An investigation into marine environments in the eastern Canadian Arctic

by

Madeleine Rosalia Prater

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Master of Science
in
Biology (Water)

Waterloo, Ontario, Canada, 2023

Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Arctic marine environments are especially vulnerable to climate change, but detailed scientific data for these ecosystems are lacking due to their remote location and the associated logistical challenges of conducting research. Arctic marine ecosystems support the culture, well-being, and nutritive needs of northern Indigenous communities, and there is an urgent need to advance knowledge that can inform effective conservation and adaptation measures. To prioritize and facilitate research in understudied Arctic marine environments, Fisheries and Oceans Canada has identified certain marine areas as ecologically and biologically significant areas (EBSAs). EBSAs are considered to be uniquely important for the Arctic environment in general, and for certain species that frequent them.

In this thesis, I first focused on synthesizing recent research that is applicable to several EBSAs in the Hudson Bay Complex. Literature published between 2011 and 2021 indicates that changes in sea surface temperature and sea ice extent are impacting primary production patterns, which are causing bottom-up shifts that affect the entire food web. Projection models indicate that these bottom-up shifts will continue in future as warming increases and sea ice declines. The species of most concern, and most reported on, in the eastern Hudson Bay EBSAs was the COSEWIC-designated threatened eastern Hudson Bay beluga, which was the focus of 62% of papers published on biota. The review highlighted ongoing gaps in research, including studies of lower trophic level biota and whole ecosystems, and will be used during preparation of an upcoming Canadian Science Advisory Secretariat (CSAS) report.

In response to the lack of research conducted on lower trophic level biota and whole food webs (reported on in chapter 2), I conducted a study on marine food web structure in Frobisher Bay, NU. Inuit who rely on the fish, mammal, and invertebrate resources of Frobisher Bay have demonstrated an interest in learning more about food webs at a variety of depths, particularly in the context of increased industrial activity in the area (i.e., construction of a deep-water port that opened in July 2023). Mid- to lower-tropic level Arctic marine species were included in the analyses, and comparisons of food web structure were made among three different depths. The trophic ecology of understudied benthic suspension feeders and benthic carnivores was examined in more detail than other functional feeding groups, and compared among depths and between groups. Three depths were included: nearshore Frobisher Bay (10 to 15 m), midshore Frobisher

Bay (20 to 45m), and offshore Frobisher Bay (260 to 351m). Food web structures were quantified using nitrogen, carbon, and sulphur stable isotope analysis. Metrics used to compare food webs included isotope ranges, isotope means, niche volume, diversity (indicated by centroid distance), redundancy (indicated by nearest neighbour distance), and evenness (indicated by standard deviation of nearest neighbour distance).

Isotope-based food web metrics were unexpectedly similar among all three depths. I hypothesize this is due to the large tidal influence in Frobisher Bay, which can move ~17km^3 of water in and out of the bay in a single day. Benthic-pelagic coupling appeared to be strongest at the midshore food web, as indicated by larger δ^{13}C and δ^{34}S ranges, higher diversity, and higher redundancy found in the food web at this depth. The isotope ecology of benthic carnivores had similar among-depth patterns as those observed for total food web structure; however, benthic suspension feeders differed at the offshore depth. Isotopic niche volume for benthic suspension feeders was largest at the offshore depth, likely due to the large sulphur range. I suggest that this could be due to more enriched δ^{34}S available at the offshore depth, potentially due to more anoxic conditions at the sediment-water interface compared to the two shallower depths.

This study represents the first comprehensive investigation of food web structure among depths in Frobisher Bay, and results highlight the uniqueness of Frobisher Bay and fill gaps in knowledge on lower trophic level Arctic marine species and their interactions among depths; however, future research is needed to further understand the tidal influence on food web structure and energy flow in Frobisher Bay.

Acknowledgements

I would like to start by thanking my supervisor Dr. Heidi Swanson for her continuous support and her never ending supply of back up plans. No matter what was thrown at us during this project, she always had a solution. I have learned so much throughout this degree and am very appreciative for all her support and guidance. I would also like to thank my supervisor Dr. Kevin Hedges for all his support and for finding samples for my project in the midst of a global pandemic. Thank you to my committee, Dr. Kirsten Müller and Dr. Simon Courtenay for their wonderful feedback and encouraging words during my constantly evolving project.

Many people were involved in sample collection even before I knew that I would be using these samples so a big thanks to all those people. Chris Lewis and team in Iqaluit led the collection of samples over several years. I would like to especially thank Dr. Ashley Ehrman for sending me samples from Frobisher Bay and being a sounding board for my analysis. I would also like to thank Dr. Tracey Loewen for assisting me with sample coordination in Winnipeg.

A special thanks to everyone in the Swanson lab for their continuous support and mentorship. Whether it was teaching me how to weigh stable isotopes for the first time, helping me with statistical errors, or reviewing my thesis chapters, everyone was super encouraging and helped me get through this chapter of my life.

Lastly, I would like to thank my family and friends who have been hearing about my project for so long and have been tremendously supportive throughout this journey. Special thanks to Fab Prater, Adrian Prater, and Robert Prater for always encouraging me to follow my own path.

Table of Contents

List of Figures

List of Tables

1.0 Introduction

Marine ecosystems in the Canadian Arctic are vast, remote, understudied, and contribute significantly to local and global economies, as well as to global environmental patterns and processes. One of the largest marine industries is fishing with the value of the top three commercial fishing species estimated at $86.3 million per year. The subsistence value of Arctic char (*Salvelinus alpinus*) is estimated at over $7 million but that does not include the benefits of improved community health, supporting cultural traditions and values, food security, and reinforcement of social connections (Department of Environment 2016). Arctic sea ice functions as a global cooling system by reflecting solar energy back into space through the albedo effect (Pistone et al. 2014; Timmermans and Marshall 2020), and marine sediments store a substantial amount of carbon, which contributes to global temperature (McGuire et al. 2009). Furthermore, the Arctic sea ice and freshwater inputs influence the Atlantic Oceanic circulation (Sévellec et al. 2017). Climate warming is affecting a myriad of physical and biological processes in Arctic marine ecosystems through both direct and indirect mechanisms (Hoover et al. 2013a; Lavoie et al. 2013; Steiner et al. 2013), and many of these effects are currently poorly understood. This is particularly true at larger scales of biological organization, such as at the scale of whole food webs, where interactions among species, and with the physical environment, are incompletely characterized. Marine ecosystems in the Canadian Arctic extend from James Bay, Ontario, to the polar shelf. More than 70% of Canada's coastal environments are located at Arctic latitudes (Niemi et al. 2019). The Canadian Arctic is home to many Indigenous people, including most of Canada's Inuit population, who have occupied the land for longer than Canadian records have existed (Simon 2011). Despite environmentally harsh conditions, a diverse array of organisms, including several charismatic megafauna mammal species (e.g., polar bears (*Ursus maritimus*), walrus (*Odobenus rosmarus*), beluga whale (*Delphinapterus leucas*)), migrating birds (e.g., eider duck (*Somateria spectabilis*)), fishes (e.g., Arctic char (*Salvelinus alpinus*), Greenland halibut (*Reinhardtius hippoglossoides*), and invertebrates (e.g., sea snails (*Limacina helicina*) and shrimp (*Pandalus borealis*) are supported by marine ecosystems in the Canadian Arctic (e.g., Niemi et al. 2019). As climate change and other stressors, including development, accelerate, it is critically important to increase our understanding of abiotic and biotic characteristics and processes that support these species, and the human populations that rely on them.

Despite the diversity and spatial expanse of Arctic marine environments, they are relatively understudied. This is partly because it is so difficult to physically obtain data, due to inclement weather and [now mostly seasonal] ice coverage (Gosselin et al. 2013; Hammill et al. 2016; Gosselin et al. 2017; Pierrejean et al. 2020). There is also a severe lack of sustainable, year-round, accessible (i.e., not a military site) northern infrastructure where research can be conducted (Beaulieu 2008). Additionally, collaboration can be difficult due to the interdisciplinary and international nature of Arctic research (Ernakovich et al. 2021). Specialization among fields such as technology, biology, social science, and health remain a challenge in Arctic research. Even within the discipline of marine biology, studies often focus on a single species or a single predator and prey relationship rather than holistic, multi-trophic level interactions (e.g., DFO 2012; Pomerleau et al. 2012; Watt et al. 2013; Doniol-Valcroze et al. 2014; DFO 2017; Gosselin et al. 2017; DFO 2020). These challenges inevitably lead to gaps in our knowledge of Arctic marine ecology.

Canada is one of five core Arctic countries including: Canada, Denmark, Norway, Russia, and the United States (Hong 2014), and is host to 25% of the world's Arctic environment (The Arctic Institute 2022). In recognition of the responsibility Canada has to protect the Arctic environment, the Canadian government has taken many efforts to encourage and regularly update research within Arctic marine environments. In 2001, Fisheries and Oceans Canada formed the Canadian Science Advisory Secretariat (CSAS) to prioritize, coordinate, and peer-review scientific research, and ultimately to provide advice on issues related to conservation, stewardship, and management of freshwater and marine resources. One of the focal topics for CSAS reports are "ecologically and biologically significant areas" (EBSAs); EBSA reports are intended to be updated at regular (i.e., once per decade) intervals. There are five Arctic marine biogeographic regions in Canada and within those regions there are 38 ecologically and biologically significant areas (Fig. 1.1) (DFO 2011). EBSA reports discuss topics such as physical oceanography, fish stocks, marine protected areas, aquatic resources, and species at risk (DFO 2011). While there is some mention of benthic habitat and invertebrates, many of the evaluation metrics for EBSAs are focused on marine mammals, birds, and fish; there is a general lack of research on benthic invertebrates (DFO 2011c). Other authors have also commented on the lack of Arctic benthic literature compared to marine mammals and fish (Wassmann et al. 2011), and that there is a need for more holistic studies in remote areas, such as the deep sea and benthic environments (Werner et al. 2016). This gap in research and knowledge regarding Arctic marine benthic environments is particularly important to address because coupling processes (e.g., benthic-pelagic coupling) that affect overall biological productivity are subject to considerable change imposed by anthropogenic stressors (Wassmann and Reigstad 2011; Hoover et al. 2013; Roy et al. 2015). In addition, benthic invertebrates can be especially helpful bio-indicators due to their relatively sessile nature and sensitivity to environmental changes (Oleszczuk et al. 2021). As such, increasing our understanding of these taxa and their habitats could advance development of future monitoring initiatives.

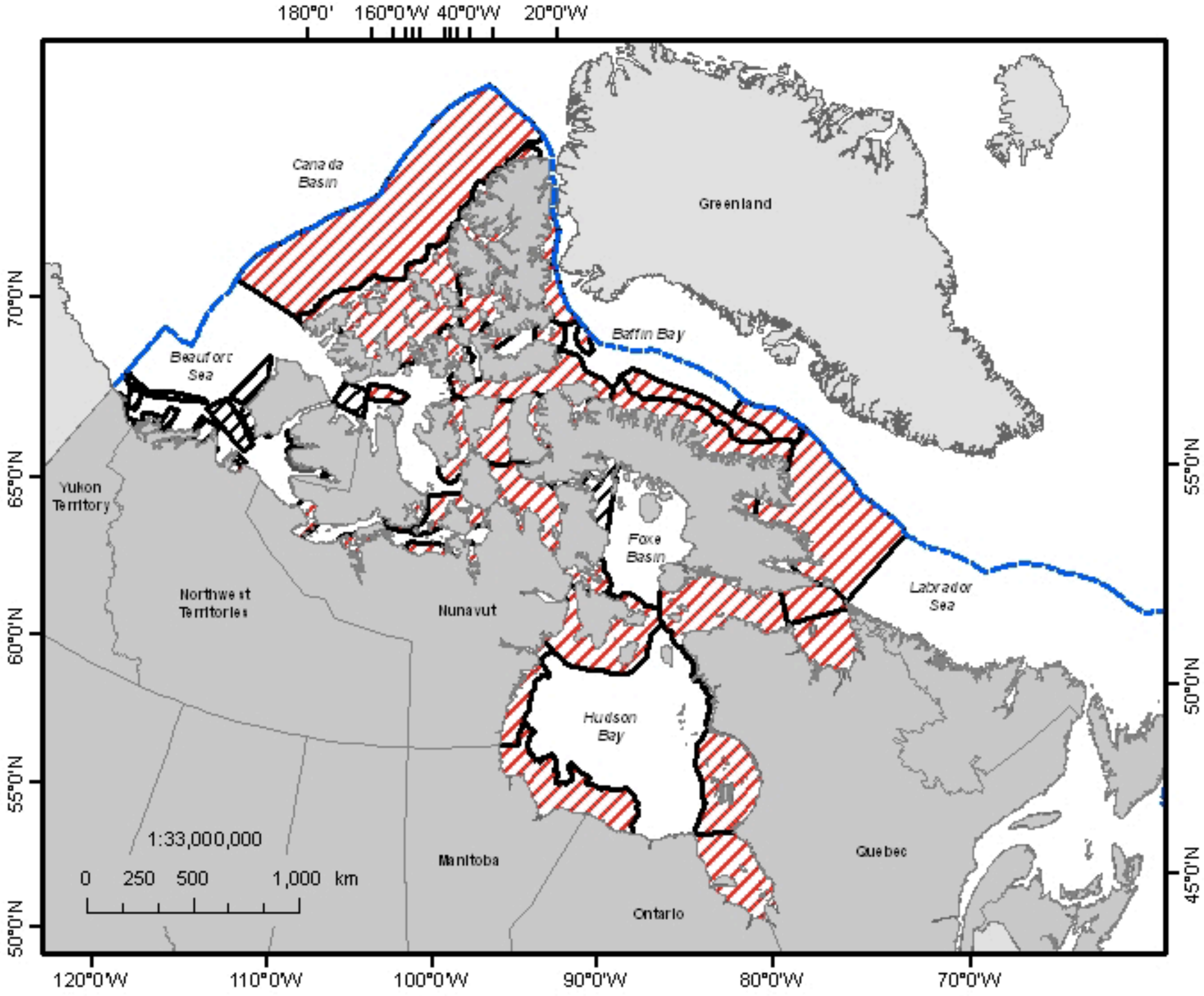

Figure 1.1. Map of the 38 EBSAs included within the five Arctic marine biogeographic regions depicted as red lines with black borders (DFO 2011c).

1.1 Arctic Marine Benthic Environments

Despite the fact that benthic marine environments in the Arctic support several species of commercial interest (Tai et al. 2019), affect species distribution and diversity across Arctic Canada, and are susceptible to climate change (Roy and Gagnon 2018), they remain quite understudied compared to pelagic environments (Bridier et al. 2021; Roy et al. 2015). Benthic habitats support 90% of diversity in Arctic marine environments (Roy and Gagon 2018) and provide essential habitats for a wide range of taxa, including macroalgae, invertebrates, fish, seabirds, and mammals (Grebmeier et al. 2006; Bluhm et al. 2011; Searles 2016; Tai et al. 2019). Benthic invertebrates comprise the base of several marine food webs in the Arctic that support species of commercial and subsistence importance, including Greenland halibut (*Reinhardtius hippoglossoides*), Northern prawn (*Pandalus borealis*), and several species of mussels and clams (Searles 2016; Tai et al. 2019). The availability and health of benthic habitats thus directly impact the livelihoods and food security of Arctic Indigenous people. Previous researchers have highlighted the need and urgency for more investigation into Arctic benthic habitat structure and function (Renaud et al. 2019).

Although they are ubiquitous and abundant in Arctic benthic environments, the role of invertebrates in benthic food webs that support subsistence and commercial harvesting activities has not received a lot of research attention. Because current diversity is so poorly characterized and varies greatly across space, invertebrates are often categorized into functional feeding groups (e.g., Stasko et al. 2018; Hilgendag et al. 2022) to facilitate comparisons. Functional feeding groups reflect habitat and feeding mode, and can include benthic suspension feeders, benthic deposit feeders, benthic surface feeders/deposit feeders, benthic carnivores, pelagic herbivores, pelagic carnivores, and benthopelagic carnivores. Categorizing invertebrates into functional feeding groups can also simplify construction and quantification of food web structure in environments where sampling is unlikely to yield full representation of taxonomic diversity, such as in Arctic benthic marine habitats.

Much of the research on Arctic aquatic (including both freshwater and marine) food web structure is focused on pelagic food webs, which are founded on the productivity of phytoplankton. Benthic primary producers such as macroalgae are also important contributors to primary production, however, including in polar marine environments. Some grazers have even demonstrated selection of specific macroalgae species (Iken et al. 1997). Benthic macroalgae can be grazed on directly by herbivores or contribute to the important detrital energy pathways that contribute to productivity in benthic food webs (Wulff et al. 2009). Food webs that rely on detrital energy (sometimes referred to as ‘brown’ food webs) are especially important in the Arctic, where light is extremely limited for several months of the year, while phytoplankton is a dominant energy source in spring and summer. Food web pathways in Arctic coastal ecosystems become more grounded in detrital energy sources toward the end of the summer and fall (McMeans et al. 2013).

Detritus is an important source of carbon for benthic food webs (Campanyá-Llovet et al. 2017), and supports the productivity of upper trophic levels (McMeans et al. 2013). There are several functional feeding groups of organisms that are important in the channeling of detrital energy from seafloor to top predators. Entry of detrital organic matter into the base of food webs is initiated by benthic deposit feeders, as they feed directly on detrital material (Campanyá-Llovet et al. 2017). Benthic suspension feeders can also feed on detritus, however they feed directly on particles (including phytoplankton) in the water column as well, which helps maintain water clarity and reduces excessive nutrient deposits to the sediment (Officer et al. 1982; Miller and Page 2012). Benthic carnivores can act as important stabilizers in benthic food webs. Depending on the season, they couple both weak and strong energy pathways and provide top predators with a less variable resource base (McMeans et al. 2013). They can also influence food webs by exerting top-down pressure, which cascades through the entire food web and prevents lower trophic level species from becoming overpopulated (Estes et al. 2011; Hui 2012). Benthic carnivores can also promote interactions between the pelagic and benthic food webs by feeding from both, which is one form of benthic-pelagic coupling (Iken et al. 2001).

Through bioturbation, contributions to habitat heterogeneity, water filtration, and benthic-pelagic coupling, benthic invertebrates are critically important to many ecosystem functions. Bioturbation, including burrowing and reworking sediment, affect many physical and biogeochemical processes that shape benthic habitats, and are carried out by several different functional feeding groups, including suspension feeders, deposit feeders, and predators (Norling et al. 2007; Queiós et al. 2013). Bioturbation processes influence pore water distribution, sediment reactivity, and nutrient fluxes (Norling et al. 2007). Bioturbators can also promote primary production of microphytobenthos by increasing nutrient availability (Lohrer et al. 2004). The diversity of benthic invertebrates contributes to habitat heterogeneity by providing different habitat processes including, enriching sediments, regulating benthic water turbulence, and bioturbation (Soltwedel and Vopel 2001; Lohrer et al. 2013), and these processes affect biodiversity (Post et al. 2017). Benthic suspension feeders, as well as several other functional feeding groups, also contribute to benthic-pelagic coupling, which shapes many other aspects of food web structure and function in Arctic marine ecosystems.

Benthic species affect nutrient cycling and resource transfer between pelagic and benthic food webs (McMeans et al. 2013). Cycling of organic matter and nutrients in generally low-productivity Arctic marine ecosystems involves the transfer of nutrients from ocean surface to ocean bottom and back (i.e., benthic-pelagic coupling). Carcasses, plankton cells, and fecal pellets, through both detrivory and remineralization, are mobilized from the ocean floor back into pelagic habitats that support key top predator fish and marine mammal species (Iken et al. 2005; Link et al. 2013). These transfer processes reflect the ecological contributions of many different benthic taxa, with each one carrying out a different function. Benthic suspension feeders, such as mussels, sponges, and filter-feeding invertebrates filter organic particles and phytoplankton from the water column and transfer them to the benthic environment (Pile and Young 2006). Suspension feeders promote sedimentation; marine benthic sediment has higher amounts of nitrogen and carbon when closely proximate individual suspension feeders are present (< 10cm) (Norkko et al. 2001). Benthic deposit feeders, such as polychaetes, amphipods, and bivalves, affect benthic-pelagic coupling through feeding and bioturbation activities. Their natural burrowing and particle ingestion reworks sediments, which helps promote nutrient cycling and oxygenation (Meysman et al. 2006). Benthic carnivores, such as carnivorous crustaceans, polychaetes, and fish are more mobile than other functional feeding groups, and directly affect benthic-pelagic coupling by consuming food from both pelagic and benthic habitats (Le Loc’h et al. 2008). Research to date clearly illustrates that the benthic environment and benthic species are critical to the proper functioning of many marine processes and functions, and that a deeper understanding of benthic marine environments is a pressing priority for research as climate change continues (Roy and Gagnon 2018).

1.2 The Influence of Climate Change on Arctic Marine Ecosystems

Climate change in the Arctic is occurring at a rate approximately three times faster than in other areas (Bintanja 2018). Climate change has already resulted in increases in sea surface temperature, reductions in sea ice extent and thickness, and changes in species distribution

(Steiner et al. 2013; Laidre et al. 2015; Alabia et al. 2018; Niemi et al. 2019). Increased CO_2 concentrations in the atmosphere also cause increased CO_2 absorption into marine waters, which results in ocean acidification. Ocean acidification can prevent the formation of, and/or damage, the shells and exoskeletons of invertebrate species through several mechanisms. Decreasing availability of the carbonate ion (CO_3^{2-}) is one of these mechanisms; many species of invertebrates require the carbonate ion to build $CaCO_3$ shells and exoskeletons, (Niemi et al. 2019). Ocean acidification is also impacting fish, as levels of PCO_2 and HCO_3^- increase in their bodies. In attempting to compensate for this via acid-base balancing, otolith growth, mitochondrial functioning, and metabolic rate may be affected (Heuer and Grosell 2014). Hoegh-Guldberg and Bruno (2010) reported that acidity is increasing twice as fast in polar oceans compared to other oceans, and that acidification-induced changes will impact food web structure. Increasing sea surface temperature in conjunction with ocean acidification has resulted in decreased energy transfer from primary producers to primary consumers and from primary consumers to secondary consumers (Ullah et al. 2018). Species distribution patterns are also changing, with some species moving northward but some species reacting in unexpected ways. This makes it difficult to predict how Arctic species will respond to climate change and which species may become established in Arctic waters (Alabia et al. 2018). It also makes it difficult to predict how food web structure and function will change.

Reductions in sea ice thickness and extent may affect benthic marine food webs in the Arctic via several different mechanisms. Although there is often a great distance between sea ice and benthic environments, sea ice plays a critical role in structuring Arctic benthic environments. The rapid loss of sea ice habitat in the Arctic is affecting marine primary producer, invertebrate, fish, and mammal populations, their foraging behaviour, and overall ecosystem dynamics (Bluhm et al. 2011; Meier et al. 2014; Laidre et al., 2015; Steiner et al. 2019; Hop et al. 2021). Scientists have found both sympagic and benthic sea-ice associated amphipods are declining in abundance. These amphipods are an important prey source for many higher trophic level species (Hop et al. 2021). Decreasing sea ice cover leads to increased light penetration, altering primary production dynamics and promoting the growth of benthic algae and macrophytes. The geographic distribution of primary producers, such as macroalgae, has been predicted to change due to increased temperature (Jueterbock et al. 2016). Benthic species as a whole may suffer with ice loss as increasing temperatures may increase pelagic grazing. Changes (either increases or decreases) in the amount and/or quality of organic matter reaching the benthic environment will also affect the ecosystem structure and function (Kędra et al. 2015).

Some authors note that with a reduction of species that depend on the sea ice, including ice-associated algae, the diversity of primary production sources will decrease (Bluhm et al. 2011). McMeans et al. (2013) studied marine benthic food webs in Cumberland Sound, Nunavut, and concluded that reduced sources of heterogeneity in primary production in response to climate change is a threat to the stability of Arctic food webs. These authors showed that different benthic species have energy channels that originate from a variety of distinct primary producers, such as phytoplankton and macroalgae, and that changes in abundance and diversity of these primary producers could reduce stability of food webs. Effects will likely be especially apparent in food webs with low redundancy (Kędra et al. 2015).

Changes in distribution of species at higher trophic levels will also likely affect benthic marine food web structure and function. Kędra et al. (2015) noted that, along with species additions, there may also be species removals from food webs and that either change can alter nutrient pathways and cause them to be less efficient, which can have profound impacts on top predators. Generalist fish species are predicted to shift poleward due to increasing temperature, and presence of new species may facilitate increased connectivity between benthic and pelagic systems (Kortsch et al. 2015). In addition to overall sea ice loss, there are also threats to benthic food webs caused by the changing temporal patterns of sea ice.

Seasonal patterns of ice formation, water temperature, primary production, and nutrient availability have profoundly shaped the structure of Arctic marine food webs. Arctic species have adapted to these patterns and several species depend on them. Climate warming, however, is changing the timing and availability of key resources, such as phytoplankton blooms, which impacts primary production and subsequently productivity at higher trophic levels. Søreide et al. (2010) investigated the Arctic zooplankton grazer *Calanus glacialis* and determined that it may need to adapt if there are changes in sea ice formation and break up, as the current timing of the peak bloom coincides perfectly with female reproduction and offspring growth. Changes in the life cycle may have cascading effects throughout the food web, as *Calanus glacialis* is an important food source for high trophic level species, such as bowhead whales (*Balaena mysticetus*) and auks (*Alcidae*).

1.3 Investigating Food Web Structure: Stable Isotope Analysis

Stable isotope analysis was first introduced as a tool for studying trophic ecology and food web structure in the 1970s (Fry 2006), and has become increasingly common in recent decades. Stable isotope ratios of carbon, nitrogen, and sulphur are frequently used (although sulphur is less commonly used) to investigate food web structure. Stable isotope ratios in biota differ among species due to fractionation and mixing (Fry 2006). Fractionation occurs because heavier isotopes react differently than lighter ones in reactions that occur during metabolism and nutrient uptake (Peterson and Fry 1987; Fry 2006).

In stable isotope analysis, the ratio of heavy to light isotopes is quantified in a sample and compared to international standards (Fry 2006). The standards that these ratios are compared to are Pee Dee limestone for carbon, atmospheric nitrogen for nitrogen, and sulphur from the Canyon Diablo meteorite (Peterson and Fry 1987). Stable isotope ratios are quantified using mass spectrometry (Peterson and Fry 1987), and are expressed as $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ for Carbon, Nitrogen, and Sulphur, respectively, where δ represents the parts per mill difference from the standard. Delta values are calculated using the equation:

$$\delta^{15}\text{N}, \delta^{13}\text{C}, \text{or } \delta^{34}\text{S } (‰) = \left(\frac{R_{Sample}}{R_{Standard}} - 1\right) x\ 1000 \qquad \text{Eq. 1}$$

where,

R represents the ratio ^{13}C:^{12}C, ^{15}N:^{14}N, or ^{34}S:^{32}S

Following the equation, δ values are higher when the heavier stable isotopes are more abundant in the sample, and vice versa. Typically, $\delta^{13}C$ and $\delta^{15}N$ are used to infer carbon source and trophic position, respectively (Wada et al. 1991; Post 2002). Delta^{15}N is used to infer trophic level because $\delta^{15}N$ typically increases ~ 3% to 5 ‰ with each trophic transfer (Peterson and Fry 1987; Montanari 2017). In contrast, $\delta^{13}C$ is used to infer carbon source, and is often used to discriminate between pelagic and benthic food sources. The $\delta^{13}C$ ratio of organisms does not change appreciably with trophic transfer, but reflects availability of dissolved inorganic carbon (DIC) for primary producers (Wada et al. 1991). Similar to $\delta^{13}C$, $\delta^{34}S$ does not change appreciably with trophic transfer, and can be used to help differentiate among different sources of basal organic matter - specifically among marine, freshwater, and terrestrial sources, but also among different marine sources (Whitney et al. 2018).

When comparing the structures of different food webs, it is often necessary to correct for among-system variability in isotope ratios in basal organisms (i.e., baseline variation; Post 2002). 'Baseline' isotope ratios can be affected by several physico-chemical attributes of the ecosystem, such as temperature, sources of nutrients, and availability of nutrients. If the baseline is not adequately characterized, then inferences drawn from comparisons may be inaccurate. Establishing an appropriate isotopic baseline is often difficult; ideally, a relatively long-lived primary consumer species that is linked to the food web of interest is selected as a baseline organism. Relatively long-lived primary consumers are preferable to primary producers because the isotopic signature of long-lived primary consumers has less temporal variance, and thus investigators can gain a more accurate representation of spatial variation (Post 2002). Ensuring the appropriate baseline is established and determining accurate predictions from food web structure is critically important but can also be quite challenging, especially in vast, remote regions such as the Arctic. Thus, establishing whether certain conclusions or inferences regarding food web structure are transferable among locations is of interest for scientists, planners, and resource managers in the Canadian Arctic.

1.4 Knowledge Gaps Addressed in this Thesis

The Canadian Science Advisory Secretariat aims to publish Ecologically and biologically significant area (EBSA) reports every decade that synthesize new information gathered for each of the EBSAs. The last EBSA report on the Hudson Bay Complex (HBC), one marine EBSA within the vast Canadian Arctic, was completed in 2011 (DFO 2011c). Given the ecological uniqueness, rising sea surface temperature, decreasing species at risk and subsistence species populations (e.g., beluga whales and narwhals), and increased shipping, (Hoover et al. 2013; Larouche and Galbraith 2016; DFO 2020; Goldsmith et al. 2020), another report that summarizes the last decade of research is timely. Smaller reports have been conducted on single EBSAs within the Hudson Bay Complex, such as Southampton Island (Loewen et al. 2020), however not all EBSAs within the HBC have received updates. Additionally, many species of interest move throughout multiple EBSAs within the HBC and thus it is important to complete a more holistic review for this area. With rapid climate change and industrial activities, including shipping, increasing in the Hudson Bay Complex, it is important to synthesize and disseminate relevant primary research to stakeholders that may not have access to peer-reviewed literature. EBSA reports are an excellent way to achieve this, as they cover a wide range of topics and are focused on rare, and endangered species, fitness consequences of species habitat loss, biological productivity and diversity, and uniqueness of habitats and species (DFO 2011c, Cobb 2011). These reports are used for management and conservation efforts and represent the most accurate and up-to-date science. When field research was paused due to COVID-related restrictions, producing EBSA reports for several areas within the Canadian Arctic became a priority.

As mentioned above, the structure and function of benthic marine food webs in the Arctic are poorly understood. Although studies on multiple invertebrate functional feeding groups are rare, some investigators have included them in recent analyses of Arctic marine food web structure (McMeans et al. 2013; Stasko et al. 2018). There was also a recent study completed on biomagnification of mercury in Frobisher Bay that included work on the coastal invertebrate food web (Hilgendag et al. 2022). Deeper sites were not included in this work, however; Inuit who rely on the fish, mammal, and invertebrate resources of Frobisher Bay have demonstrated an interest in learning more about benthic food webs at a variety of depths, particularly in the context of increased industrial activity in the area (i.e., construction of a deep-water port). Studies conducted in the Beaufort Sea, Amundsen Gulf, and the Arctic deep Canadian Basin have shown that food web structure differs among shallow and deep sites (Iken et al. 2005; Roy et al. 2015; Divine et al. 2015). Studies have found that deeper food webs tend to be longer and potentially less stable (Iken et al. 2005; Divine et al. 2015) and that feeding pattern of invertebrates may change with depth (Roy et al. 2015). Currently, there is no knowledge on how food web redundancy, diversity, niche area, trophic length, carbon sources, and sulphur sources differ among depths in Frobisher Bay, Nunavut. The lack of information about food web structure in Frobisher Bay make it difficult to predict how these food webs will change with future climate warming and increased shipping, and make monitoring and management attempts difficult or ineffective.

1.5 Thesis Structure and Research Objectives

The original overall goal of my MSc research was to investigate food web structure in Arctic marine environments. I first sought to review literature from the past decade on the eastern Hudson Bay Complex and identify gaps in the literature, with a focus on food webs along depth gradients. This work was going to be complemented by new, field-based research.

Restrictions on field work that arose from the COVID-19 pandemic, however, resulted in cancellation of both planned field seasons in the Hudson Bay Complex. I thus pivoted to complementing the literature review with a comparison of food web structure among three depths in Frobisher Bay; this undertaking involved use of existing data as well as samples that were archived (and which required processing and laboratory analysis) at Fisheries and Oceans Canada.

In Chapter 2, I present a literature review in which I reviewed 60 papers published between 2011 and 2021 on EBSAs in the eastern Hudson Bay Complex. Databases used were Web of Science and the internal Fisheries and Oceans Canada (DFO) catalogue. I summarized important findings from the literature and identified gaps in the knowledge that are meant to help shape ongoing field programs and contribute to an upcoming CSAS report. Chapter 2 revealed large gaps in research done on Arctic marine invertebrates, as well as holistic studies that include multiple invertebrate functional feeding groups and fish. In Chapter 3, therefore, I investigated invertebrate and fish food web structure in Frobisher Bay, Nunavut along a depth gradient using stable isotope analysis. Specifically, I aimed to:

1. Characterize Frobisher Bay nearshore (10 to 15m), midshore (20 to 45m), and offshore (260 to 351m) food web structures using nitrogen, carbon and sulphur stable isotope data;
2. Compare trophic ecology indices (niche area, trophic level, and $\delta^{13}C$ and $\delta^{34}S$ ranges) of two understudied functional feeding groups - benthic carnivores and benthic suspension feeders - among nearshore, midshore, and offshore depths; and,
3. Compare trophic ecology indices (niche area, trophic level, and $\delta^{13}C$ and $\delta^{34}S$ ranges) of benthic carnivores and benthic suspension feeders within depths to each other to infer interactions.

Chapter 4 is a summary and synthesis of findings from Chapters 2 and 3, and indicates future important directions for research.

2.0 Systematic Literature Review of Aquatic Marine Species and Environmental Factors in the Eastern Hudson Bay Complex

2.1 Introduction

Many resident and migratory species of ecological, social, commercial, and cultural importance rely on marine habitats in the Canadian Arctic. In recognition of the importance of marine habitats, Canada committed to designating 10% of its coastline to marine protected areas (MPAs) by 2020 (Canadian Council of Fisheries and Aquaculture Ministers 2017). Canada has the longest coastline in the world and much of it is in the Arctic, so the establishment of MPAs in the Canadian Arctic (Government of Canada 2019) is of international importance, especially because there is a global paucity of MPAs in polar regions (Yurkowski et al. 2019). This lack is due in part to the difficulty of conducting research in the Arctic, and is particularly concerning because the Arctic is subject to considerable and rapid anthropogenic-induced change. Indeed, warming in the Arctic is occurring 2 to 3 times faster than the global average (Bintanja 2018; Bush and Lemmen 2019), and is resulting in profound changes to the structure and function of Arctic marine ecosystems. Reductions in thick, multi-year ice and an increase in air and sea surface temperature (Steiner et al. 2013) are being observed, along with shifts in primary production species (Lavoie et al. 2013; Hoover et al. 2013a; Hoover et al. 2013b), abundance of marine mammals (DFO 2020; Hoover et al. 2013b), and increased potential future habitats for invasive species (Goldsmit et al. 2019). These rapid environmental changes challenge existing management and conservation plans, which ideally are grounded in up-to-date data.

Fisheries and Oceans Canada (DFO) is working to fill knowledge gaps that will enable effective and efficient monitoring, management, and conservation in Arctic marine environments (including MPAs) that are subject to continued stress from climate warming, as well as increases in shipping and industrial development. DFO collects and synthesizes rapidly accumulating literature in Canadian Science Advisory Secretariat (CSAS) reports, which include information on ecologically and biologically significant areas (EBSAs). An EBSA is a region designated by DFO to be uniquely important for the Arctic environment and the species that frequent that area (DFO 2011c). EBSAs were established to help advance establishment of management and protection strategies in areas of particular biological and ecological importance (Cobb 2011).

DFO endeavours to publish EBSA reports approximately every decade to ensure that the most recent and reliable knowledge is used to manage and protect those areas, and to assist governmental and Indigenous associations with the monitoring and management of northern resources (DFO 2011c).

Ecologically and biologically significant area reports may be useful in guiding establishment and then monitoring of MPAs, which, as stated above, are lacking in Arctic marine environments worldwide. Yurkowski et al. (2019) mapped predator diversity in Arctic marine environments and determined that existing protected areas in Canada cover only 5% to 7% of diversity hotspots in summer and winter, respectively. This highlights the need for data-driven prioritization of areas, which will ensure MPAs are placed with maximum effectiveness. To achieve this in the current research environment, which is fast-moving and involves many different groups, completed studies must be summarized regularly into accessible and synthetic formats. EBSA and other similar reports thus assist with Arctic monitoring, management, and protection, and are imperative in developing conservation plans for Arctic marine ecosystems.

Ecologically and biologically significant area reports cover many topics, but often focus on: i) endangered, rare, or declining species, as recognized by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC); ii) fitness consequences of habitat loss for particular species; iii) vulnerability, sensitivity, and resilience of species and habitats; iv) uniqueness or rarity of species and habitats; v) biological productivity and diversity; and, vi) life history and habitats used by key species for spawning, feeding, and overwintering (DFO 2011c; Cobb 2011). The review I conducted includes literature on COSEWIC-listed species, such as eastern Hudson Bay beluga whales (*Delphinapterus leucas*) (e.g., Doniol-Valcroze et al. 2011; DFO 2020), Arctic marine keystone species, such as ringed seals (*Pusa hispida*) (e.g., Luque et al. 2014), consequences of increased sea surface temperature and sea ice loss (Steiner et al. 2013), primary productivity (Lavoie et al. 2013, Sibert et al. 2011, Hoover et al. 2013a), species diversity (Carr 2012, Beazley et al. 2016), and species behaviour, including feeding ecology and migration to overwintering locations (Young and Ferguson 2014; Bouchard et al. 2015; Bailleul et al. 2012). The last EBSA report for the Hudson Bay Complex was published in 2011; I therefore reviewed sources from 2011 to 2021.

In the five Arctic marine biogeographic regions in Canada, there are 61 ecologically and biologically significant areas (EBSAs) (DFO 2011c). The most southern Arctic marine biogeographic region is the Hudson Bay Complex, which includes 13 of the 38 EBSAs in the five Arctic marine biogeographic regions. The Hudson Bay Complex (HBC) includes Hudson Bay and James Bay, and extends north to Baffin Island and east along the Hudson Strait (Fig. 2.1). The HBC is a culturally and biologically significant region in the Canadian Arctic. Hudson Bay is one of the most southern locations in the Arctic and is the most southern range for several keystone Arctic species, such as polar bears (*Ursus maritimus*) (Laforest et al. 2018). Additionally, Hudson Bay supports several threatened and endangered species and populations, as well as many Indigenous communities that rely on marine mammals and fish for subsistence. Threatened and endangered species in Hudson Bay include beluga whales (*Delphinapterus leucas*), bowhead whales (*Balaena mysticetus*), and narwhals (*Monodon monoceros*) (COSEWIC 2020, COSEWIC 2005, COSEWIC 2004). Given that the Hudson Bay forms the southern border of the Arctic, sea surface temperatures are projected to be higher than elsewhere in the Arctic, and highest in southeastern Hudson Bay and James Bay (Laforest et al. 2018). Increased sea surface temperatures, reductions in sea ice, and other anthropogenic stressors are projected to affect sources of production and benthic-pelagic coupling (Hoover et al. 2013, Oleszczuk et al. 2019), introduction of non-native species (Goldsmit et al. 2018) and changes in oceanographic conditions, such as decreases in pH (Hoover et al. 2013, de la Vega et al. 2019). Not only do these impacts highlight the urgency with which research needs to be conducted in the HBC, they also illustrate the fact that many factors influence the HBC and need to be analyzed holistically.

