Spatiotemporal variation in anadromous Arctic char (*Salvelinus alpinus*) foraging ecology and its influence on muscle pigmentation along western Hudson Bay, Nunavut, Canada

by

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Abstract

Climate-induced alterations to Arctic sea ice dynamics are influencing the availability and distribution of resources, and in turn, the nutrient and energy intake of opportunistic predators across the food web. These temporal changes in local prey communities likely influence the availability of carotenoid-rich prey types, as well as the foraging ecology of opportunistic predators that forage in the marine environment, such as anadromous Arctic char (*Salvelinus alpinus*). Despite its socioeconomic importance across its range, anadromous Arctic char foraging ecology and its influence on muscle pigmentation, particularly in relation to sea ice dynamics, remains understudied. Here, over two years (2021, 2022) with contrasting sea ice dynamics, I investigated the foraging ecology of anadromous Arctic char and its influence on their muscle pigmentation at a southern (Rankin Inlet) and northern (Naujaat) location along western Hudson Bay using a combination of stomach contents, stable isotopes ($\delta^{13}C$ and $\delta^{15}N$), highly branched isoprenoids, carotenoid spectrophotometry, and a standard muscle colour scale (DSM SalmoFan). Spatiotemporal variation in Arctic char diet occurred, where Rankin Inlet Arctic char generally consumed more fish and phytoplankton-based carbon sources, occupied a higher trophic position, and displayed a similar isotopic niche breadth compared to Arctic char in Naujaat. Invertebrates were higher in carotenoid concentration than fishes, and in association with a more invertebrate-based diet, Arctic char in Naujaat contained higher muscle carotenoid concentrations (e.g., astaxanthin) compared to Rankin Inlet Arctic char in 2021. In 2022, however, muscle carotenoid concentrations in Naujaat and Rankin Inlet Arctic char were more similar, as the diet of Arctic char in both locations was largely fish-based despite muscle colour remaining redder in Naujaat Arctic char.

Overall, the observed plastic foraging ecology of Arctic char highlights this species' ability to adjust to inter-annual variability in environmental changes, which then impacts their muscle carotenoid concentration. Such inter-annual variation in Arctic char foraging ecology is anticipated to increase with unpredictable climate-driven environmental changes in the region, which could therefore negatively affect local resource users over the long term, resulting in socioeconomic impacts across the Arctic.

Dedication

To my Grampa, “Red” Faulkner, for instilling me with a passion for the outdoors from a young age. You are deeply missed, but never forgotten.

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Contributions of Authors

This thesis is formatted a grouped manuscript, with Chapter 2 containing material from a journal article that is currently in review. Following are the author contributions for Chapters 2 and 3:

Connor Faulkner (thesis author): conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing – original draft.

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

Gail Davoren: conceptualization, methodology, supervision, writing – review & editing.

Les Harris: conceptualization, funding acquisition, methodology, writing – review & editing.

Sonny Ittinuar: investigation.

Clayton Tartak: conceptualization, funding acquisition, investigation, methodology.

Vincent L'Herault: conceptualization, funding acquisition, methodology.

Thesis Format

This thesis is formatted as a grouped manuscript. Chapter 1 provides a general introduction and background information relevant to the studies. Chapters 2 and 3 are separate manuscripts written with an individual abstract, introduction, materials and methods, results, discussion, conclusion, acknowledgements, references, tables, and figures. Chapter 4 provides a general conclusion of the studies and summarizes conclusions from Chapters 2 and 3, as well as addresses socioeconomic implications and future research stemming from the studies.

Chapter 1 General Introduction

1.1 Context

Food webs are comprised of numerous inter-linked predator-prey relationships that connect primary producers to top predators, resulting in the flow and cycling of energy throughout an ecosystem (Elton, 1927; MacArthur, 1955; Frederiksen et al., 2006). These predator-prey interactions are typically compartmentalized with boxes and arrows that can vary in size based on their frequency and strength of interaction, creating a network of both strong and weak links between species within a food web (Stouffer and Bascompte, 2011). Further, predation and competition for resources, both within and between species, can influence species interactions within ecosystems and contribute to the structuring of ecological communities (Kotler and Holt, 1989). As a result, such relationships within systems can influence species distribution and abundance, in turn causing a re-wiring of the topological structure and interaction strength of energy flow both within and across systems (Bartley et al., 2019).

Trophic omnivory and ontogenetic niche shifts can also cause variation in a species' foraging ecology, as well as overall ecosystem structure. Trophic levels describe the discrete, integer-based flow of energy within a food web from primary producers to top predators (Lindeman, 1942), which is complicated due to trophic omnivory, whereby an individual feeds at more than one trophic level within a system (Pimm and Lawton, 1978; Thompson et al., 2007). Ontogenetic niche shifts refer to the changes in resource use (e.g., foraging, habitat) of a species as individuals increase in age and/or size; a phenomenon common among animal taxa and especially well-documented among fish species (Werner and Gilliam, 1984). Such shifts create unique connections among species at various life stages which further structure local communities (Werner and Gillian, 1984; Nakazawa, 2014). As a result of trophic omnivory, species are better suited to be assigned a trophic position, which describes the continuous, non-integer-based flow of energy and provides a more accurate representation of the actual species interconnectedness within a food web (Vander Zanden and Rasmussen, 1996; Thompson et al., 2007). Further, the ecological niche of a species is defined as an "*n*-dimensional hypervolume" (Hutchinson, 1957) that outlines the suitable conditions and requirements for a species to grow, survive, and reproduce (Hutchinson, 1957; Pulliam, 2000).

Predator-prey interactions may also vary both spatially and temporally within populations due to spatiotemporal differences in prey distribution and abundance, as resources are typically not distributed uniformly in the environment and are influenced by changing environmental conditions (MacArthur and Levins, 1964; van Langevelde and Prins, 2008). Multiple models within foraging theory have predicted how individuals should respond to such heterogenous distribution of resources within the environment, including the diet width model and marginal value theorem. The diet width model generally predicts that individuals would increase their fitness by consuming a prey type that they encounter as long as the net energy gain of consumption is higher than that of their current diet (MacArthur and Pianka, 1966; Nunn et al., 2012; Kowalczyk et al., 2015). Additionally, the marginal value theorem predicts that an individual should forage in a resource patch until their rate of intake in that patch diminishes to the average rate of all patches within a habitat (Pyke et al., 1977). Overall, the foraging behaviour of a species should follow predicted resource use and rates of intake when resources are unevenly distributed within a given environment to maximize fitness.

The removal or addition of a species can also have cascading effects within an ecosystem, causing changes in resource distribution, abundance, and ultimately community structure (Paine, 1966; Vander Zanden et al., 1999). These changes in biodiversity could further influence the prey selection and diet composition of consumers, leading to potential shifts in diet (e.g., Vander Zanden et al., 1999; Dempson et al., 2002; Gaston et al., 2003) and ultimately body condition and recruitment success of individuals within a population (Nunn et al., 2012; Harwood et al., 2015). Therefore, quantifying spatial and temporal variation in diet is important to obtain information on a species' foraging ecology, which inform variations in species interactions that underly ecosystem structure and functioning, especially within rapidly changing environments (Yurkowski et al., 2016; Bartley et al., 2019).

Environmental change is rapidly occurring across the Arctic, resulting in drastic decreases in sea ice concentration and snow cover as a result of increasing sea and air temperatures (Gagnon and Gough, 2005; Gaston et al., 2012; IPCC, 2023). Collectively, these changes are having a profound effect on sea ice extent and phenology across Arctic marine habitats (Arrigo, 2014; IPCC, 2023). Such changes have altered the phenology and rates of Arctic marine primary production, impacting the amount of annual sea ice algae and pelagic phytoplankton production (Moore and Huntington, 2008; Frainer et al., 2017). In turn, these changes are providing conditions more suitable for subarctic-associated species that are more dependent on phytoplankton-derived carbon sources (e.g., capelin, *Mallotus villosus*), while potentially having negative consequences for Arctic endemic species (e.g., Arctic cod, *Boreogadus saida*; Moore and Huntington, 2008; Frainer et al., 2017). In the Arctic, higher trophic level consumers have historically relied on Arctic cod and ice-associated invertebrates (e.g., *Onisimus* spp., *Themisto* spp.; Gaston et al., 2003; Chambellant et al., 2013; Ulrich and Tallman, 2021) as their main prey sources. As a result, Arctic environments are disproportionately experiencing a northward shift in more subarctic-associated species (i.e., the "borealization" of the marine environment), leading to alterations in species interactions, distributions, and abundances (Fossheim et al., 2015; Kortsch et al., 2015; Yurkowski et al., 2017). As Arctic ecosystems are extremely vulnerable to such abrupt environmental shifts (IPCC, 2023), observed impacts on endemic species have included reductions in range, abundance, body condition, recruitment and survival, as well as shifts in diet (Gaston et al., 2003; Harwood et al., 2015; Ferguson et al., 2017).

In contrast, numerous subarctic species have benefitted from these climatic changes, such as the capelin. Capelin appear to have increased their abundance in several areas across the Canadian Arctic as documented through an increased prevalence within the diet of near-top trophic level predators (e.g., Gaston et al., 2003; Chambellant et al., 2013; Ulrich and Tallman, 2021). As many Arctic species have historically relied on highly abundant prey endemic to northern ecosystems (e.g., Arctic cod, ice-associated invertebrates; Gaston et al., 2003; Chambellant et al., 2013; Ulrich and Tallman, 2021), the introduction of new competitors, such as more subarctic-associated prey fish and invertebrates have the potential to cause bottom-up cascading effects throughout the marine ecosystem (Rose, 2005; Chambellant et al., 2013). Such shifts in resources are expected to vary spatially in response to sea ice dynamics, whereby southern locations below the Arctic Circle (66° N) are expected to be ice free longer than locations to the north (Tedesco et al., 2019), providing favourable conditions for more subarctic-associated species to increase their abundance in southerly extents of the Canadian Arctic. Therefore, ecosystem-level responses to altered species distributions and abundances may be examined by monitoring the diet of opportunistic, generalist predators that can act as sentinels in determining ecosystem-wide changes in resource availability and how these changes may vary over space and time.

1.2 General Biology of Arctic char

The Arctic char (*Salvelinus alpinus*) is the northernmost freshwater fish species, with a distribution spanning the circumpolar Arctic (Sprules, 1952; Johnson, 1980; Klemetsen et al., 2003) and have been central to the culture, economy, food security, and health of Inuit, who have relied on this species for millennia (Government of Nunavut, 2018; Harris et al., 2020). Arctic char are facultatively anadromous (Moore et al., 2016), exhibiting landlocked, freshwater resident, and anadromous forms (Johnson, 1980; Dempson and Kristofferson, 1987; Moore et al., 2014). Anadromous forms of Arctic char migrate from freshwater to marine environments to forage for approximately 30-60 days during the summer months on abundant food resources in nearshore, coastal habitats (Johnson, 1980; Dempson and Kristofferson, 1987; Moore et al., 2016). During the marine foraging period, rapid growth and energy accumulation occurs, whereby individuals can double their weight in just over a month (Dempson et al., 2002; Klemetsen et al., 2003; Rikardsen et al., 2007) while concurrently increasing lipid reserves up to five-fold (Jørgensen et al., 1997). Indeed, this marine residency is a critical period for Arctic char, as they must accumulate enough resources to sustain themselves throughout the overwintering period in low-productivity freshwater lakes where foraging activity is typically low (Moore and Moore, 1974; Harris et al., 2020; Ulrich and Tallman, 2021).

Within the marine environment, anadromous Arctic char are opportunistic, generalist foragers who consume a wide range of prey types (Dempson et al., 2002; Ulrich and Tallman, 2021), including numerous crustaceans (e.g., *Themisto* spp., *Mysis* spp., *Onisimus* spp., *Gammarus* spp.), forage fish (e.g., capelin, sand lance (*Ammodytes* spp.), sculpins (Cottidae; e.g., *Triglops* spp. and *Myoxocephalus* spp.), cod (Gadidae; e.g., Arctic cod)), polychaetes, and insects (Moore and Moore, 1974; Dempson et al., 2002; Spares et al., 2012; Harwood et al., 2015). Spatial variation in Arctic char diet has been associated with variation in prey abundance along the northern Labrador coast, where southern populations fed heavily on forage fish including capelin and sand lance, while northern populations were more reliant on invertebrates and sculpins (Dempson and Kristofferson, 1987; Dempson et al., 2002). In addition, long-term temporal changes in Arctic char diet in northern Labrador, the Beaufort Sea, and Cumberland Sound populations have shown shifts from a primarily invertebrate-based to a largely forage fish-based diet (Dempson et al., 2002; Harwood et al., 2015; Ulrich and Tallman, 2021), which is likely related to changes in prey distribution and abundance (Johnson, 1980; Dempson et al., 2002). This variability in Arctic char diet and consumption of carotenoid-rich prey types (e.g., crustaceans) may influence muscle pigmentation (Klemetsen et al., 2003), which is known to vary among populations, typically falling into white, pink, or red muscle categories (Andrews and Lear, 1956; Government of Nunavut, 2018).

Examining the influence of Arctic char diet on muscle pigmentation is important to link muscle colour to nutritional quality for humans and, thus, has socioeconomic implications. Across the Canadian Arctic, Inuit have a preference for red-muscle Arctic char (Bovin and Power, 1990), as it is said to be richer in flavour and provide higher human nutritional quality (e.g., antioxidants, vitamin A). Red-muscle pigmentation is also typically the most important characteristic to assess the human consumptive quality and determine the economic value of salmonids (Hatlen et al., 1998; Rahman et al., 2016). Therefore, red-muscle Arctic char are economically preferred by consumers and can be prepared and marketed as higher value products (i.e., fillets) than individuals with paler muscle (i.e., smoked products; S. Sadler, Kivalliq Arctic Foods manager, pers. comm.). Due to Arctic char being a key subsistence and economic resource to Inuit (Sprules, 1952; Government of Nunavut, 2018), studying the factors that influence their muscle pigmentation is necessary to examine potential socioeconomic implications across the Arctic, especially as climate change continues to impact the resources they rely on.

Despite Arctic char being a key subsistence and economic resource for Inuit (Sprules 1952; Government of Nunavut 2018), their foraging ecology and muscle pigmentation in relation to environmental variability (e.g., sea ice dynamics) has not been investigated across their range. Along the western Hudson Bay coast in the territory of Nunavut, more southern locations, such as near the community of Rankin Inlet (at 62^{o}N) generally have more ice-free days during the summer months (June to September) and therefore are less influenced by sea ice relative to more northern locations, such as Repulse Bay near the community of Naujaat (at 66^{o}N; Gupta et al. 2022). As a result, resource availability and abundance likely differ between the Rankin Inlet and Naujaat areas, in turn influencing the potential fish and invertebrate prey species composition. Therefore, this geographic location is ideal for studying spatial and temporal variation in Arctic char foraging ecology and muscle pigmentation in response to sea ice dynamics across the region.

1.3 Stomach Contents

Analyzing fish diet through the examination of stomach contents is a widely adopted practice, and is useful for identifying and quantifying prey types of dietary importance (Hyslop, 1980; Matley et al., 2015). The classification of prey items to the lowest taxonomic level and enumeration into metrics of number, weight, and occurrence have been commonly used to analyze stomach contents (Moore and Moore, 1974; Hyslop, 1980; Dempson et al., 2002; Spares et al., 2012). These metrics, which are typically quantified as the percentage of the total individuals of a certain prey type compared to the overall diet, are commonly expressed as percent number (%N), percent weight (%W) and percent frequency of occurrence (%O; Hyslop, 1980; Ulrich and Tallman, 2021). Additionally, the index of relative importance (IRI) for each prey type may be calculated by combining the values of %N, %W, and %O to express the importance of a discrete prey type or category (Liao et al., 2001; Grimaldo et al., 2009). Further, stomach fullness indices have been used to examine temporal changes in foraging activity (Hyslop, 1980; Cote et al., 2021). In numerous studies, these methods have assisted in uncovering both spatial and temporal variation in diet among fish populations (e.g., Dempson et al., 2002; Cote et al., 2021; Ulrich and Tallman, 2021).

Schoener's diet overlap index (Schoener's index) is another common metric used to examine stomach content data. Schoener's index is used to calculate the percent of diet overlap between two groups with potentially similar niche dynamics (Schoener, 1970). A Schoener's index alpha (α) value of 0 indicates no dietary overlap, an α value of 1 indicates complete dietary overlap, and an α value > 0.60 represents biologically significant diet overlap between two groups (e.g., study sites; Enders et al., 2020). Additionally, non-metric multidimensional scaling (NMDS), a type of non-parametric multivariate analysis that examines the similarity among groups, has been used to examine stomach content data. The goodness of fit for the NMDS data is reported using a stress value, whereby a value < 0.05 indicates an excellent fit, a value < 0.1 indicates good fit, and a value < 0.2 is still moderately fit although likely to provide misleading interpretations (Clarke, 1993).

Although stomach contents provide insight into the top prey species consumed by an individual or population, this method of dietary analysis is limited by rapid digestion rates of prey and typically only provides dietary information shortly before capture of the consumer, which may not reflect the general diet over space and time (Chambellant et al., 2013; Matley et al., 2015; Ulrich and Tallman, 2021). As a result, pairing stomach content analysis with stable isotope analysis and highly branched isoprenoid analysis is a powerful way of further examining diet on a broader spatial and temporal scale (Brown et al., 2013; Chambellant et al., 2013; Ulrich and Tallman, 2021).

1.4 Stable Isotopes

Stable isotope analysis provides space- and time-integrated information on the diet and habitat use of a consumer inferred from the chemical composition of various tissues (Fry et al., 1978; Peterson and Fry, 1987; Layman et al., 2012). The most common stable isotope ratios employed in ecological studies are $^{13}C/^{12}C$ and $^{15}N/^{14}N$, which are represented as the ratio of the heavy to light isotope in a sample against a reference standard and expressed as per mil (‰) in delta (δ) notation:

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

where X is ^{13}C or ^{15}N and R represents $^{13}C/^{12}C$ ($\delta^{13}C$) or $^{15}N/^{14}N$ ($\delta^{15}N$; Peterson and Fry, 1987; Post et al., 2007; Layman et al., 2012). Reference standards used are Vienna Peedee Belemnite (VPDB; carbon) and atmospheric nitrogen (N_2/AIR; nitrogen). The $\delta^{13}C$ values indicate the carbon source use of the prey of a consumer, as these ratios can differ among primary producers using different photosynthetic pathways (e.g., C_3 versus C_4 plants) and generally only increase slightly with trophic transfer (~1.0‰ enrichment; DeNiro and Epstein, 1978; Peterson and Fry, 1987; Vander Zanden and Rasmussen, 2001; Layman et al., 2012). The $\delta^{15}N$ values are typically used to indicate the trophic position of a consumer, as consumer tissues are typically enriched in ^{15}N relative to their prey by approximately 3.4‰ at each trophic step (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 1999; Vander Zanden and Rasmussen, 2001; Layman et al., 2012). Using constant trophic enrichment values, however, tends to bias trophic structure by underestimating the trophic position of top predators and dwarfing food chain length (Hussey et al., 2014).

A number of factors influence the isotopic composition of a consumer relative to their prey, including trophic fractionation, lipids, tissue turnover rates, and spatiotemporal variation in prey baseline ratios, and thus must be considered to accurately reconstruct diets using stable isotope analysis. Isotopic fractionation occurs when a consumer metabolizes and assimilates prey stable isotopes into its tissues, which causes an alteration in the ratio of heavy versus light isotopes in the consumer (Peterson and Fry, 1987; Post et al., 2007). Using a scaled enrichment approach and multiple tissue-specific diet-tissue discrimination factors allow prey and consumer stable isotope ratios to be compared for dietary reconstruction by accounting for variation in isotopic values between a consumer and its prey types (Caut et al., 2009; Hussey et al., 2014). Additionally, lipids vary in concentration among tissue types (e.g., liver versus muscle) and tend to be ^{13}C depleted compared to proteins and carbohydrates, biasing the δ^{13}C values of analyzed tissues (DeNiro and Epstein, 1978; Post et al., 2007). As a result, the presence of lipids must be accounted for through chemical lipid extraction or mathematical normalization, which provides standardized lipid corrected values for analysis (Post et al., 2007). As the chemical extraction process can influence δ^{15}N values, mathematical corrections of δ^{13}C allow the integrity of δ^{15}N to be preserved (Post et al., 2007). Further, different tissue types have characteristic turnover rates within an organism, and thus provide dietary information across multiple temporal scales (Peterson and Fry, 1987; Layman et al, 2012; Marcoux et al., 2012). Differential tissue turnover rates occur due to variable metabolic activities of tissues that dictate the rate of new tissue generation through growth and catabolic turnover processes (Grey, 2000; Vander Zanden et al., 2015). As catabolic turnover processes within tissues are closely linked to protein turnover rates, structural tissues (e.g., muscle) tend to have a slower turnover rate than other more metabolically actives tissues (e.g., liver; Tieszen et al., 1983; Waterlow, 2006; Vander Zanden et al., 2015; Canseco et al., 2021). Tissues with a higher turnover rate (e.g., liver) generally provide dietary information over the short-term (e.g., days to weeks; Tieszen et al., 1983; MacNeil et al., 2006), while tissues with a slower turnover rate (e.g., muscle) generally provide dietary information over a longer period (e.g., one to several months; Tieszen et al., 1983; MacNeil et al., 2006). Finally, isotopic composition may be influenced by variation in prey isotopic ratios (i.e., primary consumers at trophic position = 2), which are known to vary spatiotemporally (Post, 2002; Matthews and Mazumder, 2004; Smith et al., 2021). Therefore, isotopic baseline corrections of consumers should be conducted by subtracting the isotopic ratios of primary consumers from the isotopic ratios of upper-level consumers to more accurately represent local food web structure when comparing isotopic ratios between locations (Post, 2002; Black and Armbruster, 2021; Smith et al., 2021).

