



Dietary niches of endemic and range-expanding salmonids in the western Canadian Arctic

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Abstract The cumulative effects of climate change are impacting Arctic species and facilitating increased interactions between Arctic and sub-Arctic species. Anadromous Arctic char *Salvelinus alpinus* and the northern Dolly Varden *Salvelinus malma malma* are endemic Arctic fishes vulnerable to the impacts of climate change, yet our understanding of the dietary niches they occupy is limited. The recent increased occurrence of sub-Arctic Pacific salmon (*Oncorhynchus* spp.) in the western Canadian Arctic has raised concerns among Indigenous communities given the potential for competition with endemic fishes important for subsistence fisheries. Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were analyzed from Arctic char, Dolly Varden, and chum salmon *Oncorhynchus keta*, collected among four coastal Canadian Beaufort Sea locations. These fishes were captured during the summer of 2017 and 2019 during ongoing community-based fisheries monitoring programs in the Inuvialuit Settlement Region and Gwich'in Settlement Area. The trophic position

of Arctic char and Dolly Varden indicates both species rely heavily on pelagic prey enriched in $\delta^{15}\text{N}$, consistent with a diet of marine forage fishes. Chum salmon occupied a trophic position $> 3.0\text{‰}$ below the char species, which reflects a diet comprised primarily of marine invertebrates. Isotopic niche analyses revealed chum salmon do not overlap in diet with the char species during the summer marine foraging season, and thus were unlikely to compete for prey as adults. This assessment of dietary overlap informs conservation and fisheries co-management objectives of endemic fishes as their interactions with range-expanding species become more prevalent within a rapidly changing Arctic.

Keywords Arctic char · Dolly Varden · Chum salmon · Stable isotopes · Beaufort Sea

Introduction

The impacts of rapid climate change on Arctic species are cumulative to the already realized impacts on Arctic fishes (Reist et al. 2006; Huntington et al. 2020), including the increasing potential for interactions among sub-Arctic and endemic Arctic species (Bengtsson et al. 2023; von Biela et al. 2023). Thermal pressures, habitat loss, and changes in prey availability due to climate change are affecting culturally and ecologically important Arctic fishes, such as Arctic char *Salvelinus alpinus* (Linnaeus, 1758) (Bommersbach et al. 2024) and Dolly Varden *S. malma* (Walbaum, 1792). Both

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of these char species are considered important for food security among northern communities and are sensitive to stressors associated with climate change (Gallagher et al. 2013; Weinstein et al. 2024), evidenced by their decline in harvest rates in some communities in the western Canadian Arctic (Lea et al. 2021). Sub-Arctic marine fishes are responding to these same warming temperatures by shifting northward (Mueter et al. 2021; von Biela et al. 2023), including Pacific salmon species (*Oncorhynchus* spp.) that are being caught in subsistence fisheries targeting endemic Arctic salmonids (McNicholl et al. 2021; Dunmall et al. 2024). There is the potential for interaction among range-expanding salmon species and Arctic salmonids for suitable freshwater habitats (Dunmall et al. 2016; Bilous and Dunmall 2020), but the potential impact of competition driven by prey availability is not well known. Arctic salmonids rely on Arctic coastal habitats for foraging during the summer period to optimize growth and meet the energy requirements necessary to successfully overwinter (Klemetsen et al. 2003). Range-expanding species may cause diet shifts in Arctic ecosystems, such as the increased presence of capelin *Mallotus villosus* (Müller, 1776) in Arctic char diet (Yurkowski et al. 2018; Ulrich and Tallman 2021; Falardeau et al. 2022). This underscores the need to assess ecological overlap between endemic and range-expanding species in Arctic ecosystems (Dey et al. 2018; Chila et al. 2022).

Anadromous Arctic char and Dolly Varden perform seasonal migrations between freshwater and marine environments each summer to forage (Johnson 1980; Gallagher et al. 2013). However, the dietary information available for both species in the Beaufort Sea is limited (Wight et al. 2023). In the western Canadian Arctic, Arctic char consume a variety of prey that include marine crustaceans, forage fishes, and invertebrates (Harwood and Babaluk 2014). Dolly Varden are predominantly piscivorous (Stewart et al. 2009), but can also forage on sympagic amphipods (Gallagher et al. 2021) in offshore habitats. Stomach content analyses provide valuable information on preferred prey taxa, but cannot describe the niches these species occupy over a longer period of time (i.e., summer foraging). There is evidence that coastal Beaufort Sea Dolly Varden and Arctic char rely on pelagic prey sources while they forage in marine habitats (Brewster et al. 2016; Pettitt-Wade et al. 2023). However, a greater understanding of niche space is needed. Monitoring

ecological niches of vulnerable, endemic fishes is critical to understand their responses to shifting availability of resources and increased interactions with range-expanding species.

Chum salmon *Oncorhynchus keta* (Walbaum, 1792) are the most commonly harvested species of range-expanding Pacific salmon in the western Canadian Arctic (Dunmall et al. 2021). Chum salmon are generally opportunistic feeders in the marine environment, relying on a variety of invertebrates (gelatinous zooplankton, copepods, decapods, eupausiids, pteropods, squid, ctenophores) and smaller fishes (Satterfield and Finney 2002; Karpenko et al. 2007). Analyses of chum salmon diet in the Bering Sea indicate a reliance on zooplankton, with individuals inhabiting sub-Arctic regions of Alaska displaying a greater diet specialization than those found in the western Pacific Ocean (Graham et al. 2021). Although the diet of chum salmon in the Arctic is currently unknown, the potential for dietary overlap among chars and salmonids in Arctic aquatic habitats is concerning to Indigenous harvesters (Chila et al. 2022), especially given the increasing occurrence of range-expanding salmon in the western Canadian Arctic (Dunmall et al. 2024).

