Trophic ecology of culturally important subsistence fish species and assessment of diet overlap with range-expanding chum salmon (*Oncorhynchus keta*) in the Canadian Arctic

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences

University of Alberta

Abstract

Rapid climate change is occurring in the Arctic and has the potential to affect the diets and trophic dynamics of northern fish species, many of which hold great cultural value to northern communities. Fully understanding the trophic ecology of such fishes allows us to better understand their environmental niche, and being able to identify key prey items allows us to determine if key food sources are threatened by environmental changes. This allows for predictions to be made regarding the adaptation potential of fishes in the face of changing ecosystems. Additionally, global increases in water temperatures introduces the potential for opportunistic fish species to expand their ranges northward, making trophic interactions with endemic northern fishes a possibility. Understanding the trophic ecology of northern and range-expanding fishes allows us to predict the potential for trophic interactions and potentially competition, and whether or not a range expanding species may fill a vacant feeding niche in a novel environment, or if it will overlap with endemic fishes.

To assess the trophic dynamics of northern fishes, I first conducted a systematic literature review on the diets of eight fish species: Arctic char (*Salvelinus alpinus*), Dolly Varden (*S. malma*), lake trout (*S. namaycush*), bull trout (*S. confluentus*), inconnu (*Stenodus leucichthys*), broad whitefish (*Coregonus nasus*), lake whitefish (*C. clupeaformis*), and burbot (*Lota lota*). These species chosen for their importance as subsistence fishes to northern communities. This review highlighted the commonality of adaptable, generalist diets in most species, an adaptation to the harsh and variable nature of Arctic systems where prey availability can be sporadic and unpredictable. Additionally, this review highlighted several knowledge gaps regarding the trophic ecology of northern fishes, particularly for inconnu, broad whitefish, and bull trout.

Additionally, trophic studies outside of the summer months are very uncommon, resulting in a large temporal knowledge gap for most species.

Next, I analyzed the diets of range-expanding chum salmon (*Oncorhynchus* keta) caught by subsistence harvesters in the Mackenzie River basin of the Northwest Territories in order to address questions regarding the species diet and potential to compete with endemic subsistence fishes such as Dolly Varden, lake trout, and inconnu. I found that, while most salmon caught had ceased feeding upon entering fresh water, 5% of salmon sampled had recently fed while in fresh water, a deviation from established life history characteristics of Pacific salmon. Prey eaten by salmon included freshwater crustaceans, water boatmen (Family: Corixidae), least cisco, and a small bird. Despite this, the infrequency of freshwater feeding suggests that dietary interactions between salmon and the northern fishes used for comparative analyses is unlikely. This is supported by the results of stable isotope analyses, which demonstrate that salmon do not overlap with any of the endemic northern fishes on the basis of trophic level, and only Dolly Varden overlapped with chum salmon in terms of feeding habitat

My results suggest that potential for trophic niche overlap between chum salmon and Arctic freshwater fishes is not high, although more thorough analyses are needed to confirm this. Additionally, some chum salmon in the Arctic environment are exhibiting alterations from known life history traits of those found in their southern distribution. This work has implications for the management of chum salmon in the new environments to which they are expanding by demonstrating their ability to adapt to new settings, as well as the feeding niche they occupy in Arctic ecosystems. This work also has implications for the management of northern fishes by demonstrating the low risk of trophic niche overlap with a range-expanding counterpart, as well as addressing knowledge gaps regarding the trophic ecology and feeding niches of northern fishes.

Preface

This thesis is an original work by Kevin Wight. Chapter 2 has been published in *Polar Biology* as Kevin J. Wight, Darcy G. McNicholl and Karen M. Dunmall (2023) “A systematic review of the trophic ecology of eight ecologically and culturally important fish species in the North American Arctic”. *Polar Biology* 46: 409-425. K.M Dunmall conceptualized and designed this review, and K. Wight screened, extracted, and analyzed the data, and wrote the original draft. K. Wight, K.M. Dunmall, and D.G. McNicholl all partook in review and editing of subsequent drafts. The chapter appears here as submitted, with slight modifications to the naming of tables and figures to ensure consistency with the rest of the thesis.

Acknowledgements

I would like to thank my supervisors, Dr. Karen Dunmall and Dr. Keith Tierney, for their support, guidance, and encouragement throughout my time as their student. I would also like to thank my parents, sister, and partner, Nicole, for their unending love, companionship, and assistance. The members of both the Arctic Salmon lab at DFO and the Tierney Lab at UofA were some of the finest friends and colleagues I could have asked for, thank you for all of the laughs, support, feedback, camaraderie, and occasional misadventures along the way. I am also extremely grateful to the multitude of collaborators who provided samples for this project: the Hunters and Trappers Committees and Renewable Resource Boards across the NWT, the individual subsistence harvesters who submitted the salmon they found in their nets and at the end of their lines, and our DFO stock assessment collaborators – Kim Howland, Colin Gallagher (who also provided an extremely valuable review on the second chapter of this thesis, helping it to be published), Yamin Janjua and their teams. I hope the information yielded in this thesis is helpful to the aims of all involved. I would also like to thank my committee member, Dr. Greg Goss, and examiner, Dr. Mark Poesch, for their feedback and comments on this thesis which will allow parts of it to be published in the future. Finally, I would like to thank the Government of Northwest Territories for funding this work through the Cumulative Impacts Monitoring Program.

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Chapter 1: Introduction

Global climate change is altering the world's ecosystems, with outcomes in the Arctic predicted to be disproportionately severe (IPCC 2022). Climate change is the greatest threat to Arctic biodiversity, while also exacerbating all other threats (CAFF 2013). Population dynamics can be altered by shifts in species ranges dictated by environmental changes, which presents the possibility of novel interactions between endemic Arctic organisms and poleward-expanding opportunists (Kortsch et al. 2015). The potential ecological implications of these shifts means that studies assessing the ecological impacts of range-expanding organisms as they enter a new environment are needed (Wallingford et al. 2020). Understanding these impacts is crucial for the management of northern ecosystems, as range expansions can alter the species compositions of these fragile systems and potentially result in trophic restructuring or other major changes (Kortsch et al. 2015).

Given that the ranges of fishes are greatly dictated by thermal tolerances, the concept of climate-mediated range shifts is especially relevant to Arctic aquatic systems as species shift northward while the ranges of cold-adapted Arctic species become restricted (Jeppesen et al. 2012). The potential for competition between poleward-expanding fishes and endemic northern species represents a risk to northern fishes because they have strict thermal limits needed for optimal functioning and are less adaptable than temperate counterparts (Reist et al. 2006a; Gilbert and Tierney 2018). Dietary overlap between a range-expanding and endemic northern species has been recorded in lower trophic level fishes such as capelin (*Mallotus villosis*) and polar cod (*Boreogadus saida*) (McNicholl et al. 2016), and larger, migratory fishes are predicted to become increasingly common in Arctic waters in the coming decades (Kortsch et al. 2015).

Pacific salmon (*Oncorhynchus* spp.) are migratory fishes that are being observed in increasing numbers throughout the Arctic (Dunmall et al. 2013, 2018), with chum salmon (*O. keta*) in particular being predicted to continue to expand northward for thermal refuge (Yoon et al. 2014). While Pacific salmon are not wholly new to the Arctic (Stephenson 2006), the recent increases in numbers are, according to observations of local subsistence harvesters (Chila et al. 2022). The effects that Pacific salmon have on Arctic ecosystems are largely unknown. Local harvesters largely regard them as harmful, and a potential threat to valued subsistence species such as chars

(*Salvelinus* spp.) and whitefishes (*Coregonus* spp.) due to the possibility of aggression by salmon, as well as competition for habitat and especially prey resources (Chila et al. 2022). Due to the threats imposed on northern fisheries due to climate change, and the increasing presence of vagrant Pacific salmon, a working knowledge of fish diets is needed to better understand the effects of continued environmental change on trophic dynamics, as well as how salmon fit into the wider Arctic aquatic food web.

The diets and trophic dynamics of fishes are important to understand as the ecological role of a species is greatly determined by its position in the food web (Kortsch et al. 2015). Understanding the diets of fishes can aid management efforts in the face of environmental changes as it places fishes within the context of the wider ecosystem food web (Gelwick and McIntyre 2017) and provide some predictive capacity when it comes to threats to key food resources and feeding habitats. Additionally, in the case of arrivals driven by range shifts, it allows for insight into how such species may fit into a new ecosystem, and the potential for interactions with endemic species. If there is overlap in the diets of a range expanding species and an endemic species, then the risk of interactions, and potentially competition, is higher than if the range-expanding species fills a largely vacant trophic niche (Gelwick and McIntyre 2017). As such, baseline dietary data of fishes is needed to inform management decisions of northern fishes in the face of climate change.

This thesis aims to investigate the diets of Arctic fish species important to subsistence fisheries in the western Canadian Arctic, and to address the knowledge gap of the diet and, by extension, highlighting the adaptation potential of chum salmon in the fresh water. The second chapter utilized a systematic literature review to describe the diets and feeding habits of eight culturally important fish species in the North American Arctic: arctic char (*Salvelinus alpinus)*, Dolly Varden (*S. malma),* lake trout (*S. namaycush*), bull trout (*S. confluentus*), lake whitefish (*Coregonus clupeaformis*), broad whitefish (*C. nasus*), inconnu *(Stenodus leucichthys*), and burbot (*Lota lota*). This review assessed diets and feeding strategies of each species across the North American Arctic, while also noting differences across range, habitat type, and life history type. Additionally, this review noted major data gaps regarding northern fish diets, in order to help direct future research. The third chapter assessed the diet of chum salmon in the Mackenzie River basin, using samples collected by Indigenous harvesters in the Mackenzie Delta, Mackenzie River, Great Bear Lake, and Great Slave Lake. Using stomach contents and stable isotopes, the prey items consumed by chum salmon in the Mackenzie system were described, and the isotopic niche space of the species was constructed. In order to address community concerns of competition between salmon and important subsistence fishes, comparative stomach content and stable isotope analyses were preformed between salmon, and Dolly Varden, lake trout, and inconnu. These two chapters, taken together, provide a fuller picture of the feeding dynamics of eight of the most common subsistence fish species in the Arctic, identifying that chum salmon eat in the Arctic freshwater ecosystem, and providing an assessment of the potential for dietary overlap between these species.

Chapter 2: A systematic review of the trophic ecology of eight ecologically and culturally important fish species in the North American Arctic

Abstract

Rapid climate change occurring in the Arctic may affect the diet of ecologically and culturally important northern fish species. Here, a systematic literature review was completed for eight fish species found across the North American Arctic, with a focus on Inuit Nunangat, to identify major prey items, summarize feeding strategies, and highlight data gaps. Arctic Char (*Salvelinus alpinus*), Dolly Varden Char (*Salvelinus malma*), Lake Trout (*Salvelinus namaycush*), Bull Trout (*Salvelinus confluentus*), Inconnu (*Stenodus leucichthys*), Lake Whitefish (*Coregonus clupeaformis*), Broad Whitefish (*Coregonus nasus*), and Burbot (*Lota lota*), were selected as species of interest due to their ecological and cultural importance. The 74 studies reviewed indicate that these species are generalist feeders that demonstrate wide dietary niches, as well as the tendency to avoid agonistic interactions by partitioning resources when they co-occur with an overlapping species. Across coastal, lacustrine, and riverine systems, the most commonly consumed prey items are insects (Diptera spp.), as well as benthic forage fishes such as sculpins (Family: Cottidae). Insects are major prey items in riverine systems, where diets appear to be more generalized, compared to lakes. Anadromous species in coastal waters most commonly feed on various crustaceans and forage fishes. Benthic forage fishes, insects, zooplankton, and mollusks are widely consumed prey items in Arctic lakes. Burbot, Inconnu, and resident Dolly Varden had the most specialized feeding strategies, due in part to their habitat requirements and morphology, while Lake Trout and resident Arctic Char often form multiple ecotypes in lakes, some with different feeding behaviours. Knowledge gaps regarding northern fish trophic ecology are highlighted, and in particular include riverine systems and winter foraging behaviour. This review is intended to inform predictions regarding the impacts of climate change on fish tropic ecology and to guide future research.

Introduction

Climate change is predicted to affect trophic dynamics of fishes and influence geographic range shifts (Brandt et al. 2002; Jackson and Mandrak 2002; Chu et al. 2005), with outcomes anticipated to be particularly acute for the Arctic (Jansen et al. 2020; IPCC 2022; Hayden et al. 2015, Prowse et al. 2006). As temperatures continue to rise, for instance, anadromous life histories may become less common, potentially increasing competition in freshwater (Reist et al. 2006b). The increased productivity of warmer waters may result in longer growing seasons (Reist et al. 2006a) but may also increase metabolism and therefore energy intake, potentially exacerbating current food-limitations (McDonald et al. 1996). Environmental change and any resulting shifts in energy intake may also influence fish growth (Huang et al. 2021). Northward range shifts of sub-Arctic species can also impact the diet of Arctic fishes, as has already occurred with a shift to Capelin (*Mallotus villosus*) and Pacific Sandlance (*Ammodytes hexapterus*), from Arctic Cod (*Boreogadus saida*) and crustaceans as prey for Arctic Char (*Salvelinus alpinus*) in some parts of the species' range (Ulrich and Tallman 2021a; Yurkowski et al. 2018; Falardeau et al. 2017). Range-expanding species may also benefit native species by providing an alternate source of nutrients in typically oligotrophic Arctic systems, as may occur with the continued expansion of Pacific salmon into the Canadian Arctic (Dunmall et al. 2013). These range-expanding fish may also, however, compete with Arctic fishes for food, as demonstrated with a high level of diet overlap among the increased presence of Capelin and endemic Arctic Cod (McNicholl et al. 2016), and there is potential for trophic interactions between Arctic Char and Atlantic Salmon (*Salmo salar*) in the fresh water (Bilous and Dunmall 2020). The predicted northward expansion of sub-Arctic cyprinids, such as Lake Chub (*Couesius plumbeus*), may also result in competition with native planktivores, such as ciscoes (*Coregonus* spp.), and result in a shift in the prey of top predators (Reist et al. 2006a). Changes in species composition due to northward range expansions may be balanced, however, by potential losses of temperature-sensitive northern fishes, with implications cascading through the trophic web (Reist et al. 2006b). The predicted and apparent impacts of climate change on the trophic ecology of Arctic fishes are indeed complex, with reverberations extending across ecosystems (Reist et al. 2006a) and influencing the food security of northern communities (Loring et al. 2019; Lynch et al. 2016).

The feeding ecology of northern fishes is shaped by their environment, making them adapted to harsh Arctic conditions and, at the same time, particularly vulnerable to warming temperatures (Power et al. 2008; Reist et al. 2006a). Many species in Arctic waters display generalist feeding strategies, allowing them to exploit temporal variance in prey availability, as well as resources from multiple habitat types and trophic levels (Laske et al. 2018). This adaptation also minimizes agonistic interactions with other species, which conserves energy (Power et al. 2008). Generalist feeding strategies are often further coupled with migratory and facultative life history strategies, such as seasonal migrations for feeding or resident and anadromous forms, that allow selection of optimal feeding environments and food resources (Power et al. 2008). As such, most northern aquatic food chains are short, and end with one to three generalist terminal predator species. These predators often partition prey both within (e.g., specialized ecotypes), or between species when they occupy a similar trophic level (Power et al. 2008; Guzzo et al. 2016).

Arctic Char, Dolly Varden Char (*Salvelinus malma*), Lake Trout (*Salvelinus namaycush*), Bull Trout (*Salvelinus confluentus*), Broad Whitefish (*Coregonus nasus*), Lake Whitefish (*Coregonus clupeaformis*), Inconnu (*Stenodus leucichthys*), and Burbot (*Lota lota*) are ecologically and culturally important fishes in Arctic freshwater or coastal systems. These species are harvested for subsistence among many Indigenous communities and are identified as important species by northern stakeholders throughout the Canadian Arctic (Stewart et al. 2009; McNicholl et al. 2020). In addition to these species' importance for the food security and nutrition of northern Indigenous communities, fishing is also an important part of Indigenous ways of life, helping to strengthen community networks, facilitates the transmission of knowledge, and preserve cultural traditions (Proverbs et al. 2020; Galappaththi et al. 2022). The western Arctic populations of Bull Trout and Dolly Varden Char (hereafter: "Dolly Varden") are also categorized as Special Concern species under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC 2011; COSEWIC 2013). Some species, such as Arctic Char, are also commercially fished (Galappaththi et al. 2022). Additionally, these fishes serve as an important energetic link as a mid-trophic species among coastal ecosystems and as upper trophic predators in freshwater ecosystems.

In order to inform predictions regarding the effects of climate change on culturally and ecologically important fishes in the North American Arctic, a comprehensive overview of available information is required. This was done using a systematic literature review and focusing on eight key Arctic fish species occurring in riverine, lacustrine, and coastal habitats across Inuit Nunangat (traditional Inuit homelands consisting of Nunavut, the Inuvialuit Settlement Region, Nunavik, and Nunatsiavut), while also considering information gathered in the rest of the North American Arctic (the Yukon, Alaska, and the remainder of the Northwest Territories). Our objectives here are to summarize the diet information and feeding strategies of fish species with varying life-history types (resident or anadromous, where applicable) by geographic region, and highlight data gaps related to trophic ecology for these Arctic fishes. This review focuses on the North American Arctic because it was conceptualized around fish species relevant in Inuit Nunangat, and is intended to be most applicable to that region, while also including information on fish species that may become more relevant in Inuit Nunangat as thermal barriers are lowered by climate change. While focused here on the North American Arctic, these results will aid predictions regarding the impacts of climate change on northern fishes more broadly and guide future research that will, together, inform resulting management decisions and improve our understanding regarding the effects of climate change on Arctic aquatic ecosystems.

Methods

A systematic literature review was conducted to gain a thorough appraisal of diet information on eight selected fish species (Arctic Char, Dolly Varden, Lake Trout, Bull Trout, Inconnu, Lake Whitefish, Broad Whitefish and Burbot) throughout Inuit Nunangat, as well as the rest of the North American Arctic. The geographic scope of this review was restricted to studies conducted in the Yukon, Northwest Territories (NWT), Nunavut, Nunavik, Nunatsiavut, and Alaska, which encompasses the entirety of the selected species' geographic distributions in the North American Arctic. While the eight species selected were chosen primarily due to their relevance in Inuit Nunangat, the large spatial scale of this study was required in order to compile a sizeable base of information for these species, given that there is limited knowledge of their feeding ecology in northern ecosystems. Studies investigating the diets of both freshwater populations, as well as those that make marine migrations to feed, were included. To maintain consistency with the language used in the majority of studies on fish that make marine feeding migrations, the term “anadromous” was used, rather than more specific terms such as “diadromous” and “amphidromous”.

Web of Science and the Canadian Department of Fisheries and Oceans (DFO) internal catalogue were chosen as the main literature sources to use a publicly-available search engine, provide a broader temporal coverage, and to search technical reports that are not published as scientific journal articles. The search string terms (Appendix A) were the same for both searches in Web of Science and within the DFO catalogue, but the syntax was modified by removing the Web of Science-specific field tags for the DFO catalogue search. The search results were imported into an Excel (2016) spreadsheet in CSV (comma separated value) format and arranged into a database that contained title, authors, journal, abstract and DOI.

Papers were subjected to an initial screening of titles and abstracts, followed by full-text screening. Initially, only titles and abstracts of the papers were screened according to the exclusion criteria (Appendix B) to eliminate papers that did not discuss the target species, were not found within the geographic range, and/or did not have diet information obtained through stable isotope, stomach content, and/or fatty acid analyses. Stomach contents were searched for in order to meet the objective of determining specific prey items, while stable isotope and fatty acid analyses were searched for to give insight into trophic levels and broader patterns of resource use. After screening of abstracts and titles, remaining papers were then subjected to full text screening. First, papers were assessed if they contained feeding data, which was done by examining the methods and results sections, followed by a CTRL+F word search for the terms “diet”, “forag*” and “feed”, in case diet information was available elsewhere in the paper.

Following screening, the included papers were coded according to a list of questions (Appendix C) into a database that collated the relevant information contained in the papers. The coding questions were developed to record the requisite data for each species of interest, establish regional and temporal trends in feeding, as well as list diet items from stomach contents to the lowest taxonomic level (i.e., order for invertebrates, species for fishes).

The information about diet and feeding strategies (defined for the purposes of this study as the degree of generalism or specialization in the types of prey consumed, as well as factors that affect feeding behaviour such as habitat use, daily or seasonal migrations, and interactions with other species) was summarized by species and region. The range of prey items was assessed, which allowed for primary prey items to be identified, as well as variations resulting from habitat type or region. If applicable, interactions with other species were summarized to provide context for the feeding strategies displayed by the focal species, especially in cases where they interacted with one another. Tables 2.1-2.10 (available as a supplementary file titled "Online Resource 1" in published article) were constructed to give a more thorough list of recorded prey items, while also highlighting knowledge gaps by showing where diet information has been collected in each species' range (denoted by a "1" – present or "0" – absent, respectively). Regions outside of a species' range were denoted with "N/A", the ranges being verified in Sawatzky et al. (2007), Lindsey (1962), Stapanian et al. (2010), Taylor (2016), Wilson and Hebert (1996), Mee et al. (2015), and Scott and Crossman (1973).

Results

Search string and coding

The search string on Web of Science returned 323 papers and the search of the DFO catalogue returned 42, for a total of 365. Of these, 291 were excluded due to not meeting the various inclusion criteria (Appendix B), leaving 74 inclusions to be coded. Of the included publications, 11 were DFO reports, the rest being academic journal articles, and spanned from 1955 to 2022. Studies were mapped to demonstrate their geographical distribution and the number of studies done per system, with Alaska, Nunavut, and the NWT hosting the majority (Figure 2.1). Studies were largely performed in the open-water season from late spring to early fall (Figure 2.2). Arctic Char was the most frequently studied species (n = 34), followed by Lake Trout and Dolly Varden (n = 20 and 17, respectively, Figure 2.3). Analyses of stomach contents was the most common method used (n= 63), followed by stable isotope analyses (n=26) and fatty acid analyses (n = 3). The results are summarized by species, and within each species, with the information grouped by life history (i.e., resident or anadromous) if applicable, and throughout the region of known distribution (i.e., Northwest Territories, Yukon, Nunavut, Alaska, Nunavik, and Nunatsiavut) (Online Resource 1, Tables 2.1-2.10).

