

Evidence for three morphotypes among anadromous Arctic char (*Salvelinus alpinus*) sampled in the marine environment

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Abstract

Variable resource use and responses to environmental conditions can lead to phenotypic diversity and distinct morphotypes within salmonids, including Arctic char (*Salvelinus alpinus*). Despite the cultural and economic importance of Arctic char in the Inuvialuit Settlement Region (ISR), limited data exist on the extent and presence of morphological diversity in this region. This is of concern for management given climate change impacts on regional fish populations. The authors investigated morphological diversity in anadromous Arctic char sampled during their summer marine migration-residency period when seasonal harvesting occurs in a coastal mixed-stock fishery. Geometric morphometric analysis was conducted using digital photographs of live Arctic char ($n = 103$) of which a sub-set was subsequently implanted with acoustic transmitters ($n = 90$) and released, and their overwintering lakes determined using active acoustic telemetry surveys. Twenty-three morphological landmarks were established and overlaid on digital images, and nine linear measurements of the body and head were recorded. Principle component analysis and K-means clustering based on linear measurements categorised fish into three morphotypes: slender body and slim head ($n = 31$), small and short head with a small mouth ($n = 46$) and elongated head shape with large mouth ($n = 26$). Tagged individuals of the three morphotypes occupied all lakes with no distinction observed. The three Arctic char morphotypes detected in this coastal mixed-stock fishery could represent adaptation to specific feeding-movement behaviours potentially tied to juvenile residency in freshwater systems, efficient exploitation of the marine prey pulse, or are relicts from ancestral types. To the authors' knowledge, this study is the first to identify distinct Arctic char morphotypes occurring in sympatry in the marine environment. Identifying phenotypic diversity will assist management to promote the sustainability of this regional fishery.

KEYWORDS

Canadian Arctic, geometric morphometrics, marine coast, phenotypic variation, resource polymorphism, salmonid

1 | INTRODUCTION

Polymorphic populations can occur within phenotypically plastic species in response to differential habitat and resource use (i.e., resource polymorphisms) resulting in alternate morphological phenotypes (morphotypes) that are still considered the same species (Knudsen *et al.*, 2011; Skúlason & Smith, 1995; Snorrason & Skúlason, 2004). Several different ecological mechanisms can lead to the presence of morphotypes within a system. In environments where there is minimal interspecific competition and available ecological niche space, individuals of a population may expand their niche to take advantage of underutilised resources (Knudsen *et al.*, 2011; Skúlason & Smith, 1995; Smith & Skúlason, 1996). This expansion into open niche space may also reduce intraspecific competition (Svanbäck *et al.*, 2008). Alternatively, morphological divergence can occur in species-rich environments where there are resources that have not been exploited or are specific and well defined thus requiring specialised traits to obtain (Skúlason & Smith, 1995; Smith & Skúlason, 1996). Resource polymorphisms allow for the coexistence of a species within an environment that over time may play a role in divergence and speciation (Smith, 1966; Smith & Skúlason, 1996; West-Eberhard, 1989). This phenomenon occurs across a range of taxa and is determined by the environment and underlying genetic variation within a species and is crucial for understanding and managing diversity within populations (Reist *et al.*, 2013; Skúlason *et al.*, 2019), which has implications for fisheries management (Ward *et al.*, 2016).

Species from the genus *Salvelinus* are known for their phenotypic plasticity, and the diversity of observed morphotypes is reported to vary depending on region of occurrence (Jonsson & Jonsson, 2001). Arctic char (*Salvelinus alpinus*) has a circumpolar distribution and is the world's most northern freshwater fish (Johnson, 1980; Jørgensen & Johnsen, 2014; Klemetsen, 2010). It is known to exhibit between two and four sympatric lacustrine morphotypes through resource polymorphisms (Fraser *et al.*, 1998; Hindar & Jonsson, 1982; Skoglund *et al.*, 2015). Their southern range limits consist of deep cold-water lakes most likely as glacial relicts, and their evolutionary history suggests they evolved in a cold and nutrient-deficient periglacial environment (Reist *et al.*, 2013). Recently deglaciated habitats less than 10,000 years old, which are species-poor and have limited interspecific competition, have been hypothesised as a driver of observed polymorphic development in Arctic char populations (Reist *et al.*, 2013; Skúlason & Smith, 1995). This has led to the existence of Arctic char with three distinct life-history tactics: lake-resident (access to the sea, but do not migrate), migratory (i.e., anadromous) or landlocked forms (geographically isolated within a lake) (Jonsson & Jonsson, 2001; Loewen *et al.*, 2009). Although previous studies have noted differences in colouration, and head shape as well as a differential use of the limnetic, pelagic and benthic zones among lacustrine Arctic char from lakes in Norway (Hindar & Jonsson, 1982), Scotland (Walker *et al.*, 1988), Iceland (Malmquist, 1992) and Canada (Arbour *et al.*, 2011; O'Connell & Dempson, 2002), there is limited research examining variation in Arctic char morphology within the anadromous

life-history form. To date, the majority of morphometric studies have focused on landlocked Arctic char or the differences between anadromous and lake resident morphotypes within a single lake (Loewen *et al.*, 2009). Consequently, the prevalence of phenotypic diversity in anadromous populations at higher latitudes remains largely unknown.

