Food web interactions along a marine and freshwater gradient within a subarctic estuary

by

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Thesis Abstract

Food webs describe the trophic relationships between species within ecosystems. The trophic structure and interactions can vary in space and time, which can lead to changes in the food web. Ecosystems are linked together by the movement of nutrients, prey, and consumers. This movement between ecosystems is known as habitat coupling, where ecological dynamics are driven by the input of nutrients and energy from distant or adjacent habitats. Estuaries are an important link between freshwater and marine systems since they are a transition zone where species can acquire resources from both systems. The objectives of this thesis were to (1) quantify the diet composition between freshwater-and marine-derived nutrients and niche size of mobile consumers (13 fishes and 2 seal species) within the lower Churchill River, (2) quantify the trophic positions of the Churchill marine/freshwater food web for mobile consumers and to understand the ontogenetic effects on trophic position, and to (3) quantify changes in trophic structure with certain members of the fish community between 1993-1995 and 2019-2020. Results indicated habitat coupling for cisco, lake whitefish, and northern pike. These species were also found to have the greatest niche size, indicating a broader use of resources. I also found species that mainly foraged on freshwater resources occupied the secondary consumer position, whereas species that foraged on marine resources occupied the tertiary consumer position. Trophic position increased with age for cisco, fourhorn sculpin, Greenland cod, and northern pike. Six community-wide metrics of the fish assemblage (cisco, fourhorn sculpin, and lake whitefish) revealed more trophic redundancy in the 2019-2020 community. Greater trophic redundancy means that individual species are now playing similar trophic roles within the food web, which may help promote ecosystem stability and reduce vulnerability to secondary extinction events. Overall, my thesis findings have provided an understanding of the trophic structure and interactions within and between a freshwater-marine gradient within the lower Churchill River. This study highlighted how estuaries are a vital link between freshwater and marine systems and understanding trophic dynamics and connections among species in these habitats is critical for their management.

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1.0 Chapter 1: General Introduction

1.1 Background

Food webs consist of links between organisms arranged in different trophic levels, from primary producers to apex predators, with each trophic level relying on the previous level as a source of energy (Elton, 1927; Lindemann, 1942). Trophic dynamics that influence ecosystem structure and function consist of many factors such as competition, habitat use, species life history, and resource availability (Elton, 1927; Layman et al., 2015; Lindemann, 1942; Polis et al., 1997). For example, the level of food web structure and functioning depends on the variety and abundance of different nutrients/resources, which in turn can impact the level of habitat coupling in an ecosystem. Habitat coupling is the transfer of nutrients, organic matter, sediment, and species between adjacent habitats, such as marine and freshwater systems (Schindler & Scheuerell, 2002). For example, anadromous fish, such as Pacific salmon (*Oncorhynchus* sp.), will die after spawning in freshwater ecosystems, thereby transporting nutrients from a marine system to a freshwater system and providing habitat coupling between those two systems (Gende et al., 2002; Polis et al., 1997). Habitat coupling is important for nutrient cycling, predator-prey interactions, and stability or instability of the food web structure (McCann et al, 2005; Huxel & McCann, 1998; Polis et al., 1997; Schindler & Scheuerell, 2002). The trophic structure of a system is related to many interdependent factors, such as habitat and resource availability that can influence both trophic diversity and trophic redundancy. Understanding trophic diversity and species interactions can provide information on ecosystem structure and function in terms of energy flow from primary producers to top predators, with many species functioning differently within the community (Emery, 1978; Hurtubia, 1973; Polis et al., 2000; Yurkowski et al., 2018). Conversely, trophic redundancy occurs when many species are functioning similarly in the community, resulting in these species overlapping by foraging on similar prey items and occupying a more similar trophic position (Polis et al., 2000; Yurkowski et al., 2018). The trophic structure of a community can be affected by anthropogenic effects, such as gas and oil pipelines, shipping, and hydroelectric dams (Rosenberg et al., 1995). For example, management of river systems for hydroelectric power generation can result in reduced variability in the water levels that may change aquatic productivity and habitats. These changes in the freshwater environment can have a strong impact on estuarian systems since estuaries are composed of

several environmental gradients due to the mixing of marine and freshwater resulting in different habitats for different species (Elliott & Hemingway, 2002; McCann et al., 2006).

Estuaries are transition zones, where energy from a freshwater-origin mixes with energy from a marine origin and therefore allows for opportunities to investigate habitat coupling by mobile consumers. Estuaries' importance in the Arctic is not well known since they have been seldom studied, so better understanding a consumer's resource use within an estuarian system can provide more information on species interactions between freshwater and marine systems. (Kuzyk et al., 2008). Energy exchange within an estuary creates a highly productive system since species have the flexibility to acquire resources from both the freshwater and marine systems (França et al., 2011; McCann et al., 2005). Estuarian species have also been observed to have an omnivorous diet (i.e., feed on multiple trophic levels), share common resources between the marine/freshwater systems, and forage opportunistically (France, 1995; Ley et al., 1994; Polis et al., 1997). Therefore, estuarian species may have a greater dietary niche size than strictly freshwater or marine species due to the consumption of resources from both freshwater and marine systems (France, 1995; Ley et al., 1994; Polis et al., 1997). As well, mobile consumers may alter their feeding behaviours to take advantage of different resources available, which will lead to the food web being connected between different energy compartments or pathways (Rooney et al., 2006).

The Churchill River is a major river that flows through Alberta, Saskatchewan, and Manitoba and drains into Hudson Bay through the Churchill River estuary (Newbury et al., 1984). Since 1976, the Churchill River flow has been impounded at southern Indian Lake and diverted to hydroelectric generating stations along the Nelson River by the Churchill River Diversion (Kuzyk et al., 2008; Newbury et al., 1984). To increase the water levels, river accessibility, and fish abundance, a rock-filled barrier was constructed across the river in 1998, known as the Churchill River weir (Kuzyk et al., 2008). This anthropogenic disturbance to the freshwater system could have resulted in temporal changes to the system. Climate change may also result in mobile generalist species moving into systems where they previously did not occur and switching to foraging on new prey (Pecl et al., 2017; Schindler & Smol, 2006). The effects of climate change and anthropogenic activities may result in alterations to the trophic structure over time due to potential changes in basal carbon sources and shifts in the trophic positioning of

consumers. Shifts in species distributions as a result of climate warming and a re-organization of species composition can affect both community structure and functioning (Hop & Gjøsæter, 2013; Yurkowski et al., 2018). Consumers foraging on new resources could change the nutrient movement throughout the food web and result in altered and novel inter-specific interactions that can affect ecosystem stability (Bartley et al., 2019; Huxel & McCann, 1998; McCann et al., 2005).

1.2   Objective and Hypotheses

The objectives of this thesis were to quantify (1) the composition of freshwater-and marine-derived resource use and niche dynamics of mobile consumers within the lower Churchill River area (lower Churchill River, estuary, and Hudson Bay), (2) the trophic positions of the Churchill marine/freshwater food web for mobile consumers and to understand ontogenetic effects on trophic position, and (3) changes in trophic structure with certain members of the fish community between 1993-1995 with 2019-2020. This thesis consists of two data chapters: chapter two will focus on habitat coupling dynamics of mobile consumers between freshwater and marine sources and chapter three will focus on understanding the trophic structure and temporal shift in trophic diversity of mobile consumers within the lower Churchill River area. I used stable isotope analysis and stomach content analysis to address these objectives. My hypotheses for both data chapters are as follows:

Chapter 2: Habitat coupling dynamics of mobile consumers along a freshwater and marine resource gradient

Habitat coupling occurs when distant and/or adjacent habitats are connected by the movement of organisms and organic matter (Schindler & Scheuerell, 2002). Habitat coupling may affect species' diet composition, niche size, and niche overlap. Individuals in the estuary and ones that move between each system could couple resources from both the marine and freshwater systems. Here, I investigated variation in the contribution of freshwater-and marine-

derived resources at an individual and population level as well as isotopic niche size and overlap of each consumer group within the community using stable isotope mixing models. I hypothesized that:

> **H$_1$:** Species with a known life history of migration between freshwater and marine systems will couple those habitats together by using a combination of both freshwater and marine resources, whereas species with a known life history to principally reside in either freshwater or marine environments will primarily consume resources from their resident system.
>
> **H$_2$:** Species that display habitat coupling between both the freshwater and marine resources will have a larger niche than species that forage on only one resource type, either freshwater or marine. In addition, habitat coupling species will have low overlap with species who principally foraged on either one resource type
>
> **H$_3$:** Species that display habitat coupling between freshwater-and marine-derived resources will have more variability between individuals in their resource use than species that principally consume only one resource type.

> **Chapter 3:** Trophic structure and a temporal shift in trophic diversity of mobile consumers in a subarctic estuary

Species occupy different trophic positions due to variability in prey consumption. Typically, species that display an ontogenetic dietary shift may change positions within the food web throughout their life span (Cott et al., 2011). The trophic structure within this system was compared between a 25-year period, in 1993-1995 and 2019-2020, to understand if there are any potential changes in trophic diversity. High trophic diversity can promote ecosystem stability since there are many species occupying distinct positions and foraging on a diversity of prey

items. Increased trophic diversity can result in a greater strength of species interactions and redundancy in traits and trophic roles (Włodarska-Kowalczuk et al., 2019). In contrast, greater trophic redundancy has more species functioning the same within a community, which will be more resistant to secondary extinction events. I investigated the trophic structure of the Churchill marine/freshwater food web, the effect of age on the trophic position for the different fish species, and the trophic diversity between the early 1990s and 2019-2020. I hypothesized that:

> **H1:** Trophic position would increase with age and body size across all species, allowing larger individuals to forage on larger prey that sit at higher trophic positions.

> **H2:** Species that occupy a higher trophic position will have more variability in their trophic position between individuals due to a species' ability to consume a broader diversity of smaller, less mobile prey at lower trophic levels.

> **H3:** Trophic diversity within the fish community increased after the construction of the weir as a result of increased water levels and in turn habitat access for mobile fishes.

1.3 Methods

This study was conducted within the lower Churchill River area near the town of Churchill (58.7684° N, 94.1650° W), Manitoba, Canada. The Churchill River connects to Hudson Bay through the Churchill River estuary. This project focused on the summer period (June- September) because harbour seals (*Phoca vitulina*) and possibly some fish species only have access to the river after ice breakup. As the snow starts to melt with the increasing temperature in spring, a greater inflow of freshwater will enter the estuary, which will result in a pulse of freshwater energy into the estuary in spring and summer (Omstedt et al., 1994). Data were collected during July 2019 and August 2020. Fish from a variety of locations within the study area were lethally collected for internal samples (liver, muscle, stomach, and aging structures). Harbour and ringed seal (*Pusa hispida*) samples were provided by local hunters. Additional fish samples were provided by Manitoba Hydro, the Churchill Northern Studies Centre staff, North/South Consultant Inc., and local fishers. Submersed vegetation and benthic

and pelagic invertebrates were also lethally collected throughout the marine and freshwater environments to sample the possible primary producers and consumers within the food web system. Samples were collected throughout the lower Churchill River, the estuary, and Hudson Bay. Benthic and pelagic invertebrate samples, such as mussels, snails, amphipod, etc. were collected with zooplankton nets or by hand. Fish samples were collected with 2-3" monofilament gillnets or by angling.

Lab work consisted of preparing samples for stable isotope analysis and stomach content analysis. Stable isotopes have become a prominent tool in ecological studies to assess food web dynamics (Layman et al., 2012; Neubauer & Jensen, 2015). Stable isotope analysis provides a time-and space- integrated understanding of trophic relationships between organisms. Ratios of carbon isotopes (δ^{13}C) can be used to determine the original source of dietary carbon, ratios of nitrogen isotopes (δ^{15}N) are used to understand the trophic position of consumers, and ratios of sulfur isotopes (δ^{34}S) are important for estuarine systems to differentiate marine and freshwater/terrestrial resources. Different tissues were collected to provide temporal comparisons of diet, such as liver, muscle, and hair. Liver provides dietary information on a weekly scale (~15-30 days), whereas muscle provide information on a monthly scale (~1-4 months). Hair samples were used for the harbour seals since there was no liver sample. Hair is biologically inactive and will maintain an isotope signal based on the habitat the species was found in during the hair growth period (Hobson, 1999). Since harbour seal moult in August (Bajzak et al., 2012; Vincent et al., 2017), this regrown hair would represent the diet slightly before and during the moulting period (~1-2 months).

1.4   Expected Significance

The aim of this thesis was to quantify the habitat coupling, niche sizes and overlap, trophic position, and trophic structure of species in the lower Churchill River during the summer period with a particular emphasis on the relationship among fishes and seals. The Churchill River system has been seldom studied; therefore, this project will provide a greater understanding of the community structure, spatial coupling, and trophic structure of mobile consumers within the Churchill River. It also provides an opportunity for future studies

investigating temporal changes in these variables within this system, or to compare spatial variation among similar estuarine systems across the Arctic.

1.5   References

Bartley, T.J., McCann, K.S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M.M., MacDougall, A.S., Tunney, T.D., & McMeans, B.C. (2019). Food web rewiring in a changing world. *Nature Ecology & Evolution*, *3*(3), 345-354. doi: 10.1038/s41559-018-0772-3.

Cott, P.A., Johnston, T.A., & Gunn, J.M. (2011). Food web position of burbot relative to lake trout, northern pike, and lake whitefish in four sub-Arctic boreal lakes. *Journal of Applied Ichthyology*, *27*, 49-56. doi: 10.1111/j.1439-0426.2011.01843.x.

Elliott, M. & Hemingway, K. (2002). Fishes in estuaries. Oxford, UK: Blackwell Science.

Elton, C. (1927). Animal ecology. New York, NY: The MacMillan Company.

Emery, A. (1978). The basis of fish community structure: marine and freshwater comparisons. *Environmental Biology of Fishes*, *3*(1), 33-47. doi: 10.1007/BF00006307.

França, S., Vasconcelos, R.P., Tanner, S., Máguas, C., Coasta, M.J., & Cabral, H.N. (2011). Assessing food web dynamics and relative importance of organic matter sources for fish species in two Portuguese estuaries: stable isotope approach. *Marine Environmental Research*, *72*(4), 204-215. doi:10.1016/j.marenvres.2011.09.0001.

France, R., (1995). Stable nitrogen isotopes in fish: literature synthesis on the influence of ecotonal coupling. *Estuarine, Coastal and Shelf Science*, *41*(6), 737-742. doi: 10.1006/ecss.1995.0087.

Gende, S.M., Edwards, R.T., Willson, M.F., & Wipfli, M.S. (2002). Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*, *52*(10), 917-928. doi: 10.6141/0006-3568(2002)052[0917:PSIAAT]2.0.CO.

Hobson, K.A. (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, *120*(3), 314-326. doi: 10.1007/s004420050865.

Hop, H. & Gjøsæter, H. (2013). Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Marine Biology Research*, *9*(9), 878-894. doi: 10.1080/17451000.2013.775458.

Hurtubia, J. (1973). Trophic diversity measurement in sympatric predatory species. *Ecology*, *54*(4), 885-890.

Huxel, G.R. & McCann, K. (1998). Food web stability: the influence of trophic flows across habitats. *The American Naturalist*, *152*(3), 460-469.

Kuzyk, Z., Macdonald, R., Granskog, M., Scharien, R., Galley, R., Michel, C., Barber, D., & Stern, G. (2008). Sea ice, hydrological, and biological processes in the Churchill River estuary region, Hudson Bay. *Estuarine, Coastal and Shelf Science*, *77*(3), 369– 384. doi: 10.1016/j.ecss.2007.09.030.

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., & Bearhop, S. (2012). Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews*, *87*(3), 545-562. doi: 10.1111/j.1469-185X.2011.00208.x.

Layman, C.A., Giery, S.T., Buhler, S., Rossi, R., Penland, T., Henson, M.N., Bogdanoff, A.K., Cove, M.V., Irizarry, A.D., Schalk, M., & Archer, S.K. (2015). A primer on the history of food web ecology: fundamental contributions of fourteen researchers. *Food Webs*, *4*, 14-24. doi: 10.1016/j.fooweb.2015.07.001.

Ley, J., Montague, C., & Mcivor, C. (1994). Food habits of mangrove fishes: a comparison along estuarine gradients in northeastern Florida Bay. *Bulletin of Marine Science*, *54*(3), 881-889.

Lindemann, R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*, 399-417.

McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecology Letters*, *8*(5), 513-523. doi: 10.1111/j.1461-0248.2005.00742.x.

McCann, K., Rasmussen, J., Umbanhowar, J., Humphries, M. (2006). 2.4 - The role of space, time, and variability in food web dynamics. Dynamic Food Webs. Elsevier Inc., 56-70. doi: 10.1016/B978-012088458-2/50008-4.

Neubauer, P. & Jensen, O.P. (2015). Bayesian estimation of predator diet composition from fatty acids and stable isotopes. *PeerJ*, *3*, e920. doi: 10.7717/peerj.920.

Newbury, R.W., McCullough, G.K., & Hecky, R.E. (1984). The Southern Indian Lake impoundment and Churchill River diversion. *Canadian Journal of Fisheries and Aquatic Sciences*, *41*(4), 548-557. doi: 10.1139/f84-068.

Omstedt, A., Carmack, E., & MacDonald, R. (1994). Modeling the seasonal cycle of salinity in the Mackenzie shelf/estuary. *Journal of Geophysical Research*, *99*(C5), 10011-10021. doi: 10.1029/94JC00201.

Pecl, G. T., Araujo, M. B., Bell, J., Blanchard, J., Bonebrake, T. C., Chen, I., Clark, T. D., Colwell, R. K., Danielsen, F., Evengard, B., & Robinson, S. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science*, *355*(6332), 1-9.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., & Maron, J. (2000). When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution*, *15*(11), 473-475. doi: 10.1016/S0169-5347(00)01971-6.

Polis, G.A., Anderson, W.B., & Holt, R.D. (1997). Toward an integration of landscape ad food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, *281*(1), 289-316. doi: 10.1146/annurev.ecolsys.28.1.289.

Rooney, N., McCann, K., Gellner, G., & Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, *442*(7100), 265-269. doi: 10.1038/nature04887.

Rosenberg, D.M., Bodaly, R.A., & Usher, P.J. (1995). Environmental and social impacts of large scale hydroelectric development: who is listening? *Global Environmental Change*, *5*(2), 127-148. doi: 10.1016/0959-3780(95)00018-J.

Schindler, D.E., & Scheuerell, M.D. (2002). Habitat coupling in lake ecosystems. *Oikos*, *98*, 177-189.

Schindler, D. & Smol, J. (2006). Cumulative effects of climate warming and other human activities on freshwaters of arctic and subarctic Northern America. *Ambio*, *35*(4), 160-168.

2.0 Chapter 2: Habitat coupling dynamics of mobile consumers along a freshwater and marine resource gradient

2.1 Abstract

Food webs are complex systems that consist of connections by direct links between consumers and resources. These links can lead to habitat coupling, which is the transfer of nutrients, organic matter, and species between adjacent habitats or nutrient pathways. Estuaries are transition zones between freshwater and marine habitats, resulting in energy exchange between these systems. Estuaries offer flexibility for freshwater and marine species to acquire resources from both sources. The objective of this study was to quantify the diet composition between freshwater-and marine-derived resources and niche size of mobile consumers (13 fishes and 2 seal species) within the lower Churchill River. Stable isotope analysis was used to provide a time-and space-integrated understanding of trophic relationships. Cisco, lake whitefish, and northern pike caught in Goose Creek represented the habitat couplers in this system and also exhibited the greatest amount of individual variability since most individuals (75%, 56%, 65% of individuals for cisco, lake whitefish, and pike respectively) consumed a mix of both freshwater-and marine-derived resources. The largest niche sizes were found for lake whitefish ($10.70‰^3$) and Goose Creek northern pike ($9.27‰^3$) and the smallest niche sizes were found for the harbour and ringed seals ($0.04‰^3$ and $0.06‰^3$). Lake whitefish isotopic niche overlapped with the most species, which shows lake whitefish have a broader use of resources. Habitat couplers in this system were found to have more variability in their foraging strategy than the other consumers, with dietary proportions from the mixing models agreeing with the known life histories of each consumer in terms of migratory or resident movement strategies. Estuaries are vital links between freshwater and marine systems that tend to be subject to high levels of anthropogenic activity. Therefore, understanding the trophic dynamics and links among species in these habitats are critical for their management.

2.2   Introduction

Ecosystems are linked through the movement of nutrients, prey, and consumers, which can have a strong impact on the dynamics and structure of communities (Polis et al., 1997; Schreiber & Rudolf, 2008). Linkages between ecosystems can strongly influence population, consumer-resource, food web, and community dynamics by providing organisms access to more resources and habitats (Lamberti et al., 2010; Polis et al., 1997). This movement between systems is known as habitat coupling, where distant and/or adjacent habitats are connected by the transfer of organic matter and where consumers can integrate several resources from different habitats (Schindler & Scheuerell, 2002). Habitat coupling also unites cross-habitat trophic linkages that mediate key ecological processes including nutrient cycling and food web stability whereby mobile consumers take advantage of fluctuations in resource productivity between different systems (McCann et al., 2005; Rezek et al., 2020; Rooney et al., 2006). Examples of adjacent ecosystems include terrestrial-aquatic, where small streams derive most of their nutrients from litterfall (Fisher & Likens, 1973; Gregory et al., 1991; Schindler & Scheuerell, 2002), and freshwater-marine, where terrestrial/freshwater-derived resources are transported to the marine environment (Lamberti et al., 2010). These connections allow for the movement of resources between systems that consumers are able to take advantage of.

Freshwater and estuarine consumers use and respond to imported resources through the movement of marine fishes migrating back to freshwater systems (Reist et al., 2006; Polis et al., 1997; Walters et al., 2009). Freshwater systems, such as rivers, can contribute large amounts of material, such as sediments (e.g., biogenic silica), dissolved nutrients, and organic carbon to estuarine and nearshore marine systems (Conley, 1997; Lamberti et al., 2010). Marine energy can move into freshwater ecosystems by migrations of anadromous and catadromous organisms, such as salmonids (Reist et al., 2006), where nutrients from dead anadromous fish provide an important energy subsidy to freshwater systems through nutrient uptake by plants (Polis et al., 1997; Walters et al., 2009). Aquatic consumers such as fishes and marine mammals can play an important functional role as habitat couplers between systems due to their movements and flexible foraging behaviours that lead to their inter-habitat omnivory and the transfer of nutrients between different habitats (Schindler & Scheuerell, 2002). For example, anadromous cisco

(*Coregonus* spp.) have been found to use a saltwater zone during spring/early summer and then move back into a freshwater system during late summer/early fall (Morin et al., 1981).

Species that couple different habitats together may also have high levels of variability among individuals within a population in their resource use attributed to sex, ontogeny, and individuals within a cohort specializing on resources from different habitats (Matthews & Mazumder, 2004; Polis, 1984; Werner & Gilliam, 1984). A species' niche is defined as an n-dimensional hypervolume that includes an organism's interactions with biotic and abiotic factors in their environment (Hutchinson, 1957). Species known to migrate between habitats are opportunistic foragers and are known to have a more omnivorous diet by consuming resources between marine and freshwater habitats. Therefore, these migrating species likely have a larger niche size and more niche overlap with other species, possibly resulting in increased competition for resources since habitat couplers have more variability in their foraging strategies (Schindler & Scheuerell, 2002).

Estuaries are transition zones between marine and freshwater systems, where species inhabiting these connected habitats can take advantage of different resource pulses across systems (France, 1995; Polis et al., 1997). In turn, estuaries can act as important foraging habitat for many opportunistic fish and marine mammal species who can consume a wide diversity of prey items. As such, the lower Churchill River system in Manitoba, Canada is an ideal study site to investigate population and individual level variability of resource use of mobile consumers across inter-connected freshwater, estuarine and marine habitats. For example, cisco, lake whitefish (*Coregonus clupeaformis*), and brook trout (*Salvelinus fontinalis*) typically inhabit freshwater but have an anadromous life strategy and may take advantage of accessing the marine system when the ice breaks up in spring (Morin et al., 1981; Wilder, 1951). As well, the physiology of some fish, such as northern pike (*Esox Lucius*), can allow access to brackish water zones (Rohtla et al., 2012).

The objective of this chapter was to investigate the habitat coupling role of mobile consumers (13 fishes and 2 seal species) within the lower Churchill River area by quantifying their diet composition and niche dynamics using stomach content and stable isotope analysis. Stable isotopes ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) were used to investigate variation in the contribution of

freshwater-and marine-derived resource use at an individual and population level as well as isotopic niche size and niche overlap of each consumer within the community. Stable isotope analysis provides time-integrated information on habitat use and diet of a consumer (Fry, 2006) where carbon stable isotopes (δ^{13}C) are used to determine the source of dietary carbon (e.g., terrestrial/freshwater versus marine), nitrogen stable isotopes (δ^{15}N) are used to determine trophic position of consumers, and sulfur stable isotopes (δ^{34}S) are commonly used in estuarine systems to differentiate between marine-derived and freshwater-derived resources (Fry, 2006; Heady & Moore, 2013; Phillips & Eldridge, 2006). First, I hypothesized that species with a known life history of migration between freshwater and marine systems will couple those habitats together by using a combination of both freshwater and marine resources, whereas species with a known life history to principally reside in either freshwater or marine environments will primarily consume resources from their resident system. Second, I hypothesized that species that display habitat coupling between both the freshwater and marine resources will have a larger niche than species that forage on only one resource type, either freshwater or marine. In addition, habitat coupling species will have low overlap with species who principally foraged on either one resource type. Lastly, I hypothesized that species that display habitat coupling between freshwater-and marine-derived resources will have more variability between individuals in their resource use than species that principally consume only one resource type.

2.3   Methods

2.3.1   Study Site

This study was conducted within the lower Churchill River area near the town of Churchill (58.7684° N, 94.1650° W), Manitoba, Canada. Churchill is found within the subarctic which deals with short, mild temperature summers. The river connects to Hudson Bay through the estuary. Data was collected during July and August of 2019 and 2020 throughout the river, the estuary, and the coast of Hudson Bay (Figure 2-1).

2.3.2   Environmental Sampling

Surface water quality measurements (pH, dissolved oxygen, temperature, conductivity, and salinity) were taken with a YSI Professional Plus (Yellow Springs Instrument, British Columbia) at each sample collection site in the freshwater, estuarine, and marine environments throughout the lower Churchill River (Figure 2-1, Appendix A, Table A-1).

2.3.3   Sample Collection and Preparation

During data collection I tried to sample all representative fish from each habitat (marine, estuary, and freshwater). As a result, thirteen fish species were collected using a combination of gillnets and angling (collection sites for each species is found in Appendix A, Table A-2). Target fish were euthanized by a blow to the head and a cervical dislocation. Nets were set for a six-hour soak and were checked every two hours to reduce bycatch of any non-target species, such as sturgeon (Manitoba Government permits: SCP 40-19 APZ and SCP 23-20 APZ). For each fish, fork length and total length (cm), weight (g), and sex were recorded, and internal structures (muscle, liver, stomach, and otolith/cleithrum) were subsampled. Fish samples were collected late-May to September in 2019 and 2020 (Appendix A, Table A-3). Seal samples were provided opportunistically by local hunters. Four harbour seals were collected in September of 2016 and five ringed seals were collected in November 2019 and April-May 2020.

Samples of liver and muscle, which have different turnover rates, were collected from each fish to provide an understanding on any dietary shifts over the spring-summer period (Fry, 2006; Heady & Moore, 2013; Phillips & Eldridge, 2006). The whole body of smaller-sized individuals (invertebrates, three burbot (*Lota lota*), four nine-spine sticklebacks (*Pungitius pungitius*), and one sculpin (*Cottoidea* spp.)) were homogenized for analysis. Muscle and liver samples were collected from ringed seals, whereas muscle and hair samples were collected from harbour seals. Harbour seals moult in August (Bajzak et al., 2012; Vincent et al., 2017), so this regrown hair would represent the diet slightly before and during the moulting period due to representative elements circulating in the blood that are then deposited into the growing hair (Hobson, 1999). Tissues with a faster turnover rate, such as liver, provide dietary information on a weekly scale (~15-30 days) during the summer period, whereas tissues with a slower turnover

rate like muscle provide information on a monthly scale (~1-4 months) from spring to summer. Since pinnipeds moult their hair annually, hair samples contain less temporal stable isotope information than samples from mammals that have continuous hair growth (Greaves et al., 2004). Hair tissue is metabolically inert after growth and will maintain an isotope signal based on the habitat the species was found in during the hair growth period (Hobson, 1999). Since the harbour seal samples were collected in September, I will have information on their diet over a short time period (~1-2 months).

Frozen tissue samples from invertebrates, fishes, and seals were freeze-dried for 48 hours and then homogenized by hand with a mortar and pestle. Lipids were extracted from the liver, muscle, and whole-body samples with a 2:1 chloroform-methanol following procedures detailed in Bligh & Dyer (1959) and McMeans (2009). Hair samples were washed with soap and water and then left to dry overnight, then homogenized by hand with scissors. Stable isotope analysis was performed at the Chemical Tracers Laboratory, Great Lakes Institute for Environmental Research, at the University of Windsor using a Delta V Advantage Mass spectrometer (Thermo Finnigan, San Jose, CA, USA) coupled to a Costech 4010 Elemental Combustion system (Costech, Valencia, CA, USA) and a ConFlo IV gas interface. For $\delta^{13}C$ and $\delta^{15}N$ analysis, subsamples of 400-600 µg (for invertebrates, fishes, and seals) or 3000-4000 µg (for plankton) were weighed into tin capsules. For $\delta^{34}S$, 3000-6000 µg of the sample plus 300-500 µg of Vanadim Pentoxide was encapsulated. A triplicate was run for every 10th sample and the measurement of precision was 0.1‰ for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$.

Stable isotope measurements are standardized against international reference samples and reported in delta (δ) notation as per mil (‰). The isotope values are calculated as:

$$\delta X = [(R_{sample}/R_{standard}) - 1] *1000$$

where X is ^{13}C, ^{15}N, or ^{34}S, and R is the ratio of the heavy to light isotopes (e.g., $^{15}N/^{14}N$, $^{13}C/^{12}C$, and $^{34}S/^{32}S$) in the sample (R_{sample}) or an international standard ($R_{standard}$). Standards were Pee Dee Belemnite carbonate for CO_2, atmospheric nitrogen for N_2, and Canyon Diablo Troilite for SO_4 (Fry, 2006).