1.5 Highly Branched Isoprenoids

The use of highly branched isoprenoid diatom lipid biomarker analysis also allows the examination of the foraging ecology of marine organisms to provide insight into Arctic food web interactions, specifically allowing differentiation between the use of sea ice algae and phytoplankton carbon sources (Brown and Belt, 2012A; Brown et al., 2013). Numerous highly branched isoprenoid lipids are produced by specific marine diatoms (Brown et al., 2013; Brown et al., 2014) and have been detected within the tissues of both primary and upper-level consumers (specifically liver), outlining the unaltered trophic transfer of these lipids (Brown and

Belt, 2012A; Brown et al., 2013; Brown et al., 2014). Certain lipid biomarkers, such as IP_{25} and IIb are representative of foraging on sea ice-derived carbon resources (Brown and Belt, 2012A; Brown and Belt, 2012B; Brown et al., 2013; Brown et al., 2014), while others including trienes III a-d are representative of foraging on phytoplankton-derived carbon resources (Brown et al., 2013; Brown et al., 2014). Therefore, one is able to quantify the proportion of sea ice-derived or phytoplankton-derived carbon resource use within a consumer using the values of sea ice-derived or phytoplankton-derived lipids to calculate their H-Print and ice particulate organic carbon (iPOC) values (Brown et al., 2013; Brown et al., 2014; Brown et al., 2018).

Species utilizing various carbon pathways within the environment (e.g., anadromous Arctic char), such as the benthos (e.g., ice algae-derived resources) or the pelagic environment (e.g., phytoplankton-derived resources) also likely influences their muscle pigmentation (Bolduc et al., in press).

1.6 Carotenoid Pigments

Carotenoids, which are only obtained via consumer diet, are a common group of natural pigments that are synthesized by all plants and select microorganisms (Goodwin, 1986). These pigments are beneficial to the health and fitness of an organism as they play an important role in treating diseases and acting as precursors for retinol (vitamin A) within certain groups of animals (e.g., salmonids; Goodwin, 1986). Carotenoids are also responsible for pigmentation of the skin, which in some taxa, are important for attracting mates prior to reproduction (Schiedt et al., 1985; Rajasingh et al., 2007). Fish species in the family Salmonidae exhibit muscle pigmentation that typically falls along a pink-red colour gradient, primarily due to variation in the accumulation and assimilation of carotenoids present in the tissues of their crustacean prey types (Choubert and Blanc, 1993; Rajasingh et al., 2007). Astaxanthin, the carotenoid largely responsible for the red pigmentation of salmonid muscle, is known to be highly variable within and among salmonid populations and provides many fitness and nutritional benefits, including improved immune functioning, vision, mating success, gamete and offspring quality, and it can also act as an antioxidant and precursor for vitamin A (Christiansen et al., 1995; Rajasingh et al., 2007; Garner et al., 2010; Lehnert et al., 2016; Lehnert et al., 2017). The relationship between increased dietary carotenoid concentrations and carotenoid concentrations within salmonid muscle contributing to a redder colour of the muscle has been widely investigated in aquaculture (e.g., Olsen and Mortensen, 1997; Hatlen et al., 1998; Rajasingh et al., 2006; Rahman et al., 2016; Cankiriligil et al., 2022), but has seldom been studied among wild anadromous species. Muscle pigmentation is also of human interest, as red pigmented muscle is typically the most important characteristic to assess the human consumptive quality and determine the economic value of salmonids (Hatlen et al., 1998; Rahman et al., 2016). Further, Across the Canadian Arctic, Inuit have a preference for red-muscle Arctic char, as it is said to be richer in flavour and provide higher human nutritional quality (e.g., antioxidants; vitamin A). Due to the importance of these pigments to fish species and humans, studying the factors that potentially influence Arctic char muscle pigmentation is important from both a nutritional and economic lens, especially as climate change continues to impact the resources they rely on.

1.7 Objectives and Hypotheses

My overall thesis objective was to quantify spatiotemporal variation in the foraging ecology of anadromous Arctic char during their summer marine foraging period and its influence on muscle pigmentation between a southern (Rankin Inlet) and northern (Naujaat) location with different sea ice dynamics along the western Hudson Bay coast in the Kivalliq region of Nunavut. To do so, I used a combination of scientific tools, including stomach content, stable isotope, highly branched isoprenoid, carotenoid spectrophotometry analysis, and a standard muscle colour scale.

The objective of my first data chapter (Chapter 2) was to assess the foraging ecology of anadromous Arctic char in response to variable sea ice dynamics between Rankin Inlet and Naujaat along the western Hudson Bay coast using stomach contents, stable isotopes, and highly branched isoprenoids. I hypothesized that Arctic char diet will vary spatiotemporally, and predicted that Rankin Inlet Arctic char will exhibit a forage fish-based diet, and in turn, use more phytoplankton-derived carbon and occupy a higher trophic position compared to Naujaat Arctic char based on the current known distribution of forage fish species (e.g., capelin) along western Hudson Bay.

The objective of my second data chapter (Chapter 3) was to examine which diet variables (stomach contents, nitrogen stable isotope ratios ($\delta^{15}N$), and highly branched isoprenoids) are most influential on carotenoid concentration and muscle pigmentation of anadromous Arctic char. To do this, I sampled Arctic char and their invertebrate and fish prey around Rankin Inlet and Naujaat along the western Hudson Bay coast and determined carotenoid concentrations using spectrophotometry analysis and muscle colour of Arctic char using a standard scale (DSM SalmoFan). I hypothesized that Arctic char carotenoid concentration and muscle pigmentation will vary spatially in relation to dietary differences (invertebrate versus fish consumption) found between the two study sites (Faulkner et al., in review), and predicted that Naujaat Arctic char will have higher red-pigment associated carotenoid concentrations (e.g., astaxanthin) and that muscle pigmentation will fall along an orange-red colour gradient versus a pale-pink colour gradient compared to Rankin Inlet Arctic char due to a higher consumption of invertebrates that also contain higher carotenoid concentrations than fishes.

1.8 References

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Chapter 2 Spatiotemporal variation in Arctic char (*Salvelinus alpinus)* foraging ecology along western Hudson Bay, Nunavut, Canada*

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2.1 Abstract

Climate-induced alterations to Arctic sea ice dynamics are influencing the availability and distribution of resources, and in turn, restructuring Arctic marine food webs, which can be monitored by studying the foraging ecology of opportunistic predators such as anadromous Arctic char (*Salvelinus alpinus*). Despite its subsistence and economic importance, Arctic char foraging ecology across their range, particularly in relation to sea ice dynamics, remains understudied. Here, we investigate the foraging ecology of Arctic char at a southern (Rankin Inlet) and northern (Naujaat) location along western Hudson Bay, using stomach contents, stable isotopes ($\delta^{13}C$ and $\delta^{15}N$), and highly branched isoprenoids. Spatiotemporal variation in diet was observed in relation to sea ice dynamics, whereby Arctic char in Rankin Inlet consumed more fish and phytoplankton-based carbon sources, occupied a higher trophic position, and displayed a similar isotopic niche breadth compared to Naujaat. The plastic foraging ecology observed highlights the species' adaptability to inter-annual variability, although long-term resilience in the face of climate-driven changes remains unknown. This study underscores potential socioeconomic implications of changing environmental conditions on Arctic char along western Hudson Bay.

2.2 Introduction

Food webs are comprised of numerous inter-linked predator-prey relationships that connect primary producers to top predators, resulting in the flow and cycling of energy throughout an ecosystem (Elton, 1927; MacArthur, 1955; Frederiksen et al., 2006). Within these systems, numerous biotic processes influence the movement of energy among trophic links, such as predation and competition (both within and between species; Kotler and Holt, 1989), trophic omnivory (Pimm and Lawton, 1978; Thompson et al., 2007), ontogenetic niche shifts (Werner and Gilliam, 1984), and spatiotemporal heterogeneity in prey distribution and abundance (MacArthur and Levins, 1964; van Langevelde and Prins, 2008). These processes collectively contribute to the structuring of ecological communities. Additionally, abiotic processes such as environmental variability can further shape ecological communities and contribute to spatiotemporal heterogeneity in prey distribution and abundance (van Langevelde and Prins, 2008) which, in turn, influences the foraging ecology of predators.

Environmental change is rapidly occurring across the Arctic, resulting in drastic decreases in sea ice concentration and snow cover as a result of increasing sea and air temperatures (Gagnon and Gough, 2005; Gaston et al., 2012; IPCC, 2023). Collectively, these changes are having a profound effect on sea ice extent and phenology across Arctic marine habitats (Arrigo, 2014; IPCC, 2023). Such changes have altered the phenology and rates of Arctic marine primary production, impacting the amount of annual sea ice algae and pelagic phytoplankton production (Moore and Huntington, 2008; Frainer et al., 2017). In turn, these changes are providing conditions more suitable for subarctic-associated species that are more dependent on phytoplankton-derived carbon sources (e.g., capelin, *Mallotus villosus*), while potentially having negative consequences for Arctic endemic species (e.g., Arctic cod, *Boreogadus saida*; Moore and Huntington, 2008; Frainer et al., 2017). In the Arctic, higher trophic level consumers have historically relied on Arctic cod and ice-associated invertebrates (e.g., *Onisimus* spp., *Themisto* spp.; Gaston et al., 2003; Chambellant et al., 2013; Ulrich and Tallman, 2021) as their main prey sources. As a result, Arctic environments are disproportionately experiencing a northward shift in more subarctic-associated species (i.e., the "borealization" of the marine environment), leading to alterations in species interactions, distributions, and abundances (Fossheim et al., 2015; Kortsch et al., 2015; Yurkowski et al., 2017). Consequently, an increase in availability of more subarctic-associated prey fish and invertebrates have the potential to cause bottom-up cascading effects throughout the marine ecosystem (Rose, 2005; Chambellant et al., 2013). Therefore, opportunistic, generalist predators can act as sentinels in determining ecosystem-wide changes in resource availability and how these changes may vary over space and time.

Anadromous Arctic char (*Salvelinus alpinus*) have a circumpolar distribution (Johnson, 1980; Klemetsen et al., 2003) and have been central to the culture, economy, food security, and health of Inuit, who have relied on this species for millennia (Government of Nunavut, 2018; Harris et al., 2020). This species plays a key role in northern ecosystems and can act as sentinels for investigating spatiotemporal variation in resource availability given their opportunistic, generalist foraging behaviour while in the marine environment (Johnson, 1980; Ulrich and Tallman, 2021). Anadromous forms of Arctic char migrate from freshwater to marine environments to forage for approximately 30-60 days during the summer months on abundant food resources in nearshore locations (Johnson, 1980; Dempson and Kristofferson, 1987; Moore et al., 2016). During the marine foraging period, Arctic char consume a wide range of prey types (Johnson, 1980; Dempson et al., 2002; Ulrich and Tallman, 2021), including numerous crustaceans (e.g., *Onisimus* spp., *Gammarus* spp., *Mysis* spp., *Themisto* spp.), forage fish (e.g., capelin, sand lance (*Ammodytes* spp.), sculpins (Cottidae), cod (Gadidae)), polychaetes, and insects (Moore and Moore, 1974; Dempson et al., 2002; Spares et al., 2012; Harwood et al., 2015). During this time of rapid growth and energy accumulation, individuals can double their weight in just over a month (Dempson et al., 2002; Klemetsen et al., 2003; Rikardsen et al., 2007), while concurrently increasing lipid reserves up to five-fold (Jørgensen et al., 1997) before returning to freshwater to overwinter where foraging activity typically ceases (Harris et al., 2020).

Along the western Hudson Bay coast in the territory of Nunavut, more southern locations, such as near the community of Rankin Inlet (at 62^{o}N) generally have more ice-free days during the summer months (June to September) and therefore are less influenced by sea ice relative to more northern locations, such as Repulse Bay near the community of Naujaat (at 66^{o}N; Gupta et al., 2022). As a result, resource availability and abundance likely differ between the Rankin Inlet and Naujaat areas, in turn influencing the potential fish and invertebrate prey species composition. For example, capelin are commonly observed around Rankin Inlet and have only been documented as far north as Coats Island and Southampton Island (~ 62^{o}N to 65^{o}N) along western Hudson Bay (Gaston et al., 2003; Amiraux et al., 2023). Both study sites are also important Inuit subsistence and commercial harvesting locations for Arctic char, typically fished during the ice-free summer months from mid-June to late-August while Arctic char feed in the marine environment. Despite Arctic char being a key subsistence and economic resource for Inuit (Sprules, 1952; Government of Nunavut, 2018), their foraging ecology in relation to environmental variability (e.g., sea ice dynamics) has not been investigated across their range. This has implications for understanding the current state of the marine ecosystem and how future climatic changes may influence environmental conditions (e.g., sea ice dynamics), and in turn, the impact this may have on species' foraging ecology and food web interactions.

Given this paucity of information, the objective of our study was to assess the foraging ecology of Arctic char between a southern (Rankin Inlet) and northern (Naujaat) location with different sea ice dynamics along the western Hudson Bay coast using stomach contents, stable isotopes, and highly branched isoprenoids (HBIs). Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been widely applied in ecology to examine carbon source and habitat use, and trophic position (TP), respectively, among vertebrate consumers (Boecklen et al., 2011), while HBIs have been extensively used across Arctic environments to examine consumer utilization of sea ice and phytoplankton carbon sources (Brown and Belt, 2012; Koch et al., 2023). We hypothesized that Arctic char diet will vary spatiotemporally, and predicted that Rankin Inlet Arctic char will exhibit a forage fish-based diet, and in turn, use more phytoplankton-derived carbon and occupy a higher TP compared to Naujaat Arctic char based on the current known distribution of forage fish species (e.g., capelin) along western Hudson Bay.

2.3 Materials and Methods

2.3.1 Sample Collection

This study was approved by the University of Manitoba Animal Care Committee (F21-023 (AC11719)) and a Licence to Fish for Scientific Purposes was obtained from Fisheries and Oceans Canada (S-22/23-1002-NU). Arctic char were collected by angling and gillnetting between June and August in 2021 and 2022 (Table 2.1) while foraging in the estuarine and marine environments along the western Hudson Bay coast near the communities of Rankin Inlet (Diana River – 62° 49.4' N, 92° 21.5' W) and Naujaat (Sipujaqtuu – 66° 23.2' N, 86° 43.3' W and Tikiraq – 66° 26.0’ N, 86° 37.0’ W), Nunavut, which are separated by approximately 500 km (Figure 2.1). We recorded fork length (cm), round weight (kg), lipid content (%; for 2022 only), sex, and maturity status for all Arctic char, with the exception of Naujaat Arctic char in 2021 that were collected by community members. Maturity was assessed by visually examining the size and length of ovaries or testes and assigning a maturity status (immature, mature, running ripe, spent, resting, and unknown); if maturity could not be determined, a status of unknown was assigned. Despite sex and maturity being recorded, due to small sample sizes across categories, these variables could not be included in statistical analyses. Fulton’s condition factor (hereafter, body condition) was calculated using the equation:

$$K = 100 * \frac{W}{L^3},$$

where W is round weight (g) and L is fork length (cm; Getso et al., 2017). Despite body condition being recorded, due to missing data in 2021, this variable could not be included in statistical analyses. Arctic char lipid content was recorded in line with the dorsal fin just above the lateral line using a Fish Fat Meter (Distell Model FFM-692, Fauldhouse, Scotland). We also collected Arctic char stomachs to examine diet composition through stomach content analysis and livers to assess short-term diet (e.g., days to weeks; Tieszen et al., 1983; MacNeil et al., 2006) using stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and HBI ratios, as previous analysis has found that approximately 70% of HBIs within an organism are stored in liver tissues (Brown et al., 2013).

2.3.2 Sea Ice Analysis

Sea ice concentration was assessed using the L4, MUR sea ice concentration layer from the NASA Worldview dataset (https://worldview.earthdata.nasa.gov/; Smith et al., 2021). Sea ice cover was visually examined at the estuaries of both study sites and the larger marine area of

Rankin Inlet and Repulse Bay (Naujaat; Figure 2.1) to determine a local estuary and complete ice-off date for the region, respectively. Within the context of this study, the estuary is defined as the location where the river meets the ocean and where localized subsistence fishing occurs. Sea ice concentration for the larger marine area of Rankin Inlet and Repulse Bay was further examined by selecting a location central to the opening of both inlets/bays (Figure 2.1) and a sea ice concentration percentage representative of each general area was assigned. Visual assessment began on May 30 of each study year until a complete ice-off date was determined for the specific Rankin Inlet (Diana River) and Naujaat (Sipujaqtuu) study sites, as well as the larger marine area of Rankin Inlet and Repulse Bay. This date range represents the time when Arctic char typically begin their downstream migration to estuarine/marine environments (Harris et al., 2022A).

2.3.3 Stomach Content Analysis

Stomach contents were used to determine the prey species composition and relative importance of discrete prey types of Arctic char from both the Rankin Inlet and Naujaat study sites. Arctic char stomachs were categorically ranked by fullness (full, partially full, near empty, empty) and individual prey items were identified to the lowest taxonomic level possible. Otoliths and other stomach content items (i.e., digested remains, plants, gravel/sand/rocks, and other material) were also recorded, although excluded from stomach content analyses (e.g., da Silva et al., 2019) as they may accumulate in the stomachs over time and overestimate the importance of certain prey types (Battaglia et al., 2013). Diet items were enumerated and weighed following previous studies (e.g., Dempson et al., 2002; Grimaldo et al., 2009; Moreno-Sanchez et al., 2016). Counts and weights of each prey type were then summed across individual stomachs at each study site by year and used to calculate the percent number (%N), percent weight (%W), and percent frequency of occurrence (%O) for each prey type by dividing the individual prey type value by the respective total prey value of each metric (i.e., %N, %W, %O) by study site and year (Hyslop, 1980). From these values, the index of relative importance (IRI) of each prey type was calculated by summing the %N and %W, then multiplying by the %O of each prey type (Liao et al., 2001). The IRI of each prey type was then converted to a percentage (%IRI) by dividing the IRI of each prey type by the sum of the IRI values of all prey types by study site and year (Grimaldo et al., 2009). The %IRI was reported to the lowest taxonomic level possible. Further, the percentage of empty stomachs was determined by dividing the number of empty stomachs by the total number of stomachs to compare foraging activity between study sites and years (e.g., Sprules, 1952; Spares et al., 2012; Ogloff et al., 2019).

In addition to the above metrics, Schoener's diet overlap index (hereafter, Schoener's index) was calculated to determine whether the diet of Rankin Inlet Arctic char overlapped with the diet of Naujaat Arctic char within study years. Schoener's index was calculated by first grouping similar prey types into broad categories (e.g., amphipods, copepods, fish larvae) and comparing site-specific dietary proportions by both count and weight for both study years (Schoener, 1970):

$$\alpha = 1 - 0.5 * \left(\sum_{i=1}^{n} | \, P_{xi} - P_{yi} \, | \right),$$

whereby α is the Schoener's index value, P_{xi} is the proportion of the *i*th prey group in study site *x*, and P_{yi} is the proportion of the *i*th prey group in study site *y* (Enders et al., 2020). An alpha (α) value of 0 indicates no dietary overlap, an α value of 1 indicates complete dietary overlap, and an α value > 0.60 represents biologically meaningful diet overlap between two study sites (Enders et al., 2020).

2.3.4 Stable Isotope Analysis

Stable isotope ratios of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) were used to determine the carbon source use and TP of Arctic char, respectively, at both study sites. Additionally, copepods (e.g., *Calanus* spp.) were collected in each year around Rankin Inlet (2021: n = 10 net tows; 2022: n = 16) and Naujaat (2022: n = 5) using a conical zooplankton net (200-micron mesh), with the exception of Naujaat in 2021 as values from *Calanus* spp. collected nearby in 2018 and 2019 (see Amiraux et al., 2023) were used. For bulk copepods, multiple individuals sampled on the same date and at the same location were pooled to ensure sufficient material for analysis. The $\delta^{13}C$ and $\delta^{15}N$ of bulk copepods were then used to baseline correct Arctic char stable isotope ratios to account for potential spatial variation in biogeochemical processes between both study sites. Arctic char liver and bulk copepods were subsampled and freeze-dried (-50°C) or oven-dried (40°C) for 48-72 hours to remove moisture and homogenized using a mortar and pestle prior to being weighed (~1.00 mg) for stable isotope analysis at the Stable Isotopes in Nature Laboratory (SINLAB; University of New Brunswick, Fredericton, New Brunswick, Canada). Samples were analyzed using a NC2500 Elemental Analyzer (Carlo-Erba) using a PN150 Autosampler (Costech) and a Delta V Isotope Ratio Mass Spectrometer (Thermo) through a ConFlo-IV Interface (Thermo). Stable isotope ratios are reported in standard delta notation for carbon and nitrogen relative to the primary reference materials Vienna Peedee Belemnite (VPDB) and atmospheric nitrogen (N_2/AIR), respectively. Standards used in normalization were muskellunge muscle, bovine liver, and USGS61. Other standard materials run for QA/QC included acetanilide, nicotinamide, corn meal, ephedra, spirulina, IAEA-CH7, and IAEA-N2. The mean difference from certified values of each standard were ≤ 0.20 for $\delta^{13}C$ and ≤ 0.14 for

δ^{15}N. Additionally, the analytical precision derived from the standard deviation of measured standards was ≤ 0.25‰ for both δ^{13}C and δ^{15}N.