Subsistence harvesting is a vital component of life in the Inuvialuit Settlement Region (ISR) (Sawatzky & Reist, 2010; Smart, 2021; Usher, 2002). The community of Ulukhaktok, (Northwest Territories, Canada) typically harvests anadromous Arctic char using gill nets in lakes, rivers and along the coast during their summer marine migration and residency phase. Coastal subsistence fishing in the Ulukhaktok area is considered to harvest several populations of Arctic char that use different overwintering lakes, in particular Tatik and Tahiryuak lakes, which are accessible via the Kuujjua and Kuuk rivers to the northeast and southeast of Ulukhaktok, respectively (DFO, 2016a; Harwood *et al.*, 2013; Hollins *et al.*, 2022). A recent telemetry study found that Arctic char from these distinct freshwater systems are spatially segregated in the marine environment, with Arctic char from the Kuuk River making extensive use of Safety Channel, a semi-enclosed embayment east of Ulukhaktok, whereas Kuujjua River Arctic char occur primarily north of the community along Minto Inlet and the coast adjacent to Ulukhaktok (Figure 1) (Hollins *et al.*, 2022). Although Arctic char most accessible to the marine summer fishery are thought to consist primarily of individuals from the Kuuk and Kuujjua river populations, several other potential overwintering habitats are available along this region of Victoria Island. Consequently, additional subpopulations of Arctic char may be present in the marine environment during summer. In Ulukhaktok, fishing is selective for taste, texture and traditional familiarity, and smaller-sized anadromous Arctic char are highly favoured (Smart, 2021). Selective harvesting of a specific morphotype of fish could erode the distribution of phenotypic traits present within a population, reducing diversity and potentially impacting their capacity to adapt and respond to stressors such as rapid climatic shifts in the Arctic (Schindler *et al.*, 2010). Should these morphological characteristics correlate with the population of origin, then this selective harvest could also lead to specific populations experiencing disproportionate harvest pressure.

Given limited understanding on the occurrence of morphotypes within anadromous Arctic char populations, the objectives of our study were to (a) determine if distinct morphotypes are present in the marine environment within a coastal mixed-stock fishery of anadromous Arctic char harvested along the coastal region of Ulukhaktok, (b) characterise the extent of differences between morphotypes and quantify body shape variation and (c) determine if specific morphotypes are associated with an overwintering lake identified from acoustic telemetry surveys directed by traditional knowledge. Characterising the morphological diversity of anadromous Arctic char is relevant for conservation and management objectives to guide decisions on current fishing techniques such as gear type, selectivity of fish size and shape and fishing routes and timing.

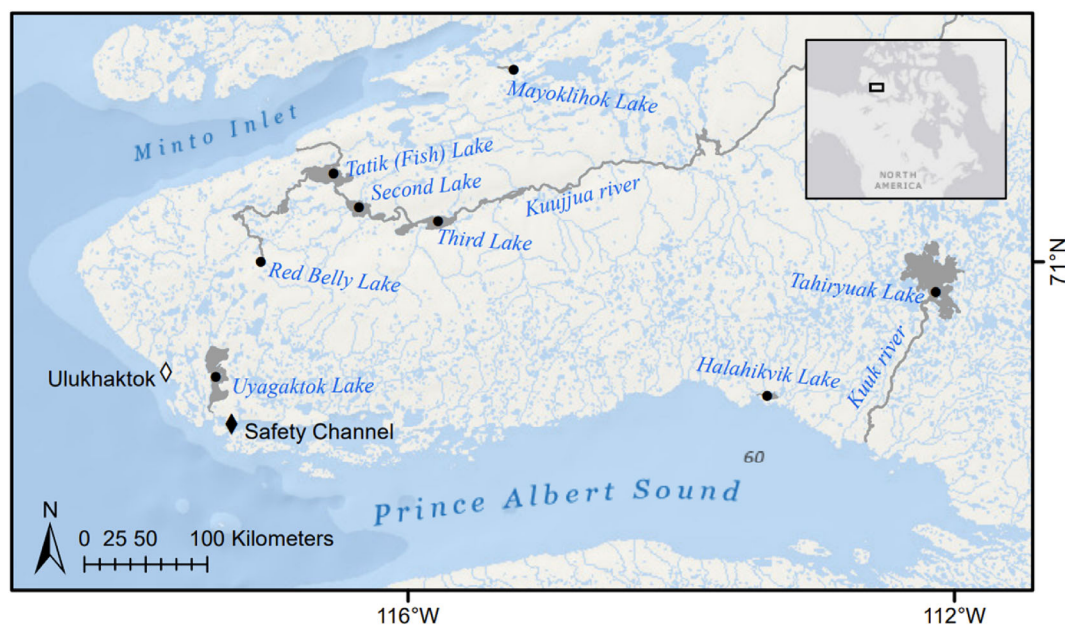


FIGURE 1 Study area located on western Victoria Island, Northwest Territories, Canada. Fish capture was conducted in Ulukhaktok (◆) and Safety Channel (◇). Lakes surveyed to detect acoustically tagged fish (●) were Tatik Lake, Second Lake, Red Belly Lake, Tahiryuak Lake, Halahikvik Lake, Uyagaktok Lake and Mayoklihok Lake. Service layer credits: Esri, Garmin, GEBCO and NOAA NGDC

2 | METHODS

2.1 | Ethical statement

The care and use of experimental animals was approved by the University of Windsor Animal Care Committee (AUPP #1803) and Fisheries and Oceans Canada Licence to Collect Fish for Scientific Purposes (LSFP # S-19/20-3000-YK) issued pursuant to Section 52 of the Fishery (*General*) Regulations. Strict procedures were followed to minimise stress and harm to fish during and after surgical procedures to implant acoustic tags ($n = 90$). These included minimising handling time and use of electrosedation instead of chemical inhibitors.

