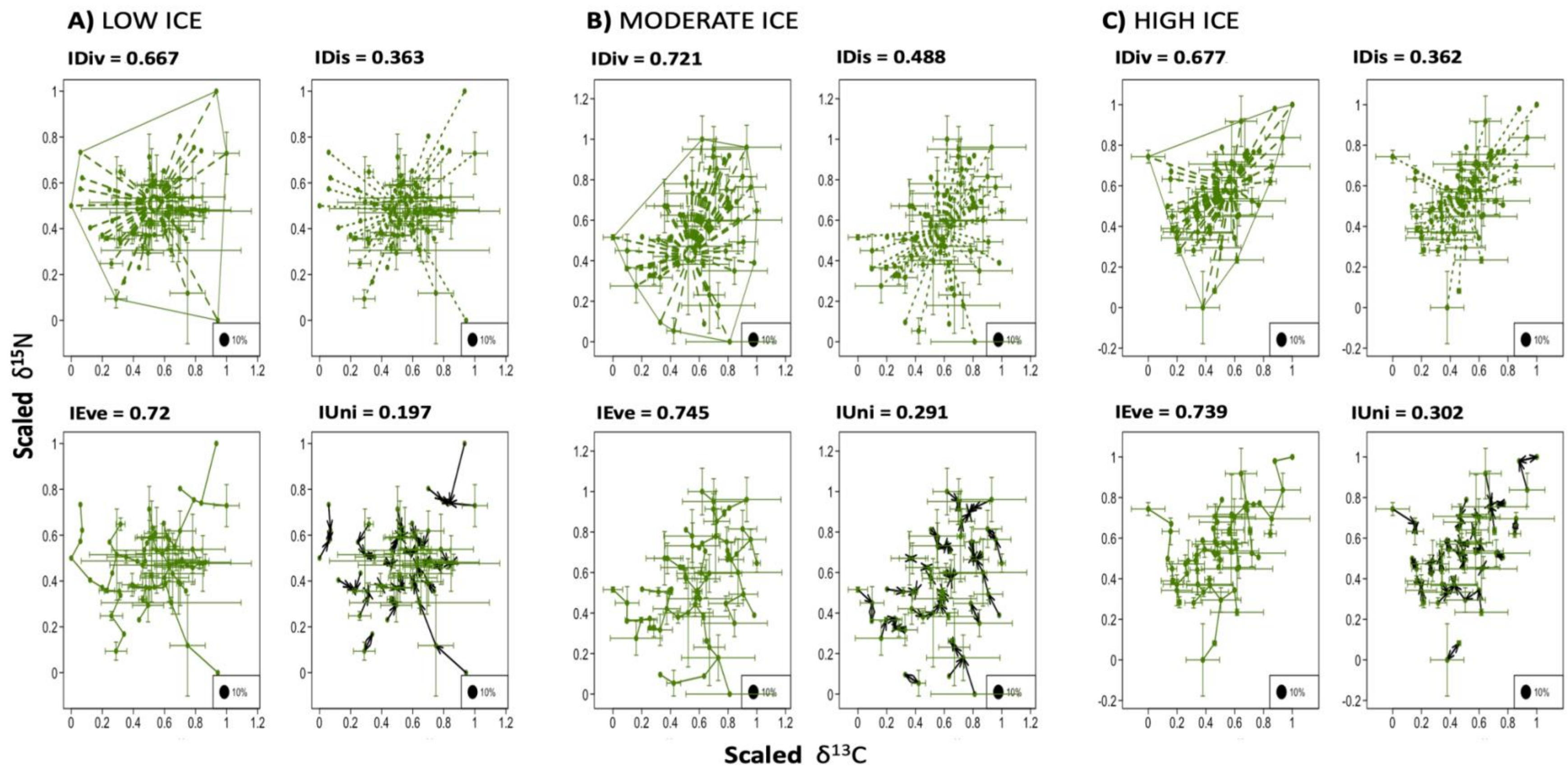

Figure S1. Biplots illustrating the isotopic diversity indices of the whole epibenthic community under contrasting sea-ice conditions. The biplots represent the mean scaled isotopic diversity indices: isotopic divergence (IDiv), dispersion (IDis), evenness (IEve), and uniqueness (IUni) of the whole epibenthic community. Isotope data of epibenthic fauna are shown in areas with different sea-ice concentrations (SIC): A) low ice (≤10% of SIC), B) moderate ice (>10 to 50% of SIC), and C) high ice (>50% of SIC). Isotopic positions of the epibenthic fauna are represented by green dots in each panel. In each area, epibenthic community $\delta^{13}C$ and $\delta^{15}N$ values are scaled between 0 and 1 to account for potentially different isotope variability in basal food resources (Cucherousset and Villéger, 2015).

