

Spatial variation in trophic interactions, food web properties, and community composition around the Belcher Islands, Nunavut

by

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Abstract

Arctic marine food web structure and function are influenced by climate-driven change and anthropogenic stressors, leading to fine-scale environmental gradients and shifts, yet these dynamics remain poorly understood in Hudson Bay. Around the Belcher Islands in southeastern Hudson Bay is the proposed Qikiqtait study area of conservation interest and is an important area for the community of Sanikiluaq, where invertebrates, fish and marine mammals are all harvested. Qikiqtait is a unique marine area due to strong upwelling and relatively colder surface water temperatures, which lead to increased mixing and therefore increased nutrient availability and productivity. However, the hydrological cycle is changing due to increasing freshwater inputs, resulting in spatially and temporally variable primary production around the islands. Yet, knowledge of fine-scale spatial (tens to hundreds of kilometres) distributions in carbon source use, community composition and trophic interactions from invertebrates to marine mammals are scarce and understudied. Using a collection of complementary biotracer tools, community metrics, environmental data, and network analyses, I quantified spatial variation in food web structure, carbon pathways, and community composition across major taxonomic groups including benthic and pelagic invertebrates, fish, and marine mammals. The marine environment north of the Belcher Islands was cooler and more saline, with less pelagic primary production availability compared to the south, where the marine environment represented more freshwater influences, with warmer and less saline water and greater concentrations of pelagic primary production indicators like colour dissolved organic matter (CDOM) and chlorophyll-a. North of the islands supported higher benthic fish richness, shrimp and stalked tunicate dominance, and an overall greater reliance on sympagic (sea ice algae-derived) carbon, whereas the south supported dominance by brittle stars and Arctic cod (*Boreogadus saida*), and relatively greater trophic positions. Sympagic carbon reliance ranged from 13.09% to 73.43% in

euphausiids (*Thysanoessa* sp.) and bearded seals (*Erignathus barbatus*), respectively, with relatively greater proportions north of the islands in benthopelagic fish, sessile invertebrates, molluscs and decapods. Trophic positions ranged from 1.97 (molluscs) to 4.28 (beluga whales (*Delphinapterus leucas*)), with generally higher values in sessile invertebrates, decapods, and echinoderms in the south, except for jellies, which had higher trophic positions in the north. Food webs in the north had greater richness and benthic connectors, while the south had a mix of benthic and pelagic connecting species, yet connectance was similar. This study provides the first comprehensive characterization of the Qikiqtait food web at fine spatial and taxonomic scales, and is the first in an Arctic ecosystem to apply such a broad and integrative suite of state-of-the-art methods on such a wide range of species. This study demonstrated how local nutrient availability shapes community composition and resource use, and these insights advance our understanding of the mechanisms structuring Arctic ecosystems and inform conservation and management efforts.

Dedication

This work is dedicated to the community of Sanikiluaq, the Arctic Eider Society and the Sanikiluaq Hunters and Trappers Association. Your support and knowledge were essential to the completion of this research.

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Table of Contents

Abstract	i
Dedication	iii
Acknowledgements	iii
Table of Contents	v
List of Tables	vii
List of Figures	viii
Contributions of Authors	ix
Thesis Format.....	ix
Chapter 1: General Introduction	1
1.1 General Introduction	1
1.2 Study Area.....	5
1.3 Study Methods.....	6
1.3.1 Stable isotopes	6
1.3.2 Highly branched isoprenoids	7
1.3.3 Community composition	8
1.3.4 Stomach content analysis using DNA metabarcoding	8
1.4 Objectives and Hypotheses	9
1.5 References	11
Chapter 2: Spatial variation in carbon source use, community composition and trophic interactions arounds the Belcher Islands, Nunavut.....	23
2.1 Abstract	24
2.2 Introduction	25
2.3 Materials and Methods	29
2.3.1 Sample collection	29
2.3.2 Hydrographic data	32
2.3.3 Community composition analysis	33
2.3.4 Highly branched isoprenoid analysis.....	34
2.3.5 Stable isotope analysis.....	36
2.3.6 Stomach content analysis.....	37
2.3.7 Trophic position analysis.....	40
2.3.8 Food web modelling with EcoDiet.....	41
2.3.8 Statistical analysis.....	44

2.4 Results	45
2.4.1 Hydrographic data	45
2.4.2 Community composition	47
2.4.3 Sea ice algae reliance across functional groups.....	49
2.4.4 Trophic positions	52
2.4.5 Network properties	55
2.5 Discussion	58
2.5.1 Environmental context.....	59
2.5.2 Benthic community composition.....	59
2.5.3 Spatial variation in sea ice algae reliance across functional groups.....	63
2.5.4 Spatial variation in trophic positions throughout the food web.....	66
2.5.5 Network properties	70
2.6 Conclusion.....	73
2.7 Acknowledgements	74
2.8 References	75
Chapter 3: General Discussion.....	100
3.1 General overview	100
3.2 Limitations	102
3.3 Significance.....	103
3.4 Future research	105
3.5 References	107

List of Tables

Table 2-1. Definitions of structural network metrics used to describe food-web topology. Metrics were calculated from directed food-web graphs from EcoDiet representing trophic interactions among taxa. Taxa richness, number of trophic links and connectance were calculated as one metric for the entire network and Out Degree and Betweenness Centrality were calculated for consumer nodes and In-Degree was calculated for each node in the network.	43
Table 2-2. Mean (\pm standard deviation) of chlorophyll a and CDOM concentrations (mg/m^3), water temperature ($^{\circ}\text{C}$), and salinity (PSU) measured at the individual stations north and south of the Belcher Islands, with regional averages (\pm standard deviation).....	46
Table 2-3. Summary of the number of species, individual organisms and biomass per square metre of fish and invertebrates north and south of the Belcher Islands.	48
Table 2-4. Estimated iPOC by functional group and region. N represents sample size. Values are posterior means and medians with 95% credible intervals derived from a Bayesian generalized linear model with a beta distributed error. Δ iPOC (South – North) reflects modelled difference between South and North and Probability of Direction (pd) indicates the certainty that the effect is positive or negative.	50
Table 2-5. Estimated trophic position (TP) by functional group and region. N denotes the sample size. Mean $\delta^{15}\text{N}$ (\pm standard deviation) are calculated. Mean and median TP are posterior values with 95% credible intervals derived from a Bayesian multiple linear regression model assuming normality. Δ TP (South – North) reflects modelled difference between South and North and Probability of Direction (pd) indicates the certainty that the effect is positive or negative.....	53
Table 2-6. In-degree, out-degree and betweenness values for selected fish taxa in the networks north and south of the Belcher Islands. In-degree represents the number of prey per taxon, out-degree represents the number of predators per taxon and betweenness indicates the extent to which a taxon serves as a connector within the network. A dash (-) indicated absence of the taxon in that region.	56

List of Figures

Figure 2-1. Map of the stations sampled in eastern Hudson Bay north and south of the Belcher Islands. Stations sampled north of the islands are in blue and stations sampled south of the island are in orange.30

Figure 2-2. 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.46

Figure 2-3. Posterior distributions of estimated iPOC 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.51

Figure 2-4. 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: 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. B: 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.54

Figure 2-5. 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.57

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Natalie Vachon (thesis author) - conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing – original draft.

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David Yurkowski - conceptualization, funding acquisition, methodology, supervision, writing – review & editing.

Thesis Format

This thesis follows a grouped manuscript format. Chapter 1 presents a general introduction and background to contextualize the research. Chapter 2 is structured as a standalone manuscript, complete with its own abstract, introduction, methods, results, discussion, conclusion, acknowledgements, references, tables, and figures. Chapter 3 offers a synthesis of the findings, highlighting key conclusions from Chapter 2, and discusses the broader significance, limitations, and directions for future research.

Chapter 1: General Introduction

1.1 General Introduction

Food webs describe feeding relationships between predators and prey and illustrate the transfer of nutrients and energy from primary consumers to top predators in an ecosystem (Lindeman, 1942; Smith & Smith, 2009). Organisms in a food web can be compartmentalized into different trophospecies, which are groups of organisms that share the same predators and prey (Kortsch et al., 2015). These trophospecies can be further compartmentalized into functional units, arranged in a web based on trophic level and carbon source use, with links denoting the passing of energy from one trophospecies to another (Kortsch et al., 2015; Paine, 1980; Stouffer & Bascompte, 2011). The number of links between organisms and trophospecies in a food web (i.e., topology) can vary and change depending on the level of species richness, primary productivity, resource availability, competition, carnivory, generalism and omnivory that altogether influence the complexity of the food web (Stouffer & Bascompte, 2011; Vander Zanden & Rasmussen, 1996).

The links in a food web can vary in interaction strength, which is the level of dependency of a particular prey item to the diet of the predator (Paine, 1980), where food webs generally consist of many weak interactions (e.g., low reliance on a specific prey item) and a few strong interactions (i.e., high reliance on a specific prey item; Bascompte et al., 2005). Generally, weak interactions can be more stabilizing than strong interactions; however, it is the overall distribution and balance of weak and strong interactions throughout a food web that confers stability (Gilbert et al., 2014; Rosenzweig, 1971). For example, generalist species that are mobile and feed on a large range of resources generally have a higher amount of interactions within a food web, but those interactions are not as strong compared to some specialist species, which rely more heavily on one or a few prey species

(Bartley et al., 2019; Kortsch et al., 2015). Changes in these interaction strengths from strong to weak may result in cascading effects, resulting in changes involving up to four trophic levels by altering feeding relationships between organisms that may otherwise be strongly co-adapted to each other (Paine, 1980). For example, the collapse of Atlantic cod (*Gadus morhua*) and other commercially exploited benthic fish species off the coast of Nova Scotia resulted in a trophic cascade, where the abundance of smaller pelagic fish increased, the abundance of herbivorous zooplankton consumed by the pelagic fish decreased, and the abundance of grey seals (*Halichoerus grypus*) that consume the pelagic fish increased (Frank et al., 2005). Additionally, Yurkowski et al. (2017) showed that with the increased availability of capelin (*Mallotus villosus*) in Cumberland Sound, Nunavut, beluga whales and Greenland halibut (*Reinhardtius hippoglossoides*) increased their consumption of forage fish leading to a long-term change in the level of intraguild predation from a more predator-prey relationship to a more competitive one. Further, the structure (i.e., topology) and function (i.e., interaction strength) of food webs are also governed by how these connections respond to environmental variation (Kortsch et al., 2015; Tews et al., 2004). For instance, in response to accelerated warming in Arctic marine ecosystems causing reduced sea ice coverage and warmer water temperatures, the introduction of larger-sized generalist species has resulted in altered topology and interaction strengths in the food web whereby the food web has shifted from one that has more specialist species and stronger interaction strengths to a food web that consists of more generalist omnivore species and weaker interactions (Kortsch et al., 2019).