Here, we focus on the summer season in the marine environment to assess the Arctic marine trophic ecology of three key salmonid species and examine the extent of niche overlap among range-expanding chum salmon and endemic Arctic char and Dolly Varden. Stable isotopes provide information that reflects trophic position ($\delta^{15}\text{N}$) and basal dietary source ($\delta^{13}\text{C}$), and their combination represents a species' dietary niche (Layman et al. 2007; Jackson et al. 2011). As they have a slower turnover rate than stomach contents, stable isotopes provide a more robust dietary niche assessment (Layman et al. 2007). Using stable isotope analyses, our objectives were to (1) assess the trophic position ($\delta^{15}\text{N}$) of anadromous Arctic char, Dolly Varden, and chum salmon in the western Canadian Arctic marine environment; (2) determine the basal dietary source ($\delta^{13}\text{C}$) among these co-occurring species; and (3) determine the extent of dietary niche overlap among endemic Arctic char and Dolly Varden with range-expanding chum salmon in an Arctic marine environment. The information gained regarding the potential for competition for food resources can be used to inform conservation

and management objectives for endemic and range-expanding species in a rapidly changing Arctic.

Methods

Sample collection

The Arctic char, Dolly Varden, and chum salmon samples used in our study were obtained from separate monitoring programs operating in the western Canadian Arctic (Table 1, Fig. 1). Char muscle samples used in this study were collected from annual community-based fisheries-dependent programs focused on monitoring Arctic char and Dolly Varden populations (Gallagher et al. 2013, 2017). Only individuals that were not in spawning form were used. In the community of Paulatuk, Northwest Territories (NT), Arctic char were collected between July 24 and August 15, 2017 at the mouth of the Hornaday River (69.35139°N; −124.06944°W) as they began to enter freshwater. Arctic char were also collected from a location locally known as Tippitiuyak, in western Darnley Bay (69.508453°N; −124.38585°W) from July 5 to August 23, 2019. Dolly Varden samples were provided by sampling programs located at Herschel Island, Yukon Territory (YT) (69.58583°N; −139.07639°W) and near the community of Aklavik, NT (Husky Channel of the Mackenzie Delta 69.6345°N; −124.38585°W). At Herschel Island, Dolly Varden were collected between August 5 and 10, 2017. In the Aklavik area, Dolly Varden were collected between August 1 and September 1, 2019. In August 2017, two Dolly Varden harvested in Aklavik were provided to the Arctic Salmon program. Although these individuals were caught inland, we assume their dietary markers obtained from muscle tissue would reflect summer foraging, as they would only have been in the Mackenzie Delta for approximately 11 days (Gallagher et al. 2021). The chum salmon samples were provided from the community-led Arctic Salmon project,

which facilitates monitoring for range-expanding species in subsistence fisheries targeting endemic fishes (Dunmall and Reist 2018). Chum salmon were collected among Beaufort Sea communities and key locations including Aklavik (68.22028°N; −135.01200°W), Herschel Island (69.58583°N; −139.07640°W), Shingle Point (68.95101°N; −137.22406°W), Paulatuk (69.35139°N; −124.06940°W), and Tuktoyaktuk (69.44278°N; −133.03110°W). The chum salmon were harvested between August 1–29, 2017, and July 15–August 21, 2019. Only those that were still in silver phase, not displaying spawning characteristics, were used.

Sample processing

To process the chum salmon, whole fish or heads were frozen and shipped to the Freshwater Institute, Winnipeg, Manitoba (Fisheries and Oceans Canada) for storage at −20 °C and processing. Fishes were then thawed, their species was confirmed, and they were processed for biological data (fork length, weight, sex, maturity). Tissue samples were removed from the left dorsal area on whole individuals, or at the base of the head if only the head was available, and frozen at −20 °C in preparation for analyses of stable isotopes. The fork length of each fish was corrected for changes associated with freezing and thawing (Babaluk et al. 2018):

$$\text{Fresh fork length} = 1.025 (\text{thawed fork length})$$

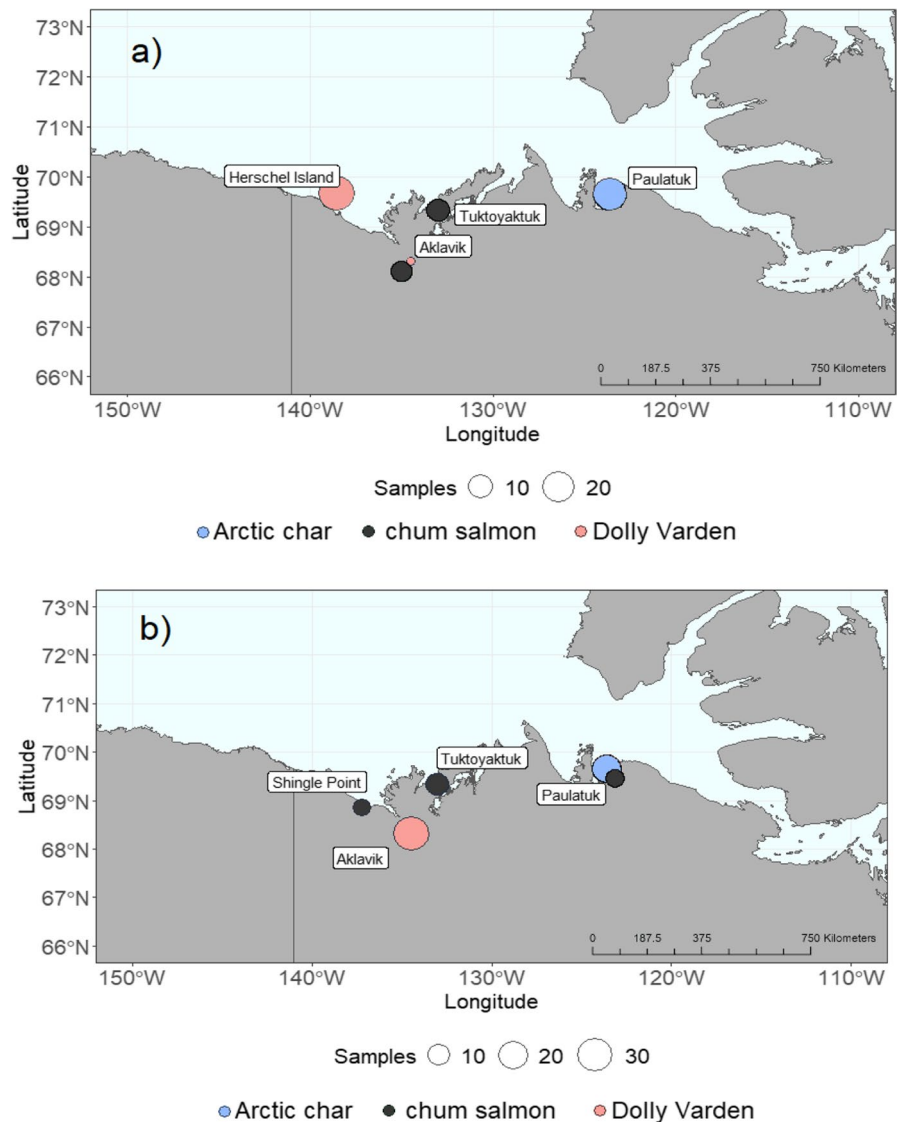
$$\text{Fresh weight} = 1.028 (\text{thawed weight})$$