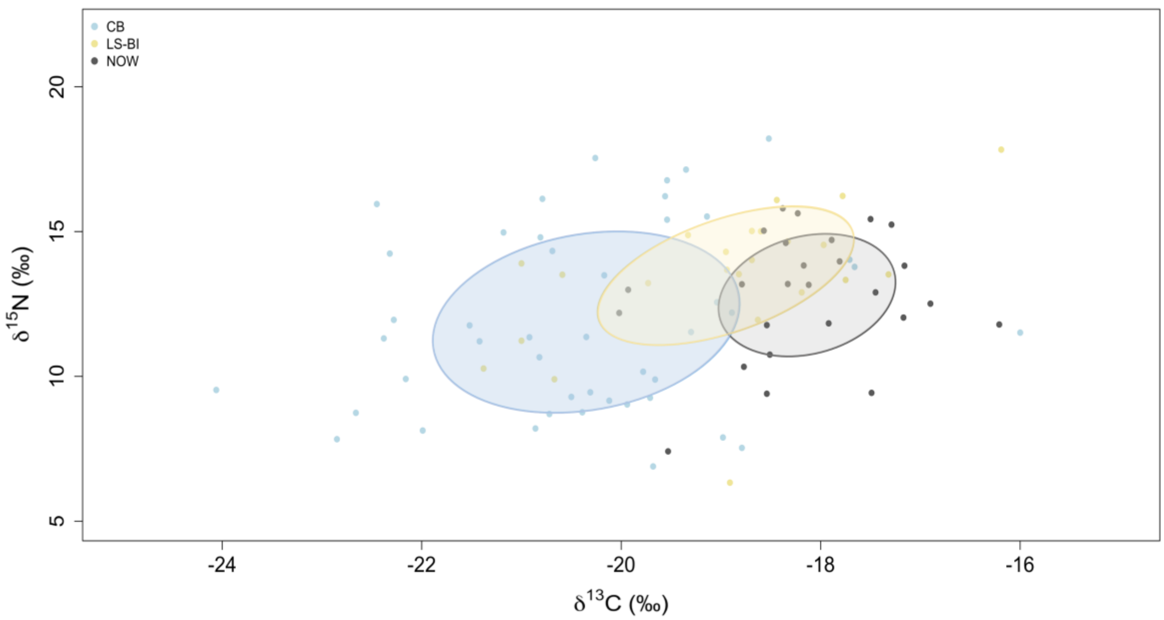

Figure S2. Biplot illustrating the isotopic niche structure of the benthic community between polynyas. The positions occupied by benthic fauna in the isotopic space are represented by dots in each $\delta^{13}C$ - $\delta^{15}N$ biplot. The representation of the ellipses (solid lines) encloses the size-corrected standard ellipses area (SEAc, fits 40% of the data) of the benthic community at A) Cape Bathurst polynya (CB; blue dots), B) Viscount-Melville Sound-Lancaster Sound-Bylot Island polynya (VMS-LS-BI; yellow dots), and C) North Water polynya (NOW; black dots).

Supporting Tables

Table S1. Data set from stations where samples were collected across regions of the Canadian Arctic Ocean.

Station	Region[a]	Sea-ice[b] condition	Water depth (m)	Sampling date[c]	Latitude[d] (N)	Longitude[d] (W)	SIC%[e]	Chl *a*[f] ($\mu g\ g^{-1}$)
W420	CB	Low	35	2011-09-26	71.05	–128.52	0 ± 0.0	5.34
W437	CB	Low	239	2011-09-28	71.83	–126.51	0 ± 0.0	2.58
W438	CB	Low	94	2011-09-29	70.59	–127.61	0 ± 0.0	5.26
W407	CB	Low	408	2011-10-02	71.07	–126.18	0 ± 0.0	2.87
407	CB	Low	392	2014-08-18	71.11	–126.07	0 ± 0.0	1.20
437	CB	Low	318	2014-08-19	71.83	–126.76	0 ± 0.0	0.90
C307	VMS	Low	368	2011-10-08	74.021	–103.062	0 ± 0.0	1.75
E301	LS-BI	Low	665	2011-10-14	74.09	–83.42	2 ± 0.1	36.43
E323	LS-BI	Low	789	2011-10-15	74.15	–80.45	4 ± 0.1	21.31
E115	NOW	Low	647	2011-10-17	76.33	–71.15	3 ± 0.1	12.39
115	NOW	Low	656	2014-07-30	76.58	–71.17	4 ± 0.0	53.00
111	NOW	Low	594	2014-07-31	76.40	–73.26	0 ± 0.0	23.10
101	NOW	Low	360	2014-08-01	76.43	–77.61	9 ± 0.1	2.30
105	NOW	Low	343	2014-08-01	76.47	–75.83	0 ± 0.0	6.50
108	NOW	Low	447	2014-08-01	76.34	–74.72	0 ± 0.0	11.10
C331	CAA	Moderate	113	2011-08-03	74.64	–97.73	40 ± 0.1	4.47
C332	CAA	Moderate	143	2011-08-04	74.60	–96.12	20 ± 0.1	23.32
C310F	CAA	Moderate	165	2011-08-08	71.30	–97.60	43 ± 0.2	2.76
C312A	CAA	Moderate	70	2011-08-09	69.17	–100.76	45 ± 0.2	8.72
C314B	CAA	Moderate	119	2011-10-06	69.00	–106.56	47 ± 0.0	12.40
312	CAA	Moderate	66	2014-08-11	69.24	–100.86	44 ± 0.2	12.80
G418	BB	Moderate	384	2016-06-28	68.11	–57.77	31 ± 0.3	N/A[g]
G503	BB	Moderate	301	2016-06-29	70.00	–57.76	18 ± 0.2	N/A
G615	BB	Moderate	615	2016-07-05	70.50	–59.52	44 ± 0.3	N/A
G703	BB	Moderate	520	2016-07-07	69.50	–58.72	29 ± 0.3	N/A
E150	BB	High	130	2011-08-01	72.74	–79.92	75 ± 0.1	2.13
E160	BB	High	726	2011-08-01	72.67	–78.58	73 ± 0.1	12.83
C314A	CAA	High	109	2011-08-10	69.00	–106.62	58 ± 0.1	7.89
309	CAA	High	335	2014-08-10	73.10	–96.18	73 ± 0.0	2.30
314	CAA	High	84	2014-08-12	69.03	–105.54	54 ± 0.2	7.30
G107	BB	High	403	2016-06-11	68.50	–59.18	82 ± 0.1	N/A
G204	BB	High	445	2016-06-15	68.71	–59.26	79 ± 0.1	N/A
G306b	BB	High	309	2016-06-18	68.99	–58.15	60 ± 0.2	N/A
G309	BB	High	360	2016-06-18	69.00	–58.74	60 ± 0.2	N/A
G507	BB	High	294	2016-06-30	70.01	–59.12	60 ± 0.3	N/A
G512	BB	High	605	2016-07-01	70.00	–60.36	84 ± 0.2	N/A