Arctic char liver and bulk copepods were not lipid extracted, with the exception of 2021 Naujaat bulk copepods from Amiraux et al., (2023). Therefore, a mathematical normalization equation was applied to the δ^{13}C ratios to account for the potential influence of lipids. Arctic char liver δ^{13}C ratios were corrected using a fish liver specific lipid normalization equation: $\Delta^{13}C = (6.059*C:N + (-22.270)) / C:N + (-1.397)$ (Logan et al., 2008), while bulk copepods were corrected using an equation developed for *Calanus hyperboreus* copepods: $\Delta^{13}C = (0.567*(C:N_{bulk})) + (-0.363)$ (Pomerleau et al., 2014). Additionally, as spatiotemporal variation in environmental conditions are known to increase the isotopic variation of consumers (Post, 2002; Matthews and Mazumder, 2004; Smith et al., 2021), Arctic char δ^{13}C ratios were baseline corrected by subtracting the isotopic ratios of primary consumers (bulk copepods, TP = 2) from the isotopic ratios of Arctic char at both study sites prior to conducting analyses to account for spatial variation in baselines of δ^{13}C (Post, 2002; Black and Armbruster, 2021; Smith et al., 2021).

To calculate the TP of Arctic char, a one source TP model (Post, 2002) was used:

$$\mathrm{TP_{consumer}} = \mathrm{TP_{baseline}} + \frac{\delta^{15}\mathrm{N_{consumer}} - \delta^{15}\mathrm{N_{baseline}}}{\Delta^{15}\mathrm{N}}.$$

We used the δ^{15}N ratios of bulk copepods as the δ^{15}N baseline which occupied a TP of 2 that were sampled in the same year Arctic char (the consumer) were sampled (e.g., McMeans et al., 2013). Diet-tissue discrimination factors (Δ^{15}N; DTDFs) from a recent meta-analysis of teleost fish by Canseco et al., (2021, see Table 4) were used, where DTDFs of 0.6 ± 0.47‰ (mean ±

standard error) for δ^{13}C and 2.8 ± 0.48‰ for δ^{15}N for fish liver were applied (Canseco et al., 2021).

2.3.5 Highly Branched Isoprenoid Analysis

HBI analysis was used to further quantify the carbon source use of Arctic char at both study sites. Arctic char liver samples were subsampled and freeze-dried for 48-72 hours to remove moisture prior to being weighed (~1.00 mg) for HBI analysis. HBI lipids were then extracted by adding an internal standard to allow later quantification, then saponified in a methanolic potassium hydroxide solution prior to completing three sequences of hexane addition, vortexing, and centrifuging, with supernatant solutions being transferred to clean vials between each sequence. The supernatant solution was then dried under a nitrogen (N_2) stream prior to being resuspended in hexane and fractionated using column chromatography to provide non-polar lipid extracts containing HBIs for analysis. For detailed methods of the HBI extraction and purification process, refer to Brown et al., (2014). Samples were run at the Freshwater Institute (Winnipeg, Manitoba, Canada) using a 7890B Gas Chromatograph (Agilent) coupled to a 5977B Mass Selective Detector (Agilent) equipped with a Purged Ultimate Union (Agilent) which facilitates pre-column backflush for analysis.

Upon analysis, H-Prints for each sample were calculated by comparing the ratio of HBIs derived from phytoplanktonic diatoms (∑ III a-d) to those derived from sea ice diatoms (∑ IP_{25} and IIb):

$$\mathrm{H-Print} = \frac{(\sum \mathrm{III})}{(\sum \mathrm{IP25} + \mathrm{II} + \mathrm{III})}.$$

In addition, ice particulate organic carbon (iPOC) values were further calculated using the H-Print values from each sample:

$$\mathrm{iPOC\ (sympagic\ carbon\ \%)} = 101.08 - 1.02 * \mathrm{H} - \mathrm{Print},$$

whereby a low iPOC value represents primary consumption of phytoplankton-derived carbon sources and a high iPOC value represents primary consumption of sea ice algae-derived carbon sources (Brown et al., 2018).

2.3.6 Statistical Analysis

To visualize whether the diet of Arctic char differed between Rankin Inlet and Naujaat by count and weight within both study years, we used non-metric multidimensional scaling (NMDS), a non-parametric multivariate method of analysis. Prior to NMDS analysis, prey count and weight data were transformed using a Hellinger transformation to improve interpretation and patterning of the data (Clarke, 1993). Transformed data were then used to construct a Bray-Curtis similarity matrix (i.e., Moreno-Sanchez et al., 2016; Adams et al., 2017) incorporating the top 20 prey types by count and weight to compare Rankin Inlet and Naujaat Arctic char. The top 20 prey types comprised a large percentage (84.0% to 99.7%) of the diet across both study years. The goodness of fit for the NMDS data was reported using a stress value: a value < 0.05 indicates an excellent fit, a value < 0.1 indicates good fit, and a value < 0.2 is still moderately fit although likely to provide misleading interpretations (Clarke, 1993). To visualize whether the diet of Arctic char differed between Rankin Inlet and Naujaat, a permutational multivariate analysis of variance (PERMANOVA) using distance matrices was run on the Hellinger transformed stomach content count and weight data using the *adonis* function from the *vegan* package in R (R Core Team, 2023).

To examine differences in Arctic char foraging ecology and determine the best predictors for the dependent variables of Arctic char baseline corrected δ^{13}C ratios (δ^{13}Cc), TP, and iPOC values, general linear models were constructed using the *lm* function from the *lme4* package in R

(R Core Team, 2023). Predictor variables included year, study site, Arctic char $\delta^{13}C_c$, TP, and iPOC. The following interactions were also included to examine their influence on dietary metrics: year and study site and study site and iPOC. Prior to model runs, predictor variables were assessed for correlation with none being highly correlated ($r < 0.5$ among all predictor variables). The top model was selected based on the examination of Akaike Information Criterion values ($\Delta AICc = 0.0$) and models with a $\Delta AICc \leq 2.0$ were considered plausible with substantial support (Burnham and Anderson, 2004). The normality and homoscedasticity of the response variables were visually assessed by examining histograms and scatterplots of the residual values. Further, the Stable Isotope Bayesian Ellipses in R or *SIBER* package in R (Adams et al., 2017; R Core Team, 2023) was used to quantify the amount of isotopic niche overlap between study sites within a year and calculate the isotopic niche breadth (Standard Ellipse Area, SEA_B: iterations = 2,000,000, burn-in = 100,000, thin by = 10) of Arctic char between and within study sites and years. Bivariate normality was visually assessed prior to the analysis of isotopic niche breadth. We estimated differences in isotopic niche breadth between study sites each year and within study sites by year using the percentage estimates from posterior probability distributions that were higher in one group compared to the other relative to the total number of estimates from the posterior distribution. All data analysis was conducted in R version 4.3.0 (R Core Team, 2023). Unless otherwise stated, all levels of statistical significance were set at $\alpha = 0.05$.

2.4 Results

2.4.1 Sea Ice

Sea ice dynamics differed between study sites in 2021, as Naujaat had relatively more sea ice and a later ice-off date than Rankin Inlet. The average sea ice concentration near Naujaat was higher than Rankin Inlet in both May (81.0% versus 66.0%) and June (75.0% versus 54.0%) of that year (Table 2.1). Rankin Inlet also had an estuary ice-off date of June 21 and a complete ice-off date of July 8, while Naujaat had an estuary ice-off date of July 4 and a complete ice-off date of July 19 in 2021. Sea ice concentration, however, was more similar between both locations in 2022 in both May (61.5% versus 67.0%) and June (61.1% versus 65.7%; Table 2.1). Further, Rankin Inlet had an estuary ice-off date of June 24 and a complete ice-off date of July 1, while Naujaat had an estuary ice-off date of June 29 and a complete ice-off date of July 6 in 2022.

2.4.2 Stomach Contents

In 2021, stomach content analysis, based on %IRI revealed that capelin (88.6%), *Centropages abdominalis* (6.4%), *Onisimus litoralis* (1.6%), *Gammarus wilkitzkii* (1.3%), and chironomids (0.6%) were the five most important prey types for Rankin Inlet Arctic char. Capelin (84.9%), *Gammarus wilkitzkii* (7.6%), crabs (*Hyas coarctatus* and *Hyas* spp.; 3.7%), sand lance (1.4%), and *Onisimus litoralis* (0.6%) were the five most important prey types in 2022. Additionally, there were three Arctic char with empty stomachs (5.1%) collected near Rankin Inlet in 2021 and 12 Arctic char with empty stomachs (24.0%) collected in 2022. In Naujaat, *Onisimus litoralis* (98.3%), mysids (1.3%), capelin (0.3%), amphipods (all remaining species; 0.1%), and fish larvae (0.1%) were the five most important prey types for Arctic char in 2021. Sculpins (*Gymnocanthus* spp., *Myoxocephalus* spp., *Triglops* spp., and Cottidae; 52.2%), *Cirripedia* larvae (nauplii and cyprid larvae; 34.2%), mysids (9.4%), copepods (all species; 1.7%), and *Themisto libellula* (0.9%) were the five most important prey types for Arctic char at this location in 2022. Additionally, no Arctic char with empty stomachs (0.0%) were collected near Naujaat in either year.

Schoener's index revealed minimal overlap between the diets of Rankin Inlet and Naujaat Arctic char in 2021 and 2022 by both prey count (2021: $\alpha = 0.32$; 2022: $\alpha = 0.10$) and weight (2021: $\alpha = 0.04$; 2022: $\alpha = 0.07$). This was further supported by the NMDS analysis, highlighting that there was virtually no overlap in ellipses for both prey count (2021: $p < 0.001$; 2022: $p < 0.001$; Figure 2.2 A,C) and weight (2021: $p < 0.001$; 2022: $p < 0.001$; Figure 2.2 B,D) over both study years.

2.4.3 Stable Isotopes and Highly Branched Isoprenoids

Arctic char δ^{13}Cc and TP, along with HBIs (iPOC values; Figure 2.3 A-C) varied by year, study site, lipid content, and body condition (Table 2.1). All model runs are in Supplementary Materials, while top and plausible models are located in Table 2.2. The best model for predicting Arctic char δ^{13}Cc ratios included year, study site, and the interaction between year and study site ($F_{3,180} = 353.2$, $p < 0.0001$, $R^2 = 0.85$), with year ($F_{1,180} = 871.8$, $p < 0.0001$), study site ($F_{1,180} = 853.8$, $p < 0.0001$), and the interaction between year and study site ($F_{1,180} = 853.8$, $p < 0.0001$) all being significant predictors of Arctic char δ^{13}Cc values (Table 2.2). The δ^{13}Cc of Rankin Inlet Arctic char was significantly higher in 2021 compared to 2022 (2.5‰ ± 0.6 versus -0.9‰ ± 0.4), while Naujaat Arctic char δ^{13}Cc was significantly higher in 2022 compared to 2021 (2.2‰ ± 0.6 versus 0.3‰ ± 0.7; Figure 2.3 A). Further, the best model for predicting Arctic char TP included year, study site, and the interaction between year and study site ($F_{3,180} = 158.2$, $p < 0.0001$, $R^2 = 0.73$), with year ($F_{1,180} = 157.0$, $p < 0.0001$), study site ($F_{1,180} = 7.6$, $p = 0.0064$), and the interaction between year and study site ($F_{1,180} = 7.6$, $p = 0.0063$) all being significant predictors of Arctic char TP (Table 2.2). Arctic char TP was significantly higher in Rankin Inlet compared to Naujaat in both 2021 (4.1 ± 0.2 versus 3.6 ± 0.3) and 2022 (4.7 ± 0.3 versus 3.9 ± 0.2) and TP was higher across both study sites in 2022 compared to 2021 (Figure 2.3 B). Finally, the best model for predicting Arctic char iPOC values included year, study site and the interaction between year and study site ($F_{3,180} = 117.5$, $p < 0.0001$, $R^2 = 0.66$), with year ($F_{1,180} = 4.8$, $p = 0.0290$) study site ($F_{1,180} = 4.8$, $p = 0.0296$), and the interaction between year and study site ($F_{1,180} = 4.8$, $p = 0.0299$) all being significant predictors of Arctic char iPOC values (Table 2.2). Arctic char iPOC values were significantly higher in Naujaat compared to Rankin Inlet in both 2021 (79.4% ± 9.1 versus 36.9% ± 16.0) and 2022 (64.1% ± 14.0 versus 31.0% ± 15.2) and iPOC values were significantly higher across both study sites in 2021 compared to 2022 (Figure 2.3 C).

In both 2021 and 2022, there was no isotopic niche overlap (0.00%) between Rankin Inlet and Naujaat Arctic char (Figure 2.4). Additionally, Arctic char isotopic niche breadth was similar between study sites across years (Rankin Inlet: 2021 = 1.17‰^{2}, 2022 = 0.97‰^{2}; Naujaat: 2021 = 1.13‰^{2}, 2022 = 0.86‰^{2}; Figure 2.4), as there was a 53% (2021) and 69% (2022) probability that the isotopic niche breadth of Rankin Inlet Arctic char was larger than the isotopic niche breadth of Naujaat Arctic char. However, there was inter-annual variability in isotopic niche breadth between years within both study sites, as there was an 83% (Rankin Inlet) and 88% (Naujaat) probability that the isotopic niche breadth of Rankin Inlet and Naujaat Arctic char was larger in 2021 than 2022, respectively.

2.5 Discussion

To our knowledge, this is the first study to characterize spatiotemporal variability in the foraging ecology of anadromous Arctic char in relation to sea ice variability. Our results further highlight the opportunistic, generalist foraging behaviour of Arctic char across their range (Johnson, 1980; Ulrich and Tallman, 2021) as evidenced by the diverse mix of forage fish and ice-associated invertebrates consumed by Arctic char at both sites. Arctic char diet variability was likely driven by spatial and inter-annual differences in sea ice cover between years and study sites, which possibly influenced the availability and distribution of local prey types.

2.5.1 Spatial Variability in Foraging Ecology

As predicted, we found that Rankin Inlet Arctic char consumed more forage fish than Naujaat Arctic char in 2021 when sea ice dynamics and ice-off dates differed between the study sites. In contrast, Rankin Inlet and Naujaat Arctic char both consumed more forage fish in 2022 when sea ice dynamics and ice-off dates were more similar between study sites. The higher consumption of forage fish was likely due to variable sea ice dynamics (e.g., sea ice concentration, open water season) influencing the availability and distribution of prey types available for Arctic char to forage on (e.g., less ice-associated invertebrates in response to a longer open water season). Southern locations along the western Hudson Bay coast generally have more ice-free days during the summer months and therefore are less influenced by sea ice relative to more northern locations within the region (Gupta et al., 2022). Therefore, it is probable that differences in environmental factors (e.g., annual ice-free days, sea ice extent) played a key role in the composition of local prey availability and distribution along the coast, influencing Arctic char diet composition in the region.

The mix of forage fish and ice-associated invertebrates consumed by Arctic char in this study is consistent with previously documented spatial variability in Arctic char diet (Dempson and Kristofferson, 1987; Dempson et al., 2002) that also showed pelagic prey-dominated diets (e.g., capelin) in more southern locations versus benthic prey-dominated diets (e.g., ice-associated invertebrates, sculpins) in more northern locations. Despite clear differences in diet, isotopic niche breadth was similar between Rankin Inlet and Naujaat Arctic char across both study years, highlighting a similar variety of resources being utilized by both populations in 2021 and 2022. These results are further supported by stomach contents, as Arctic char diet was dominated by a single prey type within individual years at both the Rankin Inlet (2021 and 2022: capelin) and Naujaat (2021: *Onisimus litoralis*; 2022: marine sculpins) study sites. This is likely due to Arctic char being less selective in their foraging habits due to residence in regions where food is limited by both seasonal and local abundance (Johnson, 1980).

As predicted, given the piscivorous diet of Rankin Inlet Arctic char (mainly consisting of capelin) and the omnivorous diet of Naujaat Arctic char (mainly consisting of ice-associated invertebrates and sculpins), Rankin Inlet Arctic char consumed more pelagic phytoplankton-based prey and occupied a higher TP than Naujaat Arctic char. This suggests that Arctic char in the Rankin Inlet ecosystem play a different trophic role (i.e., more piscivory) compared to Arctic char in the Naujaat ecosystem. Ice-associated invertebrates and sculpins have also been found to have higher iPOC values than forage fish species (~75% - 100% versus ~25% - 50%; Koch et al., 2023). Previous studies examining the diet and carbon source use of numerous Arctic char prey types found that ice-associated invertebrates (i.e., *Onisimus* spp.) largely consumed sea ice algae from benthic sediments (Gradinger and Bluhm, 2010) and exhibited significantly higher iPOC values than forage fish (i.e., capelin; Koch et al., 2023) which largely consumed pelagic copepods (Ogloff et al., 2020). Given that higher iPOC values represent the primary consumption of ice algae-derived carbon versus phytoplankton-derived carbon (Brown et al., 2018) and that relatively little sea ice net primary productivity occurs south of 66^{o}N (Tedesco et al., 2019), it is clear that Naujaat Arctic char rely significantly more on sea ice-derived carbon and ice-associated prey types (i.e., *Onisimus litoralis*, *Gammarus wilkitzkii*, sculpins) than

Rankin Inlet Arctic char. This finding suggests stronger sympagic-benthic coupling within the Repulse Bay area than the Rankin Inlet area.

Sea ice algae is richer in lipids and persists longer in the environment than pelagic phytoplankton (Smith et al., 1989; Petersen et al., 1998; Koch et al., 2023). Therefore, the higher body condition of Naujaat Arctic char compared to Rankin Inlet Arctic char in 2022 was likely associated with higher sea ice algae carbon source use, as consumers in northern locations would have more access to this lipid-rich basal resource. Further, as sea ice algae persists in the environment long after spring algae blooms (Koch et al., 2023), this lipid-rich basal resource is accessible to Arctic char prey types year-round, and therefore, Arctic char during their marine foraging period. Interestingly, previous studies examining the lipid content of potential Arctic char prey types (e.g., capelin, sand lance, *Onisimus* spp., *Gammarus* spp.) found forage fish to typically contain slightly higher amounts of lipids (16% - 33%; Anthony et al., 2000) than ice-associated invertebrates (7% - 22%; Percy and Fife, 1981). Within Cumberland Sound, Nunavut, Ulrich and Tallman, (2021) reported a long-term diet shift of Arctic char from ice-associated invertebrates to forage fish that was associated with higher Arctic char growth rates, but a decrease in body condition. These findings are supported in the current study, as in 2022, Naujaat Arctic char contained slightly higher amounts of lipids compared to Rankin Inlet Arctic char (8.9% versus 8.4%) and a higher body condition factor (1.2 versus 1.1). Therefore, despite forage fish generally containing higher amounts of lipids, a pelagic-based diet may not favour increased Arctic char body condition along the western Hudson Bay coast.

Capelin were present in Naujaat Arctic char stomachs in 2021 despite local resource users sharing that capelin have not been previously observed in the area (J.-E. Tinashlu, Naujaat local resource user, pers. comm.). As capelin respond quickly to environmental change and act as a sea canary to monitor climate-influenced changes in subarctic ecosystems (Rose, 2005), this observation may be an early sign of an increase in a previously undocumented local population in the Repulse Bay area or a northward expansion of their range along western Hudson Bay. Dempson et al. (2002) previously suggested that increased capelin consumption by Arctic char along the northern Labrador coast may have been a result of variable oceanic climate conditions. Additionally, Spares et al., (2012) first reported capelin in the diet of Arctic char along southeastern Baffin Island (Frobisher Bay), which was later documented by Ulrich and Tallman, (2021) in Cumberland Sound, approximately 300 km to the north. Indeed, such observations of capelin within upper-level consumer diets have previously acted as an early indicator of long-term ecosystem-level shifts and changes in prey availability and distribution in Hudson Bay (Gaston et al., 2003), the Beaufort Sea (Harwood et al., 2015), and Cumberland Sound (Yurkowski et al., 2018; Ulrich and Tallman, 2021). Therefore, continued monitoring of Arctic char from Naujaat will determine whether the observation of capelin presence in the diet of upper-level consumers is an early indication of a longer-term ecosystem-level shift in prey availability and distribution along northwestern Hudson Bay.

2.5.2 Temporal Variability in Foraging Ecology

Inter-annual differences in sea ice concentration and marine ice-off dates, especially around Naujaat, likely contributed to inter-annual variability in prey availability, and ultimately, the diet composition, carbon source use, and TP of Arctic char. Indeed, stomach contents revealed inter-annual variability in the diet composition of Naujaat Arctic char, whereby *Onisimus litoralis*, an ice-associated invertebrate dominated their diet in 2021, but shifted to largely consume sculpins in 2022. As ice-associated invertebrates such as *Onisimus litoralis* are endemic to Arctic near-shore ice covered locations (Gradinger and Bluhm, 2010), the absence of sea ice during the period when Arctic char were foraging in the marine environment likely influenced the prey types available for consumption. Indeed, Arctic char actively shift their foraging efforts to more abundant resources as specific prey abundance decreases (Johnson, 1980). In contrast, there was no inter-annual variability in the diet composition of Rankin Inlet Arctic char, as they principally consumed capelin in both years, suggesting capelin availability was high in both 2021 and 2022.

In Naujaat, Arctic char appeared to forage more offshore and on sculpins in 2022 compared to 2021, suggesting Arctic char may move further offshore to forage in response to current environmental conditions (Harris et al., 2022B). Given ice-associated invertebrates are common prey types for benthic-associated sculpins in the Arctic (i.e., *Myoxocephalus scorpius*), it was previously suggested that shifts in sculpin habitat use may be driven by foraging-related behaviour (Landry et al., 2019). Similarly, Arctic char move into deeper waters after marine ice-off, possibly to follow preferred prey types into deeper, offshore locations (Spares et al., 2012; Harris et al., 2020). This suggests the shift from an ice-associated invertebrate-based diet to a sculpin-based diet of Naujaat Arctic char between years is likely a combination of both a foraging and environmentally-driven shift in habitat use. Further, as both *Onisimus litoralis* and sculpins were present at the sampling location, it is possible that Naujaat Arctic char may have consumed more sculpins due to their higher availability given that Arctic char generally shift their diet towards more abundant resources (Johnson, 1980). The isotopic niche breadth of Rankin Inlet and Naujaat Arctic char was narrower in 2022 than 2021, suggesting that despite observed diet shifts of prey species between years, Arctic char used a more limited amount of resource types in both Rankin Inlet and Naujaat Arctic char populations in 2022 than in 2021.