Arctic Char

Anadromous form

Anadromous Arctic Char feed heavily on marine crustaceans and fishes, as well as mollusks and other invertebrates in some cases (Online Resource 1, Table 2.1). Anadromous individuals in the NWT feed extensively on forage fishes such as sandlance (*Ammodytes* spp.) and Capelin (Harwood et al. 2015; Harwood and Babaluk 2014). This is a shift away from diet data collected in the region during the late 1970's, which saw Arctic Char diets mainly consist of Arctic Cod, mysids and amphipods (Harwood et al. 2015). It is not known if these differences result from shifts in prey availability, predator preferences, temporal variation, or some combination thereof. Similarly, prior to 2005, most Arctic Char in Nunavut primarily fed on amphipods and mysids, which composed of up to ~80% of prey biomass, with other prey, such as Arctic Cod and sculpins (Family: Cottidae) making up the remainder (Ulrich and Tallman 2021a). After 2005, Capelin began to make up 65-75% of Arctic Char diets, while previous prey items were consumed in far lower numbers, or not at all (Ulrich and Tallman 2021a; Yurkowski et al. 2018). A similar increase in Capelin as prey, however, has not occurred across all of Nunavut. In Frobisher Bay for instance, amphipods and mysids made up nearly 95% of prey biomass consumed by Arctic Char as recently as 2009 (Spares et al. 2012) (Online Resource 1, Table 2.1). Individuals in Tariyunnuaq in the Kitikmeot region of Nunavut also feed on Capelin, as well as Pacific Herring (*Clupea pallasii*) and zooplankton but the dominant prey species is unknown (Swanson et al. 2011). Anadromous individuals in the northern areas of the archipelago consume mostly crustaceans, but information in these regions is sparse (Peet 1979). Arctic Char are opportunistic feeders in the marine environment, and their diets will likely shift in response to climate-driven changes to the marine Arctic food web. Falardeau et al. (2022) observed changes in the ∂^{13}C and ∂^{15}N signatures of individuals in the Kitikmeot Sea, Nunavut, which potentially reflect climate-driven diet shifts. Explanations for this shift could be a result the expansions in the distribution of boreal prey species, increased pelagic offshore foraging to escape warming nearshore waters, or an increase of pelagic prey availability due to earlier sea ice breakup and melting (Falardeau et al. 2022).

Anadromous Arctic Char in Nunatsiavut, off the north coast of Labrador, are largely piscivorous but also feed on crustaceans, depending on the population, and individual size (Cote et al. 2021). Long-term data collected in this region suggests that fishes such as Capelin and various Sculpins make up ~72% of prey biomass for Arctic Char, averaged across years and individual populations (Dempson et al. 2002; Dempson et al. 2008). Amphipods, mysids, and other invertebrates are also preyed upon, but only make up the majority of diets in individuals smaller than 300mm fork length (FL) (Dempson et al. 2002).

Resident form

Resident Arctic Char are primarily lacustrine generalist predators but, unlike their anadromous form, they feed in freshwater exclusively and tend to be smaller and less piscivorous. When another top predator is present (e.g., Lake Trout), resident Arctic Char forego piscivory entirely and prey more heavily on invertebrates (Klobucar and Budy 2020; Fraser and Power 1989). Such invertebrates include insects (especially chironomids and other aquatic emergents), zooplankton and gastropods (Fraser and Power 1989; Kidd et al. 1998).

Data on resident Arctic Char in the NWT are limited to summer foraging. Individuals are noted to prey on a variety of invertebrates in the Thomsen River on Banks Island, with 65% of prey items being stoneflies, craneflies, or chironomids (Stephenson 2010) (Online Resource 1, Table 2.2). Overall, there is limited information on the diet of resident Arctic Char in the NWT.

Resident Arctic Char in Nunavut most frequently consume insects, zooplankton, and crustaceans (Gallagher and Dick 2011, Curtis et al. 1995, Gallagher and Dick 2010) (Online Resource 1, Table 2.2). Larger individuals (>350mm FL) feed on small fishes (including cannibalism), except when co-occurring with Lake Trout (Kidd et al. 1998; Young et al. 2021; Vanriel and Johnson 1995). During the winter, feeding becomes less frequent but piscivorous individuals often become more cannibalistic during the winter, with smaller Arctic Char being eaten by up to 33% of large-form individuals, even in cases where they had not been cannibals during the summer (Young and Tallman 2021; Young et al. 2021; Gallagher and Dick 2010). In high-Arctic lakes such as Lake Hazen and Char Lake, which do not feature a forage fish species, cannibalism becomes the only form of piscivory (Guiger et al. 2002; Gallagher et al. 2009, Hobson and Welch 1995; Sinnatamby et al. 2012).

Resident Arctic Char in Nunavik and Nunatsiavut (particularly Gander Lake) show similar diet proclivities, with larger individuals being more piscivorous, feeding on smaller Arctic Char, Threespine Stickleback (*Gasterosteus aculeatus*), and Ninespine Stickleback (*Pungitus pungitus*), among other species (O'Connell and Dempson 2002; Power et al. 2005) (Online Resource 1, Table 2.2). Smaller individuals feed more on invertebrates, such as chironomids and other aquatic and emergent insects (Online Resource 1, Table 2.2). Resident Arctic Char in southwest Alaska are more frequently piscivorous, perhaps due to a greater diversity of forage fishes being present in these lower-latitude systems (Woods et al. 2013; Fournier and Schindler 2021). Feeding on salmon eggs and juveniles by Arctic Char occasionally occurs in these areas but to a lesser extent than do Dolly Varden, which may feed extensively on salmon eggs and juveniles found in the streams of this region. Arctic Char tend to occupy lakes and are therefore restricted to preying on Sockeye Salmon (*Oncorhynchus nerka*) populations which have runs connected to such lakes (Fournier and Schindler 2021; Morton 1982; Dennert et al. 2016; Stewart et al. 2009). Arctic Char in this region have also been recorded to consume small mammals such as shrews (Woods et al. 2013).

At the species level, resident Arctic Char are generalists but in many lakes they diverge into 2-4 distinct morphs or ecotypes which can be segregated on the basis of habitat use and feeding strategies (Reist et al. 1995; Power et al. 2005; Power et al. 2008). Arctic Char become piscivorous between 200-350 mm FL, although this can be affected by the presence of other large piscivores such as Lake Trout which will often exclude even large Arctic Char from piscivory (Klubucar and Budy 2020; Fraser and Power 1989). Outside of this scenario, large Arctic Char can form a piscivorous ecotype, often cannibalizing smaller individuals, especially in high-latitude systems with no other fish species available. Additionally, is some cases a large planktivore ecotype will also arise, as well as small and large benthivorous ecotypes (Power et al. 2008).

Dolly Varden

Anadromous form

Anadromous Dolly Varden feed primarily in coastal areas, where they consume fishes and crustaceans, feeding less frequently as they overwinter in freshwater (Online Resource 1, Table 2.3) (Stewart et al. 2009). Available information indicates anadromous Dolly Varden are heavily piscivorous at larger sizes (400 mm FL) (Stewart et al. 2009). Smaller individuals will primarily prey upon crustaceans such as mysids and amphipods, as well as chironomids in areas with a strong freshwater influence. In the Beaufort Sea, Dolly Varden often feed on sympagic (i.e., those which spent at least part of their life cycles in, or on, the sea ice) amphipods, and follow sea ice movements to do so, indicating their feeding habitat use is influenced by sea ice position and condition (Gallagher et al. 2021). Large, piscivorous individuals in the Beaufort Sea feed on a variety of fishes such as Fourhorn Sculpin (*Myoxocephalus quadricornis*), small whitefishes (*Coregonus* spp.), and others (Stewart et al. 2009) (Online Resource 1, Table 2.3). Large anadromous Dolly Varden in western Alaska feed primarily on marine fishes, such as Pacific Sandlance and Capelin, while smaller individuals feed on crustaceans, especially amphipods and malacostracans (Narver and Dahlberg 1965, Hart et al. 2015). When returning to freshwater in the fall, anadromous Dolly Varden feed infrequently until the spring migration, although various insects may be consumed during this time (Stewart et al. 2009). An exception occurs in southwestern Alaska, where some anadromous Dolly Varden make shorter coastal migrations and time their return to freshwater in the early fall to coincide with Pacific salmon runs (Sergeant et al. 2015). This allows these individuals to gorge themselves on lipid-rich salmon eggs to sustain themselves during spawning and overwintering (Sergeant et al. 2015). Salmon smolts are occasionally consumed during the winter as well (Hart et al. 2015).

Resident form

Resident Dolly Varden are primarily insectivorous and almost exclusively inhabit rivers and streams in Alaska and the Canadian Arctic. Chironomids are an important prey item, alongside other emergent insects, making up 75% or more of prey items consumed by resident Dolly Varden in many cases (Stewart et al. 2009; Parker and Huryn 2006; Milner 1994) (Online Resource 1, Table 2.4). Terrestrial insects and aquatic beetles are also occasionally eaten, with terrestrial insects becoming more prevalent as prey items later in the year (Stewart et al. 2009; Wipfli 1997). Resident Dolly Varden in the Babbage and Firth rivers in the Yukon occasionally eat amphipods and oligochaetes, which is not commonly recorded elsewhere (Stewart et al. 2009). Some large individuals will feed on small fishes, such as Arctic Grayling (*Thymallus arcticus*), as well as fish eggs, but this is not common compared to feeding on insects (Stewart et al. 2009). An exception to this is in western Alaska (e.g., Unalakleet, Chena, Iliamna, and upper Yukon rivers), where Dolly Varden ranges overlap with spawning Pacific salmon, and eggs and out-migrating juveniles, as well as scavenged flesh and dipteran larvae from dead adults make up the majority of diets when available (Jaecks and Quinn 2014; Denton et al. 2009; Denton et al. 2010; Schoen et al. 2021; Armstrong 1970). Resident individuals in an Alaskan stream feed less during winter, though they still feed on larval dipterans and stoneflies (Huryn and Benstead 2019).

Resident Dolly Varden are riverine insect specialists, with other types of invertebrates and small fishes only consumed incidentally (and only by large individuals in the case of the latter) and there appear to be no instances of resident Dolly Varden shifting their primary prey away from insects (Stewart et al. 2009). This feeding strategy is possibly shaped by morphology, given that resident Dolly Varden have smaller gapes than similarly sized Bull Trout and Arctic Char, which would necessitate feeding on smaller prey, even for larger individuals (Stewart et al. 2007). The feeding habitat use of Dolly Varden while drift foraging can be shaped by dominance hierarchies among individuals (Cullen and Grossman 2019). Larger dominant individuals occupy upstream positions in streams which allows for the first opportunity to consume drifting prey and consequently, higher foraging rates (Cullen and Grossman 2019).

Lake Trout

In Great Bear Lake, NWT, Lake Trout are noted to differentiate amongst habitat use and diet, forming several distinct morphs or ecotypes (Blackie et al. 2003). These include a more generalist ecotype and more specialized ecotypes that feed on more specific prey or at specific lake areas, although fatty acid analysis indicates that there is significant diet variation within the morphs (Chavarie et al. 2016). The generalist morph feeds on crustaceans as well as Round Whitefish (*Prosopium cylindraceum*), Slimy Sculpin (*Cottus cognatus*), adult caddisflies, ants (Formicidae spp.), and small amounts of other insects (Chavarie et al. 2016). The specialized benthic morph feed heavily on ants, as well as bivalves and mysids, but fewer fish compared to other morphs (Chavarie et al. 2016; Chavarie et al. 2021). The generalist pelagic morph feed on pelagic forage fishes (presumably *Coregonus* spp.), as well as crustaceans and terrestrial ants (Chavarie et al. 2016). The fourth morph, a pelagic piscivore, feeds on coregonids and small Northern Pike (*Esox lucius*) but also occasionally switches to Trichoptera spp. and cannibalism of the benthic morph (Chavarie et al. 2016). Each of these morphs feeds on terrestrial insects to some degree, demonstrating that, despite being more specialized ecotypes, they are still opportunistic.

In Great Slave Lake, NWT, Lake Trout exist in three different morphs but their preferred feeding habitat appears to be more related to size rather than morph (Zimmerman et al. 2009). There are shallow and deep-water piscivorous morphs, and a zooplanktivorous morph, but all three tend to forage benthically, and shift to pelagic feeding at approximately 430 mm standard length (Zimmerman et al. 2009). Smaller individuals of piscivorous morphs prey on sculpins during their benthic phase, but switch to coregonids as they grow larger and shift to pelagic feeding (Zimmerman et al. 2009). All morphs in Great Slave Lake also consume terrestrial insects opportunistically (13% occurrence averaged across morphs) (Zimmerman et al. 2009; Moshenko and Gilman 1983). Diets of Lake Trout in Great Slave Lake change throughout the year in accordance to thermal conditions (MacKenzie et al. 2022). Early in the season, foraging for terrestrial insects and littoral fishes in shallow water is more common, but Lake Trout become barricaded from nearshore prey later in the summer when the lake's upper layer reaches 15°C (MacKenzie et al. 2022).

In smaller lakes in the NWT, Nunavut, and the Yukon, Lake Trout will feed on zooplankton, insects and fishes such as stickleback, Slimy Sculpin, and others (Hulsman et al. 2016; Kidd 1996; Kidd et al. 1998) (Online Resource 1, Table 2.5). The ability of Lake Trout to resource partition is displayed in Alexie Lake, NWT, where Lake Trout, Burbot, and Northern Pike all inhabit similar trophic levels, but feed in different areas of the lake, according to stable isotope data (Guzzo et al. 2016). The diet of Lake Trout in the Thomsen River, NWT appears to be very generalized, likely due to the homogenous nature of a riverine system and contain an array of insects and fishes (Stephenson 2010). On rare occasions, Lake Trout are known to consume small mammals, as lemmings (Lemmini spp.) were found in several Lake Trout stomachs in the Thomsen River (Stephenson 2010).

Nunavut also features rare examples of anadromous Lake Trout populations that migrate to the sound of Tariyunnuaq, Nunavut, for summer feeding (Swanson et al. 2011). During these migrations to coastal areas, Lake Trout feed on Pacific Herring, Capelin, and marine crustaceans

(Swanson et al. 2011). Anadromous populations of Lake Trout are present in Husky Lakes, NWT (Kissinger et al. 2016), but there is little detailed information published about their diets.

Lake Trout in Alaska and in Nunavik are also generalist predators. Most Alaskan systems featuring Lake Trout are similar to Toolik Lake, which are relatively shallow and lack pelagic prey (MacDonald and Hershey 1992). This leads larger Lake Trout to feed on benthic fishes and mollusks, while smaller individuals feed on zooplankton closer to shore (Merrick et al. 1992; McDonald and Hershey 1992; Keyse et al. 2007, McDonald et al. 1996). In Nunavik, Quebec, larger individuals (>600 mm FL) prey heavily on other fishes and occasional crustaceans (branchiopods) (Benoit and Power 1989; Murdoch et al. 2013) (Online Resource 1, Table 2.5). Mid-size individuals (300-600 mm FL) are generalist foragers (stickleback, small Burbot and juvenile salmonids) but also feed heavily on insects (craneflies and chironomids; Benoit and Power 1989). The smallest size class of Lake Trout in these Nunavik lakes (<300 mm FL) feed mostly on dipterans (Benoit and Power 1989).

Bull Trout

The diet and feeding habits of Bull Trout in the Mackenzie River drainage are poorly understood, especially outside of summer. Juvenile Bull Trout feed on a broad array of adult and larval insects (Stewart et al. 2007) (Online Resource 1, Table 2.6). As Bull Trout grow larger, they become more piscivorous, with the shift in prey occurring when the individual is between 100-200 mm FL, and many individuals in lakes become exclusively piscivorous as adults (Stewart et al. 2007). In the NWT and Yukon, Slimy Sculpin, Arctic Grayling, Longnose Sucker (*Catostomus catostomus*), and juvenile or small Bull Trout are the preferred prey species. If available, large adults will also eat small or young birds, amphibians, snakes, and small mammals such as shrews and mice (Stewart et al. 2007). It is unknown if this species shifts its diet to avoid interspecific competition after it has reached typical piscivory sizes or if it exhibits prey preferences once it reaches such a size (Stewart et al. 2007).

Inconnu

Inconnu are a large, primarily piscivorous freshwater coregonid that are found in both resident and anadromous forms (Tallman and Howland 2017); however, diet data on Inconnu are sparse.

Inconnu in both rivers and lakes feed almost entirely on a diverse range of fishes, while invertebrates tend to only be consumed by some juveniles (Fuller 1955, Gallagher and Dick 2015; Little et al. 1995; Stuby et al. 2018). An exception to this has been recorded in Selawik Lake, Alaska, where very large individuals feed on mysids, alongside fishes (Alt, 1965). Additionally, Inconnu in the Upper Yukon and Chena rivers feed heavily on juvenile Chinook Salmon (*Oncorhychus tshawytcha*) when they are present. (Online Resource 1, Table 2.7). Anadromous individuals in the nearshore Beaufort Sea similarly feed primarily on fish, though some mysids are also consumed (32% by number of prey items consumed) (Lacho 1991).

Inconnu are comparatively specialized to other large predators because of their heavy reliance on piscivory, even in smaller individuals, in their relatively narrow habitat range (shallow, silty areas of lakes; large rivers, and brackish areas) (Fuller 1955; Smith and Sutton 2015). The linkage of individual size to level of piscivory is difficult to establish in Inconnu because small individuals occasionally eat invertebrates, but even smaller individuals have been discovered feeding on fish (Alt 1965; Fuller 1955). Thus, more work is needed to contextualize the prey preferences of Inconnu.

Lake Whitefish

Lake Whitefish is a benthic and occasionally pelagic, mid-trophic level coregonid species, primarily found in lacustrine environments and is a generalist benthic predator of aquatic invertebrates (Jessop et al. 1993). A distinct pelagic zooplanktivore ecotype forms in some instances (Bernatchez et al. 1996). It is limited by its small, subterminal mouth which is adapted for benthivory, though instances of piscivory have been recorded outside the Arctic (Pothoven and Madenjian 2013). The species is primarily freshwater but anadromous populations exist in the Mackenzie River Delta and in Alaska (Sawatzky et al. 2007). Benthic prey such as mollusks, aquatic insects, and crustaceans make up the majority of Lake Whitefish diets (Jessop et al. 1993, Little et al. 1998; Mackenzie et al. 2022; Kidd et al. 1996) In some systems, such as the Slave River, the relative importance of different prey items shifts throughout the year – ostracods make up over half of the diet during the spring, while corixids make up 68% of diets by the fall (Little et al. 1998). Lake Whitefish have a lower salinity tolerance than other coregonids, meaning that anadromous feeding is not especially common, individuals that do migrate to coastal areas to feed remain in nearshore areas (Sawatzky et al. 2007). These anadromous Lake Whitefish in Tuktoyaktuk Harbour and Liverpool Bay, NWT feed primarily on crustaceans and other invertebrates (Lacho 1991; Bond and Erickson 1993) (Online Resource 1, Table 2.8).

Broad Whitefish

Broad Whitefish are primarily an anadromous coregonid species that are generalist benthic foragers found throughout the coastal Beaufort Sea and Mackenzie River Delta; however, a lacustrine form also exists (Sawatzky et al. 2007). Anadromous Broad Whitefish found in the marine environment near Tuktoyaktuk, Northwest Territories, were found to feed heavily on copepods (98% by number), as well as some nematodes and Diptera larvae (Lacho 1991) (Online Resource 1, Table 2.9). Anadromous Broad Whitefish in Prudhoe Bay, Alaska feature a more varied diet, also feeding on copepods, but with other crustaceans and chironomids being present as well (Fechhelm et al. 1995). An exception in Broad Whitefish diets occurs in the Arctic Coastal Plain of Alaska, where adult dipterans made up 35% of the diets of several individuals (Laske et al. 2018). In comparison to Least Cisco (*Coregonus sardinella)* and Dolly Varden, Broad Whitefish occupy a lower trophic level which limits them to feeding on small mollusks and other invertebrates (Kline et al. 1998).

Burbot

Burbot are specialized piscivores that primarily inhabit benthic areas, often emerging at night to feed in littoral zones. In the NWT, adult Burbot in the Mackenzie Delta are exclusively piscivorous during the winter, feeding largely on juvenile Burbot and Northern Pike, as well as Ninespine Stickleback, among others (Gallagher and Dick 2015) (Online Resource 1, Table 2.10). Juveniles are also piscivorous, being highly cannibalistic, and eating young Northern Pike and Ninespine Stickleback (Gallagher and Dick 2015). To a lesser extent, juveniles also consume invertebrates (Online Resource 1, Table 2.10). This combination of invertebrates and small fishes has also been recorded in juveniles in the Slave River system (Little et al. 1998). Burbot piscivory increases with size, between 100–460 mm FL, reinforced by the ∂^{15}N differences between adults and juveniles (Gallagher and Dick 2015). Young Burbot that prey on fish appear to grow faster, which may explain the prevalence of cannibalism, as rapid growth would enable juveniles to grow to where they are at less risk of predation (Gallagher and Dick 2015). Winter cannibalism may also be favoured by sexually mature individuals, as the energy gained would be beneficial for spawning (Gallagher and Dick 2015). Cannibalism among Burbot appears to be more prevalent in the Mackenzie River Delta than throughout most of its North American range (Gallagher and Dick 2015). In Great Slave Lake, Burbot feed on juvenile coregonids, as well as forage fishes such as Ninespine Stickleback, Trout-Perch, and various minnows (MacKenzie et al. 2022). In the Yukon, Burbot are similarly piscivorous, with individuals in Fox and Laberge Lakes consuming Slimy Sculpin and various coregonids (Kidd 1996). In Alaska, Burbot in the Chena and Upper Yukon rivers feed on coregonids as well as juvenile Chinook Salmon when available, while in the Kuskokwim River, individuals consume various forage fishes (Schoen et al. 2021; Rausch and Adams 2000) (Online Resource 1, Table 2.10). Burbot in Nunavik consume littoral forage fishes, presumably during nightly feeding migrations (Power et al. 2009).

Burbot are the most specialized among the species reviewed. These fish are almost solely piscivorous as adults, typically feeding on littoral and some benthic fishes after reaching 460 mm total length at the latest (Gallagher and Dick 2015; Guzzo et al. 2016; Power et al. 2009). The feeding strategies of Burbot are further specialized by its photophobic and crepuscular nature, they remain at the benthos in cooler waters and protected from sunlight during the days of the open water season until nightfall, when they migrate to littoral zones to forage (Cott et al. 2015; Guzzo et al. 2016). Burbot also prefer low-complexity and soft substrates at the bottom of these lake slopes that it can burrow in during the day, which further shapes its hunting behaviour (Cott et al. 2015).

Knowledge Gaps

While consolidating available information, this review also highlighted a number of knowledge gaps relating to the diets and feeding strategies of Arctic fishes. For instance, basic year-round diet information is still needed for many Arctic species across all life-stages, especially given than current information is primarily focused on the open-water season (Figure 2.2). This is particularly apparent for Inconnu, Broad Whitefish, Lake Whitefish, and Bull Trout, which lack even basic diet data for much of their Arctic ranges (Online Resource 1, Tables 2.1-2.10). Assessing ontogenetic diet shifts is important across species as several fishes (e.g., Arctic Char, Bull Trout, Burbot) feature significant diet shifts after reaching a certain size, but it is unknown if such shifts occur in Inconnu, for example. As well, the available information focuses on lacustrine and coastal ecosystems, highlighting the need for an expansion of information about the diets of fishes in riverine habitats in the Arctic.