Lipid content can vary between tissues and individuals, where lipids are approximately 6-7 ‰ depleted in ^{13}C relative to protein (Sweeting et al., 2006). The C:N ratio is used to estimate lipid concentration where a C:N < 3.5 represents low lipid content in aquatic animals (Post et al., 2007). I calculated the C:N ratio of pure protein for liver for each fish species, which was estimated to be 3.8 based on amino acid composition (Appendix A, Table A-4) described in Bechtel & Oliverira (2006). I use the relative percentage of each amino acid from Bechtel & Oliverira (2006) and then used the chemical formula for each amino acid to find the integer of carbon and nitrogen that are found in the liver for each fish. I then divided the integer of carbon by the integer of nitrogen to get the C:N ratio. The C:N ratio was below 3.8 for each species (Table 2-1). In addition, there was no relationship between C:N ratio and $\delta^{13}C$ for any fish species based on a Kendall correlation (z = 0.758, p = 0.448) suggesting that all the lipids were successfully removed by the chloroform-methanol extraction process.

Stomach content analysis was performed on all fish species. Each prey item in the stomach was grouped into separate prey types and I noted whether the prey was whole or partially digested. If there were multiple fragments of one prey species within a stomach they would be grouped as a single prey item. Presence of mucus was noted, as well as detritus/ unidentifiable organic matter (Buckland et al., 2017). Frequency of occurrence, which provides information on prey presence/absence, was the best method to use since the prey in each stomach were only identified and not quantified. Frequency of occurrence was calculated as the number of fish containing prey divided by the total number of fish stomachs (Ahlbeck et al., 2012). Frequency of occurrence provides the sample importance to all prey types, irrespective of their mass, which may result in small prey becoming overestimated and large prey becoming underestimated. However, the benefit of estimating frequency of occurrence is it only considers counts and avoids uncertainty in accuracy of total mass of prey in stomachs due to some prey species being digested quicker than others (Baker et al., 2014). As well, some stomach content samples that were not degraded and recently consumed were cleaned and prepared for stable isotope analysis to provide a greater sample size for the 2019 samples. Three freshwater mussels were used as the freshwater source in the mixing model and two burbots and three nine-spine sticklebacks were added to the consumer group from the 2019 fish stomach contents.

2.3.4   Data Analysis

All data analyses were conducted in R v. 4.0 (R Core Team, 2021). Stable isotope values of baseline prey and consumers can vary over time and space (Cabana & Rasmussen, 1996; Fry, 2006; Post, 2002), so to determine if the mean species-specific δ^{13}C, δ^{15}N, and δ^{34}S values for each consumer tissue differed significantly between sampling years, a Wilcoxon signed-rank test was performed. I also used a Holm-Bonferroni sequential correction to account for multiple comparisons between sampling years (i.e., α = 0.05/(number of test run-rank number of pair) +1). The δ^{13}C, δ^{15}N, and δ^{34}S values were checked for normality with quantile-quantile plots and histograms, and for heteroscedasticity with residual-fitted value plots. Non-parametric tests were used to test for spatial and temporal similarity and all correlation tests due to having small sample sizes. Ringed seals were collected during two different seasons, November in 2019 and April-May in 2020. Based on the Wilcoxon signed-rank test I found no significant difference between the seasons for each stable isotope therefore the different seasoned ringed seals were combined. Northern pike and lake whitefish collected in 2019 were collected during two different time periods, May in Goose Creek and July throughout the lower Churchill River area. Based on the Wilcoxon signed-rank test I found the median difference between northern pike collected in Goose Creek and throughout the Churchill River differed significantly between May and July for δ^{15}N and δ^{34}S for muscle and liver (Appendix A, Table A-5). Therefore, northern pike were separated into two groups, one from Goose Creek and a second from the Churchill River. There were no significant differences between the locations for lake whitefish. As well, there were no significant differences between 2019-2020 for δ^{13}C and δ^{15}N for any of the other species. For δ^{34}S the average difference between the 2019 and 2020 time periods was only significant for capelin (*Mallotus villosus*) (0.80‰ muscle; Appendix A, Table A-6). I used a Bayesian mixing model (MixSIAR) to estimate contributions of freshwater and marine-derived resources to predator diet (Phillips et al., 2014). When running the MixSIAR models for each of these species separated by collection year, differentiation in resource contribution was negligible compared to model outputs with both sampling years combined (the average change in resource contribution was 0.30‰). As well, these mean differences are much lower than the range of 6.33‰ for δ^{13}C and 11.97‰ for δ^{34}S between the marine end-member blue mussel and freshwater end-member mussel.

Mixing models were run with δ^{13}C and δ^{34}S to estimate the proportion of marine- versus freshwater-derived resources used by consumers. I used the two most extreme freshwater and marine prey as sources in the mixing model (i.e., freshwater mussel and blue mussel; Table 2-2). The mixing models were run for each species separately at the population level and then again at the individual level using default uninformative priors. A test model was run with priors using some of the stomach contents and the results were similar to when the model was run without priors. Three Markov Monte Carlo chains had a length of 1,500,000 iterations, a burn-in of 1,000,000, and were thinned by 500, leaving 500 posterior estimates from the posterior probability distribution. Chain convergence was determined through the Gelman-Rubin diagnostic and all species met convergence (i.e., <1.05). The error term in the model at the population level was set to residual*process, as this type of error was found to be more accurate than previous methods of error estimation (Stock & Semmens, 2016). At the individual level, the error term was set to process only.

To account for tissue-specific differences in the stable isotope values between prey and predator, a diet-tissue discrimination factor (Δ^{13}C) was applied to each fish and seal species. For all fishes, I assumed a muscle Δ^{13}C of 1.73 ± 0.27‰ (mean ± standard deviation), a liver Δ^{13}C of 0.77 ± 1‰, and a Δ^{34}S of 0.5 ± 0.56‰ for both muscle and liver (Caut et al., 2009, Hobson et al., 1996; McCutchan et al., 2003). For harbour seals and ringed seals, the Δ^{13}C was 1.3 ± 1.2‰ for muscle, 0.6 ± 0.31‰ for liver, and 2.8 ± 0.5‰ for hair, and Δ^{34}S = 0.5 ± 0.56‰ for muscle, liver, and hair (Caut et al., 2009; Hobson et al., 1996; McCutchan et al., 2003). On a freshwater-derived resource use scale between 0% and 100%, I considered species and individuals within that species with a median posterior probability of ≤ 20% to be mainly foraging on marine sources, and a species with a median posterior probability of ≥ 80% to be mainly consuming freshwater sources.

I used nicheROVER v. 1.0 (Swanson et al., 2015) to calculate niche sizes and pairwise niche overlap between species using δ^{13}C, δ^{15}N, and δ^{34}S. Isotopic niche size (95% ellipsoid region) can describe species foraging on a variety of resources (larger niche) or using a particular resource (smaller niche), which can help with understanding resource partitioning and niche shifts, whereas niche overlap may reflect potential interactions between species (e.g., competition). Species with a larger niche will have more variability in their foraging strategy and

a more opportunistic diet. For each species, a run of 10,000 iterations was used to determine the niche size from each species' posterior probability distributions. Only one walleye (*Sander vitreus*) sample was collected, so it was not run in the mixing model due to small sample size.

The niche overlap is the probability of species A sharing an isotopic space with species B and species B sharing the isotopic space with species A. The 40% niche includes approximately 40% of the data points occurring within the ellipsoid and represents the population's core niche, whereas the 95% niche size represents the whole population. Biologically meaningful niche overlap between species is defined as a median overlap greater than 60% (Dance et al., 2018; Guzzo et al., 2013; Heuvel et al., 2019; Seubert et al., 2019). A minimum of five individuals of each species were required to calculate the niche overlap and therefore could not be run for nine-spine stickleback (muscle and liver), walleye (muscle and liver), burbot (liver), capelin (liver), trout-perch (*Percopsis omiscomaycus*) (liver), and harbour seals (hair). The harbour and ringed seals (muscle) were combined into one group.

2.4   Results

Of the thirteen fish species collected, nine species did not have empty stomachs (Table 2-3). For brook trout, fish were the preferred prey item, with the consumption of some amphipods and aquatic insects. Burbot stomachs only contained fish and some unknown organic matter. Greenland cod (*Gadus ogac*) foraged predominantly on fish and amphipods, but their stomachs also contained unknown organic matter, unknown invertebrates, and vegetation. Fourhorn sculpins (*Myoxocephalus quadricornis*) consumed a variety of resources, primarily amphipods, unknown organic matter, fish, vegetation, clams, and snails. Northern pike mainly foraged on fish, but their stomachs also contained some amphipods, aquatic insects, vegetation, snails, and leeches. All the longnose sucker (*Catostomus Catostomus*) and white sucker (*Catostomus commersonii*) stomachs contained unknown organic matter. Cisco and lake whitefish were the only species found in all habitats (Churchill River, estuary, and Hudson Bay) and had a variety of prey in their stomachs. Cisco stomach contents included amphipods, fish, vegetation, unknown organic matter, snails, and other invertebrates. Lake whitefish had the greatest variation of prey in their stomachs, which contained clams, snails, aquatic insects, vegetation,

unknown invertebrates, amphipods, ostracods, fish, mussels, leeches, and unknown organic matter. All stomachs were empty for capelin, nine-spine stickleback, trout-perch, and walleye.

Water quality measurements generally agreed with what was expected for each sampling site, but Goose Creek was found to have a higher salinity (0.35 ppt) and conductivity (673.50 µS/cm) than other sites found within the Churchill River (0.085 ppt and 158.00 µS/cm respectively; Table A-1).

2.4.1 Stable Isotopes

The consumer most depleted in ^{13}C was walleye (-28.34‰), whereas the species most enriched in ^{13}C were ringed seals (-19.85 ± 0.33‰). Predator species that had the lowest δ^{15}N values were Goose Creek northern pike (6.78 ± 0.22‰), whereas the species with the highest δ^{15}N values were harbour seals (18.06 ± 0.19‰). Species that had the lowest δ^{34}S values were longnose sucker (2.67 ± 0.23‰), whereas the species with the highest δ^{34}S values were Greenland cod (18.29 ± 0.09‰), see Table 2-1. Based on δ^{13}C and δ^{34}S biplots for the muscle data (Figure 2-2), three groups can be characterized based off the means of each isotope ratio for each species: 1) consumers with higher δ^{13}C and δ^{34}S values, which included harbour seal, ringed seal, brook trout, capelin, fourhorn sculpin, Greenland cod, and nine-spine stickleback, 2) those with the lowest δ^{13}C and δ^{34}S values, which included burbot, longnose sucker, Churchill River northern pike, trout-perch, walleye, and white sucker, and 3) fish with intermediate δ^{13}C and δ^{34}S values that included cisco, lake whitefish, and Goose Creek northern pike.

2.4.2 MixSIAR Dietary Results

Results from muscle and liver were nearly identical for each test/model run for most of the species. Therefore, the results are interpreted from the muscle tissue below with results from liver tissue provided in Appendix A. The liver tissue results are reported in the below text when they do differ from the muscle tissue. A total of eight species foraged mainly on marine resources according to the result from the mixing model and included the harbour seal (97% marine), ringed seal (99% marine), brook trout (81% marine), capelin (100% marine), fourhorn sculpin (90% marine), Greenland cod (100% marine), nine-spine stickleback (83% marine), and Goose Creek northern pike (88% marine). Five species foraged on mainly freshwater resources

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and included burbot (96% freshwater), longnose sucker (99% freshwater), Churchill River northern pike (79% freshwater), trout-perch (99% freshwater), and white sucker (99% freshwater). Three consumer species that had a mixed contribution of both freshwater and marine-derived resources (between 20% and 80% freshwater) represented the habitat couplers in this system, which were cisco (36% freshwater), lake whitefish (71% freshwater), and Goose Creek northern pike (74% freshwater) (Figure 2-3 and Table 2-1). The dietary proportions were similar for the liver tissue (Appendix A, Table A-7) for all species except for Goose Creek northern pike. Goose Creek northern pike were found to forage on mostly marine-derived resources during the spring period (liver tissue) whereas in the winter-spring period (muscle tissue) a mix of marine and freshwater-derived resources were consumed.

At the individual level, of the 285 muscle/whole body samples analyzed, 199 individuals had a ≥80% posterior probability of classification with either the marine-derived and/or freshwater-derived resources (Figure 2-4). Marine resources were principally used by all individual harbour seals, ringed seals, capelin, fourhorn sculpin, and Greenland cod, whereas all individual burbot, longnose sucker, trout-perch, and white sucker mainly consumed freshwater resources. Brook trout (15% of individuals), nine-spine stickleback (25% of individuals), cisco (75% of individuals), lake whitefish (56% of individuals), Goose Creek northern pike (65% of individuals), and the Churchill River northern pike (8% of individuals) had individuals that were between 20-80% freshwater-derived resource consumption, suggesting some variation in resource usage among individuals in these species. Cisco and lake whitefish had individuals that used both marine-derived resource and freshwater-derived resource channels. At the individual level, of the 214 liver/hair samples analyzed, 141 individuals had a ≥80% posterior probability of classification with either the marine-derived resources and/or freshwater-derived resources. The muscle and liver results were different for the brook trout and Churchill River northern pike. Based on the liver data, all brook trout consumed marine-derived resources, and 18% of Churchill River northern pike were found to consume a mix of marine-and freshwater-derived resources.

2.4.3   NicheRover Niche Size and Overlap Results

Non-overlapping 95% credible intervals were used to infer whether niche size is greater in one species compared to the other (Table 2-1 and Figure 2-5). Small niche sizes occurred for harbour seals (0.04‰^{3}, CI: 0.02-0.18), ringed seals (0.06‰^{3}, CI: 0.03-0.20), brook trout (0.09‰^{3}, CI: 0.05-0.25), Greenland cod (0.13‰^{3}, CI: 0.08-0.24), capelin (0.16‰^{3}, CI: 0.12-0.25), trout-perch (0.17‰^{3}, CI: 0.11-0.33), longnose sucker (0.21‰^{3}, CI: 0.13-0.46), burbot (0.52‰^{3}, CI: 0.27-1.69), white sucker (0.54‰^{3}, CI: 0.29-1.22), fourhorn sculpin (0.73‰^{3}, CI: 0.49-1.17), and Churchill River northern pike (0.98‰^{3}, CI: 0.62-2.25). Intermediate niche size occurred for cisco (2.00‰^{3}, CI: 1.35-3.26). The largest niche sizes occurred for lake whitefish (10.70‰^{3}, CI: 8.08-14.44) and Goose Creek northern pike (9.27‰^{3}, CI: 6.10-17.59). For the liver data, the credible intervals and niche sizes were similar to the muscle data (Appendix A, Table A-7 and Figure A-1). The probability of species A sharing an isotopic space with species B for the 95% niche sizes showed high niche overlap between cisco and fourhorn sculpin (63%); between lake whitefish with burbot (87%), longnose sucker (98%), Churchill River northern pike (93%), trout-perch (97%), and white sucker (93%), and between seals and Greenland cod (63%; see Table 2-4 and Figure 2-5). Minimal overlap occurred between a few species for the 40% niche size (Table 2-4). For liver data, lake whitefish were again found to have a high niche overlap with many other species (Appendix Table A-8).

2.5   Discussion

Within the lower Churchill River, species that exhibited the highest variability in their foraging between marine-derived and freshwater-derived resources and played the role of habitat couplers were cisco, lake whitefish, and Goose Creek northern pike. Furthermore, these species also had the largest niche sizes indicating a more diverse use of resources compared to other species. Overall, these three species, exhibited a flexible foraging strategy that allows for a shift in their resource use over the seasons and between habitats (Schindler & Scheuerell, 2002; Seubert et al., 2019). As well, significant niche overlap occurred between lake whitefish and several other fish species (burbot, longnose sucker, Churchill River northern pike, trout-perch, and white sucker) further supporting their broader use of resources within this system. At the individual level, species that are known to migrate between freshwater and marine environments

displayed the highest levels of variation among individuals in their resource channel usage, with cisco and lake whitefish having the highest proportion of individuals exhibiting a mixed foraging strategy between both marine and freshwater environments.

2.5.1   Population Level

At the population level, the dietary proportions of each species agreed with their known life histories in terms of migratory versus resident movement strategies in that cisco, lake whitefish, and northern pike migrate between fresh and marine waters and in turn, couple both habitats together by consuming both freshwater and marine-derived resources. These three species have been documented to consume fish, amphipods, and molluscs (Harvey, 2009; Rennie et al., 2009; Viljanen, 1983). Brook trout, capelin, Greenland cod, fourhorn sculpin, nine-spine stickleback, harbour seals, and ringed seals foraged principally on marine-derived resources and are known to consume a wide variety of fish, molluscs, and crustacean species (Brown & Peirce, 1998; de la Vega et al., 2016; Mikhail & Welch, 1989; Morin et al., 1981; Ogloff et al., 2020). Coastal marine and brackish water zones are the main habitat for these species and are integral for their life history cycles (Brown & Peirce, 1998; Curry et al., 2002; Matley et al., 2015; Morin & Dodson, 1986; Ogloff et al., 2020). Burbot, trout-perch, longnose sucker, white sucker, and walleye mainly foraged on freshwater-derived resources and have been reported to consume a mix of freshwater algae, benthic and pelagic invertebrates, and fish (Beeton, 1956; Edwards, 1983; Galarowicz et al., 2006; Kocovsky et al., 2014; Nelson & Dick, 2002; Saint-Jacques et al., 2000; Scott & Crossman, 1973).

Many fish species that reside in freshwater systems take advantage of the higher resource productivity found within the marine environment by migrating to those systems, as has been previously observed in the estuary and Hudson Bay (Gross et al., 1988). Based on the stomach content analysis, cisco mainly foraged on amphipods, fish, vegetation, and unknown organic matter. Within the James Bay area of the Hudson Bay complex, cisco have been found in the saltwater zone during spring and early summer and then moved back into the freshwater system in late summer/early fall (DeJong, 2017; Morin et al., 1981), which also may occur in the Churchill River system. Cisco had one of the larger niche sizes of all 16 species groups for both liver and muscle, but the niche size was larger for muscle than liver showing seasonal variability

in their resource and habitat use. The difference between tissues could be due to cisco consuming both marine-derived and freshwater-derived resources in the spring period and early summer during migration, and then focusing on marine-derived resources over the summer and early fall (Morin et al., 1981). The niche of cisco also significantly overlapped with fourhorn sculpin where both species have been reported to forage on similar invertebrate prey species (Morin & Dodson, 1986; Viljanen, 1983). However, in summer (i.e., liver) cisco did not significantly overlap with fourhorn sculpin, which may be due to timing of migration with cisco switching to more marine resources during summer.

Anadromous lake whitefish are similar to cisco in timing of migration out to a marine habitat in the summer and back to a freshwater habitat in fall (DeJong, 2017; Morin et al., 1981). These seasonal movements allow cisco and lake whitefish to capitalize on seasonal resource productivity pulses from connected freshwater and marine systems. Lake whitefish had a wide variety of prey items in their diet, consisting of clams, snails, aquatic insects, vegetation, and unknown organic matter. Lake whitefish are known to be opportunistic predators that forage on many types of freshwater and marine prey (Keva et al., 2019; Morin & Dodson, 1986; Rennie et al., 2009), which agrees with my results. Lake whitefish also had the highest levels of niche overlap with other species, further reinforcing their important role as habitat couplers in the lower Churchill River system.

Northern pike are opportunistic predators that have been reported to undertake migrations in the Baltic Sea to salinities of ~6-12 ppt and forage on marine-derived resources (DeJong, 2017; Rohtla et al., 2012). Similar to the Baltic Sea, northern pike within the Hudson Bay lowlands have been found to rely on marine-derived resources (DeJong, 2017). The marine signal found in the Goose Creek northern pike could be due to the consumption of nine-spine sticklebacks. Sticklebacks are a prey species that northern pike have been found to forage on within Alaska (Heins et al., 2016; Pintor et al., 2014) and within the Churchill system sticklebacks were found to have a marine signal in their diet. However, the differences in the northern pike dietary signals between Goose Creek and the Churchill River could also be due to the time of year samples were collected from each location. As such, northern pike could potentially be foraging on more marine resources in early spring and switch to a more freshwater diet throughout summer.

Capelin, Greenland cod, fourhorn sculpin, brook trout, nine-spine stickleback, harbour seals, and ringed seals foraged principally on marine-derived resources and had smaller niche sizes. These species are all known to mainly reside within marine systems (Morin & Dodson, 1986). Capelin feed mainly on zooplankton, such as amphipods, copepods, and euphausiids (Ogloff et al., 2020; Vesin et al., 1981). Greenland cod are omnivorous and mainly forage on fish and amphipods, which aligns with my stomach content results. Fourhorn sculpin are a benthic fish that mainly consume amphipods and small fishes (Morin & Dodson, 1986). Anadromous populations of brook trout at the northern part of their geographic ranges, which encompasses western Hudson Bay, generally migrate to the marine environment during spring to access foraging habitats and then return to a freshwater system in fall for spawning (Curry et al., 2002; Montgomery et al., 1983; Morinville & Rasmussen, 2006). Nine-spine stickleback are a cold-water adapted fish that have been found within both freshwater and marine systems and are known to inhabit coastal areas of the Arctic Ocean (Shikano et al., 2010), along with brackish systems within the littoral zone, and are abundant in estuarine systems throughout the summer season (Hynes, 1950; Morin & Dodson, 1986). The nine-spine sticklebacks collected in this study could be a saline-adapted group since they mainly foraged on marine-derived resources. Interestingly, brook trout and nine-spine stickleback were the only anadromous species within this system that did not couple the habitats together, but both species consumed more freshwater-derived resources than the other resident marine species.

Harbour seals and ringed seals are opportunistic foragers that have been documented to consume a wide variety of marine fishes and invertebrates (Brown & Peirce, 1998; de la Vega et al., 2016; Tollit et al., 1997Young et al., 2010; Yurkowski et al., 2016). Both harbour and ringed seals had smaller niche sizes than any other consumer, suggesting an exclusively marine foraging strategy (Brown & Peirce, 1998; Chambellant et al., 2013; de la Vega et al., 2016; Lydersen et al., 2017; Madgett et al., 2019; Matley et al., 2015; Tollit et al., 1997). Both the Greenland cod and seals had small niche sizes, and the seals were found to have significant niche overlap with Greenland cod. Cod are known to be a generalist apex predator and have been observed to forage on similar invertebrate and fish prey resources as seals (Ellingsen et al., 2020).

Burbot, Churchill River northern pike, trout-perch, longnose sucker, white sucker, and walleye mainly foraged on freshwater-derived resources and had small niche sizes. All six of

these species are opportunistic feeders that are omnivorous and are highly associated with a freshwater system. Burbot are the only gadiform (cod-like fish) that spend their entire life in a freshwater system (Scott & Crossman, 1973) and consume a mix of freshwater fish, insects, amphipods, and crayfish (Beeton, 1956; Lawler, 1963). Churchill River northern pike are likely only foraging within the river and on freshwater species, and they have been found to consume a variety of freshwater fish, amphipods, aquatic insects, snails, vegetation, and unknown organic matter (Harvey, 2009). Trout-perch are found in deep lakes or large streams and are considered generalists that forage on benthic invertebrates and zooplankton, especially chironomids and mayflies, as well as some fish eggs and smaller fish (Blouzdis et al., 2013; Kocovsky et al., 2014; Nelson & Dick, 2002). Catostomid fishes, known as suckers, are found to inhabit riverine and lake systems and are sensitive to environmental changes, such as changes in the carbon supplies and the availability of off-channel habitats (Welker & Scarnecchia, 2003). Both longnose and white suckers are omnivorous consumers that share similar habitat and have been observed to consume a mix of zooplankton and benthic invertebrates such as chironomid larva, gastropods, odonata, and amphipods (Edwards, 1983; Saint-Jacques et al., 2000), which supports my finding of significant niche overlap between both species. Juvenile walleye are a benthivorous fish that forage on zooplankton and small fish and are found in similar areas as trout-perch resulting in potential competition between the two species as trout-perch also consume similar resources such as benthic invertebrates and zooplankton (Blouzdis et al., 2013; Galarowicz et al., 2006; Kocovsky et al., 2014; Nelson & Dick, 2002).

2.5.2   Individual Level

A population can be made up of individuals that will specialize on a resource from one source whereas other individuals may switch their resource use by taking advantage of the resource pulses within the system (Matich et al., 2014). High variability between individuals promotes foraging flexibility for a group of species, allowing them to take advantage of a greater number of resources (Beaudoin et al., 1999), which in combination with habitat coupling, occurs in a variety of invertebrate and fish species (Elliott Smith et al., 2020). Ringed seals, capelin, fourhorn sculpin, brook trout, nine-spine stickleback, and Greenland cod had minimal variation between individuals in their energy channel usage with all individuals being mainly marine-derived resource specialists, similar to that of burbot, longnose sucker, trout-perch, and white

sucker where most individuals specialized on freshwater-derived resources. Cisco, lake whitefish, and Goose Creek northern pike, which were all the habitat coupling species in this study, exhibited a high degree of variation in their marine and freshwater resources use between individuals with no discernable difference between the summer and spring-summer diet periods. For the individuals of cisco, lake whitefish, and Goose Creek northern pike, cisco and lake whitefish were found to have individuals that specialized on both the marine and freshwater resources as opposed to Goose Creek northern pike, where individuals who specialized on a resource channel, only did so on freshwater-derived resources. This level of intraspecific variation in resource channel use between species illustrates additional complexity in the habitat coupling roles of these species and how they may take advantage of feeding on multiple sources (Elliott Smith et al., 2020). Interestingly, within a species, Goose Creek northern pike had a higher level of individual variability in resources channel use than pike collected in the Churchill River, which could be attributed to Goose Creek northern pike moving between both marine and freshwater systems or due them foraging on both freshwater and anadromous prey.

Within a population, there can be variation between individuals in their ability to tolerate different types of environment attributes, such as salinity. In addition, high variability in resource use among individuals can reduce intraspecific competition for resources, and provide food web stability (Curry et al., 2002; McMeans et al., 2013; Svanbäck & Bolnick, 2007). Brook trout, Greenland cod, nine-spine stickleback, capelin, longnose sucker, white sucker, and trout-perch had small niche sizes suggesting a reliance on only one resource type during both the spring-summer and summer time periods. Brook trout and nine-spine stickleback were the only species in this group to have a migratory life history between freshwater and marine systems (Hynes, 1950; Morin & Dodson, 1986). Brook trout could be the one of the first species to migrate to the marine system from the freshwater system each year to capitalize on the marine resource pulse. Brook trout have also been found to overwinter in a more-saline environment as observed in the St-Jean River and Saguenay River estuaries in Québec, resulting in the consumption of more marine-derived resources during winter (Castonguay et al., 1982; Morinville & Rasmussen, 2006), which also could be occurring in the lower Churchill River system. The small niche size of nine-spine sticklebacks is likely due to higher consumption of marine-derived resources.

2.6   Conclusion

This study highlighted interspecific variation in how mobile species couple energy sources along a freshwater and marine gradient (Curry et al., 2002). Habitat coupling between freshwater-derived resources and marine-derived resources occurred in migratory species (i.e., cisco and lake whitefish) and species that can physiologically tolerate a wide array of salinities such as northern pike. These species were all found to have the largest niche sizes and also the greatest amount of variability among individuals in their resource use. In addition, significant niche overlap occurred between lake whitefish and most other species, further highlighting their consistent habitat coupling role. All other species from this study foraged within one system, resulting in less variability in their resource use and smaller niche sizes. To further examine these dynamics, future work in this system could examine fish migration using otolith microchemistry, acoustic telemetry, and continuous sampling throughout the year to examine changes in habitat coupling and/or resource use across all seasons. These mobile fish and seal species are important to local community members, Indigenous communities, as well as other stakeholders since most of these species are used in substance fishing/hunting and recreational activities. Therefore, continued monitoring of these species can reveal a spring-summer change in their foraging dynamics and habitat coupling role and provide insight on potential changes to the structure and function of the ecosystem.

Previous work on habitat coupling in aquatic systems have mainly focused on understanding resource use between the benthic versus pelagic sources (Duffill Telsnig et al., 2019; Kiljunen et al., 2020; Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002). However, understanding resource use between adjacent systems, such as between freshwater and marine, is important to understand the role that estuaries provide to overall community structure and function of adjoining habitats. Migratory species typically rely on both the freshwater and marine systems for growth and reproduction, therefore this inter-connection between the marine and freshwater system is important to allow these species to complete steps within their life cycle (Morinville & Rasmussen, 2006). By understanding the foraging behaviour of different mobile consumers within the lower Churchill River we can better predict the trophic structure of the community and how to conserve these species in the future. As such, this study can be used to provide baseline information for future studies to quantify temporal changes

within the lower Churchill River as well as other estuarian systems within the subarctic. Overall, understanding variation in the habitat and resource use between and within species can aid in the management and conservation practices in these inter-connected systems in the future. This will provide a greater understanding of estuaries as an important transition zone which can then be used to track climate change and anthropogenic stressors.

2.7   References

Ahlbeck, I., Hansson, S., Hjerne, O., & Ramcharan, C.W. (2012). Evaluating fish diet analysis methods by individual-based modelling. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(7), 1184-1201. doi: 10.1139/f2012-051.

Bajzak, C., Bernhardt, W., Mosnier, A., Hammill, M., & Stirling, I. (2012). Habitat use by harbour seals (*Phoca vitulina*) in a seasonally ice-covered region, the western Hudson Bay. *Polar Biology*, *36*(4), 477-491. doi: 10.1007/s00300-012-1274-4.

Baker, R., Buckland, A., & Sheaves, M. (2014). Fish gut content analysis: robust measures of diet composition. *Fish and Fisheries*, *15*(1), 170-177. doi: 10.1111/faf.12026.