[a] Regions of sampling collection: Baffin Bay (BB), Canadian Arctic Archipelago (CAA), Cape Bathurst polynya (CB), Viscount-Melville Sound-Lancaster Sound-Bylot Island polynya (VMS-LS-BI), and North Water polynya (NOW).
[b] Sea-ice condition in ice areas: low ice (≤ 10% of SIC), moderate ice (> 10 to 50% of SIC), and high ice (> 50% of SIC).
[c] Sampling date (day/month/year).
[d] Geographic coordinates.
[e] Mean value ± standard deviation (SD) percentage of sea-ice concentration (SIC) for a period of 30 days prior to sampling.
[f] Chl *a* = Chlorophyll *a* in surface sediments.
[g] N/A indicates data not available.

Table S2. Isotopic composition of baseline food sources measured in samples collected at different locations in the Canadian Arctic Ocean.

			Suspended-POM						Sediment-POM		
Region[a]	Station	Sea-ice[b] condition	n[c]	$\delta^{15}N$ (‰)[d] SCM-POM	$\delta^{13}C$ (‰)[e] SCM-POM	n[c]	$\delta^{15}N$ (‰)[d] Bot-POM	$\delta^{13}C$ (‰)[e] Bot-POM	n[c]	$\delta^{15}N$ (‰)[d] Sed-POM	$\delta^{13}C$ (‰)[e] Sed-POM
CB	407	Low	2	4.5 ± 1.0	–25.8 ± 0.0	2	6.3 ± 3.3	–27.1 ± 0.1	2	5.7 ± 1.1	–23.6 ± 0.1
CB	437	Low	2	9.4 ± 0.0	–25.8 ± 0.2	2	7.7 ± 0.7	–28.1 ± 1.7	2	6.5 ± 0.4	–24.8 ± 0.6
CB	W.420	Low	2	5.4 ± 0.5	–27.6 ± 0.0	2	5.4 ± 0.5	–27.6 ± 0.0	3	2.1 ± 0.3	–27.4 ± 0.2
CB	W.437	Low	2	4.7 ± 0.0	–27.4 ± 0.0	0	N/A[f]	N/A	3	5.7 ± 0.5	–24.9 ± 0.3
CB	W.438	Low	2	6.5 ± 0.3	–28.1 ± 0.0	0	N/A	N/A	3	2.1 ± 0.6	–28.3 ± 0.2
CB	W.407	Low	2	6.9 ± 0.2	–25.6 ± 0.2	1	13.3	–28.5	3	6.6 ± 0.3	–25.0 ± 0.1
VMS	C.307	Low	2	6.5 ± 0.9	–25.5 ± 0.1	1	8.5	–31.3	3	7.0 ± 0.4	–22.9 ± 0.2
LS-BI	E.301	Low	2	5.5 ± 0.5	–24.9 ± 0.2	1	7.6	–26.8	3	6.0 ± 0.0	–22.8 ± 0.2
LS-BI	E.323	Low	2	5.5 ± 0.3	–24.2 ± 0.2	2	8.2 ± 0.73	–24.9 ± 0.0	3	6.3 ± 0.1	–23.0 ± 0.1
NOW	115	Low	3	8.4 ± 2.3	–25.5 ± 0.1	4	5.8 ± 2.2	–26.4 ± 1.8	2	5.7 ± 0.8	–22.5 ± 0.6
NOW	111	Low	3	7.5 ± 0.7	–25.7 ± 1.5	2	9.0 ± 0.6	–22.2 ± 1.8	2	6.3 ± 0.4	–22.3 ± 0.3
NOW	101	Low	2	7.6 ± 1.5	–24.0 ± 1.0	3	6.4 ± 0.8	–21.2 ± 3.0	2	5.8 ± 0.2	–22.6 ± 0.0
NOW	105	Low	2	5.9 ± 0.6	–25.0 ± 0.3	0	N/A	N/A	2	4.7 ± 0.3	–22.5 ± 0.6
NOW	108	Low	2	9.4 ± 2.1	–26.0 ± 1.1	0	N/A	N/A	2	5.9 ± 0.1	–22.4 ± 0.1
NOW	E.115	Low	2	5.2 ± 0.1	–27.6 ± 0.1	1	7.3	–26.6	3	5.7 ± 0.4	–23.2 ± 0.2
CAA	C.331	Moderate	2	6.5 ± 3.0	–24.9 ± 0.1	1	7.3	–22.0	3	5.8 ± 0.8	–23.2 ± 0.3
CAA	C.310F	Moderate	2	6.4 ± 0.2	–23.2 ± 0.0	1	7.5	–27.6	3	8.0 ± 1.0	–22.5 ± 0.6
CAA	C.312A	Moderate	2	7.3 ± 0.0	–23.6 ± 0.1	2	7.3 ± 0.1	–23.8 ± 0.3	3	6.4 ± 1.0	–23.1 ± 0.1
CAA	312	Moderate	3	5.5 ± 0.5	–23.5 ± 0.1	2	6.6 ± 0.6	–26.4 ± 1.1	2	6.5 ± 0.1	–23.0 ± 0.1
CAA	C.314B	Moderate	2	4.1 ± 0.1	–26.9 ± 0.2	1	8.6	–27.3	3	8.8 ± 0.5	–23.9 ± 0.1
CAA	C.332	Moderate	2	7.1 ± 0.4	–24.9 ± 0.0	1	6.8	–23.5	3	6.8 ± 0.1	–22.2 ± 0.1
CAA	314	High	2	6.8 ± 1.4	–25.3 ± 2.1	2	6.4 ± 0.0	–26.1 ± 1.0	2	7.2 ± 0.4	–22.1 ± 0.2
CAA	C.314A	High	2	5.6 ± 0.0	–24.8 ± 0.1	2	7.2 ± 0.1	–24.0 ± 0.3	3	7.2 ± 0.3	–23.4 ± 0.1
CAA	309	High	2	6.3 ± 1.2	–29.2 ± 1.2	2	7.2 ± 1.8	–24.8 ± 0.6	2	7.1 ± 0.7	–23.0 ± 0.6
BB	G.418	Moderate	0	N/A	N/A	0	N/A	N/A	1	4.8	–22.6
BB	G.615	Moderate	1	8.5	–20.1	0	N/A	N/A	1	7.4	–21.9
BB	G.107	High	1	6.7	–22.0	0	N/A	N/A	0	N/A	N/A
BB	G.204	High	1	9.1	–21.9	0	N/A	N/A	0	N/A	N/A
BB	G.306b	High	1	10.4	–21.4	0	N/A	N/A	1	5.8	–21.4
BB	E.150	High	1	6.5	–26.1	1	5.0	–24.1	3	6.3 ± 0.6	–24.4 ± 0.7
BB	E.160	High	2	5.8 ± 0.1	–26.2 ± 0.1	1	8.1	–26.9	3	7.2 ± 0.3	–22.8 ± 0.1

[a] Regions of sampling collection: Baffin Bay (BB), Canadian Arctic Archipelago (CAA), Cape Bathurst polynya (CB), Viscount-Melville Sound-Lancaster Sound-Bylot Island polynya (VMS-LS-BI), and North Water polynya (NOW).
[b] Sea-ice condition in ice areas: low ice (≤ 10% of SIC), moderate ice (> 10 to 50% of SIC), and high ice (> 50% of SIC).
[c] Number of total replicates per station and ice areas used for subsurface chlorophyll maximum particulate organic matter (SCM-POM), bottom water particulate organic matter (Bot-POM), and surface sediment particulate organic matter (Sed-POM) for stable isotope analyses.
[d] Mean values ± standard deviation of $\delta^{15}N$ (‰).
[e] Mean values ± standard deviation of $\delta^{13}C$ (‰).
[f] N/A indicates data not available.

Table S3. Benthic epifauna measurements from samples collected in different locations of the Canadian Arctic Ocean in the years 2011, 2014, and 2016.

