

# **Environmental gradients shape community composition, energy pathways, and trophic dynamics in a coastal Arctic food web**

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# co-senior

Open Research Statement: Data collected during this study are not yet publicly available. Upon acceptance of the manuscript, all data will be permanently archived in the Fisheries and Oceans Canada Open Science Data portal and a link will be provided.

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**Abstract:**

A central question in ecology is how environmental heterogeneity structures community composition and trophic organization, and whether changes in physical conditions alter energy pathways without changing overall network connectivity. Arctic food webs have generally been quantified at broader spatial scales which must average spatial heterogeneity, limiting the ability to quantify asymmetric ecosystem responses to climate- and anthropogenic-driven change at local scales. Resolving entire food webs at finer spatial scales is therefore essential to identify mechanisms linking environmental gradients to community, composition, energy flow and trophic structure. Here, we use Qikiqtait, Nunavut, Canada to characterize a coastal Arctic marine food web by integrating biotracers, DNA metabarcoding, community metrics, and network analysis across >110 species and >1200 samples, from invertebrates to marine mammals. We identified consistent north–south gradients in temperature, salinity, and primary production, with warmer, fresher, phytoplankton-dominated waters in the south and colder, more saline conditions in the north. These gradients were reflected consistently across community composition and trophic dynamics. Northern food webs exhibited higher fish species richness and stronger reliance on ice-derived carbon. Southern food webs were dominated by brittle stars and Arctic cod (*Boreogadus saida*), with greater pelagic contributions to energy pathways. Spatial differences in trophic position were most pronounced among sessile invertebrates, echinoderms, and decapods, reflecting shifts in trophic roles. Although overall food web connectance was similar across regions, species mediating energy flow north of the islands were benthic, whereas both benthic and pelagic species were central in the south. These results demonstrate that fine-scale environmental heterogeneity can reorganize energy pathways and trophic roles without altering overall network structure. In the rapidly warming Arctic, where sea ice loss and altered hydrology are increasing spatial heterogeneity, such

localized responses are likely to generate asymmetric ecosystem change. By resolving food web structure in detail at one location, this study provides mechanistic insight into how climate- and anthropogenic-driven change may propagate through Arctic marine ecosystems and informs broader predictions of ecosystem reorganization.

## 1. Introduction

Food webs describe feeding relationships and how energy and nutrients are transferred in an ecosystem, from primary producers to top predators (Lindeman, 1942; Smith & Smith, 2009). Organisms in a food web can be grouped into trophospecies, sets of species with similar predators and prey, that form functional units linked by energy flow and carbon sources (Kortsch et al., 2015; Paine, 1980; Stouffer & Bascompte, 2011). The number and strength of trophic links (i.e., topology) reflect both food web structure and function and are shaped by numerous factors such as heterogeneity in environmental conditions, species richness, productivity and resource availability, competition, and the balance of generalist and specialist interactions throughout the ecosystem (Kortsch et al., 2019; Stouffer & Bascompte, 2011; Vander Zanden & Rasmussen, 1996). This balance is composed of both strong and weak interactions, with generalist species typically contributing more weak links and specialist species maintaining stronger links that depend on fewer prey species (Bartley et al., 2019; Bascompte et al., 2005; Kortsch et al., 2015). Changes to these interaction strengths can cascade through multiple trophic levels, altering community composition, predatory-prey dynamics, and ecosystem stability (Emblemsvåg et al., 2022; Frank et al., 2005; Paine, 1980; Yurkowski et al., 2017). The structure (i.e., topology) and function (i.e., interaction strength) of food webs are also shaped by their responses to environmental variation, wherein anthropogenic processes such as climate change are altering species interactions and food

web structure across ecosystems globally (Bartley et al., 2019; Fossheim et al., 2015; Kortsch et al., 2019; Tews et al., 2004; Ward et al., 2025).

Arctic marine ecosystems are warming nearly four times faster than the global average, leading to declines in sea ice extent, thinner ice, longer ice-free seasons, and increased pelagic primary production (Arrigo et al., 2008; Hoegh-Guldberg & Bruno, 2010; Johannessen et al., 1999; Rantanen et al., 2022). These changes are causing changes in environmental heterogeneity that drive shifts in species distributions, community composition, and food web structure (Frainer et al., 2017; Kortsch et al., 2019). Loss of sea ice has facilitated the expansion of temperate-associated generalist species into Arctic waters, increasing omnivory and weakening formerly strong, specialized interactions (Fossheim et al., 2015; Kortsch et al., 2015). For example, Emblemsvåg et al. (2022) found that in the East Greenland shelf ecosystem, atmospheric warming, sea ice loss, and variability in sea surface conditions created suitable habitat for Atlantic cod (*Gadus morhua*). As a large, opportunistic, generalist apex predator, the increasing dominance of cod has reorganized the demersal fish community by reducing species richness, increasing predation on endemic Arctic species, and disrupting specialized predator-prey interactions. These changing species distributions are influencing interspecific interactions within Arctic systems and rerouting energy and carbon flows, resulting in community-wide reorganizations and rewiring of the Arctic food web (Bartley et al., 2019; Fossheim et al., 2015; Frainer et al., 2017).

A key feature of Arctic productivity is ice algae, which detaches from the underside of the ice in spring and sinks to the seafloor, providing an early, nutrient-rich food source for benthic communities (North et al., 2014; Renaud et al., 2007), in turn, supporting rapid feeding and post-winter growth. Furthermore, ice algae may be preferentially consumed by some benthic organisms over pelagic phytoplankton (McMahon et al., 2006; North et al., 2014; Renaud et al., 2007). Although the spring melt delivers the primary influx of sympagic

carbon to the ecosystem, the benthic environment also serves as an ice algal carbon bank, storing sympagic carbon in sediments throughout the year and providing an important carbon source for benthic deposit feeders (Koch et al., 2023; Koch et al., 2020; McMahon et al., 2006). Once incorporated by benthic primary consumers, sympagic carbon can be transferred through the food web from benthic primary consumers to higher trophic levels, including habitat coupling mobile consumers and marine mammals (Amiraux et al., 2023; Koch et al., 2021; Yurkowski et al., 2020). As such, shifts in the phenology, quantity, or availability of ice algae may influence the structure and function of Arctic food webs (Niemi et al., 2024). In turn, these climate- and anthropogenic-driven shifts in the structure and function of Arctic marine food webs affect Inuit communities and culture by altering the availability, nutritional quality, and reliability of harvested species from invertebrates to marine mammals, disrupting traditional harvesting practices and migration-based hunting, and increasing reliance on costly market foods (Hoover et al., 2016; Little et al., 2020; Steiner et al., 2021).

Most food web studies in the Arctic have been conducted at broad spatial scales, spanning entire seas or marine regions such as Lancaster Sound (Hobson & Welch, 1992), the Beaufort Sea (Hoover et al., 2022), the Barents Sea (Kortsch et al., 2015) and Hudson Bay (Hoover et al., 2013), typically aggregating data from coarse environmental gradients and areas encompassing thousands of square kilometres (but see Kortsch et al., 2019, Jordan et al., 2024 & Bridier et al., 2021). While valuable to detect regional abiotic-biotic patterns, these broad geographic approaches can lack the resolution needed to capture ecological responses across finer-scale environmental gradients or localized disturbances, such as marine-terminating glaciers retreating to land, hydroelectric developments altering freshwater inputs from individual rivers, and changes in sea ice formation and break-up that locally modify stratification, primary production and benthic-pelagic coupling. Furthermore, Arctic food webs are expected to shift as ice algae decline and pelagic production increases (Kedra

et al., 2015). Finer-scale studies that integrate multiple methods to track carbon sources and trophic dynamics, while accounting for climate- and anthropogenic-driven environmental heterogeneity, are therefore essential to identify trophic mechanisms most sensitive to localized environmental perturbations, and to predict how these fine-scale responses will propagate through energy flows and trophic interactions to reshape the broader food web structure.

The proposed Qikiqtait study area of conservation interest, located around the Belcher Islands in southeastern Hudson Bay, is an important harvesting area for the local community of Sanikiluaq, Nunavut (Figure 1). This system is a unique marine area characterized by strong tidal mixing and relatively cold surface water temperatures, which increase nutrient availability and productivity (Yurkowski et al., 2023). However, climate warming combined with anthropogenically induced changes to freshwater inputs is generating fine-scale (tens to hundreds of kilometres) spatial and temporal environmental heterogeneity between northern and southern Belcher Islands (Eastwood et al., 2020; Heath, 2011; Yurkowski et al., 2023). In particular, hydroelectric developments discharge significantly more freshwater during winter months (Guzzi et al., 2024), resulting in delayed ice formation and strong stratification, especially south of the Belcher Islands (Eastwood et al., 2020), conditions associated with thinner, more variable ice. Consistent with this, ice algal biomass is greater north of the islands (F. Ahmed, pers. comm.), and Inuit hunters in Sanikiluaq describe sea ice as thinner and less predictable (ELOKA [Sanikiluaq Sea Ice Project](#), accessed January 22, 2026). Together, these changes can introduce variability in the timing, magnitude, and distribution of ice-associated primary production and nutrient availability at local spatial scales (Niemi et al., 2024). Therefore, these local contrasts provide an ideal system for understanding how climate- and anthropogenic-driven changes in freshwater inputs and sea ice dynamics can cascade through Arctic marine food webs. Despite increasing evidence of these changes in

Arctic and sub-Arctic ecosystems, most of which has been documented at broad spatial scales (e.g., Hudson Bay-wide; see Pierrejean et al., 2020 and Hoover et al., 2013), our understanding of Arctic coastal community composition and food web dynamics remains limited at the local environmental gradient level. Without this level of detail, it is challenging to identify the underlying mechanisms (i.e., energy transfer, competitive interactions, and benthic-pelagic coupling) that structure Arctic coastal ecosystems and to identify the specific factors that could drive regime shifts (Fisher et al., 2015; Kortsch et al., 2019).

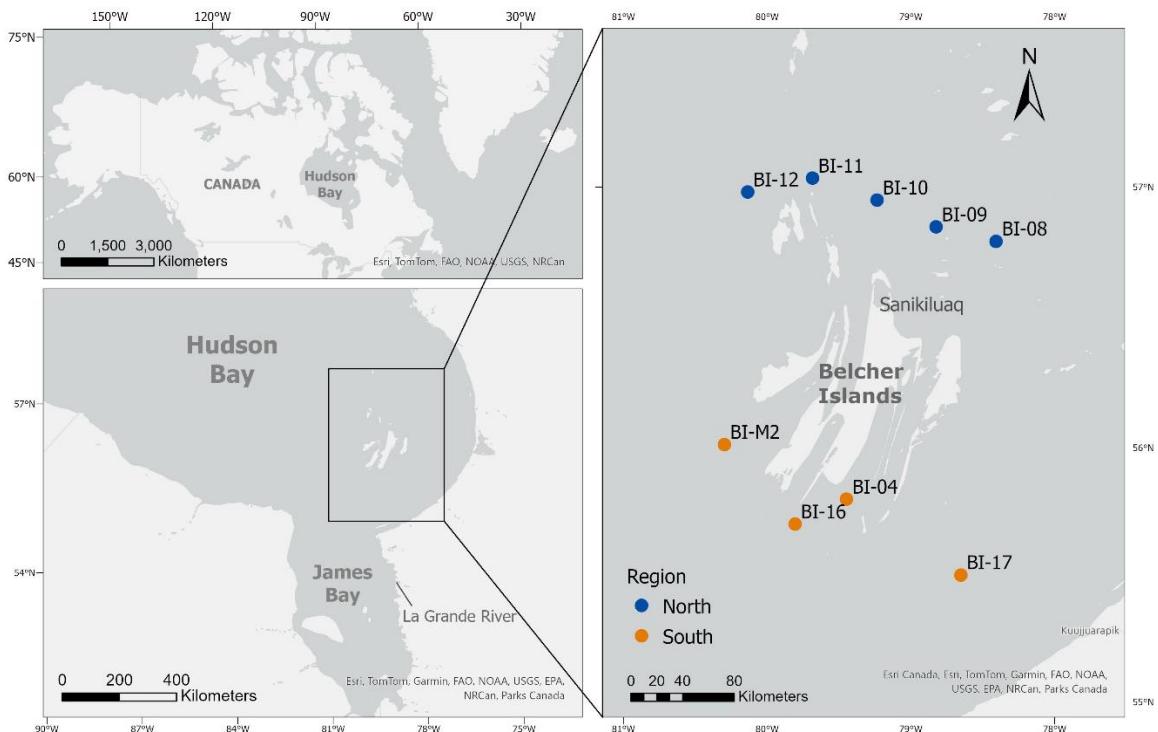
Here, our objective is to examine in depth a single Arctic coastal ecosystem to demonstrate how fine-scale spatial and environmental heterogeneity can shape local differences in food-web structure and function. Specifically, using Qikiqtait, Nunavut as our focal system, we quantify how spatial variation in environmental conditions (water temperature, salinity, FDOM and chlorophyll *a*) structure (1) community composition, (2) carbon source use (ice algae versus phytoplankton), (3) trophic roles, and (4) food web structure across all major taxonomic groups including benthic and pelagic invertebrates, fish, and marine mammals. We applied these metrics using a combination of stable isotopes, highly branched isoprenoids, DNA metabarcoding of stomach contents, and metrics of community composition, including diversity, biomass, and species richness. Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios have been widely applied in ecology to provide insight into carbon sources and habitat use, as well as trophic position (Boecklen et al., 2011), while highly branched isoprenoids have been extensively used across Arctic environments to examine consumer use of ice algae and phytoplankton carbon sources (Brown & Belt, 2012; Koch et al., 2023). EcoDiet is an R package (Hernvann et al., 2022) that combines stable isotope and stomach content data in a Bayesian model to estimate the likelihood of trophic links and the relative contributions of different prey to consumer diets, while accounting for uncertainty (Hernvann et al., 2022). EcoDiet has been applied in temperate and tropical

marine ecosystems, including the Celtic Sea (Hernvann et al., 2020) and the Gulf of Mexico (Chee et al., 2024), but this study is the first to use EcoDiet to examine food web structure in Arctic marine environments. Narrowing the geographical scope enabled us to evaluate key ecological processes that govern the structure and function of the larger marine food web (i.e., energy pathways, trophic roles, community composition, and food-web structure) in relation to localized environmental heterogeneity at a resolution not typically possible in broader surveys. Furthermore, this study offers insights into the mechanisms structuring Arctic coastal ecosystems, which can be applied more broadly to predict ecosystem vulnerability under climate-driven and anthropogenic change.