This literature review focuses on the eastern region of the Hudson Bay Complex and includes the following six EBSAs, which are detailed in DFO (2011c; including numbering conventions; see Fig. 2.1):

- 1.8 James Bay
- 1.9 Belcher Islands
- 1.10 Eastern Hudson Bay Coastline
- 1.11 Western Hudson Strait
- 1.12 Easter Hudson Strait
- 1.13 Ungava Bay

Within the 38 EBSAs across the five Arctic marine biogeographic regions, DFO (2011c) has identified 13 to be of particularly high ecological and biological significance. Four of these 13 highly significant EBSAs are included in this review: 1.9 Belcher Islands, 1.11 Western Hudson Strait, 1.12 Eastern Hudson Strait, and 1.13 Ungava Bay (DFO 2011c). The higher significance of these four EBSAs is reflected in the amount of research attention that these regions have received.

Both eastern and western Hudson Strait are considered to have high ecological and biological significance. These regions are used by migratory species that inhabit Hudson Bay during the ice-free season before either moving through the Strait in advance of the winter months or overwintering in the Strait during winter months. Scientific studies and Indigenous Knowledge have shown that several megafauna species, including beluga whales, bowhead whales, and narwhals, migrate to or through Hudson Strait each year (Brown and Fast 2012, Postma et al. 2012, Breton-Honeyman et al. 2016, Watt et al. 2013, Pomerleau et al. 2012). Studies have also been conducted on invertebrates in the Hudson Strait, and results have indicated high diversity of sponges and polychaetes (Carr 2011, Beazley et al. 2016), likely due to high plankton production that results from the oceanographic conditions (Sandstrom and Elliott 2011, Sibert et al. 2011).

The Belcher Islands and Ungava also represent regions of special biological and ecological importance in the Hudson Bay Complex. The Belcher Islands are comprised of a series of small islands in the middle of Hudson Bay. The water surrounding the islands is cooler than the water in the center of the Bay (Larouche and Galbraith 2016). Ungava Bay supports the endangered Ungava Bay beluga stock (Doniol-Valcroze and Hammill 2012a), northern Hudson Bay narwhals — which have been classified as a species of special concern by COSEWIC (Watt et al. 2013) — and ringed seals (Houde et al. 2020).

With continued and accelerating effects of anthropogenic stressors on ecosystems in the Hudson Bay Complex, an updated synthesis of relevant literature, as well as highlighting of ongoing knowledge gaps, is necessary. The objective of this review is to synthesize and evaluate recent advances in our understanding of ecosystem structure and function in EBSAs located in the eastern portion of the Hudson Bay Complex (see Fig. 2.1). Literature on the six eastern

Hudson Bay EBSAs published between 2011 and 2021 was reviewed and synthesized in preparation for an upcoming Canadian Science Advisory Secretariat (CSAS) report.

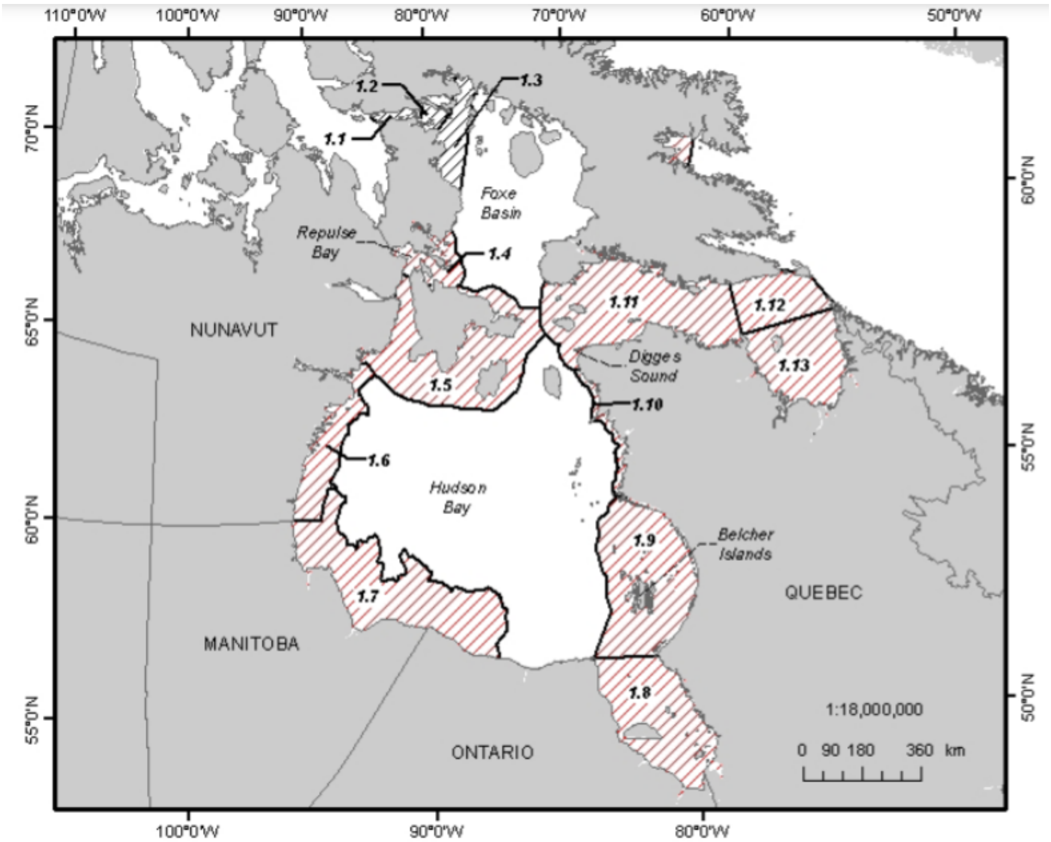

Figure 2.1. Map of the Hudson Bay Complex (HBC) and its 13 Ecologically and Biologically Significant Areas (EBSA). The focus of this review is the eastern Hudson Bay, including EBSAs 1.8 to 1.13. (DFO 2011c).

2.2 Methods

2.2.1 Search Strategy

Web of Science and the internal DFO catalogue were used in this literature review. These were chosen to reflect indexes of peer-reviewed and grey literature, respectively. Systematic searches for literature published between 2011 and March 26, 2021 were performed in each database.

The following search criteria were used in Web of Science under the field search ‘Topic’:

Table 2.1. Table of search terms used in the Web of Science Database.

Topic Field	Search Terms
Topic 1	("Hudson Bay" OR "Foxe Basin" OR "Fury and Hecla Strait" OR "Igloolik Island" OR "Rowley Island" OR "Repulse Bay" OR "Frozen Strait" OR "Southampton Island" OR "James Bay" OR "Belcher Islands" OR "Hudson Strait" OR "Ungava Bay")
AND Topic 2	(Benth* OR Invert* OR “Marine Mammal*” OR Fish* OR Pelag* OR Vegetat* OR Habitat*).
AND Topic 3	(Eco* OR Bio* OR Climat* OR Oceanograph*)
AND Topic 4	(Marine OR Coast* OR Estuar*)

The internal DFO catalogue search features were more limiting than Web of Science. An additional search requirement used for the internal DFO catalogue was limiting papers to ones written in English. The following search criteria were used in the internal DFO catalogue under the field search ‘All Fields’:

Table 2.2. Table of search terms used in the internal DFO catalogue.

Topic Field	**Search Terms**
Topic 1	DFO
AND Topic 2	“Hudson Bay”
AND Topic 3	(Eco* OR Bio* OR Climat* OR Oceanograph*)

2.2.2 Inclusion/Exclusion Criteria

The search conducted in Web of Science yielded 172 results whereas the search conducted in the internal DFO catalogue yielded 73 results. These records were screened to exclude irrelevant papers that were captured by the search. Titles and abstracts were screened, and when those passed screening, content of the whole paper was skimmed to ensure relevance. Due to time constraints and the abundance of papers published in the past decade, this review only focused on the Arctic marine environment. Papers that focused on terrestrial animals or ecosystems and freshwater ecosystems were excluded. Papers were also excluded if they: i) were conducted or focused on areas outside of the geographic area of interest (but were still somehow captured by the search) - exclusions included studies conducted in California, Norway, and western Hudson Bay (covered by a parallel review to this one, using same search criteria); ii) focused exclusively on polar bears or seabirds; or, iii) presented duplicate or redundant information that was captured in EBSA reports that were published in 2011 (Cobb 2011; DFO 2011c; Kenchington et al. 2011; Paulic & Rice 2011a; Paulic & Rice 2011b).

Of the original 172 results returned by the Web of Science search, 73 were not used due to focus outside of the geographic region of interest. A further 75 papers were excluded from the review due to irrelevance regarding biological topic (Fig. 2.2). Twenty-four papers were thus included in the final literature review from Web of Science. Of the 73 results returned from the search of the DFO internal catalogue, 27 were excluded due to focus outside of the geographic region of interest, 3 were excluded due to an irrelevant topic, 2 were removed due to duplications, and 5 were removed as they were included in previous 2011 EBSA reports (Fig. 2.2). After reviewing and eliminating articles, 36 papers were included in this review from the DFO catalogue. In total, 60 papers met the inclusion criteria and for this literature review.

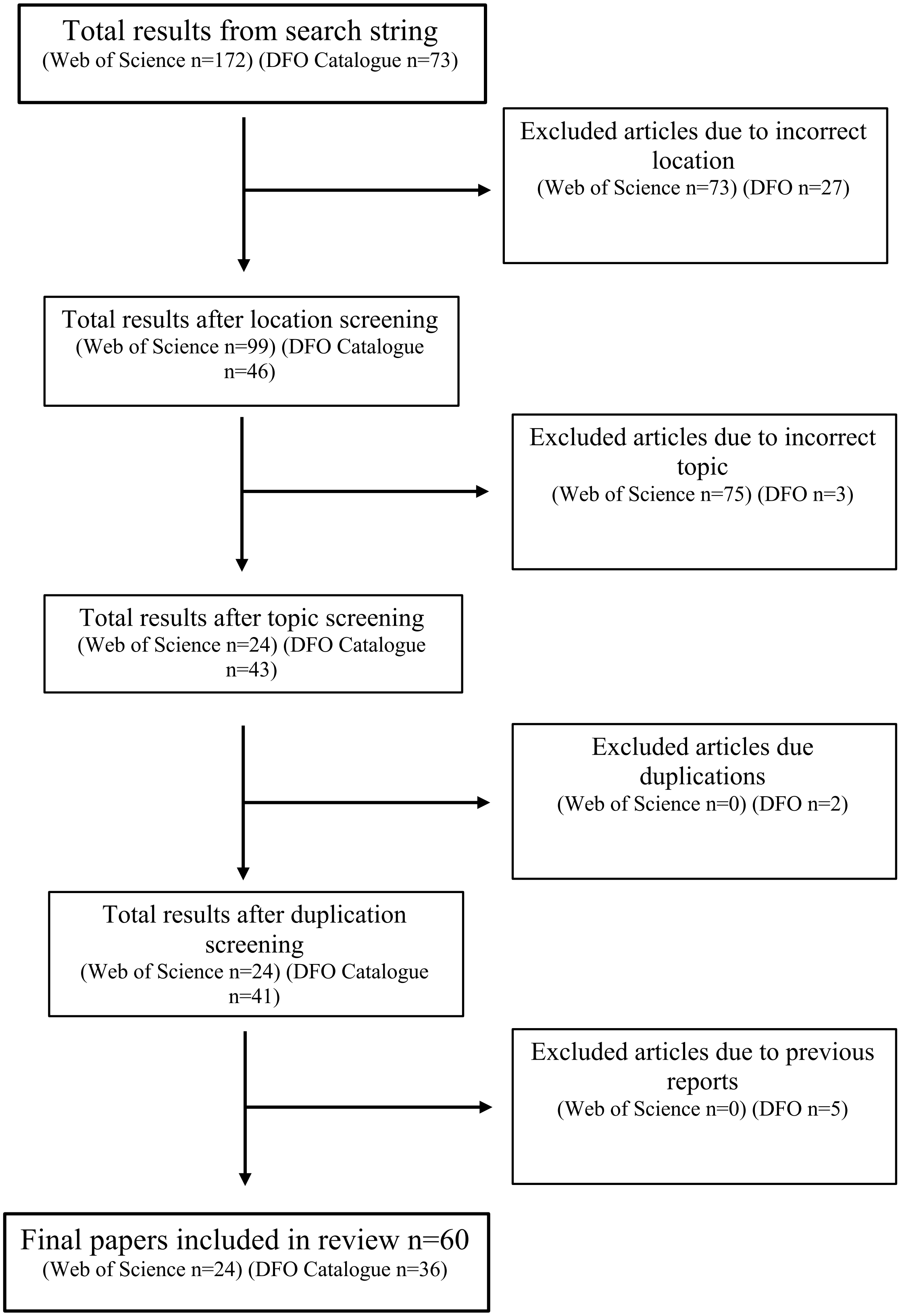

Figure 2.2. Flow chart depicting results and evaluation of papers returned from databases.

2.3 Results of Search

Taxa of interest that were represented in the retained papers included marine mammals (except polar bears), invertebrates, fish, and plankton species, and included aquatic invasive species. The papers reviewed were heavily skewed toward research on marine mammals (Fig. 2.3). Of the papers reviewed that included studies of biota, 79% focused on marine mammals, 9% focused on invertebrates, 8% focused on fish, 8% focused on primary producers, and 4% focused on aquatic invasive species. Only 4% of the 60 reviewed papers (Hoover et al. 2013a and Hoover et al. 2013b) focused on entire ecosystems - spanning from primary producers to marine mammals. Of the 79% of papers focused on marine mammals, 62% were primarily aimed at research on beluga whales.

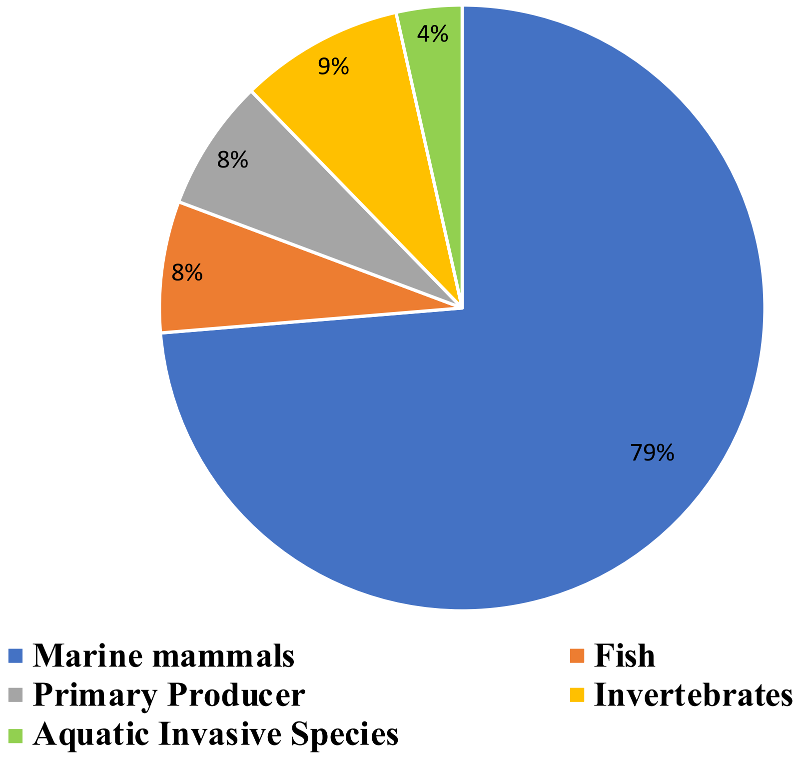

Figure 2.3. Illustration of proportional representation of broad taxonomic groups in the reviewed literature. Note: percentages add up to more than 100% because some papers included multiple groups.

Papers that focused on abiotic ecosystem components were more equally spread across different topics. There were fewer papers that focused on abiotic ecosystem components (7) compared to biotic ecosystem components (44); nine papers included both abiotic and biotic ecosystem components. There were many different abiotic topics reviewed in this paper, including rising temperatures and sea ice, nutrients, and pollutants.

This literature review spanned a 10-year period (2011 to 2021). Almost half of the papers included in this review were published in the first three years (47%) (Fig. 2.4), which was somewhat surprising as in many disciplines and/or regions, the number of published research papers is generally increasing over time. The among-year variability in published papers may reflect timing of funding cycles that are targeted for this region and should be considered by DFO in developing future funding calls that are specific to certain regions or taxa. Approximately 80% of papers published in 2016 focused on marine mammals, half of which were studies on beluga whales. This could reflect the fact that there was a 3-year management strategy for eastern Hudson Bay belugas that spanned from 2014 to 2017 (DFO 2016b, DFO 2016c, Doniol-Valcroze et al. 2016). It appeared that for beluga whales, data from aerial surveys were published ~ 2 years after collection. Beluga whale aerial surveys were conducted in 2011 and 2015 and in 2013 and 2017, 30% and 40% of the papers, respectively, were focused on analyses of new beluga survey data (DFO 2013b, Doniol-Valcroze et al. 2013, Gosselin et al. 2013, Gosselin et al. 2017, Hammill et al. 2017). A similar pattern was observed with papers focused on Atlantic walrus (*Obodenus rosmarus rosmarus*). Aerial surveys were conducted in 2014, and 20% of papers published in 2016 were focused on data collected during those surveys (Hammill et al. 2016, DFO 2016a).

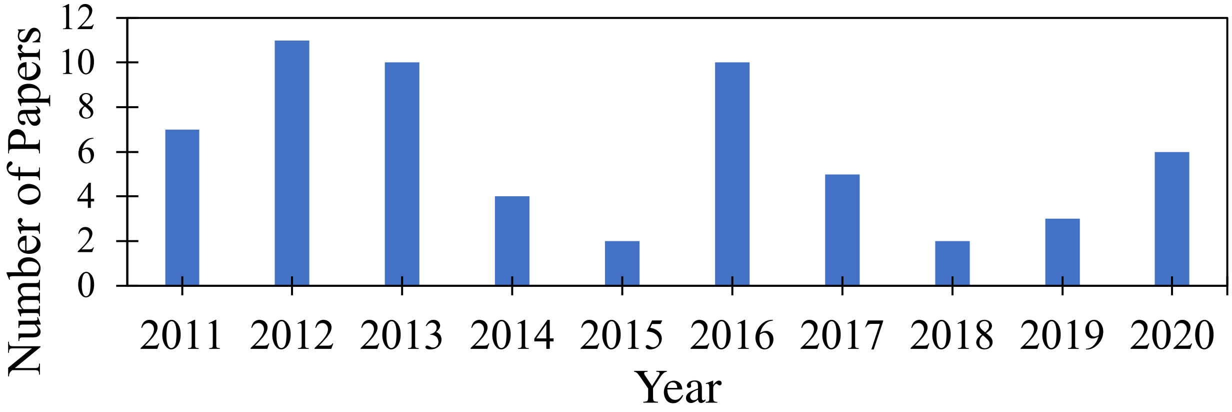

Figure 2.4. Number of papers included in the search (and retained) published in each year of interest for this review. 2021 is not included as the search was conducted on March 26, 2021.

Within the geographic region of interest – eastern Hudson Bay – some locations and sub-regions received more research attention in the past decade than others. Of papers that focused on only one area or sub-region, more research was conducted in Hudson Bay than in Hudson Strait or the Belcher Islands, and there were no papers focused solely on James Bay (Fig. 2.5). Both the Hudson Strait (including Ungava Bay) and the Belcher Islands are considered to have higher ecological and biological significance to DFO, and thus the lack of recent studies conducted in James Bay could reflect priorities of (and funding allocated by) DFO. More than half of the papers reviewed (62%) included two or more geographic areas as most of the topics and biota included in the review are not confined to one geographic area.

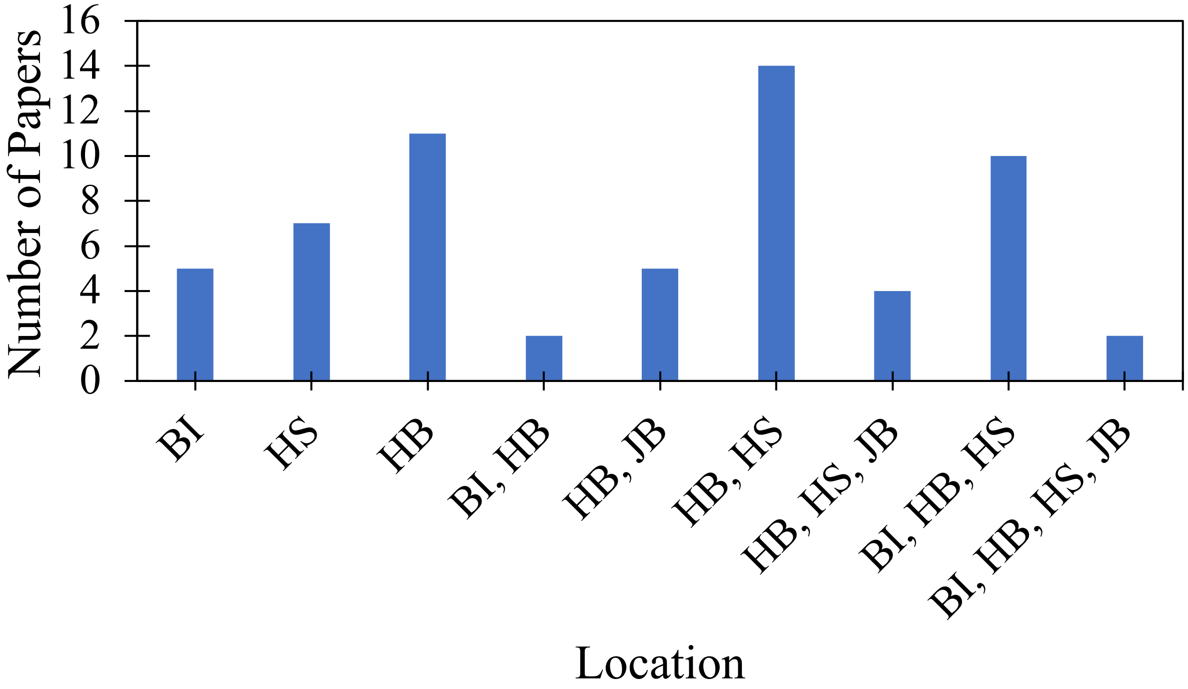

Figure 2.5. Number of papers published between 2011 and 2021 that focused on each region (and their combinations) within the study area. Abbreviations are: BI- Belcher Islands, HB- Hudson Bay, HS- Hudson Strait, and JB- James Bay.

2.4 Discussion

The eastern Hudson Bay complex is comprised of a diversity of habitats that support several resident and migratory species. The large, shallow bay receives freshwater inputs from several rivers. Estuarine habitats located at river mouths, as well as polynyas, provide critical habitats for many marine species examined in this review (DFO 2012, Brown and Fast 2012).

Resident taxa subject to recent research interest include species of whales, walruses, seals, cods, bivalves, sponges, polychaetes, zooplankton, and ice algae (Bouchard and Fortier 2011, Carr et al. 2011, Sibert et al. 2011, DFO 2012, Hoover et al. 2013a, Young and Ferguson 2014, Beazley et al. 2016, Hammill et al. 2016). The diversity of species within the Hudson Bay Complex is relatively high for an Arctic ecosystem, and is part of the reason why there are so many EBSAs within the region. Concerns regarding effects, management, and mitigation of stressors have driven much of the recent research activity in the six EBSAs in the eastern Hudson Bay Complex, including abundance, harvest, and management of key species, changes in temperature and sea ice, and fluctuations in concentrations of nutrients and contaminants.

2.4.1 Beluga Whales

Abundance and Management of Eastern Hudson Bay Beluga Stock

There are several beluga stocks specific to eastern Hudson Bay, including the eastern Hudson Bay (EHB) Beluga stock, the Ungava Bay stock, and the James Bay Beluga stock (Postma et al. 2012, DFO 2013b, DFO 2018). Beluga whales are an important subsistence food source for Inuit communities (DFO 2012) and are also of conservation concern.

The Ungava Bay beluga stock inhabits the Hudson Strait year-round (DFO 2012, Doniol-Valcroze and Hammill 2012a) and was designated as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2004. It was reconfirmed as endangered in 2020 (COSEWIC, 2020). The James Bay stock mostly inhabits James Bay (Postma et al. 2012) and does not have a COSEWIC designation. The EHB beluga stock inhabits Hudson Bay and migrates through Hudson Strait to the Labrador Sea in winter (DFO 2018). It was designated as endangered in 2004 but was reassessed as threatened in 2020. Although there is considerable among-year variability in the abundance of beluga within the EHB beluga stock, numbers increased from 3034 individuals in 2010 (Doniol-Valcroze et al. 2011) to 3819 individuals in 2015 (Gosselin et al. 2017). A recent decrease to ~3300 individuals in 2019 (DFO 2020) is the lowest recorded since 2013 (DFO 2014), however (Fig. 2.6), and is a cause for concern.

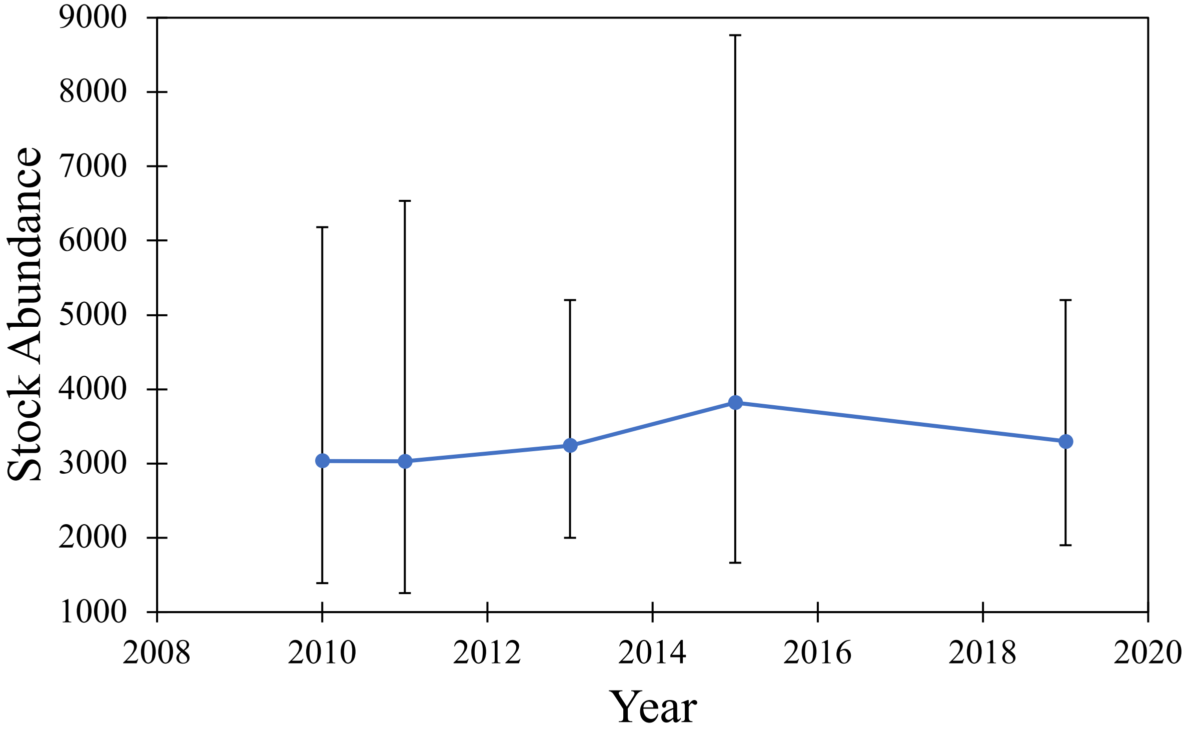

Figure 2.6. Eastern Hudson Bay (EHB) beluga stock abundance results determined from the papers reviewed that were published between 2011 and 2021. Error bars represent the 95% confidence intervals (Doniol-Valcroze et al. 2011; Doniol-Valcroze et al. 2012; DFO 2014; Gosselin et al. 2017; DFO 2020).

EBSA reports often focus on COSEWC-listed endangered species and sensitive, slow recovering species. It is important to closely monitor and manage stock dynamics and abundance of the threatened EHB beluga stock, and DFO does this through several means, including implementation of yearly harvest allocations. Models used in 2011 indicated that harvesting 50 individuals per year would result in a 50% probability of population decline (DFO 2011b, Doniol-Valcroze et al. 2011). The subsequent year it was determined that an annual harvest of 49 individuals would result in a 50% chance of the stock declining in numbers (DFO 2012; Doniol-Valcroze et al. 2012a). Harvest (59) exceeded quota (49) in 2012, which the authors of a DFO report attribute to an increase in harvest from Sanikiluaq (DFO 2013b). An increase in stock size resulted in a quota of 62 EHB belugas in 2013 (Doniol-Valcroze et al. 2013; DFO 2013b). In 2014, a new, more flexible management strategy was implemented at the request of northern community members. (DFO 2014, Doniol-Valcroze et al. 2014). Having found that probability of EHB stock decline was not significantly different when total allowable harvests were grouped into three years compared to a single year, the authors determined that the annual harvesting allocation could be changed into 3-year harvesting periods; the number of animals harvested was set at 180 individuals over three years, as long as all 180 individuals were not harvested in the first year.

Following implementation of the new management strategy in 2015 and 2016, research on beluga focused on proportion of EHB beluga harvested in different regions of eastern Hudson Bay, rather than on annual harvest. Hammill et al. (2017) used population modeling to determine how many EHB belugas could be harvested in the 2017 to 2020 period, and it was estimated that a harvest of 68 individuals per year would result in a 50% probability of decreasing stock size (Hammill et al. 2017, DFO 2018). A decrease in stock size in 2019 may have reflected harvests of 70, 74, and 98 EHB belugas in 2017, 2018, and 2019, respectively. This led to a harvest limit of 58 EHB belugas per year, which was implemented to result in a 50% probability of increasing the stock to 3 400 individuals in 5 years (DFO 2020). Generally, beluga harvests in the eastern Hudson Bay EBSAs tended to exceed quotas in the 2011 to 2021 period.

Harvests of beluga that exceed quotas may reflect, at least in part, inadequate collaboration in the development of management and conservation plans. In the Beaufort Sea region in the western Arctic, beluga populations are co-managed by boards that represent government and local Indigenous communities. Centering Indigenous communities and subsistence harvesters in the development and implementation of management plans has reduced struck/loss scenarios and wastage, and increased safety surrounding hunting practices (FJMC 2013; Wu 2018). When Indigenous communities are included in developing management guidelines, compliance with quotas and other guidelines increases (Alyes et al. 2007; Wu 2018). Although not the focus of this literature review, I did not find mention of co-management strategies or boards for beluga harvest in the Hudson Bay region. The success of the Fisheries Joint Management Committee in the Inuvialuit Settlement Region suggests that developing a more collaborative management strategy may further effective stewardship of EHB beluga.

As there are multiple beluga stocks in the HBC, it is critical to know what stocks beluga are being harvested from. As briefly mentioned, many papers published on beluga in 2016 focused on the proportion of EHB beluga being harvested from different locations in the eastern HBC. Although proportions differed between publications (DFO 2016c, Doniol-Valcroze et al. 2016, Mosnier et al. 2017, DFO 2020), 10.8% of the spring harvest (May to August) and 26.1%

of the fall/winter harvest (September to January) in Hudson Strait were represented by EHB beluga. EHB beluga represented 1.5% of the spring harvest (April 1st to June 30th) and 4.4% of the extended spring harvest (April 1st to July 14th) in the Belcher Islands (DFO 2016c, Doniol-Valcroze et al. 2016, Mosnier et al. 2017, DFO 2020). Approximately 6% of the spring harvest (Feb 1st to Aug 31st) of beluga in Ungava Bay were EHB beluga, whereas 44.5% of the fall/winter harvest (Sept 1st to July 14th) in northeast Hudson Bay were EHB beluga (DFO 2020). Understanding proportional contributions of different stocks to spatially specific, seasonal harvests can help guide management strategies by limiting harvest during certain times of the year when EHB beluga abundance is high in a particular area (DFO 2012). For example, abundance of beluga from the EHB stock peaked in the Belcher Islands in August, and thus a voluntary closure from July 15th to September 30th is effective (Doniol-Valcroze and Hammill 2012b).

Currently, harvest allocations are determined by assessing how many individuals can be harvested without increasing the probability of stock reduction to more than 50%. Several authors have stated that this method of determining annual total allowable harvests does not allow for stock recovery (Doniol-Valcroze et al. 2011, Doniol-Valcroze et al. 2012a, DFO 2014, Doniol-Valcroze et al. 2014), and have calculated harvest allocations that will promote stock growth. DFO (2013b) used precautionary methods when modeling the stock, and set two target goals of reaching 5 600 and 8 000 individuals in 25 years, based on a reference level set to 70% of the maximum stock size. Results indicated that extreme actions need to be taken to achieve maximum stock size; only a no-harvest scenario would lead to a 58% and 35% chance of reaching 5 600 and 8 000 individuals, respectively, in 25 years. This is not feasible. Harvesting 17 to 61 individuals would give the EHB stock an 80% and 50% probability of recovering to above 4000 within 50 years (DFO 2018). This would move the stock from the cautious zone it is currently designated in, to the healthy zone. Many authors throughout the decade of interest have articulated the lack of vigorous recovery initiatives present in existing management strategies.

EHB Beluga Stock Structure

Molecular data are generally lacking for beluga whales, despite the abundance of literature. This can make creating management plans difficult, as ideally these plans include genetic data (Doniol-Valcroze et al. 2016). Researchers have commented that age and sex composition of stocks is also largely unknown, and that harvesting too many reproductive females could have grave impacts for the stock (DFO 2014; Doniol-Valcroze et al. 2014). Investigators who have managed to pair molecular data with life history data have reported some important findings for the EHB stock. Doniol-Valcroze et al. (2011) determined that the mean age of the EHB beluga stock was 4.5 years younger than that of other belugas stocks, confirming that older belugas are more frequently harvested than younger ones in the EHB beluga stock. The age of harvest also increased between 1984 and 2015 (Hammill et al. 2017). Harvesting older whales in the EHB stock is concerning because calves stay with their mothers for two to three years, and it is thought that during this time calves learn migration routes from their mothers (Doniol-Valcroze et al. 2012b). Belugas appear to display site fidelity, in that they return to the same migration location as previous years, therefore learning migration routes is critical (Doniol-Valcroze et al. 2012b).

Other research has suggested that belugas are typically harvested from estuaries, and genetic data has shown that belugas killed in the same event are likely related (DFO 2012). It is thus possible that single hunting events of multiple individuals could wipe out families (DFO 2012), which would not only reduce genetic diversity, but also reduce numbers at particular sites due to the high philopatry of belugas. Lower mean stock age, along with loss of migration route knowledge, may explain why some estuaries in eastern Hudson Bay no longer support beluga (DFO 2012, Doniol-Valcroze et al. 2012b).

Feeding and Migration Behaviour of Beluga Whales

Understanding feeding and migration habitats and behaviour is critical to developing sound conservation and management plans. Data have shown that belugas that foraged more aggregately in groups tended to migrate approximately three weeks later than belugas that were more dispersed on feeding grounds (Bailleul et al. 2012). Belugas prefer waters that are cooler than 4°C, and aggregate diving behaviour has been observed in colder waters (Bailleul et al. 2012). Inuit hunters from southeastern Hudson Bay and Hudson Strait gave mixed responses about whether belugas feed during migration; however, Inuit from all communities stated that belugas ate more during the winter compared to the summer and that belugas are fattest during the early spring and thinnest in the fall (Breton-Honeyman et al. 2016). Sculpin (Cottidae), chars (Salmonidae), crustaceans, and cod (Gadidae) were the most abundant prey items reported in beluga diets by Inuit, and observations of beluga prey were similar among communities (Breton-Honeyman et al. 2016). As Bailleul et al. (2012) showed that temperature influences migrations of beluga, future climate-induced changes causing sea surface temperature to rise could impact the timing of migration and dispersal of beluga whales.

Other Beluga Stocks in Eastern Hudson Bay

Although the EHB beluga stock is the most researched, other important beluga stocks in eastern Hudson Bay include the James Bay (JB) stock and the endangered Ungava Bay (UB) stock. There is genetic overlap between the JB and EHB stocks; however, beluga from James Bay are distinct enough to be considered their own stock. Satellite telemetry data showed that belugas tagged in James Bay stayed there throughout the winter, unlike EHB beluga (Postma et al. 2012), which migrate through the Hudson Strait. The JB beluga stock is larger than the EHB stock, and results from aerial surveys indicated that abundance of JB beluga varied throughout the decade; estimates range from 8 205to19 439 individuals in 2012, 14 967 individuals in 2013, and 10 615 individuals in 2017 (DFO 2012, Gosselin et al. 2013, Gosselin et al. 2017). Whereas harvesting is the biggest threat to the EHB stock, the biggest threat to the JB stock is climate-induced changes to sea surface temperature and sea ice (Hoover et al. 2013a). When evaluating different harvest scenarios in a model, Hoover et al. (2013a) found that the JB beluga stock actually performed worse under a ‘no harvest’ scenario. The authors suspect this is because with no harvest, populations of JB beluga predators would increase. A subsequent paper by Hoover et al. (2013b) ran model scenarios of different levels of harvest and climate change; under the low climate change and constant harvest scenario, they predicted EHB belugas would be extirpated by 2069 while the JB belugas would thrive.

Recent data on abundance for the Ungava Bay beluga stock are limited. While there were no beluga sightings during their survey, Doniol-Valcroze and Hammill (2012a) determined a stock abundance of 32 individuals. A harvest of even one UB beluga could therefore have a big impact on stock size. The authors mentioned that the hunt is closed after August 31st to protect the EHB belugas that migrate through the UB area in fall, and that this management strategy increases the likelihood that belugas hunted in summer will be from the Ungava Bay stock (Doniol-Valcroze and Hammill 2012a).