Taxonomic classification	Consumer groups[a]	Ice area[b]	n[c]	$\delta^{15}N$ (‰)[d]	$\delta^{13}C$ (‰)[e]
Annelida					
Class Polychaeta					
Aglaophamus malmgreni	HC	Low ice	9	14.4 ± 0.8	–17.9 ± 0.3
A. malmgreni	HC	Moderate ice	1	14.5	–16.9
A. malmgreni	HC	High ice	4	16.3 ± 0.9	–17.1 ± 1.6
Amphicteis gunneri	OmC	Low ice	1	12.0	–18.6
Chirimia biceps biceps	HC	Low ice	4	13.9 ± 1.1	–18.8 ± 0.4
Bylgides promamme	OmC	Low ice	1	10.7	–20.8
Eunoe nodosa	HC	Low ice	1	15.0	–18.6
E. nodosa	OmC	Moderate ice	3	12.7 ± 1.7	–19.3 ± 0.6
Harmothoe extenuata	HC	Low ice	2	11.5 ± 0.4	–19.3 ± 0.2
Jasmineira sp.	HC	Low ice	3	15.0 ± 0.6	–21.2 ± 0.4
Laetmonice filicornis	HC	High ice	1	14.9	–18.0
Maldane sp.	HC	Low ice	1	16.8	–19.5
Melinna cristata	HC	Low ice	1	13.5	–18.8
Nephtys incisa	HC	Moderate ice	5	17.5 ± 0.8	–17.6 ± 0.9
N. incisa	HC	High ice	2	17.7 ± 0.8	–16.3 ± 3.5
Nephtys longosetosa	HC	Moderate ice	3	15.0 ± 1.3	–16.5 ± 1.6
Nereis zonata	HC	Low ice	1	11.4	–20.3
Nicomache sp.	HC	Low ice	2	14.7 ± 0.8	–17.9 ± 0.5
Nothria conchylega	HC	Low ice	3	12.4 ± 0.7	–19.4 ± 0.6
Phyllodocidae	HC	Low ice	1	11.9	–22.3
Scoletoma fragilis	HC	Low ice	1	15.8	–18.4
S. fragilis	HC	Moderate ice	3	13.8 ± 0.6	–20.4 ± 0.4
Spio sp.	HC	Moderate ice	2	14.2 ± 0.6	–19.7 ± 0.1
Thelepus cincinnatus	HC	Low ice	3	11.8 ± 0.9	–18.5 ± 0.5
Arthropoda					
Class Malacostraca					
Aega psora	HC	High ice	1	17.0	–19.4
Aegiochus ventrosa	HC	High ice	2	16.3 ± 0.4	–20.6 ± 0.8
Ampelisca macrocephala	PC	Low ice	3	8.1 ± 0.6	–22.0 ± 0.3
Anonyx nugax	HC	Low ice	4	14.8 ± 1.6	–20.8 ± 0.6
A. nugax	HC	Moderate ice	10	15.9 ± 1.3	–19.6 ± 0.9
A. nugax	HC	High ice	3	14.9 ± 0.9	–19.6 ± 0.4
Arctolembos arcticus	PC	Low ice	1	8.7	–22.7
Arcturus baffini	PC	Moderate ice	3	9.3 ± 0.5	–21.9 ± 0.1
Atlantopandalus propinqvus	HC	Moderate ice	1	14.4	–19.7
Boreomysis nobilis	OmC	High ice	6	11.2 ± 0.4	–20.0 ± 0.1
Calathura brachiata	HC	Low ice	1	17.5	–20.3
Diastylis rathkei	PC	Moderate ice	2	5.9 ± 0.0	–15.7 ± 2.0
Epimeria loricata	HC	High ice	1	15.4	–19.6
Eualus gaimardii	HC	Low ice	2	13.5 ± 1.2	–20.2 ± 0.0
Eualus belcheri	HC	Low ice	10	14.8 ± 1.5	–18.7 ± 0.8
Eusirus holmii	HC	High ice	1	14.3	–18.2
Halirages qvadridentatus	PC	Moderate ice	1	9.3	–18.8
Haploops laevis	PC	Low ice	3	7.8 ± 0.1	–22.8 ± 0.3
Hymenodora glacialis	HC	High ice	3	14.4 ± 0.4	–19.1 ± 0.2
Lebbeus polaris	HC	Low ice	1	15.0	–18.7