## 2. Methods

### *Sample collection*

Invertebrate and fish sampling was conducted in southeastern Hudson Bay, around the Belcher Islands, Nunavut, between approximately 80.38 to 78.14°W and from 55.5 to 57.5°N (**Error! Reference source not found.**) in August 2023 aboard the *RV William Kennedy* at nine stations located either north or south of the Belcher Islands.



**Figure 1.** Map of stations sampled. North of the islands and south of the island are blue and orange, respectively, for eastern Hudson Bay and Belcher Islands.

To collect larger zooplankton, a bongo net (two nets, 0.5-m diameter, 500- $\mu\text{m}$  mesh) was towed obliquely at each station for 15 minutes at approximately 2 knots speed-over-ground. The tow line was deployed at  $2 \text{ m s}^{-1}$  to within 10 m of the seafloor and retrieved at  $0.5 \text{ m s}^{-1}$ . Invertebrate and fish samples were sorted into the lowest taxonomic resolution possible and frozen (-20°C). In total, 805 zooplankton individuals from the north and 985 from the south were collected using the bongo net, including gelatinous zooplankton, chaetognaths, euphausiids, mysids, amphipods, pteropods and some decapods. Benthic invertebrates and fish were collected using a 3 m wide Hi-lift beam trawl, towed for 7-15 minutes at ~2 knots speed-over-ground at each station. Over  $\sim 8,566 \text{ m}^2$  in the north, 1,641 benthic invertebrates and 118 fish were collected, and over  $\sim 9,786 \text{ m}^2$  in the south, 3,390 benthic invertebrates and 99 fish were collected (Appendix S1). Benthic invertebrates collected include decapods, amphipods, molluscs, echinoderms, and sessile invertebrates, and fish collected include capelin (*Mallotus villosus*), sandlance (*Ammodytes* sp.), Arctic cod, sculpins (*Triglops murrayi*, *Icelus bicornus*, *Myoxocephalus aenaeus*, *Myoxocephalus quadricornis*), blennies (*Anisarchus medius*, *Stichaeus punctatus*, *Leptoclinus maculatus*, *Lumpenus fabricii*, *Eumesogrammus praecisus*), snailfish (*Liparis fabricii*, *Careproctus reinhardti*), alligatorfish (*Aspidophoroides olrikii*), poachers (*Leptagonus decagonus*), lump suckers (*Eumicrotremus derjugini*), eelpouts (*Lycodes polaris*), and flatfish (*Hippoglossoides platessoides*).

Additional invertebrate and fish samples were collected during coastal sampling efforts using a 1 m wide benthic sled (invertebrates) and gillnets (3-4 in) for pelagic fish. Marine mammal samples, including muscle (ringed seals (*Pusa hispida*): n = 12; bearded seals (*Erignathus barbatus*): n = 7), liver (beluga whales (*Delphinapterus leucas*): n = 20), and stomach (ringed seals: n = 12) samples were collected in 2022 and 2023 from late April to June around the Belcher Islands by Inuit hunters through subsistence harvesting and ongoing community-

based monitoring programs in collaboration between the Sanikiluaq Hunter's and Trapper's Association and Fisheries and Oceans Canada.

Fish and invertebrate samples were shipped to the Freshwater Institute, Fisheries and Oceans Canada, in Winnipeg, Manitoba, where they were taxonomically identified, measured (length and weight) and up to 20 samples per species and per region (north and south) were selected with efforts made to ensure an even distribution across stations, and processed for stable isotope and highly branched isoprenoid analysis. Muscle tissue was subsampled from larger invertebrates, and smaller invertebrates were sampled whole or pooled by species when individual organisms did not provide sufficient material, such as in chaetognaths, small amphipods, and brittle stars. Fish and marine mammals were similarly subsampled for muscle (stable isotopes), liver (highly branched isoprenoids), and stomach contents (fish stomachs preserved in 95% ethanol). The isotopic half-life ranges from weeks to a month in Arctic invertebrates and approximately 1–4 months in fish muscle (Kaufman et al., 2008; Vander Zanden et al., 2015), aligning with the open-water season when captured. For migratory species such as Arctic char (*Salvelinus alpinus*) and beluga whale, liver was used for stable isotope analysis due to its faster isotopic turnover rate (~ several weeks), reflecting a more recent diet (Vander Zanden et al., 2015) when foraging in marine waters around the Belcher Islands. All subsamples were stored in cryovials, freeze-dried (-50°C) for 48–72 hours and homogenized into a fine powder.

#### *Hydrographic data*

Hydrographic profiles were obtained using two identical Seabird 19plus V2 conductivity, temperature, and depth (CTD) sondes, each equipped with Biospherical scalar photosynthetically active radiation (PAR) sensors, Seabird SBE-43 dissolved oxygen sensors, and WetLabs ECO triplet fluorometer sensors for fluorescent dissolved organic matter

(FDOM) and relative chlorophyll *a* concentration (chl *a*), mounted on a rosette. The environmental variables used in this include water temperature (°C), salinity, chl *a* (mg m<sup>-3</sup>) and FDOM (mg m<sup>-3</sup>). To support the interpretation of biological patterns, hydrographic variables were summarized for each station. Average values of the upper 25 metres of the water column were calculated for water temperature, salinity, chl *a*, and FDOM. Regional variation in these parameters were used to contextualize spatial patterns observed in the biological data.

#### *Community composition analysis*

Community composition was assessed for the northern and southern sampling regions using metrics of biomass (g m<sup>-2</sup>), species richness, and diversity, and calculated both across each region as a whole, and within functional groups. Total biomass was calculated for each region and functional group by summing the biomass of all fish and invertebrate taxa collected by benthic beam trawl and normalizing to square meter units (g m<sup>-2</sup>) using the total areas swept by the trawl in each region. In cases where only a portion of a taxon's sample was retained for laboratory analysis (e.g., 1/8 of *Ophiura* brittle stars retained), biomass was corrected to estimate the total biomass for that taxon.

Species richness was defined as the total number of distinct taxa identified in each region and functional group, and community diversity was quantified using the Shannon diversity index (H'); Shannon, 1948), calculated as:

$$H' = - \sum_{i=1}^S p_i \ln (p_i)$$

Where p<sub>i</sub> is the proportional biomass of species i, and S is the total number of species.

Shannon's inverse diversity index was used to estimate the effective number of species (D) in each region and functional group. The resulting value represents the number of equally abundant species required to produce the observed Shannon Diversity, also described as the effective number of species (Hill, 1973; Jost, 2006):

$$D = e^{H'}$$

Diversity metrics were calculated using biomass-based data, which reflects the available energy in an ecosystem and emphasizes the contribution of larger or more ecologically influential taxa (Bambach, 1993; Singh et al., 2025).

#### *Highly branched isoprenoid analysis*

Between 5 and 9 samples of muscle (from invertebrates) and liver (from fish and marine mammals) were selected per species and per region with efforts made to achieve an even distribution across stations, where available, for HBI analysis. Liver was analysed for fish and marine mammals as it stores ~70% of the HBIs in the organism (Brown et al., 2013). In cases where individual organisms did not yield sufficient material, such as in small amphipods or the livers of small fish species such as blennies and sculpins, multiple individuals of the same species and station were combined as a single sample. Ground samples were extracted for HBIs following methods described in Belt et al. (2012), which involve a series of hexane extractions and nitrogen drying steps. Briefly, an internal standard was first added to allow later quantification. Samples were then saponified in a methanolic potassium hydroxide solution, followed by three cycles of hexane addition, vortexing, and centrifugation. The resulting supernatant was dried under a nitrogen ( $N_2$ ) stream, resuspended in hexane and fractionated by column chromatography to isolate non-polar lipid extracts

containing HBIs. The purified, non-polar lipid extracts containing HBIs were then analysed using gas chromatography-mass spectrometry (GC-MS) using a 7890B Gas Chromatograph (Agilent) coupled to a 5977B Mass Selective Detector (Agilent) equipped with a Purged Ultimate Union (Agilent) which facilitates pre-column backflush for analysis.

HBI profiles were used to calculate the H-print for each sample, representing the proportion of phytoplankton-derived HBIs (III) relative to ice algae-derived HBIs (IP<sub>25</sub> and II) (Brown & Belt, 2017):

$$H - print = \frac{III}{\sum IP_{25} + II + III}$$

A higher H-print value indicates a greater reliance on phytoplankton-derived primary carbon sources, whereas a low H-print indicated greater reliance on ice algae-derived primary carbon sources (Brown & Belt, 2017).

H-print values were further used to estimate the proportion of ice algae-derived primary organic carbon (iPOC%) using the equation below (Brown et al., 2018; Kohlbach et al., 2019).

$$iPOC(\%) = 101.8 - 1.02 * H - print$$

In this case, a higher iPOC% reflects greater primary consumption of ice algae-derived primary carbon sources, while a lower iPOC% indicates greater primary consumption of phytoplankton-derived primary carbon sources (Brown et al., 2018). To facilitate interpretation, invertebrates and fish were categorized by taxonomic and foraging traits. Fish were grouped into benthic and benthopelagic functional groups, while invertebrates were categorized as decapods, amphipods, echinoderms, molluscs, sessile invertebrates, and gelatinous zooplankton.

### *Stable isotope analysis*

In total, 1023 invertebrate (n = 578 north; n = 445 south), 177 fish (n = 108 north; n = 69 south), and 39 marine mammal samples were processed for stable isotope analysis which included up to 20 samples of muscle (from invertebrates) and liver (from migratory species like Arctic char and beluga whale) selected per species and per region, where available. Samples for stable isotope analysis were lipid extracted using a 2:1 chloroform:methanol solution, following a modified version of the Bligh and Dyer (1959) method. To prevent bias introduced by inorganic carbon in  $\delta^{13}\text{C}$  signatures, samples rich in calcium carbonate ( $\text{CaCO}_3$ ), such as brittle stars, sea stars, basket stars, feather stars and small crabs sampled whole, were split in half. One-half was acidified with 10% hydrochloric acid (HCl) until effervescence ( $\text{CO}_2$  release) ceased (Cloern et al., 2002; Fry, 1988). Acidified samples were then rinsed three times with Mili-Q water, re-dried and homogenized. The other half remained untreated to avoid acidification bias in  $\delta^{15}\text{N}$  values (Connolly & Schlacher, 2013; Jacob et al., 2005). Of the invertebrate samples, 83 were acidified (n = 11 north; n = 72 south) to remove inorganic carbon.

Homogenized samples were subsampled and analysed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Powdered material was weighed into tin capsules, with invertebrate samples ranging from 800-1000 $\mu\text{g}$ , and fish and marine mammal muscle and liver samples from 400-600 $\mu\text{g}$ . Samples were analysed at the Great Lakes Institute for Environmental Research at the University of Windsor, in Windsor, Ontario using a Delta V Advantage Mass spectrometer (Thermo) coupled to a Costech 4010 Elemental Combustion system and a ConFlo gas interface. Stable isotopes are expressed in per mil (‰) using delta ( $\delta$ ) notation as calculated using the following equation:

$$\delta X = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

Where X is  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  and R is the ratio of heavy to light isotopes ( $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ).

Isotope values are expressed relative to the ratio of international reference standards ( $R_{standard}$ ), which are Vienna PeeDee Belemnite (VPDB) and atmospheric nitrogen (AIR) for carbon and nitrogen, respectively. Values greater than the standard yield positive  $\delta$  values and values below the standard yield negative  $\delta$  values (Kelly, 2000).

Precision was assessed by the standard deviation of replicate analyses of four standards. NIST1577c, internal lab standard (tilapia muscle), USGS 40 and Urea (n=12 for all) measured  $\leq 0.20\text{\textperthousand}$  for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for all the standards. The accuracy, based on the certified values of USGS 40 (n = 12 for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) analysed through runs and not used to normalize samples showed a difference of 0.01 $\text{\textperthousand}$  for  $\delta^{15}\text{N}$  and 0.07 $\text{\textperthousand}$  for  $\delta^{13}\text{C}$  from the certified value. Instrumentation accuracy was verified throughout the analysis using NIST standards 8573, 8547 and 8574 for  $\delta^{15}\text{N}$  and 8542, 8573 and 8574 for  $\delta^{13}\text{C}$  (n = 10 for all). The mean difference from the certified values were 0.16, 0.00 and -0.17 $\text{\textperthousand}$  for  $\delta^{15}\text{N}$  and -0.21, 0.21 and 0.18 $\text{\textperthousand}$  for  $\delta^{13}\text{C}$ .