Food webs are composed of predator-prey interactions that influence species and individual survival, behaviour, and distributions as well as the biodiversity within an ecosystem (Holt, 1977; Preisser et al., 2005). Predators can have consumptive or non-consumptive effects, wherein consumptive predation occurs when predators kill and consume their prey, and non-consumptive, trait-mediated interactions occur when prey alter their

behaviour and distribution due to risks posed by predators (Preisser et al., 2005). Further, competition can directly or indirectly influence predator-prey interactions, where exploitative competitive interactions occur when a resource is shared between two species directly, and apparent competition occurs when two prey species share the same predator (Holt, 1977). Additionally, changes in prey density can alter predator consumption rates by shifting their position along the functional response curve (i.e., the rate of prey consumption at a given prey density; Hostetter et al., 2022; Solomon, 1949), and the presence of generalist, omnivorous predators can affect competition and predator-prey interactions (Condie et al., 2014; Griffith et al., 2019; Kortsch et al., 2015). Omnivory occurs when an individual feeds at more than one trophic level within a system (Pimm & Lawton, 1978), and can lead to alterations to the foraging ecology, niche structure and community composition in an area (Kortsch et al., 2015). Omnivory can differentially impact the stability of aquatic communities, where intermediate levels of omnivory can stabilize and diffuse top-down influences, thereby reducing the potential for trophic cascades (Bartley et al., 2019; Bascompte et al., 2005; Wootton, 2017).

There are several metrics that researchers use to quantify food web structure and function, including connectance, trophic positions, community composition, and carbon source use. Connectance is the degree of inter-connectivity in a food web, and is calculated as the proportion of potential trophic links that do occur ($C = L/S^2$), where L is the number of links and S is the number of different species in a food web (Dunne et al., 2002; Hattab et al., 2016; Thompson et al., 2012). The trophic position of an organism in a food web is a hierarchical assignment based on energy flow from primary producers to top predators, where the species assigned to each trophic level rely on at least one of the previous levels for energy sources (Lindeman, 1942). Metrics of community composition such as species richness and diversity are fundamental indicators of ecosystem health, with higher values typically linked

to increased ecosystem stability, productivity and ecosystem services (Palumbi et al., 2009; Tilman et al., 2014; Worm et al., 2006; Yang et al., 2025). Lastly, carbon source use from primary production can include a mix of sympagic-derived (i.e., sea ice) and pelagic-derived (i.e., phytoplankton) derived carbon, and is calculated as the percentage of sea ice derived carbon in the tissue of an organism (Belt, 2018; Brown et al., 2014). These metrics can be used to compare differences in food web structure and function with environmental conditions, such as sea ice coverage and water temperature (Amiriaux et al., 2023; Hattab et al., 2016; Kortsch et al., 2012; Pulliam, 2000; Thompson et al., 2012).

Arctic marine ecosystems are warming four times faster than the global average (Hoegh-Guldberg & Bruno, 2010; Rantanen et al., 2022). Higher temperatures in the Arctic are reducing sea ice coverage (Johannessen et al., 1999), resulting in warmer waters, and increased pelagic primary production (Arrigo et al., 2008), thus, resulting in new, suitable habitat for the range expansion of more warmer water-associated species, which have a different set of traits than Arctic species, such as larger body size, higher motility and a more generalist, omnivorous feeding behaviour (Frainer et al., 2017; Kortsch et al., 2015). These changing species distributions of generalists are influencing interspecific interactions within Arctic systems and rerouting the energy and carbon flows throughout the system, causing Arctic species to move northward, and altogether resulting in community-wide reorganizations and rewiring both the structure and the function of the ecosystem (Bartley et al., 2019; Fossheim et al., 2015; Frainer et al., 2017; Ward et al., 2025). Further, even at smaller spatial scales (e.g., southeastern Hudson Bay), the effects of changing species distributions can vary depending on abiotic factors in an area such as the presence/absence of polynyas, water temperatures or sea ice coverage (Bartley et al., 2019; Schindler, 2017).

1.2 Study Area

The study sites for this project are located north and south of the Belcher Islands in southeastern Hudson Bay, Nunavut, between 80.38 to 78.14°W and from 57.54 to 55.50°N (Figure 2-1), where the proposed Qikiqtait Study Area of conservation interest by both Inuit and Fisheries and Oceans Canada occur. This area is unique due to strong upwelling and relatively colder surface waters, which lead to increased nutrient availability and productivity (Yurkowski et al., 2023). However, the hydrological cycle is drastically changing due to increasing freshwater inputs, resulting in spatially and temporally variable primary production around the islands (Ridenour et al., 2019).

Hudson Bay has been experiencing both abiotic and biotic change over several decades (Ferguson et al., 2010; Yurkowski et al., 2023), yet the marine food webs of southeastern Hudson Bay have not yet been quantified. Further, most research on climate change and anthropogenic impacts to Arctic food webs has focused on one or a small set of key species, with little research focusing on the entire food web (Bartley et al., 2019; Gilman et al., 2010). Therefore, quantifying the structure and function that underpin the Arctic marine food web, using state of the art methods and a unique dataset that includes the entire food web from invertebrates to marine mammals at a fine scale, provides not only a reference point for future monitoring in southeastern Hudson Bay, but also critical insight into the ecological processes that drive ecosystem functioning in a rapidly changing environment. These findings will inform conservation and management efforts and contribute to a broader understanding of how environmental gradients at a relatively fine scale shape Arctic marine ecosystems.

1.3 Study Methods

1.3.1 Stable isotopes

Stable isotope ratios of animal tissues can be used to determine temporal and spatial insights into the trophic relationships and habitat use among organisms and develop trophic structure models (Layman et al., 2012; Peterson & Fry, 1987). Carbon and nitrogen stable isotope ratios are the most widely used for trophic and food web analysis applications. Carbon stable isotopic ratios of $^{13}\text{C}/^{12}\text{C}$ delineate the primary carbon source of consumers throughout the food web since producers, such as benthic macroalgae, have a diffusive boundary layer (>1mm thick), making it more ^{13}C -enriched, compared to phytoplankton (<10um thick) (France, 1995). Additionally, carbon stable isotopes generally experience less fractionation up the food web than nitrogen (Layman, 2007; Newsome et al., 2007; Peterson & Fry, 1987). Nitrogen isotopic ratios of $^{15}\text{N}/^{14}\text{N}$ reflect the relative trophic position of a species as a result of isotopic fractionation and routing between consumers and prey that are related to metabolism, protein quality and protein quantity (Caut et al., 2009; Layman, 2007, Layman et al., 2012; Post, 2002). The degree of trophic discrimination in carbon and nitrogen stable isotopes can vary due to multiple factors related to metabolism (e.g., diet, age, physiology), and therefore some taxonomic-specific discrimination factors have been developed (Caut et al., 2009). Further, because the trophic discrimination factors of $\delta^{15}\text{N}$ can vary across predators and prey, using a scaled approach with variable discrimination factors up the food web can more accurately account for taxonomic- and diet-specific variation in isotopic fractionation that occurs (Hussey et al., 2014; Stephens et al., 2023).

There are several factors one needs to account for that can bias results when conducting stable isotope analysis, including the presence of lipids and structural calcareous material in the tissues, as well as inferences on the turnover rates of stable isotopes in animal tissues. Lipids are ^{13}C depleted compared to proteins and carbohydrates because their

synthesis discriminates against the heavier ^{13}C isotope, biasing $\delta^{13}\text{C}$ values, and therefore must be accounted for via lipid extraction or normalization (DeNiro & Epstein, 1978; Post et al., 2007). Lipid extraction results in the removal of bias and uniform samples for analysis (Post et al., 2007; Sotiropoulos et al., 2004). Lastly, acidification is a technique used to remove inorganic carbonate (such as in brittle stars) that are not assimilated by predators from prey and would bias the carbon isotope signal due to carbonates being enriched in ^{12}C (Connolly & Schlacher, 2013). However, acid treatment can sometimes influence the isotope signatures of nitrogen, so it is generally used for tissues undergoing carbon stable isotope analysis only (Connolly & Schlacher, 2013). Further, it is important to be mindful that due to different metabolic activity and rate of new tissue generation, the turnover rates between tissue types can vary (Layman et al., 2012; Peterson & Fry, 1987; Vander Zanden et al., 2015). Tissues that are metabolically active and have a higher turnover rate, such as liver, provide more short-term information (days to weeks) while tissues that are relatively less metabolically active with a slower turnover rate, such as muscle, provide more long-term dietary information (e.g., several months) (MacNeil et al., 2006; Tieszen et al., 1983; Vander Zanden et al., 2015).

1.3.2 Highly branched isoprenoids

Highly branched isoprenoids (HBIs) can be used to trace sympagic and pelagic (phytoplankton-derived) carbon sources throughout the Arctic food web and are used to assess the use of sea ice algae versus phytoplankton at multiple trophic levels (Brown & Belt, 2012; Brown et al., 2013). HBIs are long chain alkenes, consisting of a 25-carbon chain with one, two or three carbon-carbon double bonds and are produced by marine diatoms associated with either sympagic or pelagic algae (Brown & Belt, 2011). IP25 (ice proxy 25) and IPSO25 (ice proxy Southern Ocean) are HBIs that are associated with sea ice algae, and HBI III is

associated with pelagic algae (Brown et al., 2014; Brown & Belt, 2012; Brown et al., 2013). The HBIs are highly stable and become embedded in organism tissues such as livers, where ~70% of the HBIs are stored (Brown et al., 2013), and can be detected in tissues of organisms throughout the food chain (Belt, 2018; Brown et al., 2014; Brown & Belt, 2012; Brown et al., 2013).

1.3.3 Community composition

Community metrics like species richness and diversity are fundamental indicators of ecosystem health, with higher values typically linked to increased ecosystem stability, productivity and ecosystem services (Palumbi et al., 2009; Tilman et al., 2014; Worm et al., 2006; Yang et al., 2025). Species richness, defined as the number of distinct species in a given area, is one of the oldest and most intuitive measures of biodiversity (Magurran, 2004). Diversity builds on richness by incorporating the relative abundance of each species. The Shannon-Wiener index is a widely used diversity metric that accounts for both richness and evenness, where evenness describes how evenly individuals are distributed across species (Magurran, 2004). The Shannon-Wiener index usually falls between 1.5 and 3.5 and this narrow range can be challenging to interpret. As an alternative, the inverse Shannon index provides a more intuitive estimate of the effective number of equally common species (Magurran, 2004; Whittaker, 1972). Further, species evenness can be quantified independently using Pielou's evenness index, which is the ratio of observed diversity to the maximum possible diversity under equal species abundance (Pielou, 1966).