Among all locations where Arctic char and Dolly Varden were collected, fishes were processed for biological data (e.g., length, sex, maturity) and tissue samples where they were harvested (Gallagher et al. 2013, 2017). Dorsal muscle samples were frozen and shipped to the Freshwater Institute in Winnipeg. The samples used for isotope analyses were selected

Table 1 Number of Arctic char, Dolly Varden, and chum salmon sampled for stable isotope analyses by location in 2017 and 2019

		Aklavik	Herschel Island	Shingle Point	Paulatuk	Tuktoyaktuk	Total
2017	Arctic char				24		24
	Dolly Varden	2	28				30
	Chum salmon	7	2			9	18
2019	Arctic char				19		19
	Dolly Varden	33					33
	Chum salmon			6	7	11	27

Fig. 1 Map of locations where either Arctic char, Dolly Varden, or chum salmon were collected **a** between July 24 and August 29, 2017, and **b** between July 5 and September 1, 2019



based on the criteria that they represented both sexes as evenly as possible and were captured within the same time period as salmon in that area (or as close as possible).

Sample analyses

Stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were used to characterize dietary niches (Layman et al. 2007; Jackson et al. 2011), including trophic position, basal carbon source, and potential for competition among co-occurring fishes (Tadokoro et al. 1996; Layman et al. 2007). Each sample of fish muscle was freeze dried for 48 h

(LAB-CONCO-FreeZone 4.5). Dried tissues were homogenized with a ceramic mortar and pestle, then weighed ($400 \pm 10 \mu\text{g}$) for stable isotope analysis. Samples were analyzed for stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopes using a continuous flow isotope ratio mass spectrometer (Thermo-Delta 5 Plus) equipped with a Costech elemental analyzer at the Freshwater Institute, Winnipeg. Ratios from stable isotopes were defined as the deviation from a standard reference material (carbon: Vienna Pee Dee Belemnite; nitrogen: atmospheric N_2) in parts per thousand (‰). Carbon and nitrogen stable isotope ratios were calculated using the following formula (Peterson and Fry 1987):

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

where X represents ^{13}C or ^{15}N , R_{sample} is the ratio ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) contained in the sample, and R_{standard} is the corresponding ratio in the reference standard. Standard deviations of repeated measurements of the certified reference materials (USGS 40 and 41a) were $<0.1\text{‰}$ for $\delta^{13}\text{C}$ and $<0.16\text{‰}$ for $\delta^{15}\text{N}$. Repeated measurements with the in-house standard produced an average deviation of $<0.08\text{‰}$ for $\delta^{13}\text{C}$ and <0.11 for $\delta^{15}\text{N}$, while standard deviations determined from duplicate samples were $<0.07\text{‰}$ for $\delta^{13}\text{C}$ and $<0.05\text{‰}$ for $\delta^{15}\text{N}$ among species. These ranges were acceptable and within the range to be compared directly (Hobson and Schell 1998). The ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and the C:N were calculated using the mass fraction for each individual.

$\delta^{13}\text{C}$ values increase by approximately 0.5 to 1.0‰ with each trophic transfer due to the enrichment of the heavier ^{13}C isotope (Deniro and Epstein 1978), yet lipids are depleted in ^{13}C relative to muscle tissue, which results in $\delta^{13}\text{C}$ values that are lower among fishes that are lipid-rich (Mcconnaughey and Mcroy 1979). Thus, fishes that differ in lipid content may rely on the similar basal carbon sources. However, without accounting for lipid bias, their $\delta^{13}\text{C}$ ratios may indicate they are occupying different niche space (Sotiropoulos et al. 2004; McNicholl et al. 2018). There is a strong correlation between C:N ratio and lipid content, such that lipid-rich muscle is often indicated by a C:N ratio of >3.5 (Mintenbeck et al. 2008). Generally, it is recommended that if the C:N ratio of a species is >3.5 then these data must be corrected with a lipid normalization model (Post et al. 2007; Logan et al. 2008).

A lipid normalization model was applied if the C:N ratio of at least one species exceeded 3.5 to standardize the $\delta^{13}\text{C}$ values among the three species, and compared against non-extracted $\delta^{13}\text{C}$ values. Only $\delta^{13}\text{C}$ values were standardized for lipid bias, while original $\delta^{15}\text{N}$ values were used in subsequent analyses. Tissue- and species-specific lipid normalization models are a stronger fit when correcting $\delta^{13}\text{C}$ ratios from lipid-rich tissues (Mcconnaughey and Mcroy 1979; Yurkowski et al. 2015); therefore, the following equation from Logan et al. (2008) was used:

$$\delta^{13}\text{C}_{\text{lipid-free}} = 0.967 \times \delta^{13}\text{C}_{\text{lipid-intact}} + 0.861$$

Standardization of consumer carbon and nitrogen to a baseline primary consumer was necessary in order to interpret basal food sources and trophic positions among species (Post 2002). Carbon and nitrogen stable isotopes vary across spatial and temporal scales (Guzzo et al. 2011), and therefore in order to interpret the dietary niches of fishes examined in this study, the mean and standard deviation among $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained from a low-trophic primary consumer collected from the same years and area were assessed. *Calanus hyperboreus*, that dominates forage copepod biomass in the study region, was used as a representative baseline for a level two trophic position (Niemi et al. 2020) and trophic enrichment factor of 3.4‰ (Post 2002) using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values gathered by the DFO-lead Canadian Beaufort Sea – Marine Ecosystem Assessment (A. Niemi unpublished data). *C. hyperboreus* were picked and frozen for analyses from bongo net samples collected at ten sites the Mackenzie Shelf (between -134.7543 and -123.4388 decimal degrees) at depths ranging between 41 and 200 m. Details about sampling and stable isotope analyses can be found in Niemi et al. (2020). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from $n=12$ samples gathered in 2017 and $n=7$ samples 2019 were compared using a Welch two sample t -test, and a non-parametric mixed-effects model was used to determine if station influenced $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ in a given year. Mean $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of *C. hyperboreus* were overlaid among the niches of Arctic char, Dolly Varden, and chum salmon to provide a prey baseline. If the standard deviation of *C. hyperboreus* $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values were less than 1.0‰ (Post 2002), it was assumed that the dietary niches observed among fishes were representative of their diet and capture location did not influence fish $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values.