It is not known whether the Belcher Islands have their own beluga stock; currently, there is no stock identified as being specific to that region. Community members from Sanikiluaq harvest approximately 69 belugas annually (DFO 2016b). They voluntarily do not harvest from July 15th to Sept 30th as EHB beluga are abundant in the area during that time (DFO 2016b). EHB beluga harvest allocations are split amongst the Belcher Islands and the 5 other EBSA locations in the Nunavik region (DFO 2016b). When it was determined that the proportion of EHB beluga harvest from Sanikiluaq was lower than models estimated in 2016, Nunavik communities wanted to re-assess the 3-year management strategy in place at the time to have the under-harvested EHB beluga whales from Sanikiluaq re-assigned to the Nunavik territory (DFO 2016b). The re-assignment never occurred because Nunavik hunters had already exceeded their quota for the first two years, and thus this strategy would have resulted in having fewer EHB beluga allocated rather than more (DFO 2016b). Management strategies and proportional allocations of harvest would likely be different if there were a Belcher Islands beluga stock, which is why further research into the presence (or not) of a Belcher Island beluga stock would be beneficial. Overall, although there is genetic and habitat overlap among the beluga stocks in the six eastern Hudson Bay EBSAs (Postma et al. 2012), stock abundances, threats (Hoover et al. 2013a), migration behaviours (Doniol-Valcroze and Hammill 2012b, Doniol-Valcroze et al. 2012b), and overwintering locations vary (Postma et al. 2012, Doniol-Valcroze and Hammill 2012b). Continuing research is thus necessary.

2.4.2 Narwhals

Narwhals (*Monodon monoceros*) are a species in the cetacean suborder that are culturally and economically important to Indigenous communities (Hoover et al. 2013a; Watt et al. 2013). Narwhals are unique in that they only inhabit Arctic areas and there are three known populations, one of which occupies northern Hudson Bay (NHB) and is comprised of 12 500 individuals (Watt et al. 2013). The NHB narwhal population inhabits an area that extends from Foxe Basin all the way to Ungava Bay, as well as EBSAs in eastern and western Hudson Strait. The NHB population migrates to Hudson Strait during the winter and returns to NHB during the summer. Narwhals are sexually dimorphic; males have a large tooth that extends into a single tusk on the front of their face, whereas females (generally) do not (Watt et al. 2013). In this review, ~9% of the papers published on biota focused on narwhals. Narwhals are designated as a species of special concern and generally only produce one calf every three years (COSEWIC, 2004); thus, information about their behaviour and abundance is important.

Diet and foraging behaviour of narwhals was analyzed by Watt et al. (2013) to determine how plastic they are and how they might respond to climate-induced changes occurring in their habitat. Although there were some similarities between male and female narwhals, it was found that males have a significantly higher $\delta^{13}C$ ratio compared to females, which likely reflects that their larger size allows them to dive deeper and feed on more benthic species compared to females. The NHB narwhal population had different isotope values compared to other populations studied (Watt et al. 2013). Compared to the other Arctic narwhal populations, the NHB population fed more on benthic prey rather than pelagic prey, likely because the NHB population occupies a relatively shallower habitat (Watt et al. 2013). The NHB narwhal population also had the highest $\delta^{15}N$ of the three Arctic populations (Watt et al. 2013). Greenland Halibut (*Reinhardtius hippoglossoides*) is a common food source for NHB narwhals, although males consumed this prey item more frequently than females (Watt et al. 2013). Although narwhals displayed some plasticity in their foraging behaviour, results from models run by Hoover et al. (2013b) indicated that if temperature continues to rise, ice continues to melt, and harvesting stays constant at 2009 levels, narwhals will be extirpated by 2069. This is quite concerning for species that prey on narwhals and the communities that depend on them as a subsistence food source.

Monitoring harvest of NHB narwhals is a critical part of developing ongoing management and conservation plans, as data suggest that narwhal abundance will decrease in the future due to climate change and harvesting pressures (Hoover et al. 2013a; Hoover et al. 2013b). Hudson and Watt (2020) determined that from 1957 to 2018 there were 4 207 narwhals harvested, averaging approximately 68 narwhals per year. The authors note that harvest was relatively low until the 1960s and has since increased. To support the development of management plans for narwhals, DFO (2011a) conducted a genetic analysis. Results indicated that all three narwhal stocks, including the Baffin Bay stock, the east Greenland stock, and the northern Hudson Bay stock, are significantly different from each other, although there is some overlap in allele frequency. The possible decline in northern Hudson Bay narwhals (Hoover et al. 2013a; Hoover et al. 2013b) is meaningful information for Hudson Strait and Ungava Bay EBSA reports as they are already classified as a species of special concern.

2.4.3 Bowhead Whales

There are two Bowhead Whale (*Balaena mysticetus*) populations in Canada, one of which is the eastern Canada-west Greenland (EC-WG) population. Bowhead whales migrate all throughout eastern Canada and western Greenland. In the winter, Bowhead whales can be found in the two EBSAs in Hudson Strait and in northern Hudson Bay, and in the summer, they occupy other areas within Hudson Bay (Pomerleau et al. 2012). Like many other whales in the Canadian Arctic, loss of sea ice is impacting available Bowhead habitat in the EBSAs of interest for this review (Hoover et al. 2013a; Hoover et al. 2013b). Furthermore, availability of prey may be affected by climate change. Pomerleau et al. (2012) reported that EC-WG Bowhead whales rely on zooplankton as a primary food source, and thus may be susceptible to climate-induced range shifts in this prey source. These same authors caution, however, that there are uncertainties and that their research may only reflect the spring/summer diet of Bowhead. Modelling results from Hoover et al. (2013a) and Hoover et al. (2013b) indicated that shifts in food webs, as a result of sea surface temperature and sea ice changes, will impact Bowhead biomass. Their projection models showed the bowhead population may increase, likely due to prey increase and low initial harvesting. Continued research and monitoring of range and population size is needed.

2.4.4 Atlantic Walrus

Atlantic Walrus (*Odobenus rosmarus rosmarus*) is the largest pinniped species in Canada. In this review, ~11% of the included papers focused on walrus. The main food source for walrus is bivalves, although they eat other invertebrates and occasionally seals when invertebrates are unavailable, usually due to deep water (DFO 2017). Mating occurs early in the year (Jan to April) and calves are born in early summer (May to June), usually one calf every three years (DFO 2017). Mature females have a pregnancy rate of approximately 33 to 35%. Walrus pregnancy rate, along with their COSEWIC status as a species of special concern (COSEWIC 2017), warrants continued monitoring and research in the Belcher Islands, Hudson Strait, and Ungava Bay EBSAs.

There are two distinct populations of walrus in Canada. The central Arctic population contains the north Foxe Basin and central Foxe Basin stocks, the Hudson Bay-Davis Strait stock, and a south and east Hudson Bay stock. Although the south and east Hudson Bay stock is considered a separate stock due to its location near the Belcher Islands EBSA, scientists in the field have stated the importance of verifying this with genetic analyses (DFO 2013a; Hammill et al. 2016).

Stock abundance and harvest reports are somewhat limited for the Atlantic walrus in the eastern Hudson Bay EBSAs. Using the information available, DFO (2013a) estimated that there were 166 walruses harvested annually from the Hudson Bay-Davis Strait stock, and that a stock size of 9 500 individuals would be needed to sustain a yearly harvest of that size. Aerial survey data conducted in 2014 indicated that the Hudson Bay-Davis Strait Stock contained ~7100 individuals (DFO 2016a, Hammill et al. 2016). This stock number can sustain a harvest of 79 to 180 individuals per year in the northern Hudson Bay and Hudson Strait (Hammill et al. 2016, DFO 2016a). Harvests reported by hunters averaged 85 individuals annually over the last five years (2010 to 2014), which was calculated to be 121 individuals removed after accounting for individuals that were struck-and-loss (DFO 2016a). Abundance of the south and east Hudson Bay stock was estimated to be ~200 individuals, which would sustain an annual harvest of 2 to 6 individuals (Hammill et al. 2016, DFO 2016a). For the south and east Hudson Bay stock, reported harvesting numbers have decreased since 2009 to an average of 2.4 individuals per year; pre-2009, the yearly harvesting average was 12 individuals. Population models indicated that the Hudson Bay-Davis Strait stock had 10 400 individuals in 1954, fell to 3 600 individuals by 1993, and rose to 7 000 individuals by 2014 (DFO 2016a). The authors reported that harvesting seems to have declined in the past 5 years (2010 to 2014) for both Hudson Bay stocks (DFO 2016a). These harvest and stock abundance data will help inform robust conservation and management strategies that allow recovery from COSEWIC ‘special concern’ status, which is especially important given the ongoing and added stresses imposed by climate change.

In a modeling exercise, the two Hudson Bay walrus stocks reacted differently to future climate-induced changes. Hoover et al. (2013a) determined that the biomass of the smaller, southern Hudson Bay population of walrus was more impacted by hunting than climate-induced changes (e.g., sea surface temperature and sea ice extent) whereas the larger, northern population was impacted by both climate change and harvest. Simulations were run until 2069 and both Hudson Bay walrus stocks were at risk of becoming extirpated due to harvest and continued ice melt and temperature increase. Simulations also showed walrus may be impacted by bottom-up changes in food webs, as their invertebrate prey showed biomass decreases in the projection models (Hoover et al. 2013b). Walrus extirpation could have significant impacts on the ecosystems within the EBSAs (Hoover et al. 2013a), and effects would likely propagate through food webs. To reduce the threat of extirpation, mitigation policies need to be implemented. Authors of a report published in 2017 (DFO 2017) reviewed current management strategies and suggested a new, flexible 5-year management strategy designed to help hunters stay within the harvest recommendations.

2.4.5 Ringed Seal

Ringed seals (*Pusa hispida*) are a small pinniped species that are found throughout Arctic Canada. Ringed seals are strong swimmers that claw holes through the sea ice for breathing. Males are slightly larger than females, and females give birth to one pup between mid-February and May and nurse them for 40 days (Luque et al. 2014). Ringed seals were the second most studied species included in this review, accounting for ~17% of papers that focused on biota. Ringed seals are a keystone Arctic species, and function as both predator and prey for several highly-valued species in Arctic marine food webs (Luque et al. 2014). Sea ice is very important for ringed seals as they use it for rest, moulting, and it is where they are most often captured as prey; they are a very important food source for both polar bears and fox (Luque et al. 2014). Seals are widespread in Arctic Canada and can be found in all of the six EBSAs included in this review.

Movement of adult seals is greatly dependent on sea ice concentration, and future changes in sea ice could impact seal reproduction and feeding (Luque et al. 2014). In a modeling study, Luque et al. (2014) showed that age, sex, sea ice concentration, day of year, and ocean depth were all important factors in predicting behaviour. Results from models also indicated that adults are more responsive to ocean depth and sea ice concentration (Luque et al. 2014). Hoover et al. (2013a) and Hoover et al. (2013b), ran projection models showing that despite future climate conditions and harvesting pressures, the HBC ecosystem can sustain ringed seal populations at increased biomass levels, possibly due to decreased predation from polar bears in the future. In contrast, Ferguson et al. (2017) determined that from 2003 to 2012 pup survival decreased, stress level increased, and seal body condition decreased significantly as duration of open water increased. These results are consistent with results of models from Luque et al. (2014) that showed that sea ice forcing and temperature will influence biomass of ringed seal in the future. These authors also note that reduced sea ice may require the seals to learn to breed on land. This may be possible, as authors of some studies have shown that seal behaviour may be more flexible than previously thought (Yurkowski et al. 2016).

Behaviour of seals differs among populations, which may suggest that seals can adapt to different habitats. Young and Ferguson (2014) investigated stable isotope signatures of western and eastern Hudson Bay ringed seals and determined that their isotopic niches are different and appear to be changing and diverging as warming occurs in the Bay. They also determined that there was more niche overlap between age classes in eastern Hudson Bay seals than in western Hudson Bay seals. Seals in different stocks are known to have different behaviours; Yurkowski et al. (2016) showed that while sea ice concentration is positively associated with resident behaviour for seals around Sanikiluaq, seals in Saglek Bay traveled more with increased ice concentration. Higher concentrations of Chlorophyll A were also associated with increased seal travel in Sanikiluaq. For both Sanikiluaq and Saglek Bay, seals dove less when resident compared to when traveling. The ice-free season was longer in Sanikiluaq and Saglek Bay compared to other locations of ringed seals at higher latitudes. The authors also discovered a latitudinal pattern in seal movement; there was a positive correlation between residence time and duration of the open water season (Yurkowski et al. 2016).

Contaminant concentrations in ringed seal muscle and liver also differ among locations. Ringed seals in eastern Arctic Canada have lower total mercury concentrations than ringed seals in the western Arctic Canada (Brown et al. 2016). In a study conducted by Brown et al. (2016), the authors found that seals collected from a population near Inukjuaq, Quebec had the lowest concentrations of total mercury in both liver and muscle tissue for subadult and adult seals. These same seals had the highest total cadmium concentrations, which the authors explain is likely due to the low trophic position occupied by this population; they are heavily reliant on amphipods (Brown et al. 2016). In another study, it was found that contaminants such as polybrominated diphenyl ethers (PBDEs) were higher in ringed seals at more southerly locations (e.g., Inukjuaq and Ungava Bay) compared to more northerly locations. The same spatial pattern was found for perfluorinated carboxylic acid (PFCA) and perfluorooctane sulfonate (PFOS) for seals in Inukjuaq (Brown et al. 2018). Another contaminant, selenium, was also found at higher levels in Hudson Bay seals compared to seals in Central Arctic Canada, Ungava/Nunatsiavut, and east Baffin Island (Houde et al. 2020).

Other authors have explored temporal trends in contaminants in ringed seals and found no relation between time and mercury concentrations in seal liver tissue; however, total mercury levels did decrease in muscle tissue in Hudson Bay (-0.91%/year) and Ungava/Nunatsiavut (-1.30%/year) seals. Unlike the Beaufort Sea and Central Arctic Canada, the North Atlantic Oscillation (NAO) index was negatively correlated with total mercury for seal muscle tissue in Hudson Bay and Ungava/Nunatsiavut as was the PNA (Pacific/North American pattern) index (Houde et al. 2020). Effects of interacting climate-induced changes on diet, habitat, behaviour, and contaminant concentrations deserve further study in the eastern Hudson Bay EBASs.

2.4.6 Polar Cod

Polar cod (*Boreogadus saida*) are part of the Gadidae family and are a species of considerable research interest. Approximately 6% of papers devoted to biotic topics in this review focused on polar cod. Polar cod are an important pelagic prey species for many higher trophic level Arctic species, such beluga whales, seabirds, narwhals, and ringed seals (Breton-Honeyman et al. 2016, Bouchard and Fortier 2011, Watt et al. 2013, Houde et al. 2020). Polar cod can also be cannibalistic. They spawn under the ice during late fall or early winter and anywhere between January and July, depending on the sub-zero temperature they occupy (Bouchard and Fortier 2011).

Literature documenting the life history of polar cod, such as hatching times and winter migrations undertaken by juveniles, provide important data for modeling effects of stressors on higher trophic levels. As cod have many predators and are very small at hatch (4 to 8 mm), previous researchers have postulated that it is advantageous for polar cod to get as big as possible before their first winter, when they migrate to deeper water (Bouchard and Fortier 2011, Bouchard et al. 2015). Bouchard and Fortier (2011) determined that Arctic areas with higher freshwater influence, such as Hudson Bay, have warmer temperatures that allow polar cod to hatch earlier. This allows them to reach a larger body size more quickly, migrate earlier in the fall, and escape predation by adult polar cod and seabirds. The authors also found that polar cod in Hudson Bay had an earlier hatch date than polar cod in the Canadian Archipelago, north Baffin Bay, and Northeast Water. As melting of multi-year sea is increasing (Steiner et al. 2013) causing higher amounts of freshwater input to Hudson Bay, it is possible that juvenile cod may start hatching earlier in future.

Hoover et al. (2013b) ran projection models with different climate change scenarios and determined that polar cod populations will likely decrease due to bottom-up and top-down forces; while abundance of polar cod prey is predicted to decrease, predation is predicted to increase. As polar cod is such a common prey source for many species at higher trophic positions within HBC EBSAs, it is critical to continue monitoring polar cod in the future.

2.4.7 Other Fish

Fish are a very important part of the Arctic ecosystem, often occupying middle trophic positions and transferring energy from lower to higher trophic levels. There are many fish species in the HBC, including sculpin (Cottidae spp.), sandlance (Ammodytidae spp.), cod (Gadiformes), and capelin (*Mallotus villosus*). Despite this, this literature search yielded no papers on single fish species, other than polar cod. Hoover et al. (2013a) and Hoover et al. (2013b) published findings on an entire HBC ecosystem model that included information on multiple fish species. Because data on fish species were so limited, they used the diets of predators, such as seabirds, to estimate fish biomass. Hoover et al. (2013a) used a fitted model to estimate biomass of fish and reported that Gadiformes had the highest biomass at 0.81 t/km and sandlance had the second highest biomass at 0.64t/km. Their model also predicted that future declines in fish biomass will be steepest for fish that rely on benthic food sources. Hoover et al. (2013a) predicted that sculpins and zoarchids will decline by -55%, sharks and rays by approximately -45%, and Gadiformes by approximately -20%. In contrast, fish that prey on pelagic species are expected to increase; sandlance and capelin, both pelagic prey fish species, will increase by 101% and 90%, respectively. Under a hypothetical "no harvest" scenario, fish biomass in the model did not change as greatly as some of the marine mammals. Although the model represents the entire HBC, fish data used in the model came from the northern portion of the Bay. Results may be different in southern Hudson Bay and James Bay (Hoover et al. 2013a), and this data gap should be addressed.

In models that simulated future climate and harvest scenarios, Hoover et al. (2013b) reported that even with the least severe scenario of consistent harvest (from 2009) and constant climate change, fish that relied on ice algae and benthic prey species (e.g., sculpin/zoarchids, Gadiformes, and sharks/rays) declined in biomass (-25% to <-75%) whereas fish that depended on pelagic prey species (e.g., sandlance and capelin) increased in biomass (25% to >75%). In predictive models, the entire food web shifted from an ice algae and benthos base, with benthic fish at a higher trophic level, to a spring bloom and zooplankton base, with pelagic fish dominating higher trophic levels. Future research should focus on collecting data that can be used to evaluate and refine these predictions.

2.4.8 Invertebrates

Invertebrates support higher trophic level species in Arctic marine food webs. Common Arctic marine invertebrates include species of polychaetes, bivalves, gastropods, echinoderms, zooplankton, and amphipods. These organisms support many fish species, including Gadiformes spp., sculpin/zoarchids, and sharks/rays, which in turn support larger fish and marine mammals (Hoover et al. 2013b). Only 9% of biotic papers from the search focused on invertebrates, demonstrating a need for more invertebrate research. Of the papers that focused on invertebrates, only sponges, polychaetes, and zooplankton had individual papers that focused solely on them.

Analyses on invertebrate diversity is especially important for the monitoring of EBSAs. Carr (2011) stated there are over 1200 species of polychaetes in Canada. She found that Hudson Bay had the lowest polychaete diversity (Terebellidae was the most common polychaete in Hudson Bay), followed by Hudson Strait which had the second lowest, although sampling efforts were lowest in this area as well. Beazley et al. (2016) published a paper on sponges using species distribution modeling, and determined that eastern Hudson Strait had a higher abundance of sponges compared to western Hudson Strait, but sponges in western Hudson Strait were more uniformly distributed. Sponges are often negatively impacted by fisheries, and thus are important to monitor as fisheries activities expand (Beazley et al. 2016).

Climate-induced effects on invertebrates are poorly understood, but there is no doubt that changes in invertebrate diversity and abundance will have bottom-up effects on megafauna species that occupy higher trophic levels. Whole-ecosystem modeling performed by Hoover et al. (2013a) and Hoover et al. (2013b) indicated that as climate change continues and sea ice declines, spring blooms of plankton will increase and catalyze a benthic to pelagic shift in lower trophic levels. The models indicated that biomass of bivalves, marine worms, and echinoderms would decrease from 0% to -25%. Other benthic biomass decreased by an average of -39%. In contrast, zooplankton increased in biomass, with macro-zooplankton increasing 71% (Hoover et al. 2013a). This could cause shifts in the biomagnification of mercury and other contaminants in

HBC food webs, as monomethylmercury biomagnifies within the zooplankton community throughout the 1 to 4 trophic levels that they occupy (Foster et al. 2012). The model produced by Hoover et al. (2013a) showed that, unsurprisingly, lower trophic levels taxa, such as zooplankton and benthic invertebrates, are more susceptible to climate change than to harvesting pressure (Hoover et al. 2013a). In an evaluation of different future scenarios, the model still resulted in a shift from dominantly benthic to dominantly pelagic production, even under a scenario of lower climate change and constant harvesting (Hoover et al. 2013b). Changes in the dominant sources of production will have bottom-up impacts, and species that currently feed on benthic invertebrates may need to find new prey species or they may be extirpated. Additionally, species that prey on pelagic invertebrates may become more abundant, but ongoing empirical data are needed to evaluate and refine these predictions.

Several environmental variables, including substrate type, have large impacts on invertebrate biomass and diversity. Pierrejean et al. (2020) identified 380 epibenthic taxa around Hudson Bay, Hudson Strait, and Ungava Bay and tested the influence of different environmental factors on diversity and biomass. The authors examined findings in the context of three spatially defined units: community 1 occupied the coastal area of Hudson Bay, community 2 occupied an area farther out into the Bay, and community 3 occupied an area in the middle of the Bay. Generally, for all three communities, particulate organic carbon content in surface water and salinity levels in bottom waters had the largest impact on epibenthic community composition. Coarse substrates in the coastal community supported the largest biomass of suspension feeders and filter feeders. The middle community had a more mixed substrate and supported an abundance of filter feeders. The third, deep community in the middle of Hudson Bay had a mud substrate and supported a large abundance of deposit feeders and filter-suspension feeders. Baseline information such as this informs future predictions and is critical as species diversity is important in designating EBSAs.

2.4.9 Primary Producers

Ice algae are an important basal food source in the Hudson Bay Complex, along with phytoplankton and detritus (Hoover et al. 2013a). Despite their fundamental role in producing energy for food webs, and the vulnerability of primary producers to climate-induced changes to sea ice and water temperature, only ~7% of papers included in this review investigated primary producers.

Biological productivity is a factor that is included in EBSA designation. The Hudson Bay Complex has many different ecosystems within it that have unique patterns of primary production. The main bay typically has low mixing and high ice algae production, whereas Hudson Strait has high mixing due to wave patterns (Sandstrom and Elliott 2011) and lower ice algae production but higher plankton production (Sibert et al. 2011). Eastern Hudson Bay and James Bay have low ice algae biomass that occurs relatively late in the season. Phytoplankton blooms in Hudson and James Bay can occur three weeks later than in Hudson Strait (Sibert et al. 2011). Ice patterns are changing rapidly with climate change, resulting in changes to algae and plankton (Hoover et al. 2013a; Hoover et al 2013b). Consistent monitoring is needed to better understand and project region-specific changes in primary producers and primary production.

As with invertebrates, benthic primary producers are expected to be negatively affected by climate change whereas pelagic primary producers are predicted to increase. Hoover et al. (2013a) determined that changes in ice are causing ice algae biomass to decline by -37% and ice detritus to decline by -27%. Conversely, pelagic production is increasing 73% and pelagic detritus is increasing 67%. This is causing bottom-up shifts that propagate through the food web (Hoover et al. 2013a; Hoover et al. 2013b). Models that project 50 years into the future also indicate an increase in phytoplankton primary production and subsurface Chlorophyll a (Lavoie et al. 2013). More intense climate change forcing in models resulted in increased pelagic phytoplankton and pelagic detritus biomass, and decreases in ice algae and ice detritus (Hoover et al. 2013b). A decrease in ice algae will be especially impactful in Hudson Bay and perhaps less impactful in Hudson Strait because Sibert et al. (2011) determined that Hudson Bay has higher ice algae levels than Hudson Strait.

In addition to monitoring shifts in composition and biomass of primary producers, it is important to know which producers can be harmful, and how their presence and abundance is responding to ongoing change. Pućko et al. (2019) found that several taxa of toxic algae, including Bacillariophyceae, Dinophyceae, Haptophyceae, and Raphidophyceae are present in the HBC. Bottom-up effects of these taxa in Arctic marine environments are poorly understood and warrant further study.

2.4.10 Aquatic Invasive Species

Climate change is increasing the risk of aquatic invasive species entering Hudson Bay and potentially outcompeting native species. Although Hudson Bay is fairly isolated, opportunities for aquatic invasive species to enter the Bay are increasing as temperature rises, sea ice melts, and the shipping season lengthens (Goldsmit et al. 2020). Ports in Hudson Bay receive both domestic and international ships and are thus at relatively high risk of invasion (Chan et al. 2012). Compounding the problem of increased shipping is the fact that Hudson Bay provides a relatively hospitable environment for several aquatic invasive species (Goldsmit et al. 2020). DFO (2015) and Goldsmit et al. (2019) determined that the current alternate water ballast exchange area should be changed from Hudson Strait, which is a high-risk area for invasive species, to a deeper and farther offshore area, such as Baffin Island or the Canadian-Greenland Ridge. This is especially important as Hudson Bay has been identified as an area that has one of the highest diversities of marine benthic invertebrates (Wei et al. 2019), cetaceans, pinnipeds, and seabirds in the Canadian Arctic (Yurkowski et al. 2019). High emphasis is placed on biodiversity in EBSAs; therefore, the threat of invasive species entering EBSAs in Hudson Bay, and potentially threatening an area which has been identified as having very high biodiversity, is of great concern and requires close future monitoring.

2.4.11 Rising Temperatures and Sea Ice

Climate change is causing both air and sea surface temperature to rise. This is occurring faster in the Arctic than in other places around the world (Bush and Lemmen 2019). Researchers of several studies agree that Hudson Bay has seen rapid warming in air temperature since the 1990s. Recent models have predicted a ~0.9°C increase in temperature each decade from 2012 to 2061 (Steiner et al. 2013). This warming in air temperature is leading to increases in sea surface temperature of ~2.7°C per century (Steiner et al. 2013). Models projecting 50 years into the future have also shown increasing trends for sea surface temperature (Lavoie et al. 2013). In fact, Hudson Bay is experiencing some of the fastest sea surface temperature increases in the Arctic, with the coastal regions being warmer than the center, with the exception of the Belcher Islands and Hudson Strait (Larouche and Galbraith 2016). Factors that influence variability in air temperature and thus sea surface temperature and sea ice include the North Atlantic Oscillation in winter and the Atlantic Multidecadal Oscillation in summer (Peterson and Pettipas

2013). Researchers are in agreement that air and sea surface temperatures are rising, which is consistent with increases in sea ice melt (Steiner et al. 2013, Larouche and Galbraith 2016, Lavoie et al. 2013).

Many species rely on sea ice (e.g., Hoover et al. 2013a, Hoover et al. 2013b). Climate change is reducing the extent and volume of sea ice each year; sea ice coverage in Hudson Bay has decreased by 7.5% to 17.8% per decade, depending on the region. There is also less multi-year ice and more seasonal, thin ice (Steiner et al. 2013). Fifty-year model projections have shown decreasing trends for sea ice concentration in Hudson Bay (Lavoie et al. 2013). Papers included in this review have shown that temperature increases and sea ice melt will decrease ice algae, potentially leading to bottom-up energy effects felt through entire food webs (Hoover et al. 2013a, Hoover et al. 2013b). Sea ice melt may also change migration patterns of marine mammals (Bailleul et al. 2012), facilitate proliferation of aquatic invasive species (Goldsmith et al. 2020), and promote ocean acidification (Steiner et al. 2013). As sea ice is an important environmental feature that species use as haul-out sites (DFO 2017), for moulting, hunting, and rest (Luque et al. 2014), sea ice loss has widespread impacts on biological productivity, biological diversity, and species life history stages, which are all key factors that are monitored in EBSAs. Consequently, future studies related to warming of the HBC and sea ice decline are critical for mitigating and understanding effects.

2.4.12 Nutrients and Pollutants

Many nutrients and pollutants are found in eastern Hudson Bay EBSAs, and concentrations are being affected by ongoing anthropogenic influences. Ocean acidification is increasing due to enhanced uptake of CO_2, a longer open water season, and increased river discharge (Steiner et al. 2013). Additionally, historic trends show surface nitrate levels in Hudson Bay decreased and are projected to continue decreasing, while levels of nitrate, phosphate, and silicate all increased at depths below 100 m, likely due to a decrease in winter mixing or stronger summer water stratification (Steiner et al. 2013). Fifty-year projection models of Hudson Bay indicate decreasing trends for sea surface salinity, nitrate concentration, surface dissolved oxygen concentration, pH, and aragonite and calcite saturation horizon depths (Lavoie et al. 2013). Shifts in these compounds and environmental factors impact biological production

(Hoover et al. 2013a) and lower trophic levels, such as invertebrates, which will affect high trophic level species through bottom-up effects.

2.4.13 Gaps in Knowledge

Although considerable research has been conducted on EBSAs in eastern Hudson Bay in the last decade, substantial gaps in knowledge remain. Many authors clearly state ongoing uncertainty in calculations and models that would be mitigated by more empirical data; more data are needed to constrain estimates on population abundance, total allowable takes, niche overlap, diets, and stock distinction (DFO 2011a, DFO 2011b, DFO 2012, Pomerleau et al. 2012, DFO 2016a). Uncertainty also results from use of different methods with similar input data. For example, in modeling estimates of abundance for the COSEWIC-listed EHB beluga stock, authors of two papers used different growth rate and struck-and-loss rates in their calculations, which led to different results in abundance (Doniol-Valcroze et al. 2013; Gosselin et al. 2013). This uncertainty and variability has implications for harvest management, which is particularly problematic when harvest is critical for food security of Indigenous peoples. More empirical data and discussion on models employed are clearly needed for several components of the Hudson Bay ecosystems.

Lack of data also directly impacted EHB beluga management strategies around the Belcher Islands, as it was unknown what proportion of beluga harvested on the islands belonged to the EHB stock. Management plans were implemented using an estimated value. A few years later, genetic analyses were conducted, and the proportional contribution of the EHB stock to the Belcher Island harvest was lower than previously thought (DFO 2016c, Doniol-Valcroze et al. 2016). The updated value, which required molecular data, allowed more evidence-based management. At present, estimates from many projection and management models are poorly constrained by lack of precision and accuracy in input values, and this lack of data must be addressed to achieve effective management and conservation, particularly because harvested species are critical to food security for many communities.

A common reason for lack of data in the HBC is a reduction in sampling and observations due to unfavourable weather conditions. Conducting Arctic research is difficult under the best circumstances; however, the best circumstances are often not encountered in the Arctic. Weather can be a big issue for aerial surveys, and it is common to have to cancel observation days due to inclement weather (Gosselin et al. 2013, Gosselin et al. 2017; Hammill et al. 2016). Most of the surveys are also conducted in the summer or the ice-free season (Pierrejean et al. 2020, Bouchard et al. 2015, Watt et al. 2013, Bouchard and Fortier 2011, Luque et al. 2014, Foster et al. 2012, Pomerleau et al. 2012, Hammill et al. 2016). The result is a profound lack of winter data for many species and ecosystem components. More data in general, and more data collected year-round would greatly increase our understanding and ability to make accurate predictions of effects of stressors.

Aerial surveys are commonly used in the Arctic, because a large area can be covered by minimal people and with minimal disruption; however, this leads to a lack of molecular data that can provide information on age structure, sex structure, health, and genetic structure (DFO 2020, DFO 2016a). Greater availability of genetic data can reduce uncertainty around estimates (Mosnier et al. 2017). In 2016 (a), DFO studied Atlantic walruses, and the authors were uncertain as to whether there was a separate south and east Hudson Bay stock, or if the Hudson Bay-Hudson Strait stock extended all the way to the south of Hudson Bay. Whether this is one or two different walrus stocks has serious implications for how the stock is managed and is important information to note for the Belcher Island EBSA report as that is the area that the south and east Hudson Bay stock inhabits. Individually, each of aerial survey and genetics methods are beneficial, but together they increase holistic understanding. This is especially important when reporting on existing EBSAs and determining which regions should be designated as EBSAs; knowing that there is a separate stock in an area or that a population in a specific region has a lower ratio of reproductive females can influence whether the region should be designated as an EBSA.

Knowledge on the eastern Hudson Bay complex is becoming increasingly abundant and available in the scientific literature; however, some topics and species receive disproportionate attention. This review highlights the bias towards research with a biotic focus. Within biotic research, there is a bias towards marine mammals. Research on fish, invertebrates, and primary producers is lacking. For example, Hoover et al. (2013a) did not have enough data on fish species in the HBC to parameterize whole-ecosystem models, and had to indirectly estimate fish biomass through seabird diet. This increased uncertainty within the results.

There were also relatively few papers published on entire ecosystems. The exceptions were Hoover et al. (2013a) and Hoover et al. (2013b). Authors of these papers modeled both bottom-up and top-down impacts of stressors, which is key to understanding how ecosystem structure, function, and services may respond to ongoing anthropogenic stressors. Continuing and expanding whole-ecosystem modeling efforts may help forecast changes in eastern Hudson Bay EBSAs with enough time to undertake mitigative management actions.

There is also a lack of traditional ecological knowledge (TEK) included in papers incorporated in this review. Of all the papers included in the literature review, only 2 papers (Brown and Fast 2012, Breton-Honeyman et al. 2016) used traditional knowledge in the methodology. Authors of some papers mentioned that Inuit were consulted or that Inuit sightings of certain species were included, but few used Indigenous knowledge as a primary method. Traditional ecological knowledge is a wealth of relatively untapped information on the HBC that could aid researchers in understanding species behaviour and stock abundance. An increase in the inclusion of traditional ecological knowledge in future scientific publications could greatly help protect and expand the knowledge on existing EBSAs.

2.5 Future Recommendations

Continued research in the six eastern Hudson Bay EBSAs equips scientists with better knowledge and understanding to protect and manage ecosystems such that they continue to have high ecological and biological significance. The best tool to ensure these areas stay protected is ample and accurate data and knowledge. Significant progress has been made with monitoring marine mammal stock abundance, especially EHB belugas; however, future mitigation strategies would be more impactful if molecular data were collected in conjunction with survey observations. This is true not only for beluga stocks but also for other marine mammals, such as walruses and narwhals. It had been more than five years since aerial surveys were conducted for some of the marine mammals included in this review, and some species, such as the EHB belugas, have seen a decrease in stock size since then. Conducting an aerial survey in the near future could thus be very important. In addition to aerial survey and molecular data, more data collected using traditional ecological knowledge would be greatly beneficial for future publications as TEK does not suffer the same limitations in terms of seasonality, time-scale, and reductionism as western science does.

In additional to expanding methodologies, topics of future research need to be expanded. Future research on fish, invertebrates, and primary producers is needed. Additionally, more research spanning multiple species and trophic levels would be greatly beneficial as these publications provide an abundance of valuable information on how species interact with each other and how a shift in one species or trophic level can propagate through an entire food web.

2.6 Conclusion

With climate change becoming an increasingly large threat for the six eastern Hudson Bay EBSAs and prediction models projecting environmental and species shifts to continue, reviews of the updated literature are important to help ensure EBSAs are managed, monitored, and protected as effectively as possible. Sixty papers were assessed in this review, which included literature published between 2011 to 2021, and there were many topics researched and published in relation to the six eastern Hudson Bay EBSAs. This review synthesized and evaluated relevant advances in the knowledge surrounding the six eastern Hudson Bay EBSAs in the past decade, and identified gaps in the literature. Marine mammals were the taxa most thoroughly studied between 2011 to 2021, with stock abundance, harvest trends, and management strategies being topics of interest for researchers. Potential threats, future shifts and abundance, and physiological changes in fish were also addressed in the literature. Diversity of invertebrates present in the six eastern Hudson Bay EBSAs was a topic of interest, as was the threat of aquatic invasive species, especially as shipping increases. A change in the alternate ballast water exchange area was proposed. The large impact of changes in sea ice and sea surface temperature on species throughout the entire ecosystem was identified, and the body of research indicates that ongoing climate change will result in shifts from more benthic-based to pelagic-based food webs. Bottom-up changes to food webs in the six EBSAs are predicted. Gaps in the literature were identified to highlight key areas for future research, and include whole-ecosystem research, research on trophic levels below marine mammals, research conducted in multiple seasons, and the include of TEK. Addressing these gaps will allow more informed parameterization of, and more accurate results from, projection, stock, and harvest models.

3.0 Food Web Structure Among Three Depths in Frobisher Bay, Nunavut

3.1 Introduction

Marine food webs are a network of complex interactions, and elucidating these interactions can provide insight into energy flow and species interactions that help us predict effects of anthropogenic stressors on ecosystem structure and function. The structure of food webs can be quantified using direct (e.g., stomach content) and/or indirect (e.g., stable isotope) diet data (Layman et al. 2007; Peterson and Fry 1987), and then analyzed and interpreted to support inferences regarding species interactions, energy flow, and the impact of environmental gradients. Food webs are often depicted as connected nodes; nodes often represent functional feeding groups or taxonomic species that are connected through direct trophic linkages, which can represent consumption and the transfer of energy, mass, and contaminants (Dunne et al. 2002). To best understand food webs, it is important to get a holistic view by including as many taxa as possible; this is especially important in the context of environmental change, as taxa can respond differently to stressors (Hoover et al. 2013; Best et al. 2015), and in the Arctic, where food webs are subject to rapid changes from both climate warming and increased human activity.

Stable isotope ratios of carbon, nitrogen, and sulphur are commonly used to investigate food web structure in Arctic marine environments, as these ratios vary in biota based on predictable fractionation and mixing processes (Fry 2006). Typically, $\delta^{13}C$ and $\delta^{15}N$ ratios are used to infer carbon source and trophic position, respectively (Wada et al. 1991; Post 2002). Delta^{15}N is often used to infer trophic level because $\delta^{15}N$ increases ~ 3 to 5 ‰ with each trophic transfer (Peterson and Fry 1987; Montanari 2017). In contrast, $\delta^{13}C$ ratios of organisms do not change appreciably with trophic transfer, but instead reflect availability and sources of dissolved inorganic carbon for primary producers (Wada et al. 1991). This allows $\delta^{13}C$ values to be used to infer carbon source, and to discriminate between freshwater and marine food sources. Terrestrial and freshwater sources of carbon are known to be more depleted in ^{13}C compared to marine sources, which can allow scientists to identify freshwater vs marine source of primary production (Hunt 1966; Schell et al. 1998; Iken et al. 2010; Pulsipher et al. 2021). Similar to $\delta^{13}C$, $\delta^{34}S$ does not change appreciably with trophic transfer, and can be used to help differentiate among different sources of basal organic matter - specifically among marine, freshwater, and terrestrial sources. Terrestrial and freshwater sources of organic matter are more depleted in ^{34}S than marine sources (Fry 2006; Whitney et al. 2018). Pelagic and benthic organisms differ in both $\delta^{13}C$ and $\delta^{34}S$ values, with pelagic organisms tending to have lower $\delta^{13}C$ and higher $\delta^{34}S$ values compared to benthic organisms. These differences allow scientists to investigate many processes related to energy flow, including organic matter pathways and benthic-pelagic coupling (Thode 1961; Hobson et al. 2002; Le Loc'h et al. 2008; Duffill-Telsnig et al. 2019).