2.2 | Study area and project co-development

The study was conducted on the western coast of Victoria Island, near Ulukhaktok, Northwest Territories (Figure 1). The coast connects with the Amundsen Gulf and has two marine inlets (Prince Albert Sound and Minto Inlet) on either side of Ulukhaktok. On the north coast of Prince Albert Sound is Safety Channel (Figure 1). The Ulukhaktok community primarily depends on this coastline and nearby lakes for subsistence harvesting. Arctic char subsistence is collaboratively managed through the Ulukhaktok Char Working Group (UCWG) and Olokhtomiut Hunters and Trappers Committee (OHTC). Through meetings, and collaborative fieldwork, the UCWG and OHTC assisted with study design, including identifying fisheries-based research questions, study sites, capture methods and conducting lake-based surveys.

2.3 | Fish sampling

Arctic char were collected in summer during the open water (*i.e.*, ice free) period in 2018 and 2019 at two coastal locations: Ulukhaktok (8–12 August 2018 and 12–14 July 2019) and western Safety Channel (16 July–3 August 2018; 18 July–5 August 2019) (Figure 1). Fish were caught by angling or gill nets set perpendicular to shore (114 or 140 mm stretch mesh-size; 22.80 m long; 1.83 m deep). Nets were set for approximately 2–13 h and regularly monitored for fish capture to minimise the time fish were caught in the net. Once a fish was caught, typically identified by a submerged float or by splashing at the surface, it was immediately secured and placed in a cooler of sea water. Individual fish were measured [fork length (mm), weighed (g)] and photographed. A standardised digital image was taken of the left lateral side of each Arctic char by laying the fish on a white mesh panel with a 1 m ruler for scale and a colour chart. Photographs were taken using a CANON Rebel i7 DSLR with 18 mm lens mounted onto a fully extended tripod. Prior to analysis, individual fish photographs were assigned a score using a quality ranking system of 1–3 for light and focus: (1) representing poor quality, (2) average and (3) excellent. Only fish with a score of three were retained for morphometric analyses ($n = 103$ of 110; 93.64%). After photographs were taken, an acoustic transmitter was surgically implanted (INNOVASEA, Nova Scotia, Canada; V13-4H; delay: 45–95s, $n = 25$, V16 4H; delay: 40–60 s, $n = 27$; delay: 45–95s, $n = 38$) and the fish released as part of a separate project investigating broad-scale movements and habitat use (Hollins *et al.*, 2022).

2.4 | Morphometric landmark coordinates

To undertake morphometric analyses, photographs were first converted to tps files via “tpsutil” (Rohlf, 2018) and imported into “tpsDig2” (Rohlf, 2018). A six-step protocol was followed before landmarks were placed on each fish. First the scale of measurement was set using the ruler placed below each fish image in “tpsDig2” (Rohlf, 2018). Second, the image was magnified until a 1 cm measurement could be clearly visualised on the ruler, the image tools button selected and a line drawn over the 1 cm ruler measurement to set the scale for each image. Scaling all photographs was required for the Procrustes fit in MorphoJ (Klingenberg, 2011) and for the extraction of accurate linear measurements. Fork length (mm) was then measured as the distance between the tip of the snout and the fork of the caudal fin. A coarse description of colouration (ventral and dorsal sections of fish) was recorded using the colour square in the image, accepting light variation in each image (*i.e.*, dim to bright depending on the time of day/cloud cover at capture). Mouth position (*i.e.*, open or closed) was recorded for quality control as fish are typically photographed with their mouth closed in standard morphometric methodology (Sandlund *et al.*, 1992; Snorrason *et al.*, 1994); nonetheless, with live fish this was not always possible. The authors of this study noted whether the caudal fin was positioned upwards or downwards as this can change the position of landmarks around the fin and influence body shape. Finally, notes regarding visual inspection of each

individual such as the position of the mouth (*i.e.*, terminal or inferior) and shape of the head were recorded. Following these steps, landmarks were assigned to individual fish selected through the quality ranking system mentioned earlier (*i.e.*, 1–3 scale). As morphological divergence within lacustrine Arctic char is generally seen in the shape of the head and the size of the body (Jonsson & Jonsson, 2001), a total of 14 standardised landmark positions were identified along the body and 9 additional landmarks were placed on the head (Figure 2) following criteria established by Skoglund *et al.* (2015).

2.5 | Assessment of fish shape using converted landmark coordinates

An initial assessment to visualise variation in body shape was undertaken using landmark data created in “tpsDig2” that were subsequently imported into MorphoJ. To remove non-shape variation in landmark positions a Procrustes superimposition was conducted, whereby the raw coordinates were translated, scaled and rotated for standardisation of landmark positioning (Mitteroecker *et al.*, 2013; Skoglund *et al.*, 2015). The new coordinates from the Procrustes were then used to construct a covariance matrix to analyse the relationship between the placement location of landmarks. These provided the core values (*i.e.*, eigenvectors and eigenvalues) required to perform principal component analysis (PCA). To visualise patterns in shape