Beaudoin, C.P., Tonn, W.M., Prepas, E.E., & Wassenaar, L.I. (1999). Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia*, *120*(3), 386-396. doi: 10.1007/s004420050871.

Bechtel, P.J. & Oliveira, A.C.M. (2006). Chemical characterization of liver lipid and protein from cold-water fish species. *Journal of Food Science*, *71*(6), S480-S485. doi: 10.1111/j.1750-3841.2006.00075.x.

Beeton, A.M. (1956). Food habits of the burbot (*Lota lota lacustris*) in the White River, a Michigan trout stream. *Copeia*, *1956*(1), 58-60.

Bligh, E.G. & Dyer, W.J. (1959). A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, *37*(8), 911-917. doi: 10.1139/y59-099.

Blouzdis, C.E., Ivan, L.N., Pothoven, S.A., Rosewell, C.R., Folet, C.J., & Höök, T.O. (2013). A trophic bottleneck?: The ecological role of trout-perch *Percopsis omiscomaycus* in Saginaw Bay, Lake Huron. *Journal of Applied Ichthyology*, *29*(2), 416-424. doi: 10.1111/jai.12023.

Brown, E. & Pierce, G. (1998). Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Marine Ecology Progress Series*, *167*, 275-289.

Buckland, A., Baker, R., Loneragan, N., & Sheaves, M. (2017). Standardizing fish stomach content analysis: the importance of prey condition. *Fisheries Research*, *196*, 126-140. doi: 10.1016/j.fishres.2017.08.003.

Cabana, G. & Rasmussen, J.B. (1996). Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Science*, *93*(20), 10844-10847. doi: 10.1073/pnas.93.10844.

Castonguay, M., FitzGerald, G.J., & Côté, Y. (1982). Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Quebec. *Canadian Journal of Zoology*, *60*(12), 3084-3091. doi: 10.1139/z82-392.

Caut, S., Angulo, E., & Courchamp, F. (2009). Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. The *Journal of Applied Ecology*, *46*(2), 443-453. doi: 10.1111/j.1365-2664.2009.01620.x.

Chambellant, M., Stirling, I., & Ferguson, S.H. (2013). Temporal variation in western Hudson Bay ringed seal *Phoca hispida* diet in relation to environment. *Marine ecology*, *481*, 269-287. doi: 10.3354/meps10134.

Conley, D.J. (1997). Riverine contribution of biogenic silica to the oceanic silica budget. *Limnology and Oceanography*, *42*(4), 774-777. doi: 10.4319/lo.1997.42.4.0774.

Curry, A.R., Sparks, D., & Sande, J. (2002). Spatial and temporal movements of a riverine brook trout population. *Transactions of the American Fisheries Society*, *131*(3), 551-560. doi: 10.1577/1548-8659(2002)131<0551:SATMOA>2.0.CO2.

Dance, K.M., Rooker, J.R., Shipley, J.B., Dance, M.A., Wells, R.J.D., & Patterson, H.M. (2018). Feeding ecology of fishes associated with artificial reefs in the northwest Guld of Mexico. *PloS One*, *13*(10), e0203873. doi: 10.1371/journal.pone.0203873.

DeJong, R.A. (2017). Life history characteristics of Lake Whitefish (*Coregonus clupeaformis*), Cisco (*Coregonus artedi*), and Northern Pike (*Esox lucius*) in rivers of the Hudson Bay Lowlands. (Masters thesis). University of Waterloo, Ontario, Canada.

de la Vega, C., Lebreton, B., Siebert, U., Guillou, G., Das, K., Asmus, R., & Asmus, H. (2016). Seasonal variation of harbour seal's diet from the Wadden Sea in relation to prey availability. *PloS ONE*, *11*(5). doi: 10.1371/journal.pone.0155727.

Duffill Telsnig, J.I., Jennings, S., Mill, A.C., Walker, N.D., Parnell, A.C., Polunin, N.V.C., & Jackson, A. (2019). Estimating contributions of pelagic and benthic pathways to consimer production in coupled marine food webs. *The Journal of Animal Ecology*, *88*(3), 405-415. doi: 10.1111/1365-2646.12929.

Edwards, E.A. (1983). Habitat suitability index models. Longnose sucker. Washington, DC: Western Energy and Land Use Team, Division of Biological Services, Research and Development, Fish and Wildlife Service, U.S. Dept. of the Interior.

Ellingsen, K.E., Yoccoz, N.G., Tveraa, T., Frank, K.T., Johannesen, E., Anderson, M.J., Dolgov, A.V., & Shackell, N.L. (2020). The rise of a mairne generalist predator and the fall of beta diversity. *Global Change Biology*, *26*(5), 2897-2907. Doi: 10.1111/gcb.15027.

France, R., (1995). Stable nitrogen isotopes in fish: literature synthesis on the influence of ecotonal coupling. *Estuarine, Coastal and Shelf Science*, *41*(6), 737-742. doi: 10.1006/ecss.1995.0087.

Lawler, G.H. (1963). The biology and taxonomy of the Burbot, *Lota lota*, in Heming Lake, Manitoba. *Journal of the Fisheries Research Board of Canada*, *20*(2), 417-433. doi: 10.1139/f63-033.

Fisher, S.G. & Likens, G.E. (1973). Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs*, *43*(4), 421-439. doi: 10.2307/1942301.

Fry, B. (2006). Stable isotope ecology. New York, NY: Springer. doi: 10.1007/0-387- 33745-8.

Galarowicz, T.L., Adams, J.A., & Wahl, D.H. (2006). The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. *Canadian Journal of Fisheries and aquatic Sciences*, *63*(8), 1722-1733. doi: 10.1139/f06-073.

Greaves, D.K., Hammill, M.O., Eddington, J.D., Pettipas, D., & Schreer, J.F. (2004). Growth rate and shedding of vibrissae in the gray seal, *Halichoerus grypus*: a cautionary note for stable isotope diet analysis. *Marine Mammal Science*, *20*(2), 296-304. doi: 10.1111/j.1748-7692.2004.tb01158.x.

Gregory, S.V., Swanson, F.J., & Cummins, K.W. (1991). An ecosystem perspective of riparian zones. *Bioscience*, *41*(8), 540-551. Doi: 10.2307/1311607.

Gross, M.R., Coleman, R.N., & McDowall, R.M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science*, *239*(4845), 1291-1293. doi: 10.1126/science.239.4845.1291.

Guzzo, M.M., Haffner, G.D., Legler, N.D., Rush, S.A., & Fisk, A.T. (2013). Fifty years later: trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lak Erie. *Biological Invasions*, *15*(8), 1695-1711. doi: 10.1007/s10530-012-0401-z.

Harvey, B. (2009). A biological synopsis of northern pike (*Esox lucius*). *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, *2885*(31).

Heady, W.N. & Moore, J.W. (2013). Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. *Oecologia*, *172*(1), 21-34. doi: 10.1007/s00442-012-2483-9.

Heins, D.C., Knoper, H., & Baker, J.A. (2016). Consumptive and non-consumptive effects of predation by introduced northern pike on life-history traits in threespine stickleback. *Evolutionary Ecology Research*, *17*, 355-372.

Heuvel, C.E., Haffner, G.D., Zhao, Y., Colborne, S.F., Despenic, A., & Fish, A.T. (2019). The influence of body size and season on the feeding ecology of three freshwater fishes with different diets in Lake Erie. *Journal of Great Lakes Research*, *45*(4), 795-804. doi: 10.1016/j.jglr.2019.05.001.

Hobson, K.A. (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, *120*(3), 314-326. doi: 10.1007/s004420050865.

Hobson, K.A., Schell, D.M., Renouf, D., & Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(3), 528-533.

Hutchinson, G.E. (1957). Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, *22*, 415–427

Hynes, H.B.N. (1950). The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *The Journal of Animal Ecology*, *19*(1), 36-58. doi: 10.2307/1570.

Keva, O., Tang, P., Käkelä, R., Hayden, B,m Taipale, S.J., Harrod, C., & Kahilainen, K.K. (2019). Seasonal changes in European whitefish muscle and invertebrate prey fatty acid composition in subarctic lake. *Freshwater Biology*, *64*(11), 1908-1920. doi: 10.1111/fwb.13381.

Kiljunen, M., Peltonen, H., Lehtiniemi, M., Uusitalo, L., Sinisalo, T., Norkko, J., Kunnasranta, M., Torniainen, J., Rissanen, A.J., & Karjalainen, J. (2020). Benthic-pelagic coupling and trophic relationships in northern Baltic Sea food webs. *Limnology and Oceanography*, *65*(8), 1706-1722. doi: 10.1002/Ino.11413.

Kocovsky, P.M., Stoneman, A.T., & Kraus, R.T. (2014). Ecology and population status of trout-perch (*Percopsis omiscomaycus*) in western Lake Erie. *Journal of Great Lakes Research*, *40*(1), 208-214. doi: 10.1016/j.jglr.2013.09.004.

Lamberti, G.A., Chaloner, D.T., & Hershey, A.E. (2010). Linkages among aquatic ecosystems. *Journal of the North American Benthological Society*, *29*(1), 245-263. doi: 10.1899/08-166.1.

Lydersen, C., Vaquie-Garcia, J., Lydersen, E., Christensen, G.N., & Kovacs, K.M. (2017). Novel terrestrial haul-out behaviour by ringed seals (*Pusa hispida*) in Svalbard, in association with harbour seals (*Phoca vitilina*). *Polar Research*, *36*(1), p.1374124. doi: 10.1080/17518369.2017.1374124.

Madgett, A.S., Yates, K., Webster, L., McKenzie, C., & Moffat, C.F. (2019). Understanding marine food web dynamics using fatty acid signatures and stable isotope ratios: improving contaminant impacts assessments across trophic levels. *Estuarine, Coastal and Shelf Science*, *227*, p. 106327. doi: 10.1016/j.ecss.2019.106327.

Matich, P., Heithaus, M.R., & Gerner, M. (2014). Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. *The Journal of Animal Ecology*, *83*(1), 199-213. doi: 10.1111/1365-2656012106.

Matley, J.K., Fisk, A.T., & Dick, T.A. (2015). Foraging ecology of ringed seals (*Pusa hispida*), beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in the Canadian High Arctic determined by stomach content and stable isotope analysis. *Polar Research*, *34*(1), p.24295-11. doi: 10.3402/polar.v34.24295.

McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecology Letters*, *8*(5), 513-523. doi: 10.1111/j.1461-0248.2005.00742.x.

Matthews, B. & Mazumder, A. (2004). A critical evaluation of intrapopulation variation of $\delta^{13}C$ and isotopic evidence of individual specialization. *Oecologia*, *140*(2), 361-371. doi: 10.1007/s00442-004-1579-2.

McCutchan, J.H., Lewis, W.M., Kendall, C., & McGrath, C.C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, *102*(2), 378-390. doi: 10.1034/j.1600-0706.2003.12098.x.

McMeans, B.C., Olin, J.A., & Benz, G.W. (2009). Stable-isotope comparisons between embryos and mothers of a placentatrophic shark species. *Journal of Fish Biology*, *75*(10), 2464-2474. doi: 10.1111/j.1095-8649.2009.02402.x.

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*, *482*, 17-28. doi: 10.3354/meps10278.

Mikhail, M.Y. & Welch, H.E. (1989). Biology of Greenland cod, *Gadus ogac*, at Saqvaqjuac, northwest coast of Hudson Bay. *Environmental Biology of Fishes*, *26*(1), 49-62. doi: 10.1007/BF00002475CODEN:EBFID3.

Montgomery, W.L., McCormick, S.D., Naiman, R.J., Whoriskey Jr., F.G.& Black, G.A. (1983). Spring migratory synchrony of salmonid, catostomid, and cyprinid fishes in Rivière à la Truite, Québec. *Canadian Journal of Zoology*, *61*(11), 2495-2502. doi: 10.1139/z83-331.

Morin, R., Dodson, J.J., & Power, G. (1981). The migrations of anadromous cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) in estuaries of eastern James Bay. *Canadian Journal of Zoology*, *59*(8), 1600-1607. doi: 10.1139/z81-219.

Morin, R. & Dodson, J.J. (1986). Chapter 15 the ecology of fishes in James Bay, Hudson Bay and Hudson Strait. *Elsevier Oceanography Series*, *44*, 293-326. doi: 10.1016/S0422-9894(08)70908-5.

Morinville, G.R. & Rasmussen, J.B. (2006). Marine feeding patterns of anadromous brook trout (*Salvelinus fontinalis*) inhabiting an estuarine river fjord. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(9), 2011-2027. doi: 10.1139/f06-097.

Nelson, P.A. & Dick, T.A. (2002). Factors shaping the parasite communities of trout-perch, *Percopsis omiscomaycus* Walbaum (Osteichthyes: Percopsidae), and the importance of scale. *Canadian Journal of Zoology*, *80*(11), 1986-1999. doi: 10.1139/z02-188.

Ogloff, W.R., Ferguson, S.H., Tallman, R.F., & Davoren, G.K. (2020). Diet of capelin (*Mallotus villosus*) in the Eastern Canadian Arctic inferred from stomach contents and stable isotopes. *Polar Biology*, *43*(9), 1273-1285. doi: 10.1007/s00300-020-02707-1.

Phillips, D.L. & Eldridge, P.M. (2006). Estimating the timing of diet shifts using stable isotopes. *Oecologia*, *147*(2), 195-203. doi: 10.1007/s00442-005-0292-0.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., & Ward, E.J. (2014). Best practices for use of stable isotopes mixing models in food-web studies. *Canadian Journal of Zoology*, *92*(10), 823-835. doi: 10.1139/cjz-2014-0127.

Pintor, L.M., McGhee, K.E., Roche, D.P. & Bell, A.M. (2014). Individual variation in foraging behavior reveals a trade-off between flexibility and performance of a top predator. *Behavioral Ecology and Sociobiology*, *68*(10), 1711-1722. doi: 10.1007/s00265-014-1779-7.

Polis, G.A. (1984). Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *The American Naturalist*, *123*(4), 541-564. doi: 10.1086/284221.

Polis, G.A., Anderson, W.B., & Holt, R.D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, *281*(1), 289-316. doi: 10.1146/annurev.ecolsys.28.1.289.

Post, D.M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, *83*(3), 703-718. doi: 10.1890/0012-9658(2002)083[0703:USITET]2.0.CO2.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., & Montaña, C.G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, *152*(1), 179-189. doi: 10.1007/s00442-006-0630-x.

R Core Team. (2021). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL https://www.R-project.org/.

Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J., & Sawatzky, C.D. (2006). General effects of climate change on Arctic fishes and fish populations. *AMBIO*, *35*(7), 370-380. doi: 10.1579/0044-7447(2006)35[370:GEOCCO]2.0.CO2.

Rennie, M.D., Sprules, W.G., Johnson, T.B., & Kraft, C. (2009). Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(12), 2096-2108. doi: 10.1139/F09-139CODEN:CJFSDX.

Rezek, R.J., Massie, J.A., Nelson, J.A., Santos, R.O., Viadero, N.M., Boucek, R.E. & Rehage, J.S. (2020). Individual consumer movement mediates food web coupling across a coastal ecosystem. *Ecosphere*, *11*(12). doi: 10.1002/ecs2.3305.

Rohtla, M., Vetemaa, M., Urtson, K, & Soesoo, A. (2012). Early life migration patterns of Baltic Sea pike *Esox lucius*. *Journal of Fish Biology*, *80*(4), 886-893. doi: 10.1111/j.1095-8649.2012.03226.x.

Rooney, N., McCann, K., Gellner, G., & Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, *442*(7100), 265-269. doi: 10.1038/nature04887.

Saint-Jacques, N., Harvey, H.H., & Jackson, D.A. (2000). Selective foraging in the white sucker (*Catostomus commersoni*). *Canadian Journal of Zoology*, *78*(8), 1320-1331. doi: 10.1139/cjz-78-8-1320.

Schindler, D.E., & Scheuerell, M.D. (2002). Habitat coupling in lake ecosystems. *Oikos*, *98*, 177-189.

Schreiber, S. & Rudolf, V.H.W. (2008). Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. *Ecology Letters*, *11*(6), 576-587. doi: 10.1111/j.1461-0248.2008.01171.x.

Scott, W. B. & Crossman, E.J. (1973). Freshwater fishes of Canada. Oakville, Ontario: Galt House Publishing.

Seubert, E.A., Hussey, N., Powers, S.P., Valentine, J.F., & Drymon, J.M. (2019). Assessing trophic flexibility of a predator assemblage across a large estuarine seascape using blood plasms stable isotope analysis. *Food Webs*, *21*, e00132. doi: 10.1016/j.fooweb.2019.e00132.

Shikano, T., Shimada, Y., Herczeg, G., & Merilä, J. (2010). History vs. habitat type: explaining the genetic structure of European nine-spined stickleback (*Pungitius pungitius*) populations. *Molecular Ecology*, *19*(6), 1147-1161. doi: 10.1111/j.1365-294X.2010.04553.x.

Stock, B.C. & Semmens, B.X. (2016). Unifying error structures in commonly used biotracer mixing models. *Ecology*, *97*(10), 2562-2569. doi: 10.1002/ecy.1517.

Svanbäck, R. & Bolnick, D.I. (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society*, *274*(1611), 839-844. doi: 10.1098/rspb.2006.0198.

Swanson, H.K., Lysy, M., Power, M., Stakso, A.D., Johnson, J.D., & Reist, J.D. (2015). A new probabilistic methods for quantifying n-dimensional ecological niches and niche overlap. *Ecology*, *96*(2), 318-324. doi: 10.1890/14-0235.1

Sweeting, C.J., Polunin, N.V.C., & Jennings, S. (2006). Effects of chemical lipid extraction and arithmetic lipid correct on stable isotope ratios of fish tissues. *Rapid Communications in Mass Spectrometry*, *20*(4), 595-601. doi: 10.1002/rcm.2347.

Tollit, D., Greenstreet, SPR., & Thompson, P. (1997). Prey selection by harbour seals, *Phoca vitulina*, in relation to variations in prey abundance. *Canadian Journal of Zoology*, *75*(9), 1508-1518.

Vander Zanden, M.J. & Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, *83*(8), 2152-2161. doi: 10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO2.

Vesin, J-P, Leggett, W.C., & Able, K.W. (1981). Feeding ecology of capelin (*Mallotus villosus*) in the estuary and western gulf of St. Lawrence and its multispecies implications. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(3), 257-267. doi: 10.1139/f81-037.

Viljanen, M. (1983). Food and food selection of cisco (*Coregonus albula* L.) in a dysoligotrophic lake. *Hydrobiologia*, *101*(1-2), 129-138. doi: 10.1007/BF00008665.

Vincent, C., Huon, M., Caurant F., Dabin, W., Deniau, A., Dixneuf, S., Dupuis, L., Elder, J-F., Fremau, M-H., Hassani, S., Hemon, A., Karpouzopoulos, J., Lefeuvre, C., McConnell, B.J., Moss, S.E.W., Provost, P., Sptz, J., Turpin, Y., & Ridouz, V. (2017). Grey and harbour seals in France: Distribution at sea, connectivity and trends in abundance at haulout sites. *Deep-Sea Research Part II: Tropical Studies in Oceanography*, *141*, 294-305. doi: 10.1016/j.dsr2.2017.04.004.

Walters, A.W., Barnes, R.T. & Post, D.M. (2009). Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. *Canadian Journal of Fisheries and Aquatic Sciences, 66*(3), 439-448. doi: 10.1139/F09-008.

Welker, T.L. & Scarnecchia, D.L. (2003). Differences in species composition and feeding ecology of catostomid fishes in two distinct segments of the Missouri River, Northern Dakota, U.S.A. *Environmental Biology of Fishes*, *68*(2), 129-141. doi: 10.1023/B:EBFI.0000003831.51734.ed.

Werner, E.E. & Gilliam, J.F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, *15*(1), 393-425. doi: 10.1146/annurev.es.15.110184.002141.

Wilder, D.G. (1951). A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis* (Mitchill)). *Journal of the Fisheries Research Board of Canada*, *9*,169– 203.

Young, B.G., Loseto, L.L., & Ferguson, S.H. (2010). Diet differences among age classes of Arctic seals: evidence from stable isotope and mercury biomarkers. *Polar Biology*, *33*(2), 153-162. doi: 10.1007/s00300-009-0693-3.

Yurkowski, D.J., Hussey, N.E., Ferguson, S.H., & Fisk, A.T. (2018). A temporal shift in trophic diversity among a predator assemblage in a warming Arctic. *Royal Society Open Science*, *5*(10), p.180259.

Yurkowski, D.J., Ferguson, S.H., Semeniuk, C.A.D., Brown, T.M., Muir, D.C.G., & Fisk, A.T. (2016). Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. *Oecologia*, *180*(3), 631-644. doi: 10.1007/s00442-015-3384-5.

2.8 Tables and Figures

Table 2-1. Fish and seal species $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ muscle values (‰, mean ± SE), plus C:N ratio (mean ± SE), the posterior medians (%) and 95% credible intervals (CI) of the freshwater-derived resources, and the mode and CI for the 95% probability niche size (‰^{3}) for each species

Species	n	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	C:N	Freshwater-derived resources (%)	Niche Size (‰^{3})
				Muscle			
trout-perch	19	-26.52 ± 0.10	9.80 ± 0.06	3.38 ± 0.37	3.06 ± 0.01	0.99 (0.97-1)	0.17 (0.11-0.33)
longnose sucker	13	-27.09 ± 0.16	7.81 ± 0.11	2.67 ± 0.23	3.11 ± 0.01	0.99 (0.96-1)	0.21 (0.13-0.46)
white sucker	10	-27.93 ± 0.36	8.21 ± 0.13	4.20 ± 0.45	3.05 ± 0.01	0.99 (0.94-1)	0.54 (0.29-1.22)
burbot	6	-25.79 ± 0.25	8.62 ± 0.51	4.89 ± 1.32	3.10 ± 0.03	0.96 (0.87-1.00)	0.52 (0.27-1.69)
northern pike CR†	13	-26.33 ± 0.41	9.74 ± 0.22	5.58 ± 0.56	3.08 ± 0.02	0.79 (0.65-0.94)	0.98 (0.62-2.25)
northern pike GC†	20	-25.53 ± 0.62	6.78 ± 0.22	15.29 ± 0.86	3.05 ± 0.01	0.74 (0.57-0.95)	9.27 (6.10-17.59)
lake whitefish	68	-23.69 ± 0.34	9.90 ± 0.22	8.41 ± 0.43	3.07 ± 0.01	0.71 (0.64-0.77)	10.70 (8.08-14.44)
cisco	28	-21.68 ± 0.35	13.57 ± 0.23	12.53 ± 0.48	3.11 ± 0.01	0.36 (0.30-0.41)	2.00 (1.35-3.26)
brook trout	7	-21.93 ± 0.28	15.26 ± 0.25	15.43 ± 0.41	3.10 ± 0.02	0.19 (0.10-0.30)	0.09 (0.05-0.25)
nine-spine stickleback	5*	-21.20 ± 0.93	11.23 ± 1.15	15.44 ± 1.16	3.06 ± 0.04	0.17 (0.04-0.30)	0.18 (0.10-0.82)
fourhorn sculpin	29	-20.64 ± 0.11	15.07 ± 0.24	15.74 ± 0.21	3.21 ± 0.01	0.10 (0.08-0.14)	0.73 (0.49-1.17)
Greenland cod	20	-19.98 ± 0.10	17.00 ± 0.17	18.29 ± 0.09	3.13 ± 0.01	0.05 (0-0.09)	0.13 (0.08-0.24)
harbour seal	4	-19.87 ± 0.23	18.06 ± 0.19	16.80 ± 0.25	3.03±0.01	0.03 (0-0.10)	0.04 (0.02-0.18)
capelin	40	-21.27 ± 0.08	14.71 ± 0.09	17.99 ± 0.08	3.16 ± 0.01	0.01 (0-0.25)	0.16 (0.12-0.25)
ringed seal	5	-19.85 ± 0.33	17.13 ± 0.38	17.12 ± 0.04	3.19 ± 0.02	0.01 (0-0.07)	0.06 (0.03-0.20)
walleye	1	-28.34	10.7	4.08	3.19		

*n=4 for $\delta^{34}S$ and niche size

†CR= Churchill River, GC= Goose Creek.

Table 2-2. Prey baseline species (invertebrates and vegetation) $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values (‰, mean ± SE) throughout the Churchill River, estuary, and Hudson Bay. Bolded species are the source members that were applied in the MixSIAR model and the trophic position equation.

Species	n	$\delta^{13}C$ (‰)	N	$\delta^{15}N$ (‰)	n	$\delta^{34}S$ (‰)
Churchill River						
snail*	7	-27.32 ± 0.57	7	3.72 ± 0.07	7	13.25 ± 1.14
leech*	7	-26.20 ± 0.73	7	6.42 ± 0.44	6	12.89 ± 2.15
freshwater mussel*	**3**	**-27.34 ± 1.17**	**3**	**4.67 ± 0.027**	**2**	**4.33 ± 0.18**
amphipod*	1	-26	1	2.4	1	17.12
midge larvae*	1	-22.18	1	8.09	1	16.77
pondweed	1	-29.22	1	3.02	1	9.87
bur-weed	1	-29.46	1	3.95	1	24.75
milfoil	1	-37.62	1	5.04	1	-13.55
Estuary						
lions mane jellyfish	2	-21.32 ± 0.65	2	13.03 ± 0.28	2	19.64 ± 0.046
midge larvae*	2	-18.79 ± 0.54	2	5.51 ± 1.22	0	
amphipod*	1	-21.7	1	8.51	0	
unknown jellyfish*	1	-20.34	1	11.88	0	
unknown vegetation	1	-32.02	1	3.47	1	6.6
Hudson Bay						
blue mussel	**13**	**-21.01 ± 0.30**	**13**	**8.58 ± 0.15**	**13**	**16.30 ± 0.20**
amphipod*	6	-18.68 ± 0.84	6	7.46 ± 0.69	3	15.09 ± 0.12
unknown mussel*	3	-17.91 ± 0.064	3	7.81 ± 0.026	3	12.23 ± 0.21
snail*	2	-18.00 ± 0.13	2	9.85 ± 0.012	2	15.18 ± 00.31
shrimp	1	-18.56	1	14.88	0	
seaweed	1	-18.64	1	4.86	1	20.62

*species that were combined for stable isotope analysis due to their small body size.

Table 2-3. The frequency of occurrence of items found in the stomachs of each fish species from the lower Churchill River area, Manitoba between 2019-2020. All stomachs were empty for capelin, walleye, trout-perch, and nine-spine stickleback.

Prey species	brook trout	burbot	cisco	fourhorn sculpin	Greenland cod	lake whitefish	longnose sucker	northern pike	white sucker
invertebrates	0.29		0.41	0.46	0.70	0.93		0.42	
benthic mollusks				0.04		0.43			
fish	0.86	0.67	0.22	0.11	0.65	0.07		0.48	
vegetation			0.19	0.07	0.05	0.19		0.09	
organic matter		0.33	0.30	0.32	0.15	0.22	1.00	0.09	1.00
# stomachs with contents	6	3	25	21	19	62	13	23	10
# empty stomachs	1	0	2	7	1	5	0	10	0

Table 2-4. Total isotopic niche overlap probability (%) of the prediction ellipsoids for the seal and fish species muscle data present in the lower Churchill River area, Manitoba based on δ^{13}C, δ^{15}N, and δ^{34}S separated by prediction ellipsoid (a- 95% region and b- 40% region). For some species sample size was insufficient to determine the niche overlap. A color gradient was applied such that darker colors coordinate with higher overlap. Significant overlap is defined as overlap ≥60%.