Further, Arctic char sea ice-derived carbon was higher in 2021, while TP was higher in 2022 at both study sites. The observed decrease in Naujaat Arctic char iPOC values and increase in TP was likely due to a shift in their dominantly-consumed prey types, while the increase in Rankin Inlet Arctic char TP seen in 2022 may be due to decreased trophic omnivory lower in the food web. Previous studies have suggested that increased trophic omnivory at lower trophic levels (i.e., primary and secondary consumers) within a system can shorten food chain length, as secondary consumers feed more omnivorously and consume a mix of primary producers and consumers (McMeans et al., 2015; de la Vega et al., 2021).

Overall, the collective inter-annual changes observed in this study may provide insight into longer-term changes along the western Hudson Bay coast. Since there is relatively less ice-associated nutrient availability currently observed south of 66^{o}N, climate change influences on both current and future sea-ice net primary productivity is believed to be negligible in these locations (Tedesco et al., 2019). Alternatively, higher latitudes (between 66^{o}N and 74^{o}N) are predicted to be most impacted by climatic changes (Tedesco et al., 2019). Given its more northerly location, the Naujaat area may be more impacted by future climatic changes (e.g., sea ice loss, longer open water seasons), collectively altering rates of sea ice-derived carbon, and in turn, the prey types that support Arctic char in this system.

2.6 Conclusion

In conclusion, spatiotemporal variation in diet was observed between the Rankin Inlet and Naujaat Arctic char populations. Given the subsistence and economic importance of anadromous Arctic char along the western Hudson Bay coast (Sprules, 1952; Government of Nunavut, 2018), changes in sea ice dynamics that impact Arctic char foraging ecology and body condition may have future socioeconomic implications within the region (e.g., food security). As such, the continued monitoring of spatiotemporal variation in the foraging ecology of opportunistic, generalist top predators that act as ecosystem sentinels, such as Arctic char along western Hudson Bay, will provide an insight into changes to Arctic marine food web structure and their potential implications on Inuit that rely on this species.

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2.9 Tables

Table 2.1: Annual mean sea ice concentration and mean (± standard deviation) of Arctic char length, weight, δ^{13}Cc, trophic position (TP), ice particulate organic carbon (iPOC) values, lipid content, and body condition by location and year.

Location/Year	**Sea ice (%)**	**n**	**Length (cm)**	**Weight (g)**	**δ^{13}Cc (‰)**	**TP**	**iPOC (%)**	**Lipid (%)**	**Body Condition**
2021									
Rankin Inlet	60.0	59	59.7 ± 8.5	2904 ± 1233	2.5 ± 0.6	4.1 ± 0.2	36.9 ± 16.0	-	1.3 ± 0.3
Naujaat	78.0	41	-	-	0.3 ± 0.7	3.6 ± 0.3	79.4 ± 9.1	-	-
2022									
Rankin Inlet	66.3	50	68.0 ± 8.2	3654 ± 1244	-0.9 ± 0.4	4.7 ± 0.3	31.0 ± 15.2	8.4 ± 2.4	1.1 ± 0.2
Naujaat	61.3	34	53.6 ± 7.8	2039 ± 787	2.2 ± 0.6	3.9 ± 0.2	64.1 ± 14.0	8.9 ± 2.6	1.2 ± 0.1

Table 2.2: Statistical results from the top (ΔAICc = 0.0) and plausible (ΔAICc ≤ 2.0) models for determining the best predictors for Arctic char δ^{13}Cc, trophic position (TP), and ice particulate organic carbon (iPOC) values. Predictor variables include: year, study site, δ^{13}Cc, trophic position (TP), and ice particulate organic carbon (iPOC), and the interactions between year and study site and study site and iPOC.

Model		**R^2**	**P-value**	**AICc**	**ΔAICc**
δ^{13}Cc ~					
	year + study site + year*study site	0.85	<0.0001	335.86	0.00
TP ~					
	year + study site + year*study site	0.73	<0.0001	14.91	0.00
iPOC ~					
	year + study site + year*study site	0.66	<0.0001	1503.14	0.00
	year + study site + δ^{13}Cc + TP	0.66	<0.0001	1504.02	0.88

2.10 Figures

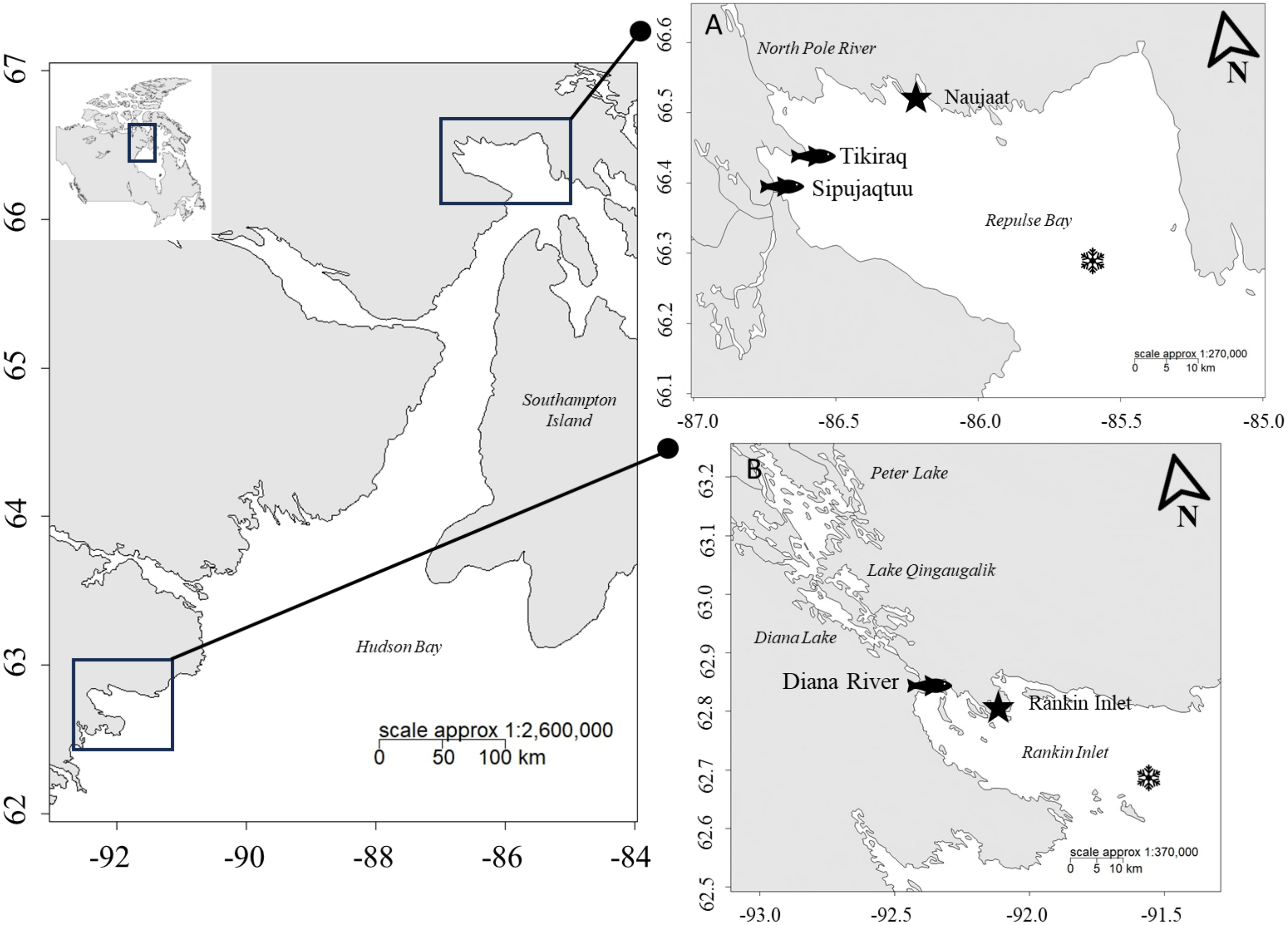

Figure 2.1: Map of the western Hudson Bay coast highlighting: A) the Sipujaqtuu and Tikiraq study sites and Repulse Bay area and B) the Diana River study site and Rankin Inlet area. The communities of Rankin Inlet and Naujaat are indicated by black stars. Snowflakes highlight the location where sea ice concentration was quantified for the Rankin Inlet and Repulse Bay areas.

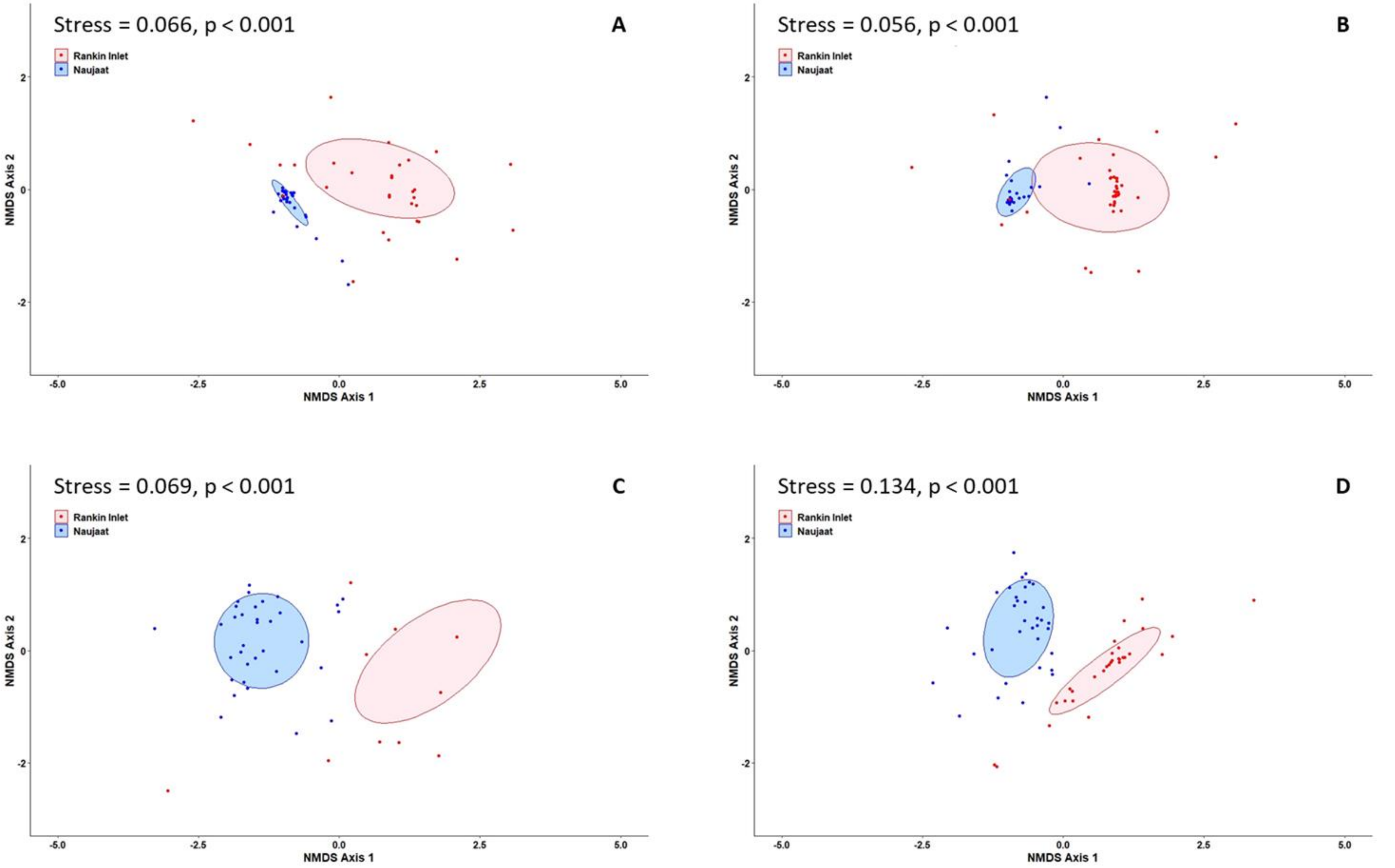

Figure 2.2: Non-metric multidimensional scaling analysis results highlighting the amount of diet overlap for the top 20 prey types of Rankin Inlet and Naujaat Arctic char by: A) 2021 prey count, B) 2021 prey weight, C) 2022 prey count, D) 2022 prey weight.

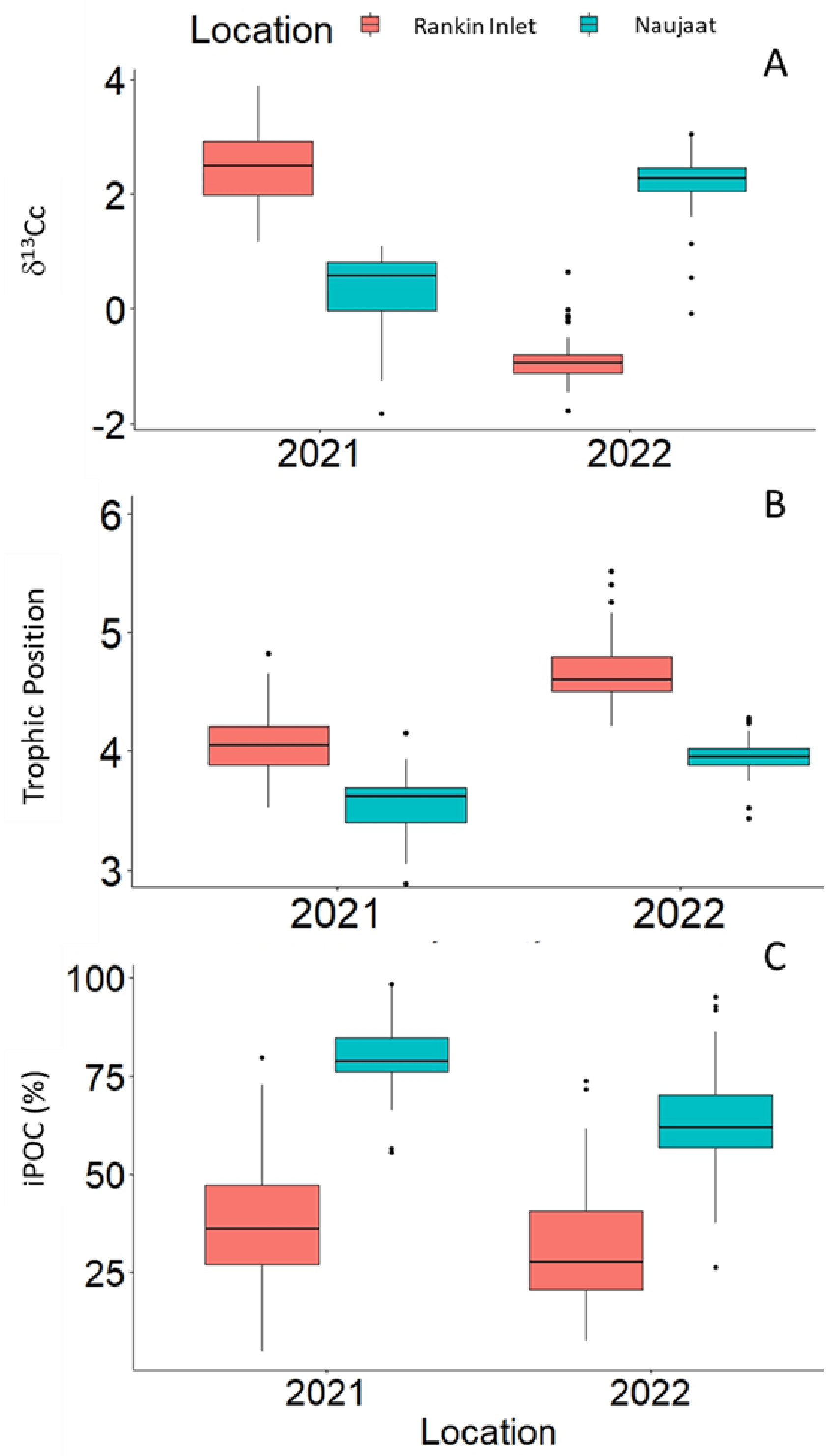

Figure 2.3: Boxplots representing the range of: A) δ^{13}Cc, B) trophic position (TP), and C) ice particulate organic carbon (iPOC) values for Rankin Inlet and Naujaat Arctic char by location and year.

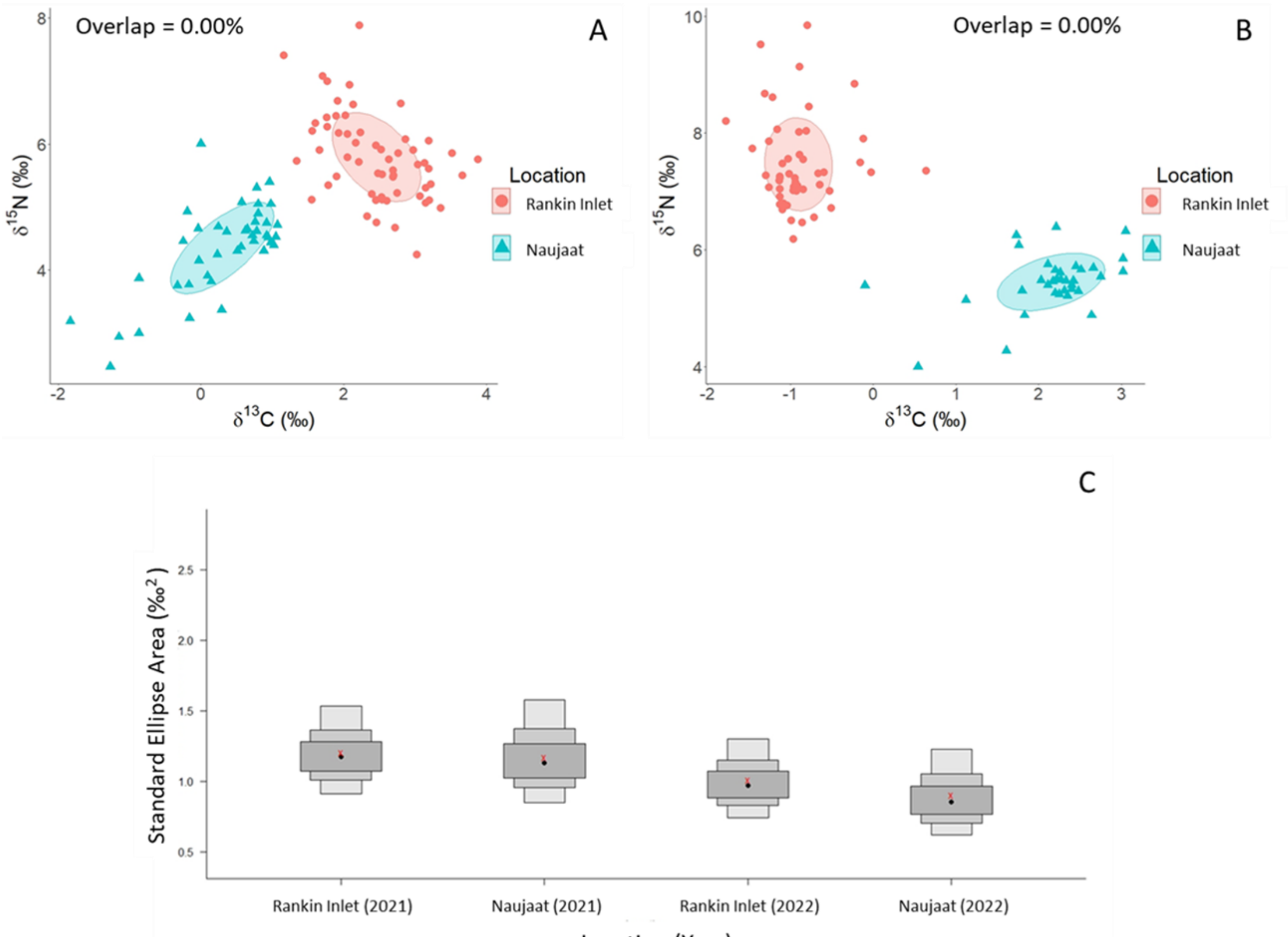

Figure 2.4: Isotopic niche breadth of Rankin Inlet and Naujaat Arctic char for: A) 2021 and B) 2022. C) Boxplots representing Bayesian mode estimates for isotopic niche breadth of Rankin Inlet and Naujaat Arctic char by location and year. Boxes indicate Bayesian credible intervals at 50% (dark grey), 75% (medium grey), and 95% (light grey).