L. polaris	HC	Moderate ice	5	13.2 ± 0.8	–18.1 ± 0.2
L. polaris	HC	High ice	11	14.3 ± 0.7	–17.3 ± 0.4
Leucothoe uschakovi	HC	Moderate ice	2	14.2 ± 0.3	–17.0 ± 0.0
Pandalus borealis	OmC	Moderate ice	7	12.5 ± 0.7	–18.2 ± 0.2
P. borealis	HC	High ice	2	13.7 ± 0.5	–18.0 ± 0.3
Pandalus montagui	HC	High ice	1	13.8	–19.3
Pontophilus norvegicus	HC	High ice	1	14.6	–17.4
Rhachotropis aculeata	HC	Low ice	1	11.8	–21.5
Sabinea sarsii	HC	High ice	2	15.1 ± 0.3	–17.2 ± 0.1
Sabinea septemcarinata	HC	Low ice	1	15.5	–19.1
S. septemcarinata	HC	Moderate ice	4	17.8 ± 0.9	–18.7 ± 0.2
S. septemcarinata	HC	High ice	1	12.9	–16.1
Saduria sabini	HC	Low ice	1	11.4	–20.9
S. sabini	HC	Moderate ice	1	14.9	–18.1
Sclerocrangon boreas	HC	Low ice	3	17.1 ± 0.4	–19.3 ± 0.4
S. boreas	HC	Moderate ice	2	15.7 ± 0.9	–18.2 ± 0.4
Sclerocrangon ferox	HC	Moderate ice	1	16.9	–17.0
Spirontocaris liljeborgii	OmC	Moderate ice	2	12.6 ± 0.2	–18.3 ± 0.3
S. liljeborgii	HC	High ice	1	13.4	–17.5
Stegocephalus inflatus	HC	Low ice	3	16.0 ± 1.0	–22.5 ± 0.0
Synidotea bicuspida	HC	Low ice	3	11.3 ± 0.3	–22.4 ± 0.1
*Themisto abyssorum**	OmC	Moderate ice	2	11.0 ± 0.3	–20.4 ± 0.5
Class Thecostraca					
Scalpellum sp.	HC	Low ice	1	13.5	–20.6
Bryozoa					
Class Gymnolaemata					
Alcyonidium gelatinosum anderssoni	HC	Low ice	4	14.7 ± 1.9	–18.3 ± 0.8
A. gelatinosum anderssoni	PC	Moderate ice	2	9.8 ± 0.2	–22.5 ± 0.8
A. gelatinosum anderssoni	HC	High ice	1	13.0	–16.2
Alcyonidium sp.	HC	High ice	1	15.5	–17.2
Alcyonidium sp.	HC	Low ice	1	13.3	–17.8
Eucratea loricata	OmC	Low ice	1	9.9	–22.2
Cnidaria					
Class Anthozoa					
Actinauge cristata	OmC	Moderate ice	4	11.7 ± 0.7	–21.1 ± 0.2
A. cristata	OmC	High ice	7	11.7 ± 1.0	–20.7 ± 0.5
Actinostola callosa	OmC	Moderate ice	1	11.1	–20.6
A. callosa	OmC	High ice	2	12.6 ± 0.2	–20.3 ± 0.5
Anemone sp.	HC	Low ice	1	15.2	–17.3
Anemone sp.	HC	Moderate ice	1	15.1	–18.2
Anthoptilum grandiflorum	OmC	Moderate ice	2	12.2 ± 0.2	–21.2 ± 0.5
Bolocera tuediae	HC	Moderate ice	1	13.4	–19.3
B. tuediae	HC	High ice	5	13.5 ± 1.0	–19.3 ± 0.2
Drifa glomerata	HC	High ice	3	13.1 ± 1.1	–19.2 ± 0.8
Liponema multicorne	HC	High ice	2	15.7 ± 0.2	–16.7 ± 0.1
Pitilella grandis	OmC	High ice	4	12.1 ± 1.0	–19.5 ± 1.8
Umbellula sp.	HC	High ice	1	14.3	–20.0
Class Hydrozoa					
Hydrozoa sp.A	PC	Moderate ice	1	9.3	–22.1
Lafoeidae	HC	Low ice	1	13.9	–21.0
Sertulariidae	OmC	Low ice	1	9.5	–24.1
Echinodermata					
Class Asteroidea					
Bathybiaster vexillifer	HC	Moderate ice	2	15.2 ± 0.6	–14.7 ± 0.7
Ceramaster granularis	HC	Moderate ice	3	18.1 ± 1.1	–15.0 ± 0.7