(a)

Species A \ Species B	brook trout	burbot	capelin	cisco	fourhorn sculpin	Greenland cod	lake whitefish	longnose sucker	northern pike Churchill River	northern pike Goose Creek	trout-perch	white sucker	seals
brook trout		0	0.2 (0-2)	37 (3-87)	57 (24-89)	3 (0-13)	0.1 (0-1)	0	0	0	0	0	10 (0-47)
burbot	0		0	0	0	0	87 (58-100)	2 (0-11)	19 (1-49)	37 (3-81)	9 (1-23)	19 (2-45)	0
capelin	0.2 (0-1)	0		3 (0-18)	10 (1-37)	12 (1-39)	0	0	0	0	0	0	3 (0-23)
cisco	2 (0-7)	0	0.2 (0-1)		25 (13-38)	0.1 (0-1)	31 (12-59)	0	5 (0-19)	0	0.1 (0-1)	0	0.3 (0-2)
fourhorn sculpin	12 (3-27)	0	2 (0-6)	63 (41-84)		4 (1-11)	8 (2-21)	0	0	0	0	0	16 (4-40)
Greenland cod	6 (0-29)	0	9 (1-25)	3 (0-23)	49 (8-90)		0	0	0	0	0	0	63 (25-97)
lake whitefish	0	8 (4-16)	0	7 (2-16)	0.9 (0-3)	0		2 (1-5)	19 (8-34)	14 (3-30)	2 (0-3)	6 (2-13)	0
longnose sucker	0	6 (0-38)	0	0	0	0	98 (87-100)		19 (0-68)	4 (0-53)	0	50 (18-87)	0
northern pike Churchill River	0	6 (0-20)	0	16 (1-52)	0	0	93 (75-100)	3 (0-11)		8 (0-50)	19 (8-33)	15 (2-37)	0
northern pike Goose Creek	0	2 (0-7)	0	0	0	0	12 (4-26)	0	0.4 (0-2)		0	0.5 (0-2)	0
trout-perch	0	27 (5-65)	0	3 (0-30)	0	0	97 (85-100)	0	55 (31-83)	5 (0-50)		3 (0-24)	0
white sucker	0	14 (2-41)	0	0	0	0	93 (73-100)	25 (7-52)	42 (9-77)	21 (0-84)	0.6 (0-4)		0
seals	2 (0-8)	0	0.4 (0-3)	0.7 (0-6)	36 (10-67)	20 (6-42)	0	0	0	0	0	0	

Table 2-4. Continued

(b)

Species A \ Species B	brook trout	burbot	capelin	cisco	fourhorn sculpin	Greenland cod	lake whitefish	longnose sucker	northern pike Churchill River	northern pike Goose Creek	trout-perch	white sucker	seals
brook trout		0	0	1 (0-11)	13 (1-35)	0.5 (0-3)	0	0	0	0	0	0	0.5 (0-5)
burbot	0		0	0	0	0	36 (10-66)	0.08 (0-1)	0.5 (0-5)	1 (0-9)	0.7 (0-4)	1 (0-8)	0
capelin	0	0		0	0.1 (0-1)	0.2 (0-1)	0	0	0	0	0	0	0
cisco	0.1 (0-1)	0	0		5 (2-10)	0	2 (0-6)	0	0.4 (0-2)	0	0	0	0
fourhorn sculpin	1 (0-5)	0	0	12 (2-27)		0.5 (0-2)	0.27 (0-2)	0	0	0	0	0	3 (0-9)
Greenland cod	0.1 (0-1)	0	0.7 (0-3)	0	0.4 (0-4)		0	0	0	0	0	0	15 (1-45)
lake whitefish	0	2 (0-4)	0	0.3 (0-1)	0	0		0.3 (0-1)	2 (1-6)	0.6 (0-3)	0.2 (0-0)	0.9 (0-2)	0
longnose sucker	0	0.2 (0-2)	0	0	0	0	4 (0-28)		0.4 (0-3)	0	0	9 (0-30)	0
northern pike Churchill River	0	0.8 (0-4)	0	0.2 (0-1)	0	0	33 (11-59)	0.2 (0-1)		0	3 (0-7)	2 (0-8)	0
northern pike Goose Creek	0	0.2 (0-1)	0	0	0	0	0.9 (0-3)	0	0		0	0	0
trout-perch	0	3 (0-17)	0	0	0	0	4 (0-24)	0	24 (10-42)	0		0	0
white sucker	0	3 (0-10)	0	0	0	0	14 (0-42)	3 (0-10)	3 (0-16)	0	0		0
seals	0.07 (0-1)	0	0	0	1 (0-6)	2 (0-7)	0	0	0	0	0	0	
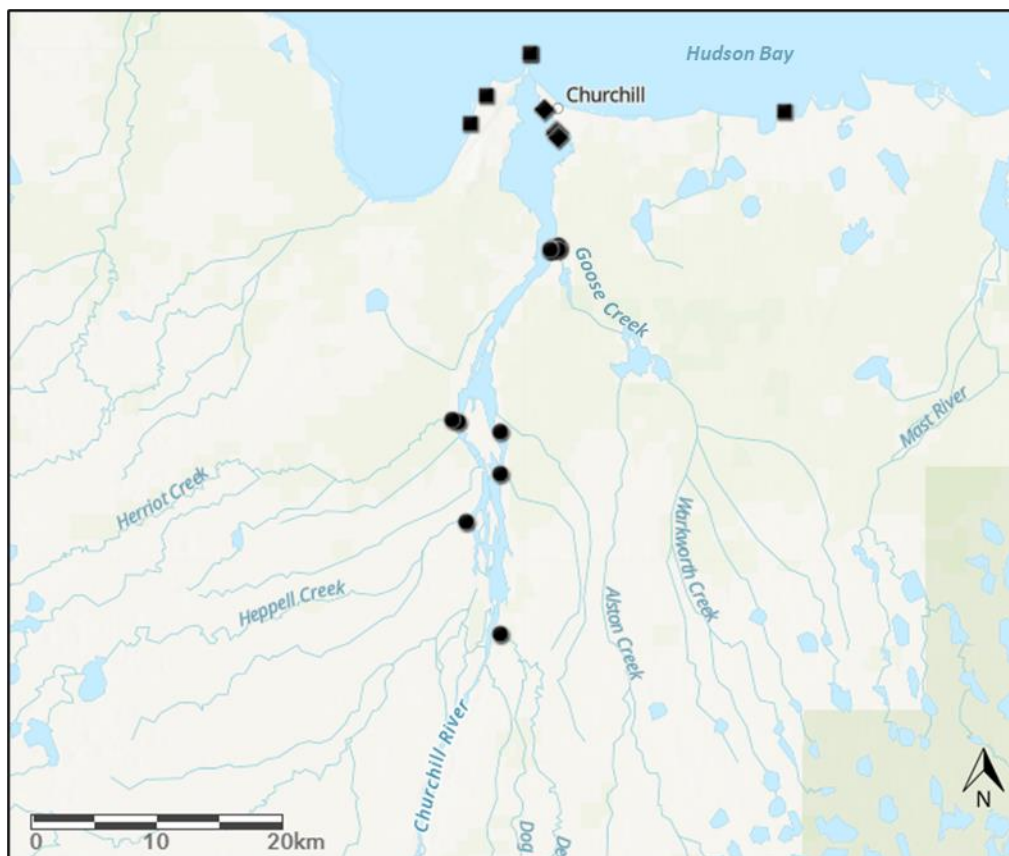
Figure 2-1. Collection sites throughout the lower Churchill River (Hudson Bay, estuary, Goose Creek, and Churchill River), Manitoba. Circles are the collection sites within the Churchill River, diamonds are the collection sites within the estuary, and squared are the collection sites within Hudson Bay.
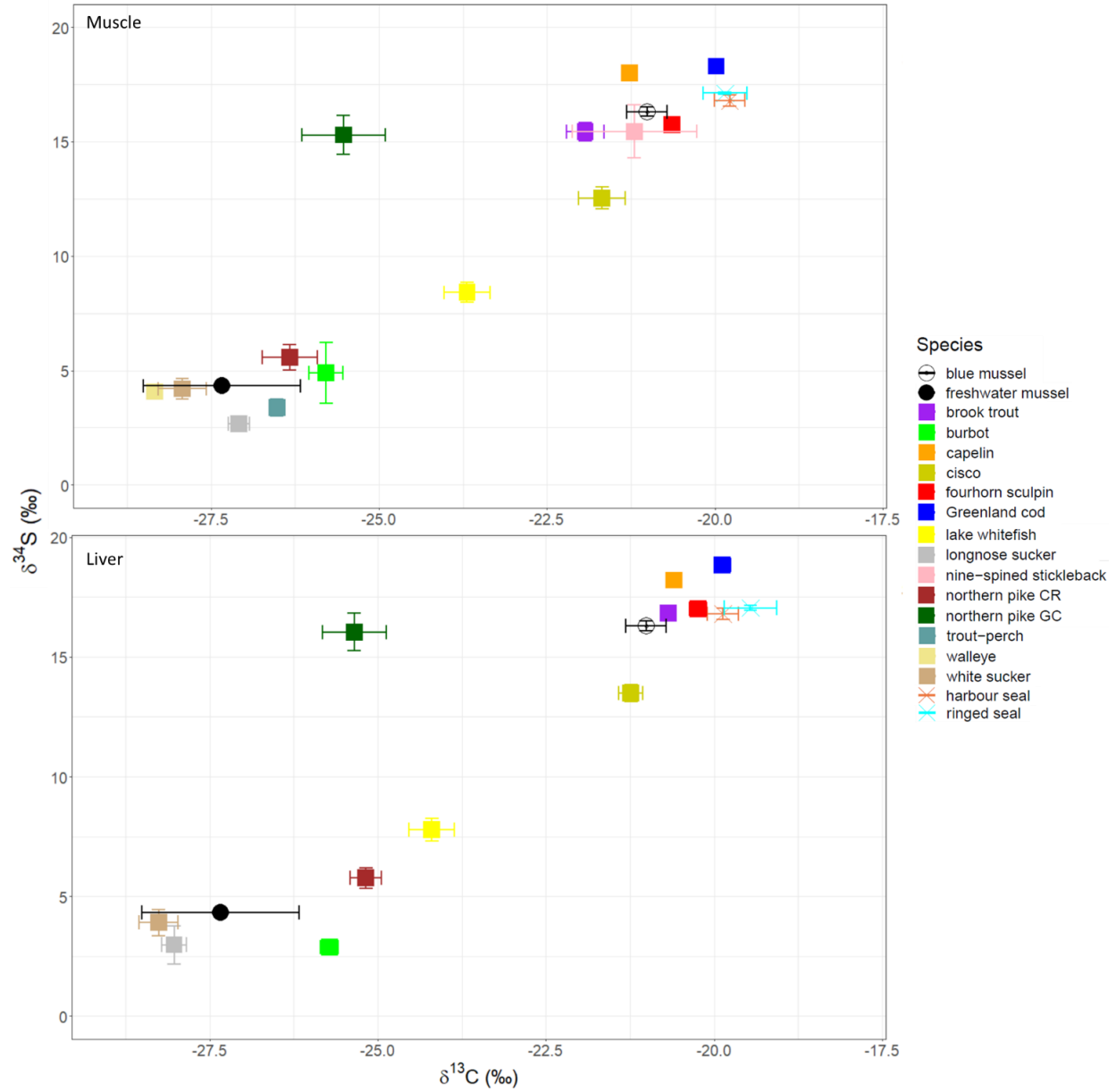
Figure 2-2. Stable isotope biplot of $\delta^{13}C$ and $\delta^{34}S$ (mean ± standard error) of muscle (top) and liver (bottom) from 16 consumers and 2 prey used as the sources for the mixing model. CR= Churchill River and GC= Goose Creek. Hair samples were used for the harbour seals instead of liver.
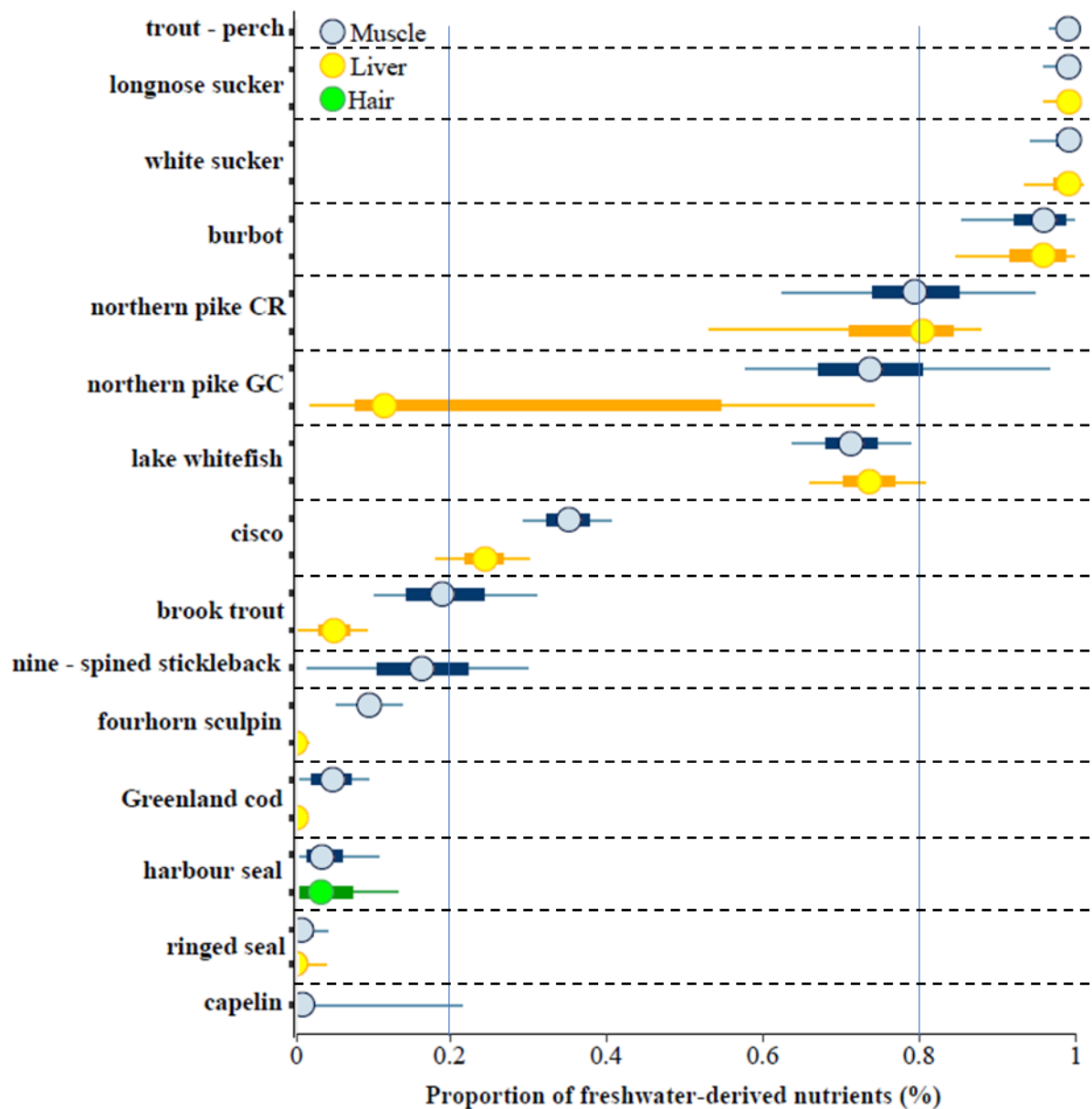
Figure 2-3. Median proportion of freshwater resource use with 50% (thick lines) and 90% credible intervals (thin lines) based on the δ^{13}C and δ^{34}S ratios for each species. Species that have a median proportion of ≤0.2 are considered to be principally foraging on marine sources, whereas species with a median proportion of ≥0.8 are considered to be mainly foraging on freshwater sources. CR= Churchill River and GC= Goose Creek.
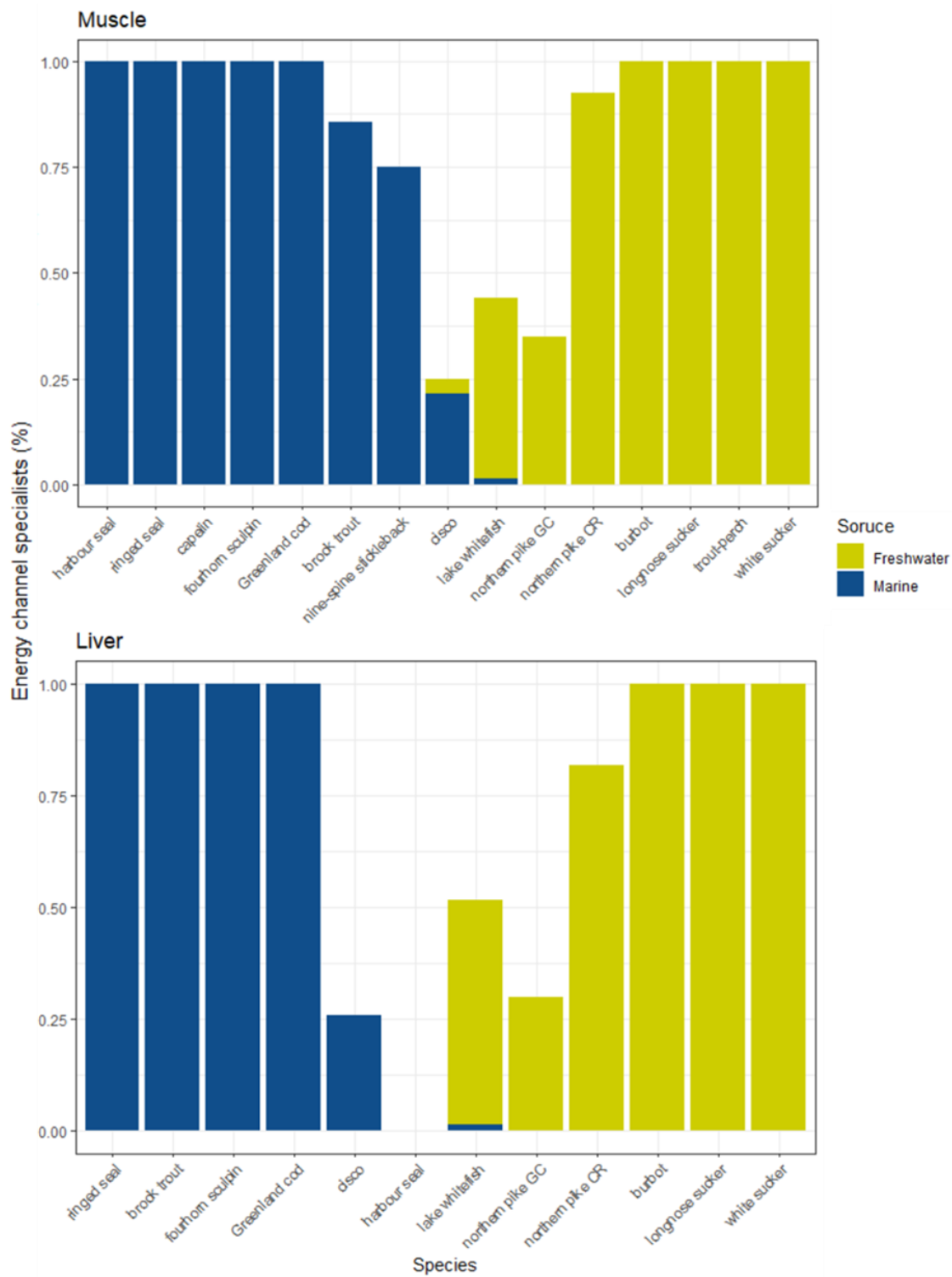
Figure 2-4. Percentage of individuals of each species consuming ≥80% freshwater-derived resources or marine-derived resources for muscle (top) and liver (bottom) tissues. CR= Churchill River and GC= Goose Creek. Hair samples were used for the harbour seals instead of liver.
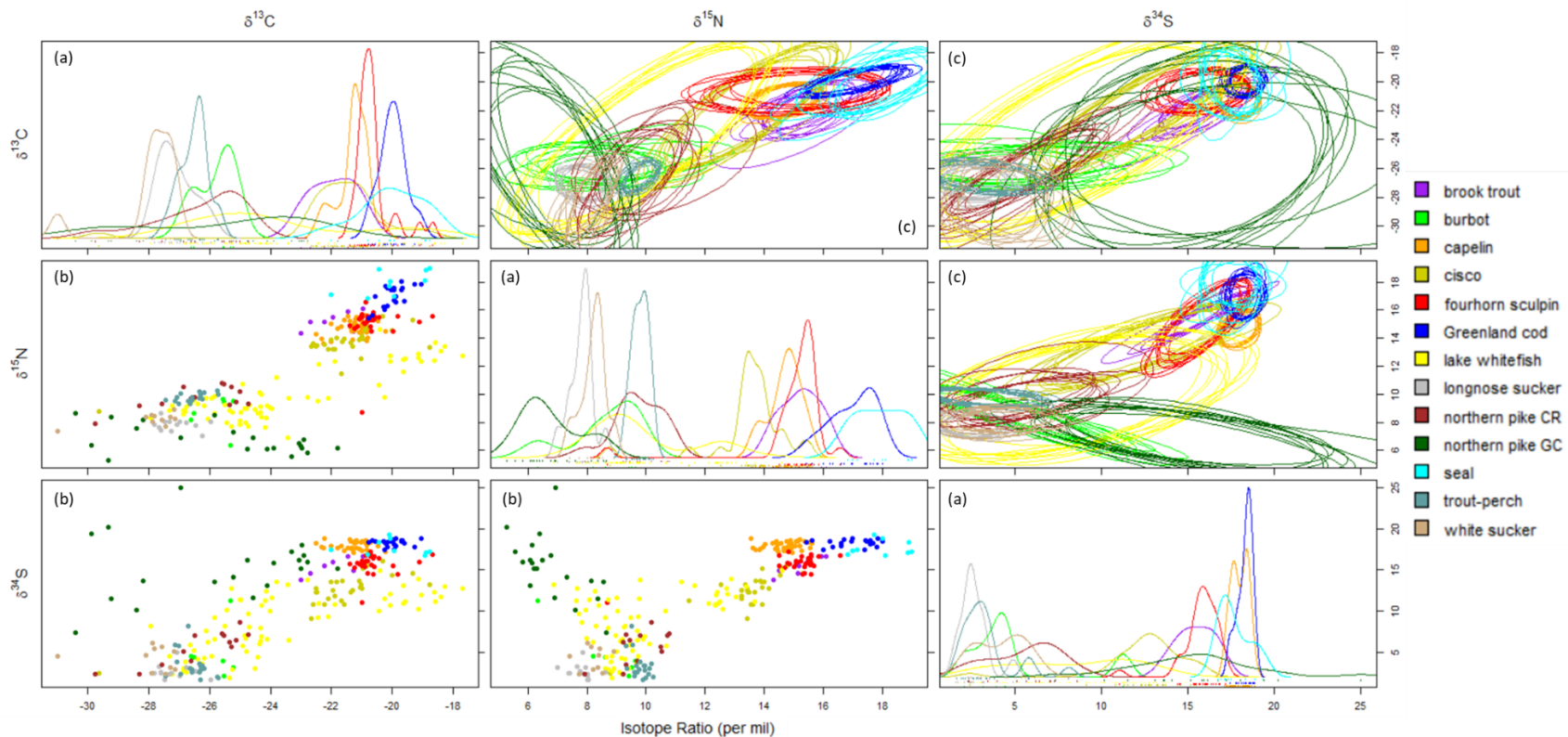
Figure 2-5. A 2-dimensional projection of ten 3-dimensional niche regions. Stable isotopes (δ^{13}C, δ^{15}N, and δ^{34}S, ‰) were used for twelve fish species groupings and one seal grouping based on muscle tissue. The line plots (a) are one-dimensional density plots. The point plots (b) are two-dimensional scatterplots or the raw stable isotope data. The elliptical projections (c) are the pairings of δ^{13}C, δ^{15}N, and δ^{34}S showing two-dimensional projections of the 95% probabilistic niche regions based on 3-dimensional data. Harbour and ringed seals were combined into one seal group. CR= Churchill River and GC= Goose Creek.

3.0 Chapter 3: Trophic structure and a temporal shift in trophic diversity of mobile consumers in a subarctic estuary

3.1 Abstract

Food webs describe trophic relationships in ecosystems between species and organizes organisms in different trophic positions. Links within a food web provide information on species interactions and ecosystem structure and function. Trophic diversity is related to factors such as habitat and nutrient availability, which can be influenced by environmental change and anthropogenic activities. For example, trophic diversity within the Churchill River may have increased after a weir was constructed in 1998 since the weir would have changed the availability of habitat space, quality, and the structure of the community by creating a physical barrier in the river. The objective of this study was to quantify the trophic position of consumers within the lower Churchill River area, as well as the trophic diversity of the community between the early 1990s, before the installation of the Churchill River weir, and 2019-2020 time period. I used stable isotopes (δ^{13}C and δ^{15}N) to quantify population and individual variation within the trophic positions for thirteen fish species and two seal species and to assess six community-level metrics between both time periods. Species that mainly foraged on freshwater resources (i.e., northern pike, white sucker, burbot, trout-perch) were at lower trophic positions (2.48-3.40) than species that foraged on marine resources (i.e., capelin, fourhorn sculpin, Greenland cod, and ringed seals; trophic positions = 3.64-5.09). Six community-wide metrics of the fish assemblage (cisco, fourhorn sculpin, and lake whitefish) revealed lower trophic diversity and more trophic redundancy in 2019-2020 than the 1993-1995 sampling period. Greater trophic redundancy means that individual species are now playing similar trophic roles within the food web, which may help promote ecosystem stability and reduce vulnerability to secondary extinction events. This project provides a greater understanding of the trophic structure of consumers in a subarctic estuary and how anthropogenic change may have affected the trophic diversity within the Churchill River and estuary.

3.2 Introduction

Food webs are complex systems of energy flow that are interconnected by direct links between consumers and resources (Elton, 1927). Organisms can then be arranged into trophic levels based on groupings of energy consumed from primary producers up to apex predators, with each trophic level relying on the previous level as a source of energy (Lindemann, 1942). The notion that many species feed omnivorously and consume prey at multiple trophic levels led to the concept of trophic position, which allowed for a more continuous measure of where species fit into the trophic hierarchy (Hobson & Welch, 1992; Vander Zanden & Rasmussen, 1996; Vander Zanden et al., 1999). Understanding the trophic structure and interactions within a system can provide information on sources of productivity and nutrient pathways (Frisch et al., 2014). Species can vary in their trophic position in relation to several abiotic and biotic factors, such as seasonal food pulses, body size, and choice of habitat (Eloranta, 2015; Hayden et al., 2019; McMeans et al., 2019; Roach et al., 2009; Romanuk et al., 2011; Sabo et al., 2010). In addition, there can be high variability in the trophic position among individuals of a species due to differential behavioural responses to resource availability.

Diet shifts can occur throughout the life span of a consumer due to changes in morphology from growth, habitat use, prey availability, and foraging strategies (Grey, 2001; Werner & Hal, 1976). Ontogenetic shifts in diet between size classes and life history stages are common for many fish species (Grey, 2001; Power et al., 2002) where the predators are usually larger than their prey, resulting in increasing trophic position with increasing body size (Layman et al., 2005). An increase in body size, and in turn gape size, allows for the use of a broad range of resources and a greater mobility between habitats across larger spatial scales (Winemiller, 1990). Therefore, quantifying ontogenetic changes in the trophic position of consumers will provide finer scale insight into the trophic dynamics of the ecosystem.

Fish occupy a wide variety of trophic positions due to their morphological (gill rakers vs. teeth) and behavioural (filter feeding vs. particulate feeding) feeding patterns (Costalago et al., 2012) and play key roles in food webs. For example, Arctic cod (*Boreogadus saida*) and capelin are key resources for top predators in the Arctic and temperate environments (Hop & Gjøsæter, 2013). Changes in the abundance, distribution, and competition of key prey fish species will

have reverberating impacts on the marine food web across all trophic levels. Therefore, these shifts in species distributions and a re-organization of species composition can affect the trophic diversity within the community (Hop & Gjøsæter, 2013; Yurkowski et al., 2018). A community with high trophic diversity will result in several species occupying many different areas of the food web, resulting in more community variability in habitat and resource use. In contrast, trophic redundancy occurs when multiple species function similarly in the community, resulting in these species using similar resources and occupying the same trophic position or area in the food web (Polis et al., 2000; Yurkowski et al., 2018). However, over time, the trophic structure of communities can dramatically change in relation to climate and anthropogenic effects (e.g., shipping and pollution), where the impacts of both are pronounced and rapidly increasing in the Arctic (Bartley et al., 2019; McCann et al., 2005; Pecl et al., 2017).

Changes in the Arctic sea ice cover and temperatures have resulted in shifts in the distribution of many mobile consumers leading to changes in the species composition of fish communities. For example, within the Barents Sea there has been a decline in the abundance of Arctic-associated fish species and an increase of more subarctic-associated fish species (Frainer et al., 2017; Pecl et al., 2017). As well, diet shifts of a predator could be due to the predator responding to changes in the prey base. Within Hudson Bay, Gaston et al. (2003) suggested a decrease of Arctic cod, due to changes in seasonal ice cover, resulted in diet shifts of a seabird predator. Similar shifts in the prey base have been found throughout Hudson Bay and will continue to impact marine mammals and seabirds who mainly rely on fish as a resource (Florko et al., 2021). Therefore, understanding the trophic structure of specific areas within Hudson Bay, such as the lower Churchill River system in the southwest, is important since the degree of trophic shifts could vary throughout the Hudson Bay region.

Given the climatic changes within Hudson Bay and increasing anthropogenic activity, the lower Churchill River system in Manitoba, Canada is an ideal study site to investigate recent (years of 2019-2020) variation in trophic position of numerous mobile consumers allowing for a comparison of the trophic diversity of some members of the community in the early 1990s, before the construction of the Churchill River weir. Since 1976, around 75-90% of the Churchill River flow had been impounded and diverted to hydroelectric generating stations along the Nelson River (Kuzyk et al., 2008; Newbury et al., 1984), resulting in reduced water flow along

the Churchill River, which has affected community members' activities on the river and possibly the fish populations (W. Coughlin, personal communication, July 16, 2019). To increase water levels and improve river accessibility and fish abundance, the Churchill River weir was constructed in 1998. The weir is 13 km upstream from the river mouth and is a 3-km long rockfill dyke that extends across the river and causes water levels to rise upstream of the structure (Kuzyk et al., 2008).

The first objective of this chapter was to quantify the trophic positions of the Churchill marine/freshwater food web for mobile consumers (13 fishes and 2 seal species) within the lower Churchill River area at the individual and population level using stable isotope analysis (δ^{13}C and δ^{15}N), as well as to understand the ontogenetic effects on trophic position for many fish species. A second objective was to quantify changes in the trophic structure with certain members of the fish community between 1993-1995 with 2019-2020. Firstly, I hypothesized that trophic position would increase with age and body size across all species, allowing larger individuals to forage on larger prey that sit at higher trophic positions. Secondly, I hypothesized species that occupy a higher trophic position will have more variability in their trophic position between individuals due to a species' ability to consume a broader diversity of smaller, less mobile prey at lower trophic levels. Lastly, I hypothesized that trophic diversity within the fish community increased after the construction of the weir as a result of increased water levels and in turn habitat availability for mobile fishes.

3.3   Methods

3.3.1   Sample Collection and Preparation

During data collection I tried to sample all representative fish from each habitat (marine, estuary, and freshwater). As a result, thirteen fish species were collected using a combination of gillnets and angling during July 2019 and August 2020. Seal samples were provided opportunistically by local hunters. To quantify any trophic shifts over the spring-summer and summer seasons, different tissues, such as muscle, liver, and hair, were used for δ^{13}C and δ^{15}N analysis (Fry, 2006; Heady & Moore, 2013; Phillips & Eldridge, 2006). See Chapter 2 for specific details on methods for fish and seal sample collections, as well as morphometric measurements and internal structures collected.

During the summers of 1993-1995, fish were collected by North/South Consultants Inc. from the Churchill River and estuary. Fish were captured using beach seines nearshore and at coastal creek mouths by gill nets in other locations. Date, locations of capture, weight (g), length (mm), and sex were recorded for each individual. Lake cisco (n=23) and lake whitefish (n=21) were caught during each sampling year and fourhorn sculpin (n=9) were only caught during 1995. Sampling details are described in Baker et al. (1993).

