

Life history variation in Arctic charr (*Salvelinus alpinus*) and the effects of diet and migration on the growth, condition, and body morphology of two Arctic charr populations in Cumberland Sound, Nunavut, Canada¹

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Abstract: Arctic charr (*Salvelinus alpinus* (Linnaeus, 1758)) are phenotypically plastic with multiple dietary–morphological relationships observed throughout their circumpolar range. Feeding strategies often differ between Arctic charr life histories and can impact size-at-age and morphological attributes. We examined growth, condition, and body morphology for two High Arctic populations of Arctic charr with anadromous and landlocked life histories. Anadromous Arctic charr had higher growth rates, achieving mean lengths two times those of landlocked Arctic charr by age 10 and had higher overall condition, particularly in the fall. Ontogenetic shifts in diet were suspected in both populations, with an abrupt shift to marine feeding in the anadromous population and a gradual shift to piscivory in the landlocked population. Morphological differences between life histories manifested most predominantly in larger eye diameter, longer pectoral and pelvic fins, and longer upper jaws of landlocked Arctic charr, suggestive of piscivorous feeding specialization of landlocked fish >350 mm. Our findings emphasize the benefits that marine feeding can have for growth and condition of freshwater fishes in Arctic environments and also convey the necessity of adaptive feeding strategies to optimize growth and condition in fishes inhabiting low-production lacustrine habitats.

Key words: adaptation, High Arctic, ontogenetic shift, freshwater, marine.

Résumé : L'omble chevalier (*Salvelinus alpinus* (Linnaeus, 1758)) s'adapte sur le plan du phénotype et présente de multiples relations diététiques–morphologiques observées dans l'ensemble de son aire de répartition circumpolaire. Les stratégies d'alimentation diffèrent souvent entre les évolutions biologiques de l'omble chevalier et peuvent avoir une incidence sur la taille par âge et les attributs morphologiques. Les auteurs ont examiné la croissance, l'état et la morphologie de deux populations d'omble chevalier du Haut Arctique aux évolutions biologiques anadrome et confinée aux eaux intérieures. L'omble chevalier anadrome affichait un taux de croissance plus élevé, atteignant une

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longueur moyenne deux fois supérieure à celle de l'omble chevalier confiné à l'âge de 10 ans et affichait un état général supérieur, particulièrement à l'automne. On suppose des changements ontogénétiques du régime alimentaire chez les deux populations, avec un virage abrupt vers l'alimentation marine chez la population anadrome et un changement graduel vers l'ichtyophagie chez la population confinée. Les différences morphologiques entre les évolutions biologiques se manifestent surtout par un diamètre oculaire plus grand, des nageoires pectorales et pelviennes plus longues et une mâchoire supérieure plus longue chez la population confinée, ce qui suggère une spécialisation ichtyophage des poissons confinés de plus de 350 mm. Les résultats mettent en évidence les avantages que l'alimentation en milieu marin peut avoir sur la croissance et l'état des poissons d'eau douce dans les milieux arctiques et font également ressortir la nécessité de stratégies d'alimentation adaptatives pour optimiser la croissance et l'état chez les poissons qui vivent dans les habitats lacustres de faible production. [Traduit par la Rédaction]

Mots-clés : adaptation, Haut Arctique, changement ontogénétique, eau douce, marin.

Introduction

Diet and feeding ecology play an important role in an organism's growth and development throughout its life cycle and may contribute to shaping its life history. The dietary needs of animals expand during ontogeny (Laegdsgaard and Johnson 2001) and the quality and quantity of prey consumed will determine an animal's overall growth and reproductive potential. Ontogenetic niche shifts (e.g., changes in feeding, habitat use, and morphology) are common in species with variable life histories (Werner and Gilliam 1984; Fryxell and Sinclair 1988; Post 2003; Kimirei et al. 2013). These shifts are related to behavioral or morphological changes during ontogeny, are often correlated with discrete growth periods in the species' life history (Werner and Gilliam 1984), and may be either as dramatic as metamorphosis in amphibians or as subtle as diet shifts in fishes (Werner and Gilliam 1984; Olson 1996).