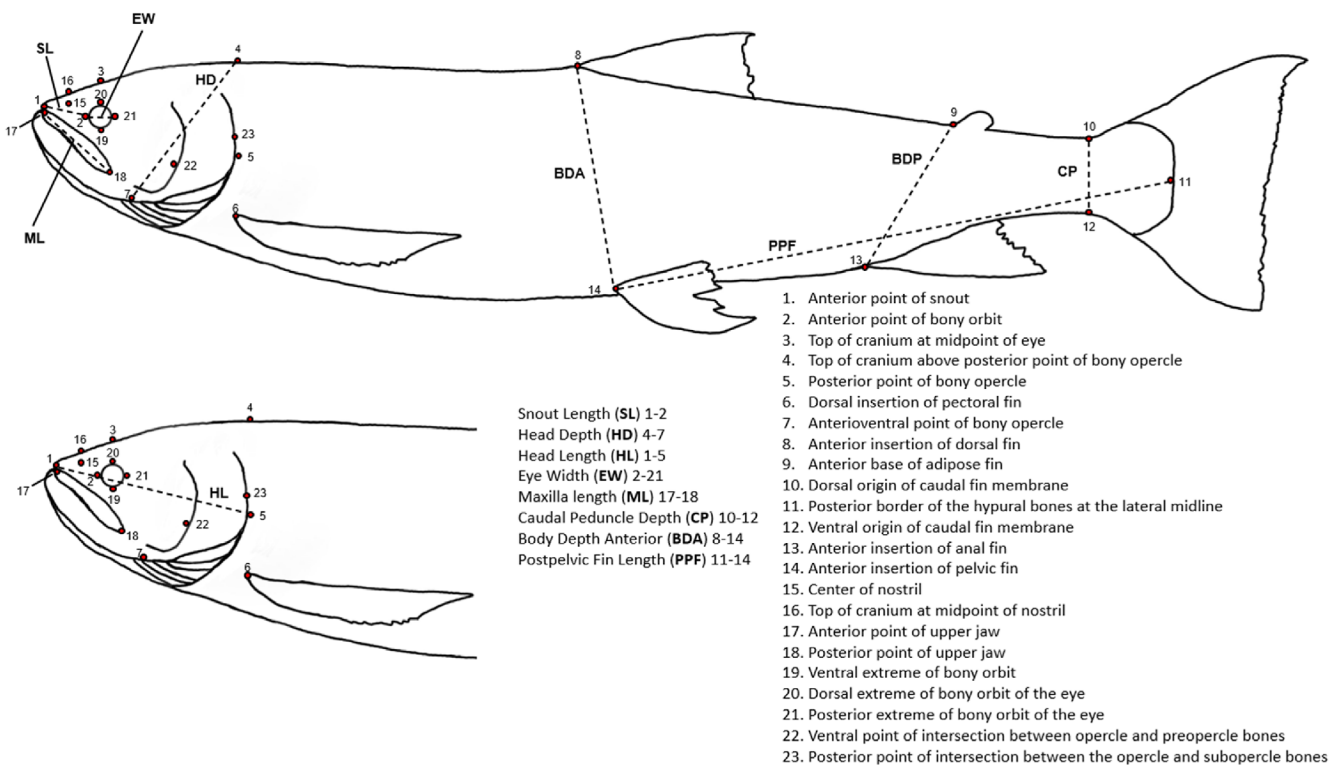


FIGURE 2 Standardised framework of landmark positions ($n = 14$ located along the body and $n = 9$ positioned specifically on the head) and associated linear measurements used in the geometric morphometric analysis of anadromous Arctic char sampled in the marine environment off the coast of Ulukhaktok, Northwest Territories. Landmarks and linear measurements defined by Skoglund *et al.* (2015) and figure modified from the same study

variation, the resulting principal component (PC) axes were plotted as a wireframe (representing the average position for each landmark for the sample population) in MorphoJ. The wireframe was created representing the entire body, including head and eye shape [wireframe landmarks: body (1, 16, 3, 4, 8, 9, 10, 11, 12, 13, 14, 7, 1), head (4, 5, 7) and eyes (2, 19, 21, 20)] (Supporting Information Figure FIGURE S1).

2.6 | Morphometric analysis using linear distances between landmark coordinates

To perform morphometric analysis, linear measurements were extracted as defined in Skoglund *et al.* (2015) from the original tps file

TABLE 1 Contribution (%) of linear trait measurements for the first two principal components (PC1 and PC2) representing variation in Arctic char morphology on the marine coast near Ulukhaktok, NT

Variable	Landmarks	PC1	PC2
Head depth (HD)	4–7	9.67	10.58
Head length (HL)	1–5	23.75	0.86
Snout length (SL)	1–2	21.50	0.69
Eye width (EW)	2–21	7.05	0.90
Maxilla length (ML)	17–18	20.01	1.37
Caudal peduncle (CP)	10–12	1.10	28.58
Body depth posterior (BDP)	9–13	4.00	27.70
Body depth anterior (BDA)	8–14	1.31	29.22
Post-pelvic fin length (PPF)	11–14	11.61	0.10
Variation explained (%)		42.3	28.1

created in “tpsDig2,” using the Geomorph package in R (Adams *et al.*, 2020; R Core Team, 2021). Linear measurements were then size-adjusted to remove the confounding effect of individual fork length using the following Equation (1):

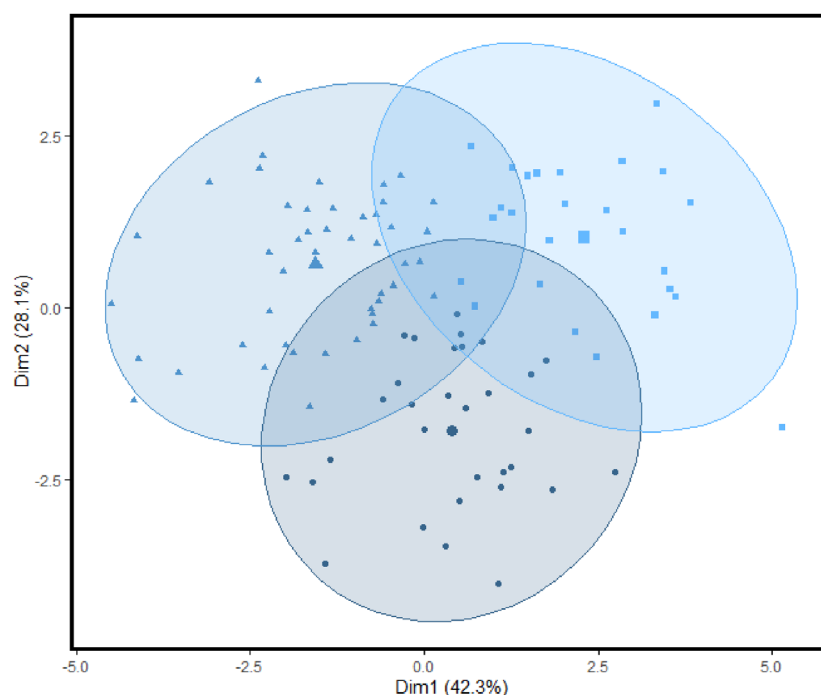
$$\log_{10} Y_i = \log_{10} M_i + b(\log_{10} L_m - \log_{10} L_i), \quad (1)$$