1.3.4 Stomach content analysis using DNA metabarcoding

Visual analysis of stomach contents is the traditional approach for studying fish diets (Hynes, 1950); however, digestion of prey can limit identification potential and there may be biases

towards certain taxonomic groups that take longer to disintegrate in the stomach (Cordone et al., 2021; Hoenig et al., 2022; Nielsen et al., 2018). Hard-bodied prey, such as crustaceans, are more easily identified visually because their exoskeletons can resist digestion and persist longer in the stomach (Carreon-Martinez et al., 2011; Nielsen et al., 2018). In contrast, soft-bodied organisms, such as worms and jellyfish, degrade rapidly during digestion and are therefore more challenging to identify morphologically (Carreon-Martinez et al., 2011). Similarly, immature prey that lack fully developed morphological features are also challenging to identify, particularly to lower taxonomic levels (Sakaguchi et al., 2017). Based on high-throughput sequencing of a standardized DNA region, DNA metabarcoding can overcome these limitations and resolve diet items to the species level, including soft-bodied or highly digested prey that are often missed by visual analysis (Nielsen et al., 2018; Pompanon et al., 2012; Symondson, 2002). DNA metabarcoding can identify diet items to species level using general primers and PCR to amplify part the CO1 gene that is found in all animals and is the most available sequence region in public libraries (Leray et al., 2013; Nielsen et al., 2018); however, the success of this method depends on both the degree of prey digestion within the stomach contents and the availability of matching sequence data in reference libraries (Liu et al., 2021).

1.4 Objectives and Hypotheses

The objective of this thesis was to assess spatial variation in trophic interactions, food web properties and benthic fish and invertebrate community composition between the north and south Belcher Islands in relation to the environment. Specifically, I compared patterns between a region of greater freshwater influence to the south of the islands and a region of lesser freshwater influence to the north. This study is based on a unique and comprehensive sample collection of an Arctic coastal food web, encompassing 82 invertebrate species and 27

fish species from both benthic and pelagic zones, and 3 marine mammal species (ringed seals (*Phoca hispida*), bearded seals, and beluga whales). To achieve these objectives, I applied a combination of scientific tools, including stomach content analysis via DNA metabarcoding, stable isotope and highly branched isoprenoid analysis.

The objective of my data chapter (Chapter 2) was to assess spatial variation in carbon source use (sea ice algae- versus phytoplankton-derived) among consumers, benthic community composition (species richness, biomass, diversity), trophic positions of consumers and food web structure between north and south of the Belcher Islands. I hypothesized that differences in hydrographic conditions (e.g., water temperature, salinity, and pelagic primary production availability) would influence carbon source use and that organisms in the north, which is not as influenced by freshwater as those to the south, would show stronger reliance on sea ice-derived carbon, higher benthic diversity and species richness, and a more complex food web structure with greater connectivity. This is based on the hypotheses that sea ice algae promotes a more productive and diverse benthos and that greater species richness can promote a food web with greater connectivity (Niemi et al., 2024; Yunda-Guarin et al., 2023).

First, I assessed spatial variation in carbon source use by quantifying the contribution of sea ice algae- and phytoplankton-derived carbon in fish and invertebrate consumers using highly branched isoprenoid analysis. Second, I examined regional differences in benthic community composition, including species richness, biomass and diversity metrics. Lastly, I examined regional variation in trophic structure by comparing trophic positions and evaluating key network metrics, including link density, connectance, in-degree (number of prey), out-degree (number of predators), and betweenness (species acting as connectors in the network).

1.5 References

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Chapter 2: Spatial variation in carbon source use, community composition and trophic interactions arounds the Belcher Islands, Nunavut

2.1 Abstract

Arctic marine food webs are undergoing rapid change as climate warming and anthropogenic stressors alter sea ice dynamics, hydrology, and primary production. The proposed Qikiqtait area of conservation interest in southeastern Hudson Bay is unique, with strong upwelling, colder surface water and increased nutrient availability, but the hydrological cycle is changing. Knowledge of fine-scale spatial patterns in carbon source use, community composition and trophic interactions across taxa are scarce and understudied. I integrated stable isotope analysis, highly branched isoprenoids, DNA metabarcoding, community metrics and network analysis to characterize the marine food web from invertebrates to marine mammals and reveal regional differences at fine spatial (tens to hundreds of kilometres) and taxonomic scales. Bearded seals and benthic fish relied most on sympagic carbon (73.43% and 68.36%), while beluga whales, ringed seals and bearded seals had the highest trophic positions (4.28, 3.91 and 3.89). North of the islands was colder and more saline, with less pelagic primary production compared to the south. The northern benthos had greater fish species richness and was dominated by shrimp and tunicates, whereas in the south, brittle stars and Arctic cod were more dominant. North of the islands, benthopelagic fish, molluscs, sessile invertebrates and decapods relied on more sympagic carbon and central consumers were more benthically associated. South of the islands, sessile invertebrates, echinoderms and decapods had higher trophic positions and central consumers were a mix of benthic and pelagic species. These results provide the first fine-scale, ecosystem-wide baselines around Qikiqtait, advancing understanding of Arctic coastal food web drivers and identifying potential vulnerabilities under climate-driven change.

2.2 Introduction

Food webs describe feeding relationships and the transfer of energy and nutrients 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 species richness, productivity and resource availability, competition, and the balance of generalist and specialist interactions throughout the ecosystem (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 few 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). Further, 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 impacts like 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, and longer ice-free seasons, and leading to increased pelagic primary production (Arrigo et al., 2008; Hoegh-Guldberg & Bruno, 2010; Johannessen et al., 1999; Rantanen et al., 2022). These changes are driving 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, Emblemstvig 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. 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; Fraimer et al., 2017). Further, a key feature of Arctic productivity is sea 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) and supports rapid feeding, post-winter growth, and may be preferentially consumed over pelagic phytoplankton by some benthic organisms (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 a sea ice algae carbon bank, storing sympagic carbon in sediments 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 (Amiriaux et al., 2023; Koch et al., 2021; Yurkowski et al., 2020). As such, shifts in the phenology, quantity or availability of sea ice algae may influence the structure and function of Arctic food webs (Niemi et al., 2024).

The proposed Qikiqtait study area of conservation interest, located around the Belcher Islands in southeastern Hudson Bay, is also an important harvesting area for the local community of Sanikiluaq. Qikiqtait is a unique marine area due to strong upwelling and relatively colder surface water temperatures, which lead to increased mixing and therefore increased nutrient availability and productivity (Yurkowski et al., 2023). However, the hydrological cycle is undergoing significant changes due to increasing freshwater inputs, resulting in spatially and temporally variable primary production around the islands (Guzzi et al., 2024; Ridenour et al., 2019; Yurkowski et al., 2023). Despite increasing evidence of these changes in Arctic ecosystems, our understanding of Arctic coastal food webs across Hudson Bay remains limited. Data on key metrics, such as connectance, trophic positions, carbon source use and community composition, are scarce in Hudson Bay, particularly at spatial scales fine enough to capture ecological patterns across the environmental gradients within a particular area of Hudson Bay. Without this level of detail, it is challenging to identify the underlying mechanisms (i.e., energy transfer, competitive interactions, and benthic-pelagic coupling) that shape this ecosystem and to identify the specific factors that could drive regime shifts (Fisher et al., 2015; Kortsch et al., 2019). Further, most research on climate change impacts to food webs focuses on one or a small key set of species, with little research focusing on the entire food web from invertebrates to top predators (Bartley et al., 2019; Gilman et al., 2010). Using a collection of complementary biotracer tools, community metrics, environmental data, and network analyses, we quantified spatial variation in food web structure, carbon pathways, and community composition across all major taxonomic groups including benthic and pelagic invertebrates, fish, and marine mammals. This study provides the first comprehensive characterization of the Qikiqtait food web at fine spatial and taxonomic scales, and is the first in an Arctic ecosystem to apply such a broad and integrative suite of state-of-the-art methods on such a wide range of species.

The objective of this study was to assess trophic interactions, food web structure and complexity, and community composition north and south of the Belcher Islands in relation to spatial variation in key marine environment characteristics including primary production, salinity and water temperature. Food web structure and function can be quantified using metrics such as connectance, trophic position, carbon source use, and community composition, which altogether can capture the number and strength of trophic interactions and the flow of energy and carbon through ecosystems (Belt, 2018; Brown et al., 2014; Dunne et al., 2002; Hattab et al., 2016; Lindeman, 1942; Thompson et al., 2012). 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 source and habitat use, and trophic position, respectively (Boecklen et al., 2011), while highly branched isoprenoids have been extensively used across Arctic environments to examine consumer use of sea ice and phytoplankton carbon sources (Brown & Belt, 2012; Koch et al., 2023). Although DNA metabarcoding of consumer stomach contents is increasingly used in diet studies, this is the first study to integrate DNA metabarcoding of stomach contents with the Bayesian hierarchical model “EcoDiet”. EcoDiet is an R package (Hervann 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 (Hervann et al., 2022). EcoDiet has been applied in temperate and tropical marine ecosystems, including the Celtic Sea (Hervann 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.

We hypothesized that regional hydrographic differences (e.g., water temperature, salinity, CDOM and chlorophyll a) would influence carbon source use and food web structure. Reflecting the more freshwater-influenced environmental conditions south of the islands, characterized by lower salinity, higher water temperatures and greater pelagic primary production availability compared to the north, we expected organisms north of the Belcher Islands to show stronger reliance on sea ice-derived carbon, greater benthic species richness and diversity, and a more complex, highly connected food web. By establishing a baseline of food web structure, carbon pathways and community composition in this region, this study provides insight into how environmental gradients shape marine ecosystems. In turn, this study offers insight into the mechanisms that structure Arctic ecosystems and, further, will provide a reference point for future studies to monitor changes and will set the stage for conservation and management in southeastern Hudson Bay.

2.3 Materials and Methods

2.3.1 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 57.54 to 55.50°N (Figure 2-1) in August 2023 aboard the *RV William Kennedy* at nine stations located either north or south of the Belcher Islands.