Comparing food web structure among sites or regions in the Arctic, as well as relating food web structure to environmental gradients, often requires that taxa are categorized into functional feeding groups. Functional feeding groups can be more comparable over relatively large spatial and/or temporal gradients than taxonomically identified organisms, because presence/absence of individual species often varies widely at scales that might not be of interest (e.g., among meso- or microhabitat scales when the interest is regional or sub-regional). This is particularly true in studies in Arctic marine systems, where study design and spatio-temporal replication of sampling are often compromised by challenging logistics.

Two prevalent functional feeding groups in Arctic marine food webs are benthic carnivores and benthic suspension feeders. Both promote benthic-pelagic coupling in ecosystems that can be very spatially and temporally variable in terms of productivity. Benthic carnivores are known to affect food webs by exerting top-down pressure via predation, and effects cascade through the entire food web to the lowest trophic levels (Estes et al. 2011; Hui 2012). Benthic carnivores feed in both pelagic and benthic food webs, which is one mechanism through which benthic-pelagic coupling occurs (Iken et al. 2001).

Benthic suspension feeders are a second important functional feeding group in Arctic marine food webs. Benthic suspension feeders affect plankton populations by filtering phytoplankton and particulate matter from the water column, and their presence can improve water quality (Lonsdale et al. 2009). Benthic suspension feeders promote benthic-pelagic coupling by digesting suspended particles and transferring undigested remains to the sediment (Newell 2004). Studying both particular functional feeding groups of interest and overall food web structure can further our understanding of ecosystem function and allow more informed predictions of effects of environmental change.

Food web structure is affected by a myriad of biotic and abiotic factors. One abiotic variable of especial interest in Arctic marine food webs is water depth, not least of which because food web structure is less well understood in deeper Arctic waters compared to shallower ones (Roy et al. 2015; Wolfl et al. 2019; Mayer et al. 2018). Many proximate variables that affect food web structure are also ultimately affected by water depth, such as amount and dominant sources of primary production (Hsiao 1988; Roy et al. 2015). Food webs vary in size, both vertically and horizontally, and previous researchers have shown that longer (vertical) food webs are often found in deeper waters (Divine et al. 2015: Iken et al. 2005). Longer food webs are thought to be less stable and may take longer to recover after a stressful or disruptive event occurs compared to shorter food webs due to the increased number of trophic levels (Pimm and Lawton 1977; Lawler and Morin 1993; Jonsson and Ebenman 1998; Chanut et al. 2020); that is, they are thought to be less resistant and less resilient to change. Characterizing food webs and identifying the more vulnerable ones may help direct research, conservation, and management efforts in the vast and poorly understood Arctic marine ecosystems.

Divine et al. (2015) examined food web structure at shallow (14 to 90 m) and deep (100 to 220 m) sites in the Beaufort Sea and found that the food web in one of the deep areas was relatively long, but that the effect of depth on food web length was inconsistent among locations. The authors highlighted the importance of determining baseline data for food web structure and energy flow in all Arctic marine environments, as these environments are facing unprecedented climate-induced changes. The variability found in food web structure along a gradient of depth highlights the need for more research in this area.

While all marine food webs in the Arctic are in general poorly understood, less is known about the structure of benthic food webs in Arctic marine ecosystems compared to pelagic food webs. Benthic food webs are thought to be more susceptible to stressors because availability of food decreases more strongly with increasing water depth in benthic food webs than in pelagic food webs (Roy et al. 2015). Benthic marine habitats support ~90% of Arctic marine diversity (Roy and Gagon 2018), and previous researchers have highlighted the need for, and urgency of, more investigation into their structure and function (Renaud et al. 2019).

As benthic food webs become more resource-constrained with increasing depth, the rate of transfer of nutrients from overlying waters to sediments (and back again - i.e., benthic-pelagic coupling) is critically important in shaping food web structure. The strength of benthic-pelagic coupling also varies with depth (Stasko et al. 2018; Sibert et al. 2011; Giordani et al. 2002); however, there are many other factors that influence this complex coupling process, including the rate and efficiency of pelagic grazing (Stasko et al. 2018), functional feeding group diversity (Caliman et al. 2007; Montoya et al. 2015; Griffiths et al. 2017; Wang et al. 2020), tidal action and resuspension activity (Mason et al. 2010; Jansen et al. 2018), and shear stress (Capet et al. 2016). Understanding how benthic food web structure varies in response to water depth could help scientists better predict how food webs will respond to climate-induced changes in primary productivity and benthic-pelagic coupling, particularly because benthic taxa are often used as bio-indicators (Oleszczuk et al. 2021). While there have been some studies on how trophic ecology of organisms and food web structure vary along gradients of water depth in Arctic marine environments (Stasko et al. 2018; Roy et al. 2015; Iken et al. 2005), our understanding remains incomplete, particularly for benthic food webs subject to current and imminent anthropogenic influences, such as food webs in Frobisher Bay, NU.

Marine food webs in Frobisher Bay support food security, through provision of a wide variety of traditionally harvested fish (e.g., Arctic Char, *Salvelinus namaycush*) and shellfish (e.g., *Mya truncata*) species, for the community of Iqaluit, NU. Frobisher Bay is subject to a wide range of local, regional, and global anthropogenic influences. Iqaluit is the most populated community in Nunavut and is home to ~7740 people (Statistics Canada 2017). Local marine food web structure is affected via wastewater inputs (Schaefer 2020), fishing, and boating (Ding and Li 2020). Additionally, a new deep-water port was recently developed in Iqaluit, and this port has been determined to be the most valuable port in the Northwest Passage in terms of container transport (Ding and Li 2020). Increases in shipping activity could impact food web structure through the introduction of invasive species (Goldsmit et al. 2018), oil spills (Satei 2018), or underwater noise (Slabbekoorn et al. 2010). Climate change will also no doubt affect food web structure in this high-latitude region. Given the importance of the Frobisher Bay environment, the current minimal knowledge on food web structures in Frobisher Bay, and both a general and local lack of knowledge of the structure and function of deep benthic food webs and benthic functional feeding groups, this study aimed to:

1. Characterize Frobisher Bay nearshore (10 to 15 m), midshore (20 to 45 m), and offshore (260 to 351 m) food web structures using nitrogen, carbon and sulphur stable isotope data;
2. Compare trophic ecology indices (niche volume, distance to centroid, nearest neighbour distance, maximum trophic level, and $\delta^{13}C$ and $\delta^{34}S$ ranges) of benthic carnivores and benthic suspension feeders among nearshore, midshore, and offshore depths; and,
3. Compare trophic ecology indices (niche volume, distance to centroid, nearest neighbour distance, maximum trophic levels, and $\delta^{13}C$ and $\delta^{34}S$ ranges) of benthic carnivores and benthic suspension feeders within depths to each other, to infer interactions.

I predicted that:

1. The nearshore and offshore food web structures would each be more isotopically similar to the midshore food web than to each other.
2. The nearshore food web would have fewer trophic levels, lower food web diversity, larger $\delta^{13}C$ and $\delta^{34}S$ ranges, and lower $\delta^{13}C$ and $\delta^{34}S$ means than the midshore and offshore food webs, due to reports of food webs being longer in deeper areas (Iken et al. 2005; Divine et al. 2015), reports of species diversity increasing with water depth (Renaud et al. 2019; Herder 2020), and the closer proximity of the nearshore food web to terrestrial and freshwater runoff, which influences nearshore $\delta^{13}C$ and $\delta^{34}S$ values (Hunt 1966; Schell et al. 1998; Iken et al. 2010; Pulsipher et al. 2021).
3. Benthic carnivores and benthic suspension feeders at the nearshore depth would have smaller $\delta^{15}N$ ranges, larger $\delta^{13}C$ and $\delta^{34}S$ ranges, and thus larger isotopic niche volume, due to the findings of previous studies that have investigated food web length and depth (Iken et al. 2005; Divine et al. 2015), and because terrestrial and freshwater inputs at the nearshore depth could provide more diverse carbon and sulphur sources (Hunt 1966; Schell et al. 1998; Iken et al 2010)

4. Benthic carnivores would occupy larger niche volume, higher trophic levels, and larger $\delta^{13}C$ and $\delta^{34}S$ ranges than benthic suspension feeders within each of the three depths, due to direct predation on both pelagic and benthic prey (Iken et al. 2001).

3.2 Methods

3.2.1 Study Area

Frobisher Bay is located adjacent to Baffin Island, NU. The capital of Nunavut, Iqaluit, is located along the coast of Frobisher Bay. The Sylvia Grinnell River discharges into Frobisher Bay between two marine inlets; Koojesse Inlet and Peterhead Inlet. Frobisher Bay is 230 km in length, and ranges from 20 to 40 km wide (Todd et al. 2016). The depth of the sea floor varies in Frobisher Bay; along almost the entire southwest side of the bay is a trough that extends to depths greater than 640 m. Calanus Shelf, also within Frobisher Bay, extends from shallow waters to depths of ~130 m before meeting the deep trough (Dunbar 1958) (Fig. 3.1). The ice-free season in Frobisher Bay starts in mid-June or July and continues until November or December (Carter et al. 2020). During this time, primary production is highest in the top 10m and decreases with depth (Hsiao 1988). The narrow shape of the bay, in combination with high tides up to 36 feet, result in turbulent conditions (Dunbar 1958). The uniquely high tide can move ~17 km^3 of water in and out of Frobisher Bay in a single day (Spares et al. 2012).

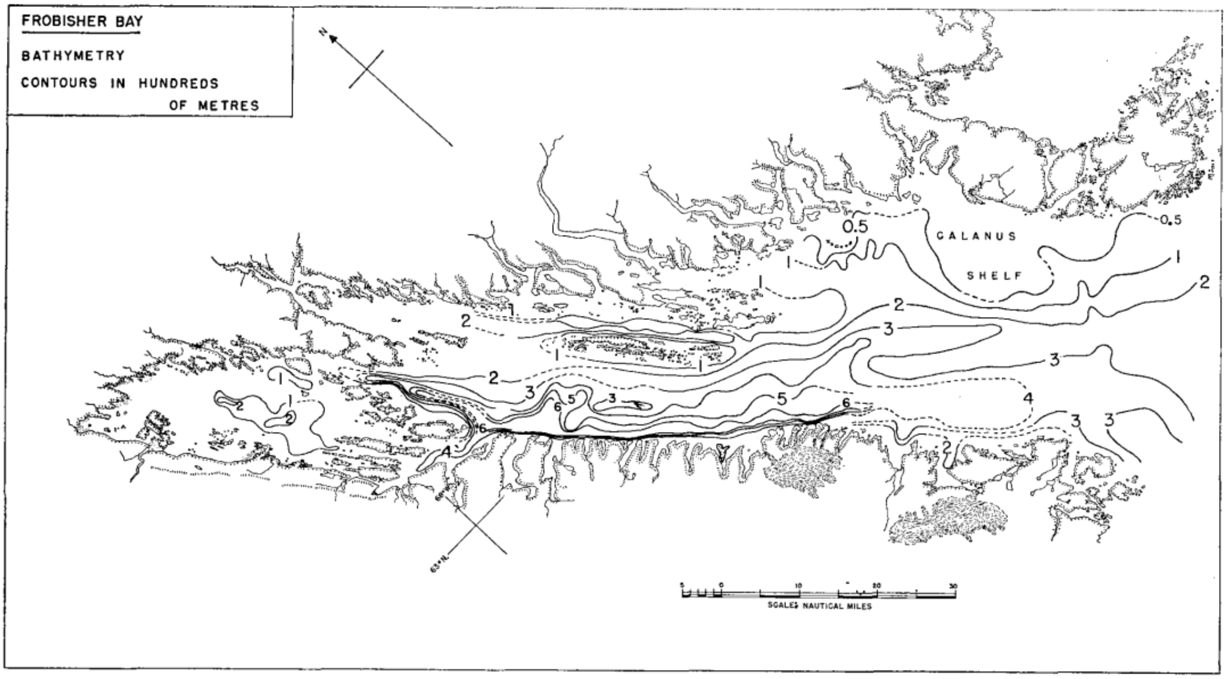

Figure 3.1. Map of Frobisher Bay with bathymetry contour lines in hundreds of meters (Dunbar 1958).

3.2.2 Sample Collection and Lab Processing

Food web structure was analyzed and compared among three broad depth categories in Frobisher Bay, Nunavut. These categories reflect sampling undertaken by project partners (Fisheries and Oceans Canada), and are hereafter referred to as Frobisher Bay nearshore (FBN; 10 to 15 m depth), Frobisher Bay midshore (FBM; 20 to 45 m depth), and Frobisher Bay offshore (FBO; 260 to 351 m depth; Fig. 3.2). FBN samples were comprised of species collected from one site in Koojesse Inlet and one site in Peterhead Inlet. The FBM samples were comprised of species collected from six different sites in Koojesse and Peterhead inlets. The FBN and FBM samples were collected during the summer of 2019 and 2020. As FBN and FBM samples were collected across two years, a t-test was conducted ($p < 0.05$) on a subset of samples to confirm that there were no statistical differences in isotope ratios of the same taxon from different years before samples were averaged together so that they only appeared once in each depth dataset. FBO samples were comprised of species collected during the summer of 2021 from three sites in the middle of the bay (Fig. 3.2). These samples and depths were used in this study due to availability and sampling constraints that resulted from the COVID-19 pandemic.

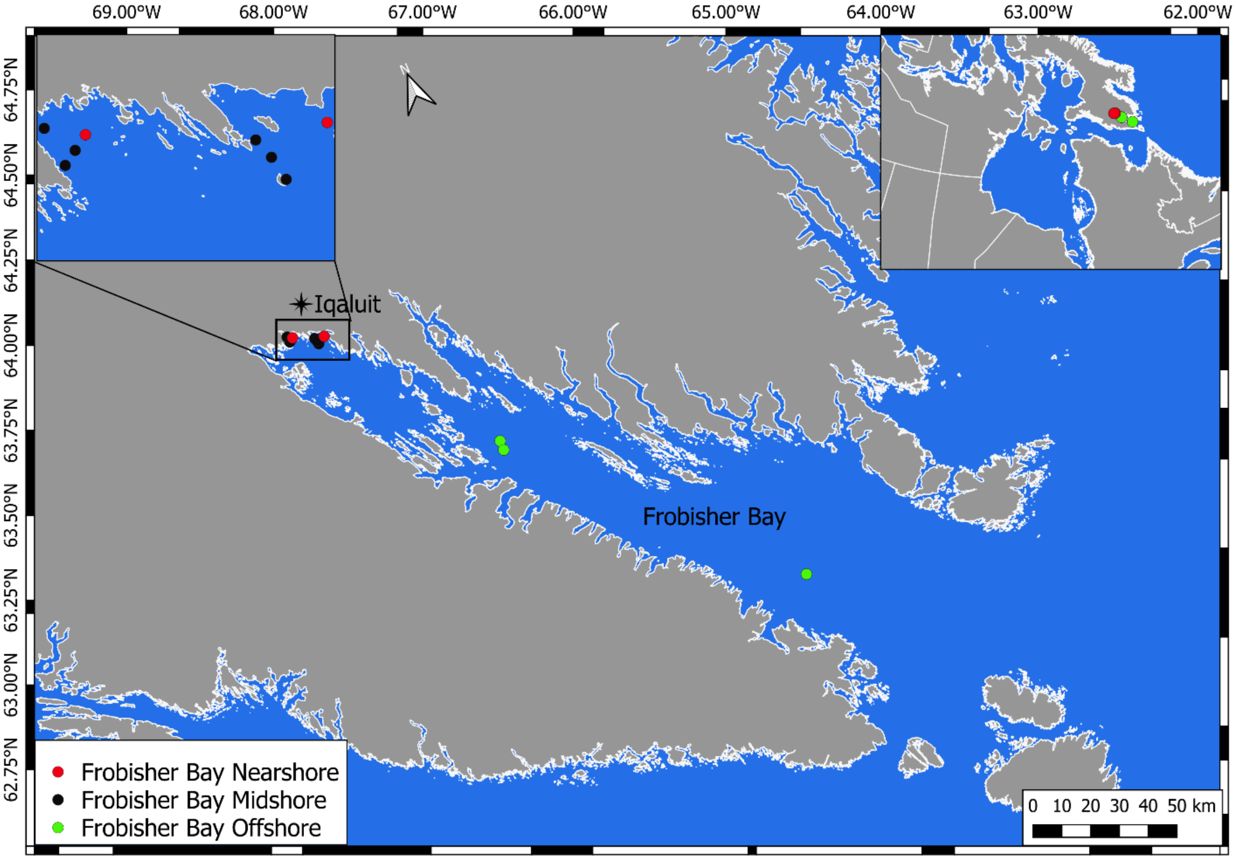

Figure 3.2. Map of Frobisher Bay including nearshore (red), midshore (black), and offshore (green) sampling locations.

Sample collection of invertebrates occurred during the summers of 2019, 2020, and 2021 using 500 µm mesh zooplankton nets, Van Veen grabs, and benthic trawls. Fish were collected using multi-mesh gill nets and benthic trawls. Identification of invertebrates and fish was done on-site to the lowest level of taxa possible, and then samples were frozen for shipping. Once samples arrived at the University of Waterloo laboratory, they were further identified to family, genus or species, with the aid of a dissection microscope when needed. A few unidentifiable samples were sent as voucher specimens to Université Laval, Quebec. Fish, crustaceans, and mollusks were further dissected to obtain the muscle tissue. When samples were too small to support analysis of stable isotope ratios, whole-body samples were used instead of muscle samples. When whole-body samples were too small, individuals of the same taxon were combined to achieve sufficient mass for stable isotope analysis.

After taxonomic identification, species were classified into different functional feeding group using the classification from Macdonald et al. (2010) (Appendix A). Classification included feeding location (i.e., pelagic, benthopelagic, or benthic) and feeding mechanism (i.e., herbivore/grazer, suspension feeder, deposit feeder, suspension/surface deposit feeder, or carnivore). In total, seven functional feeding groups were identified: pelagic carnivores (PC), pelagic herbivores (PH), benthopelagic carnivores (BPC), benthic suspension feeders (BSF), benthic deposit feeders (BSDF), benthic suspension feeders/deposit feeders (BSDF/SF), and benthic carnivores (BC). Of the seven functional feeding groups, two (benthic carnivores and benthic suspension feeders) had a sample size sufficient to conduct stable isotope analyses and statistical analyses.

Once dissected, samples were stored in a -20°C freezer until they were freeze dried at -53°C with a vacuum pressure between 0.018 mBar and 0.024 mBar for 48 hours or until completely dry. Dried samples were homogenised, whereupon samples with excess exoskeleton were acidified using 10% HCl to remove the inorganic carbon from the samples. Acidified samples were re-dried in a fume hood for 24 hours and then transferred to an oven at 50°C for 24 hours or until completely dry. If needed, samples were re-homogenized after drying. Samples were then weighed for nitrogen, carbon, and sulphur stable isotope analysis using a microbalance. Every tenth sample was duplicated to enable estimates of precision. Samples were then sent to the Environmental Isotope Laboratory at the University of Waterloo where they were run through a 4010 Elemental Analyzer (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer (CFIRMS). Delta^{34}S values were obtained using a 4010 Elemental Analyzer (Costech Instruments, Italy) coupled to an Isochrom (Micromass UK) continuous flow isotope ratio mass spectrometer (CFIRMS). Nitrogen, carbon, and sulphur delta values were determined by quantifying a ratio of heavy to light isotopes (^{13}C:^{12}C, ^{15}N:^{14}N, or ^{34}S:^{32}S) in samples and comparing them to international standards (Fry 2006). The standards used for this analysis were Vienna Pee Dee Belemnite for carbon, atmospheric AIR for nitrogen, and Vienna-Canyon Diablo Troilite meteorite for sulphur, and are expressed as δ^{13}C, δ^{15}N, and δ^{34}S for carbon, nitrogen, and sulphur, respectively, where δ represents the parts per thousand difference from the standard.

3.2.3 Data Analysis

All statistical analyses were conducted in Microsoft Excel version 16.38 and R version 4.2.0 (R Core Team, 2022), with alpha set to 0.05. Residual quantile-quantile plots were assessed for normality and the taxa Scleractinia was removed from the FBO isotope analysis to improve normality. Isotope ratios were qualitatively compared among the three depths at the taxa level, as well as between the two functional feeding groups of interest - benthic suspension feeders and benthic carnivores.

Stable isotope analysis was used to quantify food web structure at three depths - FBN, FBM, and FBO. When comparing the structures of different food webs, it is often necessary to correct for among-system variability in isotope ratios in basal organisms (i.e., baseline variation). Establishing an appropriate $\delta^{15}N$ isotopic baseline can be difficult; ideally, a relatively long-lived primary consumer species that is linked to the food web of interest is selected as a baseline organism (Post 2002). The long-lived primary consumers selected to account for baseline variation in this study were *Musculus discors* and *Musculus* sp.; if those taxa were not available, then the bivalves *Hiatella Arctica*, and *Serripes groenlandicus* were used. All isotope baseline correction was done at the site level, and was calculated as:

Equation 1: $$\text{Adjusted } \delta^{15}N \text{ value} = (\delta^{15}N_{consumer} — \delta^{15}N_{base})$$

where,
$\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value of the consumer of interest; and,
$\delta^{15}N_{base}$ is the $\delta^{15}N$ value of the chosen baseline species

Adjusted $\delta^{15}N$ values were used for all further food web data analysis. If a single taxon was collected from multiple sites within the same depth category, adjusted $\delta^{15}N$ isotope values were averaged so that each taxon was only represented once at each depth. Delta^{13}C and $\delta^{34}S$ values were also averaged so that each taxon was represented once for each depth category. Sulphur stable isotope analysis was conducted on fewer samples than carbon and nitrogen stable isotope analysis due to mass constraints; analysis of $\delta^{34}S$ requires more mass than analysis of $\delta^{13}C$ and $\delta^{15}N$ (Supplement Table 1). The fuller $\delta^{15}N$ and $\delta^{13}C$ dataset was used to determine

$\delta^{15}N$ and $\delta^{13}C$ range and means, whereas the smaller dataset including all sulphur stable isotopes was used for all other three-dimensional analysis (see below).

Trophic level was also calculated for each consumer using the following equation (Post 2002):

Equation 2: $$TL_{consumer} = [(\delta^{15}N_{consumer} — \delta^{15}N_{base})/3.4‰ + \lambda$$

where,
3.4 is the estimated average enrichment of $\delta^{15}N$ per trophic level increase;
$\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value of the consumer of interest;
$\delta^{15}N_{base}$ is the $\delta^{15}N$ value of the chosen baseline species; and,
λ is the is the trophic position of the reference species used to estimate the $\delta^{15}N$ value of the chosen baseline species (i.e. $\lambda = 2$ because a primary consumer was used as a baseline).

Several metrics are often used to quantify food web structure using two-dimensional isotope data (usually using $\delta^{15}N$ and $\delta^{13}C$) (Layman et al. 2007; Jackson et al. 2011), including: $\delta^{15}N$ and $\delta^{13}C$ range, distance to centroid (CD), total food web area (TA), nearest neighbour distance (NND), standard deviation of the nearest neighbour distance (SDNND) (Layman et al. 2007), and standard ellipse area (SEA), and standard ellipse area correct for small sample size and Bayesian implementation (SEA_C and SEA_B) (Jackson et al. 2011). Ranges of the stable isotope values provide information on the vertical and horizontal structure of a food web. Food web area, as well as distance to centroid provide information on the amount of diversity in a given food web, and distance to centroid can help identify “outliers” in the system (Layman et al. 2007). Nearest neighbour distance provides information on the amount of redundancy in a food web, whereas standard deviation of nearest neighbour distance provides information on the evenness of the distribution (Layman et al. 2007).

Sulphur stable isotope analysis, while less commonly used in food web studies, can improve aquatic food web analysis by helping differentiate between different nutrient sources (Connolly et al. 2004). All three stable isotopes ($\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$) were analyzed in this study, and thus a diversity of quantification approaches was used.

Three-dimensional isotopic analyses were conducted at the taxa level to facilitate comparison of food web structure at all three depths. Ranges of δ^{15}N, δ^{13}C, and δ^{34}S, as well as CD, NND, and SDNND were calculated using data from all three isotopes. Additional three-dimensional analysis to quantify isotopic food web volume and food web similarity were conducted using the package nicheROVER (Swanson et al. 2015). As sample size was larger for δ^{15}N and δ^{13}C analysis - due to the lower mass needed to determine stable isotope ratios - this larger dataset was used to calculate δ^{15}N and δ^{13}C range and means. To facilitate comparison with the more frequently used two-dimensional Layman et al. (2007) and Jackson et al. (2011) metrics, two-dimensional isotopic metrics were also calculated using the package SIBER (Stable Isotope Bayesian Ellipses in R). Two-dimensional analyses included: δ^{15}N, δ^{13}C, and δ^{34}S range, CD, NND, and SDNND. To estimate two-dimensional food web area, the package SIBER was used to calculate standard ellipse areas (SEA, SEA_C, and SEA_B) using areas that included 40% of the data (Jackson et al. 2011). Ellipse areas were plotted two ways: 1) δ^{15}N on the y-axis and δ^{13}C on the x-axis; and, 2) δ^{34}S on the y-axis and δ^{13}C on the x-axis. Results for all two-dimensional analyses can be found in Appendix B.

To address objective one, nearshore, midshore, and offshore food webs were quantified by δ^{15}N, δ^{13}C, and δ^{34}S ranges, food web length, CD, NND, and SDNND using three-dimensional isotopic data. The mean δ^{15}N, δ^{13}C, and δ^{34}S values were also calculated as measures of centrality for each food web. Metrics were calculated for each depth category and qualitatively compared among depth categories. To estimate isotopic food web size, food web niche volumes were calculated for each depth category using the package nicheROVER, with alpha set to 0.95. Similarity of the three food webs among depths was determined in nicheROVER by estimating posterior probability of overlap (±95% credible interval) (Swanson et al. 2015) between each pairwise combination of depths.

To address objectives two and three, trophic ecology indices for benthic carnivores and benthic suspension feeders were quantified by δ^{15}N, δ^{13}C, and δ^{34}S ranges, maximum trophic level, CD, NND, and SDNND using three-dimensional isotope data. These calculations were performed in Excel. The mean δ^{15}N, δ^{13}C, and δ^{34}S values were also calculated as measures of centrality for each food web. Functional feeding group niche region volumes were estimated using the package nicheROVER, with alpha set to 0.95. This analysis was done for benthic carnivores and benthic suspension feeders at each depth category. Trophic ecology indices were then qualitatively compared among the three depth categories for each of benthic carnivores and benthic suspension feeders. Finally, trophic ecology metrics for benthic carnivores and benthic suspension feeders were qualitatively compared to each other for each depth category.

3.3 Results and Discussion

3.3.1 Food Webs

Invertebrates represented the majority of samples analyzed for this study; 98 invertebrate taxa were identified from sample collections (Appendix A). Nineteen fish species were collected (all depths combined). The number of taxa collected was highest at the midshore depth, where 80 invertebrate taxa and 14 fish species were captured (there was adequate mass for 75 invertebrate taxa and 13 fish species for stable sulphur isotope analysis). In the nearshore depth category, 38 invertebrate taxa and 8 fish species were captured (there was adequate mass for 31 invertebrate taxa and 6 fish species for sulphur isotope analysis), and in the offshore depth category, 30 invertebrate taxa and 7 fish species were captured (there was adequate mass for 28 invertebrates and 7 fish for sulphur) (Appendix A).

Similarity Among Food Webs

Food web metrics based on three-dimensional nitrogen, carbon, and sulphur stable isotope ratios indicated that food webs were similarly structured in all three depth categories. Overlap probability plots generated in nicheROVER, visual overlap of elliptical plots, and SEA_C values (Table 3.1; Fig. 3.3; Fig. 3.4; Appendix B) all indicated little variation in food web structure among the three depth categories. This is attributed to the large overlap for all three stable isotopes ranges among the three depths (Table 3.1), as is obvious from the one-dimensional density line plots in Fig 3.4. Although I expected some overlap on the $\delta^{15}N$ axis, I did not expect to have such similar $\delta^{13}C$ and $\delta^{34}S$ means and ranges among the three depth categories (Table 3.1). I expected that there would be a gradient in $\delta^{13}C$ and $\delta^{34}S$ means from FBN to FBO due to terrestrial and freshwater influences at the nearshore depth (Hunt 1966; Schell et al. 1998; Koziorowska et al. 2016); however, $\delta^{13}C$ and $\delta^{34}S$ means and ranges were similar among the three depths. I suggest that the strong similarity in inferred organic nutrient sources ($\delta^{13}C$ and $\delta^{34}S$) among the three depths is due to the large tidal amplitude (11 m) in Frobisher Bay, which can bring ~17 km^3 of marine water in and out of the bay in one tidal cycle (Spares et al. 2012). In comparison, even during highest discharge in July, the Sylvia Grinnell

River only discharged 0.0265 km^3 of water per day between 2015 and 2021 (Government of Canada, 2023). Déry et al. (2016) determined the average annual discharge of the Sylvia Grinnell River to be 1.06 km^3 from 1964 to 2013. Lovrity (1984) determined that at 33 m in Frobisher Bay, marine water is well mixed and salinity and temperature at the bottom vary little due to high tidal currents and mixing in the area. Additionally, Dunbar (1958) determined that the high tidal amplitude in Frobisher Bay causes water 100 to 200 m deep to be warmer and have lower salinity compared to similar marine depths that lack this high tide. The strong influence of the Frobisher Bay tide on environmental conditions in deeper areas of the bay may contribute to the similarity in food web structure that I observed among the three depths.

Table 3.1. Three-dimensional isotopic Layman (2007) metrics and food web volume values (Swanson et al. 2015) calculated using $\delta^{15}N_{adj}$, $\delta^{13}C$, and $\delta^{34}S$ from taxa collected from three depth categories: Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore.

	Depth Category		
Metric	**Nearshore**	**Midshore**	**Offshore**
$\delta^{15}N_{adj}$ (‰) Range	8.90	10.64	10.06
$\delta^{15}N_{adj}$ Mean	4.02	3.92	4.84
$\delta^{13}C$ (‰) Range	11.90	14.91	11.21
$\delta^{13}C$ Mean	-18.24	-18.59	-18.44
$\delta^{34}S$ (‰) Range	6.18	11.43	7.35
$\delta^{34}S$ (‰) Mean	18.75	17.72	18.38
CD	2.79	3.49	3.14
NND	1.10	0.92	1.11
SDNND	0.64	0.63	0.74
Trophic levels	4.40	5.05	4.96

3-dimensional niche volume	329.61	844.97	596.59

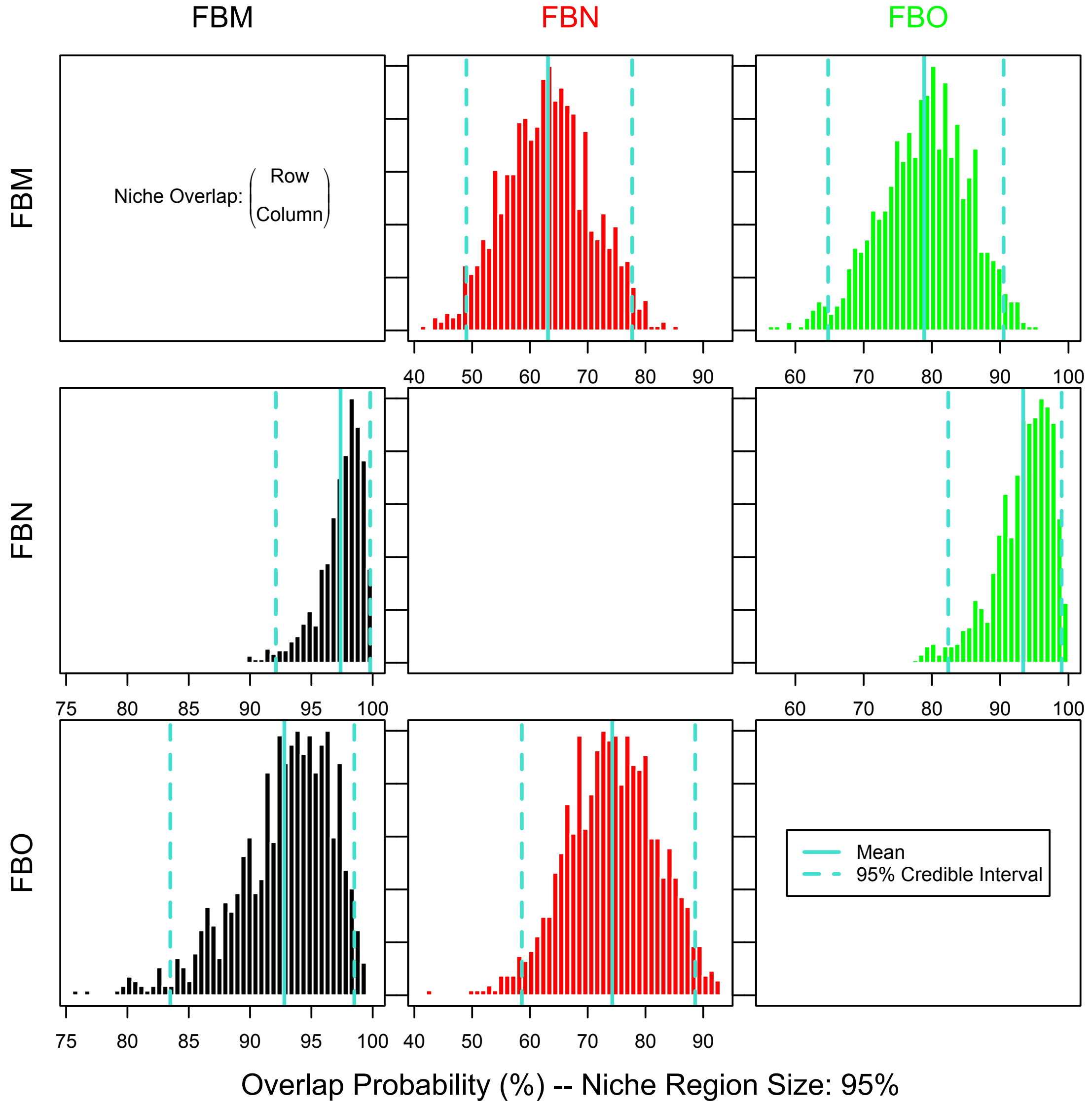

Figure 3.3. Frequency histograms for probability of overlap among the 95% food web regions estimated using three-dimensional isotopic data for Frobisher Bay midshore (black), Frobisher Bay nearshore (red), and Frobisher Bay offshore (green) food webs. The mean directional probability of overlap between all pairs is >60%. Note that the scale of X-axes differs among individual plots.

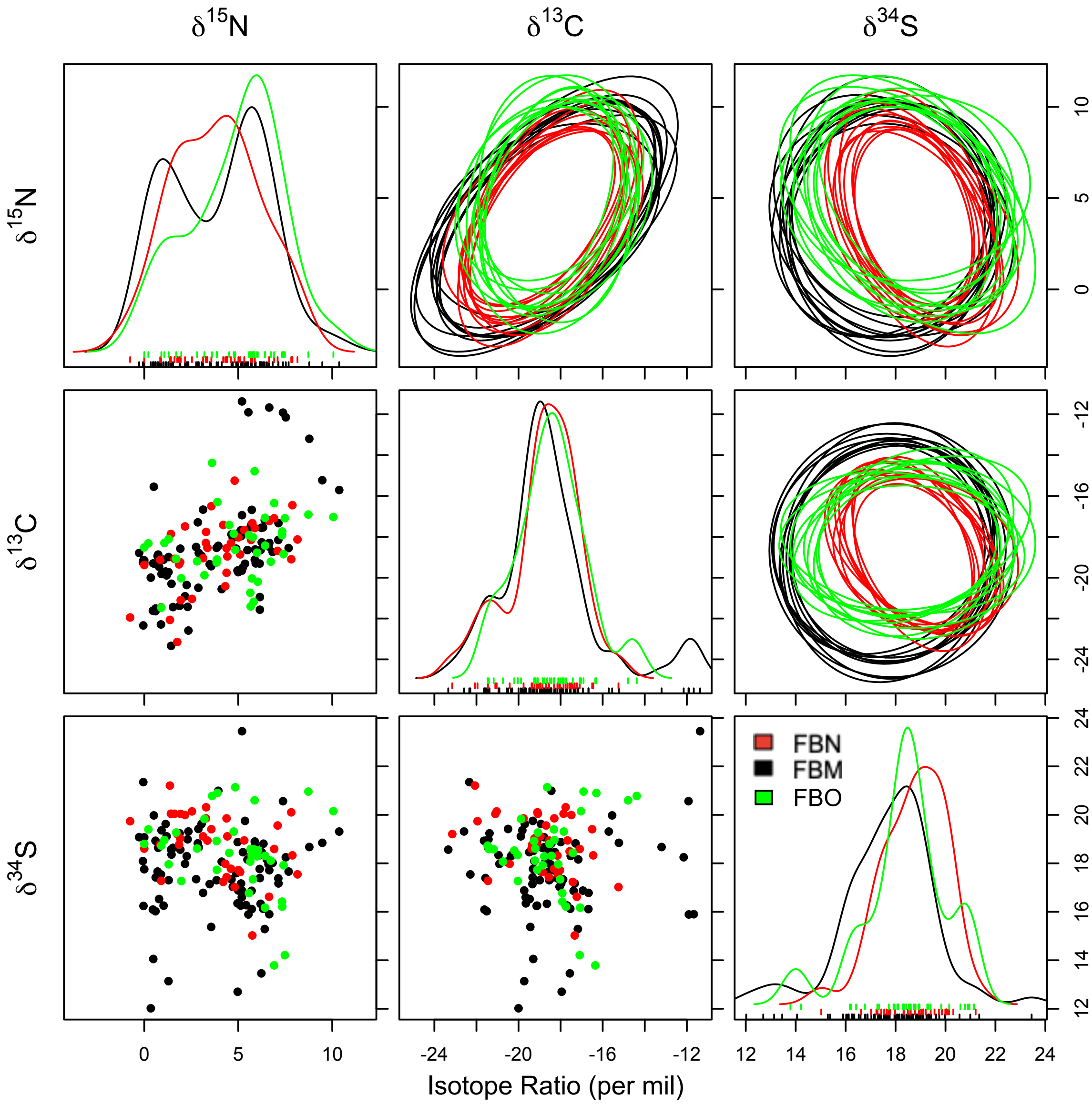

Figure 3.4. Visual representation of isotope data from each food web depth as one-dimensional density plots (lines), two-dimensional scatterplots, and two-dimensional food web niche region based on ten randomly selected elliptical projections.