Stable isotope analysis was used to provide a time-and space- understanding of trophic relationships between organisms (Fry, 2006), where carbon stable isotope ratios (δ^{13}C) reflect the source of dietary carbon (e.g., terrestrial/freshwater versus marine sources) and nitrogen stable isotope ratios (δ^{15}N) reflect the trophic position of consumers (Fry, 2006; Heady & Moore, 2013; Phillips & Eldridge, 2006). For trophic position estimates, freshwater mussels (n = 3) were used as the freshwater prey baseline species, whereas blue mussels (n = 13) were used as the marine prey baseline. As well, δ^{13}C and δ^{15}N were used together to estimate community-wide metrics to characterize decadal changes in the trophic structure of the fish community before and after the weir was constructed using three fish species (cisco, fourhorn sculpin, and lake whitefish). These three species were used since they were the only species that were caught during both time periods and are all able to take advantage of both the marine and freshwater resources. Both cisco and lake whitefish are considered anadromous species and therefore are good representatives of species that use both systems, and fourhorn sculpin are considered an estuarine species and therefore may consume both the marine and freshwater resources found within the estuary. See Chapter 2 for all details on how the 2019-2020 samples were prepared for stable isotope analysis. I confirmed lipids were successfully removed from the 2019 and 2020 samples based on the C:N ratios (Chapter 2). Stable isotope analysis was performed at the Chemical Tracers Laboratory, Great Lakes Institute for Environmental Research, at the University of Windsor during 2019-2020. A Delta V Advantage Mass spectrometer (Thermo Finnigan, San Jose, CA, USA) coupled to a Costech 4010 Elemental Combustion system (Costech, Valencia, CA, USA) and a ConFlo IV gas interface was used for the analysis. A triplicate was run for every 10th sample and have a measurement precision of 0.1‰ for both δ^{13}C and δ^{15}N. The 1993-1995 samples were analyzed at the Freshwater Institute with a duel inlet isotope ratio VG Optima mass spectrometer (Isoprime Inc., Manchester, UK) attached to an elemental analyzer

(Carlo Erba NA1500). An external laboratory working standard (Pharmamedia, a cottonseed protein) was run every 5 to 10 samples for a measurement precision of 0.07‰ and 0.05‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively. Lipids were not removed from the 1990s samples; therefore, a lipid normalization equation was applied to the $\delta^{13}C$ values to correct for the lipids not being extracted. The C:N ratios were used to normalize the $\delta^{13}C$ for lipid content. The equation for aquatic organisms is found in Post et al., (2007), $\delta^{13}C_{normalized}= \delta^{13}C_{untreated} - 3:32 + 0:99$ x C:N. The normalized $\delta^{13}C$ is comparable to the $\delta^{13}C$ after direct chemical lipid extraction (Post et al., 2007).

Fish ages were determined at AAE Tech Services Inc. in La Salle, Manitoba. Samples were either analyzed whole or sectioned (Appendix B, Table B-1). Annuli of otoliths were counted under a microscope with transmitted light. A quality assurance/quality control (QA/QC) was completed for about 60% of the 2019 samples and all the 2020 samples, where a second reader estimated the ages and then compared their age estimates to the first reader.

3.3.2 *Data Analysis*

All data analyses were conducted in R v. 4.0 (R Core Team, 2021). Stable isotope ratios of a single species can vary over time and space (Fry, 2006), therefore I determined if the mean species-specific $\delta^{13}C$ and $\delta^{15}N$ values for each tissue differed between sampling years using a Wilcoxon signed-rank test. The $\delta^{13}C$ and $\delta^{15}N$ values were checked for normality with quantile-quantile plots and histograms, and for heteroscedasticity with residual-fitted value plots. Non-parametric tests were used to test for spatial and temporal similarity and all correlation tests due to having small sample sizes. To assess if there were significant differences between the sampling years for each species a Wilcoxon signed-rank test was performed with a Holm-Bonferroni sequential correction to account for multiple comparisons. Results from these tests are found in Chapter 2. All species except for northern pike were combined. Northern pike were separated out into two groups, ones collected in Goose Creek during 2019 and others collected throughout the Churchill River during 2019 and 2020. Kendall's tau correlation tests were run to examine the correlation between trophic position and the difference in trophic position range as well as for body length and age. I examined the relationships between fish characteristics (e.g.,

age and body length) and trophic position with a linear regression on fish species with a sample size > 10. For the correlation and linear regression all significance tests had an $\alpha = 0.05$.

The scaled trophic position approach was used since the diet tissue discrimination factors ($\Delta^{15}N$) typically decrease with increasing prey $\delta^{15}N$ (Hussey et al., 2014). Therefore, trophic position for each mobile consumer was calculated using a one-source trophic position model (Post, 2002).

$$TP_{consumer} = TP_{baseline} + \frac{\delta 15 N consumer - \delta 15 N baseline}{\Delta 15 N}$$

The $\delta^{15}N$ of freshwater mussels (4.67 ± 0.03‰) was used as the baseline ($\delta^{15}N_{baseline}$) to estimate the trophic position for freshwater fishes, whereas the $\delta^{15}N$ of blue mussels (8.58 ± 0.15‰) was used to estimate the trophic position for marine fishes. Bivalvia consume microalgae, organic matter, and detritus and therefore feed at trophic position 2, which is assigned as the baseline value ($TP_{baseline}$) for the fishes (Jung et al., 2019; McMeans et al., 2013). I used freshwater mussels and blue mussels as the baseline prey species since $\delta^{15}N$ values can vary between marine and freshwater systems (Hesslein et al., 1991); therefore, using prey based on the known diet of the mobile consumers can account for that variation in $\delta^{15}N$ between each connected system ($\delta^{15}N_{consumer}$). For harbour seals and ringed seals, I used the $\delta^{15}N$ of capelin (14.71 ± 0.09‰). Capelin were used as the $TP_{baseline}$ (3.69) for harbour seals and ringed seals since both predators are mainly piscivorous and consume capelin (Ogloff et al., 2020; Thiemann et al., 2008). For the $\delta^{15}N$ of fishes, a diet-tissue discrimination factor of 3.67‰ was used for muscle and 2.80‰ was used for liver (Caut et al., 2009, Hobson et al., 1996; McCutchan et al., 2003). For ringed seals and harbour seals, I used 2.40‰, 3.10‰, and 3.00‰ for muscle, liver, and hair, respectively (Caut et al., 2009, Hobson et al., 1996; McCutchan et al., 2003).

A Bayesian inference package, SIBER v 2.1.6, in R was used to quantify the trophic diversity of the three-species fish assemblage (cisco, fourhorn sculpin, and lake whitefish) in the lower Churchill River system using six community-wide metrics (Jackson et al., 2011). Fish were collected from 1993-1995 before weir construction in 1998 and then approximately two

decades afterwards (2019-2020). I corrected for the Suess effect since there was a 25-year gap between the sampling periods. The Suess effect represents a decline in the $\delta^{13}C$ values of dissolved inorganic carbon due to the increased atmospheric CO_2 since the industrial period, which is resulting in an increase in oceanic CO_2 (Quay et al., 2003). de la Vega et al. (2019) reported a change of -0.01‰ per year in $\delta^{13}C$ values of dissolved inorganic carbon in the Arctic. Therefore, I subtracted 0.25‰ from the 1993-1995 data. For each time period, I then used SIBER to calculate four metrics measuring trophic diversity ($\delta^{13}C$ range, $\delta^{15}N$ range, mean distance to centroid, and total community area) and two metrics that estimate the extent of trophic redundancy (mean distance the nearest neighbour and standard deviation of the nearest neighbour) (Jackson et al., 2011; Layman et al., 2007). The standard ellipses represent the 40% niche size for each species, using approximately 40% of the data points within the ellipse to infer the population's core niche size. The $\delta^{13}C$ and $\delta^{15}N$ ranges are the distances between the fish assemblage in the community with the highest and lowest $\delta^{13}C$ and $\delta^{15}N$ values. These ranges represent the variability in basal carbon sources and relative trophic position between both time periods. Total community area is the total isotope area between the means of each species' niche and is less biased by convex hull extremities. The mean distance to centroid is the average Euclidean distance of each species to the $\delta^{13}C$-$\delta^{15}N$ centroid of the entire community and therefore represents species spacing between one another and provides information on the overall degree of trophic diversity. Mean nearest neighbour is the mean of the Euclidean distances to each species' nearest neighbour in bi-plot space and represents the density of species packing. The standard deviation of the nearest neighbour is a measure of the evenness of species packing in bi-plot space and is less influenced by sample size than the nearest neighbour distance (Jackson et al., 2011; Layman et al., 2007; Yurkowski et al., 2018). All six metrics were derived from 2,000,000 iterations, with a burn-in of 100,000, and thinned by 10, leaving 90,000 posterior estimates from the posterior probability distribution.

3.4   Results

3.4.1   Stable Isotopes

Consumer species that had the lowest average $\delta^{13}C$ values were walleye (-28.34‰), whereas the species with the highest average $\delta^{13}C$ values were ringed seals (-19.85 ± 0.33‰). Goose Creek northern pike had the lowest average $\delta^{15}N$ values (6.78 ± 0.22‰), whereas harbour

seals had the highest $\delta^{15}N$ value (18.06 ± 0.19‰) (Table 3-1). Three groups were characterized by the $\delta^{13}C$ and $\delta^{15}N$ muscle biplots (Figure 3-1): 1) consumers with higher $\delta^{13}C$ and $\delta^{15}N$ values, which included harbour seal, ringed seal, brook trout, capelin, cisco, fourhorn sculpin, Greenland cod, and nine-spine stickleback, 2) fish with the lowest $\delta^{13}C$ and $\delta^{15}N$ values, which included burbot, longnose sucker, Churchill River northern pike, Goose Creek northern pike, trout-perch, walleye, and white sucker, and 3) lake whitefish, which had intermediate $\delta^{13}C$ and $\delta^{15}N$ values. Similar grouping of species also occurred with liver tissue, although there were more species in the intermediate group, which included burbot, lake whitefish, Churchill River northern pike, and Goose Creek northern pike. Results from muscle and liver were nearly identical for most of the species, therefore, results are interpreted from the muscle tissue below with results from liver tissue provided in Appendix B. The liver tissue results are reported below when they differ from the muscle tissue. The raw stable isotope values for liver are found in Table B-2.

3.4.2 Trophic Positions

Trophic positions of consumers were determined by the nearest half trophic level (i.e., secondary consumers sit at trophic position 3, so individual or species between 2.5-3.4 were classified as secondary consumers) (Woodland et al., 2016). During the spring-summer period the trophic position of harbour seals, ringed seals, Greenland cod, brook trout, capelin, fourhorn sculpin, nine-spine stickleback, and walleye occupied the tertiary consumer position (trophic position ~4) and harbour and ringed seals are the apex predators (trophic position ~5; Table 3-1 and Figure 3-2). The secondary consumers (trophic position ~3) in this system were Goose Creek northern pike, longnose sucker, white sucker, lake whitefish, burbot, Churchill River northern pike, cisco, and trout-perch. Overall, the trophic positions for most species were similar between muscle and liver tissue. However, cisco, burbot, and Churchill River northern pike had a slightly higher trophic position in the summer (reflected in liver) than spring-summer time period (reflected in muscle) (Appendix B, Figure B-1). The highest level of variation in trophic position between individuals occurred in lake whitefish (muscle: 2.07-4.19, n = 68) and nine-spine stickleback (muscle: 1.54-4.37, n = 5) and the lowest level of variation between individuals was observed in trout-perch (muscle: 3.27-3.52, n = 19) (Table 3-1). Individual variability did not increase with trophic position (muscle: z = 0.20, p = 0.84, liver: z = -0.43, p = 0.67). Fish age

was found to have a moderate positive correlation with body size (z = 11.10, p <0.001, tau = 0.59).Trophic position increased with age in cisco (β = 0.042, p = 0.004, and R^2 = 0.29), fourhorn sculpin (β = 0.063, p = 0.04, and R^2 = 0.16), Greenland cod (β = 0.21, p <0.001, and R^2 = 0.59), and Churchill River northern pike (β = 0.055, p <0.001, and R^2 = 0.69; Figure 3-3). These trends were similar for liver tissue (Figure 3-3). When looking at the relationship between body size and trophic position I found the above four species still had a positive relationship (cisco: β = 0.001, p = 0.02, and R^2 = 0.20, fourhorn sculpin: β = 0.002, p = 0.004, and R^2 = 0.28, Greenland cod: β = 0.003, p <0.001, and R^2 = 0.78, and Churchill River northern pike: β = 0.001, p <0.001, and R^2 = 0.67). As well, I also found trophic position increased with body size for lake whitefish (muscle: β = 0.001, p=0.03, and R^2 = 0.07).

3.4.3   Community-Wide Metrics

The sizes of the standard ellipses areas (SEA$_c$) for cisco (recent=4.34‰^{2}, past=2.07‰^{2}) and fourhorn sculpin (recent=2.47‰^{2}, past=1.16‰^{2}) were larger in the 2019-2020 time period than the 1993-1995 time period, whereas the SEA$_c$ was smaller for lake whitefish (recent=9.31‰^{2}, past=17.52‰^{2}). All six of the community-wide metrics of trophic structure were lower in the 2019-2020 time period than the 1993-1995 time period (Figure 3-4 and 3-5). From the posterior distribution, the probability that total area would be smaller for the 2019-2020 period was 64%, which was likely a result of lake whitefish having an increase in their mean $\delta^{13}C$ value combined with a decrease in the mean $\delta^{13}C$ values for both cisco and fourhorn sculpin (Figure 3-4). The probability that $\delta^{13}C$ range (variability in basal carbon source) and $\delta^{15}N$ range (range of trophic positions) being lower in 2019-2020 versus 1993-1995 was 100% and 91% respectively. A decrease in trophic diversity also occurred as the probability that mean distance to centroid was lower in the more recent time period was 100%. As such, trophic redundancy increased as the probability of the mean nearest neighbour distance and standard deviation of nearest neighbour distance was lower in the 2019-2020 time period than the 1993-1995 time period was 65% and 99% respectively.

3.5   Discussion

This study provides one of the first descriptions of the trophic structure of a subarctic freshwater-estuarine-marine systems coupled food web and evidence of a temporal shift in the community structure of a fish assemblage. The top trophic level consumers within this system were Greenland cod, ringed seals, and harbour seals with half of all consumers (8 out of 16) occupying a tertiary consumer trophic position. Generally, species that mainly foraged on marine-derive resources occupied a higher trophic position than species that foraged mainly on freshwater-derived resources suggesting that the base resource use is different between the freshwater and marine systems. The trophic positions of three fish species (cisco, burbot, and Churchill River northern pike) increased to tertiary consumers in the summer period suggesting these species have switched to foraging on prey with higher trophic positions or on marine-derived resources. There was no observed pattern of higher trophic positioned species having more individual variability between positions. Lake whitefish were found to have the greatest amount of trophic position variability between individuals suggesting that lake whitefish use a broader suite of resources compared to the other species. The trophic position of cisco, fourhorn sculpin, Greenland cod, and Churchill River northern pike increased with age, possibly due to their body size and gape size becoming larger, and their swim hunting speed may have also increased allowing them to potentially forage on large prey items (Scharf et al., 2000). The 2019-2020 fish assemblage had less variability in basal carbon sources use and trophic position, resulting in decreased trophic diversity and increased trophic redundancy. These species now play a similar trophic role within the food web which has implications for ecosystem stability.

3.5.1   Trophic Position

Secondary consumers (trophic position ~3) in the lower Churchill River system included Goose Creek northern pike, longnose sucker, white suckers, lake whitefish, burbot, Churchill River northern pike, cisco, and trout-perch. Northern pike are generalist consumers that feed on a variety of resources from invertebrates to fish (Harvey, 2009). Northern pike from Goose Creek (mean trophic position 2.48, Table 3-1) and from the Churchill River (mean trophic position 3.37) occupied a different position which could be due to body size differences where Churchill River northern pike were much larger (412 ± 48.6 (mm)) than Goose Creek northern pike (279.6

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± 5.1 (mm)) (Table 3-2). A such, smaller individuals typically forage on small prey and gradually shift to larger prey as the consumer's body size increases (Graeb et al., 2006). Longnose (mean trophic position 2.87) and white suckers (mean trophic position 2.99) are known to forage on algae and benthic invertebrates (Edwards, 1983; Saint-Jacques et al., 2000) and there was little variation between individuals in both species. Lake whitefish (mean trophic position 3.10), northern pike, and cisco (mean trophic position 3.38) are known to have an anadromous life history or can tolerate brackish waters (Morin et al., 1981; Rohtla et al., 2012; Wilder, 1951), which can allow them access to resources from both the marine and freshwater systems. Lake whitefish forage on benthic prey, such as amphipods, snails, and mussels (Rennie et al., 2009). The highest amount of variation in trophic position between individuals occurred in lake whitefish, ranging from primary consumers to tertiary consumers, which is likely due to their different foraging strategies as a species. Some individuals of lake whitefish are potentially focusing on invertebrates while others are foraging principally on mid-trophic level fish, or that in this habitat coupling species, there is also variability between individuals where some primarily consume higher trophic position marine resources, while other individuals mainly consume lower trophic position freshwater resources. Cisco are known to be planktivorous, and feed mainly on cladocerans and copepods (Viljanen, 1983). Cisco were also found to be habitat couplers within the lower Churchill River and were found to forage on more marine-derived resources (Chapter 2), which also may explain their higher trophic position among secondary consumer species. Burbot (mean trophic position 3.19) are omnivorous and consume insects, amphipods, and fish (Beeton, 1956; Lawler, 1963). Trout-perch (mean trophic position 3.40) are generalists that forage on benthic invertebrates and zooplankton, especially chironomids and mayflies, as well as some fish eggs and smaller fish (Blouzdis et al., 2013; Kocovsky et al., 2014; Nelson & Dick, 2002).

Tertiary consumers (trophic position of ~4) were walleye, capelin, brook trout, fourhorn sculpin, nine-spine stickleback, and Greenland cod. Top predators (trophic position 5) were harbour seals and ringed seals. Tertiary consumers are known to omnivorous and can forage on a variety of prey items from vegetation, invertebrates, to fish (Blouzdis et al., 2013; Galarowicz et al., 2006; Lawler, 1963; Morin & Dodson, 1986; Vesin et al., 1981). However, the top consumers in this study had small niche sizes (see Chapter 2), showing that they were

specializing on one resource type. Walleye (mean trophic position 3.64 from Table 3-1) forage on zooplankton and fish when juveniles (~20 mm) and at larger body sizes (40-100 mm) switch to benthic invertebrates and fish (Galarowicz, 2006). Capelin (mean trophic position 3.69) feed mainly on zooplankton, such as amphipods, copepods, and euphausiids (Ogloff et al., 2020; Vesin et al., 1981). Brook trout (mean trophic position 3.80) have an anadromous life history stage and usually migrate to a marine system in spring (Montgomery et al., 1983). Brook trout forage on species available in the water current and benthos (Fechney, 1988) and feed on minnows, sticklebacks, perch, and sculpins (Ricker, 1930). Fourhorn sculpin (mean trophic position 3.85) are a benthic fish that consume mainly amphipods; however, they can also forage on plant material, molluscs, insects, mysids, polychaetes, and fish (Morin & Dodson, 1986). Nine-spine sticklebacks (mean trophic position 3.86) forage on small crustaceans, aquatic insects, and eggs and fry of fish (Hynes, 1950). Greenland cod (mean trophic position 4.35) are considered a top predator within the shallow benthic food chains of Hudson Bay and consume fishes such as capelin (Mikhail & Welch, 1989; Mouritsen et al., 2010). Ringed (mean trophic position 4.70) and harbour (mean trophic position 5.09) seals mainly consume fish, such as capelin and Arctic cod, and therefore occupy the top trophic position within this system (Ogloff et al., 2020; Thiemann et al., 2008; Yurkowski et al., 2016). Harbour seals are central place foragers and typically forage in marine waters, however in this region, harbour seals haul out on rocks in the Churchill River estuary where some individuals also move upriver, presumably to forage on freshwater-derived resources (Bajzak et al., 2013).

Based on results from Chapter 2 there was a pattern where species that primarily consumed more marine-derived resources occupied higher trophic positions than species that mainly consumed more freshwater-derived resources. Marine ecosystems are considered to be more productive than freshwater systems and consumer omnivory is usually found more often in marine systems when compared to freshwater systems (Sánchez-Hernández & Amundsen 2018). Sánchez-Hernández & Amundsen (2018) found that trophic position increased from freshwater to marine species for filter feeding, zoobenthos, benthopelagic, demersal, tropical, subtropical, and temperate species but that this relationship did not occur in herbivorous species due to their obligate consumption of primary producers. The shifts from low to high trophic positions between aquatic systems is likely due to spatial differences in prey availability, where marine

systems are typically more diverse than freshwater systems at the same latitude (Sánchez-Hernández & Amundsen 2018).

Trophic position of cisco, burbot, and Churchill River northern pike was higher in the summer period than the spring-summer period, suggesting these species may have had a shift in their foraging from lower trophic position-positioned prey (invertebrates) to consuming more higher trophic position prey (fish). This shift in the cisco and northern pike trophic position could also be due to their migration to more marine environments. Dixon et al. (2012) found Atlantic salmon (*Salmo salar*) showed an increasing gradient in trophic position from freshwater to marine ecosystems. This similar shift in diet could potentially also occur in cisco and northern pike who can migrate between the freshwater and marine systems.

3.5.2   *Body Size-Trophic Position Relationship*

Size-related constrains on prey consumption (i.e., gape size) can result in a mechanical limit to the trophic position of consumers (Scharf et al., 2000) where larger consumers typically consume smaller-sized prey items (Keppeler et al., 2021). The trophic position of cisco, fourhorn sculpin, and Greenland cod, species who mainly consume marine-derived resources, and Churchill River northern pike, who mainly consume freshwater-derived resources, increased with age. Positive trophic position-body size relationships have been found in both marine and freshwater system, but they have occurred more often in marine systems than in freshwater and terrestrial systems (Potapov et al., 2019; Keppeler et al., 2020; Keppeler et al., 2021). Dalponti et al., (2018) found piscivorous species had strong correlations between body size and trophic position for both bottom-dwelling and pelagic species (e.g., cod). Small bodied individuals that foraged on zooplankton or invertebrates have been found to have a weak correlation between body size and trophic position, due to gape limitations, therefore the body size of Atlantic cod (*Gadus morhua*) individuals is linked to their prey body size and trophic position (Kindsvater & Palkovacs, 2017), which was also observed in Greenland cod. Cisco are known to change their diet with increasing body size, with a shift towards more pelagic prey such as larger zooplankton. This shift would result in an increase in their trophic positions. Larger individuals of cisco have a greater number of gillrakers which will increase their foraging ability on pelagic resources compared to the smaller ciscoes with fewer gillrakers that will typically forage on

more benthic resources (Muir et al., 2013). Smaller individuals of shorthorn sculpin typically forage on invertebrates, while larger individuals foraged on fishes (Landry et al., 2018), which may also occur in fourhorn sculpin. Beaudoin et al. (1999) found a positive relationship between $\delta^{15}N$ and body size for pike and suggested that northern pike may have more trophic flexibility which can vary in the presence or absence of other fish species. There was no relationship between age and trophic position for lake whitefish, however there was a weak body size-trophic position relationship for them. This shows that age may not be a good predictor of trophic positions for lake whitefish, however their body size could be.

3.5.3 Community-Wide Metrics

The decrease in $\delta^{13}C$ of cisco and fourhorn sculpin between 1993-1995 and 2019-2020 could be due to an increased consumption of freshwater/terrestrial-derived resources over time or a switch to more benthic prey, whereas the increase in the $\delta^{13}C$ of lake whitefish may be a result of increased consumption of marine-derived resources or a switch to more benthic food sources in the more recent time period. Cisco, fourhorn sculpin, and lake whitefish are known to mainly forage on invertebrates, but they have been found to forging on other prey such as fish (Morin & Dodson, 1986; Rennie et al., 2009; Viljanen, 1983). Cisco and lake whitefish have been found to couple the marine and freshwater systems together (Chapter 2; DeJong 2017), which illustrates their high variability in resource use in consuming a variety of freshwater and marine invertebrates and fishes (Morin & Dodson, 1986; Rennie et al., 2009; Viljanen, 1983). The Suess effect had a negligible effect on $\delta^{13}C$ values of the three fish species assemblage since the average changes in $\delta^{13}C$ per consumer were much greater (i.e., an average of 0.6‰ than the predicted change in dissolved CO_2 of 0.25‰ over 25 years) (de la Vega et al., 2019). For all three fish species, $\delta^{15}N$ increased over time, suggesting an increase in the trophic position of each consumer which may be due to changes in the prey composition and abundance within the Churchill River and estuary. For example, grayling (*Thymallus arcticus*) are a lower trophic level consumer that have a flexible foraging strategy and mainly forage on amphipods and insects, and sometimes forage on fish (Stewart et al., 2007)., but have not been observed in the area since Manitoba Hydro lowered the water levels in this system (Edye-Rowntree, 2007). Graylings occupy a similar niche to lake whitefish and cisco, therefore after the loss of grayling in this system, there may have been increased prey availability for both lake whitefish and cisco

resulting in the increased consumption of slightly higher trophic level prey (Laske et al., 2018). Overall, the increase in trophic redundancy within the 2019-2020 community compared to the early 1990s suggests that all three fish species are now playing a more similar trophic role within the food web than they did before. Increased trophic diversity can promote ecosystem stability since there are many species occupying distinct positions across the system where different species partition and consume different food items (Włodarska-Kowalczuk et al., 2019). The loss of biodiversity can lead to a more simplified ecosystem that, in turn, can increase the community's vulnerability to extinction events. Furthermore, with several species playing the same trophic role within the community and in turn having increased competitive interactions, ecosystem stability can be reduced and foreshadow significant changes in the system (Bartley et al., 2019; Magoulick & Piercey, 2015; Yurkowski et al., 2017). However, in some cases, greater trophic redundancy may help promote ecosystem stability and reduce vulnerability to secondary extinction events (Sanders et al., 2018) where the loss of one species in the system can be replaced by another species with the same functional role. As such, it is unknown whether the change in both trophic diversity and trophic redundancy in the three fish species assemblage has increased or decreased ecosystem stability in the lower Churchill River system, which requires further investigation.

3.6   Conclusion

This study is the first to characterize the trophic structure of the lower Churchill River system with a potential application to other estuarian systems throughout Hudson Bay. The median trophic position estimates varied widely (1.39-5.21 for muscle) across all consumers. There was a pattern with species that consumed more marine-derived resources sitting at higher trophic positions than species that principally consumed freshwater-derived resources. There are differences in productivity between the marine and freshwater systems with marine systems generally being more productive than freshwater at the same latitude in some cases (Prowse et al., 2006; Sánchez-Hernández & Amundsen 2018). The results from this study can be used as a baseline for future work to monitor any future changes in the trophic position of these consumers species throughout the lower Churchill River. Continuous sampling of more species from all different body sizes is recommended to further examine the ontogenetic effects on trophic position of these consumer species. As well as continued sampling throughout each season to see

if there are any trophic position shifts based on growth over the year. Both fishes and seals are important for substance fishing/hunting and for recreational activities. Therefore, continued monitoring of these species will be important to local community members, Indigenous communities, as well as other stakeholders.

The community structure of the three fish species assemblage within the Churchill River and estuary currently has lower trophic diversity and higher trophic redundancy since the early 1990s. Anthropogenic impacts, such as the Churchill River weir which impacted the flow of water may have resulted in changes to the available habitat and resources within the system which could have been one of the likely several contributing factors that has influenced this system over time. This study can serve as a baseline to understand whether the fish community will continue to be affected by species loss or species gain, or increased competition for resources among consumers which has implications for the management and conservation of subarctic and Arctic ecosystems.

3.7 References

Bajzak, C.E., Bernhardt, W., Mosnier, A., Hammill, M.O., & Stirling, I. (2013). Habitat use by harbour seals (*Phoca vitulina*) in a seasonally ice-covered region, the western Hudson Bay. *Polar Biology*, *36*(4), 477-491. doi: 10.1007/s00300-012-1274-4.

Baker, R.F., Lawrence, M.J. & Schneider, F. (1993). Oceanography and Mid-Summer Distribution and Abundance of Plankton and Fish in the Nelson Estuary, Hudson Bay. Report prepared for Manitoba Hydro. North/South Consultants Inc., Winnipeg, Canada.

Bartley, T.J., McCann, K.S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M.M., MacDougall, A.S., Tunney, T.D., & McMeans, B.C. (2019). Food web rewiring in a changing world. *Nature Ecology & Evolution*, *3*(3), 345-354. doi: 10.1038/s41559-018-0772-3.

Beaudoin, C.P., Tonn, W.M., Prepas, E.E., & Wassenaar, L.I. (1999). Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia*, *120*(3), 386-396. doi: 10.1007/s004420050871.

Beeton, A.M. (1956). Food habits of the burbot (*Lota lota lacustris*) in the White River, a Michigan trout stream. *Copeia*, *1956*(1), 58-60.

Blouzdis, C.E., Ivan, L.N., Pothoven, S.A., Rosewell, C.R., Folet, C.J., & Höök, T.O. (2013). A trophic bottleneck?: The ecological role of trout-perch *Percopsis omiscomaycus* in Saginaw Bay, Lake Huron. *Journal of Applied Ichthyology*, *29*(2), 416-424. doi: 10.1111/jai.12023.

Caut, S., Angulo, E., & Courchamp, F. (2009). Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. The *Journal of Applied Ecology*, *46*(2), 443-453. doi: 10.1111/j.1365-2664.2009.01620.x.

Costalago, D., Navarro, J., Álvarez-Calleja, I., & Palomera, I. (2012). Ontogenetic and seasonal changes in the feeding habits and trophic level of two small pelagic fish species. *Marine Ecology*, *460*, 169-181. doi: 10.3354/meps09751.

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. doi: 10.1111/gcb.14832.

DeJong, R.A. (2017). Life history characteristics of Lake Whitefish (*Coregonus clupeaformis*), Cisco (*Coregonus artedi*), and Northern Pike (*Esox lucius*) in rivers of the Hudson Bay Lowlands. (Masters thesis). University of Waterloo, Ontario, Canada.