where Y_i is the size-adjusted linear measurement of the corresponding trait (T_{adj}), M_i is the linear measurement of the trait, b is the linear slope regression coefficient of the measured trait ($\log_{10} M_i$) against fork length ($\log_{10} L_i$) for each morph, L_m is the average fork length of all fish and L_i is the measured fork length of each fish (Arbour *et al.*, 2011; Skoglund *et al.*, 2015).

2.7 | Identifying variation in morphometric traits and establishing morphotypes

To quantify variation in the morphometric measurements among individual fish, a PCA was run on the T_{adj} using the FactoMineR package in R (Lê *et al.*, 2008). To visualise the various components of the PCA analysis, including the contributions of each T_{adj} and to determine the appropriate number of clusters, Silhouette analysis (Supporting Information Figure S2) in the R package factoextra was used. Once the optimal number of clusters was determined, a K-means algorithm was used to define unique groups using the package Cluster. Factoextra was used to visualise the cluster results. Following assignment of fish to clusters, a MANOVA was conducted using all nine T_{adj} with the clusters set as the grouping variables. Equality of covariance among groups and normality were tested using a BoxM test in the package heplots and a Shapiro-Wilk test, respectively. Each of the nine T_{adj}

FIGURE 3 Plot of principal component analysis (PCA) analysis of nine size-adjusted linear measurements (T_{adj}) from Arctic char sampled in the marine environment and the three morphotypes identified using a K-means algorithm. Cluster one = slender body; cluster two = small head traits; cluster three = elongated head traits. The centroid present within each cluster corresponds to the mean of points assigned within the cluster. Concentration ellipses have been drawn around all three clusters with 95% confidence under multivariate normal distribution. See Supporting Information Figure S3 for convex polygons fitted to clusters. Cluster ■, 1; Cluster ■, 2; Cluster ■, 3



measurements was then analysed using an ANOVA, with subsequent *post hoc* pair-wise *t*-tests to determine if differences occurred between each group. Finally, to assess if there was an effect of body condition on morphometric measurements and identified groups, Fulton's condition factor was calculated ($n = 93$, where weight was available; $K = \frac{W(g)}{L(cm)^3}$) and an ANOVA conducted. To correct for multiple hypothesis testing, *P*-values were adjusted using Bonferroni correction ($\alpha < 0.05$).

2.8 | Assessing morphotype occurrence in overwintering lakes

Following the classification of individual fish into morphotypes, their corresponding overwintering lake was assigned based on known movements from acoustic telemetry data. A portable acoustic receiver (VR100, Innovasea, Halifax, Nova Scotia) was used to detect tagged



FIGURE 4 Photographs of the three defined Arctic char morphotypes sampled in the marine environment determined from principal component analysis (PCA) and K means clustering analysis. (a) Cluster one fish [slender body with relatively small body depth anterior (BDA), body depth posterior (BDP) and caudal peduncle (CP)], (b) cluster two fish [small head traits; head depth (HD), head length (HL) and snout length (SL), with a small mouth (ML)], (c) cluster three fish [elongated head traits; HD, HL and SL, with a large mouth (ML)]