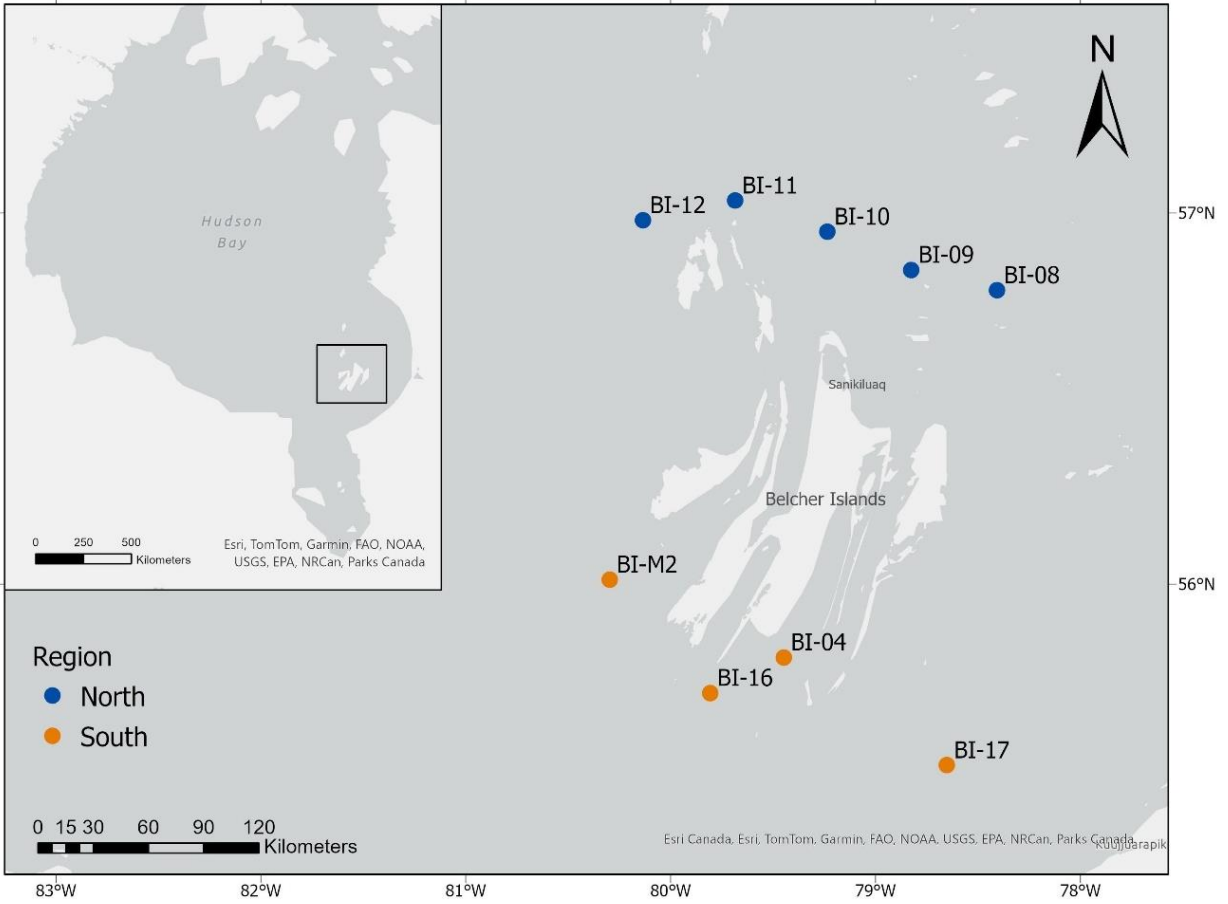


Figure 2-1. Map of the stations sampled in eastern Hudson Bay north and south of the Belcher Islands. Stations sampled north of the islands are in blue and stations sampled south of the island are in orange.

To collect larger zooplankton, a bongo net (two nets, 0.5m diameter, 500µm mesh) was towed obliquely at each station for 15 minutes at approximately 2 knots speed-over-ground. The tow line was let out at 2m/s to within 10m of the seafloor and retrieved at 0.5m/s. A flow meter was attached to each net to determine filtration volume, and an RBR Solo depth sensor was used to record depth of the tow. Invertebrate and fish samples were sorted into the lowest taxonomic resolution possible and frozen (-20°C). In total, 805 zooplankton individuals were collected from the north and 985 from the south, including jellies (n = 159, n = 15 south), arrow worms (n = 542 north, n = 820 south), euphausiids (n = 54 north, n = 0 south), mysids (n = 0 north, n = 16 south), pelagic amphipods (n = 27 north, n = 69 south), pteropods (n = 2 north, n = 4 south), decapods (n = 8 north, n = 61 south), and other amphipods (n = 13 north, n = 13 south). Benthic invertebrates and fish were collected using a 3m wide Hi-lift beam trawl, towed for 7-15 minutes at ~2 knots speed-over-ground at each station. Over ~8566 m² in the north and ~9786 m² in the south, benthic invertebrates collected include decapods (n = 1325 north, n = 395 south), amphipods (n = 200 north, n = 260 south), molluscs (n = 20 north, n = 15 south), echinoderms (n = 8 north, n = 2668 south), and sessile invertebrates (n = 88 north, n = 52 south) for a total of 1641 from the north and 3390 from the south. Fish collected included capelin and sandlance (n = 1 north, n = 1 south), Arctic cod (n = 8 north, n = 53 south), sculpins (n = 48 north, n = 2 south), blennies (n = 42 north, n = 14 south), snailfish (n = 5 north, n = 5 south), alligatorfish (n = 3 north, n = 2 south), poachers (n = 3 north, n = 20 south), eelpouts (n = 7 north) and flatfish (n = 1 north) for a total of 118 from the north and 99 from the south. Additional invertebrate and fish samples were collected during coastal sampling efforts using a benthic sled (invertebrates) and gillnets (3 - 4in) for pelagic fish. Marine mammal samples, including muscle (ringed seals: n = 12; bearded seals: n = 7), liver (beluga whales: n = 7) 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 arrow worms, small amphipods and brittle stars. Fish and marine mammals were similarly subsampled for muscle (stable isotopes), liver (highly branched isoprenoids), and stomach contents (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.

2.3.2 Hydrographic data

Hydrographic profiles were collected using conductivity, temperature, and depth (CTD) sondes. At each station, two identical, pump-type Seabird 19plus V2 CTDs were deployed, each equipped with Biospherical scalar photosynthetically active radiation (PAR) sensors,

Seabird SBE-43 dissolved oxygen sensors, and Seabird/WetLabs ECO fluorometer sensors for CDOM and Chl *a*. The environmental variables analyzed include water temperature (°C), salinity (PSU), chlorophyll *a* (mg/m³) and CDOM (mg/m³).

2.3.3 Community composition analysis

Community composition was assessed using metrics including total biomass (g/m²), species richness, diversity and evenness, and calculated separately for the northern and southern sampling regions. Total biomass was calculated for each region by summing the biomass of all fish and invertebrate taxa collected by benthic beam trawl and normalized to square meter units (g/m²) 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 *Ophiuroid* brittle stars retained), biomass was corrected to estimate the total biomass for that taxon.

The total area swept by the trawl was calculated as:

$$\text{Total Area Swept (m}^2\text{)} = \text{Trawl Width (3m)} * \text{Distance Travelled (m)}$$

Where:

$$\text{Distance Travelled} = \text{Towing Speed(m/s)} * \text{TowDuration (s)}$$

Species richness was defined as the total number of distinct taxa identified in each region and was normalized to per square metre of the area swept. Community diversity was quantified using the Shannon diversity index (H'), calculated as:

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

Where p_i is the proportional abundance (or 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. The resulting value represents the number of equally abundant species required to produce the observed Shannon Diversity:

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

To assess evenness of species distributions, Pielou's evenness index (J') was calculated as:

$$J' = \frac{H'}{\ln(S)}$$

Diversity and evenness metrics were calculated using both abundance-based (counts) and biomass-based data. Abundance-based metrics capture numerical dominance in community structure, account for rare species, and describe ecosystem complexity in terms of the number of traits present, while biomass-based metrics emphasize the contribution of larger or more ecologically influential taxa and reflect available energy in an ecosystem (Bambach, 1993; Singh et al., 2025).

2.3.4 Highly branched isoprenoid analysis

Between 5 and 9 samples of muscle (from invertebrates) and liver (from fish and marine mammals) were selected haphazardly per species and per region, 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 provide sufficient material, such as in small amphipods or the livers of small fish species like blennies

and sculpins, multiple individuals of the same species 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 gas (N₂) stream, resuspended in hexane and fractionated using 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 relative to sea ice-derived HBIs (Brown & Belt, 2017):

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

Here, III represents phytoplankton-derived carbon sources, while IP₂₅ and II represent sea ice-derived sources. A higher H-print value indicates a greater reliance on phytoplankton-derived primary carbon sources, whereas a low H-print indicated greater reliance on sea ice algae-derived primary carbon sources (Brown & Belt, 2017).

H-print values were further used to estimate the proportion of sea-ice derived primary organic carbon (iPOC%) (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 sea ice-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, invertebrate 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 jellyfish.

2.3.5 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 with carbonate-rich (CaCO_3) tissues, 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 (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 μg , and fish and marine mammal muscle and liver samples from 400-600 μg . 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 isotope ratios are expressed in per mil (‰) using delta (δ) 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 δ values and values below the standard yield negative δ 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 $\leq 0.20\%$ 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% for $\delta^{15}\text{N}$ and 0.07% 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% for $\delta^{15}\text{N}$ and -0.21 , 0.21 and 0.18% for $\delta^{13}\text{C}$.

2.3.6 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, online photos of species, and dichotomous keys, enumerated, and weighed. This method allowed for the quantification of prey that are more resistant to digestion and thus more likely to be identifiable. Hard-bodied prey such as crustaceans are more easily identified based on the shape of their exoskeleton, which are hard to digest and persist longer in the stomach. In contrast, soft-bodied organisms such as worms and jellyfish are more challenging to identify due to their rapid degradation during digestion (Carreon-Martinez et al., 2011). Similarly, immature prey that lack fully developed morphological features are also challenging to identify, particularly to lower taxonomic levels (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 15mg (or as much material 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) following the manufacturer's protocol, with an added step where 4µl of RNase A (100mg/ml) was added to each sample and incubated for 2 minutes at room temperature following the lysis stage. Extracted DNA was quantified and normalized to approximately 20ng/ul 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 mICOfintF / 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; Gielings 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-per-sample basis.

Themisto libellula was 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.

2.3.7 Trophic position analysis

Trophic positions (TPs) of consumers around the Belcher Islands were estimated using a step-wise, one-source model based on $\delta^{15}\text{N}$ values, following the approach of Post (2002). This method estimated TP using $\delta^{15}\text{N}$ values relative to a baseline primary consumer and where one can apply group-specific trophic discrimination factors (TDFs) to account for physiological and tissue-specific isotopic fractionation (Hussey et al., 2014). Therefore, I used a scaled trophic position estimation approach since tissue discrimination factors (TDF) of consumers typically decrease with increasing prey $\delta^{15}\text{N}$ values up the food web.

$$TP_{consumer} = TP_{baseline} + \frac{\delta^{15}N_{consumer} - \delta^{15}N_{baseline}}{TDF}$$

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*), which had 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 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). Alternative baseline taxa were tested for several consumers. For seals and beluga whales, other piscivorous prey including *Myoxocephalus*

sculpins were tested as alternative baselines but similarly produced TP values consistent with those based on the estimates with Arctic cod (e.g., 4.31 ± 0.17 vs. 4.28 ± 0.17 for beluga whales, 4.01 ± 0.34 vs. 3.91 ± 0.34 for ringed seals and 3.99 ± 0.27 vs. 3.89 ± 0.27 for bearded seals).