Dixon, H. J., Power, M., Dempson, J.B., Sheehan, T.F., & Chaput, G. (2012). Characterizing the trophic position and shift in Atlantic salmon (*Salmo salar*) from freshwater to marine life-cycle phases using stable isotopes. *ICES Journal of Marine Science*, *69*(9), 1646-1655. doi: 10.1093/icesjms/fss122.

Edwards, E.A. (1983). Habitat suitability index models. Longnose sucker. Washington, DC: Western Energy and Land Use Team, Division of Biological Services, Research and Development, Fish and Wildlife Service, U.S. Dept. of the Interior.

Edye-Rowntree, J. (2007). Churchill residents' use of the lower Churchill River in Manitoba. (Masters thesis) University of Manitoba, Winnipeg, Canada.

Eloranta, A.P., Kahilainen, K.K., Amundsen, P-A., Kundsen, R., Harrod, C., & Jones, R.I. (2015). Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. *Ecology and Evolution*, *5*(8), 1664-1675. doi: 10.1002/ece3.1461.

Elton, C. (1927). Animal ecology. New York, NY: The MacMillan Company.

Dalponti, G., Guariento, R.D. & Caliman, A. (2018). Hunting high or low: body size drives trophic position among and within marine predators. *Marine Ecology Process Series*, *597*, 39-46. doi: 10.3354/meps12584.

Fechney, L.R. (1988) The summer diet of brook trout (*Salvelinus fontinalis*) in a South Island high-country stream. *New Zealand Journal of Marine and Freshwater Research*, *22*(2), 163-168, doi: 10.1080/00288330.1988.9516288.

Florko, K.R.N., Tai, T.C., Cheung, W.W.L., Ferguson, S.H., Sumaila, U.R., Yurkowski, D.J., Auger-Méthé, M., & Bruyn, N de. (2021). Predicting how climate change threatens the prey base of Arctic marine predators. *Ecology Letters*, *24*(12), 2563-2575. doi: 10.1111/ele.13866.

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A.V., Fossheim, M., & Aschan, M.M. (2017). Climate-driver changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Science*, *114*(46), 12202-12207. doi: 10.1073/pnas.1706080114.

Frisch, A.J., Ireland, M., & Baker, R. (2014). Trophic ecology of large predatory reef fishes: energy pathways, trophic level, and implications for fisheries in a changing climate. *Marine Biology*, *161*(1), 61-73. doi: 10.1007/s00227-013-2315-4.

Fry, B. (2006). Stable isotope ecology. New York, NY: Springer. doi: 10.1007/0-387- 33745-8.

Galarowicz, T.L., Adams, J.A., & Wahl, D.H. (2006). The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. *Canadian Journal of Fisheries and aquatic Sciences*, *63*(8), 1722-1733. doi: 10.1139/f06-073.

Gaston, A.J., Woo, K., & Hipfner, J.M. (2003). Trends in forage fish populations in northern Hudson Bay since 1981, as determined from the diet of nestling thick-billed murres *Uria Iomvia*. *Arctic*, *56*(3), 227-233. doi: 10.14430/arctic618.

Graeb, B.D.S., Mangan, M.T., Jolley, J.C., Wahl, D.H., & Dettmers, J.M. (2006). Ontogenetic changes in prey preference and foraging ability of yellow perch: insights based on relative energetic return of prey. *Transactions of the American Fisheries Society*, *135*(6), 1493-1498. doi: 10.1577/T05-063.1.

Grey, J. (2001). Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen. *Ecology of Freshwater Fish*, *10*(3), 168-176. doi: 10.1034/j.1600-0633.2001.100306.x.

Harvey, B. (2009). A biological synopsis of northern pike (*Esox lucius*). *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, *2885*(31).

Hayden, B., Palomares, M.L.D., & Poelen, J.H. (2019). Biological and environmental drivers of trophic ecology in marine fishes – a global perspective. *Scientific Reports*, *9*(1), 11415-10. doi: 10.1038/s41598-019-47618-2.

Heady, W & Moore, J. (2013). Tissues turnover and stable isotope clocks to quantify recourse shifts in anadromous rainbow trout. *Oecologia*, *172*(1), 21-34. doi: 10.1007/s00442-012-2483-9.

Hesslein, R. H., Capel, M.J., Fox, D.E., & Hallard, K.A. (1991). Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration In the Bower Mackenzie River basin. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 2258-2265.

Hobson, K.A. & Welch, H.E. (1992). Determination of trophic relationships within high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. *Marine Ecology Progress Series*, *84*, 9-18.

Hobson, K.A., Schell, D.M., Renouf, D., & Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(3), 528-533.

Hop, H. & Gjøsæter, H. (2013). Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Marine Biology Research*, *9*(9), 878-894. doi: 10.1080/17451000.2013.775458.

Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F.J., Cliff, G., Wintner, S.P., Fennessy, S.T., Fisk, A.T., & Hessen, D. (2014). Rescaling the trophic structure of marine food webs. *Ecology Letters*, *17*(2), 239-250. doi: 10.1111/ele.12226.

Hynes, H.B.N. (1950). The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *The Journal of Animal Ecology*, *19*(1), 36-58. doi: 10.2307/1570.

Jackson, A.L., Inger, R., Parnell, A.C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER-stale isotope Bayesian ellipse in R. *The Journal of Animal Ecology*, *80*(3), 595-602. doi: 10.1111/j.1365-2656.2011.01806.x.

Jung, A.S., van der Veer, H.W., van der Meer, M.T.J., Philippart, C.J.M., & Rodrigues, C.F. (2019). Seasonal variation in the diet of estuarine bivalves. *PloS One*, *14*(6), e0217003. doi: 10.1371/journal.pone.0217003.

Keppeler, F.W., Olin, J.A., López-Duarte, P.C., Polito, M.J., Hooper-Bùi, L.M., Taylor, S.S., Rabalais, N.N., Fodrie, F.J., Roberts, B.J., Turner, R.E., Martin, C.W., & Jensen, O.P. (2021). Body size, trophic position, and the coupling of different energy pathways across a saltmarsh landscape. *Limnology and Oceanography Letters*, *6*(6), 360-368. doi: 10.1002/lol2.10212.

Kindsvater, H.K. & Palkovacs, E.P. (2017). Prredicting eco-evolutionary impacts of fishing on body size and trophic role of Atlantic cod. *Copeia*, *105*(3), 475-482. doi: 10.1643/OT-16-533.

Kocovsky, P.M., Stoneman, A.T., & Kraus, R.T. (2014). Ecology and population status of trout-perch (*Percopsis omiscomaycus*) in western Lake Erie. *Journal of Great Lakes Research*, *40*(1), 208-214. doi: 10.1016/j.jglr.2013.09.004.

Kuzyk, Z., Macdonald, R., Granskog, M., Scharien, R., Galley, R., Michel, C., Barber, D., & Stern, G. (2008). Sea ice, hydrological, and biological processes in the Churchill River estuary region, Hudson Bay. *Estuarine, Coastal and Shelf Science*, *77*(3), 369– 384. doi: 10.1016/j.ecss.2007.09.030.

Landry, J.J., Fish, A.T., Yurkowski, D.J., Hussey, N.E., Dick, T., Crawford, R.E., & Kessel, S.T. (2018). Feeding ecology of a common benthic fish, shorthorn sculpin (*Myoxocephalus scorpius*) in the high arctic. *Polar Biology*, *41*(10), 2091-2102. doi: 10.1007/s00300-018-2348-8.

Laske, S.M., Rosenberger, A.E., Wipfli, M.S., & Zimmerman, C.E. (2018). Generalist feeding strategies in Arctic freshwater fish: a mechanism for dealing with extreme environments. *Ecology of Freshwater Fish*, *27*(3), 767-784. doi: 10.1111/eff.12391.

Lawler, G.H. (1963). The biology and taxonomy of the Burbot, *Lota lota*, in Heming Lake, Manitoba. *Journal of the Fisheries Research Board of Canada*, *20*(2), 417-433. doi: 10.1139/f63-033.

Layman, C.A., Arrington, D.A., Montana, C.G., & Post, D.M. (2007). Can stable isotope ratios provide for community-wide measurements of trophic structure? *Ecology*, *88*(1), 42-48. doi: 10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO2.

Layman, C.A., Winemiller, K.O., Arrington, D.A., & Jepsen, D.B. (2005). Body size and trophic position in a diverse tropical food web. *Ecology*, *86*(9), 2530-2535. doi: 10.1890/04-1098.

Lindemann, R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*, 399-417.

Magoulick, D.D. & Piercey, G.L. (2015). Trophic overlap between native and invasive stream crayfish. *Hydrobiologia*, *766*(1), 237-246. doi: 10.1007/s10750-015-2457-0.

McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecology Letters*, *8*(5), 513-523. doi: 10.1111/j.1461-0248.2005.00742.x.

McCutchan, J.H., Lewis, W.M., Kendall, C., & McGrath, C.C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, *102*(2), 378-390. doi: 10.1034/j.1600-0706.2003.12098.x.

McMeans, B.C., Kadoya, T., Pool, T.K., Holtgrieve, G.W., Lek, S., Kong, H., Winemiller, K., Elliott, V., Rooney, N., Laffaille, P., & McCann, K.S. (2019). Consumer trophic positions respond variably to seasonally fluctuating environments. *Ecology*, *100*(2), e02570-n/a. doi: 10.1002/ecy.2570.

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*, *482*, 17-28. doi: 10.3354/meps10278.

Mikhail, M.Y. & Welch, H.E. (1989). Biology of Greenland cod, *Gadus ogac*, at Saqvaqjuac, northwest coast of Hudson Bay. *Environmental Biology of Fishes*, *26*(1), 49-62. doi: 10.1007/BF00002475.

Montgomery, W.L., McCormick, S.D., Naiman, R.J., Whoriskey Jr., F.G.& Black, G.A. (1983). Spring migratory synchrony of salmonid, catostomid, and cyprinid fishes in Rivière à la Truite, Québec. *Canadian Journal of Zoology*, *61*(11), 2495-2502. doi: 10.1139/z83-331.

Morin, R., Dodson, J.J., & Power, G. (1981). The migrations of anadromous cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) in estuaries of eastern James Bay. *Canadian Journal of Zoology*, *59*(8), 1600-1607. doi: 10.1139/z81-219.

Morin, R. & Dodson, J.J. (1986). Chapter 15 the ecology of fishes in James Bay, Hudson Bay and Hudson Strait. *Elsevier Oceanography Series*, *44*, 293-326. doi: 10.1016/S0422-9894(08)70908-5.

Mouritsen, K.N., Hedeholm, R., Schack, H.B., Møller, L.N., Storr-Paulsen, M., Dzido, J., & Rokicki, J. (2010). Occurrence of anisakid nematodes in Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*), West Greenland. *Acta Parasitologica*, *55*(1), 81-89. doi: 10.2478/s11686-010-0009-3.

Muir, A.M., Vecsei, P., Pratt, T.C., Kruegar, C.C., Power, M., & Reist, J.D. (2013). Ontogenetic shifts in morphology and resource use of cisco *Coregonus artedi*: ontogenetic shifts of *Coregonus artedi*. *Journal of Fish Biology*, *82*(2), 600-617. doi: 10.1111/jfb.12016.

Nelson, P.A. & Dick, T.A. (2002). Factors shaping the parasite communities of trout-perch, *Percopsis omiscomaycus* Walbaum (Osteichthyes: Percopsidae), and the importance of scale. *Canadian Journal of Zoology*, *80*(11), 1986-1999. doi: 10.1139/z02-188.

Newbury, R.W., McCullough, G.K., & Hecky, R.E. (1984). The Southern Indian Lake impoundment and Churchill River diversion. *Canadian Journal of Fisheries and Aquatic Sciences*, *41*(4), 548-557. doi: 10.1139/f84-068.

Ogloff, W.R., Ferguson, S.H., Tallman, R.F., & Davoren, G.K. (2020). Diet of capelin (*Mallotus villosus*) in the Eastern Canadian Arctic inferred from stomach contents and stable isotopes. *Polar Biology*, *43*(9), 1273-1285. doi: 10.1007/s00300-020-02707-1.

Pecl, G. T., Araujo, M. B., Bell, J., Blanchard, J., Bonebrake, T. C., Chen, I., Clark, T. D., Colwell, R. K., Danielsen, F., Evengard, B., & Robinson, S. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science*, *355* (6332), 1-9.

Phillips, D. & Eldridge, P. (2006). Estimating the timing of diet shifts using stable isotopes. *Oecologia*, *147*(2), 195-203. doi: 10.1007/s00442-005-0292-0.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., & Maron, J. (2000). When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution*, *15*(11), 473-475. doi: 10.1016/S0169-5347(00)01971-6.

Potapov, A.M., Brose, U., Scheu, S., & Tiunov, A.V. (2019). Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *The American Naturalist*, *194*(6), 823-839. Doi: 10.1086/705811.

Post, D.M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, *83*(3), 703-718. doi: 10.1890/0012-9658(2002)083[0703:USITET]2.0.CO2.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., & Montaña, C.G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, *152*(1), 179-189. doi: 10.1007/s00442-006-0630-x.

Power, M., Klein, G.M., Guiguer, K.R.R.A., & Kwan, M.K.H. (2002). Mercury accumulation in the fish community of a sub-arctic lake in relation to trophic position and carbon sources. *The Journal of Applied Ecology*, *39*(5), 819-830. doi: 10.1046/j.1365-2664.2002.00758.x.

Prowse, T.D., Wrona, F.J., Reist, J.D., Hobbie, J.E., Lévesque, L.M.J., & Vincent, W.F. (2006). General features of the Arctic relevant to climate change in freshwater ecosystems. *Ambio*, *35*(7), 330-338. doi: 10.1579/0044-7447(2006)35[330:GFOTAR]2.0.CO.

Quay, P., Sonnerup, R., Westby, T., Stutsman, J., & McNichol, A. (2003). Changes in the $^{13}C/^{12}C$ of dissolved inorganic carbon in the ocean as a tracer of anthropogenic CO_2 uptake. *Global Biogeochemical Cycles*, *17*(1), p.4-1-4-20. doi: 10.1029/2001GB001817.

R Core Team. (2021). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL https://www.R-project.org/.

Rennie, M.D., Sprules, W.G., Johnson, T.B., & Kraft, C. (2009). Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(12), 2096-2108. doi: 10.1139/F09-139CODEN:CJFSDX.

Ricker, W.E. (1930). Feeding habits of speckled trout in Ontario waters. *Transactions of the American Fisheries Society*, *60*(1), 64-72. doi: 10.1577/1548-8659(1930)60[64:FHOSTI]2.0.CO.

Roach, K.A., Thorp, J.H., & Delong, M.D. (2009). Influence of lateral gradients of hydrologic connectivity on trophic positions of fishes in the Upper Mississippi River. *Freshwater Biology*, *54*(3), 607-620. doi: 10.1111/j.1365-2427.2008.02137.x.

Rohtla, M., Vetemaa, M., Urtson, K, & Soesoo, A. (2012). Early life migration patterns of Baltic Sea pike *Esox lucius*. *Journal of Fish Biology*, *80*(4), 886-893. doi: 10.1111/j.1095-8649.2012.03226.x.

Romanuk, T.N., Hayward, A., & Hutchings, J.A. (2011). Trophic level scales positively with body sizes in fishes. *Global Ecology and Biogeography*, *20*(2), 231-240. doi: 10.1111/j.1466-8238.2010.00579.x.

Sabo, J.L., Finlay, J.C., Kennedy, T., & Post, D.M. (2010). The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science*, *330*(6006), 965-967. doi: 10.1126/science.1196005.

Saint-Jacques, N., Harvey, H.H., & Jackson, D.A. (2000). Selective foraging in the white sucker (*Catostomus commersoni*). *Canadian Journal of Zoology*, *78*(8), 1320-1331. doi: 10.1139/cjz-78-8-1320.

Sánchez-Hernández, J. & Amundsen, P-A. (2018). Ecosystem type shapes trophic position and omnivory in fishes. *Fish and Fisheries*, *19*(6), 1003-1015. doi: 10.1111/faf.12308.

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. doi: 10.1073/pnas.1716825115.

Scharf, F.S., Juanes, F, & Rountree, R.A. (2000). Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology*, *208*, 229-248. doi: 10.3354/meps208229.

Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J., & Sawatzky, C.D. (2007). Fish diets and food webs in the Northwest Territories: Arctic grayling (*Thymallus arcticus*). Fisheries and Oceans Canada, Winnipeg

Thiemann, G.W., Iverson, S.J., & Stirling, I. (2008). Variation in blubber fatty acid composition among marine mammals in the Canadian Arctic. *Marine Mammal Science*, *24*(1), 91-111. doi: 10.1111/j.1748-7692.2007.00165.x.

Vander Zanden, M.J. & Rasmussen, J.B. (1996). A trophic position model of pelagic food webs: impact on contaminant bioaccumulation on lake trout. *Ecological Monographs*, *66*(4), 451-477. doi. 10.2307/2963490.

Vander Zanden, M.J., Shuter, B.J., Lester, N., & Rasmussen, J.B. (1999). Patterns of food chain length in lakes: a stable isotope study. *The American Naturalist*, *154*(4), 406-416.

Vesin, J-P, Leggett, W.C., & Able, K.W. (1981). Feeding ecology of capelin (*Mallotus villosus*) in the estuary and western gulf of St. Lawrence and its multispecies implications. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(3), 257-267. doi: 10.1139/f81-037.

Viljanen, M. (1983). Food and food selection of cisco (*Coregonus albula* L.) in a dysoligotrophic lake. *Hydrobiologia*, *101*(1-2), 129-138. doi: 10.1007/BF00008665.

Watson, L.C., Stewart, D.J., & Teece, M.A. (2013). Trophic ecology of Arapaima in Guyana: giant omnivores in neotropical floodplains. *Neotropical Ichthyology*, *11*(2), 341-349. doi: 10.1590/S1679-62252013000200012.

Werner, E.E. & Hal, D.J. (1976). Niche shifts in sunfishes: experimental evidence and significance. *Science*, *191*(4225), 404-406. doi: 10.1126/science.1246626.

Wilder, D.G. (1951). A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis* (Mitchill)). *Journal of the Fisheries Research Board of Canada*, *9*,169– 203.

Winemiller, K.O. (1990). Spatial temporal variation in tropical fish trophic networks. *Ecological Monographs*, *60*(3), 331-367. doi: 10.2307/1943061.

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. doi: 10.1002/lno.11174.

Woodland, R.J., Warry, F.Y., Evrard, V., Clarke, R.H., Reich, P., & Cook, P.L.M. (2016). Niche-dependent trophic position distribution among primary, secondary and tertiary consumers. *Oikos*, *125*(4), 556-565. doi: 10.1111/oik.02486.

Yurkowski, D.J., Ferguson, S.H., Semeniuk, C.A.D., Brown, T.M., Muir, D.C.G., & Fish, A.T. (2016). Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. *Oecologia*, *180*(3), 631-644. doi: 10.1007/s00442-015-3384-5.

Yurkowski, D.J., Hussey, N.E., Fish, A.T., Imrie, K.L., Tallman, R.F., & Ferguson, S.H. (2017). Temporal shifts in intraguild predation pressure between beluga whales and Greenland halibut in a changing Arctic. *Biology Letters*, *13*(11), 20170433. doi: 10.1098/rsbl.2017.0433.

Yurkowski, D.J., Hussey, N.E., Ferguson, S.H., & Fisk, A.T. (2018). A temporal shift in trophic diversity among a predator assemblage in a warming Arctic. *Royal Society Open Science*, *5*(10), p.180259

3.8 Figures and Tables

Table 3-1. Fish and seal species $\delta^{13}C$ and $\delta^{15}N$ muscle values (‰, mean ± SE), plus the median ± SE of the trophic position, and the minimum and maximum trophic position for each species.

Species	n	$\delta^{13}C$	$\delta^{15}N$	Trophic Position	Trophic Position Range
			Muscle		
harbour seal	4	-19.87 ± 0.23	18.06 ± 0.19	5.09 ± 0.08	4.86-5.21
ringed seal	5	-19.85 ± 0.33	17.13 ± 0.38	4.70 ± 0.16	4.25-5.01
Greenland cod	20	-19.98 ± 0.10	17.00 ± 0.17	4.35 ± 0.05	3.87-4.57
nine-spine stickleback*	5	-21.20 ± 0.93	11.23 ± 1.15	3.86 ± 0.54	1.54-4.37
fourhorn sculpin	29	-20.64 ± 0.11	15.07 ± 0.24	3.85 ± 0.07	2.03-4.18
brook trout	7	-21.93 ± 0.28	15.26 ± 0.25	3.80 ± 0.07	3.56-4.05
capelin	40	-21.27 ± 0.08	14.71 ± 0.09	3.69 ± 0.02	3.35-3.92
walleye	1	-28.34	10.70	3.64	3.64
trout-perch	19	-26.52 ± 0.10	9.80 ± 0.06	3.40 ± 0.02	3.27-3.52
cisco	28	-21.68 ± 0.35	13.57 ± 0.23	3.38 ± 0.04	2.78-3.89
northern pike CR†	13	-26.33 ± 0.41	9.74 ± 0.22	3.37 ± 0.06	2.16-2.61
burbot*	6	-25.79 ± 0.25	8.62 ± 0.51	3.19 ± 0.31	1.39-3.35
lake whitefish	68	-23.69 ± 0.34	9.90 ± 0.22	3.10 ± 0.05	2.07-4.19
white sucker	10	-27.93 ± 0.36	8.21 ± 0.13	2.99 ± 0.04	2.74-3.16
longnose sucker	13	-27.09 ± 0.16	7.81 ± 0.11	2.87 ± 0.03	2.63-3.08
northern pike GC†	20	-25.53 ± 0.62	6.78 ± 0.22	2.48 ± 0.06	2.61-3.66

*some whole body samples since the species was too small

†CR= Churchill River, GC= Goose Creek.

Table 3-2. Fish and seal species body length (mm), weight (g), and age (Mean ± SE) throughout the Churchill River, Churchill River estuary, and Hudson Bay.

Species	Length (mm), n	Weight (g), n	Age, n
harbour seal	1443 ± 99, 3		
ringed seal	1227 ± 190, 5	67620 ± 11986, 5	
brook trout	440, 1		4.3 ± 0.5, 4
Burbot	255 ± 64, 4	161 ± 47, 3	3, 3
capelin	117 ± 1, 40	9 ± 1, 40	
cisco	302 ± 13, 28	466 ± 66, 28	4.9 ± 2.8, 27
fourhorn sculpin	193 ± 7, 29	89 ± 7, 28	2.7 ± 0.1, 27
Greenland cod	312 ± 13, 20	358 ± 42, 19	4.1 ± 0.2, 20
lake whitefish	337 ± 9, 68	614 ± 42, 68	5.8 ± 0.4, 66
longnose sucker	229 ± 18, 13	196 ± 71, 13	3, 2
nine-spine stickleback	33 ± 3, 2		
northern pike CR	412 ± 47, 13	756 ± 165, 13	4.4 ± 0.9, 13
northern pike GC	280 ± 5, 25	167 ± 12, 25	1.3 ± 0.11, 25
trout-perch	73 ± 1, 19	5 ± 0.1, 19	
walleye	86	5	
white sucker	251 ± 13, 10	253 ± 35, 10	3.5 ± 0.5, 2

†CR= Churchill River, GC= Goose Creek.
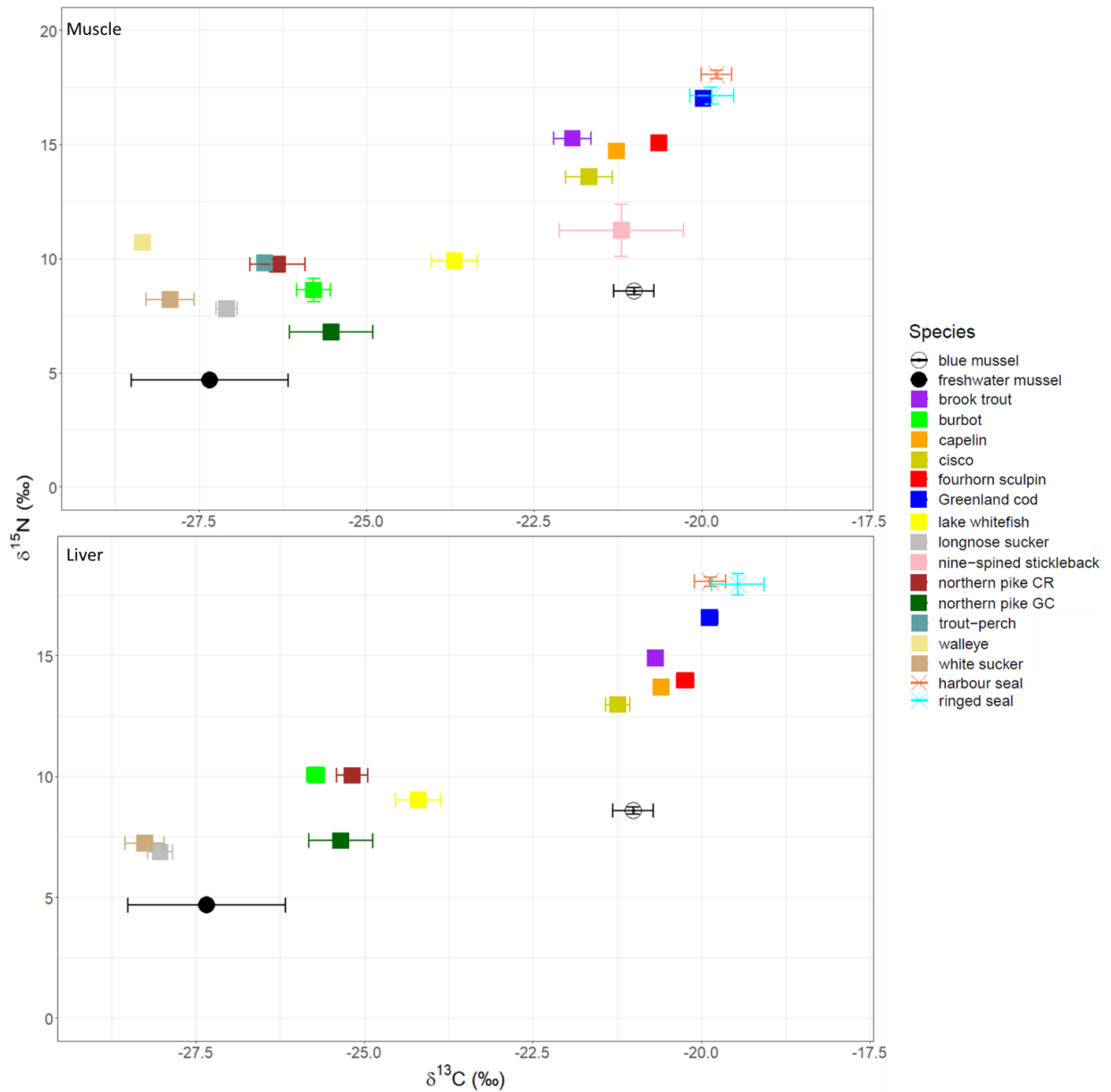
Figure 3-1. Stable isotope biplot of the mean (‰) ± standard error (SE) of δ^{13}C and δ^{15}N of the 15 consumers based on their different tissue type and 2 prey used as the prey baseline for the trophic position equation. CR= Churchill River and GC= Goose Creek. Hair samples were used for the harbour seals instead of liver.
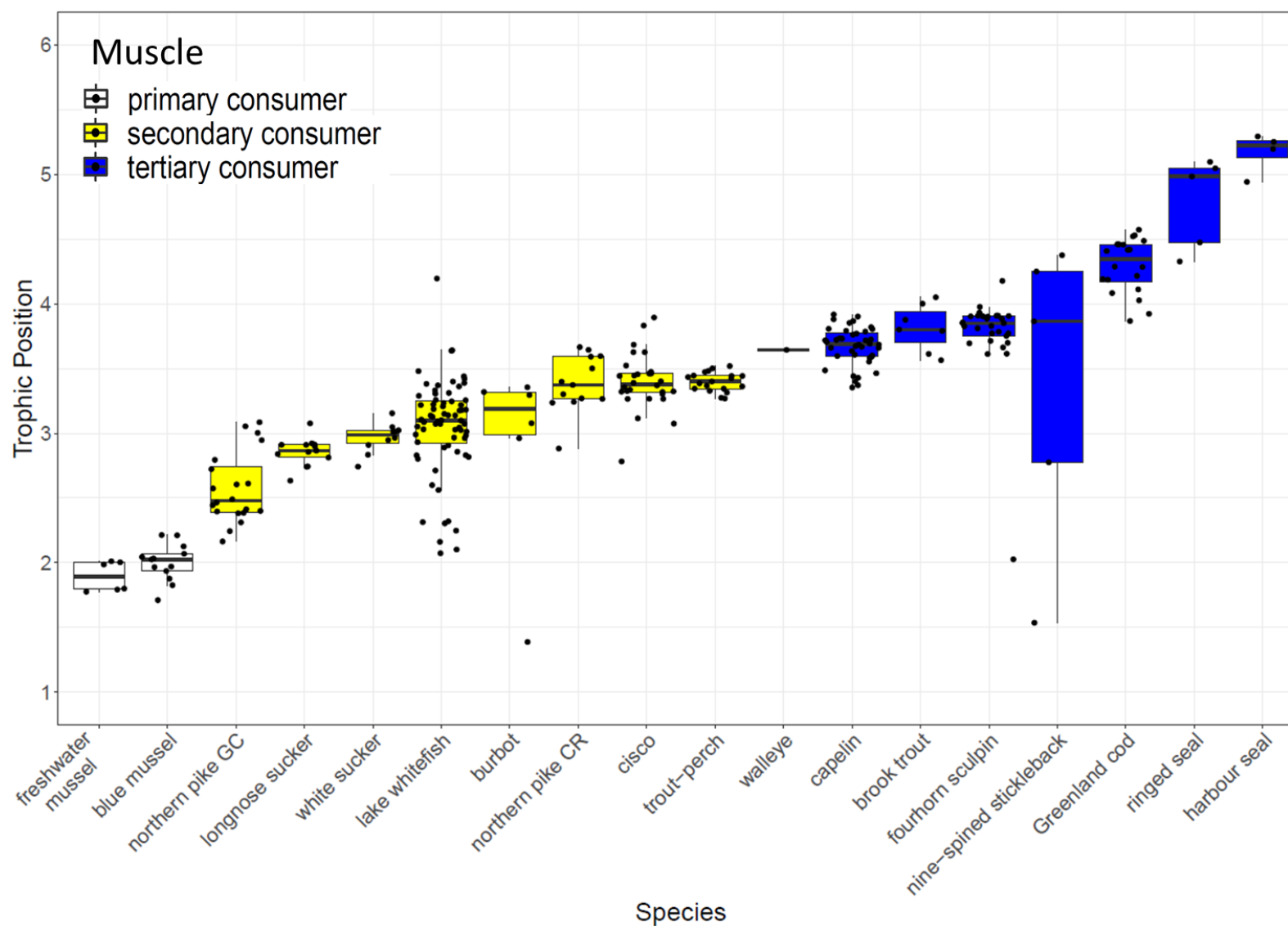
Figure 3-2. Boxplot (median and standard deviation) of consumers trophic positions within the lower Churchill River area based on muscle data. CR= Churchill River and GC= Goose Creek.