Chapter 3 You are the colour of what you eat: higher invertebrate consumption correlates with redder muscle pigmentation in anadromous Arctic char (*Salvelinus alpinus*) along western Hudson Bay, Nunavut, Canada*

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3.1 Abstract

Fish species in the family Salmonidae exhibit intra-specific variation in muscle pigmentation, primarily due to individual differences in the accumulation and assimilation of dietary carotenoids. Carotenoid pigments are first synthesized by primary producers and microorganisms, and are present in the tissues of crustaceans that serve as important prey items for salmonids. Despite anadromous Arctic char (*Salvelinus alpinus*) being a key subsistence and economic resource across Inuit Nunangat, their muscle pigmentation in relation to diet and environmental variability (e.g., sea ice dynamics) has not been investigated. Further, ecological studies in the Arctic have not examined direct correlations between carotenoid concentration and dietary composition of consumers and their prey. In this study, we examined the influence of Arctic char diet (i.e., stomach contents, stable isotopes, highly branched isoprenoids) on their muscle pigmentation, as well as the muscle pigmentation of their prey at a southern (community of Rankin Inlet) and northern (community of Naujaat) location along western Hudson Bay over two years (2021, 2022) with contrasting sea ice dynamics using carotenoid spectrophotometry analysis and a standard muscle colour scale (DSM SalmoFan). Invertebrate prey types (e.g., *Gammarus* spp., *Onisimus* spp.) contained higher carotenoid concentrations than fish prey types (e.g., marine sculpins (*Myoxocephalus* spp., capelin; *Mallotus villosus*). Due to a more invertebrate-based diet, Arctic char in Naujaat contained higher muscle carotenoid concentrations (e.g., astaxanthin) than Rankin Inlet Arctic char in 2021 (7.8 mg/kg versus 0.6 mg/kg). In 2022, muscle carotenoid concentrations of Naujaat and Rankin Inlet Arctic char were similar (2.1 mg/kg versus 1.4 mg/kg) as Arctic char in both areas had more fish-based diets, although muscle colour was still redder in Naujaat (DSM SalmoFan value: 30 versus 22). Inter-annual variation in carotenoid concentration and muscle pigmentation occurs in this species and

could affect local resource users over the long-term with unpredictable climate-driven environmental changes, resulting in socioeconomic impacts across the Arctic.

3.2 Introduction

Carotenoids, which are only obtained via consumer diet, are a common group of natural pigments that are synthesized by all plants and select microorganisms (Goodwin, 1986). These pigments are beneficial to the health and fitness of an organism as they play an important role in treating diseases and acting as precursors for retinol (vitamin A) within certain groups of animals (e.g., salmonids; Goodwin, 1986). Carotenoids are also responsible for pigmentation of the skin, which in some taxa, are important for attracting mates prior to reproduction (Schiedt et al., 1985; Rajasingh et al., 2007). Fish species in the family Salmonidae exhibit muscle pigmentation that typically falls along a pink-red colour gradient, primarily due to variation in the accumulation and assimilation of carotenoids present in the tissues of their crustacean prey types (Choubert and Blanc, 1993; Rajasingh et al., 2007). Astaxanthin, the carotenoid largely responsible for the red pigmentation of salmonid muscle, is known to be highly variable within and among salmonid populations and provides many fitness and nutritional benefits, including improved immune functioning, vision, mating success, gamete and offspring quality, and it can also act as an antioxidant and precursor for vitamin A (Christiansen et al., 1995; Rajasingh et al., 2007; Garner et al., 2010; Lehnert et al., 2016; Lehnert et al., 2017). The relationship between increased dietary carotenoid concentrations and carotenoid concentrations within salmonid muscle contributing to a redder colour of the muscle has been widely investigated in aquaculture (e.g., Olsen and Mortensen, 1997; Hatlen et al., 1998; Rajasingh et al., 2006; Rahman et al., 2016; Cankiriligil et al., 2022), but has seldom been studied among wild anadromous species.

The Arctic is experiencing a disproportionate shift in the availability and distribution of marine species as a result of increases in sea temperature and decreases in sea ice cover due to accelerated climatic changes (Fossheim et al., 2015; Kortsch et al., 2015; Yurkowski et al., 2017). For example, previous studies across the Arctic have documented increased prevalence of subarctic-associated forage fish (e.g., capelin (*Mallotus villosus*), sand lance (*Ammodytes* spp.)) within the diets of upper-level consumers that have acted as early indicators of long-term ecosystem-level shifts and changes in prey availability and distribution (e.g., Gaston et al., 2003; Harwood et al. 2015; Yurkowski et al. 2018; Ulrich and Tallman 2021), which were likely driven by climate-related environmental changes. Along the western Hudson Bay coast, southern locations (e.g., near the community of Rankin Inlet) generally have more ice-free days during the summer months (June to September) and therefore are less influenced by sea ice relative to more northern locations (e.g., near the community of Naujaat; Gupta et al., 2022). As a result, resource availability to predators in the marine environment likely differ between the Rankin Inlet and Naujaat areas; specifically, the composition of fish and invertebrate prey species. Understanding spatial variation in prey species composition has implications for local marine ecosystems and informs climate-driven changes in trophic food web interactions. These changes can be monitored by examining the diet of opportunistic, generalist predators that can act as sentinels in determining ecosystem-wide changes in resource availability and how these changes may vary over space and time.

Anadromous Arctic char (*Salvelinus alpinus*) have a circumpolar distribution (Johnson, 1980; Klemetsen et al., 2003) and have been central to the culture, economy, food security, and health of Inuit, who have relied on this species for millennia (Government of Nunavut, 2018; Harris et al., 2020). This species plays a key role in northern ecosystems and can act as sentinels for investigating spatiotemporal variation in resource availability given their opportunistic, generalist foraging behaviour while in the marine environment (Johnson 1980; Ulrich and Tallman 2021). Anadromous forms of Arctic char migrate from freshwater to marine environments to forage over an approximately 30-60-day period during the summer months on abundant food resources in nearshore, coastal habitats (Dempson and Kristofferson, 1987; Moore et al., 2016; Harris et al., 2022). During the marine foraging period, Arctic char consume a wide range of prey types, including numerous invertebrates (e.g., *Onisimus* spp., *Gammarus* spp., *Mysis* spp. (mysids), *Themisto* spp.) and fishes (e.g., capelin, sand lance (*Ammodytes* spp.), sculpins (Cottidae), cod (Gadidae); Moore and Moore, 1974; Dempson et al., 2002; Spares et al., 2012; Harwood et al., 2015; Faulkner et al., in review). Ecosystem-level climatic changes in the marine environment can therefore be expected to alter the foraging ecology of anadromous Arctic char. Indeed, a previous study examining the foraging ecology of anadromous Arctic char observed spatiotemporal diet variability in relation to sea ice dynamics, whereby Arctic char along southwestern Hudson Bay (Rankin Inlet) consumed more fish and phytoplankton-based carbon sources and occupied a higher trophic position, but displayed a similar isotopic niche breadth compared to Arctic char along northwestern Hudson Bay (Naujaat; Faulkner et al., in review).

Arctic char muscle pigmentation is known to vary among populations, typically falling into white, pink, or red muscle categories (Andrews and Lear, 1956; Government of Nunavut, 2018). Muscle pigmentation is of human interest, as red pigmented muscle is typically the most important characteristic to assess the human consumptive quality and determine the economic value of salmonids (Hatlen et al., 1998; Rahman et al., 2016). Across the Canadian Arctic, Inuit have a preference for red-muscle Arctic char (Bovin and Power, 1990), as it is said to be richer in flavour and provide higher human nutritional quality (e.g., antioxidants; vitamin A). Red muscle Arctic char is also considered an economically higher-value product, as it can be sold as whole fillets instead of being processed into other products (S. Sadler, Kivalliq Arctic Foods manager, pers. comm.). Despite Arctic char being a key subsistence and economic resource for Inuit (Sprules, 1952; Government of Nunavut, 2018), their muscle pigmentation in relation to diet and environmental variability (e.g., sea ice dynamics) has not been investigated across their range. Further, no ecological studies have examined direct correlations between carotenoid concentration and dietary composition of consumers and their prey in the Arctic. Examining the influence of Arctic char diet on muscle pigmentation along western Hudson Bay coast is important to assess the human consumptive quality and economic value of this species. Overall, studying the factors that potentially influence Arctic char muscle pigmentation is important from both a nutritional and economic lens, especially as climate change continues to impact the resources this species relies on.

The objective of this study was to examine which diet variables (stomach contents, nitrogen stable isotope ratios ($\delta^{15}N$), and highly branched isoprenoids) are most influential on carotenoid concentration and muscle pigmentation of Arctic char. To do this, we sampled Arctic char and their invertebrate and fish prey at a southern (Rankin Inlet) and northern (Naujaat) location along the western Hudson Bay coast and determined carotenoid concentrations using spectrophotometry analysis and muscle colour of Arctic char using a standard colour scale (DSM SalmoFan). Stable isotope ratios of nitrogen ($\delta^{15}N$) estimate consumer trophic positions (TP; Boecklen et al., 2011), while HBIs have been extensively used across Arctic environments to examine consumer utilization of sea ice algae versus phytoplankton carbon sources (Brown and Belt, 2012; Koch et al., 2023). We hypothesized that Arctic char carotenoid concentration and muscle pigmentation will vary spatially in relation to dietary differences (invertebrate versus fish consumption) found between the two study sites (Faulkner et al., in review). Further, we predicted that Naujaat Arctic char will have higher red-pigment associated carotenoid concentrations (e.g., astaxanthin) and that muscle pigmentation will fall along an orange-red colour gradient versus a pale-pink colour gradient compared to Rankin Inlet Arctic char due to a higher consumption of invertebrates that also contain higher carotenoid concentrations than fishes.

3.3 Materials and Methods

3.3.1 Sample Collection

Arctic char were collected by angling and gillnetting between June and August in 2021 and 2022 (Table 3.1) while foraging in the estuarine and marine environments along the western Hudson Bay coast near the communities of Rankin Inlet (Diana River – 62^o 49.4' N, 92^o 21.5' W) and Naujaat (Sipujaqtuu – 66^o 23.2' N, 86^o 43.3' W and Tikiraq – 66^o 26.0' N, 86^o 37.0' W), Nunavut, which are separated by approximately 500 km (Figure 3.1). Upon capture, we recorded fork length (cm), round weight (kg), lipid content (%; for 2022 only), muscle colour (measured using a DSM SalmoFan muscle colour scale), sex, and maturity status for all Arctic char, with the exception of Naujaat Arctic char in 2021 that were collected by community members. Maturity was assessed by visually examining the size and length of ovaries or testes and assigning a maturity status (immature, mature, running ripe, spent, resting, and unknown); if maturity could not be determined, a status of unknown was assigned. Despite sex and maturity being recorded, these variables were excluded from further analyses due to small sample sizes across categories. Fulton's condition factor (hereafter, body condition) was calculated using the equation:

$$K = 100 * \frac{W}{L^3},$$

where *W* is round weight (g) and *L* is fork length (cm; Getso et al., 2017). Despite body condition being recorded, due to missing data in 2021, this variable could not be included in statistical analyses. Arctic char lipid content was recorded in line with the dorsal fin just above the lateral line using a Fish Fat Meter (Distell Model FFM-692, Fauldhouse, Scotland) in 2022 only. We also collected Arctic char livers to assess short-term diet (e.g., days to weeks; Tieszen et al. 1983; MacNeil et al. 2006) using nitrogen stable isotopes (δ^{15}N) and HBI ratios, as previous analysis has found that approximately 70% of HBIs within an organism are stored in liver tissues (Brown et al. 2013). Further, Arctic char dorsal muscle was collected to quantify carotenoids, as muscle from this position is most representative of whole fillet carotenoid concentration (Hatlen et al., 1998). Concurrently, to compare the carotenoid concentration of prey types (e.g., *Onisimus* spp., *Gammarus* spp., *Themisto* spp., capelin, sand lance, sculpins) with Arctic char muscle, potential invertebrate prey types were opportunistically collected in the vicinity of the sampling sites in 2022 using a conical zooplankton net (200-micron mesh). Additionally, marine fish were opportunistically collected by angling or obtained fresh from Arctic char stomachs over both years in Rankin Inlet, while samples from the Naujaat area were collected in 2018 and 2019.

3.3.2 Dietary Analysis

Stomach contents were used to determine the dietary composition and relative importance of discrete prey types of Arctic char from both the Rankin Inlet and Naujaat study sites. Stomach content analysis followed methodologies in Faulkner et al., in review. In brief, individual prey items in each stomach were identified to the lowest taxonomic level possible (owing to digestion), enumerated, and weighed (e.g., Dempson et al., 2002; Moreno-Sanchez et al., 2016). Stomach contents were classified into two main groups (i.e., invertebrates versus fish) and dominant prey types within each group were used to calculate the proportion of each prey type group contributing to the dietary composition of individual Arctic char and to select key prey types to include in carotenoid spectrophotometry analysis.

Stable isotope ratios of nitrogen ($\delta^{15}N$) within liver tissue were used to determine the TP of Arctic char at both study sites. Additionally, copepods were collected in each year at each study site (see methods in Faulkner et al., in review) or obtained from Amiraux et al., 2023. Stable isotope analysis followed methodologies in Faulkner et al., in review. In brief, stable isotope ratios were measured in liver tissues of Arctic char and bulk copepods using a Delta V Isotope Ratio Mass Spectrometer (Thermo) through a Conflo-IV Interface (Thermo) at the Stable Isotopes in Nature Laboratory (SINLAB; University of New Brunswick, Fredericton, New Brunswick, Canada). Stable isotope ratios are reported in standard delta notation for nitrogen relative to the primary reference material atmospheric nitrogen (N_2/AIR). Additionally, TP was calculated using a one source TP model with *Calanus* spp. $\delta^{15}N$ values serving as the baseline (Post, 2002).

To quantify the carbon source use of Arctic char diet at both study sites, HBI ratios were measured from liver tissues of Arctic char using a 7890B Gas Chromatograph (Agilent) coupled to a 5977B Mass Selective Detector (Agilent) equipped with a Purged Ultimate Union (Agilent) at the Freshwater Institute (Winnipeg, Manitoba, Canada; see Faulkner et al., in review for more details). In brief, HBI lipids were extracted and upon analysis, H-Print values were calculated for individual Arctic char by comparing the ratio of HBIs derived from phytoplanktonic diatoms ($\sum$ III a-d) to those derived from sea ice diatoms ($\sum$ IP_{25} and IIb), and later converted to represent a value of ice particulate organic carbon (iPOC; Brown et al., 2018).

3.3.3 Muscle Pigment and Colour Analysis

Carotenoid spectrophotometry analysis was used to quantify the carotenoid concentration in Arctic char muscle and potential prey types (invertebrates and fish) collected at each study site. All available muscle tissue of smaller fish (i.e., capelin, sand lance, and larval/juvenile sculpin), dorsal muscle of larger fish (i.e., mature sculpins, cod), and whole specimens (carapace and internal tissues) of invertebrates (i.e., *Onisimus* spp., *Gammarus* spp., mysids, *Themisto* spp., and *Hyas* spp. (crab zoea)) were used to quantify carotenoids. Further, dorsal portions of Arctic char muscle samples were assigned a muscle colour value using a DSM SalmoFan between 20 and 34 (pale versus red muscle colour; e.g., Bolduc et al., in press; Figure 3.2).

Arctic char and prey type tissue samples were weighed (g), subsampled (~1.50 g), and then freeze dried (-50^{o}C) for 48-72 hours to remove moisture. Samples underwent carotenoid spectrophotometry analysis at TransBIOTech Laboratory (Levis, Quebec, Canada) using a UPC^{2} UV-Visible Spectrophotometer (Acquity) equipped with a PDA (Acquity) detector. The concentrations of eleven carotenoid pigments (α-carotene, β-carotene, astaxanthin, canthaxanthin, lutein, zeaxanthin, fucoxanthin, α-cryptoxanthin, β-cryptoxanthin, echinenone, and alloxanthin) and retinol were quantified. Astaxanthin was the carotenoid of primary interest, as it is typically found in highest concentrations within salmonid muscle and the dominant pigment in muscle colouration (Hatlen et al., 1996; Bjerkeng et al., 2000; Rajasingh et al., 2007; Garner et al., 2010). Additionally, canthaxanthin was examined, as astaxanthin and canthaxanthin in combination have been found to increase salmonid muscle pigmentation (Cankiriligil et al., 2022; Bolduc et al., in press). Retinol was also examined, as carotenoids are known to act as precursors for vitamin A which are beneficial to the health and fitness of salmonids (Rajasingh et al., 2007; Garner et al., 2010).

3.3.4 Statistical Analysis

To examine differences in Arctic char muscle pigmentation and determine the best predictors for the dependent variables of Arctic char astaxanthin, canthaxanthin, and retinol concentration in muscle, general linear models were constructed using the *lm* function from the *lme4* package in R (R Core Team, 2023). Predictor variables included year, study site, Arctic char TP, iPOC, and invertebrate proportion in the diet (hereafter, invertebrate proportion). The following interactions were also included to examine their influence on muscle pigmentation: year and study site, study site and TP, study site and iPOC, year and invertebrate proportion, and study site and invertebrate proportion. Prior to model runs, predictor variables were assessed for correlation with none being highly correlated ($r < 0.53$ among all predictor variables). The top model was selected based on the examination of Akaike Information Criterion values (ΔAICc = 0.00) and models with a ΔAICc ≤ 2.00 were considered plausible with substantial support (Burnham and Anderson, 2004). The normality and homoscedasticity of the response variables were visually assessed by examining histograms and scatterplots of the residual values. Response variables were log+1 transformed to meet the assumptions of parametric statistics. Additionally, Pearson correlation tests were run between the three response variables across all Arctic char, including between Arctic char astaxanthin and canthaxanthin concentration, astaxanthin and retinol concentration, and canthaxanthin and retinol concentration. Correlations were also run across all Arctic char between muscle astaxanthin concentration and invertebrate proportion, TP, iPOC, body condition (2022 only), muscle colour value (DSM SalmoFan), and lipid content. Further, a Student's t-test (or non-parametric equivalent) was used to test for differences between Rankin Inlet and Naujaat Arctic char muscle colour (DSM SalmoFan values) in 2022. All data analysis was conducted in R version 4.3.0 (R Core Team, 2023). Unless otherwise stated, all levels of statistical significance were set at $\alpha = 0.05$.

3.4 Results

Prey carotenoid and retinol concentration varied by prey type (invertebrates versus fish; Table 3.2). The highest prey astaxanthin concentrations were present within the whole bodies of the invertebrates: *Gammarus* spp. (80.7 ± 44.0 mg/kg), followed by *Onisimus* spp. (58.5 ± 67.7 mg/kg), mysids (11.8 ± 5.6 mg/kg), crab zoea (4.2 ± 0.2 mg/kg), and *Themisto* spp. (2.6 ± 1.0 mg/kg). Of all the prey types, sculpins (larval/juvenile: 1.0 ± 0.7 mg/kg; mature: 0.2 ± 0.2 mg/kg) were lowest in astaxanthin. Astaxanthin was absent within all other fish groups, including capelin (0.0 ± 0.0 mg/kg), sand lance (0.0 ± 0.0 mg/kg), and cod (0.0 ± 0.0 mg/kg). Canthaxanthin and retinol were present in low concentrations or absent within most prey types (Table 3.2).

All model runs for predicting Arctic char astaxanthin, canthaxanthin, and retinol muscle concentration can be found in Supplementary Materials, while top and plausible models are presented in Table 3.3. The best model for predicting Arctic char muscle astaxanthin concentration included year, study site, TP, iPOC, and the interaction between year and study site ($F_{5,178} = 41.6$, $p < 0.0001$, $R^2 = 0.54$; Table 3.3). Arctic char muscle astaxanthin concentration was significantly higher in 2021 than 2022 ($F_{1,178} = 14.9$, $p = 0.0002$), in Naujaat Arctic char compared to Rankin Inlet Arctic char muscle ($F_{1,178} = 68.3$, $p < 0.0001$), and in Arctic char occupying a lower TP ($F_{1,178} = 3.9$, $p = 0.0490$; Figure 3.3). The interaction between year and study site ($F_{1,178} = 80.5$, $p < 0.0001$) was also a significant predictor of Arctic char muscle astaxanthin concentration (Figure 3.3). Further, the best model for predicting Arctic char muscle canthaxanthin concentration included study site, TP, iPOC, and the interaction between study site and TP ($F_{4,179} = 30.4$, $p < 0.0001$, $R^2 = 0.40$; Table 3.3). Arctic char muscle canthaxanthin concentration was significantly higher in Naujaat Arctic char compared to Rankin Inlet Arctic char ($F_{1,179} = 29.1$, $p < 0.0001$) and in Arctic char with higher iPOC values ($F_{1,179} = 7.6$, $p = 0.0063$; Figure 3.4). The interaction between study site and TP ($F_{1,179} = 29.8$, $p < 0.0001$) was also a significant predictor of Arctic char muscle canthaxanthin concentration (Figure 3.4). Finally, the best model for predicting Arctic char muscle retinol concentration included year, study site, and the interaction between year and study site ($F_{3,180} = 9.2$, $p < 0.0001$, $R^2 = 0.13$; Table 3.3). The interaction between year and study site ($F_{1,180} = 7.8$, $p = 0.0059$) was a significant predictor of Arctic char muscle retinol concentration (Figure 3.5).

Further, Arctic char muscle astaxanthin and canthaxanthin concentrations were positively correlated ($r = 0.40$, $p < 0.0001$), although muscle astaxanthin and retinol ($r = -0.09$, $p = 0.2077$) and muscle canthaxanthin and retinol ($r = -0.05$, $p = 0.4871$) concentrations were not significantly correlated across all individuals. Arctic char muscle astaxanthin concentration was significantly correlated with invertebrate proportion in the diet ($r = 0.49$, $p < 0.0001$; Figure 3.3 A,D), TP ($r = -0.41$, $p < 0.0001$; Figure 3.3 B,E), iPOC (0.47, $p < 0.0001$; Figure 3.3 C,F), body condition ($r = 0.27$, $p = 0.0130$), and muscle colour ($r = 0.38$, $p < 0.0001$). In 2022, muscle colour (DSM SalmoFan values) was also higher in Naujaat Arctic char compared to Rankin Inlet Arctic char ($W = 131.0$, $p < 0.0001$; 30 ± 2 versus 22 ± 2; Table 3.1). Interestingly, Arctic char muscle astaxanthin concentration and lipid content were not significantly correlated ($r = 0.08$, $p = 0.5202$), although lipid content was only recorded for a subset of Arctic char from Rankin Inlet and Naujaat in 2022. Overall, these results support that Arctic char muscle astaxanthin concentration increased with the consumption of invertebrate prey types and consumption of more sea ice algae-based carbon sources, but decreased with the consumption of prey types occupying a higher TP (e.g., fish; Table 3.2), overall influencing the redness of Arctic char muscle.