The limited number of fish diet studies in the Arctic leads to several geographic knowledge gaps. For instance, studies in the NWT tend to be focused on the northern Great Lakes and the Mackenzie Delta, while the majority of smaller lakes and the rest of the Mackenzie River upstream of the delta remain unstudied (Figure 2.1a). The Yukon features a severe lack of diet studies, with key species such as Burbot, Inconnu, Lake Trout, Lake Whitefish, and Bull Trout having virtually no available diet information in the territory (Figure 2.1a). Additionally, there were no studies found in this review for Nunavut that consider species other than Arctic Char and Lake Trout (Figure 2.1b). The logistics of performing diet studies in remote northern areas are a limiting factor, which highlights the need to focus research efforts on constructing a baseline for each species across seasons and habitat types, to reduce redundant efforts. When comparing the diet studies reviewed here, it is apparent that variation in overall diets and feeding strategies within and among regions is low, with the biggest factor in differences between regions being latitude and its limitation on prey diversity. Therefore, studies conducted in one region are likely to be applicable to fish diets in other regions, provided the type of environment is broadly similar (i.e., data collected on a lacustrine population is unlikely to be relevant to riverine individuals of the same species). Research efforts should therefore be focused on assessing fish diets and feeding strategies on species and environments where information is sparse, extremely dated, or subject to rapid current changes, given the more extensive body of literature on the most well-studied species (i.e., lacustrine Arctic Char; Lake Trout in the northern Great Lakes and smaller Arctic lakes; resident Dolly Varden).

Discussion

This review gives a thorough appraisal of the diet and feeding behaviours of eight ecologically and culturally important mid- to upper-trophic fish species throughout the Canadian Arctic and Alaska. The species included in this review largely display generalist feeding strategies though within-species specialization did occur in several instances (e.g., Power et al. 2005; Zimmerman et al. 2009). Diet generalization is regarded as an adaptation common in northern fishes as it both reduces costly agonistic interaction with other species and allows for rapid exploitation of varied prey (Power et al. 2008; Ulrich and Tallman 2021a). The majority of fish dietary research in the region is focused on lake-resident or anadromous species during the summer. Therefore, several data gaps were identified, the most prominent being the need for information about winter feeding across species and ecosystems, as well as a lack of information available for riverine species. While some species such as Lake Trout and Arctic Char are well-studied, available information for other species is either dated (e.g., Inconnu) or limited (e.g., Lake Whitefish and Bull Trout). Diet studies on Broad Whitefish are also few in number, although two studies were recently published (Stanek et al. 2022; Leppi et al. 2022). Brewster et al. (2016) also contains information about diets and trophic niches in Dolly Varden, Broad Whitefish, Lake Whitefish, Burbot, and Inconnu, although the information was not included here as the study was not detected during keyword searches in Web of Science. There is also very little diet information available in the Yukon for the species considered, aside from Dolly Varden. Assessing the diets of fishes that are predicted to expand into the Arctic with continued warming is also important to better predict the resulting interactions with native fishes in Arctic habitats (e.g., McNicholl et al. 2016, Harris et al. 2022). Documentation of Indigenous knowledge of fish diets, as well as parameters related to diet (e.g., flesh colour and condition), is needed and would expand upon and provide additional context to current understandings (e.g., Zerehi 2016; Cott et al. 2018).

In anadromous species, crustaceans (especially copepods, amphipods, and mysids) are the most widely consumed type of prey during marine feeding migrations. This is likely due to their presence in high density patches in marine environments and ideal for northern anadromous fishes looking to maximize food intake during their short feeding periods (Ulrich and Tallman 2021a). Crustaceans make up a portion, and in many cases the majority, of diets for Arctic Char, Broad Whitefish, Lake Whitefish, Dolly Varden, and Inconnu during their marine feeding migrations. Larger individuals of these species also eat an array of fishes, most of which are benthic-dwelling coastal species such as sandlances, blennies, pricklebacks, and sculpins. The recent increase in Capelin in the diet of some Arctic Char populations appears to be an exception to this tendency (Ulrich and Tallman 2021a; Dempson et al. 2008). This is possibly a result of Capelin aggregating in large spawning shoals when Arctic Char begin their feeding migrations (Ulrich and Tallman 2021a).

Changes in sea ice breakup timing, movements, and melt onset may have impacts on the diets and feeding strategies of Arctic Char and Dolly Varden (Harris et al. 2022). In the Beaufort Sea, predation of crustaceans by these species is connected to sea ice conditions, because both species prey on sympagic crustacean species (Gallagher et al. 2021; Falardeau et al. 2022). In the Kitikmeot Sea, changes in ∂^{13}C values in Arctic Char reflect a shift towards a higher level of pelagic prey being consumed, compared to sympagic or benthic prey sources. A potential mechanism for this shift is earlier sea ice breakups and melt onset, which results in a phytoplankton bloom and in turn, a greater abundance of pelagic crustaceans present when Arctic Char arrive at sea to feed (Falardeau et al. 2022). This pattern has been observed in other Arctic predators, such as Belugas (*Delphinapterus leucas*) (Brown et al. 2017). Additionally, the shift towards more ∂^{13}C-poor prey could be explained by the warming of nearshore coastal waters, which necessitates individuals moving to cooler, offshore areas, where pelagic prey lower in carbon enrichment (Falardeau et al. 2022). Conversely, ∂^{15}N signatures have increased over time, indicating that Arctic Char occupy higher trophic levels in the Kitikmeot Sea than in the past. Falardeau et al. (2022) suggest this may be due to the increased distribution of boreal prey species (i.e., Capelin and Pacific Sandlance) into Arctic waters. Boreal species have higher tropic levels and pelagic ∂^{13}C signatures, which may explain the isotopic shift seen in Arctic Char, although further research is needed to fully understand this pattern (Falardeau et al. 2022). While Arctic Char is an adaptable feeder that can react to shifts in the food web, the species has a narrow thermal range, and the physiological consequences of warming waters will likely restrict the species' adaptability (Gilbert and Tierney 2018).

In riverine environments, diet overlap seems to be more extensive and resource partitioning is less common, possibly due to the more confined nature of such systems, or because resources may be partitioned by territorial behaviour over prime feeding areas rather than species feeding on different prey items (Arostegui and Quinn 2018; Hearn, 1987). In the Thomsen River, NWT, Lake Trout and resident Arctic Char share a large number of invertebrate prey sources, with chironomids and arachnids being the only ones exclusive to Arctic Char (Stephenson 2010). In Iliamna Lake, Alaska and its surrounding steams, Arctic Char exclude Rainbow Trout (*Oncorhynchus mykiss*) from piscivory and from feeding on benthic invertebrates alongside forage fishes; the Rainbow Trout are limited to insects (Arostegui and Quinn 2018). Conversely, in the tributaries of the same system, stream-resident Dolly Varden have significant diet overlap with stream-resident Rainbow Trout, indicating that these environments are less conducive to resource partitioning (Arostegui and Quinn 2018). Insects appear to be the most important group of prey for most fish in riverine systems, especially chironomids, trichopterans, and plecopterans, as well as other emergent and aquatic insects. Even high-level predators, such as Lake Trout and Inconnu, appear to feed upon insects more commonly when in rivers (Stephenson 2010; Alt 1965).

Lakes demonstrate clearer patterns of diet resource use and partitioning. Benthic fishes such as sculpins and sticklebacks are important prey for most piscivores, as many higher latitude Arctic lakes lack pelagic forage fishes (McDonald and Hershey 1992). Littoral foraging on prey fishes is relatively uncommon among the species considered here, limited mostly to Burbot in accordance to their nightly migrations to such areas to feed (Power et al. 2009; Guzzo et al. 2016). Inconnu also appear to specialize in piscivory in shallower waters in Great Slave Lake, although it is not known if they are specifically targeting littoral species (Fuller 1955). The importance of benthic feeding in many of these lakes is reinforced by the prevalence of mollusks (gastropods and bivalves) in the diets of Lake Whitefish, Arctic Char, and Lake Trout, with the latter two species forming benthivore-specialist ecotypes in some cases (Power et al. 2008; Chavarie et al. 2016). Zooplankton is also an important food source, especially for Arctic Char and small Lake Trout, the former of whom form a zooplanktivorous ecotype to avoid competition with piscivorous conspecifics or Lake Trout, while the latter are sometimes restricted to nearshore planktivory by larger individuals (Kidd et al. 1998; Merrick et al. 1992; Power et al. 2008).

Differences in prey items across the ranges in each species appears to be governed mostly by latitude, as food chains in the higher Arctic are simpler and less diverse (Power et al. 2008). Beyond the differences in prey diversity inherent to latitude, overall diet preferences and feeding strategies do not vary markedly within, and across, regions. Piscivorous resident Arctic Char feed on a more diverse array of fishes in western Alaska, Nunatsiavut, and Nunavik than they are in the High Arctic, due to the larger variety of different forage fishes at lower latitudes (O'Connell and Dempson, 2002; Power et al. 2009; Dennert et al. 2016). There is a greater array of invertebrates eaten by Arctic Char in these regions as well, such as leeches, hemipterans, Odonata spp., Ephemoptera spp., and various Gastropods (Woods et al. 2013; Power et al. 2009;

O'Connell and Dempson, 2002; Dennert et al. 2016). Arctic Char in places such as northern Nunavut have simpler diets, relying heavily on emergent insects and bivalves, with piscivory restricted only to the large piscivore ecotype which preys on smaller Arctic Char and the few available forage fishes such as sticklebacks (Guiger et al. 2002; Ulrich and Tallman 2021b; Gallagher and Dick 2011). Lake Trout also show some differences in their diets across their range due to changes in environment. The Lake Trout of large, deep lakes, such as Great Slave Lake and Great Bear Lake, feature a greater emphasis for some individuals on pelagic feeding upon various fishes such as ciscoes and whitefishes, as well as various crustaceans (Chavarie et al. 2016; Zimmerman et al. 2009), but at higher latitudes in smaller and shallower lakes, Lake Trout instead feed very generally on mollusks, oligochaetes, and benthic fishes (Keyse et al. 2007; McDonald and Hershey 1992; Stephenson 2010).

Continued understanding of trophic ecology and interactions of Arctic fishes for food resources will assist predictions of how native fish populations may respond to a rapidly changing Arctic (Niemi et al. 2019), or potential outcomes resulting from climate-driven distributional shifts to the north (Dunmall et al. 2013; Bilous and Dunmall 2020). Future research that addresses these gaps will contribute toward a robust baseline of diet information for northern fishes and improve understanding regarding Arctic fishes and the potential effects of climate change on Arctic ecosystems.

Acknowledgements

Funding to support this review was provided by Fisheries and Oceans Canada and the Government of Northwest Territories Cumulative Impact Monitoring Program (CIMP 221). We wish to thank Colin Gallagher as well as two anonymous reviewers for their insightful comments and suggestions to improve this manuscript.

Appendix A – Search strings: The following search strings were used to conduct the literature searches on Web of Science and the DFO catalogue. The search terms are identical and modified only to reflect differences in the syntax requirements of each search engine.

Web of Science search string:

(TS=(canad* OR alask* OR newfoundlan* OR quebec OR labrador* OR yukon OR northwest OR nunavut)) AND (TS=("arctic char*" OR "dolly varden" OR “inconnu” OR "sheefish" OR “burbot” OR "lake trout" OR “lake char*” OR "lake whitefish" OR "broad whitefish" OR "bull trout" OR "bull char*")) AND (TS=(diet* OR feed* OR “stable isotop*” OR “fatty acid” OR stomach OR prey OR food OR web OR trophic* OR niche)) NOT TS=(mercury OR contamin* OR pollution)

DFO collection search string:
(canad* OR alask*OR newfoundlan* OR quebec OR labrador* OR yukon OR northwest OR nunavut)) AND ("lake trout" OR “lake char*” OR "arctic char*" OR "inconnu" OR “sheefish” OR "dolly varden" OR "lake whitefish" OR "broad whitefish" OR "bull trout" OR “bull char*” OR "burbot") AND (diet OR feed* OR stomach OR "stable isotop*" OR "fatty acid*" OR food OR web OR trophic* OR niche) NOT (pollution OR contamin* OR mercury)

Appendix B – Exclusion criteria: Bases on which papers were included or excluded in the sample

Dimension	**Inclusion**	**Exclusion**
Geographic scope	Inuit Nunangat and the rest of Arctic Canada and Alaska	BC, Alberta, Saskatchewan, Manitoba, Ontario, Quebec outside of Nunavik, lower 49 US states, the rest of the world
Language	English and French	Non-English and non-French
Focus	Diet/Trophic ecology	Anything else
Publication type	Case studies, research articles, technical reports (DFO), manuscript reports (DFO), and research documents (DFO)	Models, predictions
Temporal scope	Current and past	Future projections
Species	Dolly Varden, Arctic Char, inconnu, broad whitefish, lake whitefish, bull trout, lake trout, burbot	Any other fish species, unless the focal species was a prey species for one of the 8 studied species, and included relevant feeding data in the paper

Appendix C – Coding questions: Questions designed for extracting diet information from each paper in a standardized manner and how that information was coded into the database

#	Column item	Description	Coding
A	Included/excluded	Is it included or excluded from analysis?	1=Included; 0=Excluded
0.1	Document Type	What kind of document is it?	J=Journal Article D=DFO report
0.2	Geographic focus	What state/province/territory does the study take place in?	Name(s)
0.3	Study area(s)	Name the bodies of water under study	Name(s)
0.4	Timeframe	When was the data collected?	Most specific dates available
0.5	Season(s)	What season(s) did the stufy occur in (Summer: Jun-Aug, Fall: Sept-Oct, Winter: Nov-Feb, Spring: Mar-May)	Sp=Spring, S=Summer, F=Fall, W=Winter
1.1	Species studied	Common names of species studies, alphabetically	Name(s)
1.1.2	Habitat type	Were specimens collected in still, coastal or flowing water systems?	F= Fluvial, L=Lacustrine,, A=Anadromous
1.2	Diet sampling method	What diet sampling technique(s) are used?	Mark "X" if applicable
1.2.1	Stomach contents	Were stomach contents analyzed?	"X"
1.2.2	Stable isotopes	Were stable isotopes analyzed?	"X"
1.2.2.1	Flesh type	Where was the flesh for SI analysis taken from?	List location(s)
1.2.3	Fatty acids	Were fatty acids analyzed?	"X"
1.3	General diet characteristics	What broad groups of prey were consumed?	Mark "X" if applicable
1.3.1	Fish	Were fish consumed?	"X"
1.3.2	Insects	Were insects or insect larva consumed?	"X"
1.3.3	Worms	Annelids, platyhelminthes, nematodes etc	"X"
1.3.4	Crustaceans	Amphipods, copepods etc	"X"
1.3.5	Molluscs	Gastropods, bivalves etc	"X"
1.3.6	Fish eggs	Eggs of other fish	"X"
1.3.7	Plankton		"X"
1.3.8	Other	Other prey items: mammals, lizards, amphibians etc	"X"
1.3.9	Please specify	List the additional prey items	List
1.4	Specific diet components	List the specific prey items to order for invertebrates, species for fishes	List
1.5	Competition/overlap with other species	If the paper describes how species react to competitors, describe here	Describe

Note: The following tables are included as online supplementary materials in the published manuscript, in a file titled “Online Resource 1”

Table 2.1: Recorded prey items of anadromous Arctic Char (*Salvelinus alpinus*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. “0” indicates that a prey item has not been recorded being consumed in the corresponding region, and “N/A” indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Arctic Cod (*Boreogadus saida*)	11	N/A	2,6	N/A	0	6
	Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*)	0	N/A	6	N/A	0	0
	Atlantic Spiny Lumpsucker (*Eumicrotremus spinosus*)	0	N/A	6	N/A	0	6
	Capelin (*Mallotus villosis*)	1	N/A	2,3,4,6	N/A	0	7,8,9
	Daubed Shanny (*Lumpenus maculatus*)	0	N/A	0	N/A	0	7
	Fourhorn Sculpin (*Myoxocephalus quadricornis*)	0	N/A	6	N/A	0	7
	Eelpouts (Lycodes spp.)	0	N/A	0	N/A	0	7
	Pacific Herring (*Clupea pallasii*)	0	N/A	3	N/A	0	0
	Pricklebacks (Stichaeidae spp.)	0	N/A	6	N/A	0	8
	Sandlance (*Ammodytes* spp.)	10, 11	N/A	0	N/A	0	7,8,9
	Threespine Stickleback (*Gasterosteus aculeatus*)	0	N/A	0	N/A	0	7
	Unspecified sculpins (Cottidae sp., *Myoxocephalus* sp., *Triglops* sp.)	0	N/A	0	N/A	0	7,8,9
Mollusca	Gastropoda	0	N/A	0	N/A	0	7
Crustaceans	Amphipoda	11	N/A	4,5,6	N/A	0	7,8,9
	Copepoda	0	N/A	4	N/A	0	7,8
	Isopoda	0	N/A	3,5	N/A	0	0
	Decapoda	0	N/A	2	N/A	0	7
	Mysida	11	N/A	4,6	N/A	0	7,8
	Malocostraca	0	N/A	4	N/A	0	7
Other	Polychaeta	0	N/A	6	N/A	0	7,8
	Unspecified zooplankton	0	N/A	3	N/A	0	0

1) Harwood and Babaluk (2014)
2) Yurkowski et al. (2018)
3) Swanson et al. (2011)
4) Ulrich and Tallman (2021a)
5) Peet (1979)
6) Spares et al. (2012)
7) Dempson et al. (2008)
8) Dempson et al. (2002)
9) Cote et al. (2021)
10) Falardeau et al. (2022)
11) Harwood et al. (2015)

Table 2.2: Recorded prey items for resident Arctic Char (*Salvelinus alpinus*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. "0" indicates that a prey item has not been recorded being consumed in the corresponding region, and "N/A" indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Arctic Char (*Salvelinus alpinus*)	0	0	2,3,4,8,10,11,12	19	14	
	Atlantic Salmon (juveniles) (*Salmo salar*)	0	0	0	0	0	16
	Lake Chub (*Couesius plumbeus*)	0	0		0	14	
	Longnose Dace (*Rhinichthys cataractae*)	0	0		21	14	
	Longnose Sucker (*Catostomus 29ucius29mus)*	0	0		0	14	
	Ninespine Stickleback (*Pungitis pungitus*)	0	0	5,6,8	21,22	0	16,17
	Slimy Sculpin (*Cottus cognatus*)	0	0	0	19,22	14	
	Sockeye Salmon (juveniles and eggs) (*Oncorhynchus nerka*)	0	0	0	18,20,22,23	0	
	Rainbow Smelt (*Osmerus mordax*)	0	0	0	0	0	16,17
	Threespine Stickleback (*Gasterosteus aculeatus*)	0	0	2,3,10	20,21,22	14,15	16,17
Mollusca	Bivalvia	0	0	5,8,9	21	15	
	Gastropoda	0	0	9	20,21,22,23	14	16,17
Crustaceans	Amphipoda	0	0	8,9	0	15	16,17
	Cladocera	0	0	5,6,7	0	0	16
	Copepoda	0	0	4,5,7	0	15	0
	Ostracoda	0	0	5,7	0	0	16
Insecta	Coleoptera	1	0	6	18	14	16,17
	Collembola	0	0	5,6	0	0	0
	Diptera	1	0	2,3,4,5,6,7,8,9,10,11,12	18,21	14	16,17
	Ephemeroptera	1	0		18	14	16
	Hemiptera	0	0		0	14	
	Lepidoptera						17
	Hymenoptera	0	0	5	18		16,17
	Orthoptera	0	0		0		17
	Plecoptera	1	0	9	18	14	16
	Trichoptera	0	0	4,5,6,7,8,13	18,19,21	14	16,17
Other invertebrates	Oligochaeta	0	0	8	18		
	Hirudinea	0	0		18		
	Nematoda				18		
	Unspecified zooplankton	0	0	8,9,11	21		
	Aranae			5,6			16
	Hydracarina	1	0	4,5,6,7,9,12	18		
Mammals	Cinereus Shrew (*Sorex cinereus*)				21		

1) Stephemson (2010)
2) Young et al. (2021)
3) Ulrich et al. (2021b)
4) Guiguer et al. (2002)
5) Gallagher and Dick (2011)
6) Gallagher and Dick (2010)
7) Sinnatamby et al. (2012)
8) Vanriel and Johnson (1995)
9) Kidd et al. (1998)
10) Young and Tallman (2021)
11) Hobson (1995)
12) Gallagher et al. (2009)
13) Peet (1979)
14) Power et al. (2009)
15) Curtis et al. (1995)
16) O'Connell and Dempson (2002)

17) Power et al. (2005)
18) Dennert et al. (2016)
19) Klobucar and Budy (2020)
20) Arostegui et al. (2018)
21) Woods et al. (2013)
22) Denton et al. (2010)
23) Fournier and Schindler (2021)

Table 2.3: Recorded prey items for anadromous Dolly Varden (*Salvelinus malma*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. "0" indicates that a prey item has not been recorded being consumed in the corresponding region, and "N/A" indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Arctic Cisco (*Coregonus autumnalis*)	0	3	N/A	0	N/A	N/A
	Arctic Cod (*Boreogadus saida*)	3	3	N/A	3	N/A	N/A
	Arctic Grayling (*Thymallus arcticus*)	0	3	N/A	0	N/A	N/A
	Capelin (*Mallotus villosis*)	0	0	N/A	1	N/A	N/A
	Dolly Varden (*Salvelinus malma*)	0	3	N/A	0	N/A	N/A
	Fourhorn Sculpin (*Myoxocephalus quadricornus*)	3	3	N/A	3	N/A	N/A
	Least Cisco (*Coregonus sardinella)*	3	3	N/A	3	N/A	N/A
	Ninespine Stickleback (*Pungitus pungitus*)	3	3	N/A	3	N/A	N/A
	Sandlance (*Ammodytes* spp.)	0	0	N/A	1,2	N/A	N/A
	Silverspotted Sculpin (*Blepsias cirrhosis*)	0	0	N/A	2	N/A	N/A
	Sockeye Salmon (*Oncorhynchus nerka*)	0	0	N/A	2	N/A	N/A
	Stout Eelblenny (*Anisarchis medius*)	3	3	N/A	3	N/A	N/A
	Whitespotted Greenling (*Hexagrammos stelleri*)	0	0	N/A	2	N/A	N/A
	Unspecified Pacific Salmon (*Oncorhynchus* sp.) eggs and smolts	0	0	N/A	5	N/A	N/A
	Unspecified Whitefishes (*Coregonus* sp.)	3	3	N/A	3	N/A	N/A
Mollusca	Bivalvia	0	3	N/A	0	N/A	N/A
	Gastropoda	0	3	N/A	0	N/A	N/A
Crustaceans	Amphipoda	3,4	3	N/A	2,3	N/A	N/A
	Euphausiacea	0	0	N/A	2	N/A	N/A
	Copepoda	3	3	N/A	3	N/A	N/A
	Isopoda	3	3	N/A	2,3	N/A	N/A
	Mysida	3	3	N/A	3	N/A	N/A
	Various crab larva	0	0	N/A	2	N/A	N/A
Insecta	Diptera	3	3	N/A	3	N/A	N/A
	Plecoptera	3	3	N/A	3	N/A	N/A
	Trichoptera	3	3	N/A	3	N/A	N/A

1) Hart et al. (2015)
2) Narver and Dahlberg (1965)
3) Stewart et al. (2009)
4) Gallagher et al. (2021)
5) Sergeant et al. (2015)