C. granularis	HC	High ice	3	16.1 ± 0.7	–15.3 ± 1.6
Ctenodiscus crispatus	HC	Low ice	13	13.0 ± 1.6	–17.2 ± 1.9
C. crispatus	OmC	Moderate ice	2	12.6 ± 0.3	–16.2 ± 0.7
C. crispatus	HC	High ice	3	13.4 ± 1.0	–16.6 ± 0.6
Henricia sp.	HC	Moderate ice	3	19.5 ± 0.7	–15.1 ± 1.0
Henricia sp.	HC	High ice	2	17.9 ± 0.5	–14.8 ± 1.4
Hippasteria phrygiana	HC	Moderate ice	2	14.7 ± 0.9	–15.4 ± 0.0
Hymenaster pellucidus	HC	Moderate ice	1	14.0	–15.8
Icasterias panopla	HC	High ice	1	13.2	–15.5
Leilaster radians	HC	High ice	1	20.5	–14.8
Leptychaster arcticus	HC	Moderate ice	2	16.2 ± 1.0	–15.5 ± 0.6
Pontaster tenuispinus	PC	Moderate ice	5	10.5 ± 0.2	–17.0 ± 1.2
Pseudarchaster parelii	HC	Moderate ice	1	17.2	–16.8
P. parelii	HC	High ice	1	17.5	–16.3
Psilaster andromeda	HC	Low ice	4	17.8 ± 1.1	–16.2 ± 0.2
Pteraster militaris	HC	High ice	1	20.2	–15.6
Stephanasterias albula	HC	Moderate ice	2	20.3 ± 1.4	–16.8 ± 0.7
S. albula	HC	High ice	2	14.7 ± 0.2	–15.0 ± 0.3
Tremaster mirabilis	HC	Moderate ice	1	19.1	–15.8
Urasterias lincki	HC	Moderate ice	1	17.3	–18.3
U. lincki	HC	High ice	4	15.0 ± 1.2	–18.6 ± 1.0
Class Crinoidea					
Heliometra glacialis	HC	High ice	1	13.4	–18.2
Class Echinoidea					
Strongylocentrotus sp.	OmC	Low ice	4	9.9 ± 1.1	–17.9 ± 1.5
Strongylocentrotus sp.	HC	High ice	3	13.2 ± 1.1	–16.5 ± 2.5
Class Holothuroidea					
Molpadia sp.	OmC	Low ice	3	11.2 ± 0.2	–21.4 ± 0.4
Molpadia sp.	HC	Moderate ice	1	17.1	–15.7
Class Ophiuroidea					
Amphiura sundevalli	OmC	Low ice	1	9.2	–20.1
Gorgonocephalus lamarckii	OmC	Moderate ice	1	12.5	–20.4
G. lamarckii	OmC	High ice	5	11.7 ± 0.8	–18.0 ± 1.2
Gorgonocephalus sp.	HC	Low ice	5	12.9 ± 1.3	–19.2 ± 3.0
Gorgonocephalus sp.	HC	High ice	5	15.5 ± 0.7	–18.8 ± 1.3
Ophiacantha bidentata	HC	Low ice	19	14.5 ± 1.6	–18.9 ± 1.2
O. bidentata	HC	Moderate ice	14	13.5 ± 1.0	–17.9 ± 2.2
O. bidentata	OmC	High ice	9	12.6 ± 0.9	–15.7 ± 1.7
Ophiacantha spectabilis	HC	Moderate ice	4	13.9 ± 0.5	–17.0 ± 1.5
Ophiocten sericeum	OmC	Low ice	12	10.6 ± 2.9	–18.4 ± 1.2
O. sericeum	PC	Moderate ice	12	7.6 ± 1.3	–17.5 ± 2.7
O. sericeum	PC	High ice	5	9.9 ± 0.6	–19.2 ± 0.9
Ophiopholis aculeata	PC	High ice	4	9.7 ± 0.2	–16.5 ± 1.2
Ophiopleura borealis	HC	Low ice	27	13.9 ± 1.4	–17.2 ± 1.1
O. borealis	HC	Moderate ice	2	13.2 ± 2.0	–15.3 ± 2.0
O. borealis	HC	High ice	6	13.8 ± 1.1	–18.0 ± 0.5
Ophiopus arcticus	PC	Moderate ice	6	10.3 ± 0.1	–17.8 ± 1.3
Ophioscolex glacialis	HC	Low ice	2	12.9 ± 0.0	–19.8 ± 0.1
O. glacialis	OmC	High ice	1	12.2	–18.8
Ophiura robusta	PC	Low ice	5	7.7 ± 1.3	–19.1 ± 0.8
O. robusta	PC	Moderate ice	7	7.9 ± 1.2	–16.9 ± 2.1
O. robusta	PC	High ice	6	6.9 ± 0.5	–16.9 ± 1.5
Ophiura sarsii	HC	Low ice	3	12.9 ± 1.1	–17.4 ± 0.1
O. sarsii	PC	Moderate ice	1	10.1	–13.5