All statistical analyses for this study were performed in R (version 4.4.3). Comparisons among species fork lengths were conducted using a Kruskal–Wallis rank sum test given that data did not satisfy the assumptions of a parametric test (i.e., failed Levene's test for homogeneity of variance). Since $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values deviated from normality (Shapiro–Wilk test) and did not meet the assumptions for homogeneity of variance, non-parametric statistical tests were employed to evaluate for differences in fork length, $\delta^{13}\text{C}$ values, and $\delta^{15}\text{N}$ values among species (Kruskal–Wallis rank sum test) within each

year. If a significant difference was observed, a post hoc test (Dunn's test) was completed to determine which groups differed significantly from one another. A mixed-effects model (Welch two sample t -test) was used to evaluate if year or location influenced $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values within each species, with the exception of Arctic char, which were only caught in one location. If there was a significant difference observed between stable isotope data collected in 2017 versus 2019, fishes collected in each year were analyzed separately. To compare stable isotope values with lipid-extracted versus non-extracted $\delta^{13}\text{C}$ values, the Welch two sample t -test was also used for each year. Fork length versus $\delta^{15}\text{N}$ values was examined among species for each year with a linear regression.

Dietary niches were examined with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in bivariate space, as a measure of overall dietary overlap among salmonids. Niche breadth (total area of convex hulls) and standard ellipse areas (SEAs) were calculated using stable isotope Bayesian ellipses in R (*SIBER*) as described by Jackson et al. (2011). Niche breadth or total area (TA) of the convex hull was calculated for each species based on the outermost points of the convex hull polygon, such that all other individuals of a species were contained within the outline of the hull. SEAs for each species were calculated within the TA as a measure incorporating approximately 95% of the data points (Jackson et al. 2011; Swanson et al. 2015), with the ellipses considered a resilient measure of niche space with variability in samples size. As samples from 2017 and 2019 for each species was less than $n=30$ for a few groups, it was necessary to apply a sample size correction to the SEAs (Jackson et al. 2011).

Bayesian inference was used to calculate the uncertainty around measures of isotopic niches. We quantified the error associated with fitting each ellipse to each species, as a result of our sample size and their distribution of isotope values in bivariate space. A Markov Chain Monte Carlo (MCMC) algorithm was used to generate a distribution of covariance matrices by combining the prior probability with the likelihood of the data for a respective covariance matrix. *SIBER* was used to create a range of ellipses that could explain the data, with the highest density of ellipses around the most likely ellipse of that species. Since it was not possible to take an average across the species' covariance matrices (i.e., cannot plot a mean, mode, or median among different species' ellipses), we

calculated each one of the ellipse areas and derived summary statistics through a loop in *SIBER* that produced a posterior distribution fitted to each species. We use these distributions to compare the size of each ellipse and the probability of one species' ellipse being smaller than another. Detailed instructions and R scripts used to produce these matrices are available on the Comprehensive R Archive Network (<https://cran.r-project.org/web/packages/SIBER/vignettes/siber-comparing-populations.html>). The extent of overlap among salmonid species was determined by calculating overlap between each pair of SEAs. The proportion of overlap assumes that one species' ellipse is the denominator, which would represent the proportion of species A that overlaps with species B, versus the proportion of B that overlaps with A.

Collaborative process

Co-management decision-makers and Arctic Salmon biologists continually share and discuss information about salmon following a collaborative process outlined in Dunmall et al. (2024). For this manuscript, the Hunters and Trappers Committees (HTCs) and Renewable Resource Councils (RRCs), including the Aklavik HTC, Tuktoyaktuk HTC, Paulatuk HTC, and Ehdiitat RRC were invited to participate as co-authors. The HTCs and RRCs (1) highlighted their concerns regarding the potential for prey competition among salmon and chars, (2) coordinated the provision of samples from harvesters and/or monitoring programs, (3) were provided a summary of the results, (4) were invited to discuss the results in a meeting and provide any interpretations (Appendix A), and (5) were given the opportunity to review their insights, which had been incorporated into the discussion. Communities that did not express interest in co-authorship are recognized in the acknowledgements section.

Results

Mean fork length (\pm SD) differed among the chars and chum salmon ($\chi^2=13.14$; $p=0.001$; $df=2$), such that Arctic char (620 ± 80 mm) were the largest, followed by chum salmon (606 ± 31 mm) and Dolly Varden (575 ± 65 mm) (Fig. 2). Post hoc tests confirmed that fork length differed significantly between

Arctic char and Dolly Varden ($Z=3.2$; $p=0.005$), and Dolly Varden and chum salmon ($Z=2.6$; $p=0.03$), but there was no significant difference between Arctic char and chum salmon. A Welch two sample t -test confirmed that, between 2017 and 2019, there was no significant difference in fork length within each species ($p>0.05$); therefore, fork lengths are combined in Fig. 2 for both years. Among chum salmon used in this analysis, $n=30$ individuals where whole (71%) and $n=12$ (29%) were heads.

Stable isotopes

Welch two sample t -test revealed that $\delta^{13}\text{C}$ values differed between 2017 and 2019 (Table 2) for Arctic char ($t=-2.81$, $p<0.05$, $df=30.12$) and Dolly Varden ($t=6.98$, $p<0.05$, $df=59.39$), and $\delta^{15}\text{N}$ values differed between years only for Dolly Varden ($t=$

-2.90 , $p<0.05$, $df=56.94$). The stable isotope values obtained from chum salmon did not differ between 2017 and 2019 ($p>0.05$). A non-parametric mixed-effects model revealed that location did not influence stable isotope results for species that were collected in multiple communities in a given year for Dolly Varden and chum salmon.