Table 2.4: Recorded prey items of resident Dolly Varden (*Salvelinus malma*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. "0" indicates that a prey item has not been recorded being consumed in the corresponding region, and "N/A" indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Arctic Grayling (*Thymallus arcticus*)	9	0	N/A	0	N/A	N/A
	Chum Salmon (juveniles and eggs) (*Oncorhynchus keta*)	0	0	N/A	6	N/A	N/A
	Coho Salmon (juveniles and eggs) (*Oncorhynchus kisutch*)	0	0	N/A	6	N/A	N/A
	Pink Salmon (juveniles and eggs) (*Oncorhynchus gorbuscha*)	0	0	N/A	6	N/A	N/A
	Sockeye Salmon (juveniles and eggs) (*Oncorhynchus nerka*)	0	0	N/A	1,2,3,7	N/A	N/A
	Unspecified fishes	9	9	N/A	6,9	N/A	N/A
Crustaceans	Amphipoda	0	9	N/A	0	N/A	N/A
Insecta	Coleoptera	0	9	N/A	1	N/A	N/A
	Diptera	9	9	N/A	1,3,4,5,7,8	N/A	N/A
	Ephemeroptera	0	9	N/A	1,4,5,8	N/A	N/A
	Hemiptera	0	0	N/A	0	N/A	N/A
	Lepidoptera	0		N/A	0	N/A	N/A
	Hymenoptera	0	9	N/A	1,2	N/A	N/A
	Orthoptera	0	0	N/A	0	N/A	N/A
	Plecoptera	9	9	N/A	1,4,5,8	N/A	N/A
	Trichoptera	0	9	N/A	1,4,5,8	N/A	N/A
Other invertebrates	Oligochaeta	0	9	N/A	5	N/A	N/A
	Hydracarina	9	9	N/A	1	N/A	N/A
	Nematoda	0	9	N/A	1	N/A	N/A

1) Dennert et al. (2016)
2) Arostegui et al. (2018)
3) Denton et al. (2010)
4) Huryn and Benstead (2019)
5) Parker and Huryn (2006)
6) Schoen et al. (2021)
7) Denton et al. (2009)
8) Milner (1994)
9) Stewart et al. (2009)

Table 2.5: Recorded prey items for Lake Trout (*Salvelinus namaycush*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. "0" indicates that a prey item has not been recorded being consumed in the corresponding region, and "N/A" indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Arctic Char (*Salvelinus alpinus*)	0	0	10	0	12	0
	Arctic Grayling (*Thymallus arcticus*)	0	0	0	16,17	0	0
	Broad Whitefish (*Coregonus nasus*)	0	9	0	0	0	0
	Brook Trout (*Salvelinus fontinalis)*	0	0	0	0	12	0
	Burbot (*Lota lota*)	1,2,6	0	0	17	11,12	0
	Capelin (*Mallotus villosis*)	0	0	18	0	0	0
	Cisco (*Coregonus artedi*)	1,2,4,6,7,8	0	0	0	11	0
	Fourhorn Sculpin (*Myoxocephalus quadricornis*)	4	0	0	0	0	0
	Lake Chub (*Couesius plumbeus*)	1	0	0	0	11	0
	Lake Trout (*Salvelinus namaycush*)	2,4,5,7	0	0	0	12	0
	Lake Whitefish (*Coregonus clupeaformis*)	1,7,8	0	0	0	12	0
	Least Cisco (*Coregonus sardinella*)	5	9	0	0	0	0
	Longnose Sucker (*Catostomus 33ucius33mus)*	1,6	9	0	0	11	0
	Pacific Herring (*Clupea pallasii*)	0	0	18	0	0	0
	Northern Pike (*Esox 33ucius*)	2	0	0	0	0	0
	Ninespine Stickleback (*Pungitis pungitus*)	1,2,4,6	0	0	0	11	0
	Slimy Sculpin (*Cottus cognatus*)	2,6	9	0	13,15,16,17	0	0
	Round Whitefish (*Prosopium cylindraceum*)	1,8	9	0	16,17	0	0
	Threespine Stickleback (*Gasterosteus aculeatus*)	0	0	10	0	11	0
	Unspecified Sculpins (Cottidae sp.)	3,5,7	0	0	0	0	0
	Unspecified Whitefishes (*Coregonus* sp.)	3	0	0	0	0	0
Mollusca	Bivalvia	2,6,7	9	0	14,17	11	0
	Gastropoda	2,7	9	0	14,15,16,17	11	0
Crustaceans	Amphipoda	6,7	9	10	0	11	0
	Cladocera	1	0	0	14	12	0
	Copepoda	1,6	0	0	14	0	0
	Isopoda	0	0	18	0	0	0
	Mysida	2,3,8	0	0	0	0	0
	Ostracoda	1,6	0	0	0	0	0
Insecta	Coleoptera	2,5,6,7	9	10	0	11	0
	Diptera	1,2,4,5,6,7	9	10	13,14,17	11,12	0
	Ephemeroptera	5	9	0	0	0	0
	Hemiptera	1,2,6	0	0	0	0	0
	Lepidoptera	2,6		10	0	0	0
	Hymenoptera	2,6,7	9	10	0	0	0
	Odonata	7		0	0	0	0
	Plecoptera	5,7	9	0	0	0	0
	Trichoptera	1,2,4,6,7	9	10	13,17	0	0
Other invertebrates	Araneae	2,6	0	0	0	0	0
	Oligochaeta	6	0	0	0	0	0
	Hirudinea	1	9	0	0	0	0
	Unspecified zooplankton	1	0	10,18	0	11	0
	Hydracarina	0	9	0	0	0	0
Mammals	Lemming (Lemmini spp.)	5	0	0	0	0	0

1) Hulsman et al. (2016)
2) Chavarie et al. (2016)
3) Zimmerman et al. (2009)
4) Blackie et al. (2003)
5) Stephenson (2010)
6) Jessop et al. (1993)

7) Moshenko and Gillman (1983)
8) MacKenzie et al. (2022)
9) Kidd (1996)
10) Kidd et al. (1998)
11) Murdoch et al. (2013)
12) Benoit and Power (1983)
13) Klobucar and Budy (2020)
14) Keyse et al. (2007)
15) McDonald and Hershey (1992)
16) McDonald et al. (1996)
17) Merrick et al. (1992)
18) Swanson et al. (2011) (marine)

Table 2.6: Recorded prey items for Bull Trout (*Salvelinus confluentus*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. "0" indicates that a prey item has not been recorded being consumed in the corresponding region, and "N/A" indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Arctic Grayling (*Thymallus articus*)	1	0	N/A	0	N/A	N/A
	Juvenile Bull Trout (*Salvelinus confluentus*)	1	0	N/A	0	N/A	N/A
	Longnose Sucker (*Catostomus 35ucius35mus*)	1	0	N/A	0	N/A	N/A
	Slimy Sculpin (*Cottus cognatus*)	1	0	N/A	0	N/A	N/A
	Diptera	1	0	N/A	0	N/A	N/A
	Ephemeroptera	1	0	N/A	0	N/A	N/A
	Plecoptera	1	0	N/A	0	N/A	N/A
	Trichoptera	1	0	N/A	0	N/A	N/A

1) Stewart et al. (2007)

Table 2.7: Recorded prey items for Inconnu (*Stenodus leucichthys*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. “0” indicates that a prey item has not been recorded being consumed in the corresponding region, and “N/A” indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Arctic Lamprey (*Lethenteron camtschaticum*)	0	0	N/A	5	N/A	N/A
	Broad Whitefish (*Coregonus nasus*)	0	0	N/A	6	N/A	N/A
	Brook Lamprey (*Lampetra planeri*)	0	0	N/A	6	N/A	N/A
	Burbot (*Lota lota)*	1	0	N/A	6	N/A	N/A
	Juvenile Chinook Salmon (*Oncorhynchus tshawytscha)*	0	0	N/A	6	N/A	N/A
	Coregonus spp.	2	0	N/A	0	N/A	N/A
	Flathead Chub (*Platygobio gracilis*)	3	0	N/A	0	N/A	N/A
	Inconnu (*Stenodus leucichthys*)	2	0	N/A	0	N/A	N/A
	Lake Chub (*Couesius plumbeus*)	0	0	N/A	6	N/A	N/A
	Lake Whitefish (*Coregonus clupeaformis*)	3	0	N/A	0	N/A	N/A
	Least Cisco (*Coregonus sardinella*)	0	0	N/A	6	N/A	N/A
	Longnose Sucker (*Catostomus 36ucius36mus*)	3	0	N/A	6	N/A	N/A
	Ninespine Stickleback (*Pungitus pungitus*)	1	0	N/A	5	N/A	N/A
	Northern Pike (*Esox 36ucius*)	1,3	0	N/A	5,6	N/A	N/A
	Rainbow Smelt (*Osmerus mordax*)	0	0	N/A	5	N/A	N/A
	Threespine stickleback (*Gasterosteus aculeatus*)	0	0	N/A	5	N/A	N/A
	Trout-Perch (*Percopsis omiscomaycus)*	3	0	N/A	0	N/A	N/A
Crustaceans	Mysida	4	0	N/A	5	N/A	N/A
Insecta	Diptera	0	0	N/A	5	N/A	N/A
	Empemeroptera	0	0	N/A	5	N/A	N/A
	Hemiptera	0	0	N/A	5	N/A	N/A
	Plecoptera	0	0	N/A	5	N/A	N/A

1) Gallagher and Dick (2015)
2) Fuller (1955)
3) Little et al. (1998)
4) Lacho (1991) (marine)
5) Stuby (2018)
6) Alt (1965)

Table 2.8: Recorded prey items of Broad Whitefish (*Coregonus nasus*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. "0" indicates that a prey item has not been recorded being consumed in the corresponding region, and "N/A" indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Mollusca	Gastropoda	1	0	0	0	N/A	N/A
Crustaceans	Amphipoda	0	0	0	2	N/A	N/A
	Copepoda	1	0	0	2	N/A	N/A
	Malacostraca	0	0	0	2	N/A	N/A
	Mysida	1	0	0	2	N/A	N/A
	Ostracoda	1	0	0	0	N/A	N/A
Insecta	Diptera	1	0	0	2	N/A	N/A

1) Lacho (1991)
2) Fechelm et al. (1995)

Table 2.9: Recorded prey items of Lake Whitefish (*Coregonus clupeaformis*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. "0" indicates that a prey item has not been recorded being consumed in the corresponding region, and "N/A" indicates that the species in question does not occur in the region.

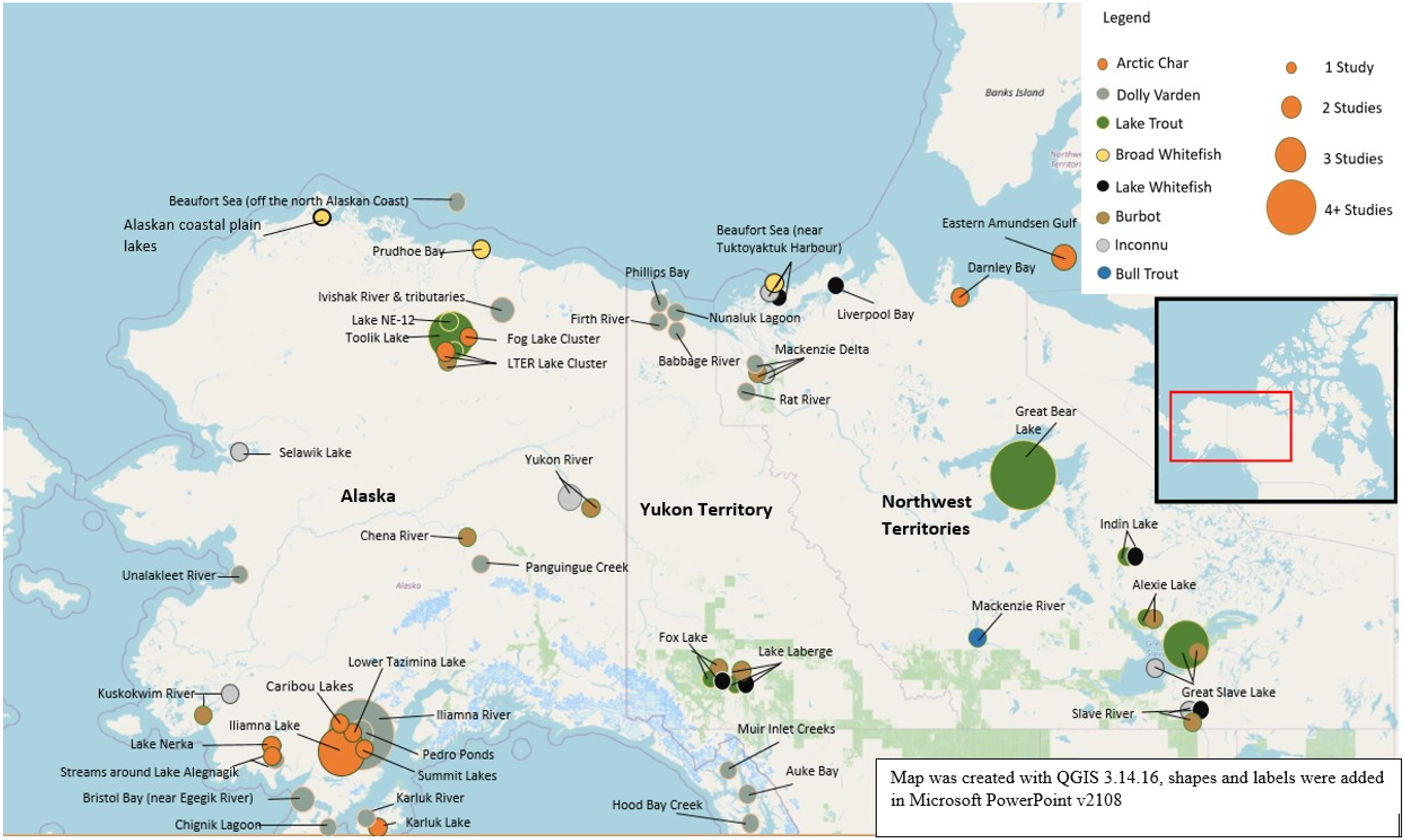
	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Ninespine Stickleback (*Pungitus pungitus*)	4	0	0	0	0	0
	Slimy Sculpin (*Cottus cognatus*)	0	5	0	0	0	0
Mollusca	Bivalvia	1,2,3	5	0	0	0	0
	Gastropoda	1,4	5	0	0	0	0
Crustaceans	Amphipoda	1,2,3,4	5	0	0	0	0
	Copepoda	2	0	0	0	0	0
	Eubranchypoda	1	0	0	0	0	0
	Isopoda	2,3	0	0	0	0	0
	Mysida	2	0	0	0	0	0
	Ostracoda	1,4	0	0	0	0	0
Insecta	Coleoptera	1,4	5	0	0	0	0
	Diptera	1,4	5	0	0	0	0
	Ephemeroptera	1,4	0	0	0	0	0
	Hemiptera	4	0	0	0	0	0
	Hymenoptera	0	5	0	0	0	0
	Trichoptera	1,2,4	5	0	0	0	0
	Zygoptera	4	0	0	0	0	0
Other invertebrates	Hydracarina	1	5	0	0	0	0
	Hirudinea	1	5	0	0	0	0
	Nematoda	2	0	0	0	0	0
	Polychaeta	2	0	0	0	0	0
	Unspecified zooplankton	0	5	0	0	0	0

1) Jessop et al. (1993)
2) Lacho (1991) (marine)
3) Bond and Erickson (1993) (marine)
4) Little et al. (1998)
5) Kidd (1996)

Table 2.10: Recorded prey items of Burbot (*Lota lota*) from available published literature. Abbreviations refer to Northwest Territories (NWT), Yukon (YT), Nunavut (NU), Alaska (AK), Nunavik (NK), and Nunatsiavut (NT), respectively. "0" indicates that a prey item has not been recorded being consumed in the corresponding region, and "N/A" indicates that the species in question does not occur in the region.

	Prey Item	**NWT**	**YT**	**NU**	**AK**	**NK**	**NT**
Fishes	Alaska Blackfish (*Dallia pectoralis*)	0	0	0	6	0	0
	Arctic Grayling (*Thymallus arcticus*)	0	0	0	5	0	0
	Arctic Lamprey (*Lethenteron camtschaticum*)	1	0	0	5,6	0	0
	Broad Whitefish (*Coregonus nasus*)	1	3	0	0	0	0
	Burbot (*Lota lota*)	1	0	0	0	0	0
	Chinook Salmon (juveniles) (*Oncorhynchus tshawytscha*)	0	0	0	5	0	0
	Goldeye (*Hiodon alosoides*)	2	0	0	0	0	0
	Humpback whitefish (*Coregonus pidschian*)	0	0	0	5	0	0
	Lake chub (*Couesius plumbeus*)	0	0	0	0	7	0
	Least Cisco (*Coregonus sardinella*)	0	3	0	5	0	0
	Lake Whitefish (*Coregonus clupeaformis*)	2	3	0	0	0	0
	Longnose Dace (*Rhinichthys cataractae*)	0	0	0	0	7	0
	Longnose Sucker (*Catostomus 39ucius39mus*)	2	0	0	0	7	0
	Ninespine Stickleback (*Pungitus pungitus*)	1,2	0	0	0	0	0
	Northern Pike (*Esox 39ucius*)	1	0	0	6	0	0
	Pacific Rainbow Smelt (*Osmerus mordax dentex*)	0	0	0	6	0	0
	Pond Smelt (*Hypomesus olidus*)	0	0	0	6	0	0
	Round Whitefish (*Prosopium cylindraceum*)	0	3	0	5	0	0
	Slimy Sculpin (*Cottus cognatus*)	0	3	0	4	7	0
	Walleye (*Sander vitreous*)	1	0	0	0	0	0
Mollusca	Gastropoda	1	0	0	0	0	0
Crustaceans	Amphipoda	1,2	3	0	0	0	0
	Copepoda	1	0	0	0	0	0
Insecta	Diptera	1	3	0	0	0	0
	Plecoptera	2	0	0	0	0	0

1) Gallagher and Dick (2015)
2) Little et al. (1998)
3) Kidd (1996)
4) Klobucar and Budy (2020)
5) Schoen et al. (2021)
6) Rausch and Adams (2000)
7) Power et al. (2009)
8) MacKenzie et al. (2022)



Map was created with QGIS 3.14.16, shapes and labels were added in Microsoft PowerPoint v2108

Figure 2.1a: Map showing the distribution and frequency of diet studies per-species in Alaska, the Yukon and the mainland NWT

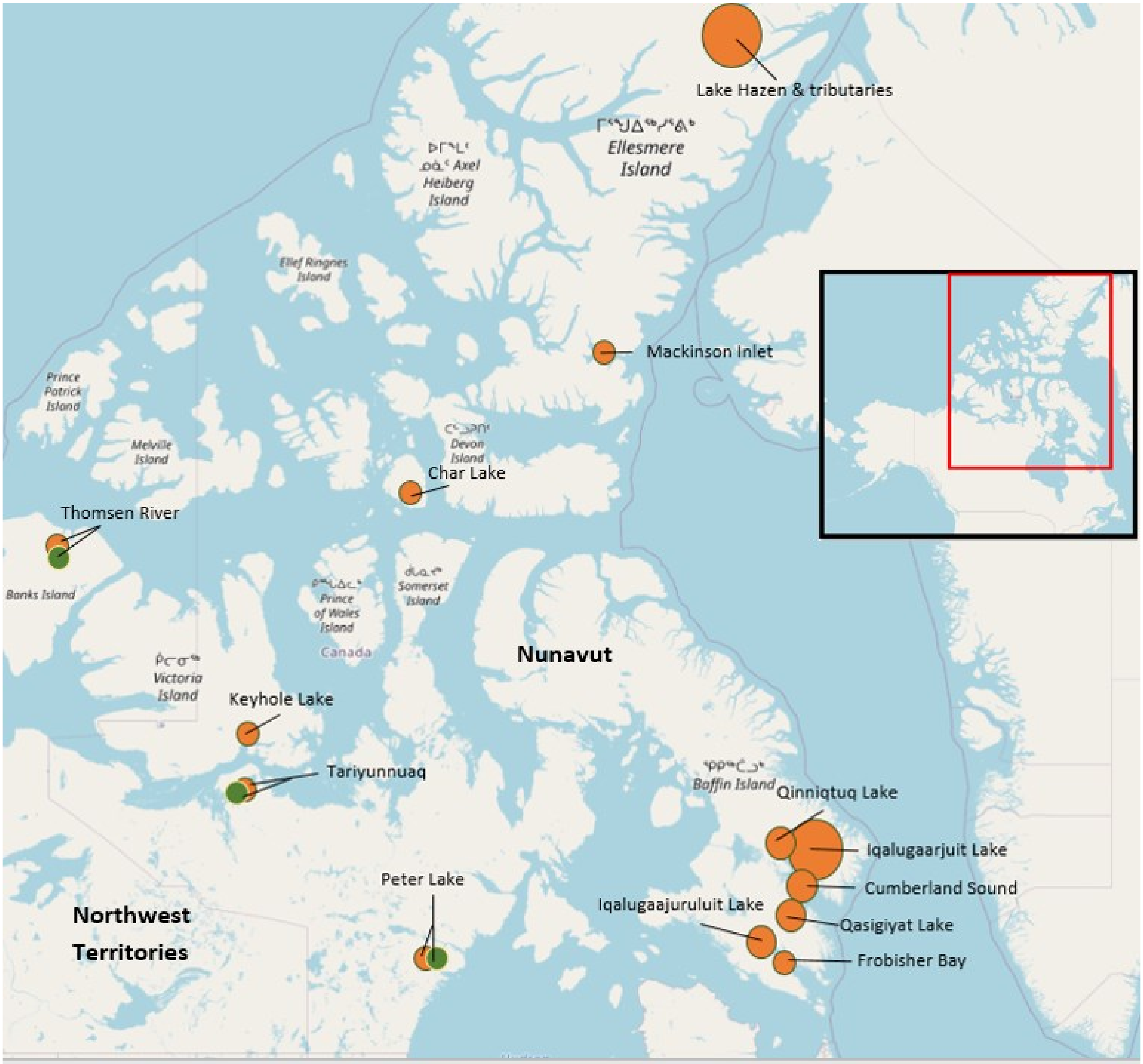


Figure 2.1b: Map showing the distribution and frequency of diet studies per-species in Nunavut and Banks Island, NWT