Previous authors who have examined effects of tidal influence on coastal ecosystems have reported effects on organic matter sources. Researchers in Australia investigated carbon in sediment cores in coastal areas and found that even with a 3 m tidal range, the surface carbon was mainly influenced by tidal transport of carbon material (Saintilan et al. 2013). As the Frobisher Bay tidal range is much larger than 3 m, tidal transport of carbon material likely influences the nearshore area. Also, due to the shape of Frobisher Bay, offshore marine sediment would be directly funneled into the nearshore and midshore areas, which could explain why the ranges in carbon and sulphur isotope ratios are so similar among the three depths in my study. Other studies have found that the tide can enrich $\delta^{13}C$ values in nearshore marine environments (Rezende et al. 1990; Bouillon et al. 2000). Authors of one study in the Bay of Fundy, which has the highest tidal amplitude in the world, reported a $\delta^{13}C$ range (-8.27‰ to -15.81‰) (Bradford et al. 2023) that was enriched relative to the typical range of $\delta^{13}C$ in marine primary producers (-10‰ to -24‰) (Hunt 1966; Fry 2006). While a definitive cause could not be stated, the authors mentioned that tidal influence may have been a factor in these enriched ratios in the Bay of Fundy (English et al. 2015; Bradford et al. 2023). While further research is necessary, tides have been known to influence sources of organic matter and energy flow in other coastal environments, and large tidal amplitude is a working hypothesis for why ranges of $\delta^{13}C$ and $\delta^{34}S$ were similar among the three depths investigated in Frobisher Bay.

Food Web Structure

Characterizing food web structures and identifying food web stability is becoming an area of increasing research focus and importance, especially in Arctic environments like Frobisher Bay that have relatively large anthropogenic influences. Shorter food webs are often considered to be more stable and may have a shorter recovery time after stressful or disruptive events occur compared to longer food webs (Pimm and Lawton 1977; Lawler and Morin 1993; Jonsson and Ebenman 1998; Chanut et al. 2020). Consistent with my predictions and with the results of some previous studies (Iken et al. 2005; Divine et al. 2015), the smallest $\delta^{15}N$ range and lowest number of trophic levels was observed in the nearshore food web, indicating shorter food web length (Table 1). The difference was small, however; the midshore and offshore food webs were longer by less than one trophic level. In contrast with predictions made, the midshore and offshore depths had similar $\delta^{15}N$ ranges and food web length (~5 trophic levels), and the offshore food web was actually slightly shorter than the midshore food web. Mean $\delta^{15}N$ was 34% higher at the offshore depth, however, indicating that more species from the offshore food web occupied higher trophic positions. Although I expected to see increasing food web length with depth, the lack of a convincing pattern among depths has been observed by authors of other Arctic marine studies (Divine et al. 2015; Bell et al. 2016).

Larger food webs with more redundancy are more stable, complex, and resilient to biodiversity loss (Sanders et al. 2018; Ziółkowska and Sokołowski 2022), which is critical for maintaining food web structure in the face of stressors. High food web redundancy in some marine environments can be attributed to strong benthic-pelagic coupling, as greater food opportunity throughout a food web allows multiple species with similar nutrient consumption to coexist within the same food web (Ying et al. 2020). Additionally, strong benthic-pelagic coupling allows basal resources to move through entire food webs, causing isotope signatures to be similar throughout food webs and redundancy to increase (Cobain et al. 2022). Both redundancy and strong benthic-pelagic coupling have been shown to increase stability and resilience in food webs (Rooney et al. 2006; Sanders et al. 2018; Ziółkowska and Sokołowski 2022). I predicted that the offshore food web would have larger ranges, higher diversity, and higher redundancy. I found, however, that the FBM food web had a larger three-dimensional niche volume and higher food web redundancy, as shown by lower nearest neighbour distance (Table 1), than the FBN and FBO food webs. Food web complexity and diversity, as indicated by three-dimensional niche volume and distance to centroid, were also higher for FBM (Table 1). The presence of diverse functional groups can enhance benthic-pelagic coupling (Caliman et al. 2007; Montoya et al. 2015; Griffiths et al. 2017; Wang et al. 2020), and future research that couples measures of taxonomic diversity and full-profile physical oceanography data with the isotope analyses presented here would allow inferences with respect to causes and effects of the slightly larger food web volume and redundancy at the midshore depth in Frobisher Bay.

In addition to larger food web volume, redundancy, and diversity, midshore Frobisher Bay had a larger $\delta^{13}C$ and $\delta^{34}S$ range than nearshore or offshore Frobisher Bay, suggesting a wider variety of carbon and sulphur resources at the midshore depth (Table 1). This is consistent with the large amounts of primary producers, macrophytes, and zoobenthic production that have previously been observed within midshore depths in Frobisher Bay (Atkinson and Wacasey 1987; Grainger 1991). In addition, particulate organic matter (POM) is an important basal nutrient source in marine food webs, and the amount and quality of POM reaching benthic environments is influenced by nearby hydrodynamics and water depth (Giordani et al. 2002). Tidal hydrodynamics could result in high quantity and quality of POM reaching the midshore depth, which would act to increase the $\delta^{13}C$ and $\delta^{34}S$ ranges at FBM via one mechanism by which benthic-pelagic coupling occurs. A study conducted in Frobisher Bay showed that at a depth of 33m, between 31% to 53% of all primary production reached the benthic environment (Atkinson and Wacasey 1987). Other authors studying the North Sea have shown that this percentage decreases at greater depths (Davies and Payne 1984), which would be consistent with the narrower $\delta^{13}C$ range observed at FBO in this study.

Although some previous studies have shown shallower depths have tighter benthic-pelagic coupling (Giordani et al. 2002; Sibert et al. 2011; Giraldo et al. 2017), the nearshore site at Frobisher Bay is unique, as discussed above, because of the particularly high tidal amplitude in the bay (Dunbar 1958). Mason et al. (2010) conducted an experimental ecosystem study and found that tidal amplitude increases resuspension of POM and transfers these nutrients out of the benthic environment and into the water column. The authors found microphytobenthos biomass was lower in the tanks that simulated tidal resuspension compared to the non-resuspension tanks. High tidal amplitude also increases shear stress which reduces accumulation of nutrients in sediment in shallow areas and instead carries them to deeper areas (Capet et al. 2016). This may explain the comparatively narrower $\delta^{13}C$ and $\delta^{34}S$ range and inferred weaker benthic-pelagic coupling at FBN, and the larger $\delta^{13}C$ and $\delta^{34}S$ range and inferred stronger benthic-pelagic coupling at FBM.

3.3.2 Functional Feeding Groups

Further data analyses were conducted on two of the seven sampled functional feeding groups: sufficient samples of benthic carnivores and benthic suspension feeders were obtained for analyses, and these two functional feeding groups are of considerable interest as they carry out very different, and very under-studied, functions in Arctic marine food webs and ecosystems. The niche region occupied by carnivores can have large impacts on overall food web structure by exerting top-down pressure, which cascades through the entire food web (Estes et al. 2011). Benthic suspension feeders can impact food webs by controlling amounts of primary production and contributing to benthic-pelagic coupling (Gili and Coma 1998; Newell 2004).

Similar to the complete food web structure analysis, the sample size for benthic carnivores was largest at the midshore depth, where 35 invertebrate taxa and 10 fish species were captured (35 invertebrate taxa and 9 fish species for sulphur). In the nearshore depth category, 17 invertebrate taxa and 6 fish species were captured (14 invertebrate taxa and 4 fish species for sulphur), and in the offshore depth category, 11 invertebrate taxa and 6 fish species were captured (11 invertebrate taxa and 6 fish species for sulphur) (Appendix A). The sample size for suspension feeders was lower than that for benthic carnivores, with nearshore, midshore, and offshore depths having sample sizes of 7, 19, and 9 invertebrate taxa, respectively (6, 18, and 8 for sulphur) (Appendix A). Species richness thus appears higher for benthic carnivores than for benthic suspension feeders in FBN, FBM, and FBO food webs, although taxonomic diversity was not the focus of this study.

Benthic Carnivores and Benthic Suspension Feeders Among Depths

Patterns in trophic ecology for benthic carnivores among the three depths were similar to those observed for whole food webs. Ranges of nitrogen, carbon, and sulphur were highest, and niche volume was largest, at FBM (Table 3.2; Fig. 3.5). The CD and NND for benthic carnivores were also highest and lowest at FBM, respectively — as they were for the entire food web analysis — indicating that benthic carnivore isotopic diversity and redundancy are higher at FBM than at the other two depths. The benthic carnivore community at the midshore depth may therefore be more stable, complex, and resilient to biodiversity loss (Sanders et al. 2018; Ziółkowska and Sokołowski 2022), which is important to consider when assessing future anthropogenic impacts. Multiple benthic carnivore taxa had similar isotope ratios, which was reflected in the relatively low NND, and it is possible that higher isotopic redundancy within the benthic carnivore functional feeding group reflects benthic-pelagic coupling (Ying et al. 2020). The larger niche width for benthic carnivores at FBM could also reflect strong benthic-pelagic coupling at this depth, as large niche width can indicate generalist or omnivory feeding (Sweeting et al. 2005; Bergmann et al. 2009), which has been found to support strong benthic-pelagic coupling (Timmerman et al. 2021).

Table 3.2: Three-dimensional isotopic Layman (2007) metrics and isotopic volume values (Swanson et al. 2015) calculated using $\delta^{15}N_{adj}$, $\delta^{13}C$, and $\delta^{34}S$ for benthic carnivores in the Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore depth categories.

	Depth Category		
Metric	**Nearshore**	**Midshore**	**Offshore**
$\delta^{15}N_{adj}$ (‰) Range	6.54	10.42	5.53
$\delta^{15}N_{adj}$ Mean	5.08	5.41	5.85
$\delta^{13}C$ (‰) Range	9.55	10.44	5.06
$\delta^{13}C$ Mean	-17.87	-18.12	-18.82
$\delta^{34}S$ (‰) Range	3.52	8.65	7.17
$\delta^{34}S$ Mean	18.73	17.83	18.13
CD	2.59	2.87	2.19
NND	1.42	1.35	1.83
SDNND	0.70	0.89	1.40
Trophic levels	4.40	5.05	4.57
3-dimensional niche volume	169.29	546.01	261.41

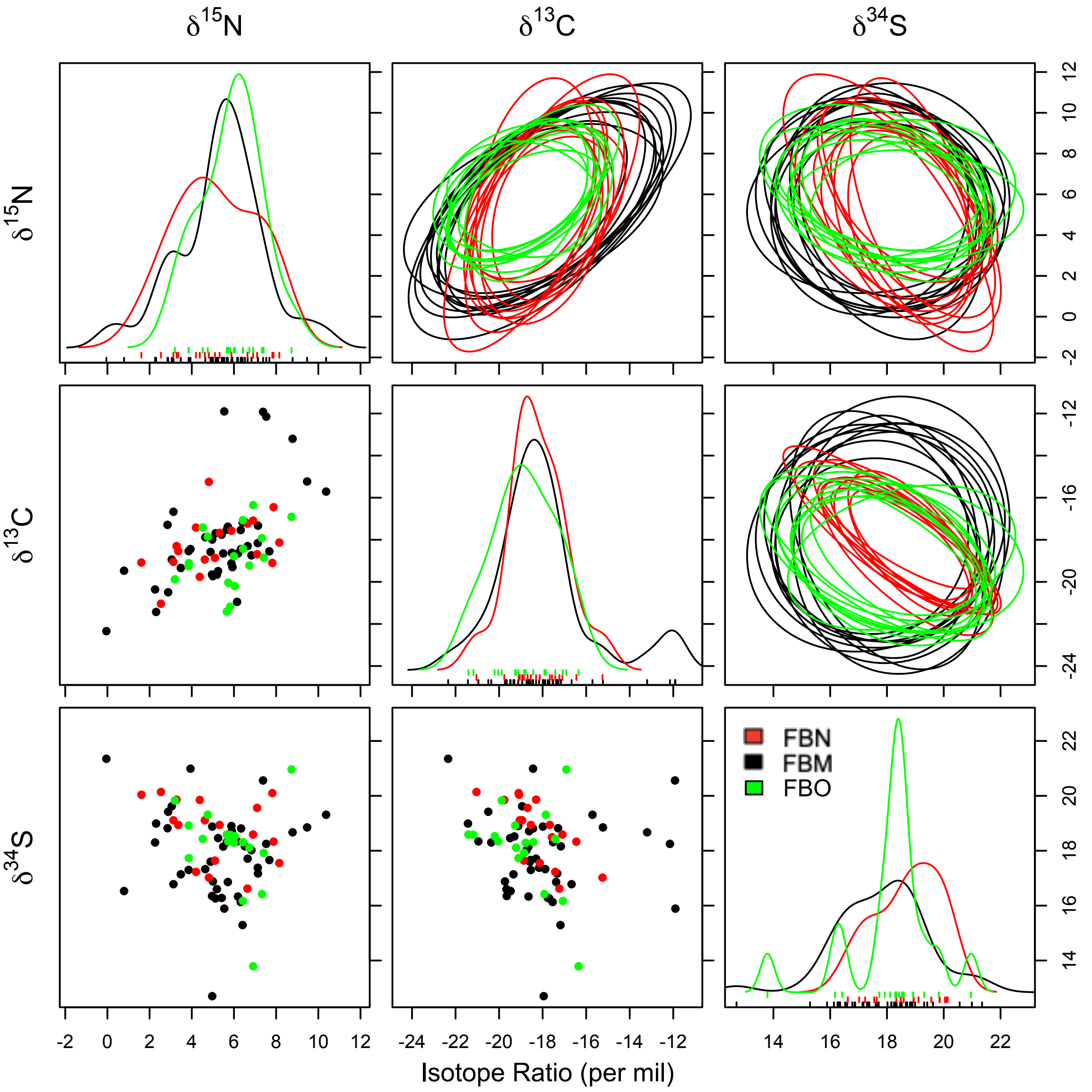

Figure 3.5. Visualization of the isotopic niche region of benthic carnivores, illustrated as one-dimensional density plots (lines), two-dimensional scatterplots, and two-dimensional projections of the three-dimensional niche regions (based on ten randomly selected ellipses; Swanson et al. 2015).

Isotopic patterns for benthic suspension feeders did not mirror the patterns observed for the whole food web analysis or for the benthic carnivore analysis. First, there was a lot of uncertainty in the niche volumes; in the bivariate ellipse projections in Figure 3.6, some ellipses of the same colour (depth) are at almost 90° to each other. This uncertainly likely reflects relatively lower sample sizes.

Fewer benthic suspension feeder taxa were captured at FBO compared to FBM, and yet the niche volume was higher at FBO than at FBM. Benthic suspension feeders captured at FBO thus appeared to occupy more unique isotopic spaces. This is further supported by the fact that NND was highest at FBO (Table 3.3), indicating redundancy was low in benthic suspension feeders at FBO. Low redundancy may mean that the benthic suspension feeder group is more vulnerable to biodiversity loss and stressors (Sanders et al. 2018; Ziółkowska and Sokołowski 2022) at the offshore depth than at the midshore or nearshore depths.

Table 3.3: Three-dimensional isotopic Layman (2007) metrics and isotopic volume values (Swanson et al. 2015) calculated using $\delta^{15}N_{adj}$, $\delta^{13}C$, and $\delta^{34}S$ for benthic suspension feeders in the Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore depth categories.

	Depth Category		
Metric	**FBN**	**FBM**	**FBO**
$\delta^{15}N_{adj}$ (‰) Range	3.65	5.63	4.84
$\delta^{15}N_{adj}$ Mean	1.93	1.39	1.67
$\delta^{13}C$ (‰) Range	4.83	3.69	3.36
$\delta^{13}C$ Mean	-17.75	-19.40	-18.87
$\delta^{34}S$ (‰) Range	1.44	2.45	3.18
$\delta^{34}S$ Mean	19.27	18.52	19.11
CD	1.55	1.55	1.70
NND	2.58	2.55	3.13
SDNND	1.29	1.96	1.67
Trophic levels	3.07	3.58	3.42
3-dimensional niche volume	29.49	78.29	114.31

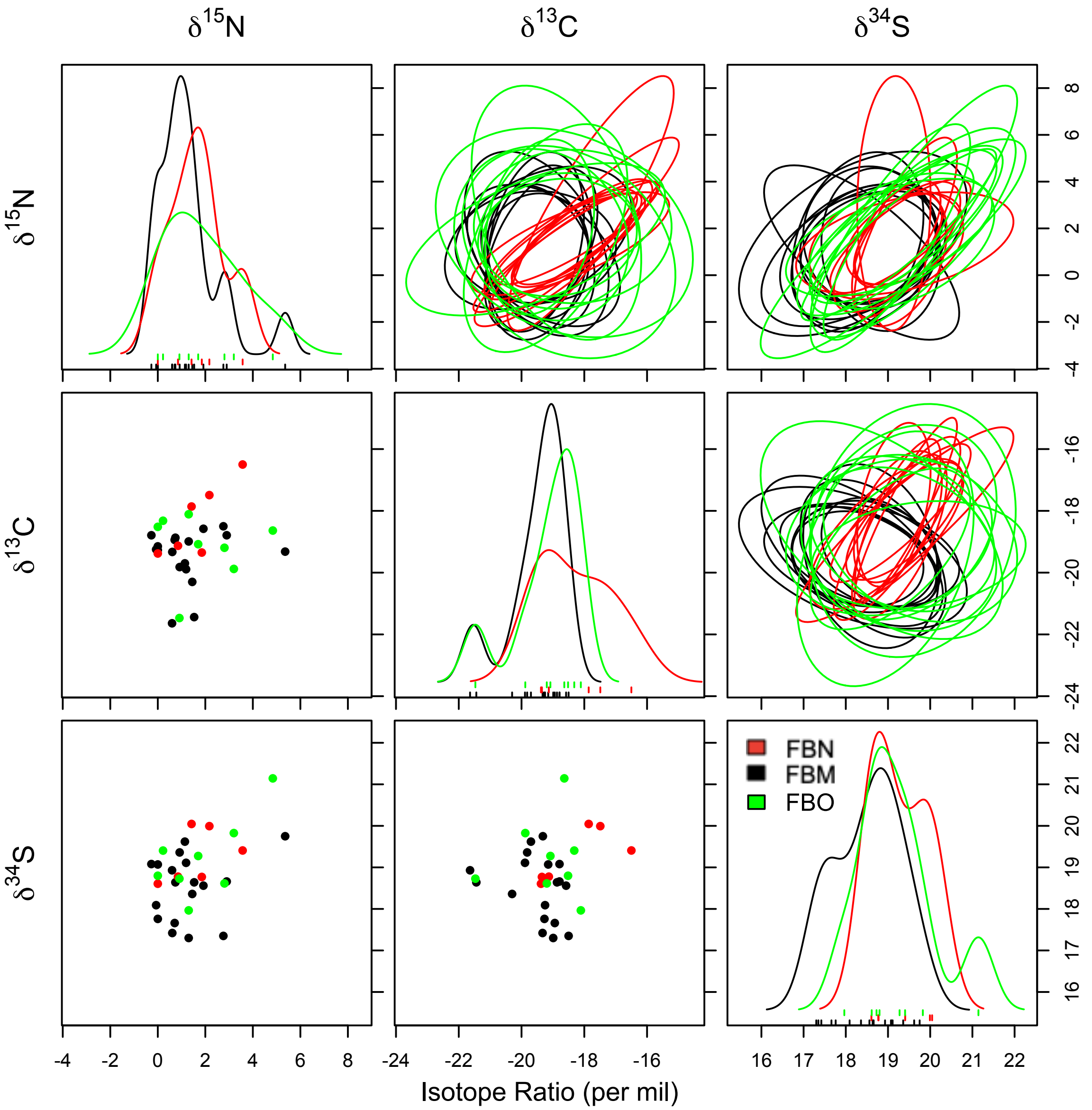

Figure 3.6. Visualization of the isotopic niche region of benthic suspension feeders, illustrated as one-dimensional density plots (lines), two-dimensional scatterplots, and two-dimensional projections of the three-dimensional niche regions (based on ten randomly selected ellipses; Swanson et al. 2015).

Benthic suspension feeders appear to play a particularly important role in the offshore food web. Not only do they occupy more unique, less redundant isotopic niches, the estimated isotopic niche volume for benthic suspension feeders at the offshore depth represents almost 20% of the whole food web volume. In contrast, benthic suspension feeders at the nearshore and midshore depths comprise less than 10% of total food web volume. The relatively large isotopic volume, as well as the higher distance to centroid for benthic suspension feeders at the offshore depth, are likely driven by the large sulphur range; δ^{34}S range for benthic suspension feeders at the offshore depth was double the range observed at the nearshore depth and 30% larger than the range observed at the midshore depth (Table 3). While the large isotopic volume observed in benthic suspension feeders at FBO was unexpected, this phenomenon may be explained by the presence of sulphate reducing bacteria. Sulphate reducing bacteria are ubiquitous in the environment and inhabit deep, anoxic marine sediment. These bacteria are able to use sulphate as an electron acceptor in metabolic processes when oxygen is not readily available, such as in anoxic zones or microzones at the sediment-water interface (Muyzer and Stams 2008; Jørgensen et al. 2019). During sulphate reduction, heavier isotopes are discriminated against, which can result in more enriched δ^{34}S being left for other organisms (Jørgensen 1979; Fry et al. 1988; Muyzer and Stams 2008; Sim et al. 2023). Antedonidae was the taxon that contributed the most to the larger sulphur range observed at FBO, and while this taxon is not known for burrowing in sediments, it does move along the seafloor and attaches to bottom substrates (Smith and Callow 2006), which could result in exposure to sources of organic matter that are enriched in δ^{34}S, Delta^{34}S samples of benthic deposit feeders and suspension feeder/deposit feeders were also relatively higher in the offshore region; however, limited sample sizes prevented statistical analysis for those functional feeding groups (Appendix A).

Alternatively, taxonomic composition of the samples could be part or all of the reason for higher δ^{34}S range at FBO. Antedonidae is the taxon that contributed the most to the larger sulphur range observed at FBO, and its sulphur value was only available for this depth (not enough biomass was available at the other depths. It is possible that this taxon may have naturally enriched sulphur values due to unique physiology that affects fractionation. It is also possible that this explanation is related to the hypothesis that there are unique sulphur sources at deeper depths that Antedonidae can capitalize on.

Benthic suspension feeder δ^{15}N mean values were relatively similar among the three depths, which was unexpected. Authors of previous studies have found that δ^{15}N values of suspension feeders increase with depth (Bergmann et al. 2009; Roy et al. 2015), possibly due to higher reliance on resuspended and degraded POM at larger water depths (Bergmann et al. 2009; Roy et al. 2015). The lack of pattern found in suspension feeders in this study may be due to the narrower depth range tested here, as well as the high tidal amplitude and consequent homogenization of resources, but further research is necessary.

Comparison Between Benthic Carnivores and Benthic Suspension Feeders

Results of nitrogen stable isotope analysis showed that benthic carnivores occupied higher trophic positions compared to benthic suspension feeders at all depths. This is consistent with the findings of other studies (Stasko et al. 2018; Włodarska-Kowalczuk et al. 2019). Also consistent with other studies (Mittermayr et al. 2014), benthic carnivores had more depleted mean $\delta^{34}S$ at all depths compared to benthic suspension feeders, although the differences were small. Fish are generally more depleted in $\delta^{34}S$ compared to invertebrates (Kwak and Zedler 1997), and the inclusion of fish in the benthic carnivore functional feeding group likely contributed to the slightly lower $\delta^{34}S$ means for benthic carnivores.

At all three depths, benthic carnivores had a larger niche volume compared to benthic suspension feeders, due to larger ranges in all three isotope ratios (Table 3.2, Table 3.3). This is likely due to the inclusion of predators and scavengers from both invertebrate and fish taxa in the benthic carnivore functional feeding group, whereas the benthic suspension feeder functional feeding group was comprised entirely of invertebrates. Additionally, many benthic carnivores are known to have generalist or opportunistic feeding behaviour (Bergmann et al. 2009; Sweeting et al. 2005); are highly mobile, and have the ability to feed on a wide range of prey items, including suspension feeders, deposit feeders, omnivores, and other carnivores. Benthic carnivores also had higher CD, lower NND, and lower SDNND than benthic suspension feeders at all three depths, indicating that the benthic carnivore functional feeding group represented more isotopic diversity, redundancy, and evenness than the benthic suspension feeder functional feeding group. Similar to the isotopic ranges and niche volume, the larger isotopic diversity (indicated by CD) represented by benthic carnivores is likely due to their wider prey range, and their role in benthic-pelagic coupling (Iken et al. 2001).

As mentioned previously, species redundancy (indicated by NND) is correlated with resiliency to biodiversity loss (Sanders et al. 2018; Ziółkowska and Sokołowski 2022); therefore, benthic carnivores may be more resilient to future climate threats than benthic suspension feeders. Higher evenness (indicated by SDNND) is positively correlated with ecosystem functioning and productivity, and within a community higher evenness allows for faster adaptation to environmental changes and maintains ecosystem productivity (Hillebrand et al. 2008). Relatively higher evenness among benthic carnivores could suggest that this functional feeding group will recover faster from environmental stresses compared to benthic suspension feeders. Overall, my results indicated that benthic carnivores occupied a large proportion of the isotopic range of the food webs analyzed, and thus greatly contribute to the stability and productivity of the food web.

3.4 Conclusion

Analyses of food web structure provide insight on energy pathways, benthic-pelagic coupling, and species interactions. Arctic marine food webs are being affected by climate-induced changes, and quantifying the current structure of these food webs is critically important. This study is the first characterization of food web structure in Frobisher Bay along a depth gradient. The unexpected isotopic similarities among all three depths (FBN; 10 to 15 m, FBM; 20 to 45 m, and FBO; 260 to 351 m) in Frobisher Bay could reflect high tidal amplitude that acts to reduce heterogeneity in biogeochemical conditions, and thus isotope ratios and food web structure, among depths. Additionally, the large $\delta^{13}C$ and $\delta^{34}S$ ranges, high redundancy (as evidenced by NND) and food web diversity (as evidenced by CD) and volume suggest strong benthic-pelagic coupling in the midshore food web. With ongoing and accelerating anthropogenic influences in Frobisher Bay, including construction of a deep sea port that opened in July 2023, these data provide a reference point against which to compare future conditions; thoroughly characterizing food webs increases our understanding of the functioning of these systems and furthers our ability to effectively monitor and predict effects of future change. Further research that directly examines the influence that the Frobisher Bay tide has on biogeochemical conditions (e.g., stable isotope values, nutrient and pollutant levels, water salinity and temperature, and benthic-pelagic coupling) and food web structure would be a useful next step.

4.0 General Conclusion

4.1 Summary

The research conducted in this thesis first provided (Chapter Two) a review and synthesis of recently published literature that furthers our understanding of ecological and physicochemical conditions in six Ecologically and Biologically Significant Areas in the eastern Hudson Bay Complex, Canada, including: James Bay, the Belcher Islands, the eastern Hudson Bay Coastline, western Hudson Strait, eastern Hudson Strait, and Ungava Bay. After collating 60 sources of information published in peer-reviewed and grey literature between 2011 and 2021, I highlighted a number of important advances, as well as knowledge gaps that need to be addressed.

Impacts of climate warming were a common theme among the papers reviewed. Available evidence suggests that environmental changes in sea surface temperature and sea ice extent are impacting primary production and are causing bottom-up shifts that propagate through entire food webs (e.g., Hoover et al. 2013a; Hoover et al. 2013b). Projection models have shown that these bottom-up shifts will continue in the future as warming increases and sea ice extent and thickness continue to decline (Hoover et al. 2013a; Hoover et al. 2013b). Hudson Bay is an area of exceptional concern for climate warming, as it forms the southern border of the Canadian Arctic environment, and sea surface temperatures are projected to be higher in this region than elsewhere in the Arctic (Laforest et al. 2018). Additionally, Hudson Bay is the southern range limit for several keystone Arctic species, and several threatened and endangered Arctic species, including polar bears (*Ursus maritimus*), narwhals (*Monodon monoceros*), and beluga whales (*Delphinapterus leucas*) (Watt et al. 2013; Laforest et al. 2018; DFO 2018). Impacts of climate warming are particularly problematic for northern Indigenous communities that rely on marine mammals, fish, and invertebrate populations in the Bay for subsistence (Berkes 1990; DFO 2012; Thompson et al. 2017). The species of most concern, as evidenced by the numerous studies published on this species, was the COSEWIC-designated eastern Hudson Bay beluga whale.

The review I conducted (Chapter two) revealed that marine mammals were vastly more studied between 2011 and 2021 than fish, invertebrates, and abiotic ecosystem components. While thorough knowledge on Arctic marine mammals is important for the future monitoring and conservation of these species, there is a gap in the knowledge regarding biota that occupy lower trophic positions and support the higher-trophic level organisms. Additional gaps in the literature identified in the review included whole-ecosystem research, research on multiple species and their interactions, and research conducted in multiple seasons. Research needs to be targeted towards these areas to determine how future climate changes will impact the eastern Hudson Bay Complex and the species that reside within its borders permanently and seasonally.

As the literature review conducted in the second chapter of this thesis revealed that lower trophic level species, such as fish and invertebrates, were greatly understudied compared to marine mammals, the third chapter of this thesis focused on the trophic ecology of fish and invertebrates in one particular marine area: Frobisher Bay, Nunavut. I investigated trophic ecology and food web structure at three depths in Frobisher Bay; this had not been studied before, and Inuit who rely on the fish, mammal, and invertebrate resources of Frobisher Bay have demonstrated an interest in learning more about benthic food webs at a variety of depths, particularly in the context of increased industrial activity in the area (i.e., construction of a deep-water port). Isotope analysis of nitrogen, carbon, and sulphur were used to infer trophic ecology and food web structure at nearshore (10 to 15 m), midshore (20 to 45 m), and offshore (261 to 350 m) locations in Frobisher Bay.

Results from this chapter differed substantially from the original predictions made, as food web structures were found to be very isotopically similar among all three depths. I hypothesized that this may be due to the large tidal amplitude in Frobisher Bay, which could cause marine environments at different depths to be more homogeneous in their nutrient sources and availability than predicted. Food web structure at the Frobisher Bay midshore depth had greater nutrient diversity, had a more complex structure, was more stable, and had higher redundancy, as indicated by the larger $\delta^{13}C$ and $\delta^{34}S$ ranges, larger niche volume, lower nearest neighbour distance, and larger distance to centroid. I inferred that these results may reflect strong benthic-pelagic coupling at this depth.

The two functional feeding groups analyzed further (benthic carnivores and benthic suspension feeders) also had similar isotopic niche overlap among depths, which I again hypothesized to be due to tidal influence. A closer examination of the trophic ecology of benthic carnivores revealed that they had a more nutrient diverse, complex, redundant, and stable niche region at the midshore depth than at the nearshore or offshore depths, which was consistent with my findings for the whole food web structure analysis. As redundancy can be attributed to strong benthic-pelagic coupling, the higher benthic carnivore redundancy at the midshore depth may indicate that this functional feeding group is contributing to inferred strong benthic-pelagic coupling at this depth, as multiple benthic carnivores with similar trophic ecology coexist in this food web (Ying et al. 2020). Benthic suspension feeders did not show this same pattern at the midshore depth. Instead, benthic suspension feeders at the offshore depth had a more nutrient diverse, complex, and redundant niche region. I suggested that this could be due to bacterial reduction of sulphate in the more anoxic conditions that could be found in the sediments of this deeper site; cycling of sulphate could provide more resuspended material that is enriched in $\delta^{34}S$ to be available for benthic suspension feeder consumption (Jorgensen 1979; Fry et al. 1988; Muyzer and Stams 2008).

4.2 Connections Between Chapter Two and Chapter Three

Insights from chapter two revealed a paucity of studies on lower trophic level species and holistic studies that include interspecific interactions and abiotic-biotic linkages. This prompted my study questions in chapter three, where I focused on lower trophic level species, and interactions among these species and with depth. Previous researchers had reported that invertebrates are influenced by many abiotic factors, such as salinity, organic carbon content, and substrate type (Pierrejean et al. 2020), all of which are affected by depth. I found few differences among the three depth categories, however, and found that tidal amplitude appeared to have a large impact on invertebrate-fish food web structure among the three depths studied.

Authors of the few papers that did focus on invertebrates in the literature review (Chapter 2) mentioned how invertebrates are poorly understood, both in terms of climate change impacts but also in terms of general ecology, particularly responses to environmental gradients. It is known that stressor-induced changes in invertebrate diversity and abundance will have bottom-up effects on megafauna species that occupy higher trophic levels, and that these impacts may be especially apparent in environments like Frobisher Bay. Frobisher Bay supports a relatively diverse and complex basal invertebrate community that directly supports the fish community, and ultimately Inuit who rely on fish (and their predators) for subsistence. Some authors reported that climate change is the largest threat to invertebrates, rather than harvesting (Hoover et al. 2013a); however, other authors have reported that the fishing industry can do severe damage to some invertebrate communities, such as sponges (Beazley et al. 2016). As different invertebrate taxa may respond differently to environmental variables and anthropogenic stressors, more studies on individual invertebrate taxa or functional feeding groups would be beneficial.

Different responses to one important environmental variable –depth– by two functional feeding groups are shown in chapter three. I found that benthic carnivores and benthic suspension feeders had different food web niche region volumes and different sulphur nutrient sources available to them at the offshore depth category. While benthic carnivore trophic ecology indices closely mirrored those of the whole food web, benthic suspension feeder ecology indices differed at the offshore region as more diverse sources of sulphur became available from inferred bacterial reduction of sulphate. As climate change is predicted to greatly impact entire bacterial communities in Arctic marine environments (Nguyen et al. 2022), benthic suspension feeders may be more sensitive to these shifts in bacteria populations compared to benthic carnivores. Therefore, studying individual functional feeding groups will more accurately predict how those groups will be impacted by climate induced changes.

An additional climate change concern highlighted in the literature review was the large impact of changes in sea ice and sea surface temperature on species throughout the entire ecosystem. Some authors suggest that there will be a shift from more benthic-based to pelagic-based food webs (Hoover et al. 2013a; Hoover et al. 2013b). This change may be especially pronounced in areas like Frobisher Bay that appear to have strong benthic-pelagic coupling. Additionally, the benthic invertebrate community in Frobisher Bay was quite diverse compared to the pelagic community. Therefore, a shift from the currently more diverse benthic community to the pelagic community in Frobisher Bay may cause serious shifts in the food web structures, and thus energy flow, within the bay.

Some climate change ramifications that were addressed in the reviewed papers in chapter two include the threat of aquatic invasive species, especially as shipping increases. The increase in Arctic shipping activity is directly applicable to the study area in chapter three of this thesis due to the recent development of a deep-sea port in Frobisher Bay. The port, which opened in July 2023, puts Frobisher Bay at greater risk for invasive species introduction. A proposed solution brought up in the literature review was a change in ballast water exchange to a deeper, offshore location (Goldsmit et al. 2019); however, research performed in chapter three of this thesis suggests that deep, offshore locations can be strongly connected to nearshore, coastal locations under certain circumstances, such as large tidal amplitudes. Therefore, any future alternate ballast water exchange area must be chosen after extensive research and while considering all possible factors and ramifications. The high connectivity among the nearshore, midshore, and offshore environments in Frobisher Bay suggest that the increasing threats of oil spills and invasive species introduction may have widespread impacts throughout the bay.

4.3 Relevance

Regular reviews of the literature are important to identify gaps in knowledge, to identify areas that need more focus, and to ensure that novel, informative, and useful knowledge contributes to improvements in management, mitigation, or conservation strategies. The review that I conducted in Chapter two covered several topics, including assessment of many marine species, abiotic factors, and projected climate change impacts, which is currently at the forefront of most Arctic environmental concerns. The literature review will contribute to the upcoming CSAS report, which is what the federal government of Canada uses to establish and help advance establishment of management and protection strategies in areas of particular biological and ecological importance.

Review of the literature also allows one to synthesize long-term data trends from multiple sources and authors. Much recent literature in eastern Hudson Bay has focused on beluga whales, and the studies reviewed through the decade will allow scientists to assess the degree to which quota management and conservation strategies were successful. There was a decrease in the EHB beluga population from 2015 to 2019 when harvest allocations were exceeded three years in a row, which may indicate that the management approach needs to be revisited.

In chapter three, I answered a novel research question that provided information on food web structure in Frobisher Bay, which Inuit communities were interested in as they rely on species included in the food webs studies for subsistence. My results unexpectedly suggest that the large tidal amplitude in the bay has far-reaching effects on food web structure, even at depths of 350 m. This is important because it reveals how connected Frobisher Bay is, even in deep offshore regions. Not only did the three food webs investigated share similar nutrient sources among depths, but findings from this work also suggested that there are strong connections between the pelagic and benthic environments via benthic-pelagic coupling. Understanding the level of connectivity among food webs at different depths in this area is becoming increasingly important as hydrologic connectivity increases the spread of anthropogenic pollutants and invasive species (Pringle 2001; Jackson and Pringle 2010). As the risk for these disruptors increases in Frobisher Bay, monitoring of the connectivity of food webs will become increasingly important. Additionally, studies have suggested that mobile marine invertebrates and fish can move to deeper environments to mitigate effects of climate change in previously inhabited areas (Poloczanska et al. 2016). However, with the tidal mixing in the bay resulting in what seems to be a fairly homogeneous environment (at least ecologically, I do not have full oceanographic data), species may need to move farther out of the bay to reach deeper, cooler environments.

4.4 Future Recommendations

Continued research in the six eastern Hudson Bay EBSAs equips scientists with better knowledge and understanding to protect and manage ecosystems such that they continue to have high ecological and biological significance. Although marine mammals were quite well studied from 2011 to 2021 in eastern Hudson Bay, methodologies used in studies were limited. Molecular data used in conjunction with survey observations could result in more impactful studies. Furthermore, aerial surveys have not been conducted for some marine mammals in over five years and some species, such as the eastern Hudson Bay belugas, have had drops in stock size since then, so conducting an aerial survey in the future could be an important priority. In addition to aerial survey and molecular data, more data collected using traditional ecological knowledge (TEK) would be greatly beneficial for future publications, as TEK does not suffer the same limitations in terms of seasonality, timescale, and reductionism as western science does.

Invertebrate community structure will likely be impacted by anthropogenic stressors and have cascading effects; however, invertebrates garner far less research attention than megafauna. With threats from climate change (Hoover et al. 2013a) and the fishing industry (Beazley et al. 2016) differing among taxa, it is especially important that more invertebrate-focused studies are conducted. In chapter three, I showed that even within the same food web, functional feeding groups appear to be influenced differently by abiotic conditions, such as redox conditions and speciation of sulphur (which then impacts isotope ratios), highlighting the importance of studies on these lower trophic level species. In addition to invertebrates, fish and primary producers were also quite understudied from 2011 to 2021 in eastern Hudson Bay, and future research efforts should focus on these taxa.