It is hypothesized that organisms adaptively select foraging strategies that optimize individual fitness (Pyke 1984). Fishes commonly undertake shifts in habitat and diet at certain points in ontogeny for the purposes of fitness and growth (Werner and Gilliam 1984; Olson 1996). A single ontogenetic shift in diet such as from an invertebrate-based diet to piscivory is common in many freshwater fishes (Werner and Gilliam 1984), whereas some species have multiple ontogenetic shifts in diet to optimize energetic return (e.g., largemouth bass (*Micropterus salmoides* (Lacepède, 1802)); Olson 1996). These shifts in diet may be necessitated by seasonal food availability, as is the case with seasonal migrations made by some salmonids that inhabit low productivity and highly seasonal freshwater habitats such as those found in the Arctic (Hendry and Stearns 2004).

Feeding ecology of Arctic fishes is often highly adaptive and not limited to one strategy given the extreme seasonality and low productivity of high-latitude freshwater ecosystems. Arctic fish exhibit numerous feeding strategies, such as feeding in different habitats (marine versus freshwater), cannibalism, or exploitation of a singular resource (benthos, zooplankton or fish), which often results in ecotype polymorphism in phenotypically plastic species such as salmonids. There is evidence for intraspecific morphs (or ecophenotypes) using different niches (e.g., planktivores, benthivores, and piscivores) within lake trout (*Salvelinus namaycush* (Walbaum in Artdi, 1792)) (Muir et al. 2015; Chavarie et al. 2016) and Arctic charr (*Salvelinus alpinus* (Linnaeus, 1758)) populations within single lacustrine systems (Johnson 1980; Riget et al. 1986; Jónasson et al. 1998; Klemetsen et al. 2003; Amundsen et al. 2008). A singular feeding strategy such as planktivory or benthivory can vary in benefits from that of a more piscivorous diet, as these strategies do not aim to optimize growth but instead optimize fitness with a smaller size at maturity (Roff 1984; Stearns 1992).

Multiple life histories of Arctic charr are known to exist allopatrically or sympatrically, including anadromous, partially anadromous, and resident populations (Hendry and Stearns 2004), all of which offer different costs and benefits. Anadromy has a positive effect on growth and fecundity due to the benefits of shifting from a freshwater to a seasonal marine-based diet (Chapman et al. 2012). The productivity offered by the ocean in temperate and northern climates far exceeds that of freshwater, with feeding in the ocean often resulting in higher growth rates, larger sizes-at-age, and greater energy stores (Gross 1987; Hendry and Stearns 2004). As such, size-at-age data have shown that sea-run fish grow faster than lake-resident fish (Johnson 1980; Kristoffersen et al. 1991; Jonsson and Jonsson 1993; Rikardsen et al. 2000) and freshwater resident fish remain smaller with lower overall growth rates (Chapman et al. 2012). The high degree of phenotypic plasticity of Arctic charr has given rise to polymorphism within the species (Jónasson et al. 1998), which may have allowed Arctic charr to become well-adapted to variable and harsh Arctic environments.

Most examinations of the dietary-morphological relationships of Arctic charr have focused on European populations (e.g., Henricson and Nyman 1976; Klemetsen and Grotnes 1980; Hindar and Jonsson 1982; Snorrason et al. 1994; Pavlov 1997; Jonsson and Jonsson 2001; Klemetsen et al. 2003; Klemetsen 2010). Comparatively little research has examined the diet, growth, and morphological characteristics of Arctic charr populations in the Canadian High Arctic (Moore and Moore 1974; Johnson 1980; Reist et al. 1995; Loewen et al. 2009; Imrie 2012), and there is no published research that compares the growth, morphological traits, and diets of Arctic charr between populations with anadromous and landlocked life histories.