Baseline primary consumer stable isotope values from *C. hyperboreus* collected by the CBS-MEA program displayed minimal variability between 2017 and 2019. A mixed-effects model indicated that sampling location did not influence stable isotope values in each year. Mean $\delta^{15}\text{N}$ ($\pm\text{SD}$) did not differ between 2017 ($8.8\pm0.4\text{‰}$) and 2019 ($9.4\pm0.4\text{‰}$) but $\delta^{13}\text{C}$ values ($\pm\text{SD}$) were significantly lower in 2017 ($-27.0\pm0.3\text{‰}$) relative to 2019 ($-26.0\pm0.9\text{‰}$). Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *C. hyperboreus* are overlaid on Fig. 4 among the SEAs of fish species

Fig. 2 Length frequency distribution of male and female Arctic char, Dolly Varden, and chum salmon samples collected among Beaufort Sea communities in 2017 and 2019

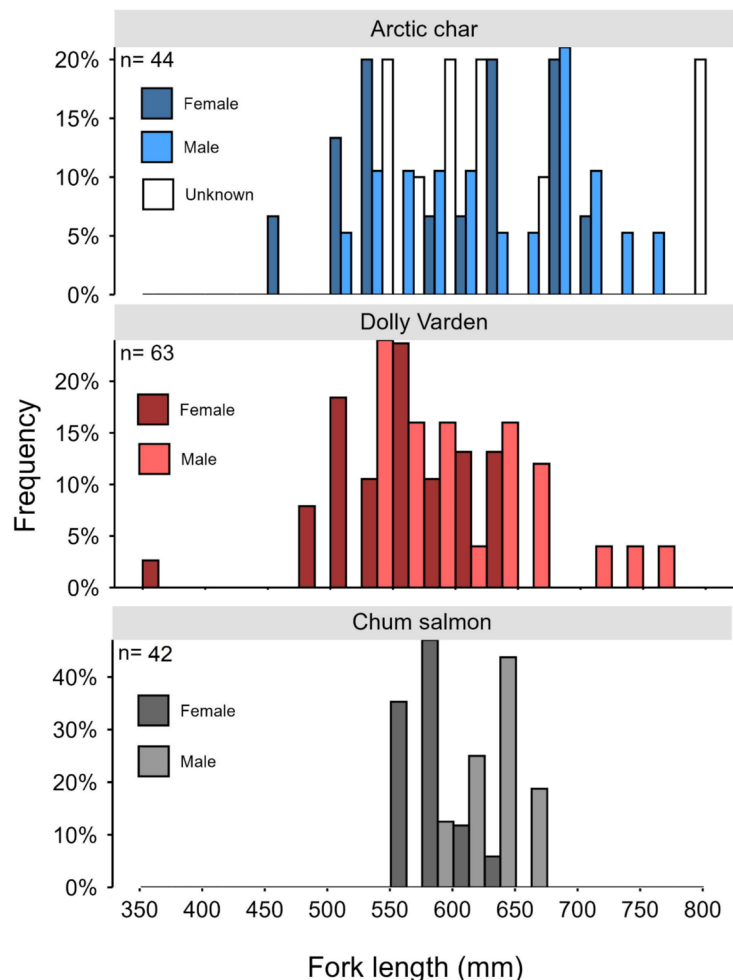


Table 2 Mean \pm SD of $\delta^{15}\text{N}$, $\delta^{13}\text{C}_{\text{lipid-intact}}$, C:N ratio, and $\delta^{13}\text{C}_{\text{lipid-free}}$ ratios for co-occurring Arctic char, Dolly Varden, and chum salmon collected among coastal Beaufort Sea locations between July–August of 2017 and 2019

Species	Year	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}_{\text{lipid-intact}}$	C:N	$\delta^{13}\text{C}_{\text{lipid-free}}$
Arctic char	2017	24	$15.6 \pm 0.5\text{‰}$	$-25.9 \pm 0.7\text{‰}$	9.6 ± 2.8	$-24.2 \pm 0.7\text{‰}$
	2019	19	$15.5 \pm 0.7\text{‰}$	$-25.5 \pm 1.1\text{‰}$	8.5 ± 3.3	$-23.4 \pm 1.0\text{‰}$
Dolly Varden	2017	30	$14.6 \pm 0.5\text{‰}$	$-24.8 \pm 0.8\text{‰}$	4.9 ± 1.0	$-23.1 \pm 0.8\text{‰}$
	2019	33	$15.0 \pm 0.4\text{‰}$	$-26.2 \pm 0.8\text{‰}$	9.3 ± 3.3	$-24.5 \pm 0.7\text{‰}$
Chum salmon	2017	18	$11.2 \pm 0.8\text{‰}$	$-20.9 \pm 0.7\text{‰}$	3.6 ± 0.5	$-19.4 \pm 0.6\text{‰}$
	2019	27	$11.3 \pm 0.9\text{‰}$	$-20.9 \pm 0.6\text{‰}$	3.3 ± 0.1	$-19.3 \pm 0.5\text{‰}$

to provide a prey baseline relative to the consumers examined in this study.