(a)
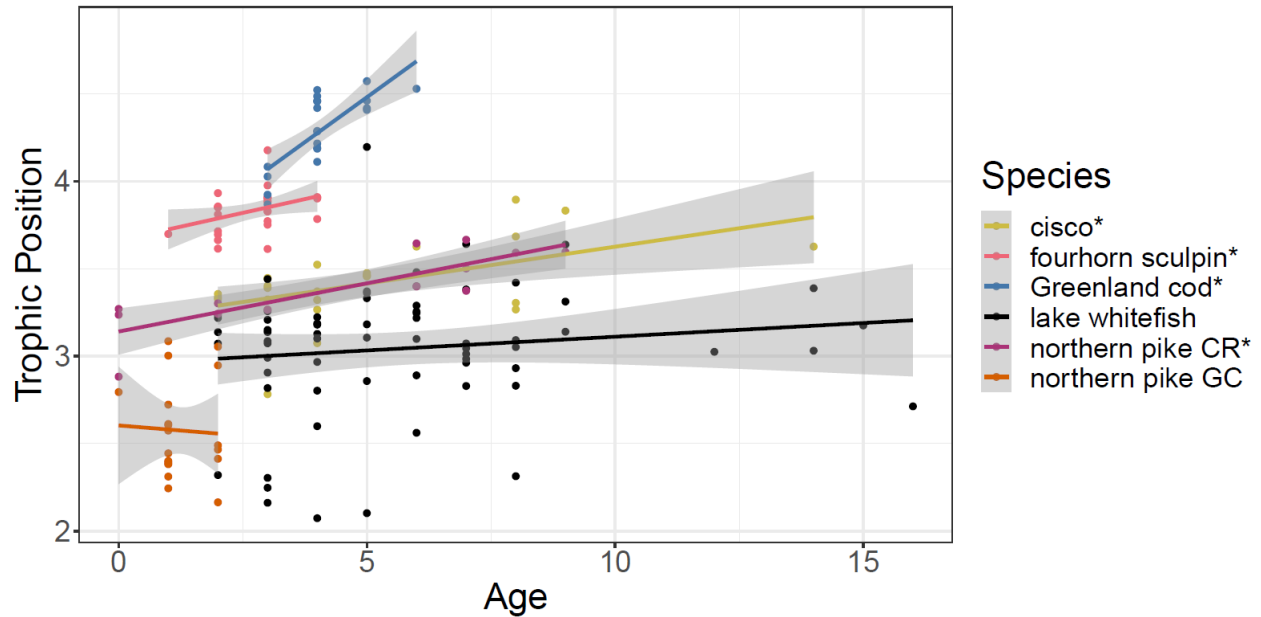
(b)
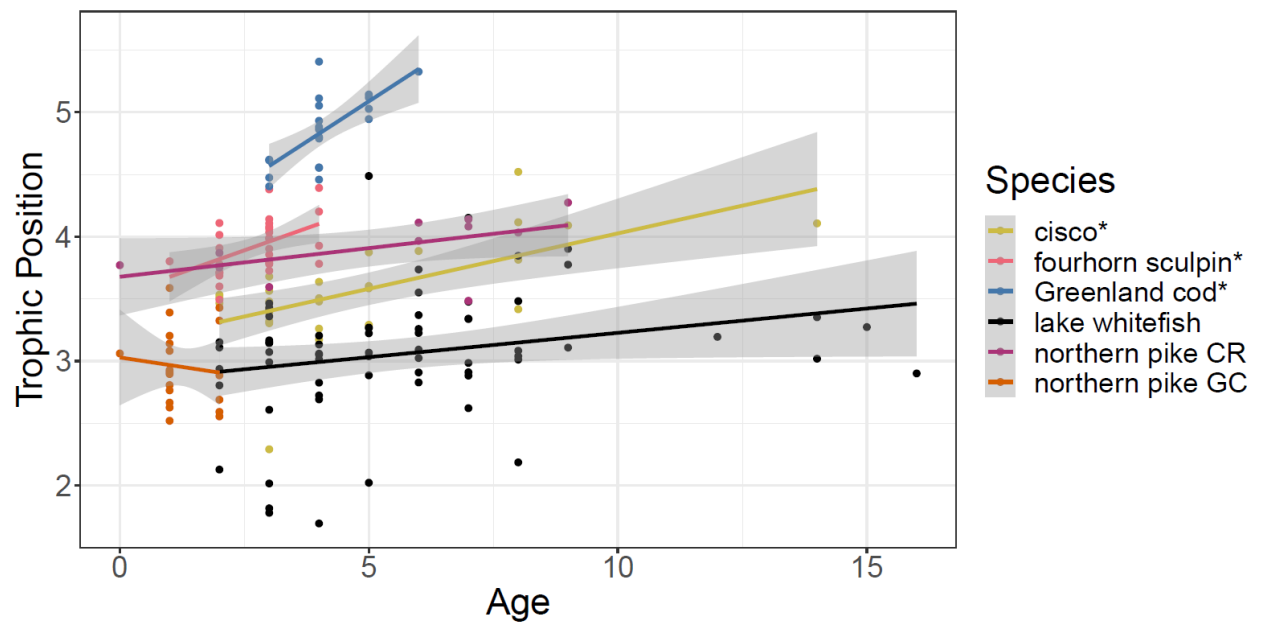
Figure 3-3. The relationship between age and trophic position of six fish groups (cisco, fourhorn sculpin, Greenland cod, lake whitefish, Churchill River northern pike (CR), and Goose Creek northern pike (GC) based on (a) muscle and (b) liver. *species with a significant relationship between body size and trophic position.
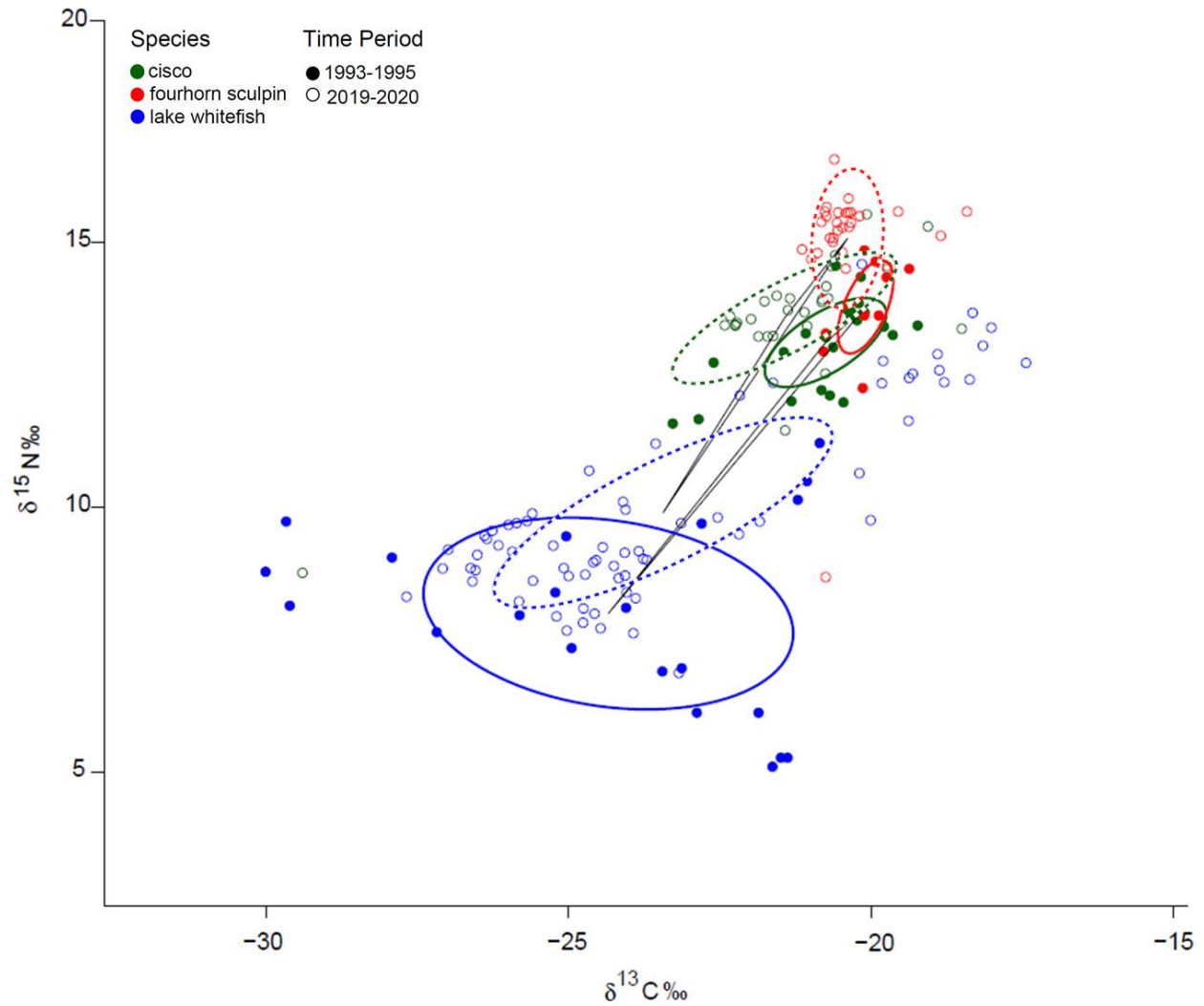
Figure 3-4. Stable isotope biplot representing the 40% isotope niche sizes (ellipses) of cisco, fourhorn sculpin, and lake whitefish during 1993-1995 and 2019-2020 within the Churchill River and Churchill River estuary. The solid black lines represent the community metric of total area. The solid ellipses lines are for the 1993-1995 community and the dashed ellipses lines are for the 2019-2020 community.
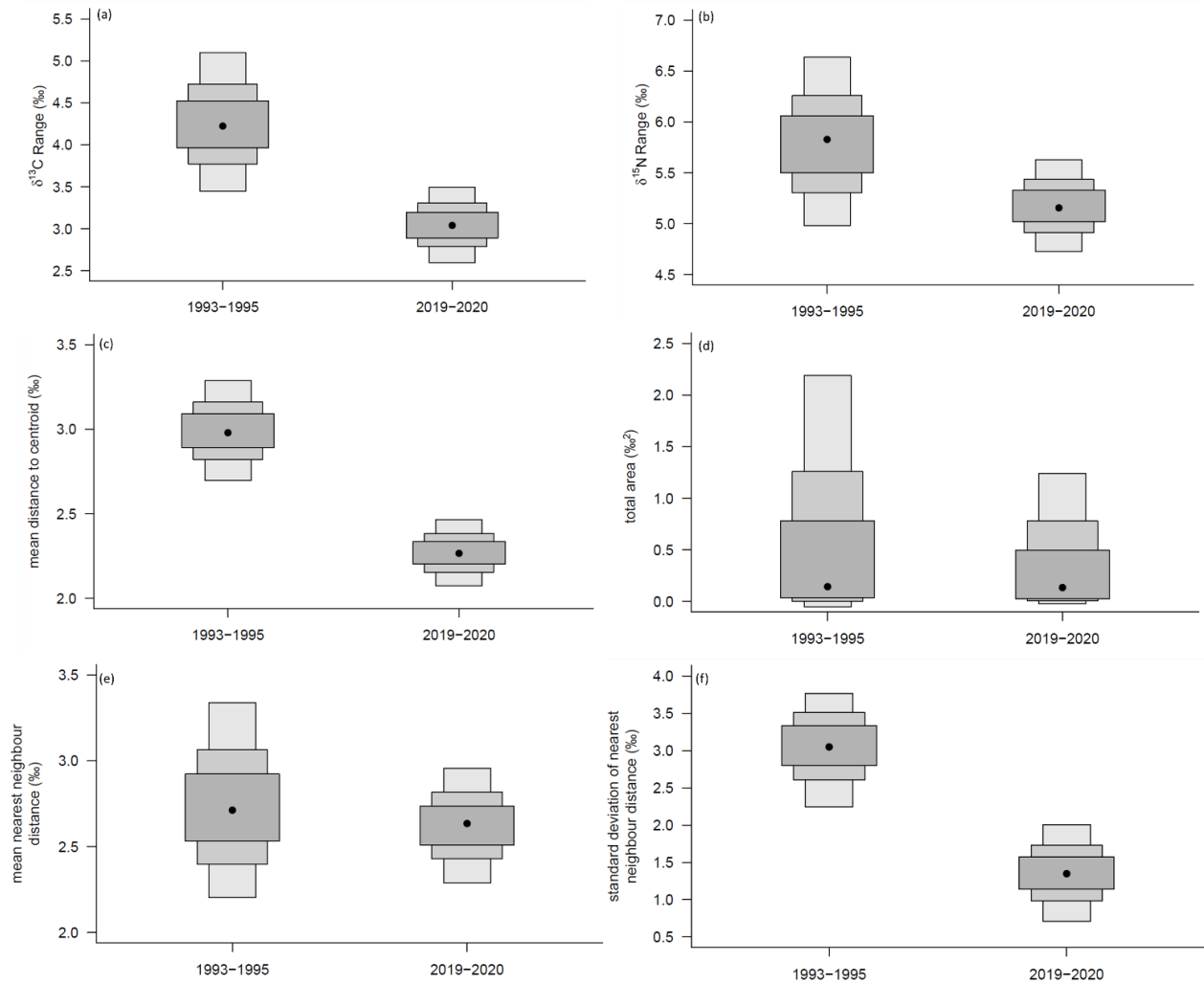
Figure 3-5. Boxplots representing the Bayesian mode estimates for each community-wide metric for the fish assemblage including (a) δ^{13}C range ‰, (b) δ^{15}N range ‰, (c) mean distance to centroid ‰, (d) total area ‰^{2}, (e) mean nearest neighbour distance ‰, and (f) standard deviation of nearest neighbour distance ‰. Boxes indicate Bayesian credible intervals at 50% (dark grey), 75% (medium grey), and 95% (light grey).

4.0   Chapter 4: Conclusion

This thesis quantified the dietary contributions of marine-and freshwater-derived resources, habitat coupling, niche size and niche overlap, and trophic positions of mobile consumers along a freshwater-marine gradient. I also quantified long-term changes in the trophic structure of a fish community over time. Migratory aquatic species rely on the connection between the marine and freshwater systems for growth and reproduction, so this connection is important to ensure these species can complete their different developmental stages. The habitat coupling species within this system were cisco, lake whitefish, and Goose Creek northern pike, which are all known to be anadromous species that can tolerate brackish water. These species also had the largest niche sizes, suggesting broader use of resources. Significant niche overlap occurred between lake whitefish and five other species examined, highlighting the broad-scale resource use of lake whitefish within this system and their important role as habitat couplers in the lower Churchill River. In addition, the habitat coupling species (i.e., cisco, lake whitefish, and Goose Creek northern pike) were also found to have the highest amount of intraspecific variation in energy channel use between the freshwater-and marine-derived resources. Additionally, this shows complexity in the habitat coupling roles of these species and how different individuals take advantage of distinctive resources between habitats (Schindler & Scheuerell, 2002; Seubert et al., 2019). There were no discernable differences between the summer and spring-summer diet for all the species except for Goose Creek northern pike who foraged on more marine-derived resources in the summer period than during the spring-summer period. As well pike caught between Goose Creek and throughout the Churchill River were found to have differences in their diet which could be due to Goose Creek northern pike moving between both the marine and freshwater systems and/or foraging on prey with a marine signal, which illustrates that there could be a seasonal shift in their resource use between habitats.

My third chapter examined trophic position variation among mobile consumer species in relation to age and investigated a temporal shift in trophic diversity of a consumer fish assemblage over time before and after the construction of the Churchill River weir. I found that trophic position increased with age in cisco, fourhorn sculpin, Greenland cod, and Churchill River northern pike. An increase in age, and in turn a larger body size, allows for the use of a broad range of resources and a greater mobility between habitats across larger spatial scales

(Winemiller, 1990). Lake whitefish were found to have a relationship between body length and trophic position but not with age and trophic position. Therefore, body length may be a better predictor of trophic position than age for some species. The trophic positions varied widely across all consumers, but higher trophic level species did not have increased variability in trophic position between individuals. Consumers that foraged on marine-derived resources occupied higher trophic positions than species that consumed freshwater-derived resources. Annual productivity of freshwater systems generally tends to be low because of low levels of nutrient inputs and low temperatures (Prowse et al., 2006; Sánchez-Hernández & Amundsen 2018). The trophic structure of the fish assemblage within the lower Churchill River changed since the early 1990s to a more trophic redundant fish assemblage. Greater trophic redundancy may help promote ecosystem stability and reduce vulnerability to secondary extinction events since the loss of one species in the system will be replaced by others since they are functioning the same within the community. Biodiversity loss can lead to a reduction in trophic redundancy, which can increase the vulnerability of ecosystems (Sanders et al., 2018). As well, if many species play the same role within the community there may also be more competition for resources between species (Bartley et al., 2019; Magoulick & Piercey, 2015; Yurkowski et al., 2017). However, increased trophic diversity can promote ecosystem stability since there are many species occupying distinct positions across the system where different species consume different prey (Włodarska-Kowalczuk et al., 2019). Therefore, both high trophic redundancy and high trophic diversity in combination can promote ecosystem stability and resilience. High diversity systems will in turn lead to greater ecosystem stability, which will result in more species interactions and redundancy in trophic roles. Furthermore, greater trophic redundancy may help reduce vulnerability to secondary extinction events with more species functioning the same within the system if a particular species is extirpated from the system (Magoulick & Piercey, 2015; Sanders et al., 2018; Yurkowski et al., 2017).

Mobile consumers (fishes and seals) within the lower Churchill River system are important for local community members, aboriginal communities, and other stakeholders since these species are used for subsistence hunting/fishing and recreational activities. Therefore, continued monitoring of this system can determine long-term changes in consumer foraging behaviour, and potential alterations to ecosystem structure and function. These results showed flexibility in the

diet of some consumers (e.g., cisco, lake whitefish, and Goose Creek northern pike) throughout the spring and summer period and how they coupled the marine and freshwater systems together. Previous studies investigating habitat coupling in freshwater and marine environments have focused on understanding vertical resource use (i.e., benthic versus pelagic sources) (Duffill Telsnig et al., 2019; Kiljunen et al., 2020; Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002), but few have focused on horizontal resource use between different systems (i.e., freshwater and marine) (DeJong, 2017). Horizontal resource use is especially important to understand in an estuarian system since aquatic migratory consumers are susceptible to climate change because they rely on two different habitats to complete their life stages. The loss of one or both habitats will result in migratory species being unable to either spawn (freshwater systems) or find more productive resources to forage on (marine system) (Pecl et al., 2017; Reist et al., 2006; Schindler & Smol, 2006). Habitat couplers are important for maintaining a diverse and productive ecosystem (Schindler & Scheuerell, 2002), and by understanding the foraging behaviour of different mobile consumers within the lower Churchill River we can better predict the trophic structure of the community and how to manage these species properly.

In conclusion, this thesis has been one of the first studies to examine the aquatic food web within the lower Churchill River system and to quantify the trophic structure and habitat coupling role of consumers along a marine and freshwater gradient. The described dietary shifts and habitat coupling may be due to species moving to safer habitats to complete certain life stages. Estuary management is important since many species use estuaries for foraging and breeding (Luxa, 2013; Morin & Dodson, 1986). As well, some species (brook trout, cisco, lake whitefish, and northern pike) may be taking advantage of foraging on more marine resources due to increased productivity compared to freshwater systems (Sánchez-Hernández & Amundsen, 2018). Understanding how the community may have changed over time will provide information to conservation managers on how to protect certain vulnerable species as well as how to prevent extinction events. For example, grayling was an important fish that use to be found within the lower Churchill River but have not been caught in the last few decades (Edye-Rowntree, 2007). The loss of this species may have resulted in changes to the fish community, as observed with the fish assemblage in Chapter 3, therefore understanding how the community functions currently and the diet and niche sizes of these consumers will help provide baseline information

for future studies and management projects. Therefore, continued monitoring of the lower

Churchill River is important to understanding any dietary shifts and trophic structure changes.

4.1 References

Bartley, T.J., McCann, K.S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M.M., MacDougall, A.S., Tunney, T.D., & McMeans, B.C. (2019). Food web rewiring in a changing world. *Nature Ecology & Evolution*, *3*(3), 345-354. doi: 10.1038/s41559-018-0772-3.

DeJong, R.A. (2017). Life history characteristics of Lake Whitefish (*Coregonus clupeaformis*), Cisco (*Coregonus artedi*), and Northern Pike (*Esox lucius*) in rivers of the Hudson Bay Lowlands. (Masters thesis). University of Waterloo, Ontario, Canada

Duffill Telsnig, J.I., Jennings, S., Mill, A.C., Walker, N.D., Parnell, A.C., Polunin, N.V.C., & Jackson, A. (2019). Estimating contributions of pelagic and benthic pathways to consumer production in coupled marine food webs. *The Journal of Animal Ecology*, *88*(3), 405-415. doi: 10.1111/1365-2646.12929.

Edye-Rowntree, J. (2007). Churchill residents' use of the lower Churchill River in Manitoba. (Masters thesis) University of Manitoba, Winnipeg, Canada.

Elliott Smith, E.A., Harrod, C., Docmac, F., & Newsome, S.D. (2020). Intraspecific variation and energy channel coupling within a Chilean kelp forest. *Ecology*, *102*(1), p.e03198. doi: 10.1002/ecy.3198.

Kiljunen, M., Peltonen, H., Lehtiniemi, M., Uusitalo, L., Sinisalo, T., Norkko, J., Kunnasranta, M., Torniainen, J., Rissanen, A.J., & Karjalainen, J. (2020). Benthic-pelagic coupling and trophic relationships in northern Baltic Sea food webs. *Limnology and Oceanography*, *65*(8), 1706-1722. doi: 10.1002/lno.11413.

Luxa, K. (2013). Food habits of harbor seals (*Phoca vitulina*) in two estuaries in the central Salish Sea. *Aquatic Mammals*, *39*(1), 10-22. doi: 10.1578/AM.39.1.2013.10.

Magoulick, D.D. & Piercey, G.L. (2015). Trophic overlap between native and invasive stream crayfish. *Hydrobiologia*, *766*(1), 237-246. doi: 10.1007/s10750-015-2457-0.

Morin, R. & Dodson, J.J. (1986). Chapter 15 the ecology of fishes in James Bay, Hudson Bay and Hudson Strait. *Elsevier Oceanography Series*, *44*, 293-326. doi: 10.1016/S0422-9894(08)70908-5.

Pecl, G. T., Araujo, M. B., Bell, J., Blanchard, J., Bonebrake, T. C., Chen, I., Clark, T. D., Colwell, R. K., Danielsen, F., Evengard, B., & Robinson, S. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science*, *355* (6332), 1-9.

Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J., & Sawatzky, C.D. (2006). General effects of climate change on Arctic fishes and fish populations. *AMBIO*, *35*(7), 370-380. doi: 10.1579/0044-7447(2006)35[370:GEOCCO]2.0.CO2.

Sánchez-Hernández, J. & Amundsen, P-A. (2018). Ecosystem type shapes trophic position and omnivory in fishes. *Fish and Fisheries*, *19*(6), 1003-1015. doi: 10.1111/faf.12308.

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. doi: 10.1073/pnas.1716825115.

Schindler, D.E., & Scheuerell, M.D. (2002). Habitat coupling in lake ecosystems. *Oikos*, *98*, 177-189.

Schindler, D. & Smol, J. (2006). Cumulative effects of climate warming and other human activities on freshwaters of arctic and subarctic Northern America. *Ambio*, *35*(4), 160-168.

Seubert, E.A., Hussey, N., Powers, S.P., Valentine, J.F., & Drymon, J.M. (2019). Assessing trophic flexibility of a predator assemblage across a large estuarine seascape using blood plasms stable isotope analysis. *Food Webs*, *21*, e00132. Doi: 10.1016/j.fooweb.2019.e00132.

Vander Zanden, M.J. & Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, *83*(8), 2152-2161. doi: 10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO2.

Winemiller, K.O. (1990). Spatial temporal variation in tropical fish trophic networks. *Ecological Monographs*, *60*(3), 331-367. doi: 10.2307/1943061.

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. doi: 10.1002/lno.11174.

Yurkowski, D.J., Hussey, N.E., Fish, A.T., Imrie, K.L., Tallman, R.F., & Ferguson, S.H. (2017). Temporal shifts in intraguild predation pressure between beluga whales and Greenland halibut in a changing Arctic. *Biology Letters*, *13*(11), 20170433. doi: 10.1098/rsbl.2017.0433.

5.0 Appendix A

Table A-1. Water quality variables (mean ± SE) collected in 2019 and 2020 throughout the lower Churchill River area, Manitoba

Year	Site	Temperature (°C)	Dissolved Oxygen (mg/L)	Conductivity (µS/cm)	Salinity (ppt)	pH
2019	Churchill River (n=8)	19.2 ± 0.6	9.5 ± 0.1	158.0 ± 13.0	0.09 ± 0.01	8.52 ± 0.09
2019	Goose Creek (n=2)	22.7 ± 0.7	11.2 ± 1.4	673.5 ± 33.5	0.35 ± 0.02	8.63 ± 0.17
2019	Estuary (n=8)	13.2 ± 0.9	10.2 ± 0.2	23018.8 ± 3791.2	19.28 ± 3.46	8.13 ± 0.06
2019	Hudson Bay (n=4)	12.6 ± 0.4	10.5 ± 0.3	33272.3 ± 66.4	28.20 ± 0.30	8.07 ± 0.06
2020	Churchill River (n=12)	16.3 ± 0.4	9.0 ± 0.2	109.6 ± 4.7	0.06 ± 0.002	8.74 ± 0.03
2020	Goose Creek (n=2)	16.3 ± 0.2	7.8 ± 1.0	358.8 ± 33.4	0.21 ± 0.022	8.69 ± 0.21
2020	Estuary (n=29)	14.3 ± 0.5	9.7 ± 0.06	4204.8 ± 1101.7	3.40 ± 0.93	9.06 ± 0.05

Table A-2. Mean (‰) ± standard error (SE) of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ for each fish and seal species based on the sampling locations. CR= Churchill River and GC= Goose Creek. Each table is divided by tissue type (a- muscle/whole body and b- liver).