Thus, our research focused on differences in growth, condition, and body morphology, and their associated influence of ontogenetic diet shifts, between allopatric populations of anadromous and landlocked Arctic charr in Nunavut, Canada. It was expected that differences in growth, seasonal condition, and between-population morphological variation would be attributed to overall differences in diet and within-population morphological variation would be associated with ontogenetic diet shifts.

Materials and methods

Study area and field collection

This study took place in two different lake systems in south Baffin Island, Nunavut (Fig. 1). Iqalugaarjuit Lake (hereafter referred to as PG027), is a small open lake system located atop Iqalugaarjuit Fjord in Cumberland Sound, Nunavut (65°44'27"N, 64°47'5"W) that supports a modest commercial quota of anadromous Arctic charr. Qinniqtuq is a small freshwater lake located 42 km west of the community of Pangnirtung in Cumberland Sound, Nunavut (66°21'13"N, 66°28'51"W). Qinniqtuq has a small population of Arctic charr that local Inuit consider landlocked given the lack of a passable connection to the marine environment and the small body size, flesh colouration, extent of parasitism, and other morphological characteristics typically associated with landlocked populations (Pangnirtung Hunters and Trappers Association, personal communication, 2011). As anadromous Arctic charr are the preferred source for both commercial and subsistence harvest, there is minimal exploitation of the landlocked Arctic charr in Qinniqtuq.

Fish were sampled from both lakes in fall and winter over a three-year period (2011–2013). Experimental gillnets with panels of 3.8 cm (1.5 in.) to 14.0 cm (5.5 in.) stretched mesh were set at varying depths. Nets placed in nearshore areas were classified as littoral habitats, whereas nets placed offshore in the middle and upper portions of the water column were classified as pelagic habitats, and those within two meters of the lake bottom were classified as benthic habitats. Nets set in March were set under the ice using a jigger board.

Fig. 1. Map of the Qinniqtuq and Iqalugaarjuit (PG027) study sites (lakes) within Cumberland Sound located on Baffin Island in Nunavut, Canada (Esri Inc. 2021; Natural Resources Canada 2013).