3.5 Discussion

This is the first study to characterize spatiotemporal variability in muscle pigmentation of anadromous Arctic char in relation to diet and sea ice dynamics, while also including correlations between carotenoid concentration and dietary composition of consumers and their prey in the Arctic. Our results support the influence of diet on muscle pigmentation using wild Arctic char; a subject that has been widely studied across the aquaculture sector although it has been seldom-studied among wild salmonids. Arctic char muscle carotenoid concentration and colour was associated with differences in the amount of invertebrate versus fish consumption, as suggested by observed relationships with Arctic char TP. Spatial and inter-annual differences in sea ice cover between years and study sites also likely influenced the availability and distribution of local prey types, and in turn Arctic char diet (see Faulkner et al., in review) and concentrations of assimilated dietary carotenoids within Arctic char muscle.

3.5.1 Spatial and Temporal Variability in Muscle Pigmentation

As predicted, we found that a higher consumption of invertebrate prey types was associated with higher levels of Arctic char red-pigment-associated carotenoid concentrations (i.e., astaxanthin), and generally, Naujaat Arctic char muscle contained higher red-pigment-associated carotenoid concentrations compared to Rankin Inlet Arctic char. The strength of the relationship, however, varied by year. The difference in the amount of invertebrates consumed by Rankin Inlet (2021: 10.6%; 2022: 13.1%) and Naujaat Arctic char (2021: 99.7%; 2022: 47.2%) across years suggests an influence on their astaxanthin concentration given the significant correlation between the proportion of invertebrates in the diet and muscle astaxanthin concentration. Interestingly, Naujaat Arctic char muscle colour still fell along an orange-red colour gradient (DSM SalmoFan value: 30) despite their muscle astaxanthin concentration being lower in 2022 (2.1 mg/kg) than 2021 (7.8 mg/kg). Given the opportunistic, generalist foraging strategy of Arctic char, their consumption of prey types with lower carotenoid concentrations in response to differences in sea ice dynamics between years, especially in Naujaat, likely contributed to lower Arctic char muscle carotenoid concentration in 2022.

The decrease in Naujaat Arctic char muscle astaxanthin concentration in 2022 relative to 2021 was likely the result of a significant decrease in the relative importance of invertebrates (e.g., *Gammarus* spp., *Onisimus* spp.) in their diet given the high astaxanthin concentration of these invertebrate prey types. Invertebrates (e.g., *Onisimus litoralis*, *Gammarus wilkitzkii*) occupy a lower TP and consume more sea ice algae from benthic sediments (Gradinger and Bluhm, 2010) compared to fish (e.g., capelin; Koch et al. 2023). In 2022, Naujaat Arctic char consumed fewer invertebrates and occupied a higher TP, although they utilized relatively consistent carbon sources across years. Therefore, it is likely that the higher consumption of fish prey types and foraging on higher TP organisms (e.g., fish versus invertebrates) and phytoplankton-based carbon resources (e.g., species with lower iPOC values) influence Arctic char muscle astaxanthin concentration by contributing less dietary carotenoids, in turn, decreasing muscle pigmentation. Similarly, in Nunavik, Quebec, Bolduc et al. (in press) found that spatial differences in Arctic char muscle astaxanthin concentration likely stemmed from differences in diet, where Arctic char with higher $\delta^{13}C$ values were more reliant on benthic prey types (e.g., invertebrates) and contained higher concentrations of astaxanthin compared to those with lower $\delta^{13}C$ values. As the Arctic continues to experience a disproportionate shift in the availability and distribution of endemic prey species (e.g., ice-associated invertebrates) towards more subarctic-associated prey species (e.g., capelin; Fossheim et al., 2015; Kortsch et al., 2015; Yurkowski et al., 2017), northern locations such as Naujaat may experience increases in prey with lower carotenoid concentrations (e.g., fish). As a result, Arctic char inhabiting more northern ecosystems may experience a shift in dominant prey types that are lower in nutritional quality (e.g., astaxanthin), in turn negatively influencing Arctic char muscle pigmentation.

In both study years, astaxanthin was found in higher concentrations than both canthaxanthin and retinol within Arctic char muscle, as would be expected given the higher metabolic turnover of canthaxanthin (Bjerkeng et al., 1992). Despite the higher concentration of astaxanthin, both astaxanthin and canthaxanthin in combination have been found to increase muscle pigmentation (Cankiriligil et al., 2022; Bolduc et al., in press). Indeed, this is supported in the current study, as Naujaat Arctic char muscle contained higher concentrations of both astaxanthin and canthaxanthin in 2021 in association with higher invertebrate consumption. However, muscle carotenoid concentrations were similar between Naujaat and Rankin Inlet Arctic char in 2022, related to higher fish consumption by Naujaat Arctic char. Further, Arctic char muscle retinol concentrations were low in both Naujaat and Rankin Inlet Arctic char muscle, which was also previously observed by Bolduc et al. (in press). Indeed, as carotenoids accumulate in various body tissues upon being metabolized, the carotenoid composition of tissues not only reflect of consumer diet, but also factors influencing metabolism (e.g., growth rate, activity; Johnston et al., 2006). The carotenoid composition of tissues is also influenced by maturity status, as mature individuals tend to redistribute carotenoids from their muscle to skin and gonads (Bjerkeng et al., 2000; Ganer et al., 2010). Therefore, retinol may be metabolized for individual nutrition (e.g., Choubert and Blanc, 1993), while astaxanthin and other carotenoids (e.g., canthaxanthin) may be reserved in muscle tissues for future offspring nutrition (e.g., Lehnert et al., 2017; Lehnert et al., 2018).

Despite the observed orange-red muscle colour but lower astaxanthin concentration of Naujaat Arctic char in 2022, a local resource user from Naujaat shared that "Arctic char are usually much oranger than this year" (J.-E. Tinashlu, Naujaat local resource user, pers. comm.). Torrissen (1985) found that within immature cultured rainbow trout (*Oncorhynchus mykiss*) fed a non-supplemented astaxanthin diet, muscle astaxanthin concentration declined rapidly after five weeks. Therefore, there may be a similar time lag between dietary carotenoid assimilation (or lack thereof) being visually reflected by Arctic char muscle colour. The interpretation of this result, however, should be considered cautiously as many other variables (e.g., fish size, sex, species; Tolasa et al., 2005) and ecological factors may further influence the accumulation and assimilation of dietary carotenoids within salmonid species.

3.5.2 Additional Influencers of Muscle Pigmentation

In addition to the influence of diet on the muscle pigmentation of Arctic char, many ecological factors can influence the accumulation and assimilation of carotenoids. Other salmonid species, such as Chinook salmon (*O. tshawytscha*), for example, exhibit a genetic-based colour polymorphism, whereby white and red morphs differ in their ability to assimilate dietary carotenoids into tissues (Lehnert et al., 2017; Lehnert et al., 2018). Such differences are known to have fitness consequences, whereby higher carotenoid concentration and, therefore, muscle pigmentation, are correlated with increased survival during egg incubation and higher offspring quality (Lehnert et al., 2017). Given the visual differences between Rankin Inlet and Naujaat Arctic char muscle colour but the similar concentrations of astaxanthin in 2022, it is plausible that there may be genetic differences between the Rankin Inlet and Naujaat Arctic char populations which influence their abilities to assimilate dietary carotenoids into their muscle. Previous Arctic char telemetry and tagging results support that there is likely limited mixing between Arctic char from our study locations, as Arctic char typically move less than the 500 km distance separating our locations during their marine residency period (Dempson and Kristofferson, 1987; Smith et al., 2024). Additionally, maturity status of salmonids has been linked to variable muscle astaxanthin concentrations, given that maturing individuals redistribute astaxanthin from their muscle to the skin and gonads during spawning (Bjerkeng et al., 2000; Garner et al., 2010). Although maturity status of Arctic char could not be explored due to small sample sizes in our study, it is probable that maturity also influenced the carotenoid concentrations of Arctic char muscle.

Another factor influencing the accumulation and assimilation of carotenoids may be variable total lipids within Arctic char muscle, as higher amounts of lipids (e.g., omega-3 fatty acids) have been linked to higher levels of astaxanthin within wild anadromous Arctic char (Bolduc et al., in press). Although our study did not examine levels of omega-3 fatty acids, Naujaat Arctic char had a similar lipid percentage compared to Rankin Inlet Arctic char (8.9% versus 8.4%) while also containing similar astaxanthin concentrations in 2022 (2.1 mg/kg versus 1.4 mg/kg). Despite Arctic char muscle astaxanthin concentration and lipid content not being significantly correlated within our study, our small sample sizes may factor in to this lack of relationship, and therefore, further study is required. It has also been reported that in addition to diet, body condition influences the accumulation of both omega-3 fatty acids and the carotenoid astaxanthin (Bolduc et al., in press). This is supported in the current study, as Arctic char muscle astaxanthin concentration and body condition were significantly correlated, suggesting that individuals with a higher body condition assimilate more carotenoids into their tissues. Overall, there are many ecological factors that influence the accumulation and assimilation of carotenoids, and therefore, further study is required to examine their influence on wild salmonid muscle pigmentation.

3.6 Conclusion

In this study, we examined Arctic char muscle pigmentation in relation to diet and correlations between the carotenoid concentration and dietary composition of consumers and their prey along western Hudson Bay in the Kivalliq region of Nunavut. As predicted, Arctic char muscle pigmentation was higher in Naujaat compared to Rankin Inlet as a result of higher invertebrate consumption. Given the subsistence and economic importance of anadromous Arctic char in the region (Sprules, 1952; Government of Nunavut, 2018), the impacts of changing sea ice dynamics and local prey composition on Arctic char muscle pigmentation may have future socioeconomic implications. As such, the continued monitoring of spatiotemporal variation in salmonid muscle pigmentation in response to changes in the foraging ecology of opportunistic, generalist top predators, such as Arctic char, can provide an indication of changes to Arctic marine food web structure and their implications on Inuit.

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3.9 Tables

Table 3.1: Mean (± standard deviation) of Arctic char length, weight, astaxanthin, canthaxanthin, and retinol concentration, SalmoFan values, lipid content, and body condition by location and year.

Location/Year	n	Length (cm)	Weight (g)	Astaxanthin (mg/kg)	Canthaxanthin (mg/kg)	Retinol (mg/kg)	SalmoFan value	Lipid (%)	Body Condition
2021									
Rankin Inlet	59	59.7 ± 8.5	2904 ± 1233	0.6 ± 0.5	0.0 ± 0.2	0.0 ± 0.0	23 ± 3	-	1.3 ± 0.3
Naujaat	41	-	-	7.8 ± 5.7	1.1 ± 2.0	0.0 ± 0.1	-	-	-
2022									
Rankin Inlet	50	68.0 ± 8.2	3654 ± 1244	1.4 ± 0.9	0.1 ± 0.2	0.0 ± 0.0	22 ± 2	8.4 ± 2.4	1.1 ± 0.2
Naujaat	34	53.6 ± 7.8	2039 ± 787	2.1 ± 2.0	0.2 ± 0.3	0.2 ± 0.5	30 ± 2	8.9 ± 2.6	1.2 ± 0.1

Table 3.2: Mean (± standard deviation) of astaxanthin, canthaxanthin, and retinol concentrations by prey category and type.

Prey Category	Prey Type	n*	Trophic Position	Astaxanthin (mg/kg)	Canthaxanthin (mg/kg)	Retinol (mg/kg)
Invertebrates	*Onisimus* spp.	5/10	2.4 ± 0.5	58.5 ± 67.7	1.5 ± 1.7	0.0 ± 0.1
	Gammarus spp.	11/13	1.9 ± 0.2	80.7 ± 44.0	0.6 ± 1.0	0.1 ± 0.2
	Mysis spp.	0/4	N/A	11.8 ± 5.6	0.5 ± 0.3	5.0 ± 1.0
	Themisto spp.	3/9	2.4 ± 0.1	2.6 ± 1.0	0.0 ± 0.0	0.2 ± 0.2
	Crab zoea (*Hyas* spp.)	3/3	2.3 ± 0.1	4.2 ± 0.2	0.4 ± 0.7	0.0 ± 0.0
Fish	Capelin	15/11	3.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Sand lance	13/5	3.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Sculpin (mature)	5/8	3.5 ± 0.5	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
	Sculpin (larval/juvenile)	3/5	3.0 ± 0.4	1.0 ± 0.7	0.0 ± 0.0	0.0 ± 0.0
	Cod	0/4	N/A	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

* Sample sizes for stable isotope analysis (left) and carotenoid spectrophotometry analysis (right) of prey types.

Table 3.3: Statistical results from the top (ΔAICc = 0.00) and plausible (ΔAICc $\leq$ 2.00) models for determining the best predictors for Arctic char astaxanthin, canthaxanthin, and retinol concentration. Predictor variables include: year, study site, trophic position (TP), ice particulate organic carbon (iPOC), and invertebrate proportion in the diet, and the interactions between year and study site, study site and TP, study site and iPOC, year and invertebrate proportion in the diet, and study site and invertebrate proportion in the diet.

Model		R^2	P-value	AICc	ΔAICc
Astaxanthin ~					
	year + study site + TP + iPOC + year*study site	0.54	<0.0001	296.65	0.00
	year + study site + year*study site	0.52	<0.0001	298.64	1.99
Canthaxanthin ~					
	study site + TP + iPOC + study site*TP	0.40	<0.0001	66.78	0.00
	year + study site + TP + iPOC + study site*TP	0.40	<0.0001	68.74	1.96
Retinol ~					
	year + study site + year*study site	0.13	<0.0001	-199.07	0.00

3.10 Figures

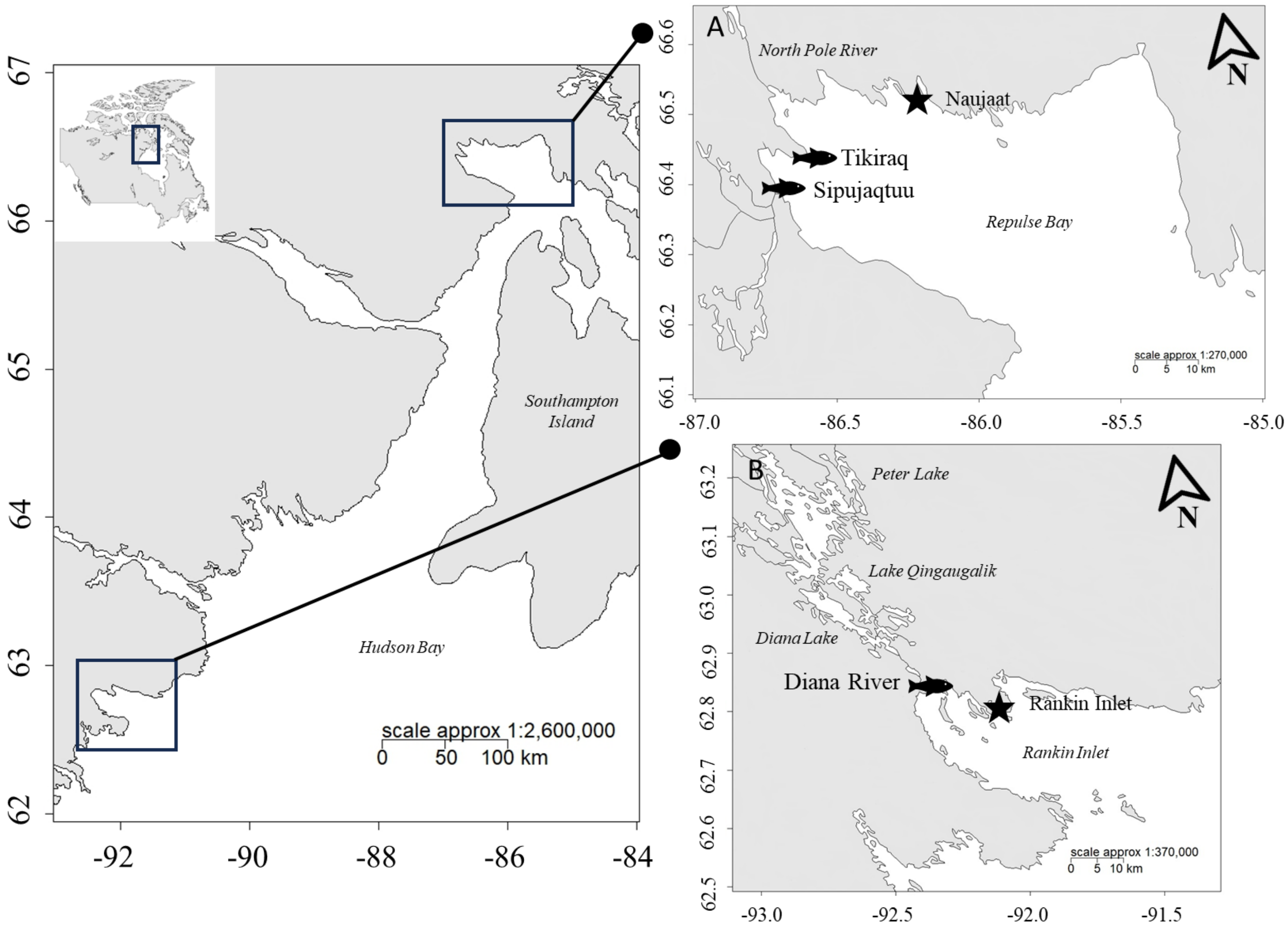

Figure 3.1: Map of the western Hudson Bay coast highlighting: A) the Sipujaqtuu and Tikiraq study sites in Repulse Bay and B) the Diana River study site in Rankin Inlet. The communities of Rankin Inlet and Naujaat are indicated by black stars.

Figure 3.2: DSM SalmoFan muscle colour scale used to assign a muscle colour value between 20 (pale muscle colour) and 34 (red muscle colour) to the dorsal portion of Arctic char muscle.

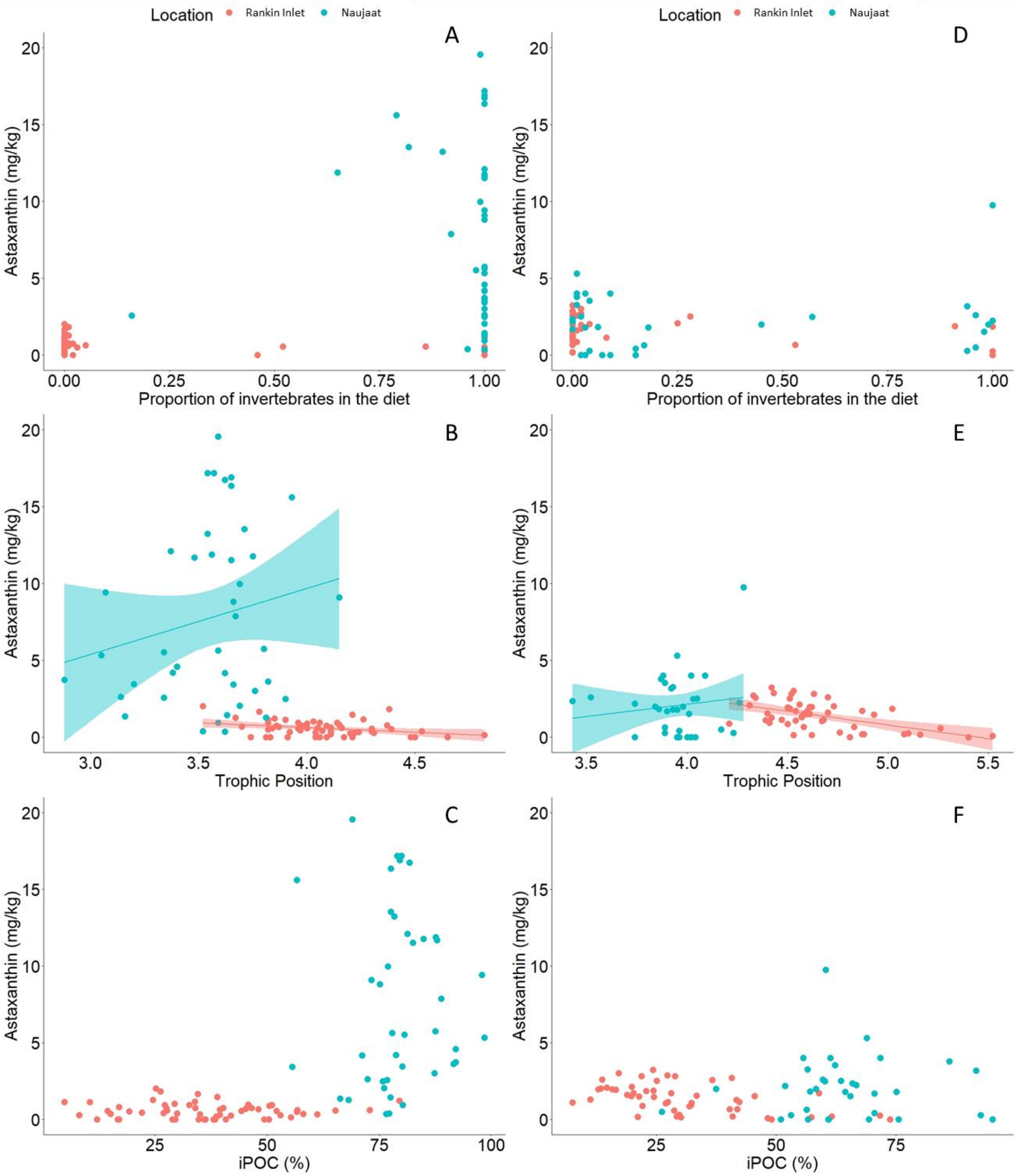

Figure 3.3: Relationships between Arctic char astaxanthin concentration and: A) 2021 invertebrate proportion in the diet, B) 2021 trophic position, C) 2021 ice particulate organic carbon (iPOC) values, D) 2022 invertebrate proportion in the diet, E) 2022 trophic position, and F) 2022 ice particulate organic carbon (iPOC) values.