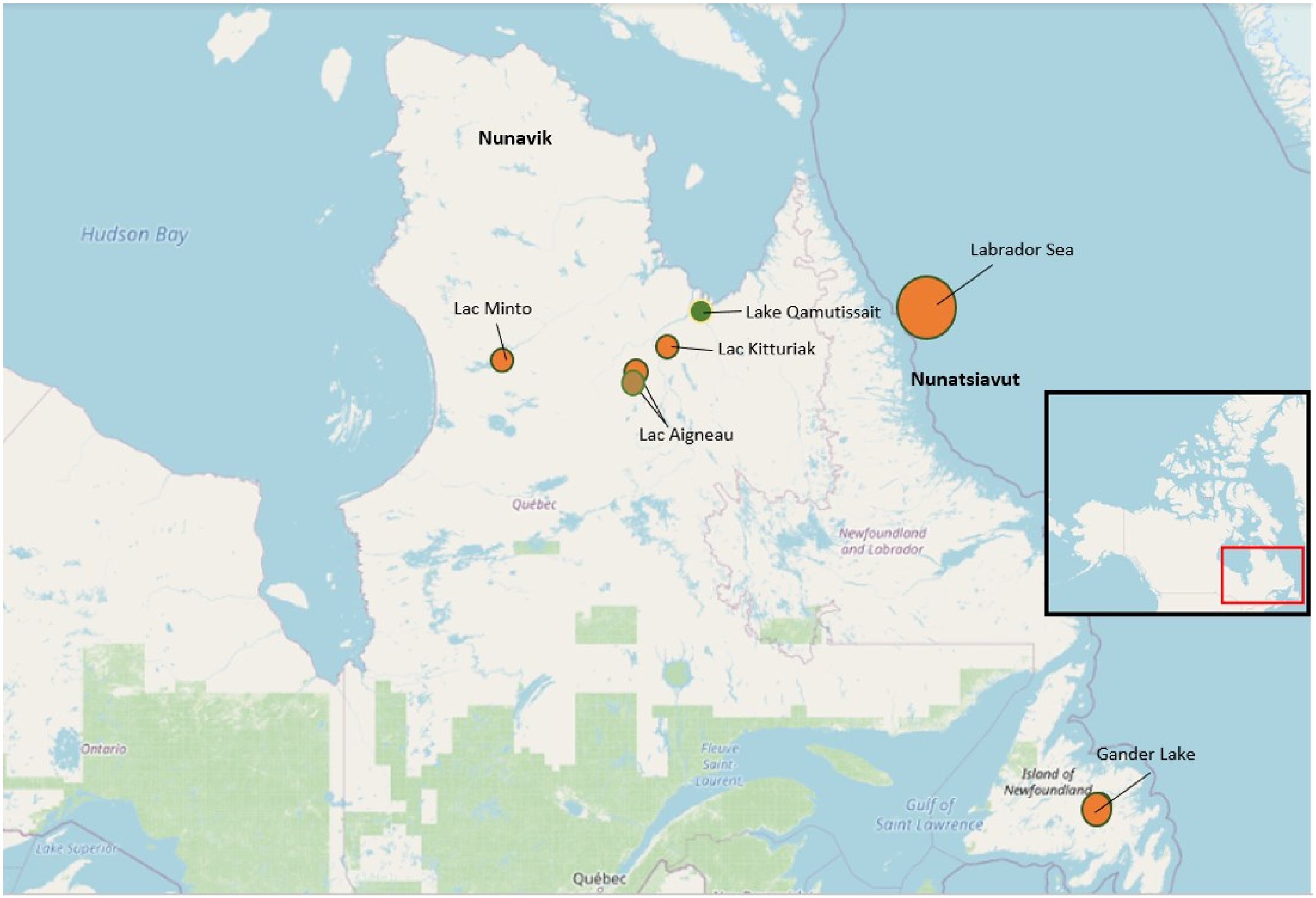


Figure 2.1c: Map showing the distribution and frequency of diet studies per-species in Nunavik and Nunatsiavut

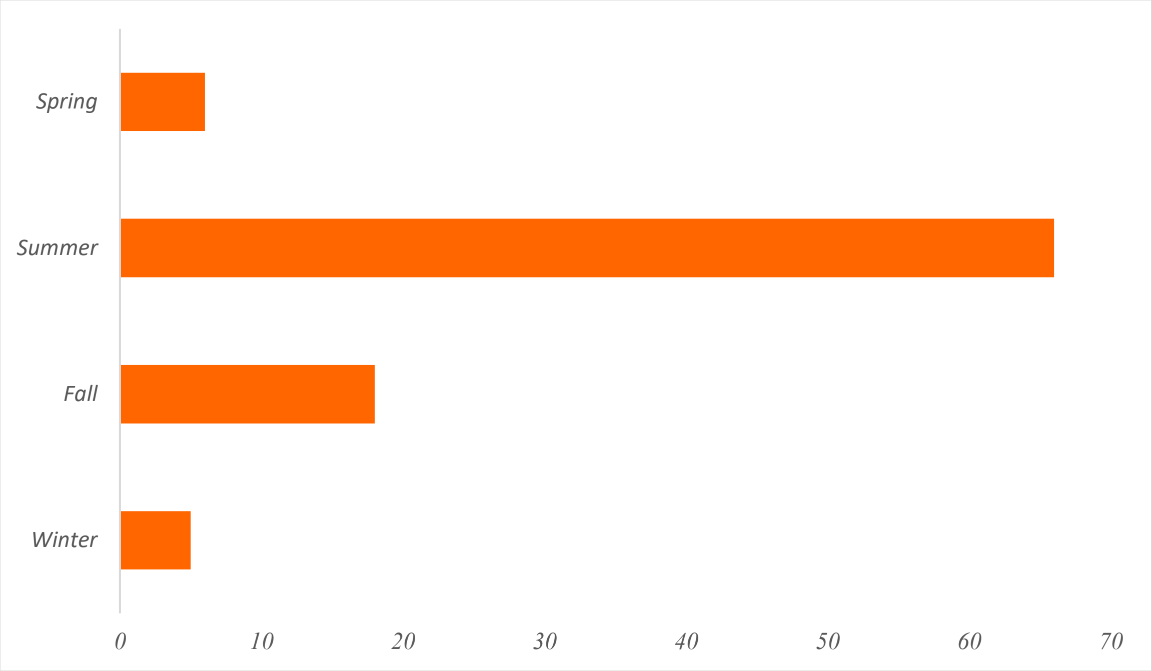


Figure 2.2 : Studies performed by season. Some studies included more than one season. Seasons were defined as summer (June-August), Fall (September-October), Winter (November-February) and Spring (March-May).

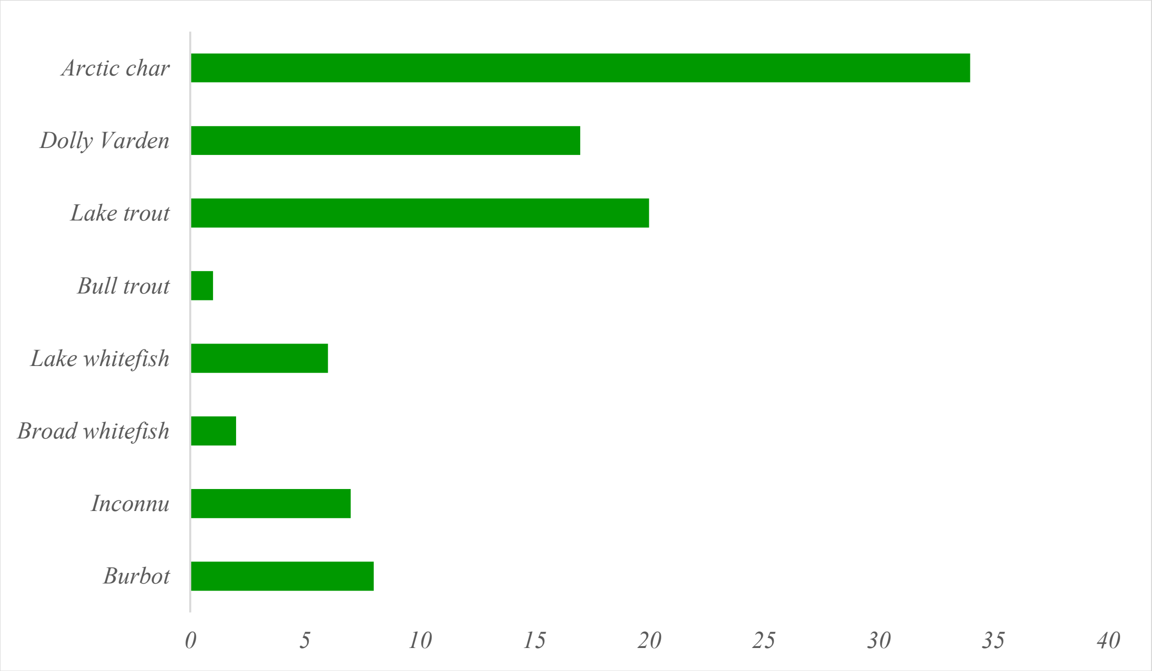


Figure 2.3: Number of available diet studies published per species in the North American Arctic. Numbers include anadromous and freshwater resident forms of all applicable species.

Chapter 3: Trophic ecology of range-expanding chum salmon (*Oncorhynchus keta*) in the Mackenzie River drainage, and potential for overlap with three key northern salmonids

Introduction

Climate change threatens to alter worldwide ecosystem dynamics, with outcomes in the Arctic being disproportionate in relation to the global average (Jansen et al. 2020; IPCC 2022). Fishes living in Arctic waterways are at particular risk from rising temperatures due to the narrow thermal ranges needed for optimal functioning (Reist et al. 2006a). There are many first-order effects that warming waters can impose on Arctic fishes such as reduced swimming performance, higher metabolic demands, increased post-exercise fatigue (Gilbert and Tierney 2018), lower gas exchange efficiency, and lowered reproductive success Reist et al. 2006a). While understanding these direct effects is extremely important in understanding how Arctic fishes may be challenged by warming waters, climate change also imposes many indirect challenges on Arctic fishes, especially with regard to their diets and trophic dynamics. Here we examine trophic ecology of a range-expanding sub-Arctic salmonid, with a focus on identifying its place in the Arctic trophic web and the potential for trophic interactions with key Arctic subsistence species.

Due to the low biodiversity found in Arctic waters, combined with high levels of unpredictability and short growing seasons, most Arctic aquatic food chains are short and necessitate generalized diets in order to minimize aggressive interactions and to exploit seasonal prey pulses (Power et al. 2008; Laske et al. 2018; Wight et al. 2023). Anadromy is common in Arctic systems with access to marine areas, as it allows some individuals to depart from harsh and unproductive Arctic freshwater systems to maximize growth potential by feeding in more productive marine areas (Power et al. 2008). Warming waters will increase productivity and potentially exacerbate food limitations in Arctic systems by increasing the metabolic demands of northern fishes, as well as increasing energy intake and growth (McDonald et al. 1996; Huang et al. 2021). This may also disincentivize anadromy because it will cause freshwater systems to become less nutrient-poor, possibly altering the population dynamics of those systems (Reist et al. 2006). Therefore, it is important to better understand the diets of Arctic fishes in order to inform effective management and conservation actions given the cumulative and continued impacts of climate change on Arctic ecosystems. Doing so allows for a better understanding of the abilities of northern fishes to adapt to changing climates, while also illustrating the adaptation potential of range-expanding species.

Climate change is also restricting the ranges of cold-adapted Arctic species, while facilitating the northward range expansion of sub-arctic species (Chu et al. 2005; Reist et al. 2006a). This increases the potential for competition in Arctic ecosystems as sub-Arctic fishes begin to expand into the southern ranges of Arctic fishes and threaten to exclude them due to their competitive advantages (Reist et al. 2006a; Sunday et al. 2012; Bilous and Dunmall 2020; Gilbert and Tierney 2018). Dietary overlap between an increasingly prevalent sub-Arctic species and an Arctic counterpart has been seen in the high degree of overlap between capelin (*Mallotus villosis*) and polar cod (*Boreogadus saida*) (McNicholl et al. 2016).

Expansion of sub-Arctic species has the potential to cause cascading effects that can impact subsistence harvests (Chila et al. 2022). Inuit harvesters have described the flesh of Arctic char (*Salvelinus alpinus*) in recent years as being paler and of lower nutritional quality, potentially as a result of the increased availability of sub-Arctic forage fishes such as capelin, which lack the high-quality nutrients and pigments of endemic Arctic prey such as Polar cod and copepods such as *Calanus glacialis* (Falardeau et al. 2022). While this is an example of an important subsistence species (Arctic char) being affected by a climate-driven range expansion at a lower trophic level, the potential for direct competition due to the arrival of sub-Arctic fishes of a similar trophic niche exists in the form of Pacific salmon (*Oncorhynchus* sp,), which are becoming increasingly common in Arctic waters (Dunmall et al. 2021).

Sporadic reports of vagrant salmon found in the Canadian Arctic have occurred for over a century, but did not indicate a pattern of increasing occurrence until the 2000's (Stephenson 2006; Dunmall et al. 2018). As a semelparous anadromous salmonid, Pacific salmon spend the majority of their adult lives in the ocean, where they move unimpeded as a response to changing conditions, such as increasing sea surface temperatures (Stephenson 2006; Dunmall et al. 2013). While the numbers of vagrant salmon have increased throughout the past two decades, the largest spikes in occurrence were observed in 2017 and 2019, which coincides with increased warming and reduction of north Pacific sea ice in those years (Huntington et al. 2020). How salmon interact with Arctic ecosystems is not fully understood, and the increasing occurrence of salmon as bycatch in Arctic subsistence fisheries has raised concerns in northern communities (Chila et al. 2022; Dunmall et al. 2021). Competition for food between salmon and native fishes is a common concern cited by subsistence harvesters, most of whom regard the increase of salmon as negative (Chila et al. 2022). The concern of trophic competition between salmon and native fishes makes assessing the diets of salmon in the Arctic necessary for assessing potential for these interactions. Chum salmon (*O. keta*) are of particular interest because they are the most commonly captured Pacific salmon species in the Canadian Arctic (Dunmall et al. 2021).

Although salmon are known to feed opportunistically at sea (Satterfield and Finney 2002; Urawa et al. 2018), it is widely accepted that Pacific salmon cease feeding entirely during their return to fresh water, with the exception of occasional egg consumption by spawning coho salmon (*O. kisutch*), chum salmon, and chinook salmon (*O. tshawytscha*) (Garner et al. 2009). In contrast, harvesters in the western Canadian Arctic have observed salmon caught in fresh water with food in their esophagi and stomachs, as well as striking readily at fishing lures, suggested the possibility of deviations from this established life history trait in the novel Arctic environment. While Indigenous harvesters in the Arctic possess an in-depth knowledge of the feeding behaviours of local subsistence species such as chars and whitefishes, most are unfamiliar with salmon due to a lack of historical presence across much of the Canadian Arctic (Chila et al. 2022). This lack of biased perspectives on salmon contributes to the raising of new research questions, including investigating the potential for freshwater feeding by mature salmon. Given the wide dietary niche of chum salmon (Urawa et al. 2018), research on feeding ecology in all environments is needed to fully understand the adaptation potential of this species and potential for dietary overlap with endemic fishes as it expands to new regions.

The goal of this study was to determine the adaptation potential of range-expanding chum salmon in the Western Canadian Arctic, situating chum salmon into the aquatic food web of that region and in doing so, adding to the information base about diets of Dolly Varden (*Salvelinus malma*), lake trout (*S. namaycush*), and inconnu (*Stenodus leucichthys*). Effort was focused across three objectives. First, to establish a baseline regarding the trophic ecology of chum salmon in the Mackenzie River system by constructing the prey assemblage and niche spaces of salmon in this novel environment using stomach contents and biomarkers; second, to fill knowledge gaps regarding the trophic ecology of Dolly Varden, lake trout, and inconnu; and lastly, to determine diet overlap between salmon and endemic species in different habitats such as the river delta and large lakes by comparing stomach and biomarker data with those of endemic fishes. This study is essential to determining the impacts salmon have in new environments they arrive in via climate-mediated range expansions, the adaptation potential of salmon as their ranges expands into new environments in order to inform decisions regarding the management of range-expanding species, and is of particular importance to northern communities as concerns of salmon affecting important endemic subsistence species have been raised.

Methods

Geographic scope

The scope of this study is the Mackenzie River drainage in the Northwest Territories, divided into four regions. These regions were the Mackenzie Delta, the mainstem of the Mackenzie river from south of Tsiigehtchic to the mouth of the river at Great Slave Lake, Great Bear Lake, and Great Slave Lake (Figure 3.1). This was done to provide four separate and unique areas where salmon are caught in the Mackenzie drainage that may illustrate differences in the diet of chum salmon in the region, and how they may interact with different endemic species found within the regions.

Sample collections and processing

Salmon

Chum salmon were collected as part of the Arctic Salmon program, which is a community-led monitoring program which uses salmon caught in the Arctic as indicators to investigate ecosystem change (Dunmall et al. 2021). This program allows harvesters operating from communities across the Canadian Arctic to voluntarily submit salmon (either whole fish or heads) in exchange for gift cards. Salmon were captured by subsistence harvesters from communities along the Mackenzie River, as well as communities located near Great Bear Lake and Great Slave Lake. Salmon heads were not able to be sexed due to the absence of gonads.

Endemic fishes

Endemic fishes used in the comparative analyses were collected as part of DFO stock assessment surveys.

Lake Trout

Lake trout were netted between July 22nd and August 1st, 2017 in the Keith Arm of Great Bear Lake using gill nets with mesh sizes between 1” and 5” set along the surface, mid-water column, and the bottom at depths between 0’ and 98’. Stomachs from these fish were analyzed and stable isotope analyses were performed. Stomach contents from lake trout netted in the southwest basin of Great Slave Lake during the final two weeks of August 2017, and the final week of July, 2019. In 2017, they were caught using benthic nets with 5.2” and 6” mesh sizes at depths of 19’ and 30’. Individuals netted in 2019 were caught using benthic gill nets with a 5.2” mesh size at 30’ deep, as well as experimental multimesh nets set in both pelagic and benthic areas at 16.5’ deep and between 30’ and 65’ respectively, featuring multiple mesh sizes randomly combined (for more information, see Zhu et al. 2017).

Inconnu

Inconnu were netted in the southwestern basin of Great Slave Lake during the final week of July, 2019 using 5.2” benthic gill nets set along the bottom at depths of 30’, as well as pelagic multimesh nets set at a depth of 16.5’.

Dolly Varden

Dolly Varden were collected from the traditional harvesting location of Ok Choo (Big Eddy), located approximately 28km southwest of Aklavik throughout August, 2019, using a gill net with a mesh size of 4” set by a local harvester.

Processing

All fish were measured for fork length from the tip of the snout to the fork of the caudal fin, and were sexed by identification of male or female gonads. Stomachs were obtained by cutting the esophagus behind the mouth and the gastrointestinal tract at the vent. Stomachs were then frozen and shipped to North/South Consultants in Winnipeg, Manitoba, where contents were identified to the lowest possible taxonomic level. Muscle samples for stable isotope analyses were pieces of epaxial muscle approximately 1” long taken from slightly behind the dorsal fin for whole fish samples. In the case of salmon submitted as heads only, the muscle was taken from slightly behind the skull. These samples were frozen and stored until freeze-dried, homogenized, weighed; and then analyzed via mass spectrometry at the DFO Freshwater Institute.

Stomach content analyses

Stomach contents from both 2017 and 2019 were analyzed when possible to provide the most complete prey assemblages possible. Multiple metrics were used to analyze stomach contents. First, percent frequency (%F), percent by number (%N), and percent by mass (%M) of prey items were calculated in order to 1) construct a general prey assemblage for each species, 2) determine how frequently each prey item was consumed and 3) assess the contribution of prey items to diet by species using both numeric and volumetric methods. These three metrics were then used to compute the Index of Relative Importance (IRI), which was chosen to concisely convey the most important prey items in each species' diet by combining all three indices, thereby reducing the inherent bias involved with using numeric or volumetric methods alone. This is a relative index that compares the prey items in relation to each other using the frequency a prey item is consumed within the fish sampled (%F), the numerical proportion of the prey item within the sample (%N), and the proportion of the prey item in the mass of prey consumed by the fishes sampled (%M). Specifically, IRI is calculated as:

$$IRI = \%F(\%N + \%M)$$

Additionally, to assess the fullness of salmon stomachs between regions, the fullness index derived by Hureau (1969) was used:

$$FI = FW/W \times 100$$

where fullness index (FI) is calculated by the weight of food (FW) divided by the weight of the fish (W), and then converted into a percentage. A nonparametric Kruskall-Wallis test and subsequent Wilcoxon rank sum test were used to test differences in FI between regions for each sampling year, given that the assumptions for a parametric alternative could not be met due to small and unequal sample sizes of stomachs from each region.

Stable isotope analysis

Biomarker analyses were restricted to samples captured in 2019 due to both sample availability and to provide consistency with regard to cross-species comparisons, which the exception of lake trout, for which only samples from 2017 were available. Stable isotope analysis (SIA) was used to determine niche space for all of the species studied. Freeze-dried fish tissues were homogenized and weighed to 400µg ± 10µug using a microbalance. Samples were placed into a tray with 100 wells. For the purposes of calibration, the reference materials USGS 40 and 41a were used twice each every twenty wells, as well as an in-house reference material synthesized at the DFO Freshwater Institute, which was used once in each sequence of reference materials. The first, 15th, 30th, 45th, 60th fish in each tray were duplicated to determine the level of variation in the samples. The niche space of salmon, characterized using $\delta^{13}C$ and $\delta^{15}N$, was compared among the different regions of the study area using a two-way ANOVA. Tukey-Kramer post-hoc test was chosen to determine where specific differences in $\delta^{13}C$ and $\delta^{15}N$ may lie, chosen due to the inequal sample sizes of chum salmon samples from each region. In order to ensure that changes in $\delta^{15}N$ were not linked to fish size, regression analysis of $\delta^{15}N$ and fork length was performed. Comparisons between isotopic data for salmon and endemic species were done by two-tailed, two sample t-tests for both $\delta^{13}C$ and $\delta^{15}N$, and were displayed visually by plotting the data points, surrounded by 95% confidence interval ellipses. Given that the tissue had not undergone lipid extraction, samples with a C:N ratio >3.5 were lipid-corrected, as suggested by Skinner et al. (2016). The correction equation used was defined by Post et al. (2007):

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$$

Results

Sample collection

Chum salmon

A total of 63 chum salmon were sampled for this study in 2017, and 182 in 2019 (164 whole fish and 18 heads) (Table 3.1). Aside from eight individuals caught in June and July, all salmon were collected between August and October. In the Delta, 36 of these fish were captured in August, with the remaining 24 being caught throughout September. With the exception of a single individual captured during late August each year, salmon were captured from Great Bear Lake throughout the month of September. Throughout the mainstem of the Mackenzie River, all individuals captured in the downstream areas in the Sahtu near Fort Good Hope were caught in August except for one in September, while all salmon caught further upstream were captured in September (38%) or October (62%). Twenty-seven salmon caught in Great Slave Lake were captured throughout September, with the remaining 11 being caught in October.

Of the 61 chum salmon sampled for stomach contents in 2017, 43 were males. Within the study regions of the Delta, mainstem of the Mackenzie River, Great Bear Lake, and Great Slave Lake, males made up 74%, 71%, 63%, and 82% of the samples, respectively (Table 3.1). Males had significantly longer mean fork lengths than females (648mm vs. 599mm; t=6.58, df-51, $p=2.44 \times 10^{-8}$). There was a significant difference in fork length of the salmon between the regions (F(3,57)=4.32, p=0.008). The Tukey HSD method revealed that chum salmon caught in Great Slave Lake had significantly longer fork lengths than those caught elsewhere ($p > 0.05$), while other regions did not differ significantly amongst each other.