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 liver (for only Arctic char), 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).

2.3.8 Food web modelling with EcoDiet

The EcoDiet statistical model was applied to integrate stable isotope data with presence/absence data from visual and metabarcoding stomach content data. 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 (Hervann 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 (Hervann 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 included a manageable number of fish families with adequate sample representation for the model, while the diversity of prey items was much higher, and grouping them below order would have resulted in too many categories with limited data and singularities. Migratory fish such as Arctic char, as well as marine mammals, were removed from the analysis due to 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 2-1 for definitions). Taxa richness, number of trophic links, link density and connectance were calculated at the network level, while out-degree and betweenness were calculated for consumer nodes, and in-degree was calculated for all nodes.

Table 2-1. Definitions of structural network metrics used to describe food-web topology. Metrics were calculated from directed food-web graphs from EcoDiet representing trophic interactions among taxa. Taxa richness, number of trophic links and connectance were calculated as one metric for the entire network and Out Degree and Betweenness Centrality were calculated for consumer nodes and In-Degree was calculated for each node in the network.

Food-web attribute	Meaning
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 ²)	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.

2.3.8 Statistical analysis

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 ($^{\circ}\text{C}$), salinity (PSU), chlorophyll a (mg/m^3) and CDOM (mg/m^3). Regional variation in these parameters were used to contextualize spatial patterns observed in the biological data.

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 sea 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 sea ice algae reliance and trophic positions included Genus as a random effect to account for repeated measures and uneven sample sizes across taxa, while 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).

2.4 Results

2.4.1 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 ± 1.49 °C vs. 7.81 ± 3.02 °C).

Indicators of primary production were also lower at the northern stations, which had lower concentrations of chlorophyll a (3.94 ± 0.69 mg/m³ vs. 4.68 ± 1.63 mg/m³) and CDOM (10.90 ± 0.69 mg/m³ vs. 15.29 ± 1.70 mg/m³). In contrast, average salinity was higher at the northern stations relative to the southern stations (27.84 ± 0.34 vs 26.51 ± 1.26 PSU) (Table 2-2; Figure 2-2). Bayesian multiple linear regression assuming normality, accounting for variation between sample stations, further supported these patterns, showing strong posterior support for higher pelagic primary production south of the islands based on CDOM (pd = 1.00, CI = 3.02 – 6.58) and chlorophyll a concentrations (pd = 0.92, CI = -0.34-1.54). 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 2-2).

Table 2-2. Mean (\pm standard deviation) of chlorophyll a and CDOM concentrations (mg/m^3), water temperature ($^{\circ}\text{C}$), and salinity (PSU) measured at the individual stations north and south of the Belcher Islands, with regional averages (\pm standard deviation).

Region	Station	Chl A (mg/m^3)	CDOM (mg/m^3)	Water temperature ($^{\circ}\text{C}$)	Salinity (PSU)
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
Average North		3.94 ± 0.69	10.90 ± 0.69	6.01 ± 1.49	27.84 ± 0.34
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
Average South		4.68 ± 1.63	15.29 ± 1.70	7.81 ± 3.02	26.51 ± 1.26

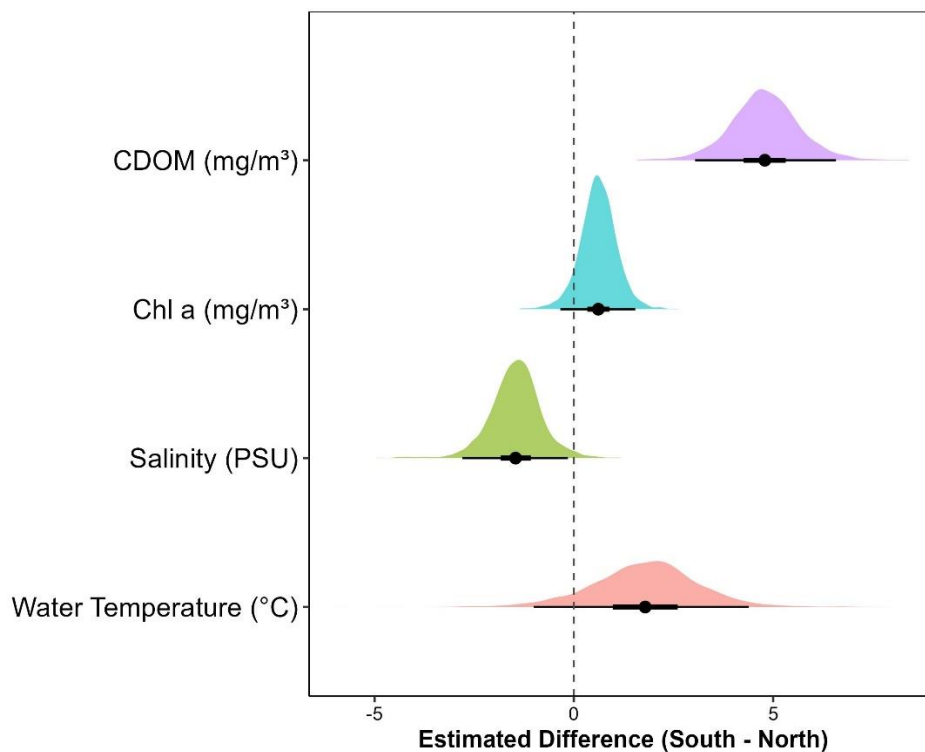


Figure 2-2. Posterior distributions of estimated differences in environmental variables (South – North) from Bayesian multiple linear regression models assuming normality, with station as a random effect. Points show the posterior mean, thick bars the 50% credible intervals, and thin bars the 95% credible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

2.4.2 Community composition

Among the fish, species richness was higher north of the islands compared to south (21 vs. 9 species, respectively), but, total fish biomass per square metre was greater in the south (0.26g/m^2) than the north (0.09g/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 (0.38g/m^2 in the north vs. 0.32g/m^2 in the south) (Table 2-3).

Based on abundance data, which can describe numerical dominance and ecosystem complexity of functional traits present, Shannon's diversity index indicated greater diversity among benthic invertebrates and fish in the north ($H' = 2.95$) compared to the south ($H' = 1.46$). In other words, the diversity in the north is equivalent to having about 19 species all equally common, whereas in the south it is equivalent to only about 4 equally common species. When calculated using biomass data (available energy), diversity was more similar between regions ($H' = 2.63$ in the north vs. 2.47 in the south), which is roughly equivalent to about 14 equally common species in the north and 12 in the south.

Pielou's evenness index, which measured how evenly individuals are distributed among species, followed the same trend. Evenness based on abundance data was higher in the north ($J' = 0.69$) than in the south ($J' = 0.36$), and evenness based on biomass data was similar between regions ($J' = 0.62$ in the north and $J' = 0.61$ in the south).

Table 2-3. Summary of the number of species, individual organisms and biomass per square metre of fish and invertebrates north and south of the Belcher Islands, where the total area trawled north in the north was ~8566 m² and the total area trawled in the south was 9786 m².

Group	Region	Total no. species	Total no. individuals	Biomass (g/m²)
Fish	North	21	119	0.09
	South	9	97	0.26
Invertebrate	North	50	1641	0.38
	South	50	3390	0.32

2.4.3 Sea ice algae reliance across functional groups

The highest overall sea ice algae reliance by a species occurred in bearded seals ($73.43\% \pm 7.55\%$), followed by benthic fish ($68.36\% \pm 25.48\%$). The overall lowest sea ice algae reliance was found in euphausiids ($13.09\% \pm 2.75\%$), beluga whales ($15.86\% \pm 3.78\%$), 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 showed 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 jellies (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 2-4; Figure 2-3). Sea ice algae reliance (iPOC%) 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).

Table 2-4. Estimated iPOC by functional group and region. N represents sample size. Values are posterior means and medians with 95% credible intervals derived from a Bayesian generalized linear model with a beta distributed error. Δ iPOC (South – North) reflects modelled difference between South and North and Probability of Direction (pd) indicates the certainty that the effect is positive or negative.

Group	North		South		Δ 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
Jellies	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

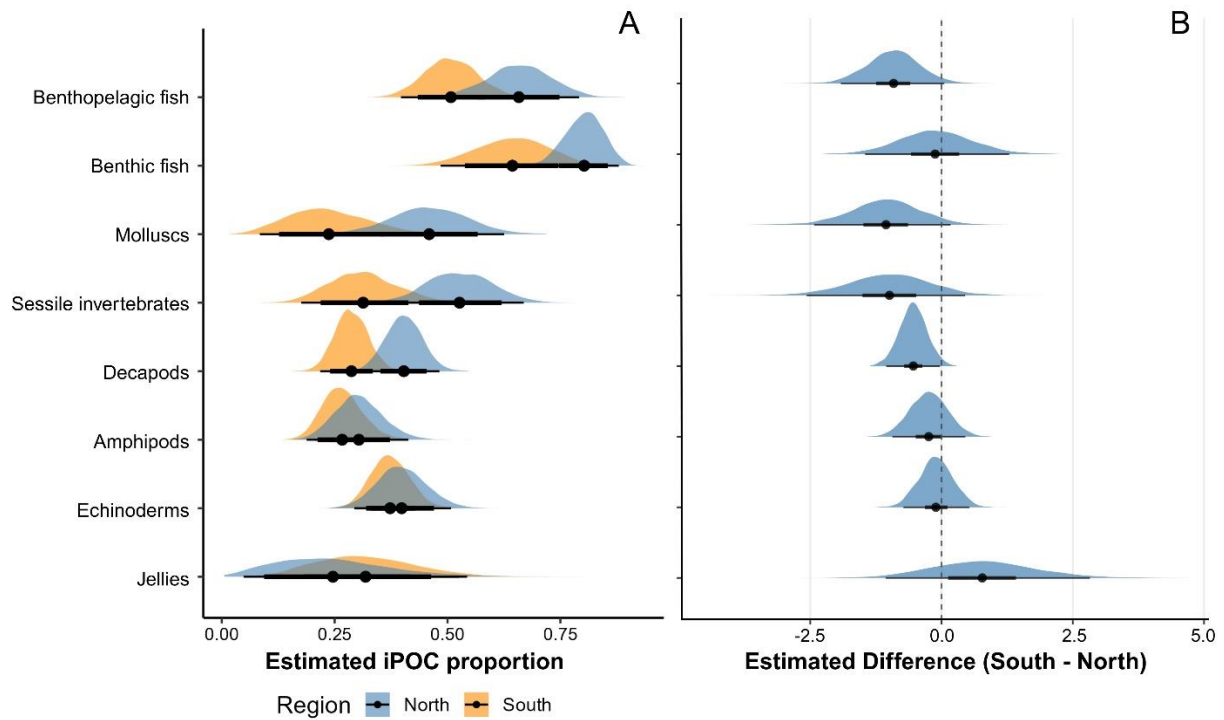


Figure 2-3. Posterior distributions of estimated iPOC proportions for each functional group by region (A) and posterior distributions of regional differences in estimated iPOC proportions (South – North) by functional group (B). A: Distributions represent posterior estimates from a Bayesian generalized 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.