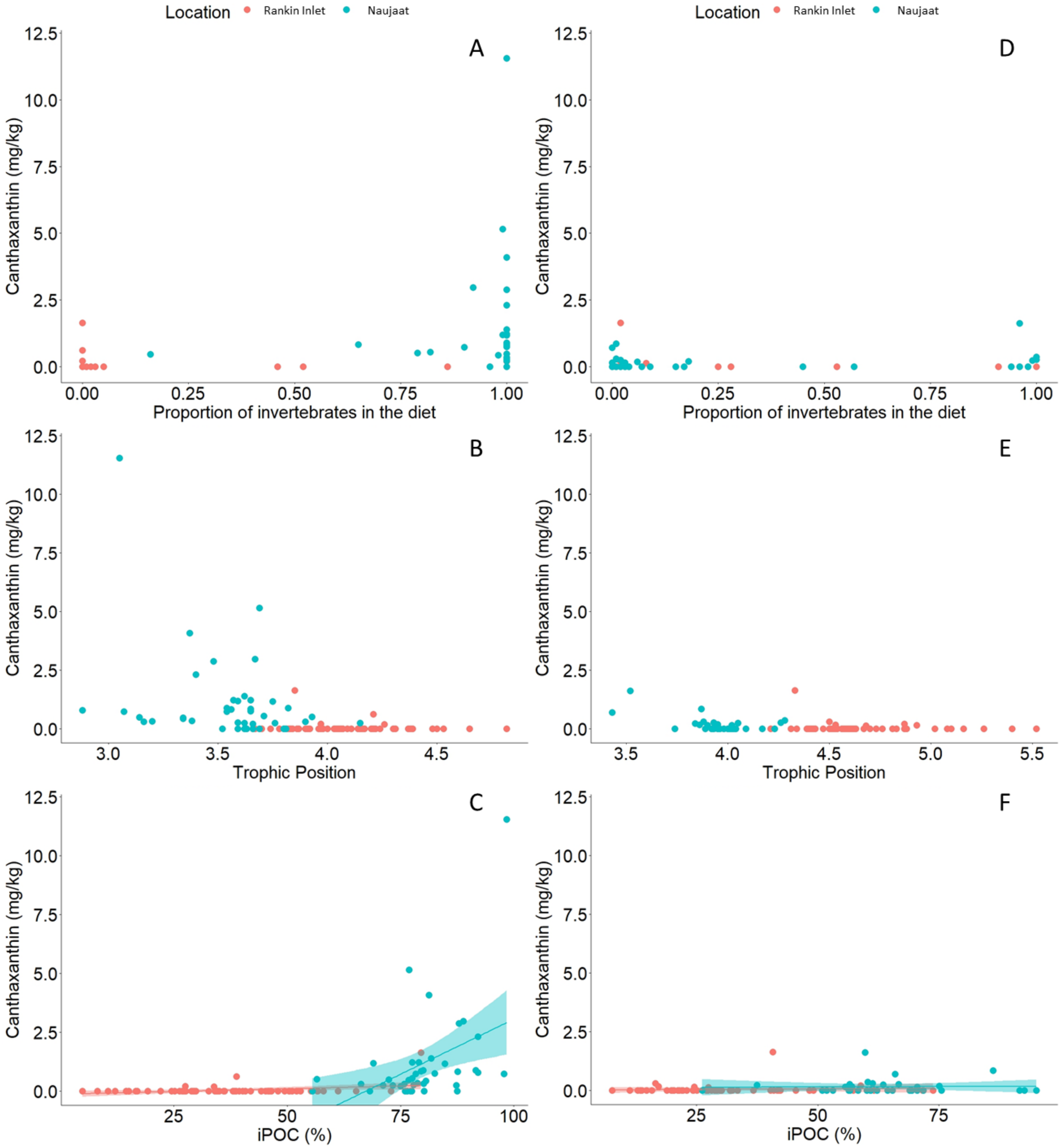

Figure 3.4: Relationships between Arctic char canthaxanthin concentration and: A) 2021 invertebrate proportion in the diet, B) 2021 trophic position, C) 2021 ice particulate organic carbon (iPOC) values, D) 2022 invertebrate proportion in the diet, E) 2022 trophic position, and F) 2022 ice particulate organic carbon (iPOC) values.

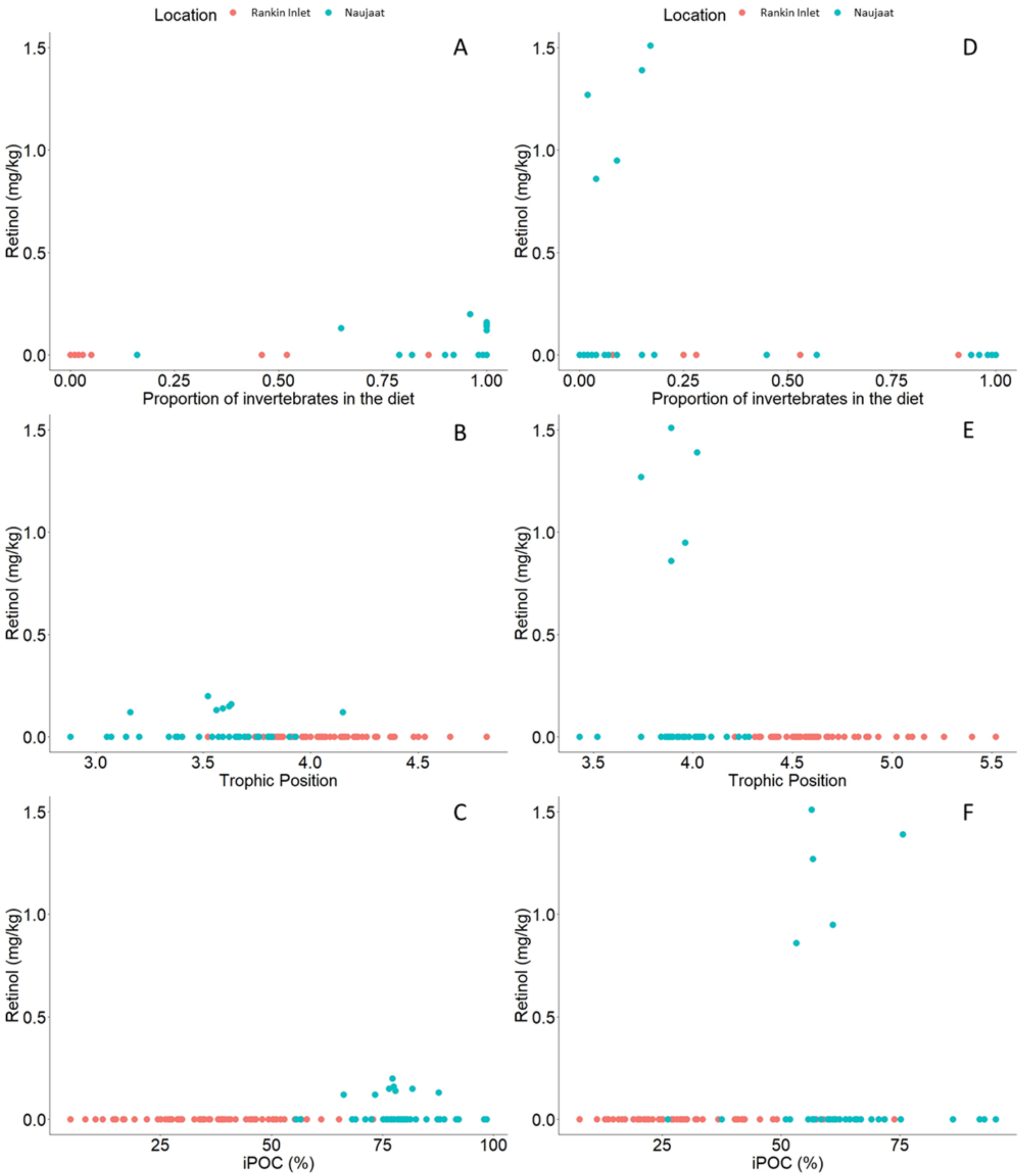

Figure 3.5: Relationships between Arctic char retinol concentration and: A) 2021 invertebrate proportion in the diet, B) 2021 trophic position, C) 2021 ice particulate organic carbon (iPOC) values, D) 2022 invertebrate proportion in the diet, E) 2022 trophic position, and F) 2022 ice particulate organic carbon (iPOC) values.

Chapter 4 General Conclusion, Socioeconomic Implications, and Future Research

4.1 General Conclusion

This is the first study to characterize spatiotemporal variability in anadromous Arctic char (*Salvelinus alpinus*) foraging ecology, specifically in relation to sea ice variability and its influence on muscle pigmentation across their range. As such, this study provides novel findings and baseline information that can guide and compliment future research in this area of the Eastern Canadian Arctic. In Chapter 2, I found that Arctic char diet differed between a southern (Rankin Inlet) and northern (Naujaat) sampling location separated by approximately 500 km along western Hudson Bay within a single foraging season when sea ice dynamics (e.g., ice-off date, sea ice concentration) differed between study sites (2021). However, I showed that when sea ice dynamics were more comparable between these two locations, diet of Arctic char was also similar (2022). These dietary differences likely reflect varying availability and distribution of local prey types associated with sea ice dynamics. More specifically, Rankin Inlet Arctic char consistently consumed forage fish, used more phytoplankton-based carbon sources, occupied a higher TP, and used a similar breadth of resources as Naujaat Arctic char. In contrast, Naujaat Arctic char generally consumed more ice-associated invertebrates in 2021 and switched to largely consume sculpins (Cottidae) in 2022, but used more ice algae-based carbon sources and occupied a lower TP than Rankin Inlet Arctic char across years.

In Chapter 3, I found that Arctic char muscle carotenoid concentration (i.e., astaxanthin) also differed between the Rankin Inlet and Naujaat study sites when diet composition and sea ice dynamics were different (2021). Muscle carotenoid concentrations, however, were more similar when diet composition and sea ice dynamics were more comparable between the two locations

(2022). Such differences in Arctic char muscle carotenoid concentration were likely due to the spatial and inter-annual differences in diet (fish versus invertebrate consumption) reported in Chapter 2. Examination of prey type carotenoid concentrations also indicated that invertebrate prey types contained higher amounts of carotenoids than forage fish prey types. Additionally, the proportion of invertebrates in the diet was significantly correlated with Arctic char muscle astaxanthin concentration, indicating that Arctic char muscle astaxanthin concentration increased when there was a higher percentage of invertebrate prey types in the diet. Naujaat Arctic char muscle carotenoid concentration was generally higher than Rankin Inlet across years, although their shift from an invertebrate-based diet to a fish-based diet in 2022 was associated with a decrease in their muscle carotenoid concentration. Interestingly, despite Naujaat Arctic char muscle containing similar carotenoid concentrations as Rankin Inlet Arctic char in 2022, their muscle colour still fell along an orange-red colour gradient on the DSM SalmoFan muscle colour scale (30 versus 22). Overall, my findings indicated Arctic char diet composition was correlated with muscle carotenoid concentration and redness, likely in response to year-specific sea ice dynamics and local availability of prey types. Lastly, as communities within the Kivalliq region of Nunavut have recently expressed interest in gaining western scientific knowledge on the diet and muscle colour of Arctic char across the region, my findings provide communities with answers to questions they directly developed and assisted in answering.

4.2 Socioeconomic Implications

It is well known that red-muscle Arctic char is preferred locally and economically as they are considered to be richer in flavour and higher in nutritional quality, and therefore can be marketed as a higher value product (Bovin and Power, 1990; S. Sadler, Kivalliq Arctic Foods manager, pers. comm.). The nutritional quality of Arctic char has been shown to be highly influenced by diet and the dynamics of local marine ecosystems in other areas across Inuit Nunangat. For example, Bolduc et al., (in press) reported that Arctic char feeding in more benthic/coastal habitats exhibited higher concentrations of astaxanthin, likely due to the consumption of invertebrates (e.g., amphipods, mysids) that are also high in astaxanthin. These results are further supported in this thesis. Future decreases in sea ice extent may provide favourable conditions for more subarctic-associated forage fish species to increase their availability within more northern locations of the Arctic, which will undoubtedly influence the foraging ecology of Arctic char and other higher trophic level species. Indeed, previous studies examining upper-level consumer diets in the Arctic have provided an early indication of long-term ecosystem-level shifts and changes in prey availability and distribution in multiple regions including Hudson Bay (Gaston et al. 2003), the Beaufort Sea (Harwood et al. 2015), and Cumberland Sound (Yurkowski et al. 2018; Ulrich and Tallman 2021). Further, Ulrich and Tallman (2021) reported a long-term diet shift of Cumberland Sound, Nunavut Arctic char from ice-associated invertebrates to capelin (*Mallotus villosus*), which resulted in higher Arctic char growth rates but a decrease in body condition. Such findings highlight that initially, climate-driven diet shifts towards more subarctic-associated species may be beneficial for Arctic consumers, such as the anadromous Arctic char, but may have negative impacts over the long term.

As red-coloured muscle of Arctic char is locally preferred (Bovin and Power, 1990), future changes in Arctic char muscle pigmentation to the less desirable pale-coloration may potentially increase food insecurity in northern communities, as residents try to find alternative nutritious food sources that are often higher in price or harder to obtain (e.g., beef, pork). If local resource users decide to consume pale-muscle Arctic char, they will likely not obtain the same nutritional value as that obtained from red-muscle Arctic char (e.g., fatty acids, vitamin A;

Bolduc et al., in press). Additionally, under the Nunavut Land Claim Agreement, Inuit have the right to sell, barter, exchange, or give wildlife that is lawfully harvested (NTI and INAC, 2018), much of which is traded or sold over informal business platforms such as social media (e.g., Facebook). For example, residents in Rankin Inlet may buy or trade products (e.g., caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*)) with residents in Naujaat (e.g., Arctic char) due to the preference of red-muscled Arctic char. Red-muscle over pale-muscle Arctic char products (e.g., fillets versus smoked products) are also sold at a higher monetary value (Connor Faulkner, pers. obs.). Therefore, future changes in Arctic char muscle pigmentation have the potential to decrease profit margins of local businesses (e.g., Kivalliq Arctic Foods, the local commercial fish processing plant in Rankin Inlet). Overall, ongoing and future climatic changes influencing sea ice dynamics, prey species availability and distribution, and in turn, Arctic char muscle pigmentation may have serious socioeconomic consequences across the Arctic, negatively impacting the food security, nutrition, and income of local residents.

4.3 Future Research

Future research on Arctic char muscle pigmentation should consider the potential influence of genetic differences between populations on muscle pigmentation, as other salmonids (e.g., Chinook salmon (*Oncorhynchus tshawytscha*)) exhibit a natural genetic-based colour polymorphism causing white and red morphs that differ in their ability to assimilate dietary carotenoids into tissues (Lehnert et al., 2017; Lehnert et al., 2018). As carotenoids contributing to muscle pigmentation provide mature individuals and their offspring with antioxidant capabilities, populations that differ genetically in their ability to assimilate dietary carotenoids may be better suited to cope with future climatic changes (e.g., increasing water temperatures).

This thesis further highlights the importance of long-term monitoring programs of opportunistic, generalist predators, such as anadromous Arctic char. Indeed, these species act as sentinels and can highlight spatiotemporal and ecosystem-wide changes in resource availability. This thesis was conducted over two years around communities with variable sea ice dynamics which may have provided extreme results (e.g., early ice-off observed in 2022). Indeed, with ongoing climatic changes across the Arctic, such events are likely to become more prevalent as increasing sea and air temperatures continue to influence sea ice concentration and snow cover within these environments (Fossheim et al., 2015; Kortsch et al., 2015; Yurkowski et al., 2017). Therefore, monitoring over longer periods will allow broader trends to be examined to better inform how climatic changes may be altering Arctic marine ecosystems. For example, Ulrich and Tallman (2021) examined the diet of Cumberland Sound Arctic char from 2002 to 2011 and reported a long-term diet shift from ice-associated invertebrates to capelin, which may not have been uncovered when examining shorter-term datasets (e.g., 2-3 years). This supports the importance of implementing long-term monitoring programs to better examine changing ecosystem-level interactions and to more accurately inform ecosystem-based management decisions.

As sea ice dynamics become more variable, determining shifts in predator and prey core use areas will also inform important areas and habitats essential for key life history activities and provide insight into how future climatic changes may impact use of these areas. Acoustic telemetry is a method to estimate home ranges, and assess dispersal and migration, habitat use, as well as species interactions (e.g., competition, predation; Hellstrom et al., 2022). Using acoustic telemetry to monitor predator and prey movements and interactions alongside research questions similar to those examined in the current thesis (e.g., sea ice extent, foraging ecology) will provide information on additional niche axes and how climate change may influence fish health (e.g., muscle pigmentation, lipid content, body condition). An Arctic char acoustic tagging program implemented in 2023 around Rankin Inlet will open the door for these research questions to be examined. In addition to Arctic char, prey species (e.g., capelin, sculpins, cod (Gadidae)) should also be included in the tagging program to increase our collective understanding of predator-prey interactions and how these may be influenced by environmental variability (e.g., sea ice dynamics, open water season), which can potentially inform ecosystem-based approaches to management. By quantifying prey species habitat use, researchers could examine whether Arctic char are able to respond to potential changes in prey behaviour and distribution, and how this may impact their long-term resilience in the face of climate-driven changes. Should earlier ice-off observed in this thesis become more commonplace in the future along western Hudson Bay, tracking Arctic char and prey species within the marine environment will allow the examination of potential trophic mismatches within the system. For example, if Arctic char are entering the marine environment earlier in response to earlier river break-up and spring ice retreat, are common prey species reliant on the timing of marine primary productivity (e.g., spring ice algae blooms) still available for foraging at that time which is crucial for energy and lipid accumulation. Alternatively, will Arctic char need to increase their energy expenditure to access prey items in new and potentially distant foraging areas? If marine habitat use areas do expand, this will likely contribute to changes in trophic interactions and increase the amount of energy necessary for Arctic char to access and obtain prey prior to their return to freshwater overwintering habitats. Further, such changes in Arctic char marine habitat use would also likely have subsistence and economic implications, as local resource users may need to travel further or to new areas to harvest this species. Overall, integrating multiple techniques within a research study (e.g., stable isotope analysis, highly branched isoprenoid analysis, acoustic telemetry) will improve understanding the mechanisms and processes that influence Arctic char foraging ecology and allow multiple integrative research questions to be concurrently examined.

4.4 References

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Supplementary Materials

Table S2.1: 2021 stomach content calculations: percent number (%N), percent weight (%W), percent frequency of occurrence (%O), index of relative importance (IRI), and percent index of relative importance (%IRI) for Arctic char in Rankin Inlet (n = 59) and Naujaat (n = 41).