### *Stomach content analysis*

Stomach content analysis was completed on fish and ringed seal stomachs following the methodology outlined in Darcy et al. (2024), with additional sterilization steps to minimize the risk of cross-contamination between samples. A subset of stomach contents was initially analysed visually. Prey items were identified to the lowest possible taxonomic resolution using field guides (Coad & Reist, 2016; Darcy et al., 2024; Lacasse et al., 2020; Nozères et al., 2014), online photos of species, and dichotomous keys (Klekowski & Węsławski, 1991),

enumerated, and weighed. This method enabled quantification of prey that are more resistant to digestion and thus more likely to be identifiable, such as hard-bodied prey like crustaceans. In contrast, soft-bodied (e.g., worms and jellyfish) and undeveloped, immature prey, are more challenging to identify due to their rapid degradation during digestion and undeveloped morphological features (Carreon-Martinez et al., 2011; Sakaguchi et al., 2017). To overcome these limitations and detect a broader range of dietary items, a DNA metabarcoding approach was used to characterize stomach contents at a finer taxonomic resolution.

For DNA analysis, stomach contents were dried, ground, and homogenized. A subsample of 15 mg, or as much material as was available, of homogenized material per stomach was used for DNA extraction. Extractions were performed using the QIAGEN DNeasy Blood & Tissue extraction kit (QIAGEN, Hilden, Germany) according to the manufacturer's protocol, with an additional step in which 4  $\mu$ l of RNase A (100 mg/ml) was added to each sample and incubated for 2 minutes at room temperature after the lysis stage. Extracted DNA was quantified and normalized to approximately 20 ng  $\mu$ l<sup>-1</sup> where possible. Where sample yields were low, extractions were retained at their original concentration. Samples were then sent to Genome Quebec's Centre d'expertise et de services (Montreal, Quebec, Canada) for DNA metabarcoding.

Metabarcoding was performed using the mICOIintF / jgHCO2198 primer pair targeting the mitochondrial COI gene region (Leray et al., 2013). These primers were originally developed for broad metazoan diversity using barcode libraries derived from marine invertebrates and fish associated with coral reef ecosystems but have since shown success across diverse marine species and regions (Leray et al., 2013; Sevellec et al., 2024; Geilings et al., 2021). Amplicon libraries were prepared using standard protocols for Illumina NextSeq PE300 sequencing (~10M reads +/- 1 reads per run). Bioinformatics processing was

conducted by the Canadian Centre for Computational Genomics (C3G) at McGill University, Montreal, Quebec.

Sequencing data was analysed for variants using C3G's GenPipes ampliconseq pipeline (Bourgey et al., 2019) using the DADA2 sequencing steps to recover single-nucleotide resolved Amplicon Sequence Variants (ASVs) from amplicon data (Callahan et al., 2016). Lastly, taxonomic assignments to the resulting ASVs were made with a naïve Bayesian classifier trained on the CO1Classifier reference database (<https://github.com/terrimporter/CO1Classifier>), which contains over 2,000,000 COI sequences from 236,247 taxa, including 185,389 species, compiled from major public barcode repositories with wide geographic ranges (i.e., GenBank and BOLD; Porter, 2017; Porter & Hajibabaei, 2018). To ensure coverage, the reference database was cross-checked against species captured in trawls around the Belcher Islands, and all species were represented, although some barcodes showed evidence of possible regional variation. ASVs with less than five reads were removed on a sample-by-sample basis.

*Themisto libellula* was the only species identified in the stomachs visually but appeared underrepresented in the metabarcoding results, even to genus and family taxonomic levels. This was likely due to high genetic variability within the genus, including the presence of cryptic species, which may hinder accurate taxonomic assignment (Tempestini et al., 2017). To address this, data from visual stomach content analysis were used to complement the metabarcoding results and confirm *Themisto* presence in relevant samples.

#### *Trophic position analysis*

Trophic positions of consumers around the Belcher Islands were estimated using a one-source model based on  $\delta^{15}\text{N}$  values, following Post (2002). This method estimated trophic position using  $\delta^{15}\text{N}$  values relative to a baseline primary consumer, where one can apply group-

specific trophic discrimination factors (TDFs) to account for physiological and tissue-specific isotopic fractionation (Hussey et al., 2014). Therefore, a scaled trophic position estimation approach was used since tissue discrimination factors (TDF) of consumers typically decrease with increasing prey  $\delta^{15}\text{N}$  values up the food web (Hussey et al., 2014).

$$TP_{consumer} = TP_{baseline} + \frac{\delta^{15}\text{N}_{consumer} - \delta^{15}\text{N}_{baseline}}{TDF}$$

Where  $TP_{consumer}$  is the trophic position of the consumer,  $TP_{baseline}$  is the trophic position of the baseline organism,  $\delta^{15}\text{N}_{consumer}$  and  $\delta^{15}\text{N}_{baseline}$  are the nitrogen isotope values (‰) of the consumer and baseline, respectively, and TDF is the group-specific trophic discrimination factor (‰). The primary baseline for most consumers was an average of several bivalve genera (e.g., *Ciliatocardium*, *Macoma*, *Hiatella*, *Ennucula*, *Chlamys* and *Mytilus*), with a mean  $\delta^{15}\text{N}$  value of 7.72‰ and were assigned a trophic position of 2. Bivalves consume microalgae, organic matter and detritus and are therefore appropriate representatives of primary consumers in this system. For ringed seals, bearded seals, and beluga whales with a primarily piscivorous diet at the time of sampling, we used Arctic cod as the baseline, with a mean  $\delta^{15}\text{N}$  value of 14.96‰ and a mean estimated TP of 3.97. This reflects the known importance of Arctic cod in the diets of these predators (Matley et al., 2015; Watt & Ferguson, 2015; Young et al., 2010), and accounts for TDF variability in consumers relative to prey  $\delta^{15}\text{N}$  (Hesslein et al., 1991).

A diet-tissue discrimination factor of 3.40‰ was used for invertebrates (Minagawa & Wada, 1984; Post, 2002). For fish, TDFs of 3.67‰ and 2.80‰ were used for muscle and Arctic char liver, respectively (Canseco et al., 2022; Caut et al., 2009; McCutchan et al., 2003). The muscle and liver diet discrimination factors used to estimate trophic position of

marine mammals were 2.4‰ and 3.1‰ for ringed and bearded seal muscle, and beluga whale liver, respectively (Caut et al., 2009; Hobson et al., 1996; McCutchan et al., 2003).

### *Food web modelling*

The EcoDiet statistical model was applied to integrate stable isotope data with presence/absence data from visual and metabarcoding analyses of stomach contents. The R package EcoDiet version 2.0.1 uses a Bayesian approach to estimate both the probability of trophic links and diet proportions of each consumer or consumer group (Hernvann et al., 2022). Uniform priors were used where stomach content data updated the prior information on food web topology and stable isotope data updated the prior information on diet proportion. The model runs in JAGS and uses Monte Carlo Markov Chain sampling to generate posterior distributions (Hernvann et al., 2022). Only a single set of trophic discrimination factors could be applied within EcoDiet for all species, and we therefore chose 3.4‰ for  $\delta^{15}\text{N}$  and 0.8‰ for  $\delta^{13}\text{C}$  based on these values being commonly applied in stable isotope ecological literature and representing averages across numerous taxa (Minagawa & Wada, 1984; Post, 2002). To ensure sufficient sample sizes for EcoDiet modelling, fish taxa were aggregated to the family level or to broader classifications where metabarcoding did not allow resolution to family, while invertebrates were grouped at the order level or higher depending on taxonomic resolution. Data were grouped in this way because the dataset comprised a manageable number of fish families with adequate sample representation for the model, whereas prey diversity was much higher, and grouping them below order would have resulted in too many categories with limited data and singularities. To support the north-south comparison, migratory species such as Arctic char and marine mammals were excluded from the analysis because of their high mobility and ability to travel between northern and southern parts of the Belcher Islands.

The igraph version 2.1.4 and NetIndices version 1.4.4.1 packages in R were used to calculate a suite of structural food web metrics, including taxa richness, number of trophic links, average link density, connectance, in-degree, out-degree and betweenness (see Table 1 for definitions). Taxonomic richness, number of trophic links, link density and connectance were calculated at the network level, while out-degree, in-degree and betweenness were calculated for consumer nodes.

#### *Statistical analysis*

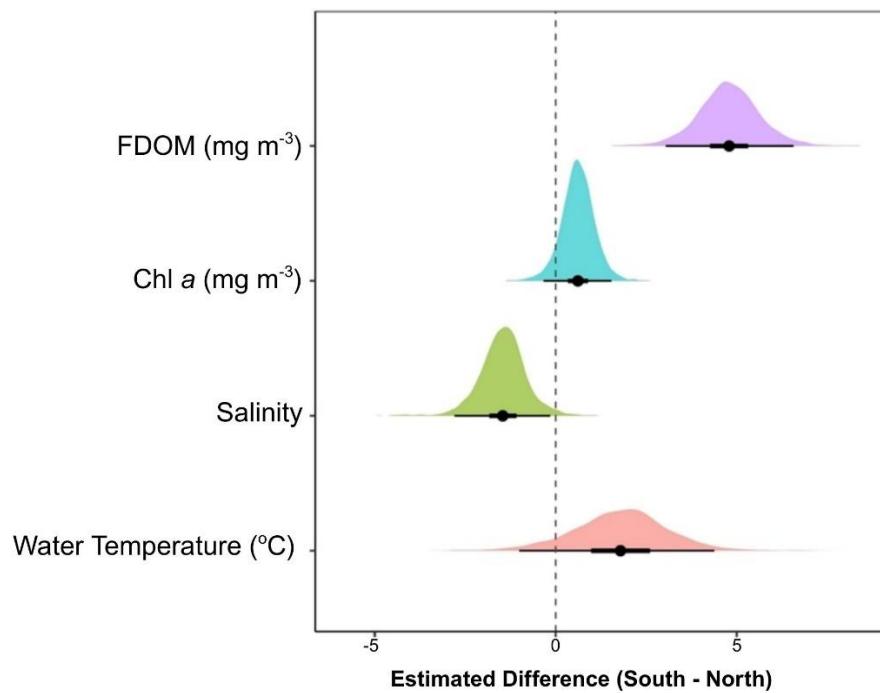
All statistical analyses were conducted using Bayesian models in the brms version 2.22.0 package in R, with model outputs explored using the tidybayes version 3.0.7 and bayestestR version 0.15.2 packages. A Bayesian generalized linear model with a beta-distributed error was used to evaluate differences in ice algae reliance across functional groups within each study region, and a Bayesian multiple linear regression assuming normality was applied to assess both variation in trophic positions and regional differences in environmental parameters. For all models, several random effect structures were tested, and model performance was compared using Leave-One-Out Cross-Validation (LOO-CV) to identify the best-fitting model using the loo version 2.8.0 package in R. The final models for ice algae reliance and trophic positions included Genus as a random effect to account for repeated measures and uneven sample sizes across taxa. Where organisms could not be identified to the genus level, broader taxonomic assignments (e.g., family) were used instead; such cases were rare and represented distinct genera from those successfully identified to genus. Similarly, the models assessing differences in environmental parameters included station as a random effect to account for spatial variability and repeated measures at each station. Model results were interpreted using posterior probability distributions, focusing on the probability and direction (pd) and the 95% credible interval (CI) of regional differences

within each functional group or environmental parameter. All analyses were conducted in R version 4.3.0 (R Core Team 2023).

### 3. Results

#### *Hydrographic data*

Hydrographic parameters varied between study sites at the time of sampling. Within the upper 25 m of the water column, stations north of the Belcher Islands exhibited lower average water temperatures compared to those in the south ( $6.01 \pm 1.49$  °C vs.  $7.81 \pm 3.02$  °C). Concentrations of chlorophyll *a* ( $3.94 \pm 0.69$  mg m<sup>-3</sup> vs.  $4.68 \pm 1.63$  mg m<sup>-3</sup>) and FDOM ( $10.90 \pm 0.69$  mg m<sup>-3</sup> vs.  $15.29 \pm 1.70$  mg m<sup>-3</sup>) were also lower in northern stations versus those in the south. In contrast, average salinity was higher at the northern stations relative to the southern stations ( $27.84 \pm 0.34$  vs  $26.51 \pm 1.26$ ; Table 2). Bayesian multiple linear regression assuming normality, accounting for variation between sample stations, further supported these patterns, providing strong posterior support for higher FDOM (pd = 1.00, CI =  $3.02 - 6.58$ ) and chlorophyll *a* concentrations (pd = 0.92, CI =  $-0.34 - 1.54$ ) south of the islands. In addition, there was strong support for warmer water temperatures (pd = 0.91, CI =  $-1.00 - 4.38$ ) and lower salinity (pd = 0.98, CI =  $-2.79 - -0.15$ ) south of the islands (Figure 2).