O. sarsii	PC	High ice	6	10.3 ± 0.9	–17.1 ± 2.2
Stegophiura nodosa	OmC	Low ice	3	9.3 ± 0.3	–19.7 ± 0.3

Mollusca					
Class Bivalvia					
Astarte borealis	OmC	Low ice	3	9.7 ± 0.6	–18.3 ± 1.3
Astarte crenata	HC	Low ice	10	16.2 ± 1.0	–17.8 ± 0.6
A. crenata	HC	Moderate ice	7	15.3 ± 1.5	–19.0 ± 1.9
A. crenata	HC	High ice	5	17.4 ± 3.2	–17.3 ± 1.6
Astarte montagui	HC	Low ice	16	15.2 ± 2.2	–19.4 ± 1.3
A. montagui	HC	Moderate ice	6	13.5 ± 1.6	–19.5 ± 1.4
A. montagui	HC	High ice	4	17.7 ± 3.6	–16.4 ± 2.9
Bathyarca glacialis	HC	Low ice	8	13.7 ± 1.0	–18.7 ± 1.1
B. glacialis	OmC	Moderate ice	8	11.3 ± 0.5	–21.2 ± 0.6
B. glacialis	OmC	High ice	5	12.7 ± 3.0	–19.4 ± 1.3
Bathyarca sp.	HC	Low ice	5	13.2 ± 0.3	–19.8 ± 0.7
Bathyarca sp.	OmC	Moderate ice	3	11.5 ± 0.4	–20.8 ± 0.2
Bathyarca sp.	HC	High ice	4	14.4 ± 2.3	–18.5 ± 0.7
Ciliatocardium ciliatum	OmC	Low ice	8	9.5 ± 1.0	–19.7 ± 1.1
Cuspidaria glacialis	HC	Low ice	6	15.5 ± 0.7	–20.1 ± 0.9
C. glacialis	HC	Moderate ice	2	14.4 ± 0.4	–19.2 ± 0.2
Ennucula tenuis	HC	Low ice	12	12.1 ± 2.2	–18.0 ± 1.9
E. tenuis	HC	High ice	3	13.4 ± 0.1	–18.6 ± 0.6
Hiatella arctica	OmC	Low ice	3	9.9 ± 0.5	–19.7 ± 0.8
H. arctica	PC	High ice	4	9.5 ± 0.3	–20.5 ± 0.4
Liocyma fluctuosa	PC	Low ice	1	8.2	–20.9
Macoma calcarea	OmC	Low ice	2	9.0 ± 0.3	–19.9 ± 0.4
M. calcarea	PC	Moderate ice	3	9.6 ± 0.3	–17.9 ± 0.4
Megayoldia sp.	PC	Low ice	8	7.4 ± 0.5	–19.5 ± 0.4
Musculus discors	PC	Low ice	2	8.8 ± 0.2	–20.4 ± 0.1
Musculus niger	OmC	Low ice	2	10.7 ± 0.8	–18.5 ± 0.6
Nuculana pernula	OmC	Low ice	3	9.5 ± 0.4	–20.3 ± 0.5
N. pernula	OmC	Moderate ice	4	11.4 ± 3.3	–20.0 ± 1.2
Similipecten greenlandicus	PC	Moderate ice	4	10.4 ± 0.9	–21.3 ± 0.6
S. greenlandicus	OmC	High ice	4	10.7 ± 0.3	–21.3 ± 0.3
Yoldia hyperborea	OmC	Low ice	3	9.3 ± 0.4	–20.5 ± 0.3
Y. hyperborea	PC	Moderate ice	3	9.7 ± 0.1	–19.2 ± 0.2
Yoldiella lenticula	PC	Moderate ice	1	7.0	–16.9
Class Caudofoveata					
Chaetodermatida	PC	Low ice	1	7.9	–19.0
Class Cephalopoda					
Bathypolypus bairdii	HC	Moderate ice	2	14.9 ± 1.3	–19.0 ± 0.8
Rossia megaptera	HC	Moderate ice	2	13.2 ± 0.2	–19.4 ± 0.1
R. megaptera	HC	High ice	3	14.0 ± 0.6	–19.5 ± 0.5
Class Gastropoda					
Boreoscala sp.	HC	Moderate ice	1	13.5	–18.1
Buccinum sp.	HC	Low ice	1	13.2	–18.1
Buccinum sp.	HC	Moderate ice	1	14.9	–17.8
Buccinum sp.	HC	High ice	1	16.2	–17.9
Calliostoma occidentale	HC	Moderate ice	2	13.7 ± 0.4	–18.9 ± 0.0
Class Polyplacophora					
Hanleya hanleyi	HC	Moderate ice	2	13.6 ± 0.4	–15.7 ± 0.8
Stenosemus albus	OmC	High ice	2	11.8 ± 0.2	–17.8 ± 0.2
Nemertea					
Nemertina sp.	HC	Moderate ice	1	15.1	–16.7
Porifera					
Class Demospongiae					
Geodia barretti	PC	High ice	2	8.5 ± 0.2	–18.3 ± 0.2