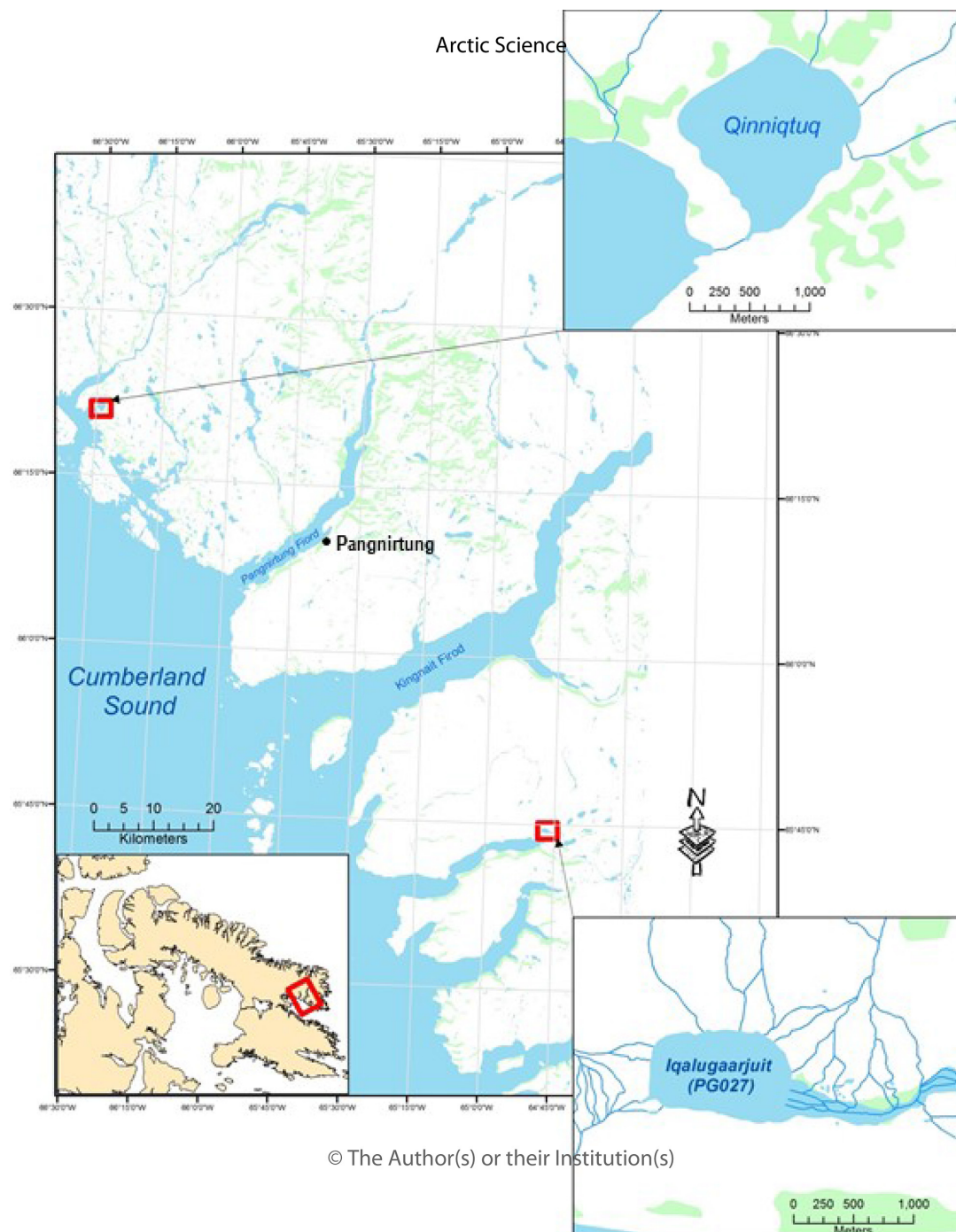
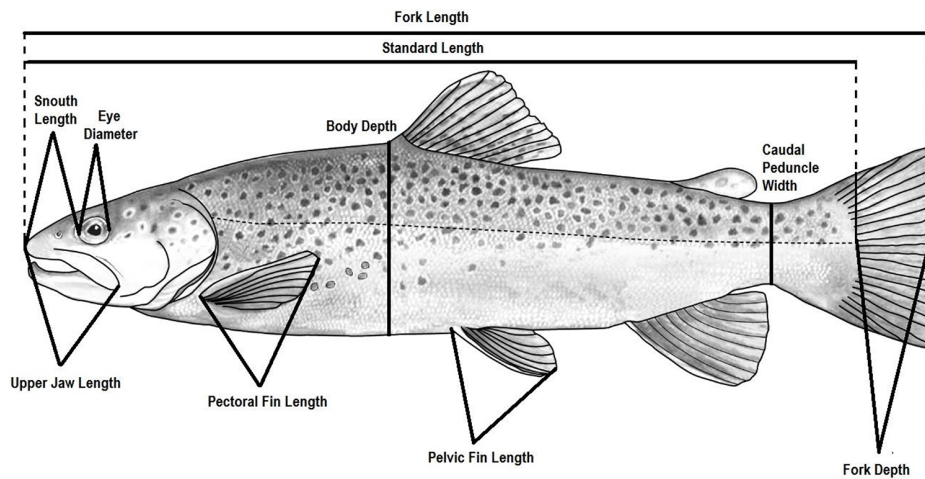


Fig. 2. Morphological characteristics measured on each Arctic charr. Diagram used with permission ([Government of Nunavut 2018](#)).