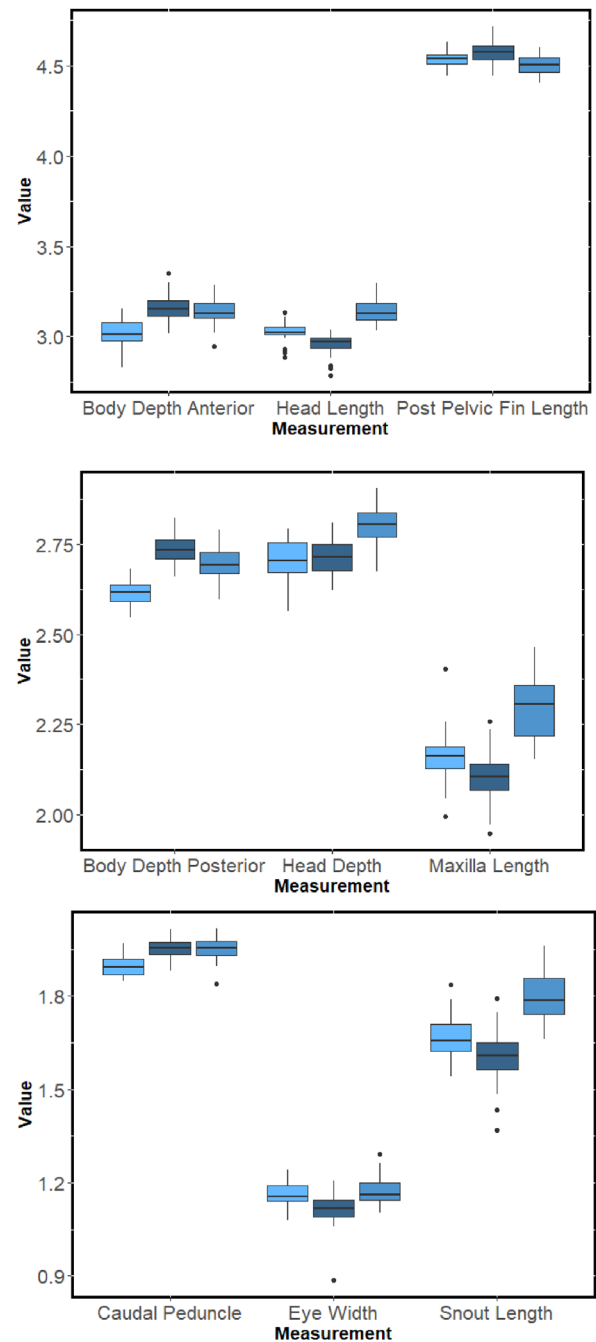


FIGURE 5 Box plots showing a comparison of the nine-size adjusted linear measurements (T_{adj}) values from the three identified anadromous Arctic char morphotypes. Cluster one fish have a slender body as indicated by lower body depth anterior (BDA), body depth posterior (BDP) and caudal peduncle (CP) values. Cluster two fish were identified by small head traits: head depth (HD), head length (HL), snout length (SL) and small mouth (ML). Cluster three fish had elongated head traits: HD, HL and SL, with a large mouth (ML). Boxplot upper and lower hinges correspond to 25th and 75th percentiles, respectively, whereas the horizontal line represents the median. Whisker length represents data range up to 1.5x the difference between the 25th and 75th percentiles. Cluster ■, 1; Cluster ■, 2; Cluster ■, 3

TABLE 2 Results of statistical comparisons for nine morphometric traits compared among three Arctic char morphotypes (ANOVA) and between each morphotype (pair-wise *t*-test)

Morphometric trait (T_{adj})	ANOVA		Difference between Arctic char morphs (pair-wise <i>t</i> -test)		
	<i>P</i> -value	<i>F</i> value	Cluster 1—Cluster 2	Cluster 1—Cluster 3	Cluster 2—Cluster 3
Head depth (HD)	<0.001	27.34	1	$P < 0.001$	$P < 0.001$
Head length (HL)	<0.001	76.38	$P < 0.001$	$P < 0.001$	$P < 0.001$
Snout length (SL)	<0.001	54.11	$P < 0.01$	$P < 0.001$	$P < 0.001$
Eye width (EW)	<0.001	15.01	$P < 0.001$	0.53866	$P < 0.001$
Maxilla length (ML)	<0.001	56.57	$P < 0.01$	$P < 0.001$	$P < 0.001$
Caudal peduncle (CP)	<0.001	31.45	$P < 0.001$	$P < 0.001$	1
Body depth posterior (BDP)	<0.001	78.68	$P < 0.001$	$P < 0.001$	$P < 0.001$
Body depth anterior (BDA)	<0.001	40.73	$P < 0.001$	$P < 0.001$	0.61
Post-pelvic fin length (PPF)	<0.001	16.96	$P < 0.01$	$P < 0.05$	$P < 0.001$

Note. Morphometric traits were determined from size-adjusted linear measurements (T_{adj}).

Arctic char among possible overwintering lakes that were identified by the UCWG, OHTC and community fishers. A total of seven lakes were surveyed for the presence of tagged fish by drilling a hole through the ice with an ice auger and deploying the hydrophone into the hole and beneath the ice, then listening and recording detections for 10–25 min per deployment (Hollins *et al.*, 2022). Lakes surveyed (n = number of VR100 deployments) were Tatik (n = 12), Second (n = 3), Red Belly (n = 5), Tahiryuak (n = 15), Halahikvik (n = 6), Uyagakto (n = 6) and Mayoklihok (n = 3) across a total of three sampling periods (4–5, 21–22 and 25 May 2019; 11, 26–27 November, 12 December 2019 and 30 May 2020, 7–9 June 2020). To assess whether overwintering lake was associated with a morphological group, a Fisher's exact test was applied due to small sample sizes.

3 | RESULTS

A total of 103 Arctic char were sampled in Ulukhaktok coastal waters (53 in 2018; 50 in 2019) ranging in size from 44.8 to 85.8 cm (mean \pm S.D. = 71.6 ± 7.2 cm) and 1500 to 7400 g (mean \pm S.D. = 4468.0 ± 1054.9 , n = 93 where weight was available). Preliminary assessment of body shape variation using landmark coordinates in MorphoJ identified that three PC axes accounted for 71.71% of the total variation. The primary factors driving this variation were divergence in head shape and body depth (Supporting Information Figure FIGURE S1).

Results from T_{adj} were in agreement with the initial assessment of shape variation observed in MorphoJ. For the PCA of the nine linear traits, PC1 represented 42.3% of the total variation (Table 1; Supporting Information Figure S3). The T_{adj} with the highest contribution to PC1 were head length (HL), snout length (SL) and maxilla length (ML) followed by post-pelvic fin length (PPF) and head depth (HD) (Table 1). This identified that head shape is the primary contributor of shape variation in this mixed-stock of anadromous Arctic char. PC2 accounted for 28.1% of the total variation (Table 1; Supporting Information Figure S3) and was heavily influenced by T_{adj} reflecting body size: caudal peduncle (CP), body depth posterior (BDP), body depth anterior (BDA) with HD.