Trophic position

The trophic position, indicated by mean $\delta^{15}\text{N}$ values, differed statistically among Arctic char, Dolly Varden, and chum salmon in 2017 ($\chi^2=107.5$, $p < 0.05$, $\text{df}=2$) and 2019 ($\chi^2=125.3$, $p < 0.05$, $\text{df}=2$). In 2017, Arctic char post hoc tests confirmed $\delta^{15}\text{N}$ values differed significantly from chum salmon ($Z=7.4$, $p < 0.01$) and Dolly Varden ($Z=3.9$, $p < 0.01$), while Dolly Varden and chum salmon also differed ($Z = -4.2$, $p < 0.01$). In 2019, the same significant differences were observed between Arctic char and Dolly Varden ($Z=2.1$, $p < 0.01$), Arctic char and chum salmon ($Z=6.9$, $p < 0.01$), and Dolly Varden and chum salmon ($Z = -5.6$, $p < 0.01$). Mean $\delta^{15}\text{N}$ (\pm SD) values were the highest overall in Arctic char followed by Dolly Varden and chum salmon (Table 2). Mean $\delta^{15}\text{N}$ values suggest that chum salmon occupy a lower trophic position relative to

char given the difference of approximately $+3.0\text{‰}$ between the two groups (Minagawa and Wada 1984; Post 2002). In 2017, there was a positive relationship between $\delta^{15}\text{N}$ values and fork length for Arctic char ($F_{1,22}=15.9$; $r^2=0.42$; $p=0.0006$) and Dolly Varden ($F_{1,28}=4.9$; $r^2=0.15$; $p=0.03$), but not for chum salmon (Fig. 3). In 2019, the strongest relationship between $\delta^{15}\text{N}$ values and fork length was observed among chum salmon ($F_{1,13}=10.4$; $r^2=0.45$; $p=0.007$) relative to Dolly Varden ($F_{1,31}=18.1$; $r^2=0.35$; $p=0.0001$). Arctic char did not display a significant relationship between $\delta^{15}\text{N}$ values and fork length in 2019.

Basal dietary source

The results of basal carbon (average $\delta^{13}\text{C}_{\text{lipid-free}}$ ratios) that contributed to the diet among Arctic char, Dolly Varden, and chum salmon differed significantly in 2017 ($\chi^2=49.81$, $p < 0.05$, $\text{df}=2$) and 2019 ($\chi^2=54.26$, $p < 0.05$, $\text{df}=2$). A post hoc test confirmed that all pairs of species differed significantly

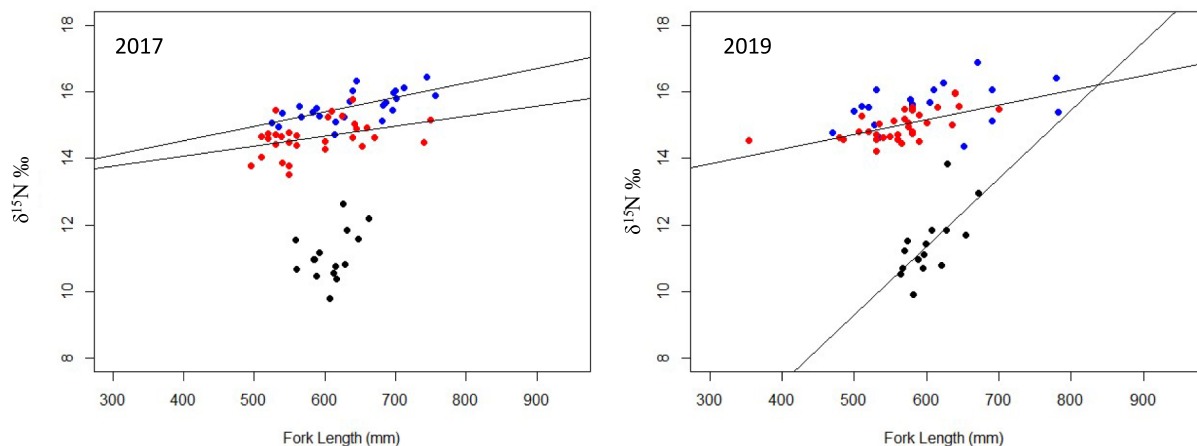


Fig. 3 $\delta^{15}\text{N}\text{‰}$ versus fork length among Arctic char=(blue), Dolly Varden=(red), and chum salmon (black) in 2017 and 2019

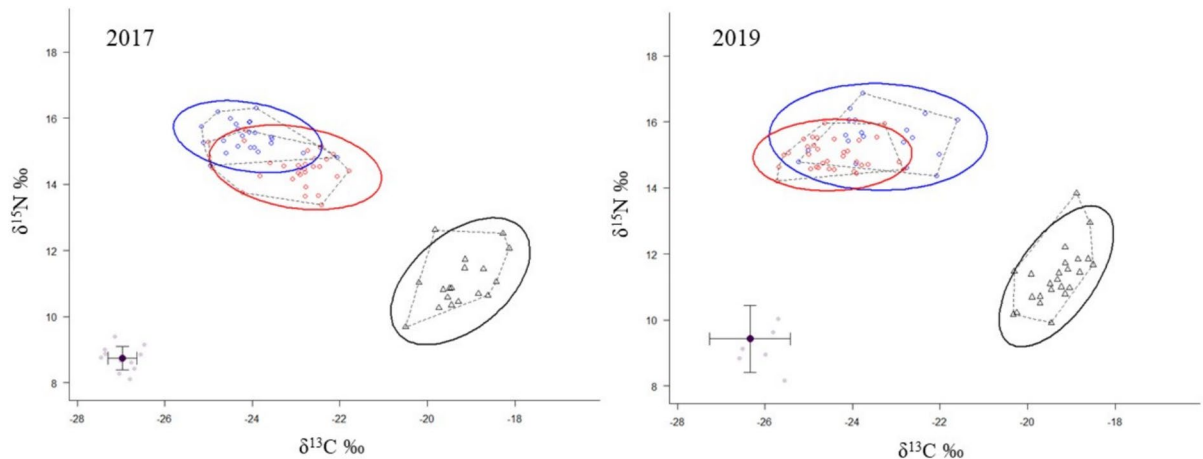


Fig. 4 $\delta^{13}\text{C}_{\text{lipid-free}}$ and $\delta^{15}\text{N}$ values among Arctic char (blue), Dolly Varden (red), and chum salmon (black). Standard ellipse areas (SEAs) at 95% confidence are indicated by solid lines and convex hulls (total area (TA)) are indicated by dashed

lines. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and individual values of bulk *C. hyperboreus* (purple) obtained from each year are overlaid among consumer ellipses

in 2017 with respect to the $\delta^{13}\text{C}_{\text{lipid-free}}$ values observed between Arctic char and chum salmon ($Z = -7.1$, $p < 0.01$), Arctic char and Dolly Varden ($Z = -3.1$, $p < 0.01$), and chum salmon and Dolly Varden ($Z = 4.5$, $p < 0.01$). Similarly in 2019, $\delta^{13}\text{C}_{\text{lipid-free}}$ values differed between Arctic char and chum salmon ($Z = -4.2$, $p < 0.01$), Arctic char and Dolly Varden ($Z = 2.4$, $p < 0.01$), and chum salmon and Dolly Varden ($Z = 7.3$, $p < 0.01$). Mean $\delta^{13}\text{C}_{\text{lipid-free}}$ (\pm SD) values were highest overall for chum salmon relative to chars (Table 2). Although the mean C:N ratio for chum salmon in 2019 fell below 3.5, their $\delta^{13}\text{C}_{\text{lipid-intact}}$ values required standardization to adequately compare niche overlap among co-occurring species.