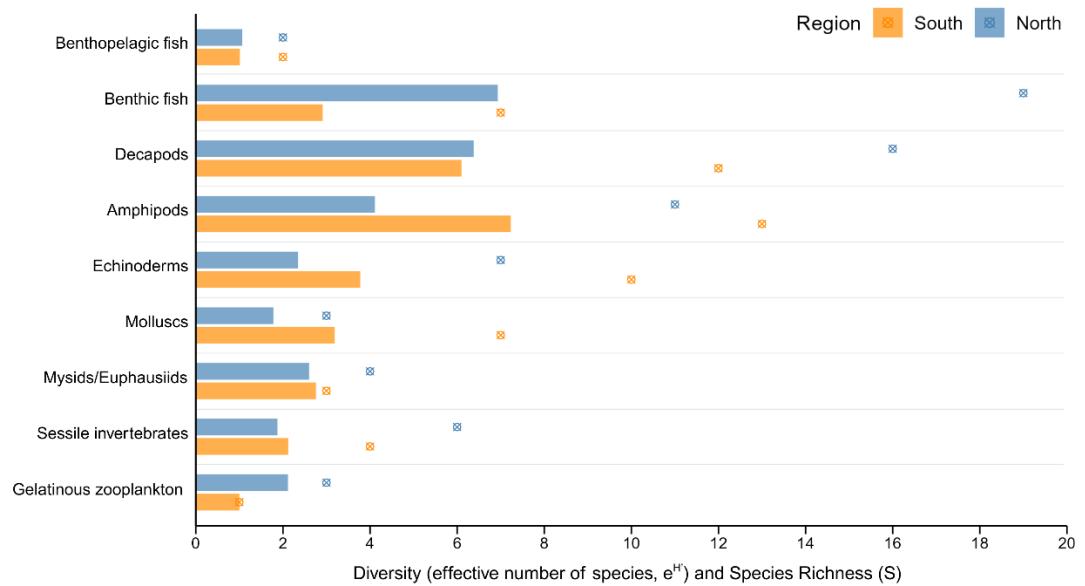
**Figure 2.** Posterior distributions of estimated differences in environmental variables (South – North) from Bayesian multiple linear regression models assuming normality, with station as a random effect. Points show the posterior mean, thick bars the 50% credible intervals, and thin bars the 95% credible intervals. Positive values indicate higher measurements in the southern region. FDOM denotes fluorescent dissolved organic matter.

### *Community composition*

Among the fish, species richness was higher north of the islands compared to the south (21 vs. 9 species, respectively); however, total fish biomass per square metre was greater in the south ( $0.26 \text{ g m}^{-2}$ ) than in the north ( $0.09 \text{ g m}^{-2}$ ). In contrast, invertebrate species richness was equivalent between regions, with 50 species observed in both the north and the south.

Similarly, invertebrate biomass per square metre was comparable between regions ( $0.38 \text{ g m}^{-2}$  in the north vs.  $0.32 \text{ g m}^{-2}$  in the south; Table 3).

Based on biomass data (available energy), diversity was similar between regions ( $H'$  = 2.63 in the north vs. 2.47 in the south), which is roughly equivalent to 14 equally common, or effective, species in the north and 12 in the south. Of the functional groups, the highest diversity north of the islands occurred in benthic fish and decapods ( $H' = 1.94$  and 1.85, respectively), equivalent to effective species numbers of approximately 7 and 6. South of the islands, the highest diversity occurred in amphipods and decapods (1.98 and 1.81, respectively), corresponding to effective species numbers of 7 and 6 (Table 3; Figure 3).

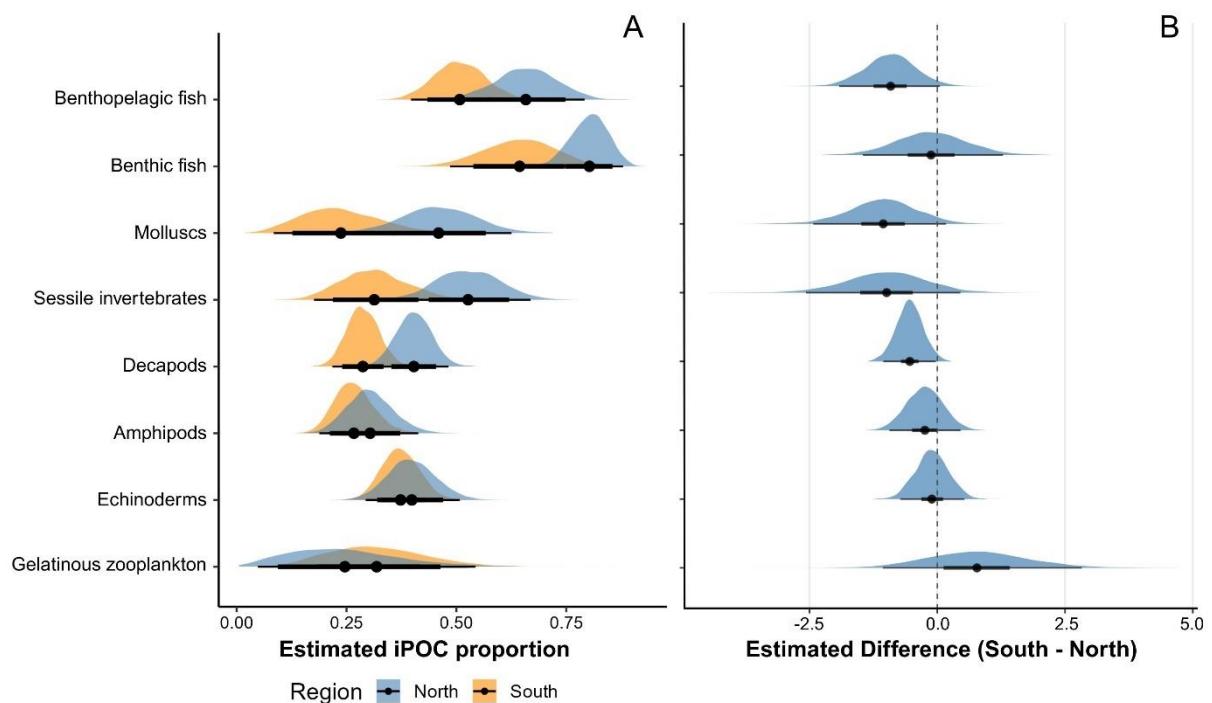


**Figure 3.** Inverse Shannon's Diversity and species richness by functional groups and region, where bars represent the effective number of species ( $e^H$ ) and the points represent observed species richness (S). Blue denotes the northern region and orange denotes the southern region.

### *Ice algae reliance across functional groups*

The highest overall ice algae reliance (iPOC%) by a species occurred in bearded seals ( $73.43\% \pm 7.55\%$ ), followed by benthic fish ( $68.36\% \pm 25.48\%$ ). The overall lowest ice algae reliance was found in euphausiids ( $13.09\% \pm 2.75\%$ ), beluga whales ( $15.59\% \pm 3.78\%$ ), and amphipods ( $22.44\% \pm 9.81\%$ ). Regionally, benthic fish and sessile invertebrates had the highest iPOC% values in the north ( $74.92\% \pm 22.91\%$  and  $53.35\% \pm 14.53\%$ , respectively), while in the south, benthic fish and benthopelagic fish had the highest iPOC% ( $56.36\% \pm 29.25\%$  and  $48.05\% \pm 38.31\%$ , respectively).

Strong posterior support for lower iPOC% in the south compared to the north was found in benthopelagic fish ( $pd = 0.97$ ;  $CI = -1.92 - 0.05$ ), decapods ( $pd = 0.98$ ,  $CI = -1.05 - -0.03$ ), molluscs ( $pd = 0.95$ ,  $CI = -2.43 - 0.17$ ), and sessile invertebrates ( $pd = 0.90$ ,  $CI = -2.57 - 0.45$ ). Moderate posterior support for higher iPOC% in the south was found in gelatinous zooplankton ( $pd = 0.79$ ,  $CI = -1.06 - 2.83$ ) and low posterior support for regional differences were observed in echinoderms ( $pd = 0.63$ ,  $CI = -0.73 - 0.53$ ), benthic fish ( $pd = 0.57$ ,  $CI = -1.45 - 1.29$ ) and amphipods ( $pd = 0.45$ ,  $CI = -0.94 - 0.45$ ) (Table 4; Figure 4). Ice algae reliance varied among marine mammal species, wherein bearded seals exhibited the highest overall average iPOC% ( $73.43 \pm 7.55\%$ ,  $n = 7$ ), followed by ringed seals ( $64.69 \pm 6.44\%$ ,  $n = 12$ ), and beluga whales had the lowest ( $15.59 \pm 3.78\%$ ,  $n = 20$ ).

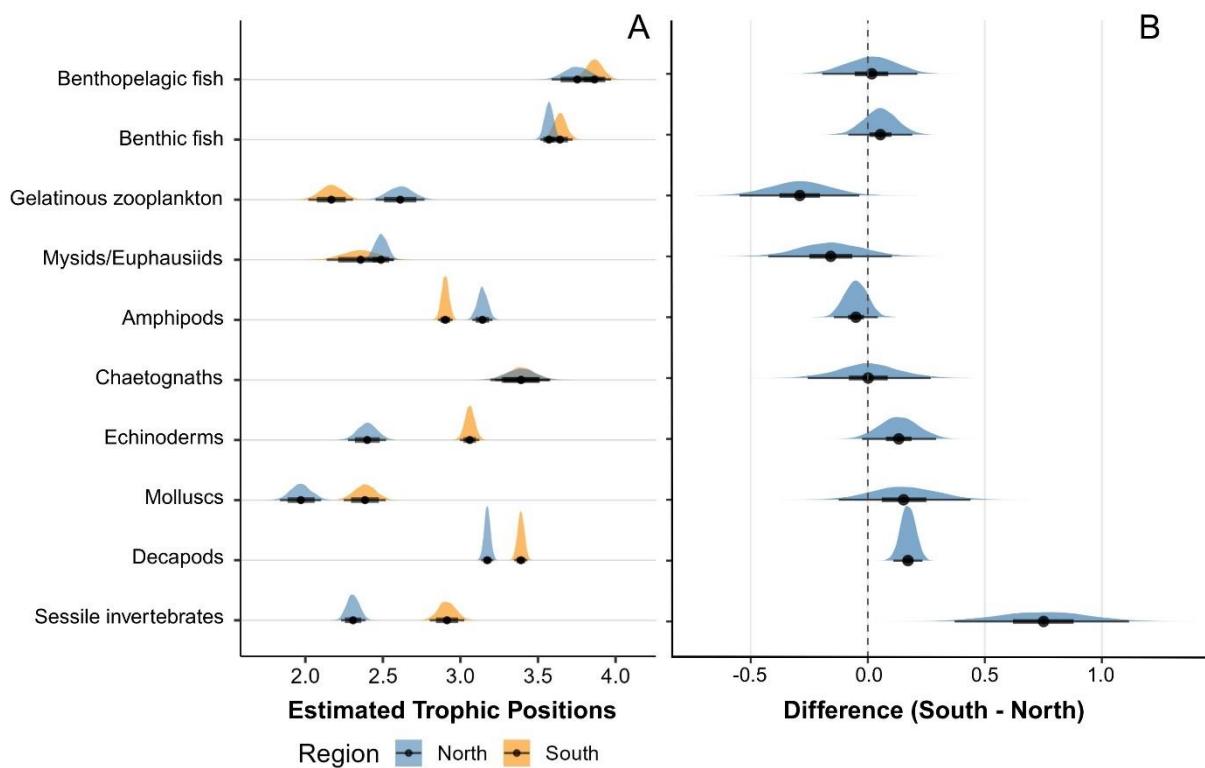


**Figure 4.** Posterior distributions of estimated iPOC (sea-ice derived primary organic carbon) proportions for each functional group by region (A) and posterior distributions of regional differences in estimated iPOC proportions (South – North) by functional group (B). A: Distributions represent posterior estimates from a Bayesian generalized linear model with a beta distributed error, grouped by functional group and region (North = blue, South = orange). Densities reflect the uncertainty in estimated mean iPOC for each group, with black lines indicating 80% and 95% credible intervals, respectively, and points representing median. B: Half-eye plots represent the posterior median (point), 50% (thick line), and 95% (thin line) credible intervals. Values are derived from a Bayesian generalized linear model with a beta distributed error with a genus-level random effect. Positive values indicate higher iPOC estimates in the South compared to the North.

### *Trophic positions*

Overall, beluga whales exhibited the highest average trophic position (TP =  $4.28 \pm 0.17$ ;  $\delta^{15}\text{N} = 15.91 \pm 0.54$ ; n = 20), followed by ringed seals (TP =  $3.91 \pm 0.34$ ;  $\delta^{15}\text{N} = 14.81 \pm 0.80$ ; n = 12), and bearded seals (TP =  $3.89 \pm 0.27$ ;  $\delta^{15}\text{N} = 14.76 \pm 0.66$ ; n = 7). Regionally specific and among fishes and invertebrates, benthopelagic fish occupied the highest trophic positions in both regions ( $3.75 \pm 0.41$  north;  $3.87 \pm 0.48$  south), followed by benthic fish ( $3.57 \pm 0.38$  north;  $3.64 \pm 0.29$  south), and chaetognaths ( $3.39 \pm 0.05$  north;  $3.39 \pm 0.18$  south).