2.4.4 Trophic positions

Overall, beluga whales exhibited the highest average trophic position (TP = 4.28 ± 0.17 ; $\delta^{15}\text{N} = 15.91 \pm 0.54$; n = 20), followed by ringed seals (TP = 3.91 ± 0.34 ; $\delta^{15}\text{N} = 14.81 \pm 0.80$; n = 12) and bearded seals (TP = 3.89 ± 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 ± 0.41 north; 3.87 ± 0.48 south), followed by benthic fish (3.57 ± 0.38 north; 3.64 ± 0.29 south) and arrow worms (3.39 ± 0.05 north; 3.39 ± 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 jellies 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 arrow worms (pd = 0.51, CI = -0.25 – 0.27) (Figure 2-4; Table 2-5).

Table 2-5. Estimated trophic position (TP) by functional group and region. N denotes the sample size. Mean $\delta^{15}\text{N}$ (\pm standard deviation) are calculated. Mean and median TP are posterior values with 95% credible intervals derived from a Bayesian multiple linear regression model assuming normality. Δ TP (South – North) reflects modelled difference between South and North and Probability of Direction (pd) indicates the certainty that the effect is positive or negative.

Group	North			South			Δ 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
Jellies	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
Arrow worms	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

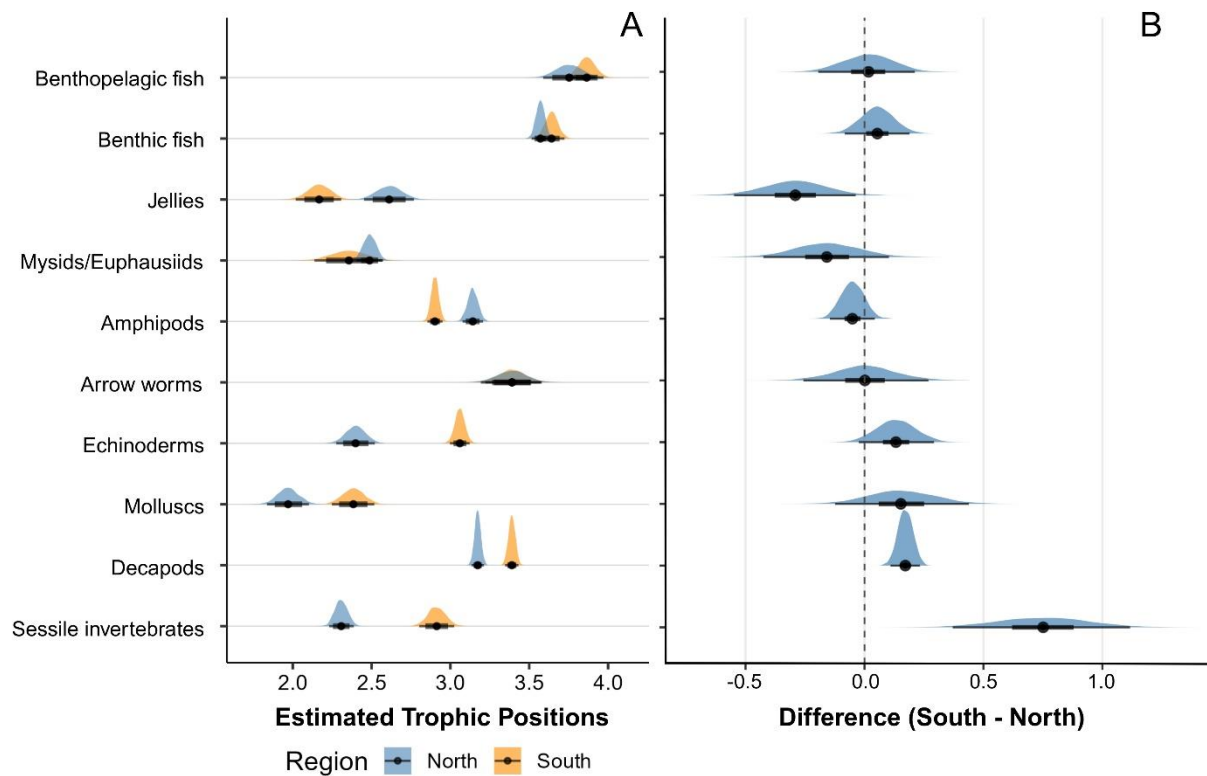


Figure 2-4. Posterior distributions of estimated trophic positions for each functional group by region (A) and posterior distributions of regional differences in estimated trophic positions (South – North) by functional group (B). A: Half-eye plots represent the posterior median (point), 50% (thick line), 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. B: 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 the median.

2.4.5 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 higher 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 between the regions (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 predator's 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 2-6). Food web network diagrams were constructed from EcoDiet posterior link probabilities, with link thickness scaled to reflect interaction strength (Figure 2-5). In both regions, benthic and benthopelagic fish families (i.e., Cottidae, Liparidae (snailfish), Gadidae) occupied central positions within the food web. The northern network displayed a greater number of strong trophic links compared to the south. Regional differences in taxa were also present, where Osmeridae (capelin) appeared as both prey and consumer in the north but were 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.

Table 2-6. In-degree, out-degree and betweenness values for selected fish taxa in the networks north and south of the Belcher Islands. In-degree represents the number of prey per taxon, out-degree represents the number of predators per taxon and betweenness indicates the extent to which a taxon serves as a connector within the network. A dash (-) indicated absence of the taxon in that region.

	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 family Salmonidae in the diet of other predators.

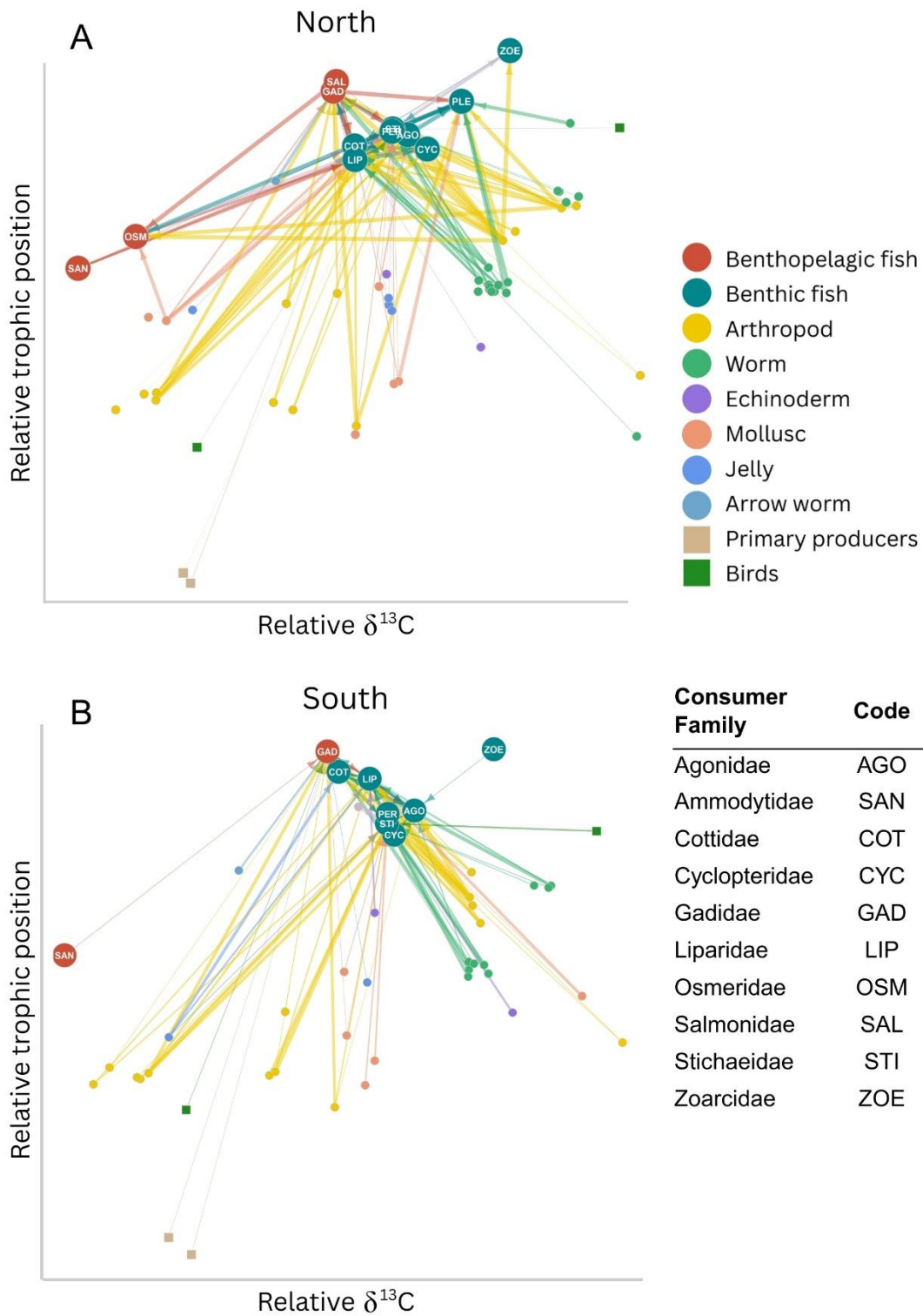


Figure 2-5. Trophic network plots for the networks north (A) and south (B) of the Belcher Islands based on EcoDiet outputs. Nodes represent taxa, with large labelled nodes indicating fish species and smaller coloured nodes representing prey taxa, coloured by phylum. The x-axis reflects relative $\delta^{13}\text{C}$ 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.

2.5 Discussion

This study provides the first comprehensive characterization of benthic community composition, carbon flow, trophic structure and food web characterization of an area within Hudson Bay (i.e., the Qikiqtait region) at a finer spatial scale (~100km x ~150km) by integrating stable isotopes, highly branched isoprenoids, DNA metabarcoding, and trophic network analysis across a wide range of taxa, from primary consumers to top predators. Regional contrasts in community composition, carbon source use, and food web structure were shaped by variation in environmental gradients. North of the Belcher Islands was characterized by cooler, saltier waters with lower pelagic production, higher benthic fish richness, greater invertebrate biomass (dominated by shrimp), and higher abundance-based diversity. In contrast, the south was more influenced by freshwater inputs, with greater pelagic productivity and dominance by brittle stars and Arctic cod. Greatest sympagic (ice algae-derived) carbon reliance was found in bearded seals and benthic fish, and organisms in the north relied on relatively more sympagic (sea ice algae-derived) carbon, especially 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, and the trophic position of jellies were higher in the north. Food web analysis showed higher species richness, link density, and broader diets in the north, but the same level of connectance between regions. Network centrality revealed more benthic connector species in the north and mixed benthic-pelagic connectors in the south, suggesting distinct but stable food web structures shaped by regional environmental conditions north and south of the islands.