Overall, male chum salmon made up the majority of salmon captured in 2019, with the sample comprising of 67% males. Within-region, only the Delta featured an even sex ratio, with the mainstem, Great Bear Lake, and Great Slave Lake samples being made up of 74%, 87%, and 67% males, respectively. Excluding 18 head-only samples which had unknown fork lengths, male chum salmon were larger on average (633mm vs. 596mm), which was a significant difference (t=6.16, df=113, $p=1.14 \times 10^{-8}$). There was a significant difference in size between salmon across the regions (F(3,138)=14.0, $p=5.09 \times 10^{-8}$). The Tukey HSD method revealed that salmon caught in Great Slave Lake and the mainstem of the Mackenzie were significantly larger than those caught in the Delta and Great Bear Lake ($p > 0.05$).

Endemic fishes

Dolly Varden

Dolly Varden captured from the Mackenzie Delta in August 2019 were predominantly female (25/34) with males having a longer mean fork length (597mm vs. 548mm), the difference of which was significant (t=2.26, df=15, p=0.03).

Lake trout

Lake trout captured in Great Bear Lake in the summer of 2017 had a predominantly male sex ratio (29/39) and a mean fork length of 623mm. Individuals captured in Great Slave Lake that year featured a slightly more males (9/17) and a mean fork length of 616mm; while in 2019, the sex ratio of the sample mostly female (5/8) and had a mean fork length of 663mm. No lake trout samples featured a significant difference in fork length based on sex.

Inconnu

In Great Slave Lake, female inconnu had a larger mean fork length (863mm vs. 770mm) which was significantly different (t=2.26, df=31, p=0.03). The sex ratio of the inconnu sampled was even.

Diet analyses

Chum salmon

The majority of salmon stomachs did not contain identifiable remains, with only 7 out of 163 across both years (4/63 in 2017 and 3/100 in 2019), or 5% of total chum salmon stomachs sampled, containing prey that could be enumerated and/or identified. Only male chum salmon fed in fresh water, and not a single identifiable prey item was recorded in a female, although this may be the result of a male-dominated sample. Feeding in the mainstem of the Mackenzie River from south of Tsiigehtchic to the mouth of the river at Great Slave Lake was limited to a single small bird consumed near Wrigley, NWT. In the Delta, one salmon in 2019 consumed an opossum shrimp of the genus *Neomysis*, although it is unknown if it is of freshwater or marine origin, given the relative proximity to the ocean (~70km). All other examples of freshwater feeding took place in the Mackenzie Basin Great Lakes. A chum salmon in 2019 fed on aquatic insects in Great Bear Lake, one of which was unidentifiable, alongside two water boatmen (Family: Corixidae), found in the lake's shallower waters (Johnson 1975). In 2017, a single chum salmon fed on a crustacean of the class Malacostraca that was not able to be identified to a lower level. In Great Slave Lake, a chum salmon that had consumed a least cisco was captured in 2017, along with two in 2019 that had eaten a least cisco and larval crustacean, respectively.

Although identifiable prey items were uncommon in the sample, many chum salmon did contain remnants of prey items in their stomachs that were in varying states of digestion, rendering them unable to be identified. In order to quantify the amounts of unidentifiable prey that had been consumed by the salmon, stomach fullness index (FI) was used. Stomach fullness in salmon across the study area was low, with an average fullness index (FI) of 0.164 in 2017, and 0.095 in 2019, with no significant difference between the years (t=1.70, df=81, p=0.09). Stomach fullness appeared to be highest in the Delta and decreased in other regions. In 2017, there was no significant difference among regions in terms of stomach fullness (H=6.98, df=3, p=0.07). In 2019, there were significant differences in stomach fullness between the regions (H=16.8, df=3, p=0.0007). Using the Wilcoxon rank sum test, salmon caught in the Delta had a significantly higher FI than the other regions, which did not differ amongst themselves (p>0.05 for Delta compared to each of the other regions).

Chum salmon demonstrated a mid-trophic level, nearshore feeding niche according to mean $\delta^{15}N$ ratios (11.4 ± 0.75) and $\delta^{13}C$ ratios (-20.9 ± 0.52). An ANOVA was performed to determine if chum salmon differed on the basis of $\delta^{13}C$ and $\delta^{15}N$ across the study area. There was no difference in $\delta^{13}C$ (F(3,156)= 0.154, p=0.21), although a significant difference in $\delta^{15}N$ was revealed (F(3,156)=4.32, p=0.005). The Tukey-Kramer method was used to determine which groups differed, being chosen instead of the Tukey HSD test due to the inequal sample sizes of salmon caught in each region. Chum salmon trophic level was significantly lower in Great Bear Lake than Great Slave Lake (p=0.006) and though not significant, the trophic level of chum salmon from Great Bear Lake tended to be slightly lower than the other regions as well (Figure 3.11). Outside of Great Bear Lake, there were no differences in trophic level between chum salmon caught in any other region. It is likely that the stable isotope data for chum salmon caught in the Mackenzie Delta reflect marine diet given the proximity to marine areas and how soon the salmon were caught following the beginning of their migration into the Mackenzie system. However, because the isotopic turnover rate of muscle in wild chum salmon is not known, it is difficult to determine to what degree these data refer marine feeding outside of the Delta, and what influence any freshwater feeding has on these results. Trophic level in the chum salmon sampled was correlated with fork length ($R^2 = 0.21$, F = 37.7, df = 1, 139, $p = 8.29 \times 10^{-9}$), although the large level of variation indicates that fork length is not the sole predictor of trophic level. Male chum salmon had a significantly higher trophic level than females (t = 3.30, df = 98, p = 0.001), which may be explained in part by males being larger on average.

Dolly Varden

In the Delta, all Dolly Varden demonstrate a broad feeding niche in terms of trophic level and resource use, in accordance with the species' generalist nature. Dolly Varden sampled in this study were caught during their migration to spawning and overwintering grounds and had ceased feeding, no identifiable stomach contents were recorded. These fish featured high mean C:N ratios (9.21 ± 3.27), as well as high mean trophic level (14.97 ± 0.45), and a large amount of variability in dietary carbon source (-26.2 ± 0.77). This species' broad range in δ^{15}N was correlated with fork length, albeit with high amounts of variation ($R^2 = 0.27$, F = 20.9, *df* = 1, 57, $p = 2.68 \times 10^{-5}$) (Figure 3.8). Overall, these Dolly Varden were upper-trophic level predators, with a high degree of variation in terms of isotopic niche space (Figure 3.5).

Lake trout

Lake trout featured varied diets, with multiple prey taxa represented, although coregonids made up the most prevalent prey in all three samples, which featured 0 empty stomachs (Figures 3.2-3.3, Table 3.2). Lake trout in Great Bear Lake featured a varied diet with 15 different invertebrate taxa being present, alongside fish such as coregonids and deepwater sculpin (*Myoxocephalus thompsonii*) (Figure 3.2, Table 3.3). Of particular note, ants (Formicidae) were consumed in large numbers by some individuals (captured in both surface and benthic nets), with individuals that had consumed them having between 56 and 462 ants in their stomachs. All individuals sampled were captured in benthic nets with the exception one which was caught in a surface net, which had eaten a large variety of terrestrial insects, as well as an unidentified salmonid. Aside from ants and a single Homopteran, terrestrial insects were not consumed by lake trout captured in benthic nets.

According to stable isotope analyses, these lake trout featured broad trophic niches, with a mean δ^{15}N ratio of 12.8 ± 0.87, and mean δ^{13}C ratios of -27.9 ± 1.74; indicating a mid-upper trophic level predator, feeding mostly in benthic and pelagic environments, albeit with large amounts of variation. The isotopic niche space did not differ significantly between individuals captured in benthic, pelagic, or surface nets. Fork length was not correlated with the trophic position of lake trout in Great Bear Lake ($R^2=0.04$, F=1.61, df=1,47, p=0.212) (Figure 3.9).

Individuals in Great Slave Lake captured in July 2017 consumed large numbers of crustaceans (copepods), while crustaceans were infrequently consumed by individuals in the August 2019 sample (Figure 3.3a, 3.3b). Conversely, the 2017 sample featured few insects, while diving beetles made up a notable proportion of the 2019 lake trout stomach contents, which may illustrate a temporal shift in prey resource use throughout the summer.

Inconnu

Inconnu sampled in Great Slave Lake in 2019 were exclusively piscivorous, aside from a single ostracod consumed by one individual. 90% of inconnu sampled had identifiable prey in their stomachs. All identifiable fish remains belonged to the Coregoninae subfamily, with the majority being whitefishes and ciscoes of the genus *Coregonus* (Figure 3.4). The isotopic niche space of inconnu corroborates the relatively narrow feeding niche of this species indicated by stomach contents. This species displayed a mid-upper mean trophic level according to δ^{15}N ratios (12.7 ± 0.42), while feeding in carbon-poor pelagic and benthic environments according to δ^{13}C ratios (-29.4 ± 0.67). Inconnu trophic level did not correlate with fork length ($R^2 = 0.29$, $F = 3.10$, $p = 0.08$) (Figure 3.10).

Dietary overlap

Chum salmon do not fully overlap with any of the chosen endemic species in terms of both trophic level and basal dietary carbon source (Figures 3.5-3.7), and stomach contents suggest that feeding is too infrequent in fresh water to constitute competition, although some prey items consumed by salmon are found in the diets of endemic fishes. Salmon and anadromous Dolly Varden captured in the Mackenzie Delta differed significantly on the basis of trophic level ($t = 23.77$, *df* = 68, $p = 1.16\text{x}10^{34}$), but featured no significant difference on the basis of δ^{13}C ($t = 0.83$, *df* = 34, $p = 0.41$) (Figure 3.5), indicating a significant overlap in terms of dietary carbon sources. Chum salmon were significantly longer in terms of fork length than Dolly Varden ($t = 4.86$, df = 91, $4.81\text{x}10^{-6}$). These data likely reflect marine feeding for both species, and it suggests that Dolly Varden feed in the same habitats as chum salmon while at sea, albeit at a higher trophic level. Ultimately, marine stomach content analyses are needed to verify this.

Salmon and lake trout in Great Bear Lake again differed significantly in terms of δ^{13}C ($t = 27.6$, *df* = 51, $p = 2.62\text{x}10^{-32}$) and δ^{15}N ($t = 10.6$, *df* = 69, $p = 3.65\text{x}10^{-16}$). There was no significant difference in fork length between the two species ($t = 0.11$, df = 51, $p = 0.91$). Despite this, the large variation amongst individual lake trout in terms of trophic level indicates that some individuals do occupy a similar trophic level to co-occurring salmon (Figure 3.6). A salmon in

Great Bear Lake ate several corixids in 2019, and aquatic hemipterans were also eaten in large quantities by a lake trout caught in a surface net during 2017, which is an instance in overlap in prey usage between the two species, though larger samples captured within similar timeframes would be needed to determine how common this is. Despite the lack of temporal overlap, the lake trout and salmon captured in Great Bear Lake used the same habitat and were captured in the same areas of the lake (Keith Arm), therefore providing a useful starting point in assessing potential overlap. In Great Slave Lake, instances of chum salmon eating least cisco provide another example in prey overlap between the two species, but occurrences are likely too low to constitute actual trophic competition.

Chum salmon and inconnu in Great Slave lake differ markedly in terms of $\delta^{13}C$ ($t = 57.4$, $df = 34$, $p = 2.01\text{x}10^{-35}$) and indicate that inconnu feed in much more benthic and pelagic habitats than salmon occurring in the same area. Trophic level was similar between the two species (Figure 3.7), but was still significantly different according to $\delta^{15}N$ ratios ($t = 5.3$, $df = 34$, $p = 5.65\text{x}10^{-6}$). Inconnu had significantly longer fork lengths than chum salmon ($t = 7.1$, $df = 43$, $8.2\text{x}10^{-9}$). Similar to lake trout, the is a small degree of diet overlap between the species due to the instances of chum salmon predating on least cisco, but competition is unlikely due to both the abundance of least cisco in the lake (Zhu et al. 2017), and the infrequency of chum salmon feeding in the lake. While these two species were caught at different times (July vs. September-October), they were caught while using the same habitat of the lakes southwestern basin.

Discussion

This study yielded novel information regarding the trophic ecology of adult chum salmon in the Canadian Arctic, including that they, on occasion and likely opportunistically, feed in fresh water in this environment. While the predation of some Pacific salmon on small amounts of eggs has been documented (Garner et al. 2009), this study recorded the consumption of prey items such as forage fishes, insects, crustaceans, and a small bird by chum salmon that had returned to freshwater. Pacific salmon typically do not eat upon returning to freshwater and operate on a fixed energy budget until spawning and their subsequent death (McVeigh et al. 2007). The presence of recently consumed, identifiable prey, as well as unidentifiable prey in varying states of digestion in fish with non-degraded digestive tracts suggests a deviation from this established life history trait can occur in vagrant salmon in the Canadian Arctic.

Salmon are known to be aggressive during spawning runs, but it is generally directed towards intruding conspecifics (McVeigh et al. 2007), rather than putative prey items. Conversely, if the salmon that fed in freshwater were doing so for the energetic gains, the low numbers of prey items consumed (particularly invertebrate prey) are unlikely to provide notable quantities of energy. The instances of feeding on nutritionally substantive prey items such as fishes occurred in the upper reaches of the study area, which may indicate that feeding for energy content in these fish is connected to distance travelled from the ocean.

While salmon are occasionally feeding in fresh water, this study has found little or no competition for food resources in the fresh water among salmon and the fresh water fishes studied. This is supported by the low frequency of feeding by salmon in fresh water, lack of resource limitations in the systems studied, and the lack of overlap in trophic niche space among chum salmon and lake trout, Dolly Varden, or inconnu. These data indicate that, even when caught in the same areas, salmon are utilizing prey resources that are both at lower trophic levels, and feature a more nearshore origin. The exception to this is Dolly Varden, which appear to eat prey originating in the same areas as chum salmon while at sea, but at a higher trophic level.

Diet results

Chum salmon

Invertebrate prey were consumed by chum salmon in small numbers in every region of the study area other than the mainstem of the Mackenzie River. Crustaceans are a major prey item for chum salmon at sea, and while they were consumed by a handful of individuals in fresh water, it is not known the purpose that this served given the numbers eaten were too small to provide energetic benefits. Foraging on insects was only recorded in Great Bear Lake, in the form of corixids (otherwise known as water boatmen). Corixids dwell along the shallow, rocky nearshore areas of the lake (Johnson, 1975). The open waters of the lake are very unproductive and inhospitable for most of the fish community, which may suggest that chum salmon are also not suited for Great Bear Lake’s open water as is restricted to shallow bays similar to the majority of the other species found in the lake (Janjua et al. 2015). The need to prey on small nearshore invertebrates in Great Bear Lake due to water conditions rather than larger prey such as fishes as seen in the more productive Great Bear Lake may account for the lower trophic level of chum salmon captured in Great Bear Lake compared to the other study regions, but a larger sample size of salmon that had fed recently in the lake would be needed to confirm this.

Consumption of larger vertebrate prey only happened in the upper reaches of the study area. Both instances of freshwater piscivory by salmon occurred in Great Slave Lake, the part of the study area furthest from the ocean. Both forage fishes consumed were least cisco, one of the most common forage fishes in all parts of the water column of the lake (Zhu et al. 2017). These least cisco had been swallowed headfirst and in the case of the individual consumed in 2019, was already in the stomach of the salmon that ate it, indicating that the esophagi and GI tracts of these fish were not atrophied to the point of being unable to accept relatively large prey items, as would typically be the case for a salmon that had undergone a significant upstream journey in fresh water. A salmon caught near Wrigley appeared to have eaten and partially digested a small bird. Chum salmon are known to have rapid digestive processes (Urawa et al. 2018), indicating that this bird had been consumed at some point during the individual's migration upriver, assuming it's digestive tract was operating at normal capacity. This is the only recorded example of a Pacific salmon consuming a bird in fresh water.

Endemic fishes

By addressing a community-driven question about potential competition among salmon and key subsistence species, this study also filled gaps regarding the diet of northern fishes, especially regarding anadromous Dolly Varden and Inconnu.

Dolly Varden

Dolly Varden had a broad trophic niche that corresponds with the broad diet of this species that has been recorded in previous studies (Stewart et al. 2009; Narver & Dahlberg 1965). The individuals in our sample featured a relatively high mean trophic level ($\delta^{15}N = 14.9 \pm 0.45$) and were between the sizes of 355-700mm FL, which is within the size range in which Dolly Varden typically begin to feed more prominently on fishes such as sculpins, anadromous coregonids, polar cod, blennies, and others (Wight et al. 2023; Stewart et al. 2009). The largest individuals are almost exclusively piscivorous (Stewart et al. 2009). The relatively ^{13}C-enriched tissues of the Dolly Varden sampled suggests a marine-influenced diet (Smith et al. 1995). However, the wide range in $\delta^{13}C$ ratios may be the result of the utilization of brackish and freshwater prey as well (Brewster et al. 2016), as Dolly Varden have been recorded feeding in those areas after leaving coastal summer feeding grounds, albeit at a much-reduced rate (Stewart et al. 2009).

Lake trout

Lake trout netted in Great Bear Lake featured the most varied diets of all the fish sampled, having eaten a variety of both fishes and invertebrates from different habitats within the sampling area on the lake (Keith Arm). Predation on cisco indicates feeding in the shallow bays of the lake where cisco are thought to reside primarily (Janjua et al. 2015); as well as very deep open waters, evidenced by the consumption of prey associated with deep, oligotrophic waters such as mysids and deepwater sculpin (Zhu et al. 2021). A wide array of terrestrial and aquatic insects were also consumed, which demonstrates seasonal exploitation of a resource pulse during the summer that lake trout living at all depths make use of in this nutrient-poor environment (Chavarie et al. 2016). This exploitation of prey in different habitats is potentially explained by the presence of four different lake trout morphotypes known to exist in the lake, which differ both on the basis of habitat use, and diet (Chavarie et al. 2016). The morphotypes of the lake trout sampled in this study were not known, but they possibly account for some of the wide variation in the diet data of these fish. A notable prey item that is consumed by lake trout in Great Bear Lake as recorded here and elsewhere is the predation on large numbers of ants (Formicidae). As part of the process of establishing new colonies, ants will make a “nuptial flight”, wherein a mass emergence of winged, reproducing individuals occurs, typically during the summer months (Hart et al. 2017). These aggregations of winged ants may get blown off-course near large bodies of water, and then sink rapidly, where they can be readily consumed by opportunistic fishes such as lake trout.

In Great Slave Lake, lake trout diets were less varied than those found in Great Bear Lake, potentially due to prey items such as fishes being more prevalent in Great Slave Lake (Vinson et al. 2021), reducing the necessity of consuming a broad range of invertebrates. During both sampling years in Great Slave Lake, lake trout were predominantly piscivorous, with consumption of aquatic invertebrates being common as well. Very few insects were consumed by individuals caught in July 2017 but they were consumed in greater numbers by those captured in August 2019 (both aquatic beetles and terrestrial insects). The difference in insect consumption between sampling years may be due to timing, given that the input of terrestrial insects into northern aquatic systems and as a result, lake trout diets, increases as the summer progresses (Vinson et al. 2021), and the 2019 lake trout samples were captured later in the summer than their 2017 counterparts. There are three different lake trout morphotypes present in Great Slave Lake which differ in morphology, but demonstrate similar patterns in habitat use (Zimmerman et al. 2009). All three morphotypes use benthic habitats as juveniles, and shift to pelagic habitats as they mature and grow larger, with a shift to pelagic feeding occurring as individuals reach sizes of >430mm. While the morphotypes of the lake trout sampled here are not known, their diets outside of insects in the 2019 sample were predominantly pelagic prey such as copepods and coregonids and all fish were over 430mm FL, corroborating the ontogenetic habitat shift recorded by Zimmerman et al. (2009).

Inconnu

Inconnu had relatively narrow diets according to both stomach contents and stable isotopes. These fish deviate from the generalist diets that most northern fishes have and instead specialize on pelagic piscivory in Great Slave Lake, specifically on coregonids. Diet data on inconnu are sparse, and taking stomach contents and stable isotopes in tandem allows us to fill a knowledge gap on this species as the few trophic studies done on inconnu typically only feature one method or the other. However, the inconnu sampled here were all fairly large and mature fish (591-1120mm FL), and the prey preferences of smaller inconnu is not as well-known. Many northern salmonids feature ontological shifts in diet with prey size being liked to age and size, but it is not known if inconnu experience such a shift, and some preexisting data suggest that inconnu become piscivorous very early in their development (Alt 1965; Fuller 1955). Further work on this species is needed to fully understand its trophic ecology.

Diet overlap

Chum salmon and Dolly Varden

Despite having smaller average fork lengths than chum salmon in this sample, Dolly Varden occupy a higher trophic level than co-occurring chum salmon. The Dolly Varden in our sample had an average fork length of 552mm, which may suggest that their diets were dominated by fishes (Stewart et al. 2009), which is not common for Chum salmon of any size (Urawa et al. 2018). This likely explains the lower trophic position of chum salmon. Ultimately, stomach content analyses of chum salmon and co-occurring anadromous chars in the Arctic are needed to determine the reason for the difference in trophic level displayed by stable isotopes. Additionally, while large adult Dolly Varden feed at a higher trophic level than chum salmon, smaller, younger individuals with more invertebrate-dominated diets may feed at a similar trophic level to chum salmon. Further work is needed to determine the possibility of trophic interaction between salmon and Dolly Varden in lower age and/or size classes.

Chum salmon and lake trout

Lake trout and salmon do not appear to share a feeding niche in Great Bear Lake. Given the breadth of prey and habitat usage by lake trout in Great Bear Lake and the low feeding frequency of chum salmon in fresh water, it is unlikely that trophic interaction occurs between these species. The samples of the two species captured in Great Bear Lake did not differ in fork length, and fork length did not correlate with trophic level in lake trout. This indicates that the difference in trophic level between the species was not due to size and that lake trout feed at higher trophic levels and on more pelagic/benthic prey than chum salmon.

Similar to Great Bear Lake, lake trout and chum salmon in Great Slave Lake had a small amount of overlap in terms of prey items, but it is unlikely to constitute competition. Least cisco were consumed by both species, but at a very low rate in the case of chum salmon (one instance in each sampling year). Least cisco are abundant in Great Slave Lake in all parts of the water column, and represent a major prey source for lake trout, as well as other upper-trophic level predators such as inconnu, northern pike, and burbot (Zhu et al. 2017). Being one of the species that dominates the makeup of Great Slave Lake’s fish community and plays a role in sustaining multiple upper-trophic level predators, the sporadic consumption of least cisco by chum salmon is not likely to introduce competition between salmon and lake trout.

Chum salmon and inconnu

Inconnu and salmon in Great Slave Lake differ in terms of isotopic niche and diet overlap does not seem to be likely. There were two instances of least cisco predation by salmon, but this likely does not indicate true niche overlap for reasons previously stated. Though the inconnu sampled in this study were considerably larger on average than chum salmon, small individuals have been recorded eating other fishes (Fuller 1955; Alt 1965). This dietary trait suggests that even if inconnu within the same size range as the salmon were sampled, they would still feature fish-dominated diets, while chum salmon feed opportunistically on prey that result in lower δ^{15}N ratios.