Differences in food web structure among nearshore, midshore, and offshore depths in Frobisher Bay did not conform to expected predictions. We suggest that this is due to the large tidal amplitude in the bay; however, this study was not designed to look at tidal influence specifically. Future studies in Frobisher Bay and in other high tidal amplitude environments, such as the Bay of Fundy in Nova Scotia, should look at the influence of tidal amplitude along a depth gradient to confirm this assertion. The deepest sites sampled in this study were 261 to 350 m, and tidal influence was inferred to be strong at this depth, so future studies should extend this depth range and determine at what depths tidal influence lessens. Additionally, I focused on nitrogen, carbon, and sulphur stable isotopes but tidal influence would impact many other abiotic and biotic factors, which future researchers should investigate. With anthropogenic influences projected to substantially increase in marine environments, it is critical to know how large the hydrologic connectivity impact area is for environmental disruptors such as invasive species introduction, oil spills, and other anthropogenic pollution.

4.5 Final Remarks

The literature review conducted in chapter two was the first of its kind, in that it included all six EBSAs in eastern Hudson Bay and included more than a decade of conducted research. I synthesised relevant research and highlighted research biases towards marine mammals and gaps in knowledge for lower trophic level species such as fish, invertebrates, and primary producers. The identification of knowledge gaps allowed me to develop a relevant research question regarding lower trophic level food web structures in Frobisher Bay, and how they differ among depths. This research question was of interest to Inuit communities as they rely on species from the food webs studied for subsistence. This study represents the first in-depth analysis of food web structure among nearshore, midshore, and offshore depth categories in Frobisher Bay. Results suggest food web structure among the three depths share very similar nitrogen, carbon, and sulphur nutrient sources, which I suggest is due to the large tidal amplitude in the bay. Additionally, benthic-pelagic coupling was inferred to be strong in this region, especially at the midshore depth, as indicated by higher food web complexity, volume, diversity, redundancy, and nutrient ranges. Benthic carnivores had similar among-depth patterns in trophic ecology compared to the whole food web, whereas benthic suspension feeders at the offshore site differed somewhat, likely due to more enriched $\delta^{34}S$ availability from bacterial reduction of sulphur in deeper, potentially more anoxic conditions. Results from this thesis will provide the first knowledge of food web structure at different depths in Frobisher Bay and can be used in future CSAS reports to help with management and conservation strategies in eastern Hudson Bay.

References

References that apply to material in the main thesis text

Alabia, I. D., García Molinos, J., Saitoh, S., Hirawake, T., Hirata, T., & Mueter, F. J. (2018). Distribution shifts of marine taxa in the Pacific Arctic under contemporary climate changes. *Diversity and Distributions, 24*(11), 1583-1597.

Atkinson, E. G., & Wacasey, J. W. (1987). Sedimentation in Arctic Canada: Particulate organic carbon flux to a shallow marine benthic community in Frobisher Bay. *Polar Biology, 8*, 3-7.

Ayles, B., & Hoyt, A. Adaptive fisheries co-management in the Western Arctic. *UBC Press,*, 125-150.

Bailleul, F., Lesage, V., Power, M., Doidge, D. W., & Hammill, M. O. (2012). Migration phenology of beluga whales in a changing Arctic. *Climate Research, 53*(3), 169-178.

Beaulieu, J. (2008). Beacons of the north research infrastructure in Canada's Arctic and subarctic. Ottawa, Ont: *Canadian Polar Commission = Commission Canadienne des affaires polarise.*

Beazley, L., Murillo, F. J., Kenchington, E., Guijarro, J., Lirette, C., Siferd, T., Treble, M., Wareham, V., Baker, E., & Bouchard Marmen, M. (2016). Species distribution modelling of corals and sponges in the eastern Arctic for use in the identification of significant benthic areas. *Ocean and Ecosystem Sciences Division, Maritimes Region, Fisheries and Oceans Canada.*

Bell, L. E., Bluhm, B. A., & Iken, K. (2016). Influence of terrestrial organic matter in marine food webs of the Beaufort Sea shelf and slope. *Marine Ecology Progress Series, 550*, 1-24.

Bergmann, M., Dannheim, J., Bauerfeind, E., & Klages, M. (2009). Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. *Deep Sea Research Part I: Oceanographic Research Papers, 56*(3), 408-424.

Berkes, F. (1990). Native subsistence fisheries: A synthesis of harvest studies in Canada. *Arctic,*, 35-42.

Best, R. J., Stone, M. N., & Stachowicz, J. J. (2015). Predicting consequences of climate change for ecosystem functioning: Variation across trophic levels, species and individuals. *Diversity and Distributions, 21*(12), 1364-1374.

Bintanja, R. (2018). The impact of Arctic warming on increased rainfall. *Scientific Reports, 8*(1), 1-6.

Bluhm, B. A., Gebruk, A. V., Gradinger, R., Hopcroft, R. R., Huettmann, F., Kosobokova, K. N., Sirenko, B. I., & Weslawski, J. M. (2011). Arctic marine biodiversity: An update of species richness and examples of biodiversity change. *Oceanography, 24*(3), 232-248.

Bouchard, C., & Fortier, L. (2011). Circum-Arctic comparison of the hatching season of polar cod *boreogadus saida*: A test of the freshwater winter refuge hypothesis. *Progress in Oceanography, 90*(1-4), 105-116.

Bouchard, C., Thorrold, S. R., & Fortier, L. (2015). Spatial segregation, dispersion and migration in early stages of polar cod *boreogadus saida* revealed by otolith chemistry. *Marine Biology, 162*(4), 855-868.

Bouillon, S., Mohan, P. C., Sreenivas, N., & Dehairs, F. (2000). Sources of suspended organic matter and selective feeding by zooplankton in an estuarine mangrove ecosystem as traced by stable isotopes. *Marine Ecology Progress Series, 208*, 79-92.

Bradford, M. A., Mallory, M. L., & O'Driscoll, N. J. (2023). Mercury bioaccumulation and speciation in coastal invertebrates: Implications for trophic magnification in a marine food web. *Marine Pollution Bulletin, 188*, 114647.

Breton-Honeyman, K., Hammill, M. O., Furgal, C. M., & Hickie, B. (2016). Inuit knowledge of beluga whale (*delphinapterus leucas*) foraging ecology in Nunavik (Arctic Quebec), Canada. *Canadian Journal of Zoology, 94*(10), 713-726.

Bridier, G., Olivier, F., Chauvaud, L., Sejr, M. K., & Grall, J. (2021). Food source diversity, trophic plasticity, and omnivory enhance the stability of a shallow benthic food web from a high-Arctic fjord exposed to freshwater inputs. *Limnology and Oceanography,* doi:10.1002/lno.11688

Brown, L., & Fast, H. (2012). An overview of important ecological and biological marine features in Nunavut based on local knowledge. *Canadian Manuscript Report of Fisheries and Aquatic Sciences 2976,* Retrieved from https://publications.gc.ca/collections/collection_2012/mpo-dfo/Fs97-4-2976-eng.pdf

Brown, T. M., Fisk, A. T., Wang, X., Ferguson, S. H., Young, B. G., Reimer, K. J., & Muir, D. C. (2016). Mercury and cadmium in ringed seals in the Canadian Arctic: Influence of location and diet. *Science of the Total Environment, 545*, 503-511.

Brown, T. M., Macdonald, R. W., Muir, D. C., & Letcher, R. J. (2018). The distribution and trends of persistent organic pollutants and mercury in marine mammals from Canada's eastern Arctic. *Science of the Total Environment, 618*, 500-517.

Bush, E., & Lemmen, D. S. (2019). Canada's changing climate report. *Government of Canada,* , 444.

Caliman, A., Leal, J. J., Esteves, F. A., Carneiro, L. S., Bozelli, R. L., & Farjalla, V. F. (2007). Functional bioturbator diversity enhances benthic–pelagic processes and properties in experimental microcosms. *Journal of the North American Benthological Society, 26*(3), 450-459.

Campanyà-Llovet, N., Snelgrove, P. V., & Parrish, C. C. (2017). Rethinking the importance of food quality in marine benthic food webs. *Progress in Oceanography, 156*, 240-251.

Canadian Council of Fisheries and Aquaculture Ministers (CCFAM) Oceans Task Group. (2017). Report on Canada's network of marine protected areas. *Fisheries and Oceans Canada Ottawa, Ontario,*

Capet, A., Meysman, F. J., Akoumianaki, I., Soetaert, K., & Grégoire, M. (2016). Integrating sediment biogeochemistry into 3D oceanic models: A study of benthic-pelagic coupling in the Black Sea. *Ocean Modelling, 101*, 83-100.

Carr, C. M. (2012). Polychaete diversity and distribution patterns in Canadian marine waters. *Marine Biodiversity, 42*(2), 93-107.

Carter, N., Dawson, J., & Weber, M. (2020). Arctic corridors and northern voices: Governing marine transportation in the Canadian Arctic. *University of Ottawa*.

Chan, F. T., Bronnenhuber, J. E., Bradie, J. N., Howland, K. L., Simard, N., Bailey, S. A. (2012). Risk Assessment for Ship-Mediated Introductions of Aquatic Nonindigenous Species to the Canadian Arctic. *Canadian Science Advisory Secretariat, ON (Canada)*

Chanut, P. C., Siebers, A. R., & Robinson, C. T. (2020). Flood disturbance affects macroinvertebrate food chain length in an alluvial river floodplain. *Freshwater Biology, 65*(3), 490-501.

Cobain, M. R., McGill, R. A., & Trueman, C. N. (2022). Stable isotopes demonstrate seasonally stable benthic-pelagic coupling as newly fixed nutrients are rapidly transferred through food chains in an estuarine fish community. *Journal of Fish Biology,*

Cobb, D. G. (2011). Identification of ecologically and biologically significant areas (EBSAs) in the Canadian Arctic. *Canadian Science Advisory Secretariat* , 30.

Connolly, R. M., Guest, M. A., Melville, A. J., & Oakes, J. M. (2004). Sulfur stable isotopes separate producers in marine food-web analysis. *Oecologia, 138*, 161-167.

COSEWIC. (2004). COSEWIC assessment and update status report on the narwhal (monodon Monoceros) in Canada. *Committee on the Status of Endangered Wildlife in Canada*, 50.

COSEWIC. (2005). COSEWIC assessment and update status report on the bowhead whales (*balaena mysticetus*) in Canada. *Committee on the Status of Endangered Wildlife in Canada*

COSEWIC. (2020). COSEWIC assessment and status report on the beluga whale *(delphinapterus leucas*). *Committee on the Status of Endangered Wildlife in Canada* Retrieved from https://www.Canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments-status-reports/beluga-whale-2020.html#toc7

Davies, J. M., & Payne, R. (1984). Supply of organic matter to the sediment in the northern North Sea during a spring phytoplankton bloom. *Marine Biology, 78*, 315-324.

de la Vega, C., Jeffreys, R. M., Tuerena, R., Ganeshram, R., & Mahaffey, C. (2019). Temporal and spatial trends in marine carbon isotopes in the Arctic Ocean and implications for food web studies. *Global Change Biology, 25*(12), 4116-4130.

Department of Environment. (2016). Nunavut fishing strategies. *Government of Nunavut,*

Déry, S. J., Stadnyk, T. A., MacDonald, M. K., & Gauli-Sharma, B. (2016a). Recent trends and variability in river discharge across northern Canada. *Hydrology and Earth System Sciences, 20*(12), 4801-4818.

DFO. (2011a). Advice regarding the genetic structure of Canadian narwhal *(monodon monoceros*). *Canadian Science Advisory Secretariat Science Advisory Report*

DFO. (2011b). Harvest advice for Nunavik beluga *(delphinapterus leucas*). *Canadian Science Advisory Secretariat Science Advisory Report*

DFO. (2011c). Identification of ecologically and biologically significant areas (EBSA) in the Canadian Arctic. *Canadian Science Advisory Secretariat Science Advisory Report 2011/055,*

DFO. (2012). Harvest advice for Nunavik beluga (*delphinapterus leucas*). *Canadian Science Advisory Secretariat Science Advisory Report 2011/080,*

DFO. (2013a). Estimates of abundance and total allowable removals for Atlantic walrus *(odobenus rosmarus rosmarus)* in the Canadian Arctic. *Canadian Science Advisory Secretariat Science Advisory Report*

DFO. (2013b). Harvest advice for Nunavik beluga *(delphinapterus leucas). Canadian Science Advisory Secretariat Science Advisory Report*

DFO. (2014). Harvest advice and effects of a flexible total allowable take system for Nunavik beluga (*delphinapterus leucas*) (c2014). *Canadian Science Advisory Secretariat, 005*

DFO. (2015). Risk assessment of alternate ballast water exchange zones for vessel traffic to the eastern Canadian Arctic. *Canadian Science Advisory Secretariat,*

DFO. (2016a). Estimates of abundance and total allowable removals for Hudson Bay-Davis Strait and south and east Hudson Bay Atlantic walrus (*odobenus rosmarus rosmarus*) stocks. *Canadian Science Advisory Secretariat Science Advisory Report. 2015/063,* DFO. (2016b). Update to the proportion of eastern Hudson Bay beluga harvested and implications for harvest allocations in Nunavik. *Canadian Science Advisory Secretariat Science Advisory Report*

DFO. (2016c). Updated genetic mixture analysis of Nunavik beluga (*delphinapterus leucas*) harvests. *Canadian Science Advisory Secretariat Science Advisory Report*

DFO. (2017). Impacts of flexible quota system on walrus (*odobenus rosmarus rosmarus*) harvesting. *Canadian Science Advisory Secretariat Science Advisory Report*

DFO. (2018). Harvest advice for eastern and western Hudson Bay beluga (*delphinapterus leucas*). *Canadian Science Advisory Secretariat Science Advisory Report*

DFO. (2020). 2020 Harvest advice for eastern Hudson Bay beluga (*delphinapterus leucas*). *Canadian Science Advisory Secretariat Science Advisory Report*

Ding, C. Z., & Li. (2022). Research on the shipping network structure under the influence of Arctic routes. *GeoJournal*. doi:10.1007/s10708-020-10296-z.

Divine, L. M., Iken, K., & Bluhm, B. A. (2015). Regional benthic food web structure on the Alaska Beaufort Sea shelf. *Marine Ecology Progress Series, 531*, 15-32.

Doniol-Valcroze, T., Hammill, M. O., & Lesage, V. (2011). Information on abundance and harvest of eastern Hudson Bay beluga (delphinapterus leucas). *Canadian Science Advisory Secretariat Advisory Report. 2010/121,*

Doniol-Valcroze, T., Hammill, M. O., & Lesage, V. (2012a). Information on abundance and harvest of eastern Hudson Bay beluga (*delphinapterus leucas*). *Canadian Science Advisory Secretariat Advisory Report*

Doniol-Valcroze, T., Lesage, V., & Hammill, M. O. (2012b). Management Implications of Closure of Estuaries to Hunting of Beluga in Nunavik. *Canadian Science Advisory Secretariat.*

Doniol-Valcroze, T., & Hammill, M. O. (2012a). Information on abundance and harvest of Ungava Bay beluga 2012. *Canadian Science Advisory Secretariat Advisory Report. 2011/126*

Doniol-Valcroze, T., & Hammill, M. O. (2012b). Harvest advice for beluga in the Belcher, King George, and sleeper Islands in relation to the eastern Hudson Bay stock *Fisheries and Oceans Canada, Science, Quebec Region.*

Doniol-Valcroze, T., Hammill, M. O., & Gosselin, J. (2013). Population modeling and harvest advice under the precautionary approach for eastern Hudson Bay beluga (*delphinapterus leucas*). *Canadian Science Advisory Secretariat= Secrétariat Canadien de consultation*

Doniol-Valcroze, T., Gosselin, J., & Hammill, M. O. (2014). Impacts of a flexible total allowable take system on beluga conservation in the Nunavik marine region. *Canadian Science Advisory Secretariat Advisory Report*

Doniol-Valcroze, T., Hammill, M. O., Turgeon, S., & Postma, L. D. (2016). Updated analysis of genetic mixing among Nunavik beluga summer stocks to inform population models and harvest allocation. *Fisheries and Oceans Canada, Ecosystems and Oceans Science.*

Duffill Telsnig, J. I., Jennings, S., Mill, A. C., Walker, N. D., Parnell, A. C., & Polunin, N. V. (2019). Estimating contributions of pelagic and benthic pathways to consumer production in coupled marine food webs. *Journal of Animal Ecology, 88*(3), 405-415.

Dunbar, M. J. (1958). Physical oceanographic results of the "calanus" expeditions in Ungava Bay, Frobisher Bay, Cumberland Sound, Hudson Strait and northern Hudson Bay, 1949–1955. *Journal of the Fisheries Board of Canada, 15*(2), 155-201.

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences, 99*(20), 12917-12922.

English, M. D., Robertson, G. J., & Mallory, M. L. (2015). Trace element and stable isotope analysis of fourteen species of marine invertebrates from the Bay of Fundy, Canada. *Marine Pollution Bulletin, 101*(1), 466-472.

Ernakovich, J. G., Eklund, N., Varner, R. K., Kirchner, N., Jeuring, J., Duderstadt, K., Granebeck, A., Golubeva, E., & ASIAQ participants. (2021). Is a common goal a false hope in convergence research?: Opportunities and challenges of international convergence research to address Arctic change. *Earth's Future, 9*(5), e2020EF001865.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., & Jackson, J. B. (2011). Trophic downgrading of planet earth. *Science, 333*(6040), 301-306.

Ferguson, S. H., Young, B. G., Yurkowski, D. J., Anderson, R., Willing, C., & Nielsen, O. (2017). Demographic, ecological, and physiological responses of ringed seals to an abrupt decline in sea ice availability. *PeerJ, 5*, e2957.

Fisheries Joint Management Committee. (2013). Beaufort sea beluga management plan.(4) Retrieved from https://www.beaufortseapartnership.ca/wp-content/uploads/2015/04/Beaufort-Sea-Beluga-Management-Plan-2013.pdf

Foster, K. L., Stern, G. A., Pazerniuk, M. A., Hickie, B., Walkusz, W., Wang, F., & Macdonald, R. W. (2012). Mercury biomagnification in marine zooplankton food webs in Hudson Bay. *Environmental Science & Technology, 46*(23), 12952-12959.

Fry, B., Gest, H., & Hayes, J. (1988). 34S/32S fractionation in sulfur cycles catalyzed by anaerobic bacteria. *Applied and Environmental Microbiology, 54*(1), 250-256.

Fry, B., & Sherr, E. B. (1989). δ13C measurements as indicators of carbon flow in marine and freshwater ecosystems. Paper presented at the *Stable Isotopes in Ecological Research,* 196-229.

Fry, B. (2006). Stable isotope ecology. *Springer.*

Gili, J., & Coma, R. (1998). Benthic suspension feeders: Their paramount role in littoral marine food webs. *Trends in Ecology & Evolution, 13*(8), 316-321.

Giordani, P., Helder, W., Koning, E., Miserocchi, S., Danovaro, R., & Malaguti, A. (2002). Gradients of benthic–pelagic coupling and carbon budgets in the Adriatic and northern Ionian Sea. *Journal of Marine Systems, 33*, 365-387.

Giraldo, C., Ernande, B., Cresson, P., Kopp, D., Cachera, M., Travers-Trolet, M., & Lefebvre, S. (2017). Depth gradient in the resource use of a fish community from a semi-enclosed sea. *Limnology and Oceanography, 62*(5), 2213-2226.

Goldsmit, J., Archambault, P., Chust, G., Villarino, E., Liu, G., Lukovich, J. V., David, G., & Howland, K. L. (2018). Projecting present and future habitat suitability of ship-mediated aquatic invasive species in the Canadian Arctic. *Biological Invasions, 20*(2), 501-517.

Goldsmit, J., Nudds, S. H., Stewart, D. B., Higdon, J. W., Hannah, C. G., & Howland, K. L. (2019). Where else? assessing zones of alternate ballast water exchange in the Canadian eastern Arctic. *Marine Pollution Bulletin, 139*, 74-90.

Goldsmit, J., McKindsey, C. W., Schlegel, R. W., Stewart, D. B., Archambault, P., & Howland, K. L. (2020). What and where? predicting invasion hotspots in the Arctic marine realm. *Global Change Biology, 26*(9), 4752-4771.

Gosselin, J., Doniol-Valcroze, T., & Hammill, M. O. (2013). Abundance estimate of beluga in eastern Hudson Bay and James Bay, summer 2011. *Fisheries and Oceans Canada, Science*.

Gosselin, J., Hammill, M. O., & Mosnier, A. (2017). Indices of abundance for beluga (*delphinapterus leucas*) in James Bay and eastern Hudson Bay in summer 2015. *Canadian Science Advisory Secretariat (CSAS)*.

Government of Canada. (2019). Canada's marine protected and conserved areas. Retrieved from https://www.dfo-mpo.gc.ca/oceans/conservation/areas-zones/index-eng.html#MCTtable

Government of Canada. (2023). Daily discharge graph for Sylcia Grinnell River near Iqaluit (10UH001) [NU]. Retrieved from https://wateroffice.ec.gc.ca/report/statistics_e.html?start_year=2015&end_year=2023&start_month=01&end_month=12&y1Max=1&y1Min=1&mean1=1&scale=normal&mode=Graph&stn=10UH001&dataType=Daily&parameterType=Flow&year=2021

Grainger, E. H. (1991). Exploitation of Arctic sea ice by epibenthic copepods. *Marine Ecology Progress Series.Oldendorf, 77*(2), 119-124.

Grebmeier, J. M., Cooper, L. W., Feder, H. M., & Sirenko, B. I. (2006). Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic. *Progress in Oceanography, 71*(2-4), 331-361.

Griffiths, J. R., Kadin, M., Nascimento, F. J., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gãrdmark, A., & Järnström, M. (2017). The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology, 23*(6), 2179-2196.

Hammill, M. O., Mosnier, A., Gosselin, J. F., Higdon, J. W., Stewart, D. B., Doniol-Valcroze, T., Ferguson, S. H., & Dunn, J. B. (2016). Estimating abundance and total allowable removals for walrus in the Hudson Bay-Davis Strait and south and east Hudson Bay stocks during September 2014. *Fisheries and Oceans Canada, Ecosystems and Oceans Science*.

Hammill, M. O., & Canadian Science Advisory Secretariat. (2017). Management approaches, abundance indices and total allowable harvest levels of belugas in Hudson Bay. *Canadian Science Advisory Secretariat (CSAS).*

Herder, E. C. (2020). Temporal and spatial changes in benthic mollusc (bivalves and gastropods) communities in inner Frobisher Bay, Nunavut, Baffin Island over fifty years.

Herman, P., Middelburg, J. J., Van de Koppel, J., & Heip, C. (1999). Ecology of estuarine macrobenthos. *Advances in Ecological Research, 29*(780), 195-240.

Heuer, R. M., & Grosell, M. (2014). Physiological impacts of elevated carbon dioxide and ocean acidification on fish. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology, 307*(9), R1061-R1084.

Hilgendag, I. R., Swanson, H. K., Lewis, C. W., Ehrman, A. D., & Power, M. (2022). Mercury biomagnification in benthic, pelagic, and benthopelagic food webs in an Arctic marine ecosystem. *Science of the Total Environment, 841*, 156424.

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology, 89*(6), 1510-1520.

Hobson, K. A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J. M., & Fortier, M. (2002). A stable isotope model for the north water food web: Implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep-Sea Research II, 49*

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science, 328*(5985), 1523-1528.

Hong, N. (2014). Emerging interests of non-arctic countries in the Arctic: A Chinese perspective. *The Polar Journal, 4*(2), 271-286.

Hoover, C., Pitcher, T., & Christensen, V. (2013a). Effects of hunting, fishing and climate change on the Hudson Bay marine ecosystem: I. re-creating past changes 1970–2009. *Ecological Modelling, 264*, 130-142.

Hoover, C., Pitcher, T., & Christensen, V. (2013b). Effects of hunting, fishing and climate change on the Hudson Bay marine ecosystem: II. ecosystem model future projections. *Ecological Modelling, 264*, 143-156.

Hop, H., Vihtakari, M., Bluhm, B. A., Daase, M., Gradinger, R., & Melnikov, I. A. (2021). Ice-associated amphipods in a pan-arctic scenario of declining sea ice. *Frontiers in Marine Science, 8*, 743152.

Houde, M., Taranu, Z. E., Wang, X., Young, B., Gagnon, P., Ferguson, S. H., Kwan, M., & Muir, D. C. (2020). Mercury in ringed seals (*pusa hispida*) from the Canadian Arctic in relation to time and climate parameters. *Environmental Toxicology and Chemistry, 39*(12), 2462-2474.

Hsiao, S. I. (1988). Spatial and seasonal variations in primary production of sea ice microalgae and phytoplankton in Frobisher Bay, Arctic Canada. *Marine Ecology Progress Series,*, 275-285.

Hudson, J. M., & Watt, C. A. (2020). Northern Hudson Bay narwhal (*monodon monoceros*) catch statistics in Canada from 1957-2018. *Can. Tech. Rep. Fish. Aquat. Sci. 3390: Vii,*, 77.

Hui, D. (2012). Food web: Concept and applications. *Nature Education Knowledge,* Retrieved from https://www.nature.com/scitable/knowledge/library/food-web-concept-and-applications-84077181/

Hunt, J. M. (1966). The significance of carbon isotope variations in marine sediments. Paper presented at the *Advances in Organic Geochemistry. Proceedings of the Third International Congress, London,, 32* 27-35.

Iken, K., Barrera-Oro, E. R., Quartino, M. L., Casaux, R. J., & Brey, T. (1997). Grazing by the Antarctic fish (*notothenia coriiceps*): Evidence for selective feeding on macroalgae. *Antarctic Science, 9*(4), 386-391.

Iken, K., Brey, T., Wand, U., Voigt, J., & Junghans, P. (2001). Food web structure of the benthic community at the porcupine abyssal plain (NE Atlantic): A stable isotope analysis. *Progress in Oceanography, 50*(1-4), 383-405.

Iken, K., Bluhm, B. A., & Gradinger, R. (2005). Food web structure in the high Arctic Canada basin: Evidence from δ 13 C and δ 15 N analysis. *Polar Biology, 28*, 238-249.

Iken, K., Bluhm, B., & Dunton, K. (2010). Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography, 57*(1-2), 71-85.

Jackson, C. R., & Pringle, C. M. (2010). Ecological benefits of reduced hydrologic connectivity in intensively developed landscapes. *Bioscience, 60*(1), 37-46.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable isotope Bayesian ellipses in R. *Journal of Animal Ecology, 80*(3), 595-602.

Jansen, J., Hill, N. A., Dunstan, P. K., McKinlay, J., Sumner, M. D., Post, A. L., Elèaume, M. P., Armand, M. K. Warnock, J. P., & Galton-Fenzi, B. K. (2018). Abundance and richness of key Antarctic seafloor fauna correlates with modelled food availability. *Nature Ecology & Evolution, 2*(1), 71-80.

Jonsson, T., & Ebenman, B. (1998). Effects of predator–prey body size ratios on the stability of food chains. *Journal of Theoretical Biology, 193*(3), 407-417.

Jorgensen, B. B. (1979). A theoretical model of the stable sulfur isotope distribution in marine sediments. *Geochimica Et Cosmochimica Acta, 43*(3), 363-374.

Jørgensen, B., Findlay, A., & Pellerin, A. (2019). The biogeochemical sulfur cycle of marine sediments. *Microbiological Chemistry and Geomicrobiology, 10*

Jueterbock, A., Smolina, I., Coyer, J. A., & Hoarau, G. (2016). The fate of the Arctic seaweed (*fucus distichus*) under climate change: An ecological niche modeling approach. *Ecology and Evolution, 6*(6), 1712-1724.

Kędra, M., Moritz, C., Choy, E. S., David, C., Degen, R., Duerksen, S., Ellingsen, I., Gorska, B., Grebmeier, J., & Kirievskaya, D. (2015). Status and trends in the structure of Arctic benthic food webs. *Polar Research, 34*(1), 23775.

Kenchington, E., Link, H., Roy, V., Archambault, P., Siferd, T., Treble, M., & Wareham, V. (2011). Identification of mega- and macrobenthic ecologically and biologically significant areas (EBSAs) in the Hudson Bay complex, the western and eastern Canadian Arctic. *Canadian Science Advisory Secretariat,*

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of Arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B-Biological Sciences, 282*(1814), 31-39. doi:10.1098/rspb.2015.1546

Koziorowska, K., Kuliński, K., & Pempkowiak, J. (2016). Sedimentary organic matter in two Spitsbergen fjords: Terrestrial and marine contributions based on carbon and nitrogen contents and stable isotopes composition. *Continental Shelf Research, 113*, 38-46.

Kwak, T. J., & Zedler, J. B. (1997). Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia, 110*, 262-277.

Laforest, B. J., Hébert, J. S., Obbard, M. E., & Thiemann, G. W. (2018). Traditional ecological knowledge of polar bears in the northern Eeyou marine region, Québec, Canada. *Arctic, 71*(1), 40-58.

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., Ferguson, S. H., Wiig, Ø., Boveng, P., & Angliss, R. P. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology, 29*(3), 724-737.

Larouche, P., & Galbraith, P. S. (2016). Canadian coastal seas and great lakes sea surface temperature climatology and recent trends. *Canadian Journal of Remote Sensing, 42*(3), 243-258.

Lavoie, D., Lambert, N., & Van der Baaren, A. (2013). Projections of future physical and biogeochemical conditions in Hudson and Baffin Bays from CMIP5 global climate models. *Fisheries and Oceans Canada= Pêches et océans Canada.*

Lawler, S. P., & Morin, P. J. (1993). Food-web architecture and population-dynamics in laboratory microcosms of protists. *American Naturalist, 141*(5), 675-686. doi:10.1086/285499

Layman, C., Arrington, D., Montaña, C., & Post, D. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology (Durham), 88*(1), 42-48. doi:10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Le Loc'h, F., Hily, C., & Grall, J. (2008). Benthic community and food web structure on the continental shelf of the Bay of Biscay (northeastern Atlantic) revealed by stable isotopes analysis. *Journal of Marine Systems, 72*(1-4), 17-34.

Link, H., Piepenburg, D., & Archambault, P. (2013). Are hotspots always hotspots? the relationship between diversity, resource and ecosystem functions in the arctic. *PLoS One, 8*(9), e74077.

Loewen, T. N., Hornby, C., Johnson, M., Chambers, C., Dawson, K., MacDonell, D., Bernhardt, W., Gnanpragasam, R., Pierrejean, M., & Choy, E. (2020). Ecological and biophysical overview of the Southampton Island ecologically and biologically significant area in support of the identification of an area of interest. *Canadian Science Advisory Secretariat (CSAS) Research Document 2020/032.*

Lohrer, A. M., Thrush, S. F., & Gibbs, M. M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature, 431*(7012), 1092-1095.

Lohrer, A. M., Rodil, I. F., Townsend, M., Chiaroni, L. D., Hewitt, J. E., & Thrush, S. F. (2013). Biogenic habitat transitions influence facilitation in a marine soft-sediment ecosystem. *Ecology, 94*(1), 136-145.

Lonsdale, D. J., Cerrato, R. M., Holland, R., Mass, A., Holt, L., Schaffner, R. A., Pan, J., & Caron, D. A. (2009). Influence of suspension-feeding bivalves on the pelagic food webs of shallow, coastal embayments. *Aquatic Biology, 6*, 263-279.

Lovrity, J. E. (1984). Oceanographic data from Frobisher bay in the eastern Canadian Arctic for the years 1982 and 1983. *Arctic Biological Station, Department of Fisheries and Oceans*.

Luque, S. P., Ferguson, S. H., & Breed, G. A. (2014). Spatial behaviour of a keystone Arctic marine predator and implications of climate warming in Hudson Bay. *Journal of Experimental Marine Biology and Ecology, 461*, 504-515.

Macdonald, T. A., Burd, B. J., Macdonald, V. I., & Van Roodselaar, A. (2010). Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. *Fisheries and Oceans Canada= Pêches et océans Canada.*

Mason, E. T. P. R. P., & Sanford, L. P. (2010). Effect of tidal resuspension on benthic–pelagic coupling in an experimental ecosystem study. *Marine Ecology Progress Series, 413*, 33-53.

Mayer, L., Jakobsson, M., Allen, G., Dorschel, B., Falconer, R., Ferrini, V., Lamarcher, G., Snaith, H., & Weatherall, P. (2018). The nippon Foundation—GEBCO seabed 2030 project: The quest to see the world's oceans completely mapped by 2030. *Geosciences, 8*(2), 63.

McGuire, A. D., Anderson, L. G., Christensen, T. R., Dallimore, S., Guo, L., Hayes, D. J., Heimann, M., Lorenson, T. D., Macdonald, R. W., & Roulet, N. (2009). Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs, 79*(4), 523-555.

McMeans, B. C., Rooney, N., Arts, M. T., & Fisk, A. T. (2013). Food web structure of a coastal Arctic marine ecosystem and implications for stability. *Marine Ecology Progress Series, 482*, 17-28.

Meier, W. N., Hovelsrud, G. K., Van Oort, B. E., Key, J. R., Kovacs, K. M., Michel, C., Hass, C., Granskog, M., Gerland, S., & Perovich, D. K. (2014). Arctic sea ice in transformation: A review of recent observed changes and impacts on biology and human activity. *Reviews of Geophysics, 52*(3), 185-217.

Meysman, F. J., Middelburg, J. J., & Heip, C. H. (2006). Bioturbation: A fresh look at Darwin's last idea. *Trends in Ecology & Evolution, 21*(12), 688-695.

Miller, R. J., & Page, H. M. (2012). Kelp as a trophic resource for marine suspension feeders: A review of isotope-based evidence. *Marine Biology, 159*, 1391-1402.

Mittermayr, A., Fox, S. E., & Sommer, U. (2014). Temporal variation in stable isotope composition (δ13C, δ15N and δ34S) of a temperate zostera marina food web. *Marine Ecology Progress Series, 505*, 95-105.

Montanari, S. (2017). Discrimination factors of carbon and nitrogen stable isotopes in meerkat feces. *Peerj, 5*, e3436. doi:10.7717/peerj.3436

Montoya, D., Yallop, M. L., & Memmott, J. (2015). Functional group diversity increases with modularity in complex food webs. *Nature Communications, 6*(1), 7379.

Mosnier, A., Hammill, M. O., Turgeon, S., & Postma, L. (2017). Updated analysis of genetic mixing among beluga stocks in the Nunavik marine region and Belcher Sslands area: Information for population models and harvest allocation. *Canadian Science Advisory Secretariat.*

Muyzer, G., & Stams, A. J. (2008). The ecology and biotechnology of sulphate-reducing bacteria. *Nature Reviews Microbiology, 6*(6), 441-454.

Newell, R. I. (2004). Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: A review. *Journal of Shellfish Research, 23*(1), 51-62.

Nguyen, H. T., Lee, Y. M., Hong, J. K., Hong, S., Chen, M., & Hur, J. (2022). Climate warming-driven changes in the flux of dissolved organic matter and its effects on bacterial communities in the Arctic ocean: A review. *Frontiers in Marine Science, 9*, 968583.

Niemi, A., Ferguson, S., Hedges, K., Melling, H., & Michel, C. (2019). State of Canada's Arctic seas. *Can. Tech. Rep. Fish. Aquat. Sci.,*, 189.

Norkko, A., Hewitt, J. E., Thrush, S. F., & Funnell, T. (2001). Benthic-pelagic coupling and suspension-feeding bivalves: Linking site-specific sediment flux and biodeposition to benthic community structure. *Limnology and Oceanography, 46*(8), 2067-2072.

Norling, K., Rosenberg, R., Hulth, S., Grémare, A., & Bonsdorff, E. (2007). Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series, 332*, 11-23.

Officer, C. B., Smayda, T. J., & Mann, R. (1982). Benthic filter feeding: A natural eutrophication control. *The University of Rhode Island*.

Oleszczuk, B., Michaud, E., Morata, N., Renaud, P. E., & Kędra, M. (2019). Benthic macrofaunal bioturbation activities from shelf to deep basin in spring to summer transition in the Arctic ocean. *Marine Environmental Research, 150*, 104746.

Oleszczuk, B., Grzelak, K., & Kędra, M. (2021). Community structure and productivity of Arctic benthic fauna across depth gradients during springtime. *Deep Sea Research Part I: Oceanographic Research Papers, 170*, 103457.

Paulic, J., & Rice, J. (2011a). Identification of ecologically and biologically significant areas (EBSAs) in the Canadian Arctic. *Proceedings Series,*, 047.

Paulic, J., & Rice, J. (2011b). Identification of ecologically and biologically significant areas (ESBAs) in the Canadian Arctic, June 14-17, 2011, Winnipeg, Manitoba. *Canadian Science Advisory Secretariat,*

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics, 18*, 293-320. doi:10.1146/annurev.es.18.110187.001453

Peterson, I. K., & Pettipas, R. G. (2013). Trends in air temperature and sea ice in the atlantic large aquatic basin and adjoining areas. *Fisheries and Oceans Canada= Pêches et océans Canada.*

Pierrejean, M., Babb, D. G., Maps, F., Nozais, C., & Archambault, P. (2020). Spatial distribution of epifaunal communities in the Hudson Bay system, patterns and drivers. *Elementa: Science of the Anthropocene, 8*(1)

Pile, A. J., & Young, C. M. (2006). The natural diet of a hexactinellid sponge: Benthic–pelagic coupling in a deep-sea microbial food web. *Deep Sea Research Part I: Oceanographic Research Papers, 53*(7), 1148-1156.

Pimm, S. L., & Lawton, J. H. (1977) Number of trophic levels in ecological communities. *Nature (London), 268*(5618), 329-331.

Pistone, K., Eisenman, I., & Ramanathan, V. (2014). Observational determination of albedo decrease caused by vanishing Arctic sea ice. *Proceedings of the National Academy of Sciences, 111*(9), 3322-3326.

Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Moore, P. J., Richardson, A. J., & Schoeman, D. S. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science,*, 62.

Pomerleau, C., Lesage, V., Ferguson, S. H., Winkler, G., Petersen, S. D., & Higdon, J. W. (2012). Prey assemblage isotopic variability as a tool for assessing diet and the spatial distribution of bowhead whale (*balaena mysticetus*) foraging in the Canadian eastern Arctic. *Marine Ecology Progress Series, 469*, 161-174.

Post, A. L., Lavoie, C., Domack, E. W., Leventer, A., Shevenell, A., Fraser, A. D., & NBP 14-02 Science Team. (2017). Environmental drivers of benthic communities and habitat heterogeneity on an east Antarctic shelf. *Antarctic Science, 29*(1), 17-32.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology, 83*(3), 703-718.

Postma, L. D., & Canadian Science Advisory Secretariat. (2012). Beluga whales in James Bay: A separate entity from eastern Hudson Bay belugas? *Canadian Science Advisory Secretariat= Secrétariat Canadienne de consultation*

Pringle, C. M. (2001). Hydrologic connectivity and the management of biological reserves: A global perspective. *Ecological Applications, 11*(4), 981-998.