Geodia macandrewii	PC	Moderate ice	5	8.8 ± 0.8	–18.2 ± 0.3
Polymastia hemisphaerica	HC	Moderate ice	1	16.9	–18.6
P. hemisphaerica	HC	High ice	1	17.0	–17.9
Polymastia sp.	HC	Moderate ice	2	15.7 ± 2.2	–16.9 ± 0.6
Polymastia sp.	HC	High ice	1	17.4	–16.6
Porifera sp. A	HC	High ice	3	14.6 ± 0.6	–18.7 ± 0.4
Tentorium semisuberites	HC	High ice	1	17.4	–17.9
Thenea muricata	HC	High ice	2	16.2 ± 0.3	–18.5 ± 0.1

[a] Consumer groups: primary TL consumers (PC), omnivorous consumers (OmC), and high TL consumers (HC).
[b] Sea-ice condition in ice areas: low ice (≤ 10% of SIC), moderate ice (> 10 to 50% of SIC), and high ice (> 50% of SIC).
[c] Number of total replicates per taxon and ice areas used for stable isotope analyses.
[d] Mean values ± standard deviation of $\delta^{15}N$ (‰).
[e] Mean values ± standard deviation of $\delta^{13}C$ (‰).
[*] *Themisto abyssorum*, a species considered pelagic, was included in the analyses because it was present among our benthic samples.

Table S4. Results of the quantitative community-wide niche metrics of the whole epibenthic communities and epibenthic trophic groups (high consumers, omnivorous consumers, primary consumers) under contrasting sea-ice conditions.

Metric	**Ice area[a]**		
***Standard ellipse metrics* (‰^{2})**	**Low ice**	**Moderate ice**	**High ice**
Whole epibenthic community			
Ellipse area (TA)	56.00	76.35	55.71
Standard ellipse area (SEAb)	12.68	18.26	12.30
Standard ellipse area core (SEAc)	12.87	18.54	12.51
Epibenthic trophic group			
High TL consumers			
Ellipse area (TA)	37.68	33.67	30.83
Standard ellipse area (SEAb)	8.55	8.52	8.73
Standard ellipse area core (SEAc)	8.75	8.72	8.91
Omnivorous consumers			
Ellipse area (TA)	8.63	10.59	6.81
Standard ellipse area (SEAb)	3.12	4.26	2.67
Standard ellipse area core (SEAc)	3.28	4.54	2.84
Primary TL consumers			
Ellipse area (TA)	7.27	21.52	9.25
Standard ellipse area (SEAb)	3.09	9.40	6.96
Standard ellipse area core (SEAc)	3.33	10.08	8.12

[a] Sea-ice concentration (SIC) across ice areas: low ice (≤10% of SIC), moderate ice (>10 to 50% of SIC), and high ice (>50% of SIC).