Niches and overlap

The niches of Arctic char and Dolly Varden were similar in size and position, relative to the niche of chum salmon at a lower trophic position in 2017 and 2019. In 2017, Dolly Varden had the largest overall total ellipse area (4.8‰^2), followed by chum salmon (4.1‰^2) and Arctic char (3.3‰^2). The corrected Standard Ellipse Areas (SEAs) among Dolly Varden, chum salmon, and Arctic char that encompass 95% of the data were 1.3, 1.5, and 1.0‰^2 respectively. In 2019, Arctic char had the largest overall total ellipse area (5.7‰^2), followed by chum salmon

(4.2‰^2) and Dolly Varden (3.6‰^2). The corrected Standard Ellipse Areas (SEAs) among 2019 Arctic char, chum salmon, and Dolly Varden were 2.2, 1.2, and 1.1‰^2 , respectively. In both years, there was no overlap between the char and salmon ellipses, suggesting the probability of one group occurring within the dietary niche of the other was 0% (Fig. 4). The SEA of chum salmon did not overlap with Dolly Varden or Arctic char; therefore, the likelihood of overlap was not calculated. In 2017, the likelihood of Dolly Varden occurring within the niche of Arctic char was 54.4% while the likelihood of Arctic char occurring within the niche of Dolly Varden was 40.0%. In 2019, the likelihood of Dolly Varden occurring within the niche of Arctic char was 83.9% while the likelihood of Arctic char occurring within the niche of Dolly Varden was 39.8%.

Discussion

Stable isotope analyses indicate that Dolly Varden and Arctic char maintained a piscivorous diet at a higher trophic position with evidence of foraging in the coastal-marine and offshore-marine environments, whereas chum salmon occupied a lower trophic niche than the chars and were more likely eating zooplankton from nearshore habitats. Arctic char and Dolly Varden were similar in niche size and

position, with a high-degree of trophic overlap. There was no evidence of trophic overlap between anadromous endemic chars and range-expanding chum salmon among the coastal habitats of the western Canadian Arctic. Although chum salmon are caught in the same subsistence nets as either char species in the western Canadian Arctic (Dunmall et al. 2021), these range-expanding fish do not appear to compete for marine-derived resources with these Arctic endemic fish. Primary consumer baselines obtained from bulk *C. hyperboreus* carbon and nitrogen stable isotopes indicate there was minimal variation among sites in 2017 and 2019. Therefore, we assume that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values observed in the fish are a reflection of their diet and habitat use (Kjeldgaard et al. 2021), despite the wide spatial scale these fishes were collected. Given that the standard deviation in $\delta^{15}\text{N}$ values was low and did not differ significantly between 2017 and 2019 ($<1\text{‰}$), we can assume that mean trophic fractionation observed among fishes is approximately 3.4‰.

The trophic position informed by ^{15}N stable isotope values suggest that both char species rely heavily on forage fishes. Capelin and other forage fishes such as Pacific sand lance *Ammodytes hexapterus* Pallas, 1814 are common prey items found in the stomach contents of Dolly Varden (Stewart et al. 2009) and Arctic char (Harwood and Babaluk 2014; McNicholl et al. 2024); they are the most likely prey enriching ^{15}N values analyzed in this study. This is not consistent with other studies that suggest crustaceans (e.g., amphipods and copepods) are a primary prey source for Arctic char in Nunavut (Ulrich and Tallman 2021) and more recent analyses of Dolly Varden (Gallagher and Johnson 2025). There is a positive relationship for Dolly Varden in both years and Arctic char in 2017 between fork length and $\delta^{15}\text{N}$ ratios, indicating that as individuals continue to grow, they consume larger, higher trophic prey taxa. In 2017, Arctic char caught at the mouth of the Hornaday River near Paulatuk displayed a positive relationship between fork length and $\delta^{15}\text{N}$, but the relationship was not significant in 2019. Although there were no significant differences in mean $\delta^{15}\text{N}$ or fork length between 2017 and 2019 among Arctic char, stomach content analyses among 2017 Arctic char from Darnley Bay indicated that capelin contributed to approximately 93% of their diet (Gallagher unpublished data). Although no stomach content data are available for 2019 Arctic

char, capelin were notably more abundant in the area in 2017 relative to 2019 (McNicholl et al. 2024), and potentially contributed more to diet than other prey items in that year. A positive relationship between $\delta^{15}\text{N}$ and fork length is commonly observed in salmonids, particularly when larger individuals exhibit a more piscivorous diet (Klobucar and Budy 2020; Pettitt-Wade et al. 2023).

The depleted $\delta^{13}\text{C}$ in Dolly Varden and Arctic char indicate that the basal carbon source contributing to the diet of these species includes both coastal and offshore sources. The SEA among 2017 Arctic char was notably smaller than in 2019 and more depleted in ^{13}C , suggesting that they relied on fewer prey types that were derived from marine sources. This supports the interpretation that Arctic char in Darnley Bay may have relied more on capelin in 2017 compared to 2019. Arctic cod are also known to aggregate along the continental shelf of the Beaufort Sea (Walkusz et al. 2013), and the movement of Alaskan Dolly Varden suggests they travel onto the Beaufort Shelf during the summer and may be consuming cod (Courtney et al. 2018). The range of $\delta^{13}\text{C}$ values from this study are comparable to the Arctic char from the neighboring Kitikmeot Sea, Nunavut (NU) (Falardeau et al. 2022), and from Melville Sound, NU (Swanson et al. 2010), and suggest that Beaufort Sea Arctic char display a piscivorous foraging behavior in coastal- and offshore-marine habitats.