A limitation of this study was the unavailability of endemic fish samples in Great Bear Lake and Great Slave lake that overlapped temporally with salmon, with inconnu being caught several months prior to the arrival of salmon in Great Slave Lake in 2019, and lake trout in Great Bear Lake being from a different year and an slightly earlier seasonal timeframe than the salmon used for comparative stable isotope analyses. However, these results are still worthwhile starting points for comparative trophic analyses for salmon in the Arctic and these species, due to the fact that they were caught in the same habitats. Additionally, we assumed that the isotopic values from salmon heads did not differ from those of whole fish, where the muscle samples were taken from behind the dorsal fin.

Future directions

Future work regarding stable isotope research on salmon in the Arctic must be done to determine the effects of isotopic turnover. The isotopic turnover rate of adult chum salmon is not known, and the transition of salmon into spawning phase individuals additionally has unknown affects. Given that isotopes in muscle only turn over during periods of growth (Perga and Gerdeaux 2005), isotopic data in salmon may cease providing an accurate picture of trophic niche after the salmon stops growing and maintaining tissues as it devotes energy to spawning. It is also unknown how that would relate to salmon in the Arctic particularly, since the presence of feeding and digesting individuals indicates that tissue maintenance may still be ongoing while in Arctic freshwater systems like the Mackenzie drainage. A potential solution would be to utilize liver tissues, which are regulatory in nature and turn over continually (Perga and Gerdeaux 2005), and we recommend that future work investigates this further. Additionally, future work is needed to confirm that isotopic values do not differ significantly between dorsal muscle samples taken near the head or behind the dorsal fin.

There were several limitations in the use of stable isotopes for this study, due to its design. Water samples and primary produces were not sampled for a reference point regarding environmental δ^{15}N levels. This was due to the usage of archival samples submitted by community harvesters in remote locations from prior harvest years, making the collections of any type of sample other than fish tissues not feasible. This has the potential to skew stable isotope results and make drawing definitive conclusions regarding the niche space of the fishes sampled difficult. Likewise, lipid extractions were not performed on the fishes sampled, meaning a correction equation had to be used. While mathematical corrections are generally adequate, they are not necessarily the best fit for all types of tissues compared to chemical lipid extractions (Logan et al. 2008). Due to the caveats listed here and in the preceding paragraphs, it is difficult to make definite conclusions regarding trophic interactions between salmon and Arctic fishes, although this work may be used as a baseline for further study.

In order to fully understand the trophic niche and adaptation potential of chum salmon in the Canadian Arctic, marine diets must be documented. Chum salmon are opportunistic and highly adaptable marine feeders in their traditional range (Urawa et al. 2018), and it remains to be seen if they feed similarly in the Canadian Arctic Ocean. The isotopic niche space of salmon caught in the Mackenzie Delta is highly C^{13}-enriched, suggesting a heavily nearshore marine-influenced diet in fish that have recently entered the Mackenzie River system. Knowing how chum salmon react to the changes in sea conditions and prey availabilities in the Arctic marine environment will provide us a fuller picture of this species' adaptation potential by demonstrating how it responds to unpredictable and cold Arctic marine waters.

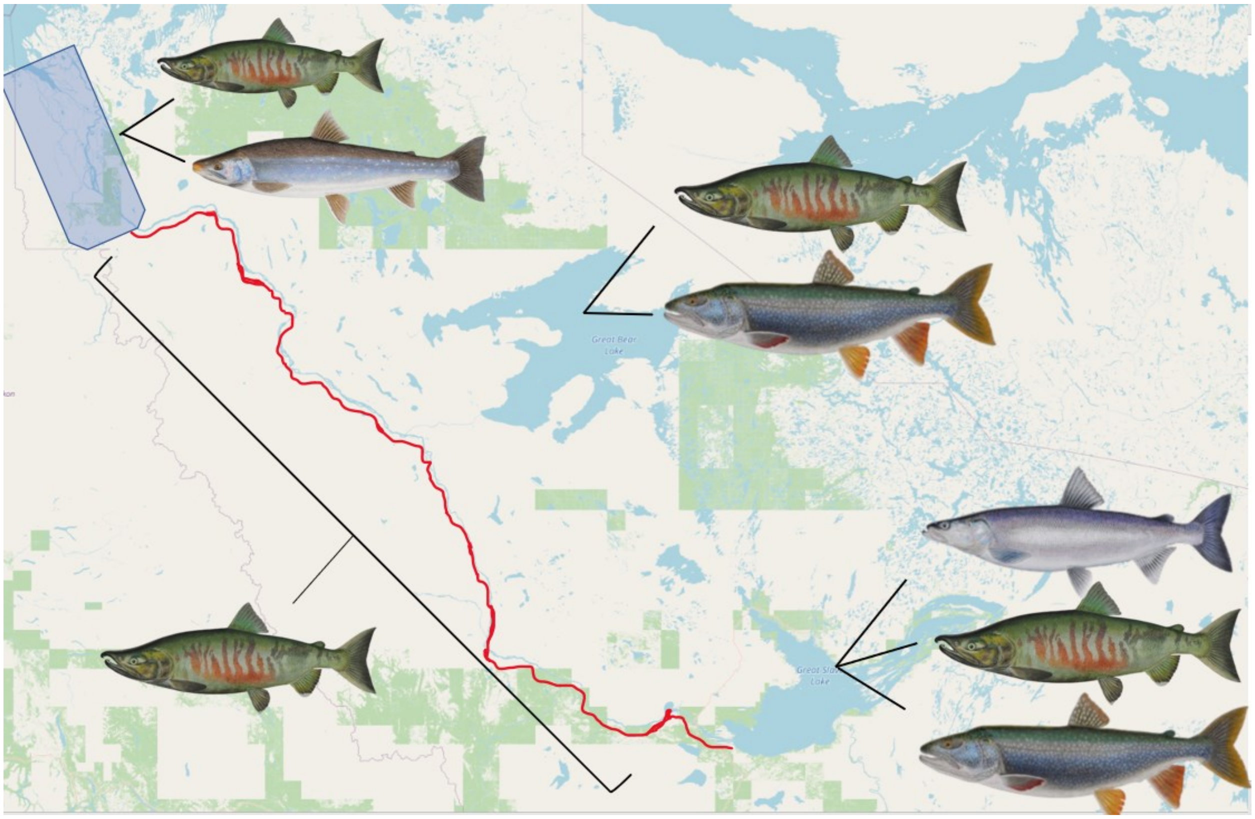


Figure 3.1: Map detailing the fish collected from the different regions of this study. Dolly Varden (*Salvelinus* malma) and chum salmon (*Oncorhynchus* keta) were collected from the Delta region (overlaid in blue); chum salmon were collected from the mainstem of the Mackenzie (approximated in red); lake trout (*Salvelinus namaycush*) and chum salmon were collected in Great Bear Lake; and those species, as well as inconnu (*Stenodus leucichthys*) were collected from Great Slave Lake.

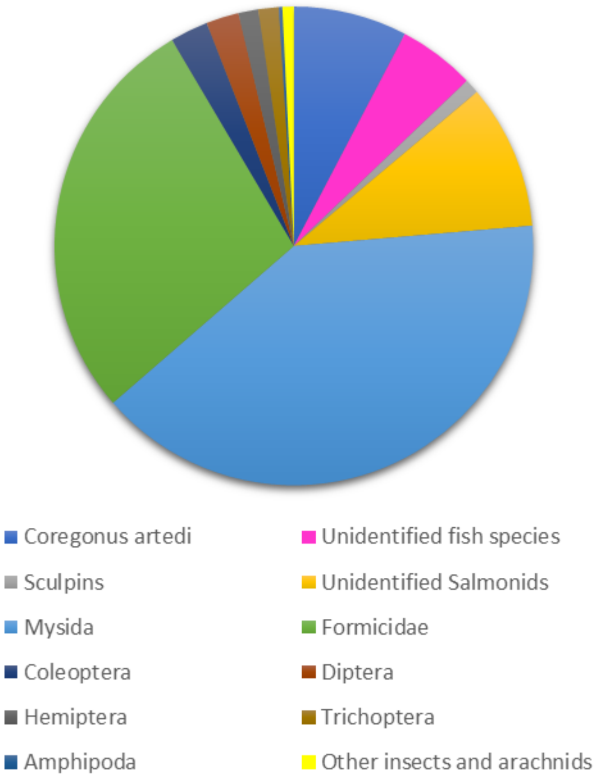
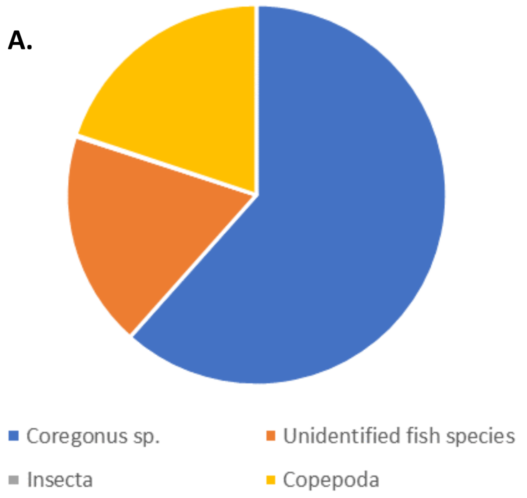


Figure 3.2: Stomach contents of lake trout (*Salvelinus namaycush)* caught in Great Bear Lake in 2017 by Index of Relative Importance (n = 9). Note: The category "Other insects and arachnids" is composed of Homoptera, Neuroptera, Odonata, Lepidoptera, Plecoptera, and unidentified insects and arachnids. "Sculpins" includes deepwater sculpin (*Myoxocephalus thompsonii*) and unidentified sculpins. Amphipods were present in the sample but made up too small of a portion to be visible



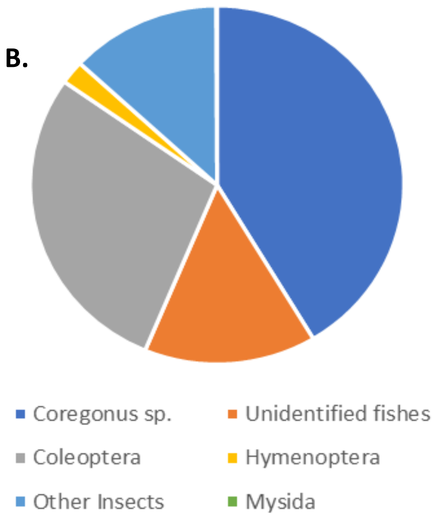


Figure 3.3a: Stomach contents of lake trout (*Salvelinus namaycush)* caught in Great Slave Lake in July, 2017 by Index of Relative Importance (n = 17). Note: The category "Insecta" is composed of Odonata and unidentified insects, making up too small of a portion to be visible.
Figure 3.3b: Stomach contents of lake trout (*Salvelinus namaycush)* caught in Great Slave Lake in August, 2019 by Index of Relative Importance (n = 8). Note: The category "Other insects" is composed of Diptera, Hemiptera, Trichopera and unidentified insects. Mysids were present in the sample but made up too small of a portion to be visible

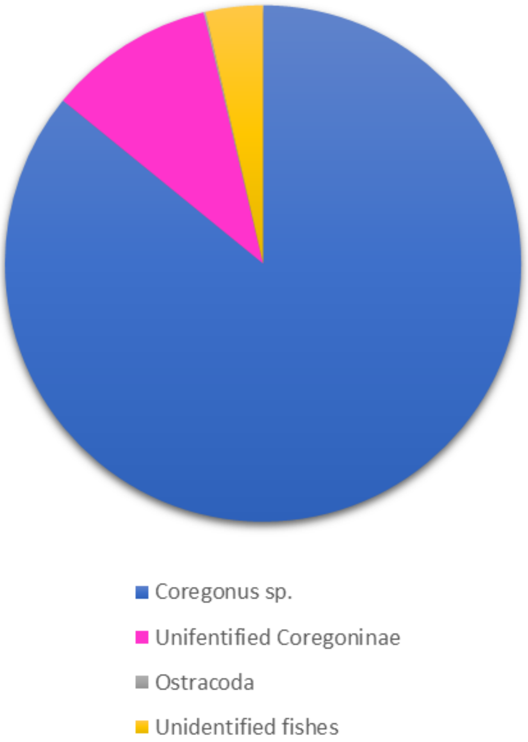


Figure 3.4: Stomach contents of inconnu (*Stenodus leucichthys)* caught in Great Slave Lake in 2019 by Index of Relative Importance (n = 11). Note: Ostracods were present in the sample but made up too small of a portion to be visible

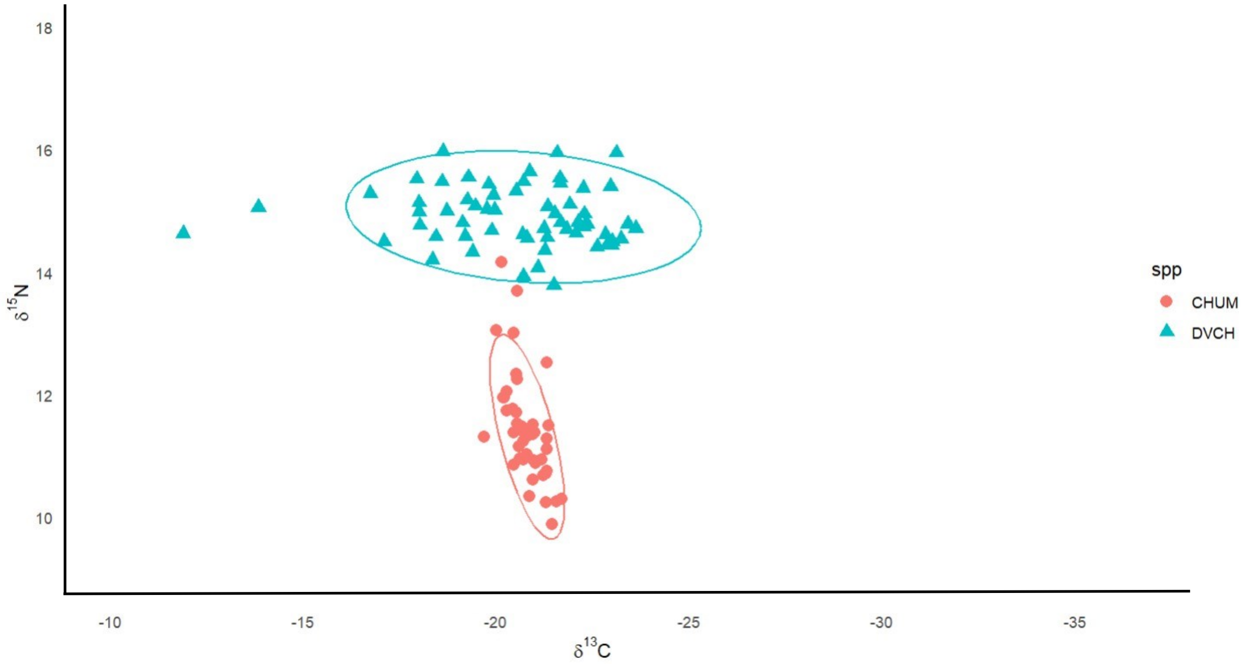


Figure 3.5: Isotopic niche space of chum salmon (*Onchorhynchus keta*) and Dolly Varden (*Salvelinus malma*) in the Mackenzie Delta in 2019

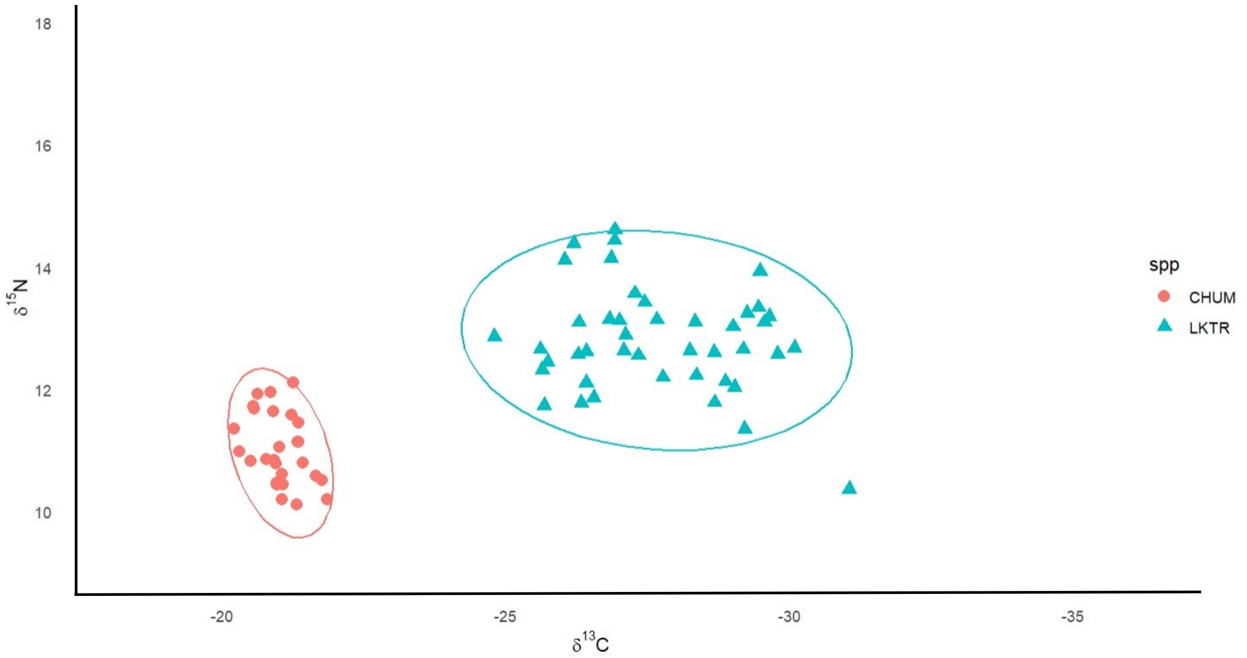


Figure 3.6: A comparison of the Isotopic niche space of chum salmon (*Onchorhynchus keta*) and lake trout (*Salvelinus namaycush*) in Great Bear Lake in 2019 and 2017, respectively. Although the samples were from different years, the two species were caught in the same habitat.

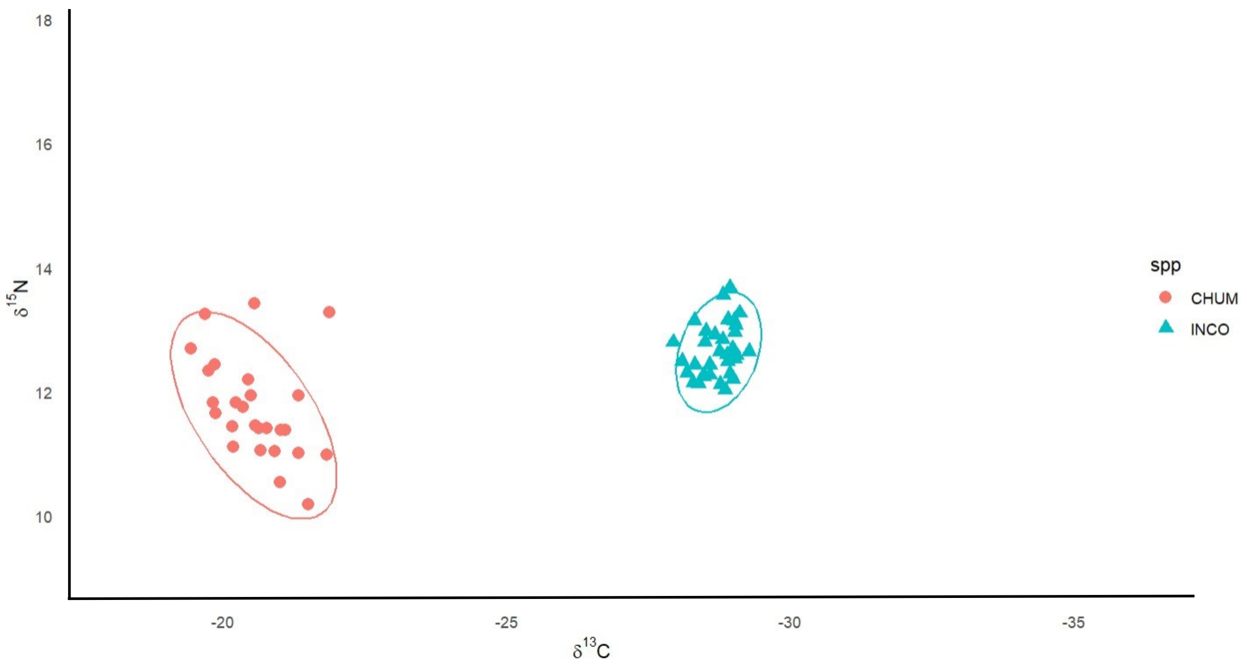


Figure 3.7: Isotopic niche space of chum salmon (*Onchorhynchus keta*) and inconnu (*Stenodus leucichthys*) in Great Slave Lake, 2019.

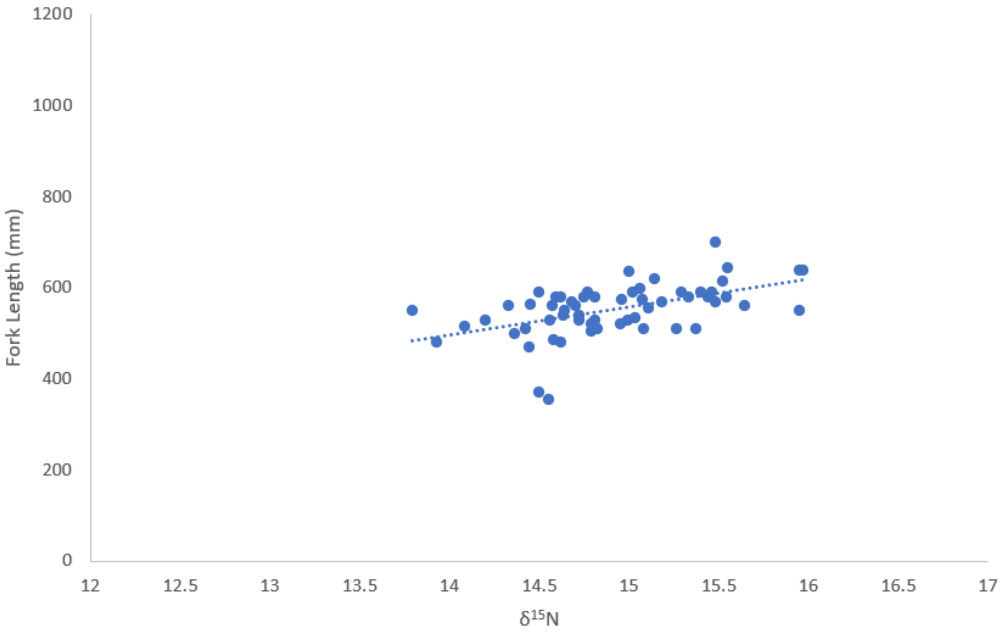


Figure 3.8: Fork length vs. trophic position of Dolly Varden (*Salvelinus malma*) caught in the Mackenzie Delta in 2019.