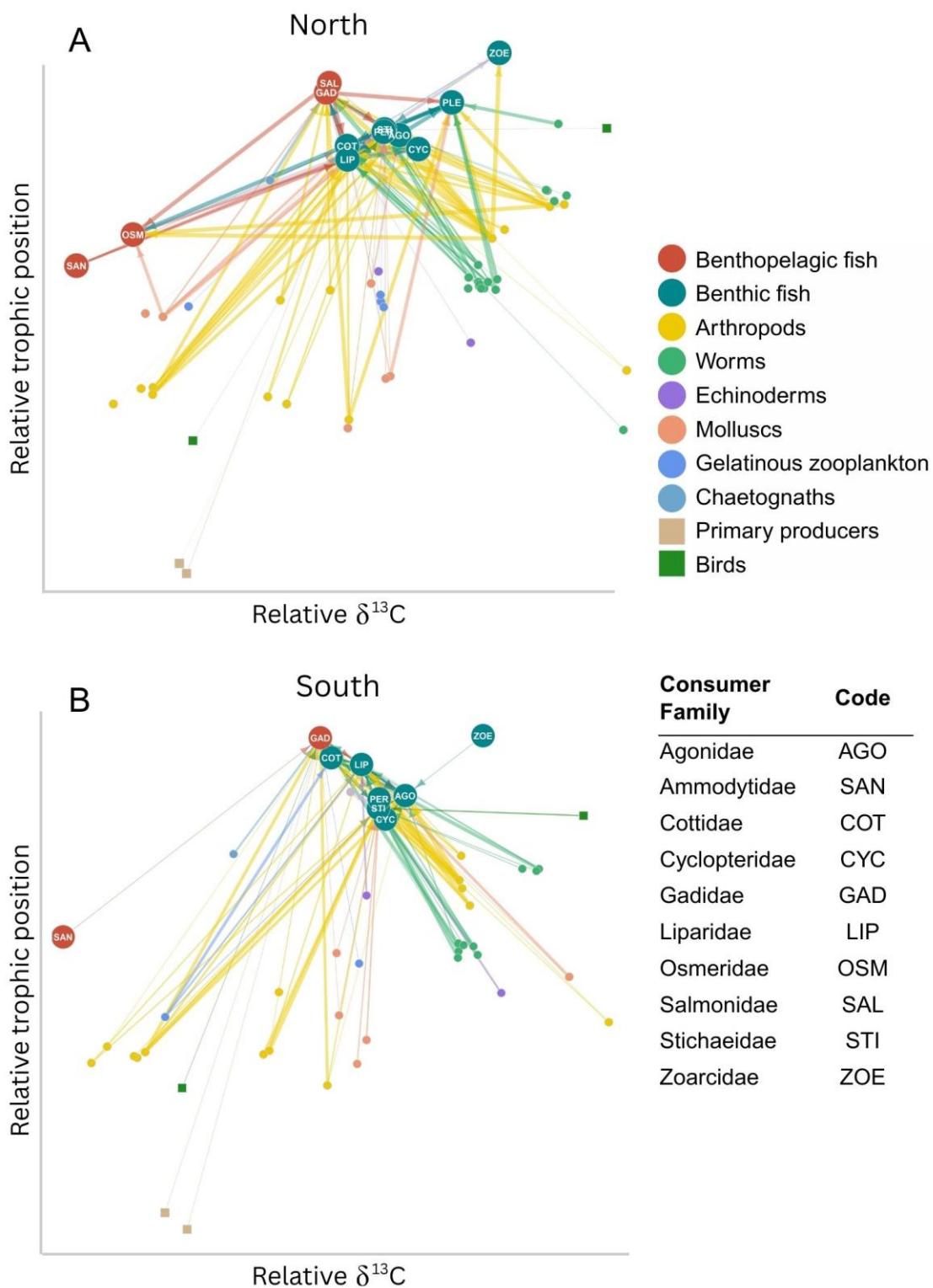
Strong posterior support for higher trophic positions in functional groups south of the Belcher Islands was found for sessile invertebrates (pd = 1, CI = 0.37 – 1.12), decapods (pd = 1, CI = 0.11 – 0.23), and echinoderms (pd = 0.95, CI = -0.02 – 0.29). Conversely, there was strong support for lower trophic positions for gelatinous zooplankton south of the islands (pd = 0.99, CI = -0.54 – -0.04). Moderate posterior support for higher trophic positions in the south was observed in benthic fish (pd = 0.78, CI = -0.08 – 0.19) and molluscs (pd = 0.87, CI = -0.12 – 0.44) and for lower trophic positions in the south in amphipods (pd = 0.85, CI = -0.15 – 0.04) and mysids and euphausiids (pd = 0.88, CI = -0.42 – 0.10). Lastly, there was lower posterior support for regional differences in benthopelagic fish (pd = 0.57, CI = -0.19 – 0.21) and chaetognaths (pd = 0.51, CI = -0.25 – 0.27) (Figure 5; Table 5).



**Figure 5.** Posterior distributions of estimated trophic positions for each functional group by region (A) and posterior distributions of regional differences in estimated trophic positions (South – North) by functional group (B). A: Distributions represent posterior estimates from a Bayesian multiple linear regression model assuming normality, grouped by functional group and region (North = blue, South = orange). Densities reflect the uncertainty in estimated mean trophic position for each group, with black lines indicating 80% and 95% credible intervals, respectively and points representing median. B: Half-eye plots represent the posterior median (point), 50% (thick line), and 95% (thin line) credible intervals. Values are derived from a Bayesian multiple linear regression model assuming normality, with a genus-level random effect. Positive values indicate higher trophic position estimates in the South compared to the North.

### *Network properties*

Food web structure and key taxa differed between regions north and south of the Belcher Islands in that taxa richness, number of trophic links and average link density were all greater in the food web north of the Belcher Islands (61, 151 and 2.48, respectively), compared to the food web south of the islands (47, 86 and 1.83). Despite these differences, connectance was identical within each region (0.04). North of the islands, Stichaeidae (blennies) and Cottidae (sculpins) exhibited the highest in-degree values (number of prey), feeding on 45 and 36 taxa, respectively. In the south, Stichaeidae and Gadidae (cod) had the highest number of prey items (28 and 25, respectively). For out-degree, Agonidae (poachers) and Cottidae were the most frequently consumed consumer taxa in the north (each in 6 predators' diets), while Cottidae had the highest out-degree in the south (appearing in 4 predator species' stomachs). Betweenness centrality was highest for Cottidae and Stichaeidae in the north (205 and 166), and Gadidae and Stichaeidae had the highest betweenness values in the south (72 and 66; Table 6). Food web network diagrams were constructed from EcoDiet posterior link probabilities, with link thickness scaled to reflect interaction strength (Figure 6). In both regions, benthic and benthopelagic fish families (i.e., Cottidae, Liparidae (snailfish), Gadidae) occupied central positions within the food web. The northern network exhibited stronger trophic links than the southern network. Regional differences in taxa were also evident: Osmeridae (capelin) appeared as both a prey and a consumer in the north but was absent in the south. Similarly, although Salmonidae were not included as predators due to their high motility, salmonid DNA was detected in the stomach contents of northern consumers (i.e., Cottidae, Liparidae, Osmeridae and Stichaeidae) but not in the south. Lastly, DNA from birds, dinoflagellates, diatoms, and algae were detected in fish stomachs in both regions, highlighting unexpected or incidental feeding interactions.



**Figure 6.** Trophic network plots for the networks north (A) and south (B) of the Belcher Islands based on EcoDiet outputs. Nodes represent taxa, with large labelled nodes indicating fish species and smaller coloured nodes representing prey taxa, coloured by phylum. The x-axis reflects relative  $\delta^{13}\text{C}$  values and the y-axis reflects relative trophic position. Directed edges (arrows) represent predicted trophic links, with line thickness scaled to the probability of interaction.

#### 4. Discussion

This study provides what is among the most comprehensive characterizations of benthic community composition, carbon flow, trophic structure, and food web organization in the Arctic, regardless of area coverage. By focusing in-depth at localized spatial scale (~100 km), our work adds important spatial context with localized environmental heterogeneity, including trophic and community dynamics, for other explorations of Arctic food webs that tend to cover more spatially extensive regions. Clear regional contrasts emerged, with pronounced differences in interspecific interactions and trophic dynamics structured by fine-scale environmental heterogeneity, revealing patterns that would have been averaged or obscured had the system been treated as a single, homogenous area. North of the Belcher Islands, waters were cooler, saltier, with lower relative chlorophyll *a*, higher benthic fish richness, and greater invertebrate biomass (dominated by shrimp). In contrast, the south was more influenced by freshwater inputs, with a greater standing stock of pelagic chlorophyll *a*, and dominance by brittle stars and Arctic cod. The highest sympagic (ice algae-derived) carbon reliance was observed in bearded seals and benthic fish, and organisms in the north relied on relatively more sympagic carbon, particularly benthopelagic fish, sessile invertebrates, molluscs and decapods. Highest trophic positions occurred in beluga whales, ringed seals, and bearded seals, while sessile invertebrates, decapods, and echinoderms held higher trophic positions in the south. Food web analysis showed more benthically centred connector species in the north and mixed benthic-pelagic connectors in the south, suggesting distinct but stable food web structures shaped by local environmental heterogeneity north and south of the islands.

#### *Environmental context*

Environmental conditions differed in the upper 25 m of the water column between the north and south regions of the Belcher Islands. South of the islands, higher FDOM and water temperatures, along with lower salinity, reflect a stronger freshwater influence. These differences are consistent with the influence of freshwater inputs to the south of the islands (Eastwood et al., 2020), originating in part from James Bay and the La Grande River in Quebec, which has experienced extensive hydroelectric developments and variable freshwater outputs throughout the year (Guéguen et al., 2011; Guzzi et al., 2024). In contrast, higher salinity and colder water temperatures north of the islands, together with greater ice algae biomass (F. Ahmed, pers. comm.), are consistent with a more classically Arctic-derived system relative to the freshwater-influenced system in the south, which may experience more variable ice conditions and less predictable primary production regimes (Arrigo et al., 2008). Together, this fine-scale environmental heterogeneity sets the stage and supports the observed variation in carbon pathways, community structure, and trophic interactions across regions, discussed in more detail below.

#### *Benthic community composition*

Regional differences in community composition around the Belcher Islands likely reflect underlying spatial variation in resource availability and physical habitat structure. Although invertebrate biomass and species richness were similar between regions, the north supported higher fish species richness and abundance-based diversity. This is consistent with its cooler, more saline waters and greater ice algae biomass (F. Ahmed, pers. comm.), that may favour more species-rich benthic fish assemblages and benthic-associated taxa such as shrimp (*Argis*, *Eualus*) and stalked tunicates (*Boltenia*), which dominated both numerically and in biomass. In contrast, south of the islands supported higher fish biomass (driven by Arctic cod), benthic invertebrate communities dominated by brittle stars (*Ophiurida* spp.), and

greater bivalve richness. Brittle star-dominated communities are common in Arctic marine ecosystems and globally (Gage, 2004; Volage et al., 2021), where brittle stars can contribute >50% of epibenthic biomass, and can reach densities up to 500 per m<sup>-2</sup> (Piepenburg & Schmid, 1996, 1997). Brittle stars can occupy a wide range of substrates and, although often classified as suspension feeders, they are also known to be opportunistic generalist suspension feeders, with the ability to also capture and consume small prey (Volage et al., 2021; Warner et al., 1982; Yokoyama & Amaral, 2008). Through suspension-feeding, brittle stars can enhance benthic-pelagic coupling, capturing nutrients from the water column and recycling them to the seafloor (Ambrose et al., 2001; Blicher & Sejr, 2011; Dinevik et al., 2025). Lastly, despite their low caloric value, brittle stars are common prey of crabs and fishes, as seen in the stomach of a snailfish south of the Belcher Islands (Burukovsky et al., 2021; Hüssy et al., 2016), consistent with their prominence in the south, where benthic fish richness and thus predation pressure was lower.

In contrast, abundance and biomass north of the islands were dominated by shrimp, where multiple shrimp species co-occurred in the region, likely facilitated by specialized feeding behaviours. For example, *Eualus* targets pelagic prey such as copepods, *Spirontocaris* and *Lebbeus* feed on benthic invertebrates such as hydrozoans and foraminiferans, and *Pandalus* forages on diatoms, zooplankton, and other invertebrates (Birkely & Gulliksen, 2003; Yunda-Guarin et al., 2025). Shrimp are also known to be sensitive to environmental changes, particularly during early developmental stages (Storm & Pedersen, 2003). Their higher abundance in the north may reflect more stable temperature regimes and salinity gradients compared to environmental shifts observed in the south, however, these relationships may shift with continued climate change. The high abundance of shrimp north of the islands may serve as an important resource for higher trophic levels, as shrimp are documented as key prey for marine mammals such as bearded seals and beluga

whales (Finley & Evans, 1983; Quakenbush et al., 2015). Further, north of the islands, shrimp were found in the stomachs of multiple fish groups including alligatorfish, cod, flatfish, sculpins, and blennies, whereas south of the islands, they were only detected in cod stomachs. The overall biomass north of the islands was also dominated by stalked tunicates. These tunicates are not typically foraged on, but are known to form biogenic habitats (Francis et al., 2014), increasing structural complexity and heterogeneity in an environment, providing shelter, and altering hydrodynamic conditions. Off the east coast of Canada, stalked tunicate beds are associated with higher abundances of brachiopods and sessile cnidarians and provide shelter for larger mobile species such as fish and crabs (Francis et al., 2014). These beds likely play a similar role in Qikiqtait.

Fish assemblages also reflected spatial contrasts, with species richness considerably higher in the north (21) than in the south (9). Multiple species of benthic fish were found in the north but not the south, including fourline snakeblennies, eelpouts, flatfish, lumpfish, and sculpins, which are all species that feed largely on benthic prey like worms and crustaceans (Coad & Reist, 2016). Greater ice algae biomass north of the islands may contribute to this pattern by supporting benthic communities that benefit from an early, high-quality carbon input in spring, promoting post-winter growth and reproduction and sustaining a richer benthic prey base from higher trophic levels like fish (Niemi et al., 2024; Amirault et al., 2022). Fish biomass was higher in the south, driven by the dominance of Arctic cod. Stomach content analysis showed that cod primarily foraged pelagically and consumed calanoid copepods, *Themisto* amphipods, and chaetognaths, consistent with previous studies (Maes et al., 2022; Majewski et al., 2016; Walkusz et al., 2013; Walkusz et al., 2011). Arctic cod are also an important prey resource for marine mammal predators such as beluga whales, ringed seals, and bearded seals (Matley et al., 2015; Quakenbush et al., 2015; Young et al.,

2010), and in fish such as Arctic char (Harwood et al., 2015; Ulrich & Tallman, 2021; Yurkowski et al., 2018).