All biological measurements and samples were obtained in the field from dead fish. Fork length (FL) to the nearest mm, round weight to the nearest 1 g, sex, maturity stage, and gonad weight to the nearest 0.5 g were recorded, and sagittal otoliths were removed for subsequent age analysis. Stomachs that contained food items were removed whole and stored in 90% ethanol. Snout length, eye diameter, upper jaw length, pectoral fin length, pelvic fin length, body depth, caudal peduncle width, FL, and standard length were obtained from the left side of each fish to the nearest 0.01 mm with digital calipers (Fig. 2). Fork depth was calculated by subtracting standard length from FL. This suite of morphological measurements were adapted from [Loewen et al. \(2009\)](#), [Cadrian \(2005\)](#), and [Reist et al. \(1995\)](#) and have been used in previous Arctic charr studies to discriminate between phenotypic groups ([Reist et al. 1995](#); [Adams and Huntingford 2002](#); [Alekseyev et al. 2002](#); [Kristofferson 2002](#); [Loewen et al. 2009](#)).

Age determination

Ages were estimated from whole otoliths except when the estimated age was more than 11 for fish from Qinniqtuq or more than 12 for fish from PG027. In these instances, the age estimated from the whole otolith was replaced with an age estimated from the sectioned otolith. Ages for when sectioned otoliths were used were determined from preliminary analysis of ages estimated from both whole and sectioned otoliths for a subsample of fish. Otoliths were sectioned by embedding the whole otolith in epoxy resin and then cutting through the nucleus perpendicular to the sulcus with a BuehlerTM Isomet 1000 sectioning saw.

Data analyses

Growth

Growth curves and growth comparisons between populations based on length at age data were calculated with the Gompertz growth function:

$$L_i = L_{\infty} e^{-e^{-g(t_i - t^*)}} + \varepsilon_i$$

where L_i is FL at age t_i , L_{∞} is the mean asymptotic FL, t^* is the age at the inflection point, g is the instantaneous growth rate at the inflection point, and ε_i is a normally distributed error

term for the i th fish (Ogle et al. 2017). The Gompertz growth function was fit to observed data using non-linear least-squares (`nls()` in R v4.0.1 (R Core Team 2020)) and `GompertzFuns()` from the FSA v0.8.30 package (Ogle et al. 2020). Differences in Gompertz model growth parameters between populations were assessed by using an extra sums-of-squares test to identify the most parsimonious significant model from a family of eight models where all three, two, one, or no parameters differed between populations (Ogle 2016; Ogle et al. 2017).

Condition

Weight–length relationships were assessed as a measure of condition within and between populations and seasons. Sexes were pooled for analysis and somatic weight (round weight – gonad weight) was used to avoid seasonal, spawning-related bias in weights caused by differences in maturity stage. Condition was examined with a linear model that included \log_e weight as the response variable, \log_e FL as a covariate, season and population as dichotomous explanatory variables, and all two- and three-way interactions among \log_e FL, season, and population. Statistical significance of each term was determined with this model using Type I SS F tests. All interaction terms with the \log_e FL covariate were non-significant such that the slopes of the \log_e weight – \log_e FL relationships were the same for all season–population combinations. Thus, a second linear model was fit where all non-significant terms from the first model were removed. We described relative condition from this second model by predicting the ratio of mean weights at the overall (i.e., across all season–population combinations) mean FL for all season–population combinations using the `emmeans` v1.5.0 package in R (Lenth 2020).