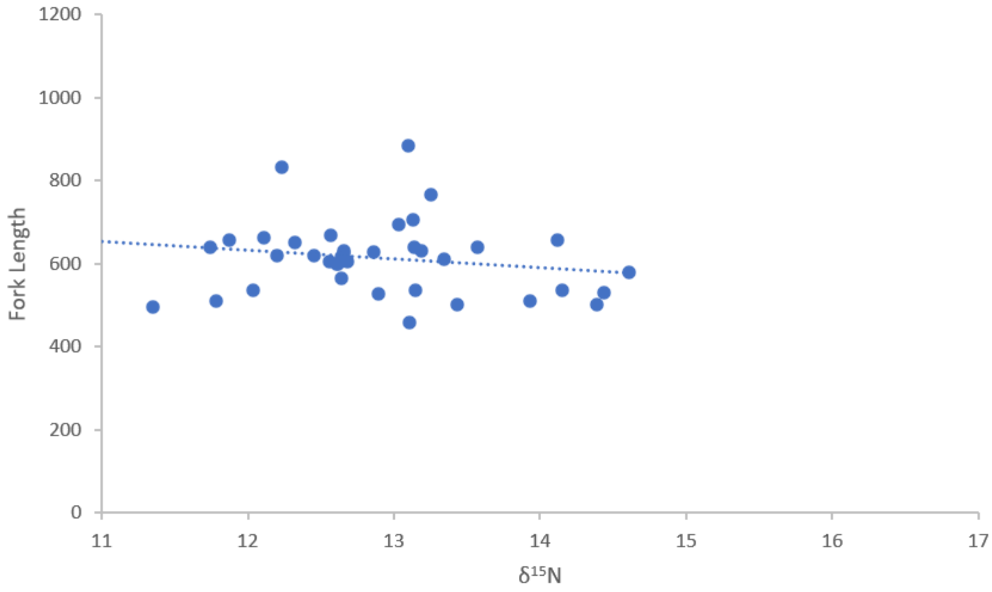


Figure 3.9: Fork length vs. trophic position of lake trout (*Salvelinus namaycush*) captured in Great Bear Lake in 2017.

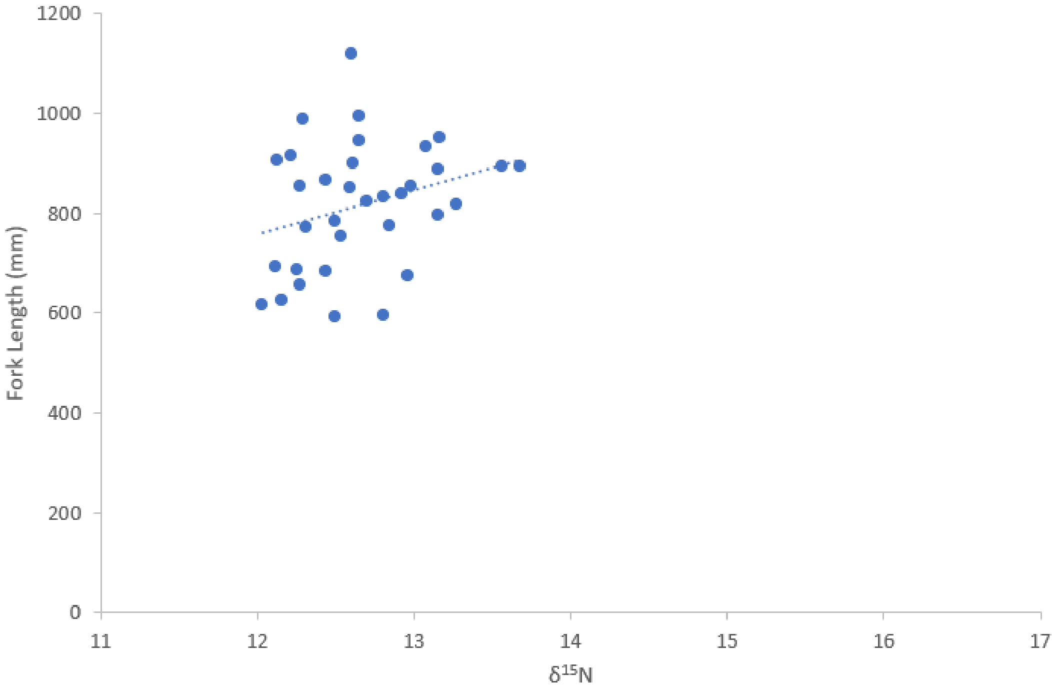


Figure 3.10: Fork length vs. trophic position of inconnu (*Stenodus leucichthys*) in Great Slave Lake, 2019.

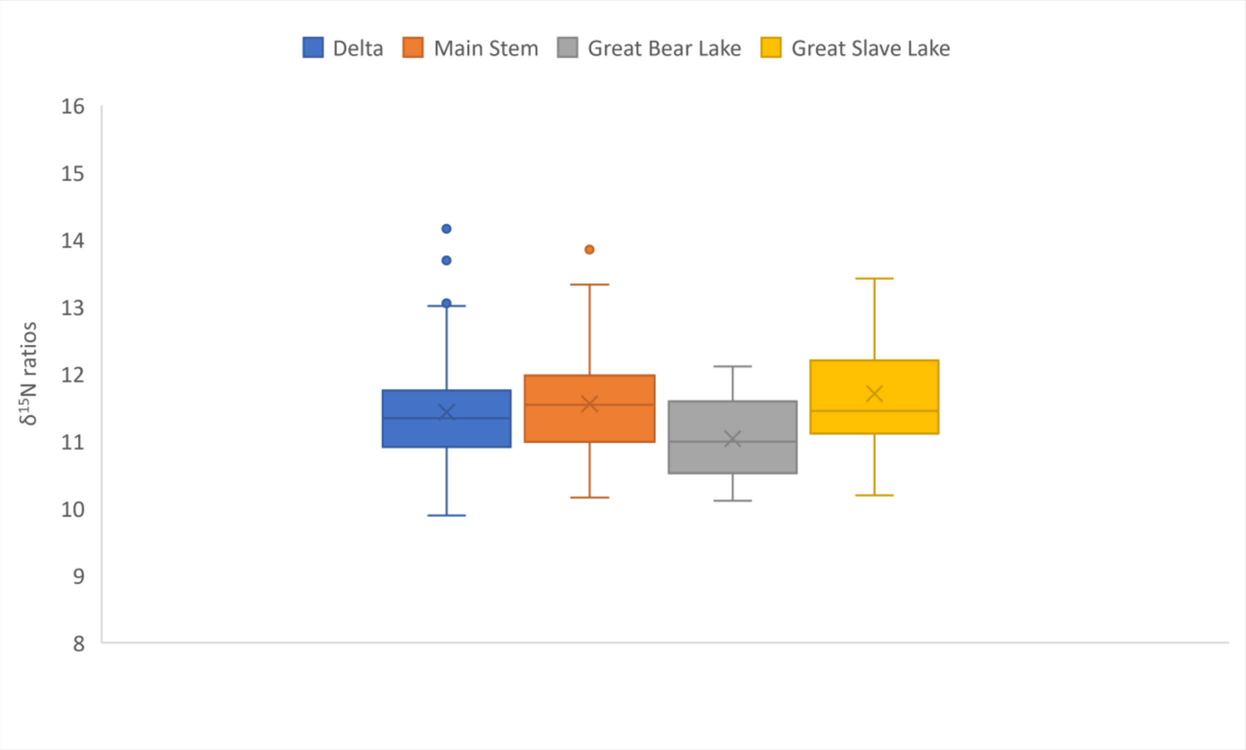


Figure 3.11: Differences in trophic position in chum salmon (*Oncorhynchus keta*) across the four regions studied. The trophic position of salmon caught in Great Bear Lake was significantly lower than the other regions.

Table 3.1: Catch data for all species sampled organized as male/female/unknown. Note: Fishes harvested in 2017 were used for stomach content analyses only, aside from Great Bear Lake lake trout, which were also used for stable isotope analyses.

Region	Species	2017	2019
Delta	Chum	12/6	17/17/11
	Dolly Varden	0	9/25 (Muscle only)
Great Bear Lake	Chum	5/3	26/5
	Lake trout	29/10 (Muscle and stomachs)	0
Mainstem	Chum	17/7	37/13/7
Great Slave Lake	Chum	9/2	18/9
	Inconnu	0	17/17
	Lake trout	9/8	3/5 (Stomachs only)

Table 3.2: Stomach contents of lake trout (*Salvelinus namaycush*) caught in Great Slave Lake in 2017 (n = 17) and 2019 (8)

	2017				2019			
Prey Organism	**%F**	**%N**	**%M**	**IRI**	**%F**	**%N**	**%M**	**IRI**
Fishes	100%	10.9%	95.6%	10646	100%	5.00%	60.6%	6516
Coregonus sp.	100%	9.40%	70.9%	8029	62.5%	5.00%	72.1%	4791
Unidentified fish remains	88.2%	1.60%	25.6%	2398	100%	n/a	18.5%	n/a
Insecta	29.4%	1.00%	0.500%	16.6	50.0%	92.4%	8.60%	5051
Odonata (Dragonflies and damselflies)	11.8%	0.600%	0.500%	12.9	n/a	n/a	n/a	n/a
Coleoptera (Beetles)	n/a	n/a	n/a	n/a	37.5%	84.3%	3.52%	3294
Dytiscidae (Predaceous diving beetles)	n/a	n/a	n/a	n/a	25.0%	3.00%	0.200%	80.8
Unidentified Coleoptera	n/a	n/a	n/a	n/a	25.0%	81.3%	3.32%	2115
Diptera (Flies)	n/a	n/a	n/a	n/a	12.0%	0.51%	0.007%	6.5
Hemiptera (True bugs)	n/a	n/a	n/a	n/a	12.5%	1.01%	0.02%	12.9
Corixidae (Water boatmen)	n/a	n/a	n/a	n/a	12.5%	1.01%	0.02%	12.9
Hymenoptera (Bees, wasps and ants)	n/a	n/a	n/a	n/a	25.0%	9.09%	0.700%	244
Formicidae (Ants)	n/a	n/a	n/a	n/a	12.5%	1.01%	0.04%	13.1
Unidentified Hymenoptera	n/a	n/a	n/a	n/a	12.5%	8.08%	0.660%	109
Trichoptera (Caddisflies)	n/a	n/a	n/a	n/a	12.5%	0.51%	0.0400%	6.9
Unidentified insects	29.4%	0.310%	0.003%	3.70	25.0%	n/a	4.35%	n/a
Crustacea	29.4%	88.2%	0.009%	2593	12.5%	0.510%	0.004%	6.40
Copepoda	41.8%	88.2%	0.009%	2593	n/a	n/a	n/a	n/a
Mysida	n/a	n/a	n/a	n/a	12.5%	0.510%	0.004%	6.40
Digested remains	11.8%	n/a	3.00%	n/a	37.5%	n/a	0.790%	n/a

Proportion of empty stomachs in total sample of fish captured in 2017: 0/17, and 2019: 0/8

Table 3.3: Stomach contents of lake trout (*Salvelinus namaycush*) caught in Great Bear Lake in 2019 (n = 9)

Prey Organism	% F	% N	% M	IRI
Fishes	88.9%	1.67%	29.7%	2785
Cottidae (Unidentified sculpins)	11.1%	0.440%	3.79%	47.0
Myoxocephalus thompsonii (Deepwater sculpin)	11.1%	0.110%	1.18%	14.3
Salmonidae	44.4%	0.440%	23.9%	1078
Coregonus artedi (Cisco)	22.2%	0.170%	21.2%	474
Unidentified fish/fish remains	88.9%	0.660%	3.44%	320
Arachnida	11.1%	0.110%	0.0150%	1.40
Insecta	77.8%	63.8%	3.56%	5236
Coleoptera (Beetles)	33.3%	2.65%	2.11%	158
Diptera (Flies)	55.6%	2.27%	0.190%	136
Chironomidae (Nonbiting midges)	44.4%	0.440%	0.0200%	20.4
Culicidae (Mosquitoes)	11.1%	0.110%	0.00700%	1.30
Hemiptera (True bugs)	33.3%	2.16%	0.310%	82.3
Corixidae (Water boatmen)	22.2%	0.220%	0.150%	8.20
Homoptera	22.2%	0.110%	0.00200%	2.50
Hymenoptera	33.3%	50.6%	1.43%	1731

Formicidae (Ants)	33.3%	50.3%	1.41%	1721
Vespidae (Wasps)	11.1%	0.280%	0.0200%	3.30
Lepidoptera (Moths & butterflies)	11.1%	0.500%	0.100%	6.70
Neuroptera (Lacewings)	11.1%	0.280%	0.0200%	3.30
Odonata (Dragonflies & demselfies)	11.1%	0.110%	0.580%	7.70
Plecoptera (Stoneflies)	11.1%	0.0600%	0.00400%	0.700
Trichoptera (Caddisflies)	22.2%	3.43%	0.420%	85.5
Unidentified insect remains	11.1%	0.0600%	0.00100%	0.700
Crustacea	66.7%	34.5%	3.01%	2500
Amphipoda	33.3%	0.440%	0.00700%	14.9
Mysida	66.7%	34.0%	3.00%	2469
Digested remains	88.9%	n/a	31.1%	n/a
Plant material	55.6%	n/a	0.0200%	n/a

Proportion of empty stomachs in total sample of fish captured: 1/10 (10%)

Table 3.4: Stomach contents of inconnu (*Stenodus leucichthys*) caught in Great Slave Lake in 2019 (n = 11)

Prey Organism	% F	% N	% M	IRI
Fishes	100%	98.0%	100%	19800
Coregoninae	100%	85.7%	78.6%	16434
Coregonus sp.	100%	75.5%	71.0%	14654
Unidentified fish remains	18.2%	12.2%	21.4%	611.7
Crustacea	9.10%	2.00%	0.000100%	18.5
Ostracoda	9.10%	2.00%	0.000100%	18.5
Digested remains	36.4%	n/a	0.300%	n/a
Plant material	9.10%	n/a	0.00300%	n/a

Proportion of empty stomachs in total sample of fish captured: 0/11

Table 3.5: Stomach contents of chum salmon (*Oncorhynchus keta*) caught in the Mackenzie Delta in 2017 (n = 15) and 2019 (n = 2)

	2017				2019			
Prey Organism	**%F**	**%N**	**%M**	**IRI**	**%F**	**%N**	**%M**	**IRI**
Fishes	26.7%	n/a	86.4%	n/a	50.0%	50.0%	42.9%	4643
Unidentified fish remains	26.7%	n/a	86.4%	n/a	50.0%	50.0%	42.9%	4643
Crustacea	0%	n/a	0%	n/a	50.0%	50.0%	21.4%	3571
Mysidcea	0%	n/a	0%	n/a	50.0%	50.0%	21.4%	3571
Digested remains	66.7%	n/a	3.47%	n/a	0%	0%	0%	0
Plant material	40.0%	n/a	10.1%	n/a	0%	0%	0%	0

Proportion of empty stomachs in total sample of fish captured in 2017: 4/19 (21.5%), and in 2019: 14/16 (87.5%)

Note: % N and therefore IRI was not able to be calculated for 2017 because none of the remains were enumerable.

Table 3.6: Stomach contents of chum salmon (*Oncorhynchus keta*) caught in Great Bear Lake in 2017 (n = 13) and 2019 (n = 1)

	2017				2019			
Prey Organism	**%F**	**%N**	**%M**	**IRI**	**%F**	**%N**	**%M**	**IRI**
Fishes	38.4%	n/a	3.07%	n/a	n/a	n/a	n/a	n/a
Unidentified fish remains	38.4%	n/a	3.07%	n/a	n/a	n/a	n/a	n/a
Crustacea	7.69%	n/a	0.480%	n/a	n/a	n/a	n/a	n/a
Malacostraca	7.69%	n/a	0.480%	n/a	n/a	n/a	n/a	n/a
Unidentified invertebrate remains	7.69%	n/a	>0.00100%	n/a	n/a	n/a	n/a	n/a
Insecta	n/a	n/a	n/a	n/a	100%	100%	100%	20000
Hemiptera (Corixidae)	n/a	n/a	n/a	n/a	100%	66.7%	72.9%	13957
Unidentified insect remains	n/a	n/a	n/a	n/a	100%	33.3%	27.1%	6045
Digested remains	61.5%	n/a	6.30%	n/a	n/a	n/a	n/a	n/a
Plant material	61.5%	n/a	90.2%	n/a	n/a	n/a	n/a	n/a

Proportion of empty stomachs in total sample of fish captured in 2017: 13/26 (50%), and 2019: 10/11 (91.0%)

Note: % N was not able to be calculated in the 2017 fish because none of the remains were enumerable.

Table 3.7: Stomach contents of chum salmon (*Oncorhynchus keta*) caught in Great Slave Lake in 2017 (n = 2, *Coregonus sardinella* was in the esophagus of the individual that ate it) and 2019 (n = 2)

	2017				2019			
Prey Organism	**%F**	**%N**	**%M**	**IRI**	**%F**	**%N**	**%M**	**IRI**
Fishes	100%	n/a	100%	n/a	50.0%	50.0%	99.9%	7500
Coregonus sardinella	50.0%	n/a	99.9%	n/a	50.0%	50.0%	99.9%	7500
Unidentified fish remains	50.0%	n/a	0.000700%	n/a	n/a	n/a	n/a	n/a
Unidentified Crustacea	n/a	n/a	n/a	n/a	50.0%	50.0%	0.00001%	2500

Proportion of empty stomachs in total sample of fish captured in 2017: 10/13 (77%) and 2019: 16/18: 89.0%

Note: % N was not able to be calculated in 2017 because none of the remains were enumerable aside from the single *C. sardinella*

Chapter 4: Conclusion & future directions

The second chapter of this thesis established the prevalence of generalist feeding strategies as an adaptation to the lack of diversity, productivity, and predictability inherent to Arctic systems. Through the systematic review of the trophic ecology of eight fish species, each relied upon by subsistence harvesters across the region, the necessity of adaptable diets, as well as the ability to partition resources or habitats in lakes is crucial. However, due to the more confined nature of lotic systems, partitioning of prey resources does not appear to occur. There is a near complete absence of diet data for northern fishes during winter months. The challenging conditions of Arctic regions constrain studies in temporal coverage to only the ice-free summer months. Lastly, this review highlights that bull trout, inconnu, and broad whitefish lack sufficient diet data regardless of season.

The third chapter focuses on chum salmon, which are expanding their presence in the Mackenzie River drainage. Driven by community concerns of trophic competition between chum salmon and endemic subsistence species, this chapter examines the specific trophic ecology of chum salmon and determines how this will fit into established trophic landscape of this system. Most notably, these chum salmon were seen to deviate from the established behaviour of all Pacific salmon, in fresh water. During spawning, the digestive systems of Pacific salmon typically degrade as energy is diverted towards reproduction (Quinn 2018) so they do not feed aside from some instances of egg consumption (Garner et al. 2009). Conversely, the salmon sampled for this study had largely intact digestive systems, with several having identifiable prey in their stomachs at the time of their capture, demonstrating opportunistic feeding throughout the study area, with freshwater feeding becoming slightly more common as distance from the sea increased. Despite this, culturally relevant fishes such as Dolly Varden, lake trout, and inconnu are not at apparent risk for trophic competition with chum salmon due to both the low frequency of freshwater feeding by chum salmon and their preference for nearshore carbon-enriched diets, as demonstrated stable isotope analyses. However, more thorough analyses on the trophic ecology of chum salmon in this system are needed to confirm this.

Overall, this thesis has laid out the trophic dynamics of important northern fishes and determined how an increasingly-prevalent, range-expanding Pacific salmon species fits into the trophic landscape of the Mackenzie River basin. Additionally, the adaptation potential of chum salmon in the novel Arctic environment was explored in changes from established life history characteristics such as the feeding and digestion of prey items in fresh water. This work aids in northern fisheries management in several ways. First, it provides the necessary background to monitor food availability for culturally relevant northern fish species. Secondly, it provides baseline data to aid in future management of chum salmon populations in the Northwest Territories by detailing the dietary needs of the species while in an Arctic freshwater system, as well as the potential interactions with endemic fishes. Finally, it allows managers to address community concerns regarding feeding competition between chum salmon and established northern fishes.

Future dietary studies on northern fishes should focus on ensuring an adequate baseline of information is established for all important subsistence species. Bull trout and broad whitefish remain heavily understudied throughout their Arctic ranges. While this study updated the literature regarding the diet and trophic position regarding inconnu in Great Slave Lake, significant knowledge gaps regarding the diet of inconnu in marine and riverine environments still exist. Trophic studies in the winter should also be conducted if possible, in order to provide a full span of temporal coverage to our understanding of fish diets. The logistical difficulties of scientific field studies in the winter may be able to be partially overcome with a larger focus on community-led research that utilizes samples collected by Indigenous harvesters who are on the land year-round.

Further work is necessary to identify the feeding habits of chum salmon in the Arctic marine environment, as this is a further potential avenue for competition with marine-dwelling forms of subsistence fishes such as inconnu, arctic char, whitefish, and Dolly Varden. While the stable isotope data presented in chapter three of the salmon captured in the Mackenzie Delta likely reflects marine feeding, the exact prey items consumed by chum salmon in the Beaufort Sea remain unknown. The relatively low trophic level of these salmon indicates a heavy invertebrate input, but the exact species need to be determined before competition with any Arctic marine species can be ruled out. Chum salmon are specialized to eat and process large quantities of invertebrate prey that is of poor individual nutritional quality (Urawa et al. 2018), which could induce a competitive effect on any endemic species that utilize the same prey species. Despite the discovery of some chum salmon feeding in fresh water in the Canadian Arctic, chum salmon still do the majority of their feeding at sea, which means there is still a large knowledge gap in the species' Arctic trophic ecology.

Future work should also expand to other salmon species caught in the Canadian Arctic – particularly pink salmon (*O. gorbuscha*) and sockeye salmon, as they are also increasingly being harvested in the western Canadian Arctic (Dunmall et al. 2021). Sockeye salmon are known to have a higher cold tolerance than other species of Pacific salmon (Welch et al. 1995), which indicates that they may feed in colder waters in the Arctic, nearer to sea ice. This may put them in competition with fish such as Dolly Varden, which often feed on sympagic amphipods near sea ice (Gallagher et al. 2021). The diets of pink salmon in the Canadian Arctic must be investigated as well. Work in northern Norway has demonstrated that, while pink salmon feed nearer to shore than Arctic char, there is still a moderate degree of dietary overlap (Bengtsson et al. 2023). Similar dynamics may occur in Canadian Arctic waters and need to be investigated in order to assess the potential for competition between the species. Finally, as efforts to monitor the potential reproduction of salmon in the Arctic continue, the potential for trophic competition between juvenile salmon and endemic fishes remains a concern, should reproducing populations be established. A single juvenile chum salmon that was captured on the Alaskan North Slope in 2017 exhibited a high degree of isotopic trophic overlap with co-occurring Arctic cisco (*C. autumnalis*) juveniles (Dunmall et al. 2022).

Summary of suggested future directions:

1) Ensure baseline year-round diet data is known for all important Arctic subsistence species.
2) Determine the marine diets of chum salmon in the Canadian Arctic in order to fully understand the trophic ecology of the species in Arctic environments,
3) Investigate the trophic ecology of other salmon species being caught across the Canadian Arctic in increasing numbers, such as pink salmon and sockeye salmon.
4) Monitor for successful salmon reproduction in the Arctic, in order to determine the potential for trophic competition between juvenile salmon endemic fishes.

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