Compositional differences in abundance and biomass were reflected in patterns of diversity north and south of the islands. Biomass-based metrics emphasize the contribution of larger taxa and reflect available energy in an ecosystem (Bambach, 1993; Singh et al., 2025). Biomass-based diversity was similar between regions, suggesting that the overall availability of biomass for resource use remained comparable. However, when functional groups were analysed independently, clear regional differences emerged. Among the fish, the greatest diversity was found in benthic fish north of the islands (species richness = 19; effective number of species  $\approx 7$ ), where these fish also relied more heavily on ice algae carbon sources. As secondary and tertiary consumers, this pattern is consistent with greater ice algae biomass in the north likely supporting a richer benthic prey base. Among invertebrates, decapods and amphipods exhibited the highest species richness and effective number of species across both regions. Despite substantially higher decapod biomass north of the islands, the effective number of species was similar between regions, reflecting comparable evenness among dominant taxa. This pattern is consistent with size-spectrum theory, which predicts relatively stable energy partitioning across trophic or size classes despite shifts in total biomass (Boudreau & Dickie, 1992). In contrast, amphipods showed similar species richness across regions (north = 11; south = 13), but nearly twice the biomass and effective number of species in the south ( $\approx 7$ ) compared with the north ( $\approx 4$ ). In both regions, the biomass of benthic amphipods was dominated by two species, *Acanthostepheia malmgreni* and *Anonyx nugax*; however, their stronger dominance in the north, where they comprised 67% of the total amphipod biomass, compared to 48% in the south, skewed evenness and resulted in a lower effective number of species in the north.

Temperature, salinity, and productivity are widely acknowledged drivers of community composition in Arctic marine systems (Cusson et al., 2007; Macpherson, 2002; Pierrejean et al., 2020). Pierrejean et al. (2020) identified salinity and surface-water particulate organic carbon content as primary drivers of community composition throughout Hudson Bay. Sediment type and benthic topography can also drive variation in benthic community structure (Dewenter et al., 2023; Kraan et al., 2010), and data on benthic habitat features remain sparse at fine scales in the Canadian Arctic (Cusson et al., 2007; Pierrejean et al., 2020). Biological structures may also contribute to habitat heterogeneity, where the high biomass of the stalked tunicate *Boltenia ovifera* north of the islands may support the more diverse benthic assemblages observed. Species-specific traits further influence their distributions, where responses to environmental gradients may vary taxonomically (Ehrman et al., 2022; Loreau & de Mazancourt, 2013; Saeedi et al., 2022). For example, predictors of community composition differ across taxonomic groups, such as silicate levels for brittle stars and light availability for cephalopods like squid (Saeedi et al., 2022). South of the Belcher Islands, the high abundance of brittle stars might be related to their tendency to aggregate in large groups and form dense patches, as a large portions were collected from a single station. These nuances emphasize the need to assess diversity and species assemblages at finer spatial resolutions to identify underlying regional drivers of community composition in Arctic ecosystems (Michel et al., 2012; Willis & Whittaker, 2002).

#### *Spatial variation in ice algae reliance across functional groups*

Ice algal reliance (iPOC%) was highest overall in bearded seals ( $73.4\% \pm 7.6\%$ ), consistent with their benthic foraging habits (Pauly et al., 1998), wherein adult bearded seals use specialized vibrissae (whiskers) to detect benthic prey (Young et al., 2010). Regionally, benthic fish exhibited the highest proportions of sympagic carbon in both areas (north: 74.9%

$\pm 22.9\%$ ; south:  $56.4\% \pm 29.3\%$ ), reflecting foraging on benthic invertebrates (annelids, arthropods, and molluscs) and other benthic fishes.

Ice algal reliance was consistently lower south of the islands among primary consumers, including molluscs, sessile invertebrates, and decapods. The mollusc (primarily *Chlamys islandica*) and sessile invertebrate (sponges, tunicates, and anemones) species used here are mainly epibenthic suspension feeders, filtering phytoplankton, detritus, and other particles from the water column, though anemones are more opportunistic, also consuming small invertebrates and zooplankton (Crawford, 1992; Shick, 1991; Yahel et al., 2007). Decapods (i.e., composed of primarily shrimp in this study) are benthic and epibenthic foragers that feed on diatoms, zooplankton, and other invertebrates (Yunda-Guarin et al., 2025). The largest regional difference within this species group was observed in parrot shrimp (*Spirontocaris spinus*), with individuals north of the islands showing ice algal reliance values of  $>40\%$ , compared to  $<25\%$  in the south, potentially driving the overall regional pattern. Because suspension feeders like molluscs and sessile invertebrates primarily reflect the availability of carbon sources in the water column (Gili & Coma, 1998), their diets in the north likely reflect greater ice algae availability, whereas benthic and epibenthic foragers like decapods may reflect both resource availability and dietary choice, as some invertebrates are capable of selectively feeding on the more nutritious ice algae-derived resources when present (McMahon et al., 2006).

Once incorporated by benthic primary consumers, sympagic carbon can be transferred through the food web to higher trophic levels, including mobile consumers and marine mammals (Amiriaux et al 2023; Koch et al., 2021, Yurkowski et al, 2020). Mobile, opportunistic species such as ringed seals and benthopelagic fish can act as habitat couplers, feeding across benthic and pelagic systems and facilitating energy transfer between sympagic, pelagic (phytoplankton-derived), and benthic (macroalgae) resource channels. Ice

algal reliance patterns in benthopelagic fish (primarily Arctic cod) mirrored those of decapods, with higher values in the north. Stomach content analysis showed that, while Arctic cod in both areas fed on a range of both pelagic and benthic invertebrates, the Arctic cod north of the islands consumed more shrimp and benthic fish compared to those in the south, potentially contributing to their greater ice algal reliance via benthic foraging. This is further consistent with the northern benthic biomass being dominated by shrimp.

Overall, our results suggest that carbon from ice algae plays a more prominent role through the food web north of the Belcher Islands than in the south. Ongoing climate change is altering the dynamics of ice algae production and availability (Arrigo et al., 2008; Frainer et al., 2017; Ji et al., 2013; Kahru et al., 2016) and rising Arctic temperatures are leading to reduced sea ice coverage, age, and thickness, resulting in increased light penetration and enhanced phytoplankton production (Comiso, 2012; Johannessen et al., 1999). These changes favour generalist fish species with broad diets and greater mobility (Fosseim et al., 2015; Kortsch et al., 2015; Sunday et al., 2015). Comparatively, more specialized organisms may be at a greater risk due to narrower dietary niches and less dietary flexibility (Fosseim et al., 2015; Frainer et al., 2017). In the Barents Sea, for example, Cautain et al. (2022) found that the proportion of sympagic carbon in the tissues of megafauna was highly correlated ( $r^2 = 0.754$ ) with sea ice duration. As such, shifts in the timing, quantity or availability of ice algae may influence the structure and function of Arctic food webs (Niemi et al., 2024). For example, the resulting shift toward more phytoplankton sources would reduce the availability of nutrient-rich ice algae-derived carbon sources for key benthopelagic couplers, with potential cascading effects on higher trophic levels, including bearded seals, which currently obtain >70% of their diet from ice algae-derived sources.

#### *Spatial variation in trophic positions throughout the food web*

Across the full spectrum of sampled invertebrates, fish, and marine mammals, trophic positions ranged from a low of 1.97 in molluscs north of the Belcher Islands to a high of 4.28 in beluga whales. There were regional differences in the trophic positions of invertebrates like sessile invertebrates, decapods, echinoderms and gelatinous zooplankton, each occupying higher trophic positions south of the Belcher Islands except for gelatinous zooplankton, which occupied lower trophic positions south of the islands. The sessile invertebrates are primarily suspension/filter feeders, and are restricted to the available resources in the water column that can be filtered, such as particulate organic matter from primary producers, resuspended detritus, and potentially small zooplankton (Shick, 1991; Yahel et al., 2007). Relatively higher proportions of ice algae-derived carbon sources in sessile invertebrates north of the islands indicate greater reliance on pelagic resources south of the islands. Regional differences in trophic positions among sessile invertebrates could reflect the filtering of small zooplankton, or spatial variation in baseline  $\delta^{15}\text{N}$  due to greater freshwater influence south of the islands. Kuzyk et al. (2010) reported that  $\delta^{15}\text{N}$  from riverine discharge entering the Hudson Bay can vary widely throughout the water column due to nutrient utilization and post phytoplankton production processes, sometimes leading to enrichment in  $^{15}\text{N}$ . Thus, observed regional differences could result from both zooplankton resource availability and differences in isotopic baselines.

Echinoderms also had higher trophic positions south of the islands compared to the north, and in both areas showed broader trophic diversity, with trophic positions ranging from 2.0 (brittle star) to 3.77 (basket star) in the north and 2.31 (sea cucumber) to 4.84 (*Pteraster* sea star) in the south. This reflects the wide spectrum of feeding strategies in Echinodermata, from detritivory and herbivory (urchins; Rohonczy et al., 2024; Scheibling & Hatcher, 2001), to suspension feeding with the ability to capture and consume small prey (brittle stars, sea cucumbers, basket stars; Emson et al., 1991; Volage et al., 2021; Warner et al., 1982;

Yokoyama & Amaral, 2008), to carnivory (sea stars; Gaymer et al., 2004). The *Pteraster* sea star had the highest trophic position of both areas, and have been reported to feed on sponges, benthic cnidaria, and can scavenge on upper pelagic predators (Katrín et al., 2006; Sargent et al., 1983). Amiraux et al. (2023) found a similar trophic position for the *Pteraster* sea star around the Southampton Islands (4.2) and posited that these megafaunal-predatory sea stars are the benthic equivalent of the top predator polar bear of the pelagic realm.

Decapods also exhibited higher trophic positions south of the islands and also have a wide breadth of foraging strategies. For example, the larger, benthic-associated *Sabinea* and *Argis* species had the highest trophic positions overall (*Argis*: 3.71 north, 3.72 south, *Sabinea* 4.10 north, 4.03 south) and forage on infauna such as detritus, cumacea (hooded shrimp), small bivalves and polychaetes (Kobiakov, 2024; Squires, 1965). Other species, such as *Pandalus*, *Eualus*, *Lebbeus* and *Spirontocaris*, typically forage at lower trophic levels and more epibenthically on diatoms and zooplankton (Yunda-Guarin et al., 2025), and had an overall range in trophic positions of 2.69 – 3.31 in the north and 2.83 – 3.46 in the south. The higher trophic position in decapods south of the islands are primarily represented in the epibenthic foragers, suggesting that they may have been feeding on more pelagic-associated zooplankton. This is corroborated by the proportions of ice algae-derived carbon sources, in which decapods north of the islands relied more on ice algae carbon sources than those in the south. Greater ice algae availability north of the islands likely supports direct coupling to primary production, whereas in areas with fewer ice algae sources, decapods may feed at higher trophic levels. This pattern illustrates how fine-scale environmental heterogeneity can restructure trophic roles within a functional group over small spatial scales.

Finally, gelatinous zooplankton occupied a higher trophic position north of the islands and commonly forage on microplankton, zooplankton and ichthyoplankton (fish larvae; Graham & Kroutil, 2001; Javidpour et al., 2016; Titelman et al., 2007). As suitable habitat for

gelatinous zooplankton such as jellyfish expands, their predatory nature may allow them to outcompete fish in stressful environments (Lynam et al., 2011). For example, in the Irish Sea, overfishing and rising water temperatures correlate with increased jellyfish abundance, and because they forage on ichthyoplankton, they could prevent fish stocks from recovering (Lynam et al., 2011). Around the Belcher Islands, the higher trophic position of gelatinous zooplankton north of the islands is consistent with low abundance and biomass of the primary pelagic forager, Arctic cod, potentially reducing competition for pelagic resources.

Regionally, benthopelagic fish occupied the highest trophic positions in both regions (north: 3.75, south: 3.87), followed by benthic fish (north: 3.57, south: 3.64) and chaetognaths (3.39 in both). The benthopelagic fish group (primarily Arctic cod) north of the islands consumed a wide array of prey (copepods, decapods, chaetognaths, and benthic fish) and showed higher proportions of ice algae-derived carbon in their tissue, whereas south of the islands, they were feeding primarily on copepods and chaetognaths, with lesser contributions from other taxa and lower proportions of ice algae-derived carbon.

Chaetognaths were found in the diet of Arctic cod in both regions, and despite their small size, occupied the third highest trophic level in both regions, reflecting their pelagic carnivory and competition with juvenile fish for zooplankton resources like copepods (Grigor et al., 2015).

In both regions, benthic fish occupied the second highest trophic position. North of the islands, the larger sculpin *Myoxocephalus* reached a trophic position of 4.17, feeding on polychaetes, crabs and *Anonyx* amphipods. The eelpout *Lycodes*, despite its small size with an average length of just 53 mm, reached a trophic position of 4.07, with a generalist benthivore diet of primarily arthropods. South of the islands, the sea tadpole *Careproctus* had the highest trophic position (4.01), also with a small size of 53 mm, and was feeding on both *Anonyx* amphipods (TP of 3.48 south of the islands) and *Cyanea* jellies. There is growing

concern about the role of jellyfish in Arctic food webs, as their expanding distribution and increasing importance as prey may contribute to regime shifts (Dischereit et al., 2024), and they are frequently undetected in traditional morphometric stomach content analysis.

Previous studies have identified crustaceans, amphipods, polychaetes, and decapods as the primary prey of sea tadpoles (Eriksen et al., 2020; Falk-Petersen et al., 1998), and the detection of *Cyanea* in the stomachs of sea tadpoles here confirms DNA metabarcoding as a robust tool for tracking the consumption of gelatinous prey items in Arctic food webs.