The estimated optimal number of morphological groups based on T_{adj} using a Silhouette Analysis was three (Supporting Information Figure S2) and the K-means clustering approach assigned each fish to a cluster (Figure 3; Supporting Information Figure S4). Cluster one fish had slender bodies with relatively small BDA, BDP and CP measurements (Figures 4 and 5). Cluster two fish had a small and short head (HD, HL, SL), with a small mouth (ML) (Figures 4 and 5). Cluster three fish had an elongated head shape (HD, HL, SL) and large mouth (ML) (Figures 4 and 5). Significant differences were found among all nine T_{adj} morphometric traits (ANOVA, $P < 0.001$; Table 2), and the nine T_{adj} differed significantly among the three Arctic char morphs (MANOVA, $F_{18,186} = 18.157$, $P < 0.001$, Pillai trace = 1.27). Body depth (BDA) and tail depth CP were similar in clusters two and three, whereas HD was similar in clusters one and two, and eye width (EW) was similar in clusters one and three ($P > 0.5$ for all these comparisons, pair-wise *t*-test; Table 2; Figures 4 and 5). All remaining T_{adj} comparisons between each morphotype were significant (pair-wise *t*-test, $P < 0.05$; Table 2). Fulton's condition factor did not vary among the three morphological groups (ANOVA, $F_{2,90} = 2.285$, $P = 0.108$) indicating that body condition was not a confounding variable (Supporting Information Table S1).

Of the 103 fish sampled, it was possible to assign 33 tagged fish to one of two known overwintering lakes: Tahiryuak Lake [n = 23; cluster one (n = 4), cluster two (n = 12), cluster three (n = 7)] and Tatik Lake [n = 11; cluster one (n = 3), cluster two (n = 4), cluster three (n = 4)]. The remaining fish (n = 69) could not be assigned given they were not detected in a specific lake during acoustic surveys. Fisher's exact test showed no significant difference between the number of Arctic char morphotypes from Tahiryuak or Tatik lakes, indicating no association between morphotype and overwintering lake ($P = 0.709$).

4 | DISCUSSION

This study is the first documentation of Arctic char morphotypes in the marine environment and provides evidence for morphological

variation within anadromous Arctic char in the Canadian Arctic. Three morphotypes of Arctic char were identified with the primary differences found in head shape and body depth. The observation of anadromous morphotypes within a coastal mixed-stock fishery is in agreement with the documented morphological diversity found within the Salmonidae family (Reist *et al.*, 2013) and Arctic char species (Jonsson & Jonsson, 2001). Although the sample size was small, the lack of association between morphotype and overwintering lake raises questions on the evolutionary and ecological drivers of morphotypes in anadromous Arctic char.

To date, morphological studies on *Salvelinus* spp. have primarily focused on lacustrine populations, and research on morphological variation in Arctic char has consistently been conducted in areas where the number of morphotypes was previously identified (Garduño-Paz *et al.*, 2012; Jónsson & Skúlason, 2000; Skoglund *et al.*, 2015; Walker *et al.*, 1988). These studies have focused on distinct variation among individuals such as colouration (O'Connell & Dempson, 2002; Power *et al.*, 2005), marked differences in body depth/shape (Arbour *et al.*, 2011; Garduño-Paz *et al.*, 2012) or between lake-resident and anadromous life-history strategies when present in fresh water (Loewen *et al.*, 2009). The presence and diversity of anadromous Arctic char morphotypes in the Ulukahktok area was not known a priori, allowing for an unbiased assessment of morphotype occurrence. The divergence in head morphology and body depth within anadromous Arctic char sampled in the Ulukahktok-Safety Channel region matches common morphological variation seen within lacustrine populations (Jonsson & Jonsson, 2001). The results support the assessment that variation documented within lacustrine Arctic char populations using PCA analyses resembles a gradient relationship between morphs instead of distinct and separate clusters (Gíslason *et al.*, 1999; Reist *et al.*, 1995). This spectrum of morphotypes with inherent overlap (Fraser *et al.*, 1998; Reist *et al.*, 1995; Skoglund *et al.*, 2015) is thought to represent a “plasticity-first” evolution in nature where phenotypic plasticity can produce developmental variants in response to abiotic and biotic environmental variation to enhance fitness (Ghalambor *et al.*, 2015; Levis & Pfennig, 2016; Robinson & Parsons, 2002).

The life history of anadromous Arctic char begins in the freshwater environment, where spawning takes place and alevins develop into juveniles. During this period, young remain resident in the lake system feeding and growing until they attain a suitable body size to undertake their first seasonal marine migration (Scott & Crossman, 1973). As a result of the varied habitats and resources anadromous Arctic char encounter over their lifetime, the authors identify four possible explanations for the morphological divergence observed within Arctic char from the Ulukahktok region.

Accepting the small sample size of tracked fish that could be assigned to a lake, morphotypes were equally distributed across the two primary overwintering lakes. If morphotype divergence occurred in fresh water in response to resource or habitat availability, this could suggest both overwintering lakes have similar environments to support the existence of the three morphotypes. In this scenario, morphological divergence could potentially be an artefact of ecological differentiation during juvenile development (Esin *et al.*, 2018; Nakano

et al., 2020; Parsons *et al.*, 2011). The age of first marine migration can be up to approximately 6 years for anadromous Arctic char (Dempson & Green, 1985; Klemetsen *et al.*, 2003). Therefore, sustained year-round foraging in freshwater lake habitat and intraspecific competition for resources among juveniles could drive the observed morphological variation. Nonetheless, further lake-specific information would be required to confirm this hypothesis (e.g., habitat surveys, winter sampling of fish and further morphometric analysis).