(a)

Marine Mammal	δ13C Muscle				δ15N Muscle				δ34S Muscle			
	2019		2020		2019		2020		2019		2020	
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE
Churchill River												
harbour seal	4	-19.87 ± 0.23	0		4	18.06 ± 0.19	0		4	16.80 ± 0.25	0	
ring seal	1	-20.9	4	-19.58 ± 0.26	1	16.03	4	17.41 ± 0.34	1	17.03	4	17.15 ± 0.05

Fish	$\delta^{13}C$ Muscle				$\delta^{15}N$ Muscle				$\delta^{34}S$ Muscle			
	2019		2020		2019		2020		2019		2020	
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE
Hudson Bay												
brook trout	5	-21.71 ± 0.32	2	-22.48 ± 0.52	5	15.37 ± 0.29	2	14.89 ± 0.57	5	15.66 ± 0.44	2	14.86 ± 1.09
capelin	20	-21.09 ± 0.08	20	-21.46 ± 0.13	20	14.89 ± 0.11	20	14.53 ± 0.12	20	18.39 ± 0.05	20	17.58 ± 0.06
cisco	20	-21.69 ± 0.16	6	-20.33 ± 0.47	20	13.65 ± 0.09	6	14.46 ± 0.39	20	12.53 ± 0.31	6	14.43 ± 0.65
fourhorn sculpin	8	-20.13 ± 0.30	0		8	15.17 ± 0.13	0		8	15.88 ± 0.37	0	
Greenland cod	20	-19.98 ± 0.10	0		20	17.00 ± 0.17	0		20	18.29 ± 0.09	0	
lake whitefish	2	-19.78 ± 0.66	15	-19.94 ± 0.40	2	11.61 ± 0.97	15	12.49 ± 0.29	2	10.08 ± 0.14	15	12.02 ± 0.38
Estuary												
burbot	0		1	-25.3	0		1	6.34	0		1	11.26
cisco	0		1	-21.67	0		1	11.45	0		1	11.3
fourhorn sculpin	20	-20.83 ± 0.07	1	-21	20	15.35 ± 0.10	1	8.68	20	15.92 ± 0.12	1	11.05
lake whitefish	2	-21.34 ± 1.09	5	-24.01 ±0.52	2	9.62 ± 0.13	5	9.76 ± 0.61	2	10.32 ± 1.16	5	6.55 ± 1.43
Churchill River												
burbot	2	-26.58 ± 0.07	3	-25.43 ± 0.11	2	8.41 ± 0.21	3	9.53 ± 0.06	2	4.44 ± 0.04	3	3.07 ± 0.54
cisco	0		1	-29.65	0		1	8.76	0		1	2.41
lake whitefish	20	-24.66 ± 0.44	20	-25.85 ± 0.25	20	9.33 ± 0.23	20	8.80 ± 0.16	20	8.33 ± 0.74	20	5.52 ± 0.64
longnose sucker	1	-27.65	12	-27.05 ± 0.17	1	7.65	12	7.82 ± 0.12	1	3.21	12	2.62 ± 0.25
northern pike	7	-25.40 ± 0.22	6	-27.40 ± 0.63	7	9.92 ± 0.24	6	9.53 ± 0.40	7	7.10 ± 0.29	6	3.80 ± 0.57
nine-spine stickleback	3	-22.60 ± 0.21	2	-19.10 ± 1.05	3	12.61 ± 0.56	2	9.15 ± 2.27	3	16.60 ± 0.10	1	11.97
trout-perch	0		19	-26.52 ± 0.10	0		19	9.80 ± 0.06	0		19	3.38 ± 0.37
walleye	0		1	-28.34	0		1	10.7	0		1	4.08
white sucker	2	-27.23	8	-28.11 ± 0.43	2	8.64 ± 0.27	8	8.10 ± 0.13	2	4.08 ± 1.00	8	4.23 ± 0.53
Goose Creek												
lake whitefish	4	-24.78 ± 0.48	0		4	7.95 ± 0.50	0		4	10.30 ± 1.05	0	
northern pike	20	-25.53 ± 0.62	0		20	6.78 ± 0.22	0		20	15.29 ± 0.86	0	

Table A-2. Continue

(b)

Marine Mammal	δ¹³C Liver 2019 n	Mean ± SE	2020 n	Mean ± SE	δ¹⁵N Liver 2019 n	Mean ± SE	2020 n	Mean ± SE	δ³⁴S Liver 2019 n	Mean ± SE	2020 n	Mean ± SE
Churchill River												
harbour seal*	4	-20.66 ± 0.46	0		4	17.94 ± 0.37	0		4	18.49 ± 0.40	0	
ring seal	1	-20.8	4	-19.13 ± 0.27	1	16.82	4	18.24 ± 0.46	1	16.88	4	17.09 ± 0.12

Fish	δ¹³C Liver 2019 n	Mean ± SE	2020 n	Mean ± SE	δ¹⁵N Liver 2019 n	Mean ± SE	2020 n	Mean ± SE	δ³⁴S Liver 2019 n	Mean ± SE	2020 n	Mean ± SE
Hudson Bay												
brook trout	5	-20.80 ± 0.10	3	-20.49 ± 0.03	5	15.05 ± 0.15	3	14.63 ± 0.39	5	16.58 ± 0.25	3	17.25 ± 0.59
capelin	15	-20.58 ± 0.09	8	-20.65 ± 0.24	15	13.73 ± 0.14	8	13.61 ± 0.17	1	18.2	0	
cisco	20	-21.46 ± 0.19	6	-20.40 ± 0.32	20	12.78 ± 0.12	6	14.21 ± 0.42	20	13.04 ± 0.28	6	15.53 ± 0.77
fourhorn sculpin	8	-19.82 ± 0.39	0		8	14.27 ± 0.22	0		8	16.81 ± 0.37	0	
Greenland cod	20	-19.88 ± 0.12	0		20	16.57 ± 0.18	0		20	18.83 ± 0.10	0	
lake whitefish	2	-20.09 ± 1.33	15	-20.58 ± 0.41	2	11.81 ± 0.92	15	11.76 ± 0.29	2	10.22 ± 1.06	15	11.88 ± 0.51
Estuary												
burbot	0		0		0		0		0		0	
cisco	0		1	-21.79	0		1	9.39	0		1	10.3
fourhorn sculpin	20	-20.41 ± 0.09	0		20	13.85 ± 0.13	0		20	17.07 ± 0.15	0	
lake whitefish	2	-21.54 ± 0.70	5	-23.44 ± 0.72	2	8.78 ± 0.16	5	8.54 ± 0.47	2	6.12 ± 3.11	5	7.54 ± 1.58
Churchill River												
burbot	0		3	-25.72 ± 0.13	0		3	10.06 ± 0.05	0		3	2.87 ± 0.33
cisco	0		0		0		0		0		0	
lake whitefish	20	-25.25 ± 0.40	20	-26.51 ± 0.32	20	8.26 ± 0.25	20	7.83 ± 0.20	20	7.24 ± 0.85	20	5.21 ± 0.69
longnose sucker	1	-27.66	12	-28.06 ± 0.19	1	6.97	12	6.86 ± 0.15	1	12.54	12	2.19 ± 0.11
northern pike	7	-24.98 ± 0.24	4	-25.52 ± 0.56	7	10.08 ± 0.22	4	9.96 ± 0.48	7	6.48 ± 0.47	4	4.54 ± 0.66
nine-spine stickleback	0		0		0		0		0		0	
trout-perch	0		0		0		0		0		0	
walleye	0		0		0		0		0		0	
white sucker	1	-26.71	7	-28.48 ± 0.22	1	8.06	7	7.11 ± 0.15	1	6.00	7	3.61 ± 0.53
Goose Creek												
lake whitefish	4	-25.24 ± 0.45	0		4	8.03 ± 0.51	0		4	7.80 ± 0.70	0	
northern pike	20	-25.35 ± 0.47	0		20	7.34 ± 0.20	0		20	16.04 ± 0.78	0	

*tissue samples for harbour seals was hair

Table A-3. The month and year each fish species was collected throughout the Churchill River, estuary, and Hudson Bay, Manitoba

Species	n	Collection Date
brook trout	5	19-Jul
	3	20-Jun
burbot	2	19-Jul
	1	20-Aug
	3	20-Sep
capelin	20	19-Jun
	20	20-Jun
cisco	20	19-Jul
	6	20-Jun
	1	20-Aug
	1	20-Sep
fourhorn sculpin	28	19-Jul
	1*	20-Aug
Greenland cod	20	19-Jul
lake whitefish	4	19-May
	24	19-Jul
	15	20-Jun
	24	20-Aug
longnose sucker	1	19-Jul
	12	20-Sep
nine-spine stickleback	3	19-May
	2	20-Aug
northern pike CR	7	19-Jul
	2	20-Aug
	4	20-Sep
northern pike GC	20	19-May
trout-perch	19	20-Sep
walleye	1	20-Sep
white sucker	2	19-Jul
	5	20-Aug
	3	20-Sep

Table A-4. Amino acid composition of arctic fish liver carboxylesterase. The C:N ratio of pure protein was calculated to be ~3.8 based on the amino acid composition of the arctic fish liver tissues. AF = arrow tooth flounder; BS = big mouth sculpin; FS = flat head sole; PH = Pacific halibut; PS = pink salmon; WP = walleye pollock; RF = spiny head rock fish.

Amino Acid	Molecular Formula	#Cs	#Ns	C x integer							N x integer							
				AF	BS	FS	PH	PS	WP	RF	AF	BS	FS	PH	PS	WP	RF	
Alanine	$C_3H_7NO_2$	3	1	18.84	19.11	18.9	20.22	17.97	19.98	18.84	6.28	6.37	6.3	6.74	5.99	6.66	6.28	
Arginine	$C_6H_{14}N_4O_2$	6	4	45.48	45.66	41.46	41.4	50.4	38.46	38.16	30.32	30.44	27.64	27.6	33.6	25.64	25.44	
Aspartic acid	$C_4H_7NO_4$	4	1	36.88	36.44	38.48	38.2	37.52	36.6	39.96	9.22	9.11	9.62	9.55	9.38	9.15	9.99	
Glutamic acid	$C_5H_9NO_4$	5	1	61.9	60.8	60.8	61.35	69.1	61.45	62.75	12.38	12.16	12.16	12.27	13.82	12.29	12.55	
Glycine	$C_2H_5NO_2$	2	1	9.72	14.2	10.78	10.64	10.3	11.16	9.48	4.86	7.1	5.39	5.32	5.15	5.58	4.74	
Histidine	$C_6H_9N_3O_2$	6	3	16.8	15.42	17.76	16.62	16.56	16.56	17.22	8.4	7.71	8.88	8.31	8.28	8.28	8.61	
Isoleucine	$C_6H_{13}NO_2$	6	1	29.7	26.52	29.1	28.14	27.24	29.7	29.22	4.95	4.42	4.85	4.69	4.54	4.95	4.87	
Leucine	$C_6H_{13}NO_2$	6	1	52.5	47.52	51.48	51.96	47.82	54.84	54.72	8.75	7.92	8.58	8.66	7.97	9.14	9.12	
Lysine	$C_6H_{14}N_2O_2$	6	2	55.38	49.8	56.7	51.36	50.58	43.14	52.8	18.46	16.6	18.9	17.12	16.86	14.38	17.6	
Methionine	$C_5H_{11}NO_2S$	5	1	14.7	15.2	13.3	16.75	17.15	16.85	14.45	2.94	3.04	2.66	3.35	3.43	3.37	2.89	
Phenylalanine	$C_9H_{11}NO_2$	9	1	45.36	43.92	47.88	44.46	46.98	47.88	50.13	5.04	4.88	5.32	4.94	5.22	5.32	5.57	
Proline	$C_5H_9NO_2$	5	1	21.85	24.65	21.9	20.85	24.05	23	21.55	4.37	4.93	4.38	4.17	4.81	4.6	4.31	
Serine	$C_3H_7NO_3$	3	1	14.07	15.69	15.15	15.75	13.26	15.09	14.25	4.69	5.23	5.05	5.25	4.42	5.03	4.75	
Threonine	$C_4H_9NO_3$	4	1	22.92	21.84	23	23	19.72	25.16	23.44	5.73	5.46	5.75	5.75	4.93	6.29	5.86	
Tyrosine	$C_9H_{11}NO_3$	9	1	39.15	33.39	33.93	38.16	40.14	37.08	36.09	4.35	3.71	3.77	4.24	4.46	4.12	4.01	
Valine	$C_5H_{11}NO_2$	5	1	32.45	31.2	32.6	34.3	29.65	34.5	33.95	6.49	6.24	6.52	6.86	5.93	6.9	6.79	C:N ratio
Total		84	22	517.7	501.36	513.22	513.16	518.44	511.45	517.01	137.23	135.32	135.77	134.82	138.79	131.7	133.38	3.79

Table A-5. Wilcoxon Rank Sum Squares test results (p-values) comparing stable isotope ratios between May and July for northern pike and lake whitefish collected in 2019 based on tissue type. The bolded values indicate significant differences between years (Holm-Bonferroni sequential correction to α).

Species	Location	Tissue	p-values $\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
northern pike	GC-CR	Muscle	0.19	**<0.001**	**<0.001**
lake whitefish	GC-CR	Muscle	1.00	0.04	0.24
lake whitefish	GC-E	Muscle	0.13	0.13	1.00
lake whitefish	GC-HB	Muscle	0.13	0.13	0.80
northern pike	GC-CR	Liver	0.79	**<0.001**	**<0.001**
lake whitefish	GC-CR	Liver	0.91	0.85	0.63
lake whitefish	GC-E	Liver	0.13	0.53	0.80
lake whitefish	GC-HB	Liver	0.13	0.13	0.27

Table A-6. Wilcoxon Rank Sum Squares test results (p-values) comparing stable isotope ratios between 2019 and 2020 for each species and tissue type. The bolded values indicate significant differences between years (Holm-Bonferroni sequential correction to α).

Species	Tissues	p-values $\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
brook trout	Muscle	0.38	0.57	0.57
burbot	Muscle/ whole body	0.13	0.53	0.53
capelin	Muscle	0.01	0.03	**<0.001**
cisco	Muscle	0.07	0.82	0.30
lake whitefish	Muscle	0.62	0.22	0.41
longnose sucker	Muscle	0.31	0.62	0.31
nine-spine stickleback	Whole body	0.20	0.20	0.50
northern pike CR	Muscle	0.01	0.45	0.001
white sucker	Muscle	0.18	0.27	1.00
sculpin	Muscle	0.41	0.12	0.11
seals*	Muscle	0.56	0.11	0.29
brook trout	Liver	0.04	0.57	0.39
capelin	Liver	1.00	0.59	
cisco	Liver	0.05	0.06	0.08
lake whitefish	Liver	0.53	0.31	0.78
longnose sucker	Liver	0.77	0.92	
northern pike CR	Liver	0.41	0.93	0.04
white sucker	Liver	0.25	0.25	0.25
ringed seals	Liver	0.40	0.40	0.80

*harbour and ringed seal muscle data were combined.

Table A-7. Fish and seal species δ^{13}C, δ^{15}N, and δ^{34}S liver values (‰, mean ± SE), plus C:N ratio (mean ± SE), the posterior medians (%) and 95% credible intervals (CI) of the freshwater-derived resources, and the mode and CI for the 95% probability niche size (‰^{3}) for each species.

Species	n	δ^{13}C	δ^{15}N	δ^{34}S	C:N	Freshwater-derived resources (%)	Niche Size (‰^{3})
				Liver			
longnose sucker	13	-28.03 ± 0.18	6.87 ± 0.14	2.98 ± 0.80	3.47 ± 0.05	0.99 (0.96-1.00)	0.77 (0.46-1.68)
white sucker	8	-28.26 ± 0.29	7.23 ± 0.18	3.91 ± 0.55	3.53 ± 0.13	0.99 (0.93-1)	0.42 (0.24-1.15)
burbot	3	-25.72 ± 0.13	10.06 ± 0.05	2.87 ± 0.33	3.24 ± 0.02	0.96 (0.85-1)	
northern pike CR†	13	-25.18 ± 0.23	10.04 ± 0.19	5.77 ± 0.43	4.32 ± 0.36	0.81 (0.55-0.91)	0.71 (0.41-1.63)
lake whitefish	68	-24.20 ± 0.34	9.03 ± 0.23	7.78 ± 0.47	3.34 ± 0.02	0.74 (0.67-0.81)	12.62 (9.60-16.97)
cisco	27	-21.24 ± 0.18	12.97 ± 0.22	13.49 ± 0.35	3.26 ± 0.03	0.24 (0.18-0.29)	0.79 (0.53-1.34)
northern pike GC†	20	-25.35 ± 0.47	7.34 ± 0.20	16.04 ± 0.78	4.51 ± 0.19	0.12 (0.04-75)	5.72 (3.68-10.42)
brook trout	8	-20.68 ± 0.08	14.89 ± 0.17	16.83 ± 0.27	3.22 ± 0.03	0.05 (0.01-0.09)	0.06 (0.04-0.17)
harbour seal	4	-19.87 ± 0.23	18.06 ± 0.19	16.80 ± 0.25	4.00 ± 0.26	0.03 (0-0.14)	0.003 (0.002-0.02)
ringed seal	5	-19.46 ± 0.39	17.95 ± 0.45	17.05 ± 0.10	3.33 ± 0.02	0.008 (0-0.05)	0.003 (0.002-0.01)
fourhorn sculpin	28	-20.24 ± 0.13	13.97 ± 0.11	17.00 ± 0.15	5.31 ± 0.21	0.005 (0-0.02)	0.36 (0.24-0.60)
Greenland cod	20	-19.88 ± 0.12	16.57 ± 0.18	18.83 ± 0.10	3.13 ± 0.01	0.004 (0-0.02)	0.11 (0.07-0.21)
capelin	23*	-20.60 ± 0.10	13.69 ± 0.11	18.20	3.16 ± 0.02		

*n=1 for δ^{34}S

†CR= Churchill River, GC= Goose Creek.

Individual liver results

At the individual level, of the 214 liver/hair samples analyzed, 141 individuals had a ≥80% posterior probability of classification with either the marine-derived resource and/or freshwater-derived resource channels. The liver results were similar to the muscle results for the following species. Marine resources were consumed by all individuals of ringed seals, fourhorn sculpin, and Greenland cod, whereas all individuals of burbot, longnose sucker, and white sucker relied mainly on freshwater resources. Cisco (26% of individuals), lake whitefish (51% of individuals), and Goose Creek northern pike (70% of individuals) had individuals that were between 20-80% for their posterior medians.

Table A-8. Total isotopic niche overlap probability (%) of the prediction ellipsoids for the seal and fish species liver data present in the lower Churchill River area, Manitoba based on $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ separated by prediction ellipsoid (a- 95% region and b- 40% region). A color gradient was applied such that darker colors coordinate with higher overlap. Significant overlap is defined as overlap $\geq$60%.

(a)

	Species B									
Species A	brook trout	cisco	fourhorn sculpin	Greenland cod	lake whitefish	longnose sucker	northern pike Churchill River	northern pike Goose Creek	white sucker	seal
brook trout		65 (18-97)	55 (20-89)	5 (0-22)	0.2 (0-2)	0	0	0	0	4 (0-26)
cisco	5 (1-13)		15 (5-28)	0.2 (0-1)	53 (27-80)	0	0.7 (0-5)	0	0	0.1 (0-1)
fourhorn sculpin	14 (3-35)	43 (17-72)		0.2 (0-2)	3 (0-22)	0	0	0	0	0.09 (0-1)
Greenland cod	5 (0-22)	3 (0-34)	0.7 (0-5)		0	0	0	0	0	1 (0-10)
lake whitefish	0	5 (1-10)	0.07 (0-0)	0		8 (4-15)	11 (5-22)	13 (3-30)	6 (2-12)	0
longnose sucker	0	0	0	0	95 (80-100)		0.5 (0-5)	2 (0-10)	51 (24-80)	0
northern pike Churchill River	0	0.7 (0-5)	0	0	97 (84-100)	0.4 (0-3)		4 (0-31)	0.8 (0-6)	0
northern pike Goose Creek	0	0	0	0	20 (7-38)	0.3 (0-2)	0.3 (0-2)		0.1 (0-1)	0
white sucker	0	0	0	0	98 (86-100)	68 (35-94)	1 (0-13)	1 (0-13)		0
seal	2 (0-11)	1 (0-11)	0.2 (0-2)	2 (0-13)	0	0	0	0	0	

Table A-8. Continue.

(b)

	Species B									
	brook trout	cisco	fourhorn sculpin	Greenland cod	lake whitefish	longnose sucker	northern pike Churchill River	northern pike Goose Creek	white sucker	seal
brook trout		3 (0-17)	8 (0-26)	0.3 (0-2)	0	0	0	0	0	0
cisco	0.5 (0-2)		2 (0-5)	0	6 (1-16)	0	0	0	0	0
fourhorn sculpin	1 (0-5)	2 (0-9)		0	0	0	0	0	0	0
Greenland cod	0.1 (0-1)	0	0		0	0	0	0	0	0
lake whitefish	0	0.3 (0-1)	0	0		1 (0-3)	1 (0-4)	0.6 (0-2)	0.8 (0-2)	0
longnose sucker	0	0	0	0	16 (1-48)		0	0.06 (0-1)	12 (2-28)	0
northern pike Churchill River	0	0	0	0	31 (8-64)	0		0	0	0
northern pike Goose Creek	0	0	0	0	2 (0-6)	0	0		0	0
white sucker	0	0	0	0	18 (6-57)	22 (6-47)	0	0		0
seal	0.2 (0-1)	0	0	0	0	0	0	0	0	

(Species A labels the rows)

Niche overlap liver results

For the liver, higher isotopic niche overlap occurred between cisco and brook trout (65%); between lake whitefish with longnose sucker (95%), Churchill River northern pike (97%), and white sucker (98%), and between longnose sucker and white sucker (68%).
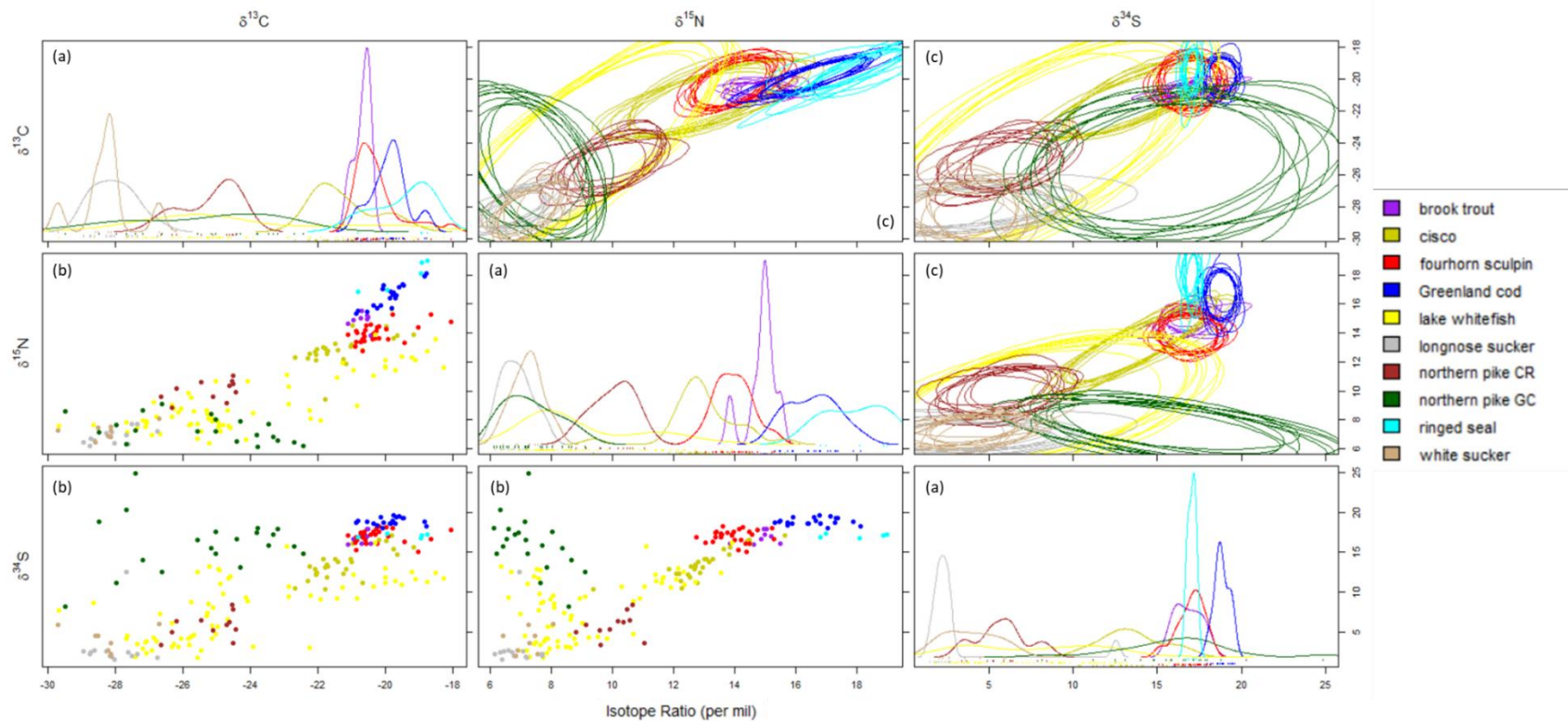
Figure A-1. A 2-dimensional projection of ten 3-dimensional niche regions. Stable isotopes (δ^{13}C, δ^{15}N, and δ^{34}S, ‰) were used for twelve fish species groupings and one seal grouping based on liver tissue. The line plots (a) are one-dimensional density plots. The point plots (b) are two-dimensional scatterplots or the raw stable isotope data. The elliptical projections (c) are the pairings of δ^{13}C, δ^{15}N, and δ^{34}S showing two-dimensional projections of the 95% probabilistic niche regions based on 3-dimensional data. CR= Churchill River and GC= Goose Creek.

6.0 Appendix B

Table B-1. The total number of fish sent for aging out of the total number of fish sent for stable isotope analysis during 2019 and 2020. Structures sent for analysis were either the otolith or cleithrum or preopercular bones. Samples were either sectioned, crack and burned, or analyzed whole. *when cleaning the structures, several cleithrum were actually preopercular bones which are less accurate for aging in northern pike.

Year	2019			2020		
Species	**Structure**	**Analyzed**	**Number**	**Structure**	**Analyzed**	**Number**
brook trout	Ototlith	Sectioned	3	Ototlith	Crack and Burn	1
burbot				Ototlith	Crack and Burn	3
cisco	Ototlith	Crack and Burn	1	Ototlith	Crack and Burn	7
		Whole	1			
		Sectioned	18			
fourhorn sculpin	Ototlith	Sectioned	27			
Greenland cod	Ototlith	Sectioned	20			
lake whitefish	Ototlith	Crack and Burn	22	Ototlith	Crack and Burn	40
		Whole	5			
longnose sucker				Ototlith	Sectioned	3
northern pike	Cleithrum	Whole	27	Cleithrum*	Whole	6
white sucker				Ototlith	Sectioned	2

Table B-2. Fish and seal species $\delta^{13}C$ and $\delta^{15}N$ liver values (‰, mean ± SE), plus the median ± SE of the trophic position, and the minimum and maximum trophic position for each species.

Species	n	$\delta^{13}C$	$\delta^{15}N$	Trophic Position	Trophic Position Range
			Liver		
harbour seal*	4	-19.87 ± 0.23	18.06 ± 0.19	5.09 ± 0.12	4.85-5.44
ringed seal	5	-19.46 ± 0.39	17.95 ± 0.45	4.87 ± 0.15	4.45-5.15
Greenland cod	20	-19.88 ± 0.12	16.57 ± 0.18	4.87 ± 0.07	4.40-5.41
brook trout	8	-20.68 ± 0.08	14.89 ± 0.17	4.28 ± 0.06	3.88-4.48
northern pike CR†	13	-25.18 ± 0.23	10.04 ± 0.19	3.97 ± 0.07	3.48-4.27
fourhorn sculpin	28	-20.24 ± 0.13	13.97 ± 0.11	3.92 ± 0.04	3.49-4.39
burbot	3	-25.72 ± 0.13	10.06 ± 0.05	3.91 ± 0.02	3.90-3.96
capelin	23	-20.60 ± 0.10	13.69 ± 0.11	3.82 ± 0.04	3.48-4.23
cisco	27	-21.24 ± 0.18	12.97 ± 0.22	3.51 ± 0.08	2.29-4.52
lake whitefish	68	-24.20 ± 0.34	9.03 ± 0.23	3.09 ± 0.06	1.69-4.49
white sucker	8	-28.26 ± 0.29	7.23 ± 0.18	2.93 ± 0.06	2.63-3.21
northern pike GC†	20	-25.35 ± 0.47	7.34 ± 0.20	2.90 ± 0.07	2.52-3.59
longnose sucker	13	-28.03 ± 0.18	6.87 ± 0.14	2.76 ± 0.05	2.54-3.09

*hair samples were used for the harbour seal since there was no liver sample
†CR= Churchill River, GC= Goose Creek.
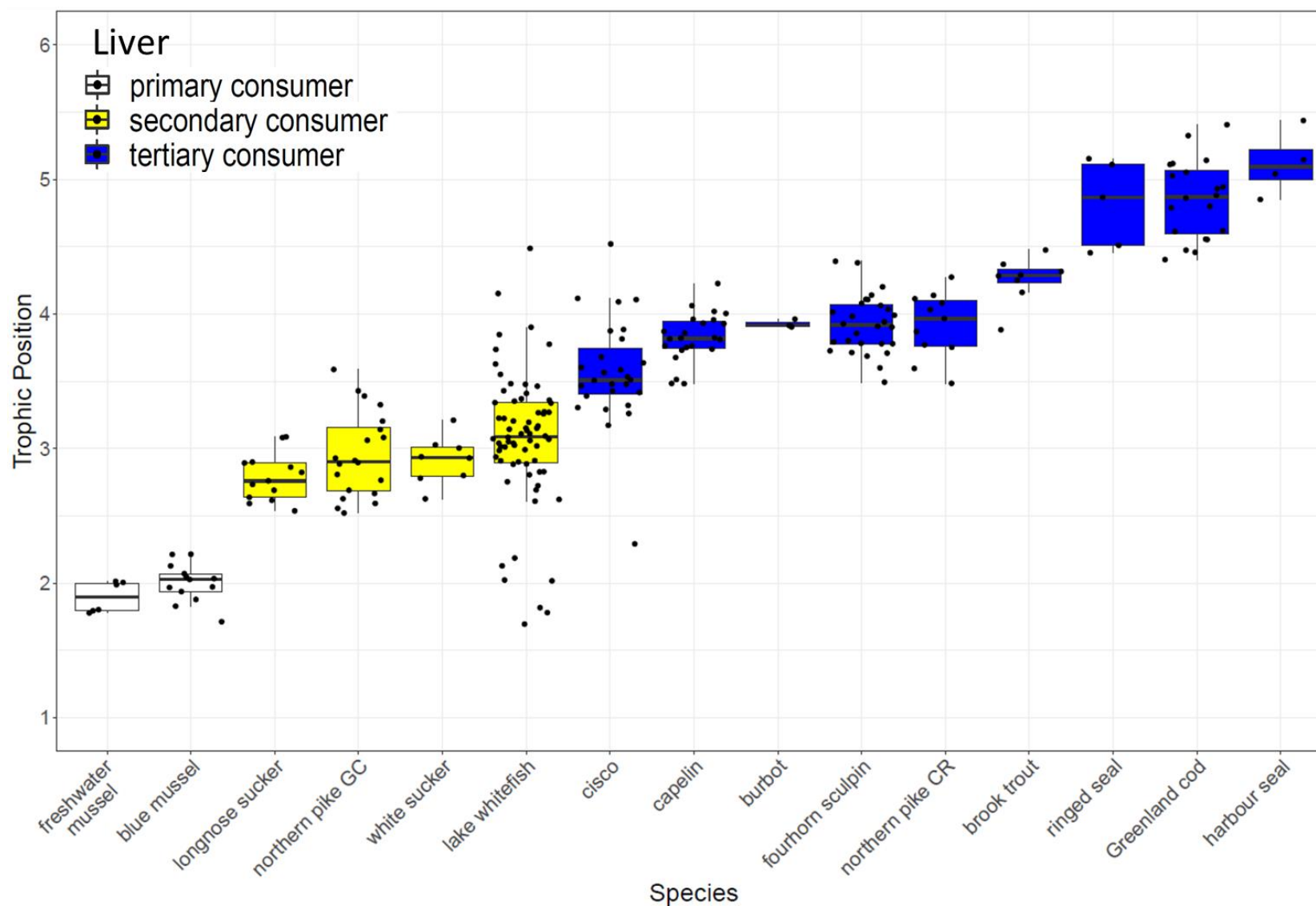
Figure B-1. Boxplot (median and standard deviation) of consumers trophic positions within the lower Churchill River area based on liver data. Hair samples were used for the harbour seals instead of liver. CR= Churchill River and GC= Goose Creek.