As top predators, beluga whales had the highest mean trophic positions (4.28), consistent with their diet of primarily pelagic fish such as Arctic cod and capelin (Breton-Honeyman et al., 2016; Kelley et al., 2010). Ringed seal and bearded seal trophic positions followed closely (3.91 and 3.89, respectively), where ringed seals opportunistically feed on a wide array of fish (capelin, sandlance, Arctic cod, sculpin, blennies) and pelagic and benthic invertebrates (mysids, euphausiids, amphipods, decapods; Chambellant et al., 2013; Dehn et al., 2007; Ogloff et al., 2019; Yurkowski et al., 2016), and bearded seals consume a mix of fish such as Arctic cod and sculpins, and benthic invertebrates such as whelks and shrimp (Finley & Evans, 1983; Young et al., 2010). The higher trophic positions of benthopelagic fish, which was primarily composed of Arctic cod, and had similar trophic positions to that of the seals and beluga whales, suggests that the marine mammals are likely feeding on a mix of Arctic cod and lower trophic level fish, such as capelin (TP = 2.83, n = 1) and sandlance (TP = 2.64, n = 1), as well as invertebrates.

### *Network properties*

The comparative analysis of food web properties north and south of the Belcher Islands revealed differences and similarities in complexity and organization that are likely associated with underlying environmental and community composition gradients. The higher number of

nodes and links, along with greater link density in the northern region, reflects greater species richness and interaction diversity relative to the southern region. Notably, despite these differences, connectance was similar between the regions, indicating that the complexity of trophic relationships scaled predictably with community size and richness. Kortsch et al. (2015) found that the northward expansion of typically larger, generalist, and opportunistic species can lead to food webs with higher connectance as a result of the broad dietary niches of most consumers. The southern region's greater freshwater influence, warmer waters, and lower salinity were expected to support more generalist species and therefore higher connectance. However, the similar connectance observed across regions provides no evidence of food web restructuring among the regions.

The greater number of nodes and higher link density observed north of the Belcher Islands likely reflect greater ice algae biomass and both biogeographic and habitat heterogeneity, which supports the region's elevated species richness (61 taxa in the north versus 47 in the south). Trawl data similarly revealed higher benthic fish richness in the north, providing the structural basis for increased link density and suggesting broader prey resource availability. In turn, this may facilitate broader dietary breadth among consumers. These findings are consistent with work in the Barents Sea, where habitat heterogeneity was positively associated with species richness and link density (Kortsch et al., 2019). In this study, species with broader diets were not newcomers but characteristic Arctic taxa, suggesting that local prey availability, rather than species turnover, as seen in other ecosystems such as the Barents Sea (Kortsch et al., 2015), is driving this pattern.

Network centrality metrics, particularly betweenness centrality, reveal distinct regional differences in the roles of certain species as connectivity hubs within the trophic network. Betweenness centrality among the fish in the food web north of the islands was dominated by benthic taxa, specifically sculpins and blennies. This suggests a benthically

centred food web structure, where small benthic fish are important channels of energy and nutrient flow throughout the food web. In contrast, the food web south of the islands showed a combination of benthic and benthopelagic species (blennies and cod) dominating betweenness centrality, reflecting a more pelagically influenced food web. This signals different bottom-up drivers between systems, wherein benthic productivity and complexity drive trophic interactions among species in the north versus pelagic-driven energy inputs shaping the food web in the south. The prominence of small, benthic fishes as network hubs underscores the ecological importance of these lesser-studied species in maintaining food web cohesion and functional stability, an aspect frequently overlooked in Arctic marine ecology which traditionally focuses on commercially or ecologically dominant taxa (Dey et al., 2018).

Salmonids (Arctic char) were not included as predators in this study, yet salmonid DNA was detected in the stomachs of four fish families north of the islands (sculpins, snailfish, capelin and blennies), and no occurrences in the stomach samples south of the islands. Arctic char spawn in the freshwater system and begin migrating to the marine environment after 4-5 years, by which time they would likely be larger than the fish containing their DNA. This suggests these fish were likely scavenging on the remains of Arctic char rather than preying on them directly. Blennies also showed the strongest associations with avian DNA, which may reflect opportunistic feeding behaviour, such as scavenging bird carcasses or ingestion of bird feces from the seafloor. Additionally, DNA signatures of dinoflagellates, diatoms, and brown algae were detected primarily in Greenland cod (*Gadus ogac*), a known generalist predator, and in blennies collected north of the islands, likely representing transient or secondary prey items. These unique detections represent the utility of using DNA metabarcoding in stomach content analysis for identifying cryptic

trophic interactions and dietary components that are often missed by traditional visual stomach content analysis.

## 5. Limitations

This study faced several limitations that may have affected interpretations, particularly regarding the resolution of environmental gradients and dietary data. Analyses at the level of individual stations would have better accounted for variation in environmental parameters and depth across sites. However, due to limited sample sizes, stations were pooled into north and south areas. For example, although brittle stars were dominant south of the islands, most were collected at a single station, which may reflect a local feature rather than a widespread pattern. Nonetheless, very few brittle stars were collected at northern stations, supporting the conclusion that brittle star dominance is a feature more representative of southern sites and represents regional differences. Furthermore, within-region variability was lower than between-region differences, reinforcing the strength of the regional patterns detected in this study.

Although overall DNA metabarcoding improved dietary resolution relative to visual stomach content analysis, it was not without limitations. Some prey taxa may have been underrepresented due to incomplete reference libraries, particularly for Arctic taxa. For instance, *Themisto* amphipods were observed in stomach contents but rarely detected via DNA metabarcoding, likely due to genomic plasticity or gaps in reference sequences for Hudson Bay species. Further, some taxa could not be resolved to species or genus level due to DNA degradation or insufficient species or regional representation in the reference database. Lastly, this study used a single primer pair, whereas other studies have improved coverage by combining multiple primers targeting the same or different genes. However, the target gene used here (CO1) is the most widely used and is well represented in reference

libraries, and many studies also rely on a single region (Gielings et al., 2021). These limitations highlight the value of a mixed approach, with a subsample of stomachs visually analysed to validate and supplement molecular findings where needed.

The application of EcoDiet was similarly constrained by data availability. Stomach content data were primarily available only for fish consumers, while literature describing quantitative diet composition for many Arctic invertebrates remains scarce. Additionally, stable isotope data were not available for several prey taxa (e.g., small copepods or worms) that were not captured in the trawls or pelagic nets. These sample sizes and data gaps required the aggregation of taxa into broader groups to achieve model convergence, potentially masking some even finer scale trophic dynamics or differences between regions. Ultimately, despite these limitations, this study provides the first fine-scale, multi-taxa assessment of food web structure and function in a model Arctic system characterized by spatial heterogeneity in freshwater influence and ice algae availability at a scale of 10s to 100s of kilometres, using a unique dataset spanning more than 120 species, including community composition data from over 5000 organisms, stable isotope analyses from more than 1200 individuals, highly branched isoprenoid analysis on a subset of over 250 samples, and DNA metabarcoding of over 200 stomachs.

## **6. Conclusion**

Herein, the integration of multiple tools revealed clear regional differences in community composition, resource use and food web structure. South of the Belcher Islands, organisms tended to rely less on ice algae-derived carbon than in the north, with trophic positions generally higher, reflecting less ice algae supply. Food web structure also differed, with north of the islands supporting broader diet breadths and benthically centred key connector species, whereas the food web south of the islands exhibited narrower diets and a mix of benthic and

pelagic central species. Despite these regional contrasts, overall food web connectance was similar across regions, indicating that the food web south of the islands, while more strongly influenced by freshwater inputs, has a similar level of structural complexity to the north.

These results suggested that freshwater influence, likely driven by currents from James Bay and runoff from rivers along the coast of southeastern Hudson Bay alongside La Grande River in James Bay, which has several large hydroelectrical developments, alters baseline nutrient dynamics and primary production regimes across this relatively small latitudinal gradient (55.5° to 57.5°) between north and south of the Belcher Islands. Mid-trophic level organisms in Arctic ecosystems remain understudied (Hoover et al., 2013), yet they are both harvested by the local communities like Sanikiluaq (scallops, sea cucumbers and urchins) and act as key benthic-pelagic couplers, supporting many higher-trophic-level and locally harvested species such as Arctic char, Greenland cod, ringed and bearded seals, and beluga whales.

Our study demonstrated how local environmental variability has potential implications for these harvested species through disruptions to benthic-pelagic coupling, shifts in prey biomass, and changes in prey quality. This work also highlights the role of smaller, lesser-studied fish (i.e., benthic fishes) as key species and emphasizes the value of whole food web evaluations in Arctic marine ecology, which traditionally focuses on commercially or ecologically dominant taxa and charismatic species (Dey et al., 2018). Studies conducted over broader spatial scales, spanning hundreds to thousands of kilometres, can average or obscure fine-scale variation in food web structure and function, including energy pathways, trophic roles, network characteristics, and community composition, particularly as it relates to climate and anthropogenically-driven local environmental gradients or perturbations. By contrast, we demonstrated that examining ecosystems at finer spatial scales (tens to hundreds of kilometres) reveals significant differences in ecosystem structure associated with

anthropogenic and climate-driven change. Together, these findings underscore the need for fine-scale, ongoing monitoring to inform conservation and management decisions under a rapidly changing Arctic climate.

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## **8. Conflict of Interest Statement**

The authors declare no conflicts of interest.

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## Tables

Table 1. Definitions of structural network metrics used to describe food web topology.

<b>Food-web attribute</b>	<b>Meaning</b>
Taxa Richness (S)	Total number of taxa (nodes) in the food web.
Number of trophic links (L)	Total number of feeding interactions (edges) among the taxa in the network.
Link Density (=L/S)	Average number of links per taxon. Reflects the degree of dietary generalism across the web (Tylianakis et al., 2007).
Connectance (=L/S <sup>2</sup> )	Proportion of all possible trophic links that are realized. Indicates the overall complexity of interconnectivity of the food web (Warren, 1994).
In-Degree	Number of incoming edges to a node; the number of consumers (predators) that feed on a given taxon.
Out-Degree	Number of outgoing edges from a node; the number of prey consumed by a given taxon.
Betweenness Centrality	Frequency with which a node lies on the shortest paths between all other pairs of nodes. Represents the taxon's role in connecting parts of the network.

Table 2. Environmental variables measured at the individual stations north and south of the Belcher Islands, with regional averages.

Region	Station	Chl <i>a</i> (mg m <sup>-3</sup> )	FDOM (mg m <sup>-3</sup> )	Water temperature (°C)	Salinity
North	BI-08	3.72 ± 0.64	10.73 ± 0.53	6.73 ± 0.83	27.57 ± 0.08
	BI-09	3.92 ± 0.38	11.08 ± 0.62	5.51 ± 1.13	27.93 ± 0.16
	BI-10	4.31 ± 0.55	10.66 ± 0.59	5.96 ± 1.33	27.90 ± 0.23
	BI-11	4.39 ± 0.69	10.70 ± 0.47	6.67 ± 1.24	27.67 ± 0.27
	BI-12	3.37 ± 0.61	11.36 ± 0.91	5.19 ± 1.20	28.13 ± 0.48
<b>Average North</b>		<b>3.94 ± 0.69</b>	<b>10.90 ± 0.69</b>	<b>6.01 ± 1.49</b>	<b>27.84 ± 0.34</b>
South	BI-04	5.22 ± 1.82	13.57 ± 0.66	8.03 ± 2.02	26.99 ± 0.51
	BI-16	4.47 ± 1.48	15.77 ± 0.44	5.93 ± 1.10	27.14 ± 0.50
	BI-17	4.79 ± 0.91	16.20 ± 1.25	11.18 ± 3.01	24.86 ± 1.50
	BI-M2	3.71 ± 1.50	17.34 ± 0.72	5.76 ± 2.80	26.66 ± 1.09
<b>Average South</b>		<b>4.68 ± 1.63</b>	<b>15.29 ± 1.70</b>	<b>7.81 ± 3.02</b>	<b>26.51 ± 1.26</b>

Note: Chl *a* = chlorophyll *a* (mg m<sup>-3</sup>); FDOM = fluorescent dissolved organic matter (mg m<sup>-3</sup>)

Table 3. Summary of community composition by functional group north and south of the Belcher Islands.

Functional Group	North						South					
	N	N m <sup>-2</sup>	S	Biomass (g m <sup>-2</sup> )	H'	e <sup>H'</sup>	N	N m <sup>-2</sup>	S	Biomass (g m <sup>-2</sup> )	H'	e <sup>H'</sup>
Benthopelagic fish	9	0.023	2	0.024	0.06	1.06	54	0.006	2	0.187	0.01	1.01
Benthic fish	110	0.013	19	0.068	1.94	6.93	33	0.003	7	0.072	1.07	2.91
Decapods	1341	0.157	16	0.165	1.85	6.38	422	0.043	12	0.102	1.81	6.1
Amphipods	200	0.023	11	0.004	1.41	4.11	260	0.027	13	0.008	1.98	7.23
Echinoderms	8	0.001	7	0.012	0.85	2.35	2675	0.273	10	0.186	1.33	3.78
Molluscs	20	0.002	3	0.005	0.58	1.78	15	0.002	7	0.005	1.16	3.19
Mysids/ Euphausiids	245	0.029	4	0.004	0.96	2.6	7	0.001	3	7.7x10 <sup>-5</sup>	1.01	2.76
Sessile invertebrates	88	0.01	6	0.188	0.63	1.87	45	0.005	4	0.018	0.75	2.12
Gelatinous zooplankton	7	0.001	3	0.001	0.75	2.12	1	0.000 1	1	0.002	0	1
<b>Totals</b>	<b>2029</b>	<b>0.237</b>	<b>71</b>	<b>0.471</b>	<b>2.63*</b>	<b>14*</b>	<b>3512</b>	<b>0.359</b>	<b>59</b>	<b>0.581</b>	<b>2.47*</b>	<b>12*</b>

\*Totals for  $H'$  and  $e^{H'}$  represent overall diversity metrics and are not additive across functional groups.