Pućko, M., Dionne, K., & Michel, C. (2019). Occurrence of toxin-producing marine algae in the Canadian Arctic and adjacent waters. *Canadian Manuscript Report of Fisheries and Aquatic Sciences, 3180*(vii), 27.

Pulsipher, M. A., Schiffbauer, J. D., Jeffrey, M. J., Huntley, J. W., Fike, D. A., & Shelton, K. L. (2021). A meta-analysis of the steptoean positive carbon isotope excursion: The SPICEraq database. *Earth-Science Reviews, 212*, 103442.

Queirós, A. M., Birchenough, S. N., Bremner, J., Godbold, J. A., Parker, R. E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P., & Van Colen, C. (2013). A bioturbation classification of European marine infaunal invertebrates. *Ecology and Evolution, 3*(11), 3958-3985.

R Core Team. (2022). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria. URL Https://Www.R-Project.Org/.,*

Renaud, P. E., Wallhead, P., Kotta, J., Włodarska-Kowalczuk, M., Bellerby, R. G., Rätsep, M., Slagstad, D., & Kukliński, P. (2019). Arctic sensitivity? suitable habitat for benthic taxa is surprisingly robust to climate change. *Frontiers in Marine Science, 6*, 538.

Rezende, C. E., Lacerda, L. D., Ovall, A., Silva, C., & Martinelli, L. A. (1990). Nature of POC transport in a mangrove ecosystem: A carbon stable isotopic study. *Estuarine, Coastal and Shelf Science, 30*(6), 641-645.

Rooney, N., McCann, K., Gellner, G., & Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature, 442*(7100), 265-269.

Roy, V., & Gagnon, J. (2018). Natural history museum data on Canadian Arctic marine benthos. *Marine Biodiversity, 48*(3), 1357-1367.

Roy, V., Iken, K., Gosselin, M., Tremblay, J., Bélanger, S., & Archambault, P. (2015). Benthic faunal assimilation pathways and depth-related changes in food-web structure across the Canadian Arctic. *Deep Sea Research Part I: Oceanographic Research Papers, 102*, 55-71.

Saintilan, N., Rogers, K., Mazumder, D., & Woodroffe, C. (2013). Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. *Estuarine, Coastal and Shelf Science, 128*, 84-92.

Sanders, D., Thébault, E., Kehoe, R., & Frank van Veen, F. J. (2018). Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences, 115*(10), 2419-2424.

Sandstrom, H., & Elliott, J. A. (2011). Internal waves observed by SLAR imagery collected by AES ice branch 1978-1985. *Canadian Technical Report of Hydrography and Ocean Sciences 276,*, 166.

Satei, S. (2018). The legal status of the Northwest Passage: Canada's jurisdiction or international law in light of recent developments in Arctic shipping regulation? *Sustainable shipping in a changing Arctic* (pp. 241-252) Springer.

Schaefer, C. M. (2020). *Mya truncata* as a bioindicator of chronic municipal wastewater exposure and anthropogenic activity in Frobisher Bay, NU. *The University of Manitoba*.

Schell, D. M., Barnett, B. A., & Vinette, K. A. (1998). Carbon and nitrogen isotope ratios in zooplankton of the Bering, Bhukchi and Beaufort Seas. *Marine Ecology Progress Series, 162*, 11-23.

Searles, E. (2016). To sell or not to sell: Country food markets and Inuit identity in Nunavut. *Food and Foodways, 24*(3-4), 194-212.

Sévellec, F., Fedorov, A. V., & Liu, W. (2017). Arctic sea-ice decline weakens the Atlantic meridional overturning circulation. *Nature Climate Change, 7*(8), 604-610.

Sibert, V., Zakardjian, B., Gosselin, M., Starr, M., Senneville, S., & LeClainche, Y. (2011). 3D bio-physical model of the sympagic and planktonic productions in the Hudson Bay system. *Journal of Marine Systems, 88*(3), 401-422.

Sim, M. S., Woo, D. K., Kim, B., Jeong, H., Joo, Y. J., Hong, Y. W., & Choi, J. Y. (2023). What controls the sulfur isotope fractionation during dissimilatory sulfate reduction? *ACS Environmental Au, 3*(2), 76-86.

Simon, M. (2011). Canadian Inuit: Where we have been and where we are going. *International Journal, 66*(4), 879-891.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., & Popper, A. N. (2010). A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution, 25*(7), 419-427.

Smith, A. M., & Callow, J. A. (2006). *Biological adhesives*. Germany: Springer.

Soltwedel, T., & Vopel, K. (2001). Bacterial abundance and biomass in response to organism-generated habitat heterogeneity in deep-sea sediments. *Marine Ecology Progress Series, 219*, 291-298.

Søreide, J. E., Leu, E. V., Berge, J., Graeve, M., & Falk-Petersen, S. (2010). Timing of blooms, algal food quality and *calanus glacialis* reproduction and growth in a changing Arctic. *Global Change Biology, 16*(11), 3154-3163.

Spares, A. D., Stokesbury, M. J., O'Dor, R. K., & Dick, T. A. (2012). Temperature, salinity and prey availability shape the marine migration of Arctic char, *salvelinus alpinus*, in a macrotidal estuary. *Marine Biology, 159*, 1633-1646.

Stasko, A. D., Bluhm, B. A., Michel, C., Archambault, P., Majewski, A., Reist, J. D., Swanson, H., & Power, M. (2018). Benthic-pelagic trophic coupling in an Arctic marine food web along vertical water mass and organic matter gradients. *Marine Ecology Progress Series, 594*, 1-19. doi:10.3354/meps12582

Statistics Canada. (2017). Cape dorset, HAM [census subdivision], Nunavut and Baffin, REG [census division], Nunavut (table).

Steiner, N. S., Cheung, W. W., Cisneros-Montemayor, A. M., Drost, H., Hayashida, H., Hoover, C., Lam, J., Sou, T., Sumaila, U. R., & Suprenand, P. (2019). Impacts of the changing ocean-sea ice system on the key forage fish Arctic cod (*boreogadus saida*) and subsistence fisheries in the western Canadian Arctic—Evaluating linked climate, ecosystem and economic (CEE) models. *Frontiers in Marine Science, 6*, 179.

Steiner, N., Azetsu-Scott, K., Galbraith, P., Hamilton, J., Hedges, K., Hu, X., Janjua, M. Y., Lambert, N., Larouche, P., & Lavoie, D. (2013). Climate change assessment in the Arctic basin part 1: Trends and projections: A contribution to the aquatic climate change adaptation services program. *Fisheries and Oceans Canada= Pêches et océans Canada*.

Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., & Reist, J. D. (2015). A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology, 96*(2), 318-324.

Sweeting, C. J., Jennings, S., & Polunin, N. (2005). Variance in isotopic signatures as a descriptor of tissue turnover and degree of omnivory. *Functional Ecology,*, 777-784.

Tai, T. C., Steiner, N. S., Hoover, C., Cheung, W. W. L., & Sumaila, U. R. (2019). Evaluating present and future potential of Arctic fisheries in Canada. *Marine Policy, 108*, 103637. doi:10.1016/j.marpol.2019.103637

The Arctic Institute. (2022). Canada. Retrieved from https://www.thearcticinstitute.org/country-backgrounders/Canada/

Thode, H. G., Monster, J., & Dunford, H. B. (1961). Sulphur isotope geochemistry. *Geochimica Et Cosmochimica Acta, 25*(3), 159-174.

Thompson, K., Picard, C. R., & Chan, H. M. (2017). Polycyclic aromatic hydrocarbons (PAHs) in traditionally harvested bivalves in northern British Columbia, Canada. *Marine Pollution Bulletin, 121*(1-2), 390-399.

Timmermans, M., & Marshall, J. (2020). Understanding Arctic ocean circulation: A review of ocean dynamics in a changing climate. *Journal of Geophysical Research: Oceans, 125*(4), e2018JC014378.

Timmerman, C., Giraldo, C., Cresson, P., Ernande, B., Travers-Trolet, M., Rouquette, M., Denamiel, M., & Lefebvre, S. (2021). Plasticity of trophic interactions in fish assemblages results in temporal stability of benthic-pelagic couplings. *Marine Environmental Research, 170*, 105412.

Todd, B. J., Shaw, J., Campbell, D. C., & Mate, D. J. (2016). Preliminary interpretation of the marine geology of Frobisher Bay, Baffin Island, Nunavut. *Summary of Activities,*, 61-66.

Ullah, H., Nagelkerken, I., Goldenberg, S. U., & Fordham, D. A. (2018). Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation. *PLoS Biology, 16*(1), e2003446.

Wada, E., Mizutani, H., & Minagawa, M. (1991). The use of stable isotopes for food web analysis. *Critical Reviews in Food Science & Nutrition, 30*(4), 361-371.

Wang, S. C., Liu, X., Liu, Y., & Wang, H. (2020). Benthic-pelagic coupling in lake energetic food webs. *Ecological Modelling, 417*, 108928.

Wassmann, P., Duarte, C. M., Agusti, S., & Sejr, M. K. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology, 17*(2), 1235-1249.

Wassmann, P., & Reigstad, M. (2011). Future Arctic ocean seasonal ice zones and implications for pelagic-benthic coupling. *Oceanography, 24*(3), 220-231.

Watt, C. A., Heide-Jørgensen, M. P., & Ferguson, S. H. (2013). How adaptable are narwhal? A comparison of foraging patterns among the world's three narwhal populations. *Ecosphere, 4*(6), 1-15.

Wei, C., Cusson, M., Archambault, P., Belley, R., Brown, T., Burd, B. J., Edinger, E., Kenchington, E., Gilkinson, K., & Lawton, P. (2019). Seafloor biodiversity of Canada's three oceans: Patterns, hotspots and potential drivers. *Diversity and Distributions, 26*(2), 226-241.

Werner, K., Fritz, M., Morata, N., Keil, K., Pavlov, A., Peeken, I., Nikolopoulos, A., Findlay, H., Kędra, M., & Majaneva, S. (2016). Arctic in rapid transition: Priorities for the future of marine and coastal research in the Arctic. *Polar Science, 10*(3), 364-373.

Whitney, E. J., Beaudreau, A. H., & Howe, E. R. (2018). Using stable isotopes to assess the contribution of terrestrial and riverine organic matter to diets of nearshore marine consumers in a glacially influenced estuary. *Estuaries and Coasts, 41*(1), 193-205.

Włodarska-Kowalczuk, M., Aune, M., Michel, L. N., Zaborska, A., & Legeżyńska, J. (2019). Is the trophic diversity of marine benthic consumers decoupled from taxonomic and functional trait diversity? isotopic niches of Arctic communities. *Limnology and Oceanography, 64*(5), 2140-2151.

Wölfl, A., Snaith, H., Amirebrahimi, S., Devey, C. W., Dorschel, B., Ferrini, V., Huvenne, V., Jakobsson, M., Jencks, J., Johnston, G., Lamarche, G., Mayer, L., Millar, D., Pedersen, T., Picard, K., Reitz, A., Schmitt, T., Visbeck, M., Weatherall, P., & Wigley, R. (2019). Seafloor mapping – the challenge of a truly global ocean bathymetry. *Frontiers in Marine Science, 6* doi:10.3389/fmars.2019.00283

Wulff, A., Iken, K., Quartino, M. L., Al-Handal, A., Wiencke, C., & Clayton, M. N. (2009). Biodiversity, biogeography and zonation of marine benthic micro-and macroalgae in the Arctic and Antarctic. *Botanic Marina*. 491-507.

Ying, R., Cao, Y., Yin, F., Guo, J., Huang, J., Wang, Y., Zheng, L., Wang, J., Liang, H., & Li, Z. (2020). Trophic structure and functional diversity reveal pelagic-benthic coupling dynamic in the coastal ecosystem of Daya Bay, China. *Ecological Indicators, 113*, 106241.

Young, B. G., & Ferguson, S. H. (2014). Using stable isotopes to understand changes in ringed seal foraging ecology as a response to a warming environment. *Marine Mammal Science, 30*(2), 706-725.

Yurkowski, D. J., Auger-Méthé, M., Mallory, M. L., Wong, S. N., Gilchrist, G., Derocher, A. E., Richardson, E., Lunn, N., Hussey, N., & Marcoux, M. (2019). Abundance and species diversity hotspots of tracked marine predators across the North American Arctic. *Diversity and Distributions, 25*(3), 328-345.

Yurkowski, D. J., Semeniuk, C. A., Harwood, L. A., Rosing-Asvid, A., Dietz, R., Brown, T. M., Clackett, S., Grgicak-Mannion, A., Fisk, A., & Ferguson, S. H. (2016). Influence of sea ice phenology on the movement ecology of ringed seals across their latitudinal range. *Marine Ecology Progress Series, 562*, 237-250.

Ziółkowska, M., & Sokołowski, A. (2022). Variation of food web structure in macrobenthic communities in low diversity system as determined by stable isotope-based community-wide metrics. *Estuarine, Coastal and Shelf Science, 274*, 107931.

References that apply to material in Appendix A

Ambrose, W., Clough, L., Tilney, P., & Beer, L. (2001). Role of echinoderms in benthic remineralization in the Chukchi Sea. *Marine Biology, 139*(5), 937-949.

Auel, H., & Werner, I. (2003). Feeding, respiration and life history of the hyperiid amphipod *themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. *Journal of Experimental Marine Biology and Ecology, 296*(2), 183-197.

Banse, K. (1995). Zooplankton: Pivotal role in the control of ocean production: I. biomass and production. *ICES Journal of Marine Science, 52*(3-4), 265-277.

Barreto, F. S., & Bauer, K. K. (2019). Genetic evidence for alloparental care and frequent multiple paternity in the brooding sea star (*leptasterias sp.). Marine Biology, 166*(3), 1-12.

Bell, J. J. (2008). The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science, 79*(3), 341-353.

Bergmann, M., Soltwedel, T., & Klages, M. (2011). The interannual variability of megafaunal assemblages in the Arctic deep sea: Preliminary results from the HAUSGARTEN observatory (79 N). *Deep Sea Research Part I: Oceanographic Research Papers, 58*(6), 711-723.

Birkely, S. R., & Gulliksen, B. (2003). Feeding ecology in five shrimp species (*decapoda, caridea*) from an Arctic fjord (Isfjorden, sSalbard), with emphasis on *sclerocrangon boreas* (phipps, 1774). *Crustaceana-International Journal of Crustacean Research-, 76*(6), 699-716.

Bjørdalsbakke, L. K. (2011). Population structure, parasitism and prey preference in *sclerocrangon boreas* and *S.ferox*, Svalbard.

Blake, D. B., Breton, G., & Gofas, S. (1996). A new genus and species of asteriidae (asteroidea; echinodermata) from the upper cretaceous (coniacian) of Angola, Africa. *Paläontologische Zeitschrift, 70*(1), 181-187.

Böer, M., Gannefors, C., Kattner, G., Graeve, M., Hop, H., & Falk-Petersen, S. (2005). The Arctic pteropod *clione limacina*: Seasonal lipid dynamics and life-strategy. *Marine Biology, 147*(3), 707-717.

Boyce, D. G., Frank, K. T., & Leggett, W. C. (2015). From mice to elephants: Overturning the 'one size fits all' paradigm in marine plankton food chains. *Ecology Letters, 18*(6), 504-515.

Burgos-Rubio, V., De la Rosa, J., Altamirano, M., & Espinosa, F. (2015). The role of patellid limpets as omnivorous grazers: A new insight into intertidal ecology. *Marine Biology, 162*, 2093-2106.

Coad, B. W., & Reist, J. D. (2004). *Annotated list of the Arctic marine fishes of Canada* Fisheries and Oceans Canada Winnipeg.

Coleman, C. O. (1990). Bathypanoploea schellenbergi holman & watling, 1983, an antarctic amphipod (crustacea) feeding on holothuroidea. *Ophelia, 31*(3), 197-205.

Conlan, K., Hendrycks, E., Aitken, A., Williams, B., Blasco, S., & Crawford, E. (2013). Macrofaunal biomass distribution on the Canadian Beaufort Shelf. *Journal of Marine Systems, 127*, 76-87.

Crisp, D. J., & Southward, A. J. (1961). Different types of cirral activity of barnacles. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 243*(705), 271-307.

Denisenko, S. G., Denisenko, N. V., Lehtonen, K. K., Andersin, A., & Laine, A. O. (2003). Macrozoobenthos of the Pechora Sea (SE Barents Sea): Community structure and spatial distribution in relation to environmental conditions. *Marine Ecology Progress Series, 258*, 109-123.

Diffenthal, M., & Horton, T. (2007). Stephonyx arabiensis (crustacea: Amphipoda: Lysianassoidea: Uristidae), a new deep-water scavenger species from the Indian Ocean, with a key to the genus *stephonyx*. *Zootaxa, 1665*(31-4), 1.

Fankboner, P. V. (1978). Suspension-feeding mechanisms of the armoured sea cucumber *psolus chitinoides clark*. *Journal of Experimental Marine Biology and Ecology, 31*(1), 11-25.

Fauchald, K., & Jumars, P. A. (1979). The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review,*

Fernández, D. E., Pérez, D. E., Luci, L., & Carrizo, M. A. (2014). An early cretaceous astropectinid (echinodermata, asteroidea) from Patagonia (Argentina): A new species and the oldest record of the family for the southern hemisphere. *Andean Geology, 41*(1), 210-223.

Goldberg, W. M. (2002). Feeding behavior, epidermal structure and mucus cytochemistry of the scleractinian *mycetophyllia reesi*, a coral without tentacles. *Tissue and Cell, 34*(4), 232-245.

Graeve, M., Kattner, G., & Piepenburg, D. (1997). Lipids in Arctic benthos: Does the fatty acid and alcohol composition reflect feeding and trophic interactions? *Polar Biology, 18*(1), 53-61.

Gravem, S. A., & Morgan, S. G. (2017). Shifts in intertidal zonation and refuge use by prey after mass mortalities of two predators. *Ecology, 98*(4), 1006-1015.

Hallanger, I. G., Ruus, A., Herzke, D., Warner, N. A., Evenset, A., Heimstad, E. S., Gabrielsen, G. W,. & Borgå, K. (2011). Influence of season, location, and feeding strategy on bioaccumulation of halogenated organic contaminants in Arctic marine zooplankton. *Environmental Toxicology and Chemistry, 30*(1), 77-87.

Hays, B. (2016). Can skeletal morphology support new molecular phylogenies of antedonidae (crinoidea: *Comatulida*)? *Nova Southeastern University*.

Hilgendag, I. R., Swanson, H. K., Lewis, C. W., Ehrman, A. D., & Power, M. (2022). Mercury biomagnification in benthic, pelagic, and benthopelagic food webs in an Arctic marine ecosystem. *Science of the Total Environment, 841*, 156424.

Hodgson, A. (1999). The biology of siphonariid limpets (gastropoda: Pulmonata). *Oceanography and Marine Biology: An Annual Review,* (37), 245–314.

Hou, Z., & Sket, B. (2016). A review of gammaridae (crustacea: Amphipoda): The family extent, its evolutionary history, and taxonomic redefinition of genera. *Zoological Journal of the Linnean Society, 176*(2), 323-348.

Kane, J. E. (1963). Observations on the moulting and feeding of a hyperiid amphipod. *Crustaceana, 6*(2), 129-132.

Kharlamenko, V. I., Zhukova, N. V., Khotimchenko, S. V., & Svetashev, V. I. (1995). Fatty acids as markers of food sources in a shallow-water hydrothermal ecosystem (Kraternaya Bight, Yankich Island, Kurile Islands). *Marine Ecology Progress Series, 120*, 231-241.

Lange, L., & Griffiths, C. L. (2014). Large-scale spatial patterns within soft-bottom epibenthic invertebrate assemblages along the west coast of South Africa, based on the nansen trawl survey. *African Journal of Marine Science, 36*(1), 111-124.

Latyshev, N. A., Khardin, A. S., & Kiyashko, S. I. (2001). Fatty acids as markers of starfish food sources. Paper presented at the *Doklady Biological Sciences,, 380*(1) 489-491.

Løkken, T. S. (2013). Carbon source and trophic structure along a depth gradient in Isfjorden, Svalbard. *UiT Munin,*

Macdonald, T. A., Burd, B. J., Macdonald, V. I., & Van Roodselaar, A. (2010). Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia, *Fisheries and Oceans Canada= Pêches et océans Canada.*

Madin, J., Angkirim, M. A., Yassine, M., & Nor'azlan, S. N. (2022). Feather star community in Sepanggar Bay, Sabah. *The Marine Ecosystems of Sabah,*, 153.

Madio, B., King, G. F., & Undheim, E. A. (2019). Sea anemone toxins: A structural overview. *Marine Drugs, 17*(6), 325.

McTigue, N. D., & Dunton, K. H. (2017). Trophodynamics of the Hanna shoal ecosystem (Chukchi Sea, Alaska): Connecting multiple end-members to a rich food web. *Deep Sea Research Part II: Topical Studies in Oceanography, 144*, 175-189.

Messing, C. G. (1997). Living comatulids. *The Paleontological Society Papers, 3*, 3-30.

Millar, R. H. (1971). The biology of ascidians. *Advances in marine biology* (pp. 1-100) Elsevier.

Mladenov, P. V., Carson, S. F., & Walker, C. W. (1986). Reproductive ecology of an obligately fissiparous population of the sea star *stephanasterias albula stimpson*. *Journal of Experimental Marine Biology and Ecology, 96*(2), 155-175.

North, C. A., Lovvorn, J. R., Kolts, J. M., Cooper, L. W., & Grebmeier, J. M. (2019). Discriminating trophic niches of carnivorous benthic macroinvertebrates with gut contents, stable isotopes, and fatty acids. *Marine Ecology Progress Series, 631*, 49-66.

Orr, J. W., Spies, I., Stevenson, D. E., Longo, G. C., Kai, Y., Ghods, S., & Hollowed, M. (2019). Molecular phylogenetics of snailfishes (cottoidei: Liparidae) based on MtDNA and RADseq genomic analyses, with comments on selected morphological characters. *Zootaxa, 4642*(1), 1–79.

Pasternak, A. F., Drits, A. V., & Flint, M. V. (2017). Feeding, egg production, and respiration rate of pteropods *limacina* in Arctic seas. *Oceanology, 57*(1), 122-129.

Petersen, J. K. (2007). Ascidian suspension feeding. *Journal of Experimental Marine Biology and Ecology, 342*(1), 127-137.

Ravelo, A. M., Konar, B., Bluhm, B., & Iken, K. (2017). Growth and production of the brittle stars *ophiura sarsii* and *ophiocten sericeum* (echinodermata: Ophiuroidea). *Continental Shelf Research, 139*, 9-20.

Renaud, P. E., Løkken, T. S., Jørgensen, L. L., Berge, J., & Johnson, B. J. (2015). Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Frontiers in Marine Science, 2*, 31.

Sargent, P. S., Hamel, J., & Mercier, A. (2019). The life history and feeding ecology of velvet shell, *velutina velutina* (gastropoda: Velutinidae), a specialist predator of ascidians. *Canadian Journal of Zoology, 97*(12), 1164-1176.

Schell, D. M., Barnett, B. A., & Vinette, K. A. (1998). Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort Seas. *Marine Ecology Progress Series, 162*, 11-23.

Schnabel, K. E., & Hebert, P. D. (2003). Resource-associated divergence in the Arctic marine amphipod *paramphithoe hystrix*. *Marine Biology, 143*(5), 851-857.

Shick, J. M., Edwards, K. C., & Dearborn, J. H. (1981). Physiological ecology of the deposit-feeding sea star *ctenodiscus crispatus*: Ciliated surfaces and animal-sediment interactions. *Marine Ecology Progress Series, 5*, 165-184.

Simone, L. R. L., & Seabra, M. I. G. (2017). Shell and body structure of the plesiomorphic pulmonate marine limpet *siphonaria pectinata* (linnaeus, 1758) from Portugal (gastropoda: Heterobranchia: Siphonariidae). *Folia Malacologica, 25*(3)

Sokolova, M. N. (1959). On the distribution of deep-water bottom animals in relation to their feeding habits and the character of sedimentation. *Deep Sea Research (1953), 6*, 1-4.

Stasko, A. D., Bluhm, B. A., Michel, C., Archambault, P., Majewski, A., Reist, J. D., Swanson, H., & Power, M. (2018). Benthic-pelagic trophic coupling in an Arctic marine food web along vertical water mass and organic matter gradients. *Marine Ecology Progress Series, 594*, 1-19. doi:10.3354/meps12582

Vannier, J., Steiner, M., Renvoisé, E., Hu, S., & Casanova, J. (2007). Early Cambrian origin of modern food webs: Evidence from predator arrow worms. *Proceedings of the Royal Society B: Biological Sciences, 274*(1610), 627-633.

Watling, L. (1993). Functional morphology of the amphipod mandible. *Journal of Natural History, 27*(4), 837-849.

Watson, C., & Faulwetter, S. (2017). Stylet jaws of chrysopetalidae (annelida). *Journal of Natural History, 51*(47-48), 2863-2924.

Watts, J., & Tarling, G. A. (2012). Population dynamics and production of *themisto gaudichaudii* (amphipoda, hyperiidae) at south Georgia, Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography, 59*, 117-129.

Whitehouse, G. A., Buckley, T. W., & Danielson, S. L. (2017). Diet compositions and trophic guild structure of the eastern Chukchi Sea demersal fish community. *Deep Sea Research Part II: Topical Studies in Oceanography, 135*, 95-110.

Wilding, T., Black, K., & Hughes, D. (2017). SARF098C: PAMP refreshment study-the association between emamectin benzoate use and crustacean assemblages around Scottish fish-farms. *University of the Highlands and Islands*.

Wiltse, W. I. (1980). Predation by juvenile *polinices duplicatvs* (say) on *gemma gemma* (totten). *Journal of Experimental Marine Biology and Ecology, 42*(2), 187-199.

Wlodarska, M., Weslawski, J. M., & Gromisz, S. (1997). A comparison of the macrofaunal community structure and diversity in two Arctic glacial bays-a old one off Franz Josef land and a warm one off spitsbergen. *Oceanographic Literature Review, 2*(44), 133.

Wood, H. L., Spicer, J. I., Kendall, M. A., Lowe, D. M., & Widdicombe, S. (2011). Ocean warming and acidification; implications for the Arctic brittle star *ophiocten sericeum*. *Polar Biology, 34*(7), 1033-1044.

Yamakami, R., & Wada, S. (2022). Stomach contents of the deep-water whelks *buccinum kashimanum* and *neptunea sp.* (caenogastropoda: Buccinidae) off the coast of Cape Esan, southwestern Hokkaido, Japan, in the western north Pacific Ocean. *Venus (Journal of the Malacological Society of Japan), 80*(1-2), 40-46.

Zinkann, A., Wooller, M. J., O'Brien, D., & Iken, K. (2021). Does feeding type matter? contribution of organic matter sources to benthic invertebrates on the Arctic Chukchi Sea shelf. *Food Webs, 29*, e00205.

Appendix A- Taxonomic classifications

Table A-1. Table of all the taxa included in the food web analysis study and the corresponding depths, functional feeding group, sample size, isotope values, and references for functional feeding group identification.

Taxa	Depth	Functional Feeding Group	n	δ^{15}Nadj (‰)	δ^{13}C (‰)	δ^{34}S (‰)	References
Actiniaria	FBM	BC	1	3.94	-18.44	20.99	Madio et al. 2019
Actiniaria	FBO	BC	1	3.20	-19.88	19.83	Madio et al. 2019
Ascidiacea	FBM	BSF	1	1.14	-19.70	19.62	Millar 1971; Petersen 2007
Chaetognatha	FBM	BPC	1	6.15	-21.57	17.39	Schell et al. 1998; Vannier et al. 2007
Annelida							
Polychaeta							
Chrysopetalidae gn.	FBO	BC	1	6.91	-16.35	13.79	Fauchald and Jumars 1979; Watson et al. 2017
Euphrosinidae	FBM	BC	1	5.49	-18.65	18.15	Fauchald and Jumars 1979
Harmothoe sp.	FBN	BC	2	4.20	-17.42	17.23	Macdonald et al. 2010
Harmothoe sp.	FBM	BC	2	5.13	-17.69	16.26	Macdonald et al. 2010
Polynoidae gn.	FBN	BC	6	3.36	-18.54	18.94	Fauchald and Jumars 1979
Polynoidae gn.	FBM	BC	7	5.71	-17.38	16.86	Fauchald and Jumars 1979
Polynoidae gn.	FBO	BC	1	6.00	-18.78	18.29	Fauchald and Jumars 1979
Nereididae	FBM	BC	1	5.19	-19.66	16.60	Fauchald and Jumars 1979
Terebellida							
Pista maculata	FBN	BSDF	4	0.90	-21.45	17.28	Macdonald et al. 2010
Pista maculata	FBM	BSDF	21	0.60	-21.51	16.02	Macdonald et al. 2010
Sabellidae gn.	FBM	BSF	9	1.45	-20.30	18.36	Fauchald and Jumars 1979; Macdonald et al. 2010
Sabellidae gn.	FBO	BSF	2	2.81	-19.20	18.61	Fauchald and Jumars 1979; Macdonald et al. 2010

Terebellidae gn.	FBO	BSDF	7	1.97	-20.03	17.27	Fauchald and Jumars 1979; Macdonald et al. 2010
Arthropoda							
Amphipoda							
100-500um Bulk zooplankton	FBN	PH		1.37	-22.07	21.21	Banse 1995; Hallanger et al. 2011; Boyce et al. 2015
>1000um Bulk zooplankton	FBN	PH		1.76	-23.15	19.21	Banse 1995; Hallanger et al. 2011; Boyce et al. 2015
100-500um Bulk zooplankton	FBM	PH		2.35	-22.59	19.31	Banse 1995; Hallanger et al. 2011; Boyce et al. 2015
>1000um Bulk zooplankton	FBM	PH		1.43	-23.34	18.56	Banse 1995; Hallanger et al. 2011; Boyce et al. 2015
Anonyx sp.	FBN	BC	2	7.82	-19.10	20.10	Macdonald et al. 2010; McTigue and Dunton 2017
Anonyx sp.	FBM	BC	20	6.15	-20.95	18.34	Macdonald et al. 2010; McTigue and Dunton 2017
Anonyx sp.	FBO	BC	3	5.82	-21.18	18.58	Macdonald et al. 2010; McTigue and Dunton 2017
Calliopiidae gn.	FBN	BC	2	2.54	-21.04	20.14	Macdonald et al. 2010
Calliopiidae gn.	FBM	BC	1	2.31	-21.43	18.99	Macdonald et al. 2010
Gammaridae gn.	FBN	BPC	2	1.94	-21.10	20.04	Macdonald et al. 2010
Lepidepecreum gn.	FBN	BC	2	1.61	-19.08	20.04	Macdonald et al. 2010
Lepidepecreum gn.	FBM	BC	3	3.13	-16.67	16.78	Macdonald et al. 2010
Oedicerotidae	FBM	BC	1	5.00	-19.73	16.88	Macdonald et al. 2010
Paramphithoe hystrix	FBM	BC	1	0.79	-19.47	16.53	Coleman 1990; Watling 1993; Schnabel and Hebert 2003
Rhachotropis aculeata	FBM	BC	8	4.96	-19.65	16.35	Macdonald et al. 2010
Themisto libellula	FBM	PC	4	2.17	-20.91	17.98	Auel and Werner 2003
Themisto sp. 1	FBM	PC	1	1.88	-21.38	19.24	Kane 1963; Watts and Tarling 2012; Løkken 2013
Themisto sp. 2	FBM	PC	1	1.49	-22.24		Kane 1963; Watts and Tarling 2012; Løkken 2013
Stegocephalus sp.	FBN	BC	1	4.62	-18.94	19.11	Macdonald et al. 2010
Stegocephalus sp.	FBM	BC	13	4.89	-18.58	17.60	Macdonald et al. 2010
Stegocephalus sp.	FBO	BC	3	6.73	-19.22	18.11	Macdonald et al. 2010
Uristidae gn.	FBN	BC	2	3.13	-19.05	19.11	Diffenthal and Horton 2007; Wilding et al. 2017
Uristidae gn.	FBM	BC	11	2.88	-13.60	19.42	Diffenthal and Horton 2007; Wilding et al. 2017
Cirripedia	FBM	BSF	7	0.60	-21.64	18.93	Crisp and Southward 1961; Ambrose et al. 2001; Macdonald 2010

Copepoda							
Calanus	FBM	PH	3	0.89	-22.29	17.54	Schell et al. 1998; Løkken 2013
Cumacea							
Diastylis sp.	FBM	BSDF/SF	2	0.46	-21.62	16.09	Macdonald et al. 2010
Decapoda							
Argis dentata	FBN	BPC	3	5.75	-17.33	15.02	Stasko et al. 2018
Argis dentata	FBM	BPC	20	6.23	-17.56	13.46	Stasko et al. 2018
Argis sp.	FBO	BPC	8	7.48	-17.09	14.21	Zinkann et al. 2021
Eualus sp.	FBN	BPC	4	5.01	-18.03	17.72	Macdonald et al. 2010
Eualus gaimardii belcheri	FBM	BPC	3	5.15	-17.97	17.17	Birkley and Glliksen 2003
Eualus gamairdii belcheri	FBO	BPC	1	7.34	-17.74	16.21	Birkley and Glliksen 2003
Eualus gaimardii gaimardii	FBM	BPC	5	5.20	-16.94	16.87	Birkley and Glliksen 2003
Lebbeus polaris	FBN	BPC	4	4.61	-18.31	17.78	Birkley and Glliksen 2003
Lebbeus polaris	FBM	BPC	30	4.71	-18.05	17.03	Birkley and Glliksen 2003
Lebbeus polaris	FBO	BPC	5	5.57	-17.92	16.77	Birkley and Glliksen 2003
Lebbeus groenlandicus	FBN	BPC	3	12.28	4.38	-18.56	Macdonald et al. 2010; Stasko et al. 2018
Lebbeus groenlandicus	FBM	BPC	13	5.72	-16.68	16.11	Macdonald et al. 2010; Stasko et al. 2018
Lebbeus groenlandicus	FBO	BPC	1	5.78	-18.02	17.34	Macdonald et al. 2010; Stasko et al. 2018
Sabinea sp.	FBN	BC	4	3.28	-18.30	19.86	Macdonald et al. 2010
Sabinea sp.	FBM	BC	1	6.52	-17.16	18.16	Macdonald et al. 2010
Sabinea septemcarinata	FBM	BC	8	6.41	-17.18	15.29	Stasko et al. 2018
Sclerocrangon sp.	FBN	BC	1	6.64	-17.23	16.62	Bjørdalsbakke 2011
Sclerocrangon boreas	FBM	BC	10	6.32	-17.54	16.13	Birkley and Glliksen 2003
Spirontocaris sp.	FBM	BC	21	5.42	-17.76	16.28	Birkley and Glliksen 2003; Macdonald et al. 2010
Spirontocaris sp.	FBO	BC	4	6.42	-17.07	16.17	Birkley and Glliksen 2003; Macdonald et al. 2010
Isopoda							
Arcturus baffini	FBN	BSF	2	1.42	-17.86	20.05	Graeve et al. 1997

Arcturus baffini	FBM	BSF	22	1.53	-21.44	18.64	Graeve et al. 1997
Saduria sabini	FBM	BC	5	4.97	-17.95	12.70	Stasko et al. 2018
Mysida							
Mysis sp.	FBN	PH	1	1.91	-19.24	19.03	Stasko et al. 2018; Hilgendag et al. 2022
Mysis sp.	FBM	PH	11	3.56	-19.44	15.38	Stasko et al. 2018; Hilgendag et al. 2022
Pantopoda							
Boreonymphon sp.	FBM	BC	1	2.26	-20.36	18.30	Macdonald et al. 2010
Boreonymphon sp.	FBO	BC	3	3.85	-19.26	18.92	Macdonald et al. 2010
Nymphon sp	FBM	BC	12	3.48	-19.34	17.14	Macdonald et al. 2010
Nymphon sp.	FBO	BC	3	3.86	-19.11	17.73	Macdonald et al. 2010
Pisces							
Gadiformes							
Boreogadus saida	FBN	PC	9	4.31	-20.36	18.03	Whitehouse et al. 2017; Hilgendag et al. 2022
Boreogadus saida	FBM	PC	12	4.12	-20.56	18.07	Whitehouse et al. 2017; Hilgendag et al. 2022
Perciformes							
Careproctus kidoi	FBO	BC	3	5.73	-20.04	18.34	Orr et al. 2019
Careproctus reinhardti	FBN	BPC	2	5.68	-17.87	18.32	Coad and Reist 2004
Careproctus reinhardti	FBM	BPC	6	6.25	-18.27	18.46	Coad and Reist 2004
Cyclopterus lumpus	FBM	BPC	13	6.14	-19.31	17.77	Coad and Reist 2004
Eumicrotremus spinosus	FBN	BC	3	5.56	-18.29		Coad and Reist 2004
Eumicrotremus spinosus	FBM	BC	8	5.88	-19.12	18.90	Coad and Reist 2004
Eumicrotremus spinosus	FBO	BC	4	6.04	-20.20	18.53	Coad and Reist 2005
Gymnelus viridis	FBN	BC	4	8.15	-18.13	17.55	Coad and Reist 2006
Gymnelus viridis	FBM	BC	7	7.68	-18.55	17.66	Coad and Reist 2007
Gymnocanthus tricuspis	FBN	BC	2	7.10	-18.69	19.56	Coad and Reist 2008
Gymnocanthus tricuspis	FBM	BC	4	7.13	-18.16	17.38	Coad and Reist 2004
Gymnocanthus tricuspis	FBO	BC	1	7.33	-17.92	16.42	Coad and Reist 2009

Icelus bicornis	FBM	BPC	15	6.61	-18.47	17.81	Coad and Reist 2010
Icelus spatula	FBN	BC	4	5.10	-18.86	17.64	Coad and Reist 2011
Icelus spatula	FBM	BC	17	6.83	-18.74	18.02	Coad and Reist 2011
Leptagonus decagonus	FBO	BC	2	6.43	-18.43	18.31	Coad and Reist 2011
Lycodes eudipleurostictus	FBM	BC	2	6.19	-18.65	16.33	Coad and Reist 2011
Lycodes polaris	FBM	BC	1	7.74	-17.80		Coad and Reist 2012
Myoxocephalus octodecemspinosus	FBN	BC	1	7.88	-16.45	18.33	Coad and Reist 2011
Myoxocephalus scorpioides	FBM	BC	3	5.90	-18.62	18.71	Coad and Reist 2011
Myoxocephalus scorpius	FBM	BC	2	6.34	-18.44	18.81	Coad and Reist 2011
Myoxocephalus quadricornis	FBN	BC	2	4.81	-19.79		Coad and Reist 2011
Myoxocephalus quadricornis	FBM	BC	3	5.25	-19.49	18.46	Coad and Reist 2011
Triglops nybelini	FBO	BC	1	5.66	-21.41	18.59	Coad and Reist 2012
Triglops pingelii	FBM	BC	5	5.93	-19.30	18.52	Coad and Reist 2013
Triglops pingelii	FBO	BC	2	7.41	-18.85	17.92	Coad and Reist 2014
Pleuronectiformes							
Reinhardtius hippoglossoides	FBO	BPC	1	5.64	-20.74	18.07	Coad and Reist 2014
Echinodermata							
Asteroidea							
Asteriidae gn.	FBN	BC	1	3.22	-16.17		Blake et al 1996 and Latyshev et al. 2001
Astropectinidae gn.	FBN	BC	1	4.49	-17.13		Fernándex et al. 2014
Astropectinidae gn.	FBO	BC	1	8.73	-16.91	20.96	Fernándex et al. 2014
Crossaster pupposus	FBM	BC	2	9.47	-15.23	18.85	Macdonald et al. 2010
Crossaster sp.	FBM	BC	2	10.37	-15.71	19.31	Macdonald et al. 2010
Ctenodiscus crispatus	FBO	BSDF	1	10.06	-17.03	20.15	Shick et al. 1981; Denisenko et al. 2003; Macdonald et al. 2010
Leptasterias sp.	FBN	BC	4	4.81	-15.25	17.02	Gravem and Morgan 2017; Barreto & Bauer 2019; North et al. 2019
Leptasterias sp.	FBM	BC	3	5.54	-11.90	15.89	Gravem and Morgan 2017; Barreto & Bauer 2019; North et al. 2019