Chum salmon in the Arctic appear to spend more time in the coastal environment, foraging on invertebrates while also potentially seeking suitable freshwater habitats for spawning. We did not observe a difference in stable isotope values in chum salmon between 2017 and 2019, which contrasts with Arctic char and Dolly Varden, which displayed more temporal variability. The $\delta^{13}\text{C}$ values among chum salmon were more enriched (approximately 4.5‰) relative to both char species, suggesting that chum salmon are consuming prey from relatively nearshore habitats (Fry 1981; Schell et al. 1998). $\delta^{15}\text{N}$ values observed among zooplankton collected along the nearshore shelf of the Beaufort Sea (Stasko et al. 2017) generally fall between 8.5 and 10.0‰ while forage fishes were between 12.5 and 14.0‰ (Stasko et al. 2017; McNicholl et al. 2018). This suggests Beaufort Sea chum salmon forage on lower trophic prey, and likely rely upon a zooplankton-based diet, given their comparable $\delta^{15}\text{N}$ values to those found among

Alaskan populations. The range of $\delta^{13}\text{C}$ values of nearshore shelf zooplankton and forage fish found in the Beaufort Sea (-27.5 to -26.0‰ and -25.5 to -23.5‰ respectively) indicates that chum salmon caught in this region rely on nearshore-coastal prey sources relative to those derived from offshore-marine sources (Johnson and Schindler 2009). Based on the date of harvest, the timing of salmon movement into the Beaufort Sea (Dunmall et al. 2024), a swimming speed of approximately 36 km/day (Tanaka et al. 2001), and a timeframe of approximately 116–173 days when stable isotopes derived from muscle tissues reflect feeding (Weidel et al. 2011), we expect these results to indicate foraging between the Chukchi Sea and the Alaskan North Slope (Dunmall et al. 2024). In comparison, chum salmon in the Pacific Ocean are less enriched in $\delta^{13}\text{C}$ relative to chum salmon in the Beaufort Sea, which is characteristic of pelagic-marine foraging (Johnson and Schindler 2002; Hunt et al. 2022). The $\delta^{15}\text{N}$ values reported in this study are within the range (10.7 to 11.5‰) of those found in a meta-analysis of chum salmon analyzed in the North Pacific and Alaska (Johnson and Schindler 2009).

Between 2017 and 2019, chum salmon demonstrated less variability in SEAs, suggesting they may utilize prey taxa from similar basal sources, relative to Arctic char and Dolly Varden. This smaller niche and minimal temporal variability of chum salmon is interesting given this species is known consume a wide range of prey taxa in the north Pacific Ocean (Karpenko et al. 2007). It is possible that the availability of prey taxa is limited relative to those in the Pacific Ocean as they travel from the Chukchi Sea, potentially constricted by cold water (Dunmall et al. 2024). Although there is substantial spatial variation among sampling locations in this study, the effect of location on stable isotope values was not significant, and we therefore assume the results are reflective of marine foraging in the coastal Beaufort Sea between the North Slope of Alaska and southern Amundsen Gulf. Chum salmon were collected from the largest spatial scale among the three species, yet their observed niche variability was smaller compared to Arctic char and Dolly Varden, which display relatively localized movements (Harwood and Babaluk 2014; Gallagher et al. 2021; Hollins et al. 2022).

Anadromous Arctic char and Dolly Varden are important indicators to assess ecosystem-level

changes in a warming Arctic marine environment (Smith et al. 2024; Pearce et al. 2024). Monitoring dietary markers provides a tangible tool to detect a change in trophic dynamics among char species as the prevalence of range-expanding species increases (Bommersbach et al. 2024) and endemic fish species exhibit shifts in their foraging behavior (Faulkner et al. 2024). In their anadromous form, Arctic char rely on coastal habitats during the open-water period for foraging and growth (Klemetsen et al. 2003), yet there is growing evidence that there is a decline in anadromy among populations (Finstad and Hein 2012). Their reliance on rivers to complete their anadromous life history results in trade-offs that are energy intensive and increase mortality in their early years, contributing to their sensitivity relative to lake-resident forms (Jensen et al. 2019). The anadromous form of Dolly Varden is an important indicator for the coastal Beaufort Sea and adjacent freshwater habitats, where some of the most accelerated rates of climate-driven coastal erosion and permafrost melt are occurring (Lantz et al. 2008; Mochnacz et al. 2010; Whalen et al. 2022). There are outlying cases where Arctic char and Dolly Varden co-occur (Sawatzky and Reist 2021), and their ranges may increase in overlap in response to climate-induced change (Weinstein et al. 2024). The cumulative impact of endemic species shifting their ranges (Faulkner et al. 2024) while increasing in overlap with range-expanding sub-Arctic species requires further investigation. Understanding the niches of these species may help explain the impacts of spatiotemporal changes to their habitat use in response to changing climate.

Here, we have expanded our understanding of the dietary niches of important Arctic fishes and range-expanding chum salmon in the Beaufort Sea; however, many knowledge gaps remain. Future efforts could focus on assessing the diets of other range-expanding salmon species, including pink salmon *O. gorbuscha* (Walbaum, 1792) and sockeye salmon *O. nerka* (Walbaum, 1792), which are also incidentally harvested in the western Canadian Arctic (Dunmall et al. 2021). This is of particular significance to subsistence fishers in Arctic waters that rely upon endemic fishes where food security is increasingly uncertain (Chila et al. 2022). Furthermore, understanding the potential impacts of climate change on prey (e.g., availability, diversity, phenology) and foraging behavior for anadromous Arctic fishes in the

western Canadian Arctic is of particular importance, especially with ongoing sea ice change (Harris et al. 2022). As prey availability becomes more variable in the Arctic and as sub-Arctic fishes continue to expand northward, the potential for competition between range-expanding and endemic fishes is likely to increase in the western Canadian Arctic, which would be cumulative to the impacts of warming temperatures on Arctic fishes.

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Author contribution DM: conceptualization, methodology, data analysis, and writing of the original manuscript. CG: conceptualization, provision of samples, data analysis, and review and editing. Tuktoyaktuk Hunters and Trappers Committee: conceptualization, investigation, and sample acquisition. KD: conceptualization, funding acquisition, project administration, resources, supervision, writing, review and editing.

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Data availability Data are available upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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