Note:  $N$  = number of individuals;  $N m^{-2}$  number of individuals per square metre trawled;  $S$  = species richness (total number of species);  $H'$  = Shannon's diversity index;  $e^{H'}$  = effective number of species (inverse Shannon's diversity index).

Table 4. Estimated iPOC by functional group and region with modelled difference between South and North and the probability of a positive or negative effect.

Group	North		South		$\Delta$ iPOC (South – North) (95% CI)	Probability of Direction
	N	Median iPOC (95% CI)	N	Median iPOC (95% CI)		
Benthic fish	10	0.80 (0.72-0.88)	6	0.65 (0.49-0.79)	-0.11 (-1.45-1.29)	0.57
Benthopelagic fish	9	0.66 (0.52-0.79)	13	0.51 (0.40-0.62)	-0.92 (-1.92-0.05)	0.97
Amphipods	15	0.30 (0.21-0.41)	20	0.26 (0.19-0.36)	-0.24 (-0.94-0.45)	0.45
Echinoderms	18	0.40 (0.29-0.51)	29	0.37 (0.29-0.46)	-0.10 (-0.73-0.53)	0.63
Gelatinous zooplankton	2	0.23 (0.05-0.53)	4	0.31 (0.13-0.54)	0.79 (-1.06-2.83)	0.79
Sessile invertebrates	11	0.53 (0.39-0.67)	8	0.31 (0.18-0.46)	-1.01 (-2.57-0.45)	0.90
Decapods	32	0.40 (0.33-0.48)	32	0.29 (0.22-0.36)	-0.54 (-1.05 -0.03)	0.98
Molluscs	8	0.46 (0.29-0.63)	4	0.23 (0.08-0.43)	-1.07 (-2.43-0.17)	0.95

Note: N denotes sample size, values are posterior medians with 95% credible intervals derived from a Bayesian generalized linear model with a beta distributed error.  $\Delta$  iPOC (South – North) reflects modelled difference between South and North and Probability of Direction indicates the certainty that the effect is positive or negative.

Table 5. Estimated trophic position (TP) by functional group and region, with calculated mean  $\delta^{15}\text{N}$ , posterior median trophic positions, modelled differences in trophic positions between South and North and the probability of a positive or negative effect.

Group	North			South			$\Delta$ TP (South – North) (95% CI)	Probability of Direction
	N	Mean $\delta^{15}\text{N}$	Median TP (95% CI)	N	Mean $\delta^{15}\text{N}$	Median TP (95% CI)		
Benthic fish	97	13.48 $\pm 1.41$	3.57 (3.52-3.62)	43	13.74 $\pm 1.07$	3.64 (3.56-3.72)	0.05 (-0.08-0.19)	0.78
Benthopelagic fish	11	13.87 $\pm 1.59$	3.75 (3.59-3.92)	26	14.56 $\pm 1.76$	3.86 (3.76-3.97)	0.02 (-0.19-0.21)	0.57
Amphipods	69	11.60 $\pm 1.12$	3.14 (3.08-3.21)	133	10.78 $\pm 1.76$	2.90 (2.85-2.95)	0.05 (-0.15-0.04)	0.85
Echinoderms	19	9.07 $\pm 1.76$	2.40 (2.28-2.52)	78	11.32 $\pm 2.55$	3.06 (3.00-3.12)	0.13 (-0.02-0.29)	0.95
Gelatinous zooplankton	12	9.80 $\pm 0.96$	2.61 (2.45-2.77)	15	8.29 $\pm 0.76$	2.17 (2.02-2.31)	-0.29 (-0.54- -0.04)	0.99
Sessile invertebrates	47	8.76 $\pm 1.80$	2.31 (2.23-2.39)	24	10.82 $\pm 0.92$	2.91 (2.80-3.02)	0.75 (0.37-1.12)	1.00
Decapods	191	11.70 $\pm 1.62$	3.17 (3.13-3.21)	157	12.44 $\pm 1.25$	3.39 (3.35-3.43)	0.17 (0.11-0.23)	1.00
Molluscs	17	7.62 $\pm 1.42$	1.97 (1.84-2.10)	17	9.02 $\pm 1.36$	2.38 (2.25-2.52)	0.15 (-0.12-0.44)	0.87
Chaetognaths	8	12.44 $\pm 0.17$	3.39 (3.19-3.58)	10	12.45 $\pm 0.6$	3.39 (3.22-3.57)	0.00 (-0.25-0.27)	0.51
Mysids/ Euphausiids	45	9.37 $\pm 0.36$	2.49 (2.40-2.57)	6	8.94 $\pm 0.42$	2.36 (2.14-2.57)	-0.16 (-0.42-0.10)	0.88

Note: N denotes sample size, mean  $\delta^{15}\text{N}$  ( $\pm$  standard deviation) are calculated values, median TPs are posterior values with 95% credible intervals derived from a Bayesian multiple linear regression model assuming normality.  $\Delta$  TP (South – North) reflects modelled difference between South and North and Probability of Direction indicates the certainty that the effect is positive or negative.

Table 6. Calculated network metrics for selected fish taxa in the networks north and south of the Belcher Islands.

Family	In Degree		Out Degree		Betweenness		
	North	South	North	South	North	South	
Benthic fish	Agonidae	10	12	6	3	16	20
	Cottidae	36	6	6	4	205	21
	Cyclopteridae	8	0	1	1	1	0
	Liparidae	19	16	3	1	14	9
	Stichaeidae	45	28	4	3	166	66
	Zoarcidae	2	0	2	1	0	0
	Pleuronectidae	12	-	1	-	14	-
	Perciformes*	0	0	1	1	0	0
Benthopelagic fish	Osmeridae	6	-	1	-	0	-
	Salmonidae**	0	-	4	-	0	-
	Ammodytidae	0	0	4	1	0	0
	Gadidae	13	25	5	3	9	72

\*Taxon identified at a higher taxonomic level due to limited resolution in diet data.

\*\*Salmonid predators were not included as a predator in the network analysis; values reflect occurrences of Salmonidae in the diet of other predators.

Note: In-degree represents the number of prey per taxon, out-degree represents the number of predators per taxon, betweenness indicates the extent to which a taxon serves as a connector within the network, and a dash (-) indicated absence of the taxon in that region.

## APPENDIX S1

**Table S1.** Species included in each analysis, organized by functional group, indicating inclusion in community composition, stable isotope (SI), highly branched isoprenoid (HBI), and stomach content analysis (SCA). Community composition analyses include only organisms collected by benthic trawl to allow normalization by area swept. For SI, HBI, and SCA, functional groups were supplemented with samples collected during coastal sampling when necessary to achieve adequate sample sizes. For some HBI and SI analyses, reported values represent the number of analytical samples rather than individual organisms, as multiple individuals were sometimes pooled to obtain sufficient material.

Functional Group	Common name	Species name	Analyses			
			Community composition	SI	HBI	SCA
Marine mammals	Beluga	<i>Delphinapterus leucas</i>		20	20	
	Bearded seal	<i>Pusa hispida</i>		12	12	12
	Ringed seal	<i>Erignathus barbatus</i>		7	7	
Benthic fish	Alligatorfish	<i>Leptagonus decagonus</i>	23	23	2	22
	Blennies	<i>Anisarchus medius</i>	19	21	2	19
		<i>Eumesogrammus praecisus</i>	3	3		3
		<i>Leptoclinus maculatus</i>	17	25	2	21
		<i>Lumpenus fabricii</i>	1	1		1
		<i>Stichaeus punctatus</i>	4	4	1	4
	Eelpout	Stichaeidae	2	2		2
		<i>Lycodes polaris</i>	7	7		2
		<i>Hippoglossoides platessoides</i>	1	1	1	1
		<i>Eumicrotremus derjugini</i>	1	1		1
		<i>Aspidophoroides olrikii</i>	5	5		5
	Sculpins	<i>Icelus bicornis</i>	8	7	1	7
		<i>Icelus sp.</i>	2	2		2
		<i>Myoxocephalus aenaeus</i>	1	1		1
		<i>Myoxocephalus quadricornis</i>	2	3	3	3
		<i>Triglops murrayi</i>	36	23	7	19
		Cottidae	1	1		1
	Snailfish	<i>Careproctus reinhardti</i>	2	2		2
		<i>Liparis fabricii</i>	6	6	2	5
		<i>Liparis sp.</i>	2	2		1
Benthopelagic fish	Arctic char	<i>Salvelinus alpinus</i>		5	5	5
	Capelin	<i>Mallotus villosus</i>		1	1	
	Cod	<i>Boreogadus saida</i>	61	28	11	28
		<i>Gadus ogac</i>		2	2	2
	Sandlance	<i>Ammodytes sp.</i>	1	1		1
Amphipods	Benthic amphipods	<i>Acanthostepheia malmgreni</i>	89	40	10	
		<i>Ampelisca eschrichtii</i>	2	2		
		Ampeliscidae	38	18		
		<i>Anonyx nugax</i>	68	40	12	

		<i>Anonyx sp.</i>	1		
		<i>Arrhis phyllonyx</i>	29	14	
		<i>Eusirus cuspidatus</i>	30	21	
		<i>Haploops sp.</i>	2	1	
		<i>Monoculodes sp.</i>	14	7	
		<i>Onisimus sp.</i>	1	1	
		<i>Paroedicerus lynceus</i>	1		
		<i>Rhachotropis aculeata</i>	17	16	
		<i>Stegocephalus inflatus</i>	3	1	
		<i>Syrrhoe crenulata</i>	28	2	
		<i>Themisto abyssorum</i>	3	1	
	Pelagic amphipods	<i>Themisto libellula</i>	133	38	13
		<i>Hyperia galba</i>	1		
Chaetognaths	Arrow worms	Chaetognatha		18	
Decapods	Shrimp	<i>Argis dentata</i>	360	40	6
		<i>Eualus belcheri</i>	10	10	1
		<i>Eualus fabricii</i>	426	21	
		<i>Eualus gaimardii</i>	103	31	3
		<i>Eualus macilentus</i>	119	40	5
		<i>Eualus sp.</i>	55	8	
		<i>Lebbeus groenlandicus</i>	9	9	
		<i>Lebbeus polaris</i>	28	21	2
		<i>Lebbeus sp.</i>	158	20	
		<i>Pandalus montagui</i>	124	40	7
		<i>Pandalus sp.</i>	1		
		<i>Sabinea septemcarinata</i>	178	42	20
		<i>Sabinea sp.</i>	12	1	
		<i>Spirontocaris sp.</i>	11	2	
		<i>Spirontocaris spinus</i>	126	40	15
	Crabs	<i>Hyas c. alutaceus</i>	34	21	5
		<i>Hyas sp.</i>	5		
		<i>Pagurus sp.</i>	4	2	
Echinoderms	Sea stars	<i>Henricia sp.</i>	5	5	
		<i>Leptasterias groenlandica</i>	14	14	8
		<i>Leptasterias polaris</i>			3
		<i>Pteraster militaris</i>	1	1	1
		Asteroidea	20	4	
	Sun stars	<i>Solaster endeca</i>			1
		<i>Crossaster papposus</i>			1
	Basket star	<i>Gorgonocephalus sp.</i>	1	1	1
	Brittle stars	<i>Ophiocten sericeum</i>	7		
		<i>Ophiocten sp.</i>	1		
		<i>Ophiopholis aculeata</i>	2	1	
		<i>Ophiopus arcticus</i>	24	1	
		Ophiurida	2588	21	5
	Feather star	<i>Helicometra glacialis</i>	7	7	
	Sea cucumber	<i>Cucumaria frondosa</i>		12	16

	Urchin	<i>Strongylocentrotus sp.</i>	13	30	11
Gelatinous zooplankton	Ctenophora	Ctenophora		3	1
	Cubozoan	Cubozoa	1	2	
	Hydrozoan	<i>Euphysa sp.</i>		2	
	Scyphozoans	<i>Cyanea capillata</i>	2	14	5
		<i>Aurelia aurita</i>		5	
	Unknown cnidarian	Cnidaria	5	1	
Molluscs	Bivalves	<i>Chlamys islandica</i>	4	11	12
		<i>Ciliatocardium ciliatum</i>	3	1	
		<i>Ennucula tenuis</i>	1	1	
		<i>Hiatella arctica</i>	18	8	
		<i>Macoma calcarea</i>	1	1	
		<i>Mytilus sp.</i>		1	
	Gastropods	<i>Cylichna alba</i>	1		
		<i>Margarites groenlandicus</i>	2	1	
		<i>Margarites sp.</i>		3	
		<i>Patella sp.</i>	1		
		<i>Plicifusus kroyeri</i>	4	2	
		<i>Clione limacina</i>		4	
		<i>Limacina helicina</i>		1	
Mysids/ Euphausiids	Mysid	<i>Mysis sp.</i>	11	9	
	Euphausiids	<i>Thysanoessa longicaudata</i>	10	7	
		<i>Thysanoessa rashii</i>	76	21	
		<i>Thysanoessa sp.</i>	155	14	
Sessile invertebrates	Anemones	Actiniaria	2	2	
		<i>Stomphia coccinea</i>	40	19	7
	Barnacle	<i>Balanus sp.</i>	32	13	
	Sponge	Porifera	13	13	6
	Tunicates	<i>Boltenia ovifera</i>	43	21	5
		Ascidia	3	3	1