Pteraster sp.	FBM	BC	2	2.85	-17.29	18.82	Macdonald et al. 2010
Solaster syrtensis	FBM	BC	2	7.38	-11.92	20.56	Lange and Griffiths 2014
Solaster sp.	FBM	BC	1	8.78	-13.20	18.67	Lange and Griffiths 2014
Stephanasterias albula	FBN	BC	2	6.04	-11.49		Mladenov et al. 1986
Stephanasterias albula	FBM	BC	1	7.53	-12.15	18.25	Mladenov et al. 1986
Crinoidea							
Antedonidae gn.	FBM	BSF	1	3.63	-17.95		Messing 1997; Hays 2016; Madin et al. 2022
Antedonidae gn.	FBO	BSF	2	4.84	-18.64	21.14	Messing 1997; Hays 2016; Madin et al. 2022
Echinoidea							
Strongylocentrotus sp.	FBM	BSF	4	1.19	-19.89	19.11	Macdonald et al. 2010
Strongylocentrotus sp.	FBO	BSF	1	0.91	-21.47	18.73	Macdonald et al. 2010
Holothuroidea							
Psolus	FBM	BSF	1	1.92	-18.58	18.56	Fankboner 1978; Kharlamenko et al. 1995
Molpadia	FBM	BSDF/SF	1	0.51	-15.55	19.98	Sokolova 1959
Ophiuroidea							
Amphiuria sp.	FBN	BSDF/SF	4	4.42	-18.96		Macdonald et al. 2010
Amphiuria sp.	FBM	BSDF/SF	25	4.42	-12.96		Macdonald et al. 2010
AmphiurIa sp.	FBO	BSDF/SF	6	3.89	-16.30	20.90	Macdonald et al. 2010
Ophiacantha bidentata	FBN	BSDF/SF	2	7.00	-16.50		Stasko et al. 2018
Ophiacantha bidentata	FBM	BSDF/SF	22	6.65	-11.67	15.90	Stasko et al. 2018
Ophicantha bidentata	FBO	BSDF/SF	5	5.87	-14.79	20.60	Stasko et al. 2018
Ophiocten sericeum	FBM	BSDF/SF	3	4.03	-9.56		Wood et al. 2011; Conlan et al. 2013; Ravelo et al. 2017
Ophiocten sericeum	FBO	BSDF/SF	3	3.61	-14.38	20.78	Wood et al. 2011; Conlan et al. 2013; Ravelo et al. 2017
Ophiuridae gn.	FBM	BSDF/SF	1	5.20	-11.37	23.45	Macdonald et al. 2010
Stegophiura nodosa	FBN	BSDF	4	3.15	-11.25		Wlodarska et al. 1997 and Denisenki et al 2003
Stegophiura nodosa	FBM	BSDF	34	3.87	-8.43		Wlodarska et al. 1997 and Denisenki et al 2003
Stegophiura nodosa	FBO	BSDF	2	3.68	-10.27		Wlodarska et al. 1997 and Denisenki et al 2003

Mollusca							
Bivalvia							
Astarte sp.	FBN	BSF	1	1.85	-19.35	18.77	Macdonald et al. 2010
Astarte sp.	FBM	BSF	6	0.92	-19.82	19.36	Macdonald et al. 2010
Astarte sp.	FBO	BSF	2	1.70	-19.08	19.27	Macdonald et al. 2010
Chlamys sp.	FBM	BSF	2	-0.27	-18.79	19.08	Macdonald et al. 2010
Entodesma sp.	FBM	BSF	1	0.71	-18.94	17.66	Macdonald et al. 2010
Ennucula tenuis	FBM	BSDF/SF	4	0.35	-20.00	12.02	Macdonald et al. 2010
Hiatella Arctica	FBM	BSF	16	0.74	-18.87	18.64	Denisenko et al. 2003; Macdonald et al. 2010
Hiatella Arctica	FBO	BSF	6	1.07	-18.30	18.96	Denisenko et al. 2003; Macdonald et al. 2010
Lyonsia sp.	FBM	BSF	2	0.61	-19.33	17.42	Macdonald et al. 2010
Macoma sp.	FBM	BSDF/SF	4	1.03	-19.12	16.25	Macdonald et al. 2010
Musculus discors	FBN	BSF	2	0.00	-19.38	18.61	Macdonald et al. 2010
Musculus sp.	FBN	BSF	1	0.85	-19.13	18.78	Macdonald et al. 2010
Musculus discors	FBM	BSF	6	0.00	-19.15	19.07	Macdonald et al. 2010
Musculus discors	FBO	BSF	3	0.00	-18.52	18.80	Macdonald et al. 2010
Musculus niger	FBO	BSF	1	0.22	-18.32	19.40	Macdonald et al. 2010
Mya sp.	FBM	BSF	7	1.30	-18.99	17.30	Macdonald et al. 2010
Mya arenaria	FBO	BSF	2	1.30	-18.11	17.96	Macdonald et al. 2010
Nuculana Pernula	FBM	BSDF	4	1.29	-19.73	13.14	Macdonald et al. 2010; McTigue and Dunton 2017
Nuculana sp.	FBM	BSDF	5	-0.04	-19.14	16.24	Macdonald et al. 2010
Serripes groenlandicus	FBM	BSF	1	0.00	-19.27	17.76	Denisenko et al. 2003; Macdonald et al. 2010; McTigue and Dunton 2017
Similipecten groenlandicus	FBM	BSF	4	-0.07	-19.25	18.09	Løkken 2013; Renaud et al. 2015; McTigue and Dunton 2017
Yoldiella sp.	FBM	BSDF	3	0.48	-19.30	14.05	Macdonald et al. 2010
Gastropoda							
Buccinum sp.	FBN	BC	7	5.88	-17.57	18.49	Macdonald et al. 2010; McTigue and Dunton 2017
Buccinum cf. finmarkianum	FBM	BC	4	6.65	-18.30	17.71	Macdonald et al. 2010

Buccinum scalariforme	FBM	BC	2	5.66	-17.52	18.31	Macdonald et al. 2010
Buccinum sp.	FBM	BC	5	4.64	-17.88	17.33	Macdonald et al. 2010; McTigue and Dunton 2017
Buccinum sp.	FBO	BC	1	4.76	-17.85	19.31	Macdonald et al. 2010; McTigue and Dunton 2017
Buccinidae gn.	FBN	BC	1	5.32	-17.67	18.94	Macdonald et al. 2010
Colus sp.	FBM	BC	7	4.97	-17.99	18.88	Macdonald et al. 2010
Lepeta sp.	FBN	BSF	1	3.65	-14.55		Burgos-Rubio et al. 2015
Limneria undata	FBM	BC	2	3.05	-18.94	19.62	Sargent et al. 2019
Margarites Groenlandicus umbilicus	FBN	BSDF/SF	7	3.29	-17.76	20.31	Macdonald et al. 2010
Margarites sp.	FBN	BSF	2	3.57	-16.50	19.41	Macdonald et al. 2010
Margarites sp.	FBM	BSF	8	2.76	-18.50	17.35	Macdonald et al. 2010
Mohnia sp.	FBM	BC	5	7.14	-17.33	17.17	Bergmann et al. 2011
Neptunea sp.	FBN	BC	3	6.91	-17.09	18.59	McTigue and Dunton 2017; North et al. 2019; Yamakami and Wada 2022
Neptunea sp.	FBO	BC	3	4.52	-17.42	18.43	McTigue and Dunton 2017; North et al. 2019; Yamakami and Wada 2022
Polinices sp.	FBM	BC	1	3.85	-18.54	17.30	Wiltse 1980
Pteropoda	FBN	PC	1	-0.75	-21.95	19.74	Bōer et al. 2005; Pasternak et al. 2017
Pteropoda	FBM	PC	1	-0.05	-22.34	21.35	Bōer et al. 2005; Pasternak et al. 2017
Solariella obscura	FBN	BSF	3	2.17	-17.49	19.99	Macdonald et al. 2010
Velutinidae gn.	FBN	BC	1	4.38	-19.76	19.85	Sargent et al. 2019
Williama sp.	FBM	BSF	1	5.36	-19.32	19.75	Hodgson 1999; Simone and Seabra 2017
Porifera	FBM	BSF	4	2.90	-18.79	18.66	Bell 2008
Porifera	FBO	BSF	1	2.18	-18.17	13.94	Bell 2008
Scleractinia	FBO	BSF	1	3.26	-11.66	20.78	Goldberg 2002

Appendix B Two-dimensional stable isotope analysis

Table B-1. Layman (2007) metrics and SIBER values (Jackson et al. 2011) calculated using $\delta^{15}N_{adj}$ and $\delta^{13}C$ from taxa collected from three depth categories: Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore.

	Depth Category		
Metric	**Nearshore**	**Midshore**	**Offshore**
$\delta^{15}N_{adj}$ (‰) Range	8.90	10.64	10.06
$\delta^{15}N_{adj}$ Mean	4.02	3.92	4.84
$\delta^{13}C$ (‰) Range	11.90	14.91	11.21
$\delta^{13}C$ Mean	-18.24	-18.59	-18.44
CD	2.63	3.23	2.79
NND	0.68	0.43	0.78
SDNND	0.59	0.42	0.74
Trophic levels	4.40	5.05	4.96
TA	63.79	93.21	64.54
SEA	14.01	19.75	15.95
SEA_C	14.33	19.96	16.41

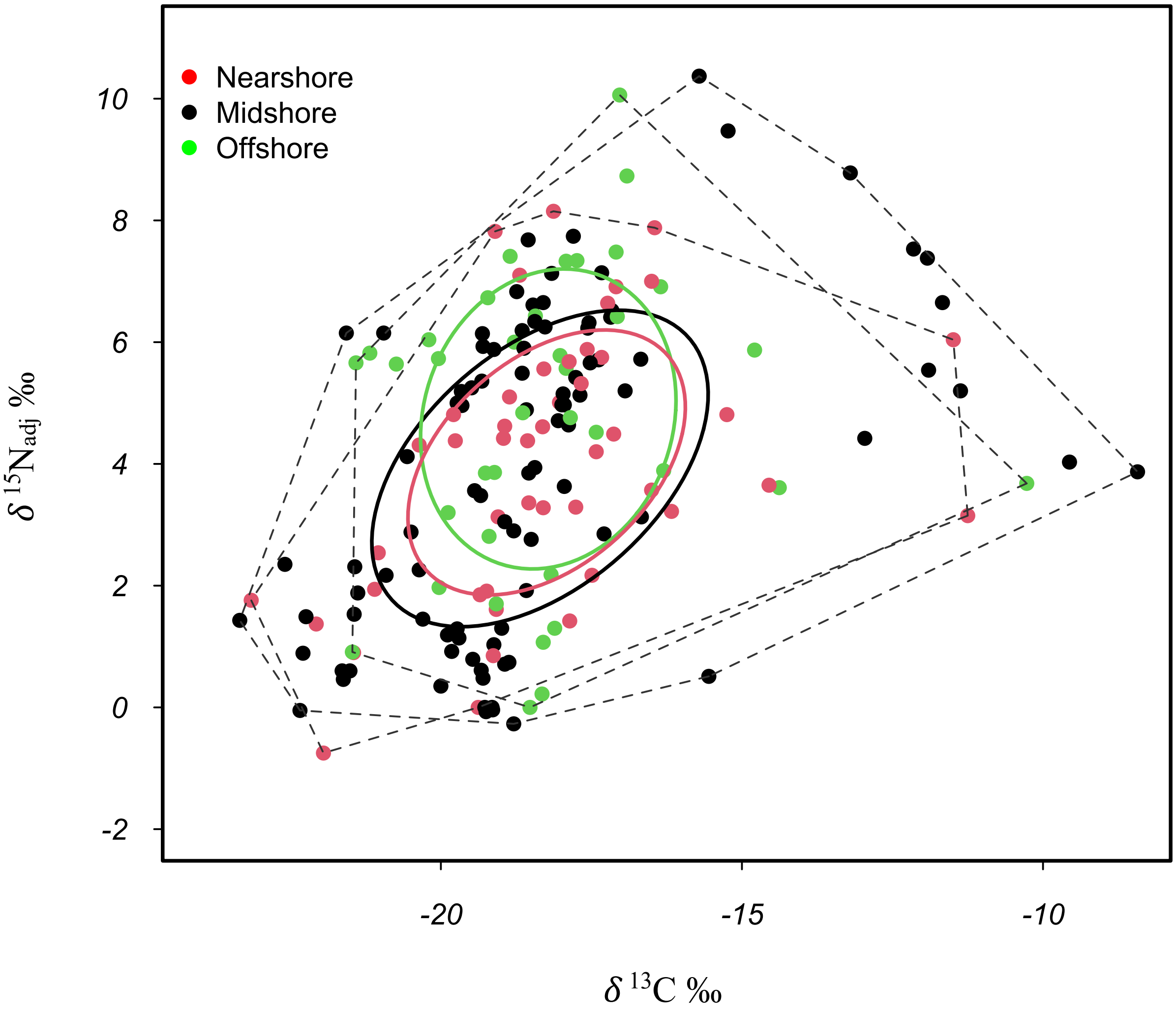

Figure B-1. Standard ellipse area corrected for small sample size, set to 40% inclusivity (SEA$_C$; solid lines) and total area of convex hulls (dotted lines) for food webs in Frobisher Bay nearshore (red), Frobisher Bay midshore (black), and Frobisher Bay offshore (green) using $\delta^{15}N_{adj}$ and $\delta^{13}C$ values.

Table B-2. Layman (2007) metrics and SIBER values (Jackson et al. 2011) calculated using the two-dimensional δ^{34}S by δ^{13}C plot from taxa collected from three depth categories: Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore.

	Depth Category		
Metric	**Nearshore**	**Midshore**	**Offshore**
δ^{34}S (‰) Range	6.18	11.43	7.35
δ^{34}S (‰) Mean	18.75	17.72	18.38
CD	1.76	2.30	1.95
NND	0.55	0.45	0.51
SDNND	0.46	0.49	0.32
TA	28.22	93.58	29.32
SEA	6.16	13.27	8.84
SEA_C	6.34	13.42	9.11

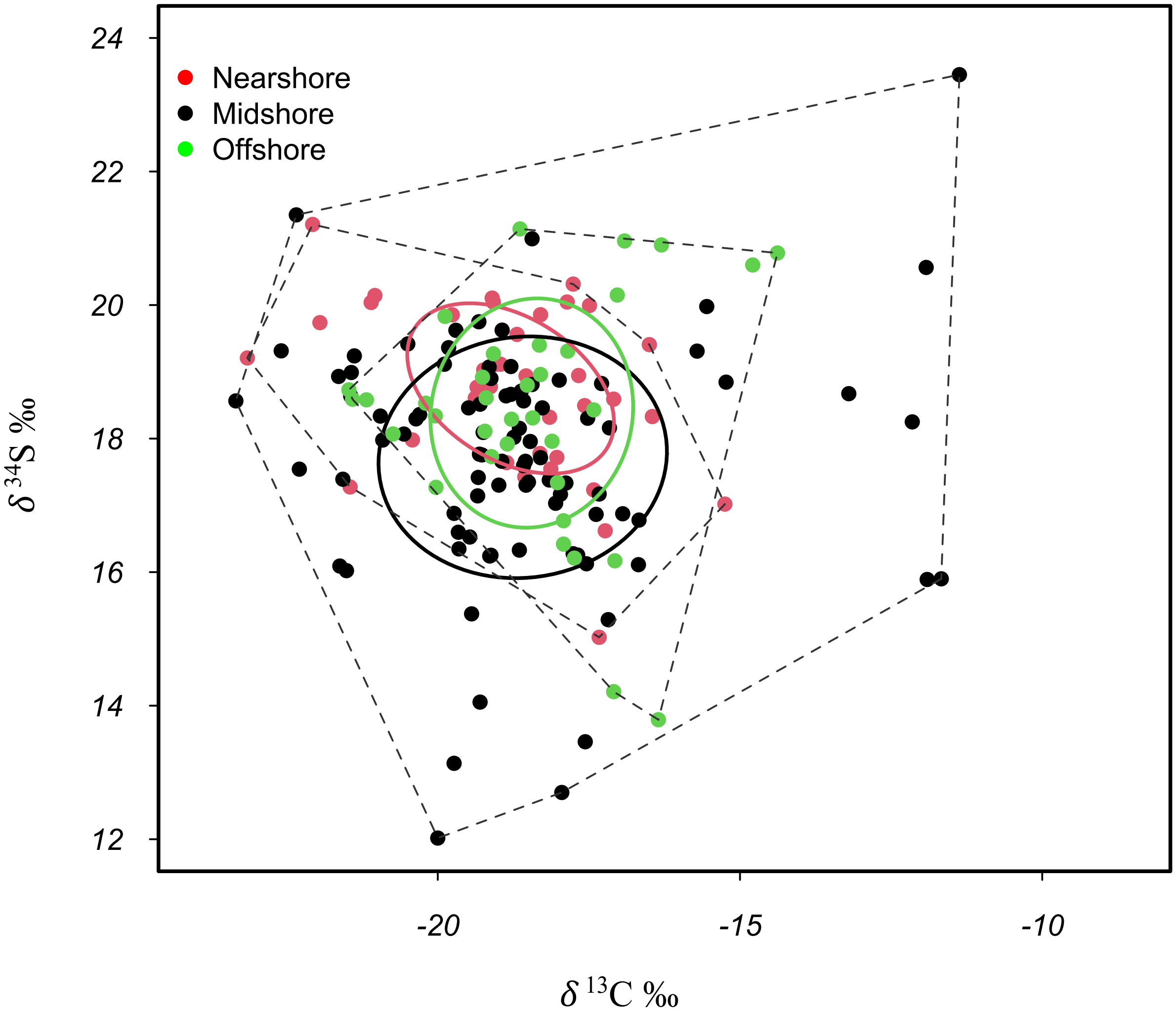

Figure B-2. Standard ellipse area corrected for small sample size, set to 40% inclusivity (SEA$_C$; solid lines) and total area (dotted lines) for food webs in Frobisher Bay nearshore (red), Frobisher Bay midshore (black), and Frobisher Bay offshore (green) using δ^{34}S and δ^{13}C values.

Table B-3. Layman (2007) metrics and SIBER values (Jackson et al. 2011) calculated using the $\delta^{15}N_{adj}$ by $\delta^{13}C$ for benthic carnivores collected from three depth categories: Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore.

	Depth Category		
Metric	**Nearshore**	**Midshore**	**Offshore**
$\delta^{15}N_{adj}$ (‰) Range	6.54	9.58	5.53
$\delta^{15}N_{adj}$ Mean	5.08	5.54	5.85
$\delta^{13}C$ (‰) Range	9.55	9.53	5.06
$\delta^{13}C$ Mean	-17.87	-17.88	-18.82
CD	2.18	2.29	1.82
NND	0.91	0.51	0.62
SDNND	0.85	0.46	0.39
Trophic levels	4.40	5.05	4.57
TA	33.01	52.82	14.37
SEA	10.27	11.24	6.18
SEA_C	10.76	11.51	6.59

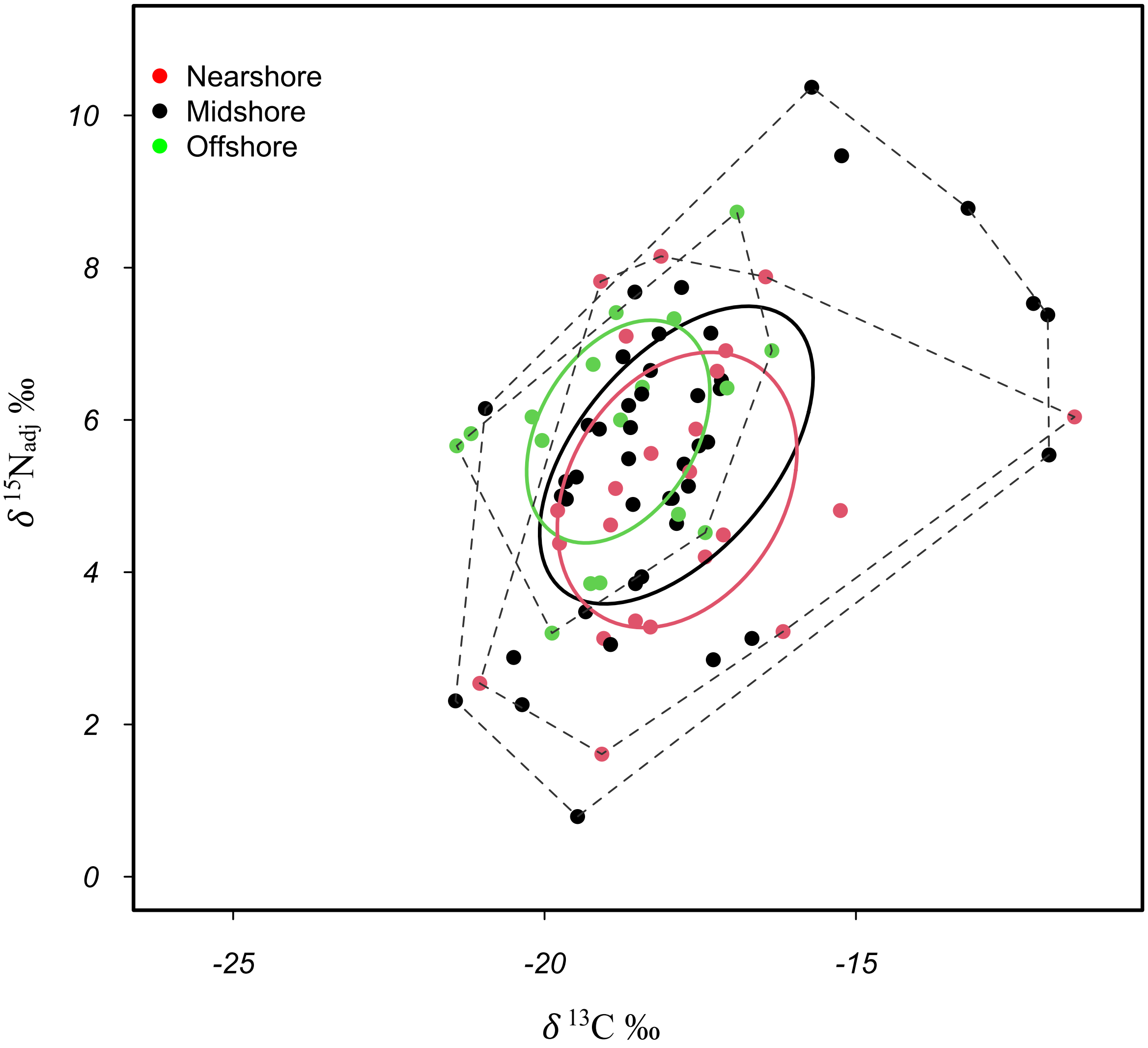

Figure B-3. Benthic carnivore standard ellipse area corrected for small sample size, set to 40% inclusivity (SEA$_C$; solid lines) and total area (dotted lines) for benthic carnivore niche region in Frobisher Bay nearshore (red), Frobisher Bay midshore (black), and Frobisher Bay offshore (green) food webs using $\delta^{15}N_{adj}$ and $\delta^{13}C$ values.

Table B-4. Layman (2007) metrics and SIBER values (Jackson et al. 2011) calculated using the two-dimensional δ^{34}S by δ^{13}C plots for benthic carnivores collected from three depth categories: Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore.

	Depth Category		
Metric	**Nearshore**	**Midshore**	**Offshore**
δ^{34}S (‰) Range	3.52	8.65	7.17
δ^{34}S Mean	18.73	17.75	18.13
CD	1.48	2.11	1.66
NND	0.58	0.60	0.75
SDNND	0.43	0.61	0.64
TA	9.15	53.96	17.77
SEA	3.29	10.20	6.66
SEA_C	3.49	10.25	7.10

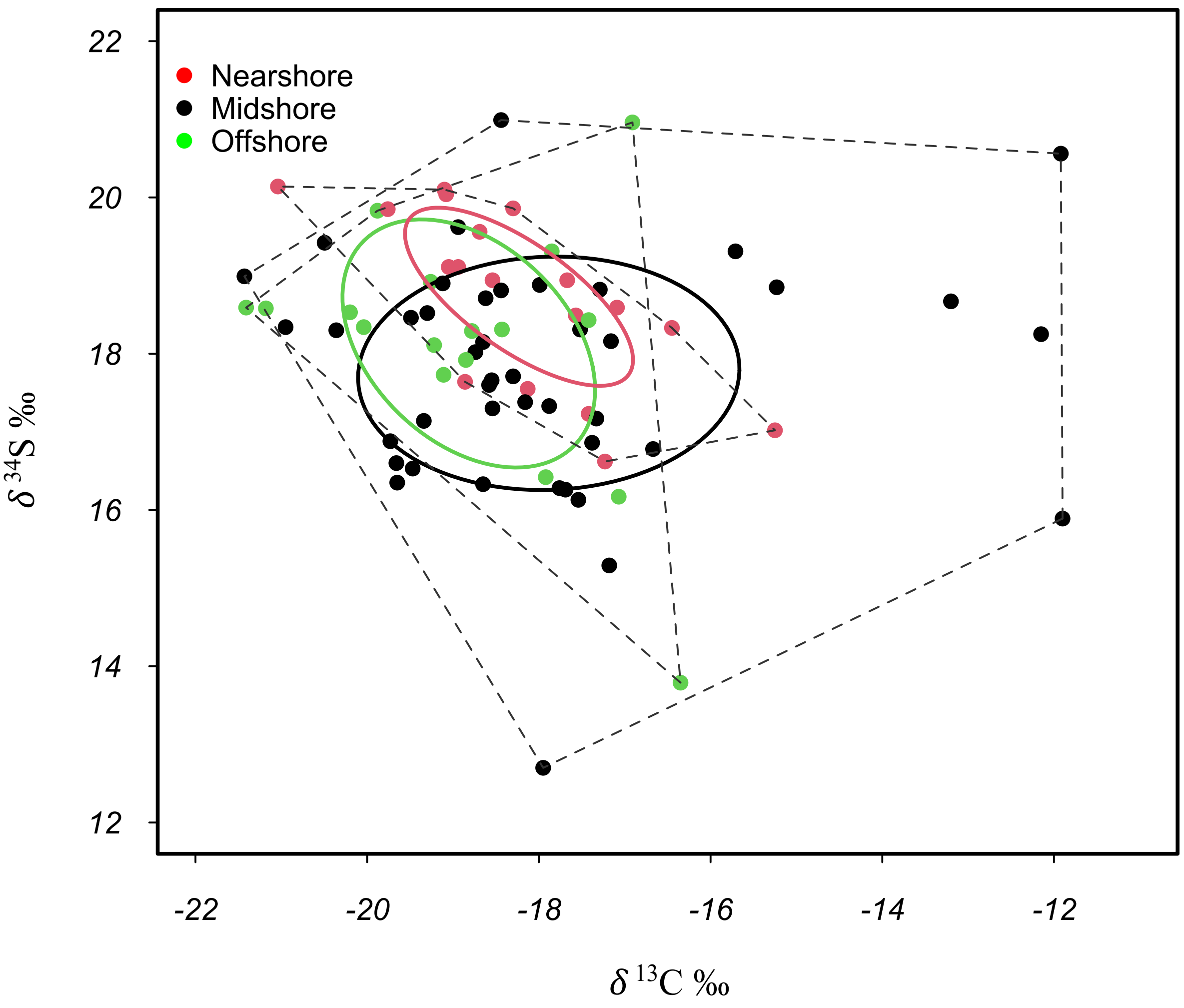

Figure B-4. Benthic carnivore standard ellipse area corrected for small sample size, set to 40% inclusivity (SEA$_C$; solid lines) and total area (dotted lines) for benthic carnivore niche region in Frobisher Bay nearshore (red), Frobisher Bay midshore (black), and Frobisher Bay offshore (green) food webs using δ^{34}S and δ^{13}C values.

Table B-5. Layman (2007) metrics and SIBER (Jackson et al. 2011) values, calculated using the $\delta^{15}N_{adj}$ by $\delta^{13}C$ values for benthic suspension feeders from the Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore depth categories.

	Depth Category		
Metric	**FBN**	**FBM**	**FBO**
$\delta^{15}N_{adj}$ (‰) Range	3.65	5.63	4.84
$\delta^{15}N_{adj}$ Mean	1.93	1.39	1.67
$\delta^{13}C$ (‰) Range	4.83	3.69	3.36
$\delta^{13}C$ Mean	-17.75	-19.40	-18.87
CD	1.78	1.40	1.45
NND	1.16	0.50	0.98
SDNND	0.47	0.52	0.83
Trophic levels	3.07	3.58	3.42
TA	5.98	11.79	8.37
SEA	3.77	4.05	4.87
SEA_C	4.52	4.29	5.57

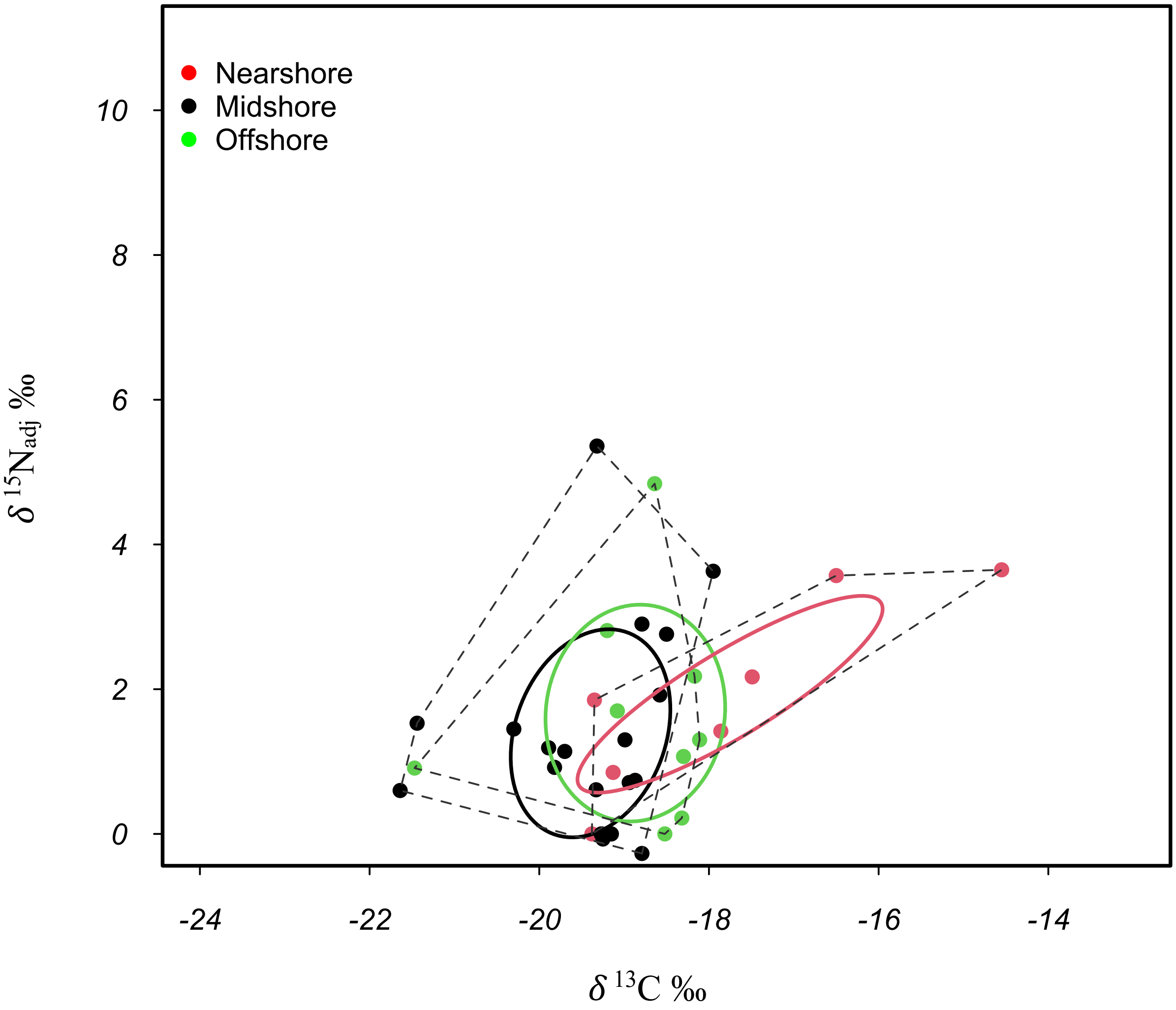

Figure B-5. Benthic suspension feeder standard ellipse area corrected for small sample size, set to 40% inclusivity (SEA$_C$; solid lines) and total area (dotted lines) for benthic suspension feeder niche region in Frobisher Bay nearshore (red), Frobisher Bay midshore (black), and Frobisher Bay offshore (green), using $\delta^{15}N_{adj}$ and $\delta^{13}C$ values.

Table B-6. Layman (2007) metrics and SIBER (Jackson et al. 2011) values, calculated using the δ^{34}S by δ^{13}C values for benthic suspension feeders from the Frobisher Bay nearshore, Frobisher Bay midshore, and Frobisher Bay offshore depth categories.

Benthic Suspension Feeder	**Depth Category**		
Metric	**FBN**	**FBM**	**FBO**
δ^{34}S (‰) Range	1.44	2.45	3.18
δ^{34}S Mean	19.27	18.52	19.11
CD	1.20	1.05	1.09
NND	0.41	0.34	0.91
SDNND	0.38	0.16	0.73
TA	1.64	4.36	5.18
SEA	1.62	2.07	3.16
SEA_C	2.02	2.20	3.68

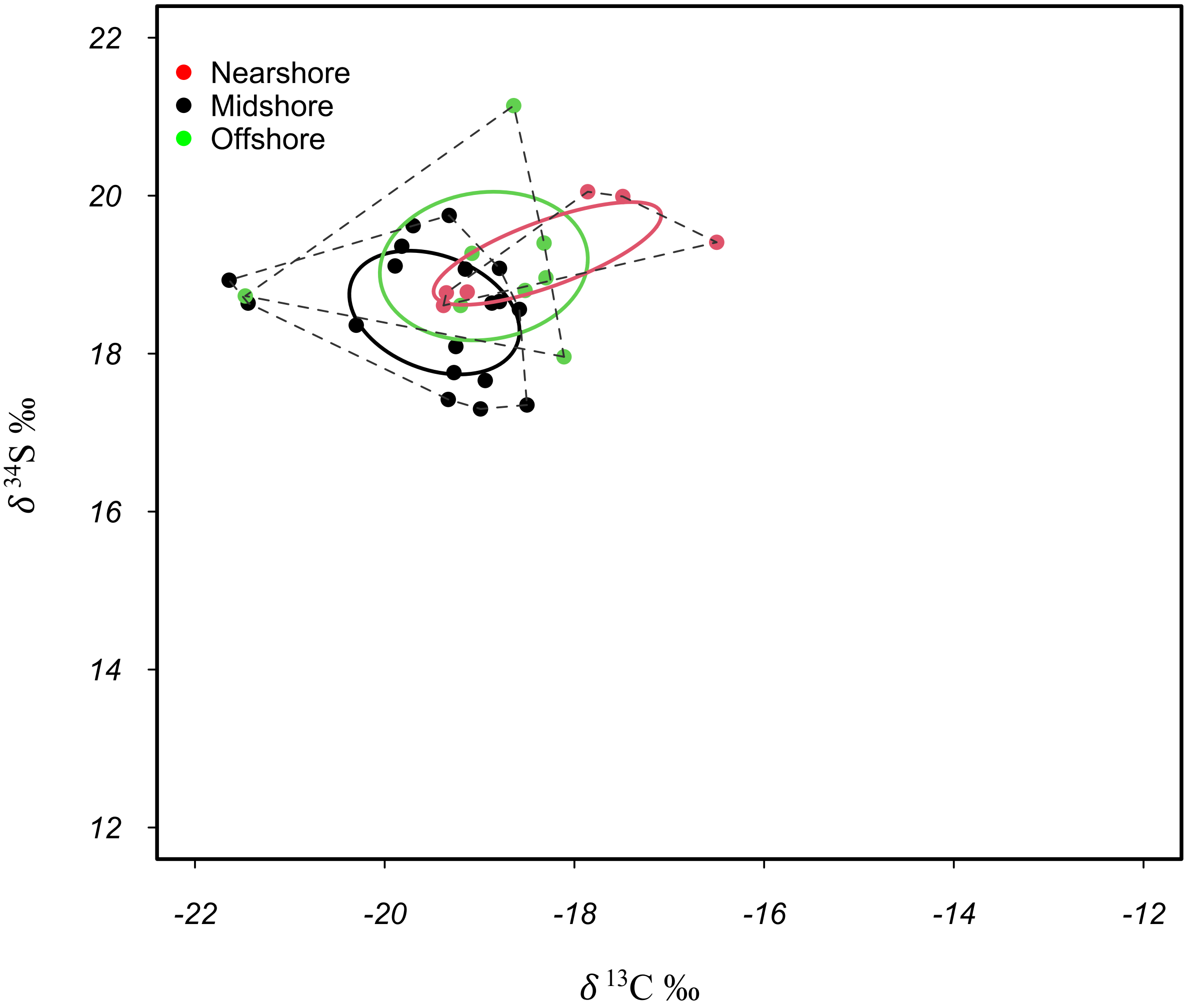

Figure B-6. Benthic suspension feeder standard ellipse area corrected for small sample size, set to 40% inclusivity (SEA_C; solid lines) and total area (dotted lines) for benthic suspension feeder niche region in Frobisher Bay nearshore (red), Frobisher Bay midshore (black), and Frobisher Bay offshore (green), using δ^{34}S and δ^{13}C values.