2.5.1 Environmental context

Environmental conditions differed in the upper 25m of the water column between the north and south regions of the Belcher Islands. South of the islands, higher chlorophyll a, CDOM 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, particularly from James Bay and the La Grande River, which has experienced extensive hydroelectric developments and variable freshwater outputs throughout the year (Guéguen et al., 2011; Guzzi et al., 2024). These conditions support greater phytoplankton biomass, photosynthetic activity, and pelagic primary production, providing more resources for pelagic feeders (Li et al., 2019). These regional environmental differences set the stage and support the observed variation in carbon pathways, community structure and trophic interactions across regions, which are discussed in more detail below.

2.5.2 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, consistent with cooler, more saline waters with relatively less pelagic primary production, 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/abundance, and can reach densities up to 500/m² (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 generalists, suspension feeding with the ability to capture and consume small prey (Volage et al., 2021; Warner et al., 1982; Yokoyama & Amaral, 2008). Despite their low caloric value, brittle stars are common prey of crabs and fishes (as seen in the stomach of snailfish south of the Belcher Islands) (Burukovsky et al., 2021; Hüsey et al., 2016), and suspension-feeding brittle stars can enhance benthic-pelagic coupling (Ambrose et al., 2001; Blicher & Sejr, 2011; Dinevik et al., 2025), consistent with their prominence in the south, where pelagic production was higher and benthic fish richness (and thus predation pressure) was lower.

In contrast, abundance and biomass north of the islands were dominated by shrimp, potentially due to a combination of cooler and more stable temperatures, and more suitable habitat conditions such as soft sediments that support epibenthic and deposit-feeding strategies (Birkely & Gulliksen, 2003; Krawczyk et al., 2024; Li et al., 2020). 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). Furthermore, the decapod group (primarily composed of shrimp) exhibited greater reliance on sea ice algae-derived carbon in the north compared to the south, suggesting increased benthic foraging on a more nutritionally rich sympagic resource. 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 primary production compared to the recent environmental shifts observed in the south. The high abundance of shrimp north of the islands may serve as

an important resource for higher trophic levels. 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 (*Aspidophoroides*), cod (*Boreogadus*), flatfish (*Hippoglossoides*), sculpins (*Icelus*, *Triglops*, *Myoxocephalus*) and blennies (*Leptoclinus*), whereas south of the islands, shrimp were only detected in cod (*Boreogadus* and *Gadus*). 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 structure complexity and heterogeneity in an environment, providing shelter, and altering hydrodynamic conditions. Off the east coast of Canada, stalked tunicate beds are associated with greater abundance of brachiopods and sessile cnidarians, and provide shelter for larger, mobile species like fish and crabs (Francis et al., 2014), and these beds likely play a similar role in Qikiqtait.

Fish assemblages also reflected spatial contrasts, where species richness was considerably higher in the north (21) compared to the south (9). Multiple species of benthic fish were found in the north and not the south, such as the fourline snakeblenny (*Eumesogrammus*), eelpouts (*Lycodes*), flatfish (*Hippoglossoides*), lumpstickers (*Eumicrotremis*) and sculpins (*Icelus* and *Triglops*), which are all species that feed largely on worms (indicating a soft benthos) and crustaceans (Coad & Reist, 2016). Fish biomass was greater in the south, driven by the dominance of Arctic cod, reflecting both a large catch at one southern station and relatively higher local pelagic productivity supporting cod aggregations. Stomach content analysis showed that cod primarily consumed calanoid copepods, *Themisto* amphipods, and arrow worms, consistent with previous studies (Maes et al., 2022; Majewski et al., 2016; Walkusz et al., 2013; Walkusz et al., 2011). Arctic cod is 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 strongly reflected in patterns of diversity and evenness north and south of the islands. Abundance-based metrics, which capture numerical dominance, account for rare species, and describe ecosystem complexity in terms of the number of traits present (Bambach, 1993), were higher in both diversity and evenness in the north compared to the south. This pattern was driven by the numerical dominance of brittle stars in the south, where they accounted for ~75% of all individuals, skewing the numerical evenness. In contrast, biomass-based metrics emphasize the contribution of larger taxa and reflect available energy in an ecosystem (Bambach, 1993; Singh et al., 2025), and biomass-based diversity was more similar between regions, suggesting that, despite numerical differences, the overall availability of biomass for resource use remained comparable.

Arctic marine community composition can be shaped by complex interactions among physical and biological factors, including primary productivity (and its source), sediment characteristics, topography, and species-specific traits (Anderson, 2008; Cusson et al., 2007; Loreau & de Mazancourt, 2013; Macpherson, 2002; Michel et al., 2012; Pierrejean et al., 2020; Rosenzweig, 1995; Yang et al., 2025). While temperature, salinity, and productivity are widely acknowledged drivers in Arctic 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 tunicates 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 ophiuroids and light availability for cephalopods (Saeedi et al., 2022). South of the Belcher Islands, the high abundance of brittle stars might be an effect of their tendency to aggregate in large groups and form dense patches, as most 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), as climate change is rapidly altering environmental conditions, with cascading effects on biodiversity, food web connectivity and structure and ecosystem functioning (Hattab et al., 2016; Michel et al., 2012).

2.5.3 Spatial variation in sea ice algae reliance across functional groups

Sea ice algal reliance (iPOC%) was highest overall in bearded seals ($73.4\% \pm 7.6\%$), aligning with findings reporting a similar average among bearded seals across the Canadian Arctic ($68.0\% \pm 29.7\%$; Ferguson et al., 2025). This high reliance is 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.

Sea ice algal reliance was consistently lower south of the islands in primary consumers such as molluscs, sessile invertebrates, and decapods. The molluscs (primarily *Chlamys islandica*) and sessile invertebrates (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 the species in this group was observed in parrot shrimp (*Spirontocaris spinus*), with individuals north of the islands showing sea ice algal reliance values of >40%, compared to <25% in the south, potentially driving the overall regional pattern. These results align with those found by Combaz et al. (2025), where deposit feeders and predators/scavengers (e.g., shrimp) relied more on sympagic carbon sources compared to suspension feeders. Because suspension feeders like molluscs and sessile invertebrates primarily reflect the availability of carbon sources in the water column, their diets in the south likely reflect greater pelagic nutrient 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 sea 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 from benthic primary consumers 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 and pelagic (phytoplankton-derived) resource channels. Sea 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 sea ice algal reliance via benthic foraging. This is further consistent with the north being dominated by shrimp in terms of both benthic biomass and abundance.

Among marine mammals, bearded seals showed the highest sea ice algae reliance, followed by ringed seals and beluga whales, reflecting their feeding strategies wherein bearded seals forage benthically (Pauly et al., 1998; Young et al., 2010), whereas ringed seals are generalist predators feeding on prey from both the benthic and pelagic zones (Chambellant et al., 2013; Dehn et al., 2007; Ogloff et al., 2019; Yurkowski et al., 2016), and beluga whales are primarily foraging on pelagic-associated capelin and other fish species like Arctic cod (Breton-Honeyman et al., 2016; Kelley et al., 2010). Together, these results suggest that carbon from sea ice algae plays a more prominent role through the food web north of the Belcher Islands than in the south, which has greater pelagic primary production. By linking sea ice algae reliance to food web connections and community composition, we can begin to trace the flow of difference carbon sources throughout the food web in relation to environmental conditions. Ongoing climate change is altering the dynamics of sea 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 pelagic primary production (Comiso, 2012; Johannessen et al., 1999). These changes favour generalist fish species with broad diets and greater mobility (Fossheim 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 (Fossheim 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 on megafauna was highly correlated ($r^2 = 0.754$) with sea ice duration. As such, shifts in the timing, quantity or availability of sea ice algae may influence the structure and function of Arctic food webs (Niemi et al., 2024). The greater contribution of sea ice algae-derived carbon to the food web north of the islands, together with colder and more saline waters, suggests that future warming and increased freshwater influence (as observed south of the islands) could shift northern carbon pathways toward more pelagic sources. This would reduce the availability of nutrient-rich sea ice algae-derived carbon sources for key benthic-pelagic couplers, with potential cascading effects to higher trophic levels, including bearded seals, which currently obtain >70% of their diet from sea ice algae-derived sources.

2.5.4 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 jellies, each occupying higher trophic positions south of the Belcher Islands except for jellies, 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, re-suspended detritus, and potentially small zooplankton (Shick, 1991; Yahel et al., 2007). Relatively higher proportions of sea ice algae-derived carbon sources in sessile invertebrates north of the islands indicate a greater consumption of pelagic resources south of the islands. Regional differences in trophic

positions in the sessile invertebrates could be representative of small zooplankton being filtered, or spatial variation in baseline $\delta^{15}\text{N}$ as an effect of the higher freshwater influences south of the islands, where we observed higher CDOM and chlorophyll a concentrations. 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 $\delta^{15}\text{N}$. Thus, observed regional differences could be a result of 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 has been reported to feed on sponges, benthic cnidaria, and can scavenge on upper pelagic predators (Katrin 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 sea ice algae-derived carbon sources, where decapods south of the islands were relying on less sea ice algae carbon sources compared to those in the north.

Finally, jellies 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 like jellies 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 increasing water temperatures correlate with an increase in jellyfish abundance, and because they forage on ichthyoplankton, this could prevent fish stocks from recovering (Lynam et al., 2011). Around the Belcher Islands, higher trophic position of jellyfish 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 arrow worms (3.39 in both). The benthopelagic fish group (primarily Arctic cod) north of the islands consumed a wide array of prey (copepods, decapods, arrow worms, and benthic fish) and showed higher proportions of sea ice algae-derived carbon in their tissue, whereas south of the islands, they were feeding primarily on copepods and arrow worms, with lesser

contributions from other taxa and lower proportions of sea ice algae-derived carbon. Arrow worms 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 53mm, 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 53mm, and were 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 (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 have specialized vibrissae to feed on 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.

2.5.5 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 the same 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 that have higher connectance as a result of 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 between regions suggests no current evidence of food web restructuring between the regions. Over time, though, continued anthropogenic and climate-driven change may render the conditions south of the islands to be increasingly favourable for the expansion of generalist predators, potentially altering food web structure in the future.