		Rankin Inlet					**Naujaat**				
		%N	%W	%O	IRI	%IRI	%N	%W	%O	IRI	%IRI
Fish	*Ammodytes* spp.	0.8	1.6	5.1	12.3	0.1	0.0	0.0	0.0	0.0	0.0
	Cottidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.1	0.0
	Cyclopterus lumpus	0.6	1.7	13.6	31.3	0.4	0.0	0.0	0.0	0.0	0.0
	Mallotus villosus	22.5	84.6	67.8	7265.8	88.6	0.0	2.7	19.5	53.6	0.3
	Fish larvae	0.0	0.0	0.0	0.0	0.0	0.2	0.2	12.2	5.9	0.0
	Individual fish	1.3	3.1	5.1	21.9	0.3	0.0	0.0	0.0	0.0	0.0
	Fish remains	-	7.9	54.2	-	-	-	0.1	7.3	-	-
Polychaeta	Nereididae	0.1	0.0	1.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Nereis spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
	Nereis pelagica	0.5	0.2	8.5	5.3	0.1	0.0	0.0	0.0	0.0	0.0
	Enipo spp.	0.2	0.1	5.1	1.1	0.0	0.0	0.0	0.0	0.0	0.0
	Polychaeta	0.0	0.1	3.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Mollusca	Mollusca	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
Gastropoda	*Margarites groenlandicus umbilicalis*	0.1	0.0	1.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0
	Margarites olivaceus	0.1	0.0	1.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Arachnida	Hydracarina	0.4	0.0	1.7	0.7	0.0	0.0	0.0	2.4	0.0	0.0
Insecta	Chironomidae	6.2	0.0	8.5	52.7	0.6	0.0	0.0	2.4	0.0	0.0
	Tipulidae	0.0	0.0	0.0	0.0	0.0	0.0	0.2	7.3	1.4	0.0
	Diptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.1	0.0
	Ameletidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.0	0.0
	Ephemeroptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0

	Plecoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
	Limnephilidae	0.4	0.1	1.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0
	Trichoptera	0.1	0.0	1.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Insecta	0.1	0.0	1.7	0.1	0.0	0.0	0.0	4.9	0.0	0.0
Cirripedia	*Cirripedia* nauplii larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
Copepoda	*Calanus* spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
	Calanus hyperboreus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
	Centropages abdominalis	34.3	0.0	15.3	524.0	6.4	0.0	0.0	0.0	0.0	0.0
	Eurytemora hirudinoides	0.1	0.0	1.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0
	Calanoida	0.1	0.0	1.7	0.1	0.0	0.0	0.0	2.4	0.0	0.0
	Cyclopina spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.0	0.0
	Cyclops scutifer	0.0	0.0	0.0	0.0	0.0	0.1	0.0	12.2	0.7	0.0
	Triconia spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
	Cyclopoida	0.1	0.0	1.7	0.2	0.0	0.0	0.0	2.4	0.0	0.0
	Harpacticus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.6	0.4	0.0
	Tisbe spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.0	0.0
	Harpacticoida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Malacostraca	Malacostraca	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
Amphipoda	*Weyprechtia pinguis*	0.1	0.0	1.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Gammaracanthus loricatus	5.3	0.0	5.1	27.2	0.3	0.0	0.0	12.2	0.3	0.0
	Gammaridae spp.	0.7	0.0	1.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0
	Gammarus wilkitzkii	16.1	0.2	6.8	110.2	1.3	0.1	0.1	17.1	2.6	0.0
	Hyperiidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.0	0.0
	Themisto libellula	0.0	0.0	0.0	0.0	0.0	0.0	0.1	14.6	2.4	0.0
	Ischyrocerus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.8	0.2	0.0
	Ischyrocerus anguipes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0
	Monoporeia affinis	0.0	0.0	0.0	0.0	0.0	0.1	0.1	19.5	2.4	0.0
	Onisimus litoralis	8.5	0.1	15.3	130.6	1.6	95.9	94.7	97.6	18598.7	98.3
	Onisimus glacialis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0

	Onisimus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.1	0.0
	Uristidae spp.	0.2	0.0	1.7	0.4	0.0	0.0	0.0	0.0	0.0	0.0
	Amphipoda	0.1	0.5	6.8	3.7	0.0	0.0	0.7	12.2	8.5	0.0
Decapoda	Brachyura larvae	0.4	0.0	3.4	1.4	0.0	0.0	0.0	0.0	0.0	0.0
	Crangonidae larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.1	0.0
	Decapoda larvae	0.1	0.0	1.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda	*Dajus mysidis*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.3	0.0	0.0
Mysida	*Mysis* spp.	0.8	0.0	13.6	11.4	0.1	3.5	0.9	56.1	247.1	1.3

Table S2.2: 2022 stomach content calculations: percent number (%N), percent weight (%W), percent frequency of occurrence (%O), index of relative importance (IRI), and percent index of relative importance (%IRI) for Arctic char in Rankin Inlet (n = 50) and Naujaat (n = 34).

		Rankin Inlet					**Naujaat**				
		%N	%W	%O	IRI	%IRI	%N	%W	%O	IRI	%IRI
Fish	*Ammodytes* spp.	1.5	5.5	10.0	70.0	1.4	0.0	0.0	0.0	0.0	0.0
	Gymnocanthus tricuspis	0.0	0.0	0.0	0.0	0.0	1.6	10.1	23.5	274.9	2.5
	Myoxocephalus scorpius	0.1	0.3	2.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0
	Myoxocephalus spp.	0.0	0.0	0.0	0.0	0.0	3.0	32.0	79.4	2773.5	25.6
	Triglops spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.3	0.0
	Triglops pingelii	0.0	0.0	0.0	0.0	0.0	0.0	0.5	2.9	1.5	0.0
	Cottidae	0.0	0.0	0.0	0.0	0.0	4.7	25.7	85.3	2591.4	24.0
	Boreogadus saida	0.5	2.3	2.0	5.6	0.1	0.0	0.0	0.0	0.0	0.0
	Gadidae	0.5	4.6	4.0	20.4	0.4	0.0	0.0	0.0	0.0	0.0
	Mallotus villosus	23.0	69.7	46.0	4263.4	84.9	0.0	0.0	0.0	0.0	0.0
	Stichaeus punctatus	0.1	1.3	2.0	2.8	0.1	0.0	0.0	0.0	0.0	0.0
	Fish larvae	0.0	0.0	0.0	0.0	0.0	0.5	2.2	23.5	63.7	0.6
	Individual fish	0.3	0.8	2.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0
	Fish remains	-	13.6	60.0	-	-	-	10.2	76.5	-	-
Polychaeta	*Nereis* spp.	0.1	0.1	4.0	0.8	0.0	0.0	0.0	2.9	0.1	0.0
	Nereis pelagica	1.4	0.7	10.0	21.0	0.4	0.0	0.2	8.8	1.5	0.0
	Polychaeta	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bivalvia	Bivalvia	0.1	0.0	2.0	0.3	0.0	0.2	0.0	2.9	0.5	0.0
Gastropoda	*Limacina helicina*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Gastropoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8	0.2	0.0
Insecta	*Pterostichus adstrictus*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Chironomidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Dolichopodidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	Simuliidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Tipulidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Ameletidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Hymenoptera	0.7	0.0	2.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0
	Perlodidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Thysanoptera	0.1	0.0	2.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
	Insecta	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crustacea	Crustacea	-	0.0	0.0	-	-	-	0.0	5.9	-	-
Copepoda	Copepoda	0.0	0.0	0.0	0.0	0.0	2.7	0.0	29.4	79.6	0.7
	Acartia longiremis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.8	0.4	0.0
	Acartia spp.	0.1	0.0	2.0	0.3	0.0	0.1	0.0	8.8	0.5	0.0
	Calanus spp.	0.0	0.0	0.0	0.0	0.0	0.2	0.0	26.5	6.4	0.1
	Calanus hyperboreus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.1	0.0
	Clausocalanidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Diaptomidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Calanoida	0.0	0.0	0.0	0.0	0.0	0.7	0.0	44.1	31.6	0.3
	Cyclops spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.1	0.0
	Cyclops scutifer	0.0	0.0	0.0	0.0	0.0	0.2	0.0	11.8	1.9	0.0
	Cyclopina spp.	0.5	0.0	2.0	1.1	0.0	0.0	0.0	2.9	0.0	0.0
	Cyclopoida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.1	0.0
	Ectinosomatidae	0.1	0.0	2.0	0.3	0.0	0.0	0.0	23.5	1.2	0.0
	Ectinosoma spp.	0.3	0.0	2.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
	Pseudobradya spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.0	0.0
	Harpacticidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Harpacticus chelifer	0.1	0.0	2.0	0.3	0.0	0.0	0.0	2.9	0.1	0.0
	Harpacticus uniremis uniremis	4.4	0.0	2.0	8.8	0.2	0.0	0.0	11.8	0.2	0.0
	Harpacticus spp.	0.5	0.0	6.0	3.3	0.1	0.1	0.0	32.4	4.0	0.0
	Zaus spp.	0.0	0.0	0.0	0.0	0.0	0.1	0.0	29.4	1.9	0.0

	Amonardia arctica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8	0.2	0.0
	Amonardia spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Miraciidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Tisbe spp.	0.0	0.0	0.0	0.0	0.0	0.1	0.0	17.6	2.5	0.0
	Tisbe furcata	5.2	0.0	2.0	10.4	0.2	0.3	0.0	29.4	7.9	0.1
	Thalestridae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Harpacticoida	0.3	0.0	2.0	0.5	0.0	1.1	0.0	44.1	47.3	0.4
Cirripedia	*Cirripedia* cyprid larvae	0.1	0.0	2.0	0.3	0.0	12.1	0.1	85.3	1033.9	9.6
	Cirripedia nauplii larvae	0.0	0.0	0.0	0.0	0.0	16.2	0.1	41.2	673.4	6.2
	Balanus spp. nauplii larvae	0.0	0.0	0.0	0.0	0.0	48.1	0.2	41.2	1990.3	18.4
Ostracoda	*Philomedes* spp.	0.0	0.0	0.0	0.0	0.0	0.1	0.0	41.2	3.5	0.0
Malacostraca	Malacostraca	0.0	0.0	6.0	0.0	0.0	0.0	0.0	8.8	0.3	0.0
Amphipoda	*Gammaracanthus loricatus*	0.7	0.0	2.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0
	Gammarus lacustris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Gammarus setosus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.1	0.0
	Gammarus wilkitzkii	37.0	1.1	10.0	380.8	7.6	0.0	0.0	2.9	0.0	0.0
	Gammarus spp.	0.5	0.0	4.0	2.2	0.0	0.0	0.0	2.9	0.0	0.0
	Gammaridae	0.0	0.0	0.0	0.0	0.0	0.1	0.0	5.9	0.5	0.0
	Hyperiidae	0.1	0.0	2.0	0.3	0.0	0.0	0.0	17.6	0.9	0.0
	Hyperia galba	0.3	0.0	2.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0
	Hyperoche medusarum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.1	0.0
	Themisto libellula	0.0	0.0	0.0	0.0	0.0	0.2	1.2	64.7	93.2	0.9
	Themisto abyssorum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Quasimelita formosa	0.1	0.0	2.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
	Paroediceros lynceus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.8	0.1	0.0
	Oedicerotidae	0.4	0.0	2.0	0.8	0.0	0.0	0.0	8.8	0.2	0.0
	Pontogeneia inermis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Pontoporeia femorata	0.1	0.0	2.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
	Orchomenella minuta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0

	Anonyx nugax	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Onisimus glacialis	0.4	0.0	2.0	0.8	0.0	1.0	0.6	5.9	9.1	0.1
	Onisimus litoralis	5.1	0.1	6.0	30.9	0.6	1.0	3.2	11.8	48.8	0.5
	Onisimus spp.	0.0	0.0	0.0	0.0	0.0	0.6	0.7	8.8	11.6	0.1
	Amphipoda	0.0	0.0	14.0	0.7	0.0	0.0	1.1	26.5	29.1	0.3
Cumacea	Cumacea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.8	0.1	0.0
Isopoda	Bopyridae	0.0	0.0	0.0	0.0	0.0	0.2	0.0	17.6	2.7	0.0
	Dajus mysidis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	23.5	1.5	0.0
	Isopoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
Mysida	*Mysis* spp.	0.4	0.0	4.0	1.6	0.0	3.9	11.1	67.6	1015.6	9.4
	Mysidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
Decapoda	*Hyas coarctatus*	7.8	0.0	10.0	78.2	1.6	0.0	0.0	0.0	0.0	0.0
	Hyas spp.	5.9	0.0	18.0	106.2	2.1	0.1	0.0	20.6	1.2	0.0
	Pagurus bernhardus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.0	0.0
	Pagurus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Spirontocaris phippsii	0.0	0.0	0.0	0.0	0.0	0.7	0.4	2.9	3.3	0.0
	Caridea	0.0	0.0	0.0	0.0	0.0	0.1	0.0	17.6	1.6	0.0
	Caridea zoea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
	Decapoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0
Euphausiacea	Euphausiidae	0.7	0.0	2.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0
Echinodermata	Echinoidea	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table S2.3: Statistical results from all models for determining the best predictors for Arctic char δ^{13}Cc. Predictor variables include: year, study site, trophic position (TP), and ice particulate organic carbon (iPOC), and the interactions between year and study site and study site and iPOC.

Model	**R^2**	**P-value**	**AICc**	**ΔAICc**
year + study site + year*study site	0.85	<0.0001	335.86	0.00
year + study site + TP + iPOC + year*study site	0.86	<0.0001	337.96	2.11
year + TP + iPOC	0.20	<0.0001	649.02	313.16
year + study site + TP + iPOC	0.21	<0.0001	650.45	314.60
year	0.16	<0.0001	654.32	318.47
TP + iPOC	0.15	<0.0001	658.56	322.70
study site + TP	0.15	<0.0001	658.70	322.84
study site + TP + iPOC	0.16	<0.0001	659.03	323.17
TP	0.11	<0.0001	664.42	328.56
study site + iPOC + study site*iPOC	0.09	0.0005	672.74	336.89
null	-	-	684.64	348.79
study site	0.00	0.3408	685.79	349.93
iPOC	0.00	0.5599	686.36	350.51
study site + iPOC	0.01	0.6149	687.81	351.95

Table S2.4: Statistical results from all models for determining the best predictors for Arctic char trophic position (TP). Predictor variables include: year, study site, δ^{13}Cc, and ice particulate organic carbon (iPOC), and the interactions between year and study site and study site and iPOC.

Model	**R^2**	**P-value**	**AICc**	**ΔAICc**
year + study site + year*study site	0.73	<0.0001	14.91	0.00
year + study site + δ^{13}Cc + iPOC + year*study site	0.73	<0.0001	17.45	2.54
year + study site + δ^{13}Cc + iPOC	0.72	<0.0001	20.08	5.17
year + δ^{13}Cc + iPOC	0.56	<0.0001	100.38	85.47
study site + δ^{13}Cc + iPOC	0.52	<0.0001	116.84	101.92
study site + δ^{13}Cc	0.50	<0.0001	122.65	107.73
δ^{13}Cc + iPOC	0.45	<0.0001	141.53	126.61
Study site + iPOC + study site*iPOC	0.45	<0.0001	143.01	128.10
study site + iPOC	0.43	<0.0001	145.62	130.70
study site	0.41	<0.0001	149.74	134.83
iPOC	0.35	<0.0001	169.34	154.42
year	0.30	<0.0001	181.97	167.05
δ^{13}Cc	0.11	<0.0001	225.97	211.05
null	-	-	246.19	231.27

Table S2.5: Statistical results from all models for determining the best predictors for Arctic char ice particulate organic carbon (iPOC) values. Predictor variables include: year, study site, δ^{13}Cc, and trophic position (TP), and the interaction between year and study site.

Model	**R^2**	**P-value**	**AICc**	**ΔAICc**
year + study site + year*study site	0.66	<0.0001	1503.14	0.00
year + study site + δ^{13}Cc + TP	0.66	<0.0001	1504.02	0.88
year + study site + δ^{13}Cc + TP + study site*year	0.66	<0.0001	1506.18	3.04
study site + TP	0.62	<0.0001	1520.20	17.05
study site + δ^{13}Cc + TP	0.63	<0.0001	1520.53	17.38
study site	0.61	<0.0001	1524.32	21.18
study site + δ^{13}Cc	0.61	<0.0001	1526.34	23.20
year + δ^{13}Cc + TP	0.39	<0.0001	1612.92	109.77
δ^{13}Cc + TP	0.38	<0.0001	1613.77	110.62
TP	0.35	<0.0001	1619.63	116.49
year	0.04	0.0049	1690.52	187.38
null	-	-	1696.48	193.34
δ^{13}Cc	0.00	0.5599	1698.21	195.06

Table S3.1: Statistical results from all models for determining the best predictors for Arctic char astaxanthin concentration. Predictor variables include: year, study site, trophic position (TP), ice particulate organic carbon (iPOC), and invertebrate proportion in the diet, and the interactions between year and study site, study site and TP, study site and iPOC, year and invertebrate proportion in the diet, and study site and invertebrate proportion in the diet.

Model	**R^2**	**P-value**	**AICc**	**ΔAICc**
year + study site + TP + iPOC + year*study site	0.54	<0.0001	296.65	0.00
year + study site + year*study site	0.52	<0.0001	298.64	1.99
study site + invertebrate proportion + study site*invertebrate proportion	0.44	<0.0001	302.91	6.25
study site + invertebrate proportion	0.35	<0.0001	327.62	30.97
study site + TP + iPOC + invertebrate proportion	0.35	<0.0001	330.71	34.05
year + study site + TP + iPOC + invertebrate proportion	0.35	<0.0001	332.46	35.80
year + invertebrate proportion + year*invertebrate proportion	0.33	<0.0001	334.49	37.84
iPOC + invertebrate proportion	0.30	<0.0001	340.55	43.90
study site + iPOC + study site*iPOC	0.40	<0.0001	340.75	44.09
TP + invertebrate proportion	0.29	<0.0001	341.88	45.23
study site + TP + iPOC + study site*iPOC	0.40	<0.0001	342.29	45.64
year + study site + TP + iPOC + study site*iPOC	0.40	<0.0001	344.15	47.50

study site + TP + iPOC + study site*TP	0.37	<0.0001	351.52	54.87
year + study site + TP + iPOC + study site*TP	0.38	<0.0001	352.44	55.79
invertebrate proportion	0.23	<0.0001	354.33	57.68
year + invertebrate proportion	0.23	<0.0001	355.45	58.80
study site + TP	0.33	<0.0001	360.36	63.71
study site	0.32	<0.0001	360.65	64.00
study site + TP + iPOC	0.33	<0.0001	362.40	65.74
study site + iPOC	0.32	<0.0001	362.44	65.78
year + study site + TP + iPOC	0.33	<0.0001	363.15	66.50
year + TP + iPOC	0.26	<0.0001	378.88	82.22
TP + iPOC	0.25	<0.0001	379.13	82.48
iPOC	0.21	<0.0001	386.66	90.01
TP	0.19	<0.0001	392.26	95.61
year	0.01	0.1016	427.93	131.28
null	-	-	428.58	131.93

Table S3.2: Statistical results from all models for determining the best predictors for Arctic char canthaxanthin concentration. Predictor variables include: year, study site, trophic position (TP), ice particulate organic carbon (iPOC), and invertebrate proportion in the diet, and the interactions between year and study site, study site and TP, study site and iPOC, year and invertebrate proportion in the diet, and study site and invertebrate proportion in the diet.

Model	R^2	P-value	AICc	ΔAICc
study site + TP + iPOC + study site*TP	0.40	<0.0001	66.78	0.00
year + study site + TP + iPOC + study site*TP	0.40	<0.0001	68.74	1.96
year + study site + TP + iPOC + year*study site	0.39	<0.0001	72.19	5.41
study site + TP + iPOC + study site*iPOC	0.36	<0.0001	78.70	11.92
year + study site + TP + iPOC + study site*iPOC	0.36	<0.0001	80.86	14.08
year + study site + year*study site	0.34	<0.0001	82.82	16.04
study site + iPOC + study site*iPOC	0.34	<0.0001	83.01	16.23
study site + TP + iPOC + invertebrate proportion	0.34	<0.0001	90.70	23.92
TP + iPOC	0.31	<0.0001	90.87	24.09
year + study site + TP + iPOC + invertebrate proportion	0.35	<0.0001	91.20	24.41
year + TP + iPOC	0.31	<0.0001	92.72	25.94
study site + TP + iPOC	0.31	<0.0001	92.97	26.19
year + study site + TP + iPOC	0.31	<0.0001	94.79	28.01

iPOC + invertebrate proportion	0.31	<0.0001	96.00	29.22
TP + invertebrate proportion	0.31	<0.0001	96.00	29.22
iPOC	0.26	<0.0001	99.45	32.67
study site + iPOC	0.27	<0.0001	100.34	33.56
study site + invertebrate proportion + study site*invertebrate proportion	0.29	<0.0001	100.98	34.20
study site + TP	0.25	<0.0001	103.95	37.17
TP	0.22	<0.0001	110.33	43.55
study site + invertebrate proportion	0.24	<0.0001	110.50	43.72
study site	0.20	<0.0001	115.21	48.43
year + invertebrate proportion + year*invertebrate proportion	0.23	<0.0001	116.04	49.26
year + invertebrate proportion	0.19	<0.0001	122.38	55.60
invertebrate proportion	0.18	<0.0001	122.52	55.74
year	0.06	0.0010	144.82	78.04
null	-	-	153.66	86.87

Table S3.3: Statistical results from all models for determining the best predictors for Arctic char retinol concentration. Predictor variables include: year, study site, trophic position (TP), ice particulate organic carbon (iPOC), and invertebrate proportion in the diet, and the interactions between year and study site, study site and TP, study site and iPOC, year and invertebrate proportion in the diet, and study site and invertebrate proportion in the diet.

Model	R^2	P-value	AICc	ΔAICc
year + study site + year*study site	0.13	<0.0001	-199.07	0.00
year + study site + TP + iPOC + year*study site	0.13	<0.0001	-194.92	4.15
study site + iPOC + study site*iPOC	0.10	0.0002	-192.55	6.52
year + study site + TP + iPOC + study site*iPOC	0.12	0.0005	-191.00	8.07
study site + TP + iPOC + study site*iPOC	0.10	0.0006	-190.73	8.35
year + study site + TP + iPOC + study site*TP	0.11	0.0006	-190.55	8.52
study site + iPOC	0.08	0.0005	-190.44	8.64
study site	0.07	0.0003	-190.36	8.71
year + study site + TP + iPOC	0.10	0.0007	-190.23	8.85
study site + TP + iPOC + study site*TP	0.10	0.0010	-189.55	9.53
study site + TP	0.08	0.0008	-189.52	9.55
study site + TP + iPOC	0.08	0.0011	-189.08	9.99
year + TP + iPOC	0.08	0.0013	-188.82	10.25
year	0.03	0.0313	-181.69	17.39
iPOC	0.02	0.0542	-180.74	18.33

TP	0.01	0.1380	-179.22	19.86
null	-	-	-179.05	20.02
TP + iPOC	0.02	0.1434	-178.84	20.23
study site + invertebrate proportion + study site*invertebrate proportion	0.18	<0.0001	-176.02	23.05
study site + invertebrate proportion	0.13	<0.0001	-168.31	30.77
study site + TP + iPOC + invertebrate proportion	0.14	<0.0001	-165.58	33.50
year + study site + TP + iPOC + invertebrate proportion	0.14	0.0002	-163.40	35.67
iPOC + invertebrate proportion	0.05	0.0100	-153.84	45.24
year + invertebrate proportion + year*invertebrate proportion	0.06	0.0246	-151.90	47.17
year + invertebrate proportion	0.03	0.0581	-150.24	48.84
TP + invertebrate proportion	0.03	0.1059	-149.01	50.06
invertebrate proportion	0.01	0.2268	-148.02	51.05