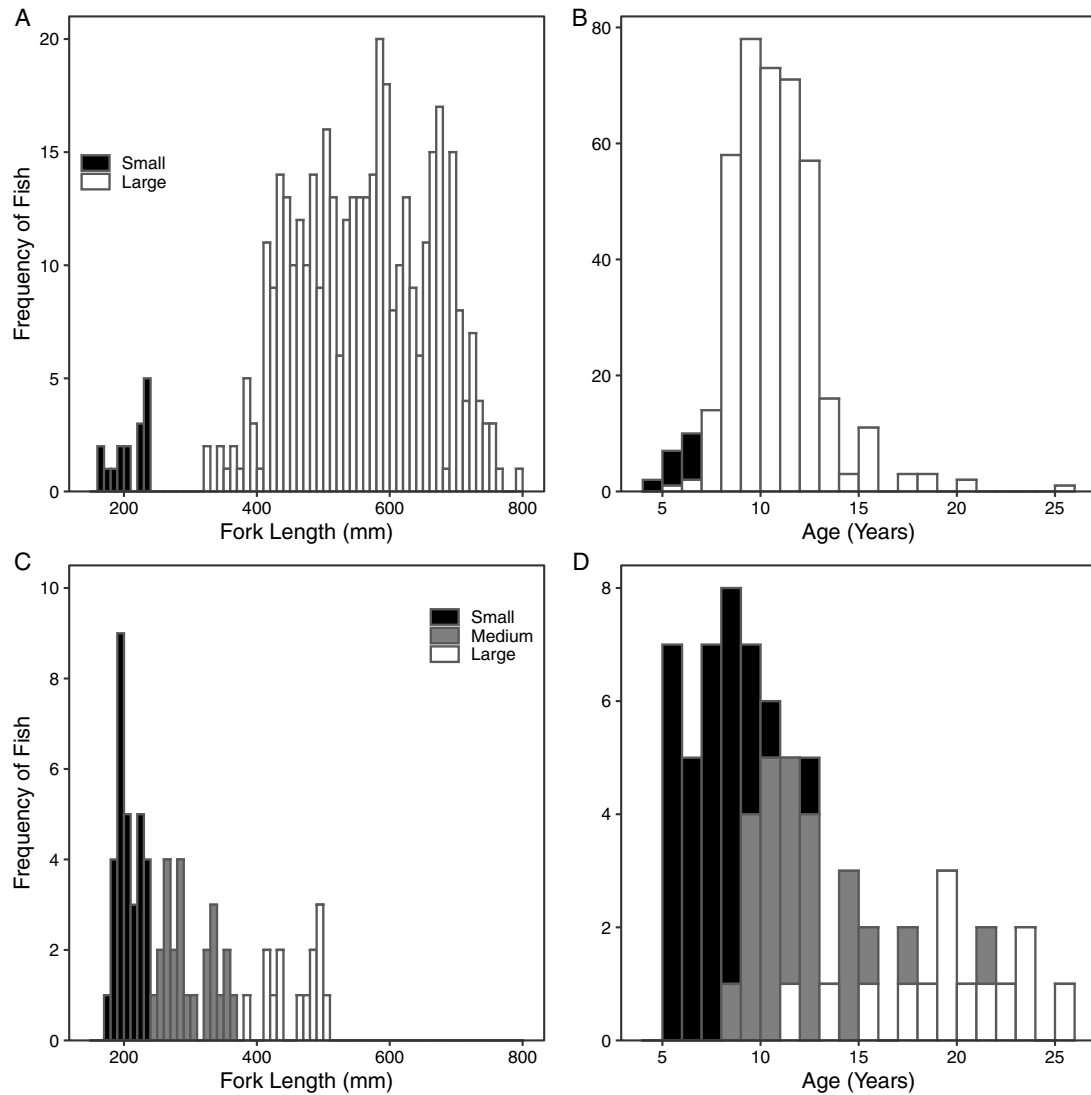
Morphometrics

We examined potential differences between anadromous and landlocked populations for each morphometric variable with general additive models (GAM; Wood 2017) that included a smoother term for FL, as we expected each morphometric variable to be related to FL. To further isolate potential differences between the two populations, separate from the effect of size, we restricted the comparison to only fish from both populations that were <525 mm FL (Rohlf 1990; Freckleton 2002; Parsons et al. 2003; Jensen et al. 2008). The GAM were fit using `gam()` from the `mgcv` v1.8–34 package (Wood 2017) with p -values for the differences between the two populations derived from a Wald test as described by Wood (2017). We used a conservative $\alpha = 0.005$ to account for multiple tests across the morphometric variables.