The greater number of nodes and higher link density observed north of the Belcher Islands likely reflected 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 wider diet breadths 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). Similarly, larger and more connected food webs, often shaped by range-expanding species, have been linked to increased dietary generalism and omnivory (Kortsch et al., 2015; Pecuchet et al., 2020). However, in this study, species with broader diets were not newcomers but characteristic Arctic taxa, suggesting that local prey availability, rather than species turnover, is driving this pattern. Moreover, reliance on sympagic carbon was higher in the north across several taxonomic groups, supporting the notion that sea ice algae enhances benthic productivity and complexity, thereby promoting wider diet breadths (Niemi et al., 2024).

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 centered 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. Supporting these observations, the fish with the greatest in-degree (number of prey taxa per predator) were the same as those with the greatest

betweenness, emphasizing that key benthic and benthopelagic fishes act as versatile consumers. Similarly, out-degree results identified poachers and sculpins as the most consumed fish taxa in the north, and sculpins as the most consumed fish taxa in the south, suggesting their key role as energy sources sustaining multiple predators. The prominence of small, benthic fishes in 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 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. The salmonid species in this region (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.

2.6 Conclusion

Overall, our integrative and collective use of multiple tools to characterize the Qikiqtait food web revealed clear regional differences in community composition, resource use and food web structure. Organisms north of the Belcher Islands tended to have a greater reliance on sea ice algae-derived carbon, while trophic positions were generally higher in the south, reflecting more primary pelagic consumer resource availability. 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 between 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. Sessile invertebrates and molluscs showed greater reliance on sea ice algae-derived source north of the islands, where stalked tunicates were also among the top contributors to benthic biomass. While nutrients from phytoplankton and riverine discharge are available in both regions, sea ice algae is more nutrient-dense, particularly in essential fatty acids (Amiriaux et al., 2019). These sessile organisms act as key benthic-pelagic couplers and biogenic habitat modifiers, contributing both nutritional resources to secondary consumers and structural complexity to the benthos, thereby supporting food web stability and broader community structure and function. This novel work provides a regional baseline of food web structure, carbon pathways and community composition, and will inform conservation and management processes in southeastern Hudson Bay, a region experiencing climate-driven and anthropogenic changes.

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Chapter 3: General Discussion

3.1 General overview

My MSc thesis investigated fine-scale spatial variation in Arctic coastal food web structure and function across multiple taxonomic groups around the Belcher Islands in southeastern Hudson Bay, a region of ecological and cultural significance and part of the proposed Qikiqtait study area of conservation interest. This study provided the first fine-scale, ecosystem-wide characterization of trophic structure, carbon source use and community composition across benthic invertebrates, fish and marine mammals in this region.

Chapter 2 used a suite of biotracers ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes and highly branched isoprenoids), DNA metabarcoding for diet analysis, along with environmental data and network analysis to explore variation in community composition, carbon source use and trophic interactions north and south of the Belcher Islands. Overall trophic positions ranged from 1.97 (molluscs) to 4.28 (beluga whales), with the highest values observed in marine mammals and the lowest in jellies and molluscs. Bearded seals and benthic fish exhibited the highest overall sympagic carbon reliance (73.43% and 68.36%, respectively), and euphausiids and beluga whales exhibited the lowest overall sympagic carbon reliance (13.09% and 15.86%, respectively).

Waters north of the islands were colder and saltier, with lower pelagic primary production availability, greater fish species richness, a benthos dominated by shrimp and stalked tunicates, and greater abundance-based diversity and evenness. Sympagic (sea ice-derived) carbon reliance was higher north of the islands, particularly in sessile invertebrates, molluscs, decapods and benthopelagic fish. The northern food web was also more taxonomically rich, with a higher average link density and benthic fish acting as central consumer species. In contrast, waters south of the islands were warmer and fresher (i.e., less

saline), reflecting stronger freshwater influence, and also had greater indicators of pelagic productivity (CDOM and chlorophyll a). The benthic community composition south of the islands was dominated by brittle stars and Arctic cod, with generally lower sympagic carbon source use and higher trophic positions, particularly in sessile invertebrates, echinoderms and decapods. Central consumers in the food web south of the islands were a mix of benthic and benthopelagic species, and overall food web connectance was comparable between regions.

My results suggested that freshwater influence, likely driven by currents from James Bay and runoff from La Grande River (housing several large hydroelectrical developments), alters baseline nutrient dynamics and primary production regimes across this relatively small latitudinal gradient (55.6° to 57.0°) between north and south of the Belcher Islands. These environmental gradients likely drive resource use, trophic structure, community compositions and species interactions. Given that sympagic carbon is more nutritionally dense than pelagic sources, these findings suggest that increased freshwater inputs and reductions in sea ice may especially impact sessile or less mobile benthic taxa that rely on the nutrients in the water column, such as tunicates, anemones, sponges, barnacles, scallops, mussels and sea cucumbers, many of which play important roles in benthopelagic coupling. While studies conducted over broader spatial scales (i.e., hundreds to thousands of kilometres) likely overlook fine-scale variation, my thesis demonstrated that examining ecosystems at finer spatial scales (tens to hundreds of kilometres) can reveal significant differences in ecosystem structure in response to anthropogenic and climate-driven change. These results provide a critical ecological baseline for the Qikiqtait region and emphasize the need for ongoing monitoring to inform conservation and management decisions under a rapidly changing Arctic climate.

3.2 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, there were a limited number of samples, especially those for highly branched isoprenoid analysis, so all stations in the south and all in the north had to be bulked as one area to reach suitable sample sizes. This may have masked finer-scale variation in community composition, trophic positions and resource use. For example, while brittle stars were dominant in both biomass and abundance south of the islands, the majority were collected at a single station. Given that brittle stars often form dense, localized aggregations, this observation may reflect a local feature rather than a widespread characteristic of the community composition south of the islands. Nonetheless, very few brittle stars were collected at all five northern stations, supporting the conclusion that brittle star dominance is a feature more representative of southern sites and represent regional differences. Furthermore, variability between the stations within each region was lower than the differences observed between north and south, reinforcing the strength of the regional patterns detected in this study and the quality of the dataset for this region.

Although overall DNA metabarcoding enhanced dietary resolution compared to visual stomach content analysis, there were limitations. Some prey taxa may have been underrepresented due to incomplete reference libraries, particularly for Arctic taxa. For instance, *Themisto* amphipods were visually 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 either to DNA degradation or insufficient species or regional representation in the reference database. 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 covered in reference libraries, and many studies also rely on a single region (Gielings et al., 2021). Lastly, although the EcoDiet model used here did not require diet quantity data, a limitation of DNA metabarcoding is that it cannot reliably estimate relative quantities of diet items because of primer bias (Liu 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 the 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, often lacking diet proportion data to the taxonomic specificity required. Additionally, stable isotope data were not available for many of the smaller or soft-bodied prey taxa (e.g., small copepods or worms) that were not captured via the trawls or pelagic nets. These sample sizes and data gaps required the aggregation of taxa into broader groups in order for the model to meet convergence, potentially masking some even finer scale trophic dynamics or differences between regions. Ultimately, while this study provides the first fine-scale, multi-taxa assessment of food web structure and function around Qikiqtait, addressing these limitations will help improve these analyses.

3.3 Significance

This study is the first comprehensive characterization of the Qikiqtait food web at fine spatial and taxonomic scales and is the first in an Arctic ecosystem to apply such a broad and integrative suite of state-of-the-art methods on such a wide range of species. Although applying EcoDiet and applying DNA metabarcoded stomach content data to EcoDiet has been proposed as a future direction in the literature (Hervann et al., 2022; Kuile et al., 2022;

Thompson et al., 2025), this study is the first to do so. Further, this study 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).

This study also provided key insights into marine ecosystem health and resilience in Hudson Bay, a rapidly changing Arctic marine region experiencing both climate-driven and anthropogenic change. Mid-trophic level organisms in this region remain chronically understudied (Hoover et al., 2013), yet they are both harvested by the local community of Sanikiluaq (scallops, sea cucumbers and urchins) and support 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 nutrient availability shaped community composition and resource use, with potential implications for these harvested species through disruptions to benthic-pelagic coupling, shifts in prey biomass, and changes in prey quality. As anthropogenic and climate-driven change progresses in the Arctic, the resulting alterations in prey availability and nutrient pathways may cascade through the food web, altering both ecosystem structure and function, as well as the resources available for harvested species.

By providing the first fine-scale, ecosystem-wide baseline of community composition, resource use, and trophic interactions north and south of the Belcher Islands, this study establishes a reference point from which to detect and monitor future change. Our results demonstrate that, by examining patterns at fine spatial and taxonomic scales, we can reveal relationships that broader-scale studies may overlook. In turn, these insights advance our understanding of the mechanisms structuring Arctic ecosystems and inform conservation and management efforts that can be applied in the future and to other systems.

3.4 Future research

Future research should prioritize long-term monitoring of this region, as Arctic marine regions are experiencing significant species distribution shifts linked to climate-driven changes. For example, Arctic char have shifted diets from ice-associated invertebrates to pelagic fish like capelin in areas experiencing variable sea ice dynamics ((Faulkner et al., 2024; Ulrich & Tallman, 2021) and ringed seals have changed their foraging patterns, increasing niche size in relation to shifts in forage fish abundance (Yurkowski et al., 2016). Given that generalist predators adapt to prey availability, continued monitoring of prey availability in this region could enable an integration of predator resource use, spatial variation and prey availability. Furthermore, characterizing benthic habitat features such as sediment type and structural benthic features may explain spatial variations in organism distributions and identify correlations among habitat characteristics, environmental parameters, resource use and biodiversity.

While this study used broad taxonomic groups, future research should incorporate the emerging application of functional trait analysis. This approach categorizes organisms by traits (e.g., size, motility, foraging strategy) rather than taxonomy, recognizing that even within a Family or Order, species may exhibit a wide range of traits that influence spatial variation in habitat use, resource use and trophic roles. A first step here would be to identify the traits most relevant to ecosystem function, then these traits could be used as a way to monitor the functional diversity of the ecosystem, as well as the status of key ecosystem features such as species abundances and distributions shift. For example, traits such as “filter feeding” can be linked to ecosystem processes like benthic-pelagic coupling and nutrient cycling, and “calcareous” organisms can be used to monitor calcification in an ecosystem (Fraschetti, 2025). Similarly, (Bevilacqua et al., 2009) found that molluscs (benthic filter feeders) can serve as effective indicators of benthic health, suggesting that species already

present around the Belcher Islands can be used as surrogates from which to monitor ecosystem change. Further, future research should also prioritize targeting prey taxa that were underrepresented here, particularly infauna like polychaetes as well as small pelagic species like copepods that were abundant in the stomach contents. Finally, to contextualize these findings more broadly, comparative studies across other Arctic regions should also be conducted, relating food web structure to varying environmental parameters, spatial gradients and sea ice characteristics across coastal areas in the Canadian Arctic as well as between coastal and offshore areas.

3.5 References

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