Alternatively, the three morphotypes of anadromous Arctic char could occur in response to fish maximising consumption of seasonal prey resources in the marine environment (Gross *et al.*, 1988). During the marine residency phase, Arctic char can double their body weight and exponentially increase body fat stores in preparation for overwintering and spawning in fresh water where feeding is thought to cease to conserve energy (Jørgensen & Johnsen, 2014; Klemetsen *et al.*, 2003). Anadromous Arctic char exploit diverse prey resources during the marine phase, including, fishes, amphipods, crustaceans and zooplankton that occupy different vertical niches (Dempson *et al.*, 2002; Moore & Moore, 1974). Given Arctic char is considered to be an ecological generalist (Reist *et al.*, 2013), it is possible these morphs arose to occupy all available niches in the marine environment (Klemetsen *et al.*, 2003) with specialised morphotypes often feeding more efficiently than intermediate forms (Guiguer *et al.*, 2002). In contrast to sub-Arctic populations of Arctic char, populations found at higher latitudes experience marked seasonal differences in food availability (Jørgensen & Johnsen, 2014) that is likely a major driving force in the evolution of the anadromous life-history strategy (Gross *et al.*, 1988). In these environments, Arctic char migrate to the sea in spring when ice breaks up to take advantage of the seasonal pulse of prey resources tied with the productivity bloom (Dempson & Green, 1985; Gilbert *et al.*, 2016; Hammer *et al.*, 2021; Hammer *et al.*, 2022). As a result, the long slender body morph (cluster one) could indicate a planktivorous feeding strategy in the marine environment (Jonsson & Jonsson, 2001; Robinson & Parsons, 2002; Skoglund *et al.*, 2015). The smaller head and body size features of cluster two fish could be beneficial for benthic feeding (Jonsson & Jonsson, 2001; Knudsen *et al.*, 2011), whereas the elongated head and large mouth of cluster three fish could indicate they are primarily piscivorous (Jonsson & Jonsson, 2001; Skúlason *et al.*, 1989). Consequently, morphological variation in anadromous Arctic char in this study may not be driven by resource availability in lakes during the adult life stage unless presumed low consumption rates or cessation of feeding during winter still require a degree of niche partitioning (Jørgensen & Johnsen, 2014), or density dependence tied with low activity rates drives variable habitat selection.

A third possible explanation is that the observed morphotypes are relicts from ancestral lake populations (Behnke, 1972; Reist *et al.*, 2013). This would suggest head-body shape variation is redundant for consuming the high diversity of prey available in the marine environment. Although morphological divergence could represent sexual dimorphism, the authors were unable to assess the effect of sex given the majority of photographed fish were released alive. Further study will be required to determine whether the three morphotypes

are driven by the occupation of different ecological niches during the juvenile life stage or are relicts, and to evaluate the effect of sex. Stomach content analysis and/or stable isotope analysis (e.g., nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$)) of tissues in conjunction with genomics could address this question.

Acoustic telemetry has shown that Arctic char in the vicinity of Ulukhaktok seasonally inhabit overwintering lakes that correspond to divergent marine migration routes and residency areas, with migration timing potentially modulated by total migratory distance (i.e., Tatik vs. Tahiryuak lake) (Hollins *et al.*, 2022). This variability in marine migration timing and space use may increase selective pressure on fish that occupy certain overwintering lakes, depending on the timing when harvesting occurs along the coast during the summer marine phase. For example, Arctic char with longer freshwater migration distances may spend less time in marine foraging grounds targeted by fisheries and are consequently less likely to be captured in deployed gears (Hollins *et al.*, 2022). In addition, Tatik Lake experiences higher fishing pressure compared to other lakes during winter based on the distance fishers need to travel to harvest and the associated logistics, such as fuel costs (DFO, 2016a; Gallagher *et al.*, 2021). Given that the identified morphotypes that appeared to be evenly distributed across both lakes and Arctic char were sampled at the same location in the marine environment using similar techniques to the subsistence fishery, it is unlikely that lake selection or variable timing of marine harvesting by fishers from Ulukhaktok would alter the spatial distribution of morphotypes. As a result, the potential for phenotypic erosion tied to selective removal of specific morphotypes is considered low (Hollins *et al.*, 2018; Schindler *et al.*, 2010) but requires further investigation. It is possible that specific morphotypes are more vulnerable to fisheries through a mechanism independent of selection on habitat use and behaviour (Alós *et al.*, 2014; Hollins *et al.*, 2018). For example, Arctic char from cluster two and three had larger anterior and posterior body depths compared to the slender form of cluster one. Therefore, these larger-bodied fish could be more easily retained in gill nets, increasing their risk of capture compared to the slender form that had the lowest occurrence in this study. This latter point is of importance given the community is reported to favour consumption of small-sized anadromous Arctic char (DFO, 2016b), and there is increasing evidence that fishing gear and fishing habits can selectively remove phenotypes related to the preferred catch (Ljungberg *et al.*, 2020) or depth selected (Olsen *et al.*, 2012), which can be directly correlated with morphotype (Olsen *et al.*, 2012).

Arctic char is an important resource for subsistence harvesting in the Canadian Arctic (Sawatzky & Reist, 2010; Smart, 2021; Usher, 2002), but the sustainable harvest of this species depends on relevant knowledge to implement management strategies that account for its variable ecology and intraspecific diversity (Harris *et al.*, 2016). Anadromous Arctic char populations are vulnerable to environmental stressors such as climate change as freshwater and marine habitats are being differentially affected (Reist *et al.*, 2013). The effects of environmental and anthropogenic stressors, while still largely unknown, could have long-term impacts on Arctic char populations and the fisheries that help sustain northern communities.

With concerns raised by harvesters in Ulukhaktok over the decline of favoured small-sized Arctic char, recent low capture rates of fish and increasing prevalence of Pacific salmon (Chila *et al.*, 2021; DFO, 2016a; DFO, 2016b; Smart, 2021), information on the life history of anadromous stocks is essential. Identifying and conserving diversity within fish populations, such as the morphotypes identified here, is necessary to maintain stability and resilience of ecosystems to disturbances amid the enhanced anthropogenic stressors currently threatening northern aquatic systems.

AUTHOR CONTRIBUTIONS

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SUPPORTING INFORMATION

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