Diet

Diet analysis was only conducted for the landlocked population of Arctic charr given the near complete absence of food in the stomachs of the anadromous Arctic charr. As the diversity of prey items in the stomach contents of landlocked Arctic charr was low, we summarized diet simply as the percent of stomachs by whether either fish or invertebrates occurred. Simple linear regression was used to examine length of prey consumed in relation to Arctic charr FL. Logistic regression was used to predict the FL at which landlocked Arctic charr switch from an invertebrate-based to a fish-based diet. Given that only one fish had stomach contents containing both fish and invertebrates, any Arctic charr with fish in its stomach was considered piscivorous. Percent stomach content was examined visually in relation to class size and season.

Fig. 3. Distributions of fork lengths and estimated ages for anadromous (A–B) and landlocked (C–D) Arctic charr separated by broad size categories. Note that the y-axis scales differ among all panels.



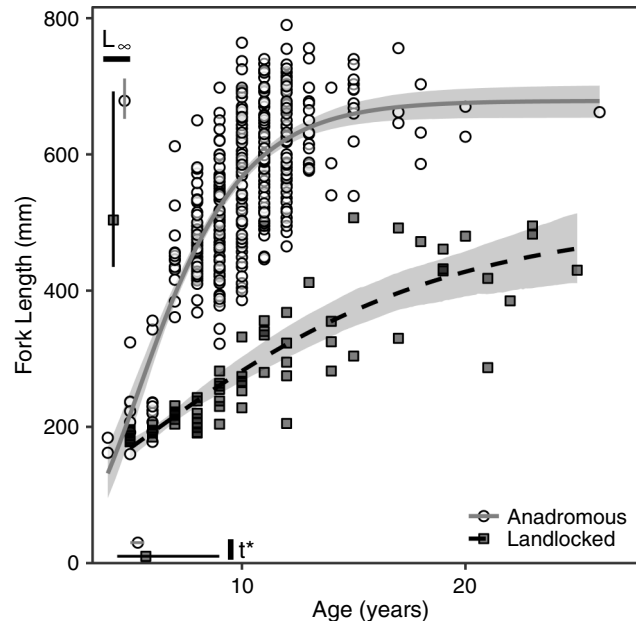
Results

General

Study sites yielded notably different sample sizes with 409 anadromous Arctic charr sampled from PG027 and 69 landlocked Arctic charr sampled from Qinnigtug across all sampling seasons and years. Seasonal catch rates differed between systems, with 197 anadromous fish sampled from PG027 and 27 landlocked fish sampled from Qinnigtug in the two winter sampling seasons.

Anadromous Arctic charr were between 160 mm and 790 mm FL with a distinct group of small fish <240 mm FL, whereas landlocked Arctic charr were between 178 mm and 507 mm FL without distinct size groups (Fig. 3). To aid comparisons in later analyses we categorized all fish into “small” (<240 mm FL), “medium” (240–374 mm FL), and “large”

Fig. 4. Fork length-at-age data with fitted Gompertz growth curves for anadromous and landlocked Arctic charr. Point and interval estimates for the mean asymptotic length (L_{∞}) are shown along the y-axis and point and interval estimates for the inflection point age (t^*) are shown along the x-axis for both forms of Arctic charr. Note that L_{∞} but not t^* was significantly different between anadromous and landlocked Arctic charr.



(≥ 375 mm FL) categories. Only seven anadromous Arctic Charr were categorized as “medium”, so these fish were included within the “large” category. Ages within these size categories overlapped very little for anadromous fish where all “small” anadromous fish were ages 4–6 and 99% of “large” anadromous fish were older than age 6, with a maximum age of 26 (Fig. 3). Age overlap among size categories was also not substantial for landlocked fish where most (94%) of “small” fish were ages 5–9, most (83%) “medium” fish were ages 9–14, and most (86%) “large” fish were age 15 or older, with a maximum age of 25 (Fig. 3). Thus, our size categories also largely correspond to distinct age categories.

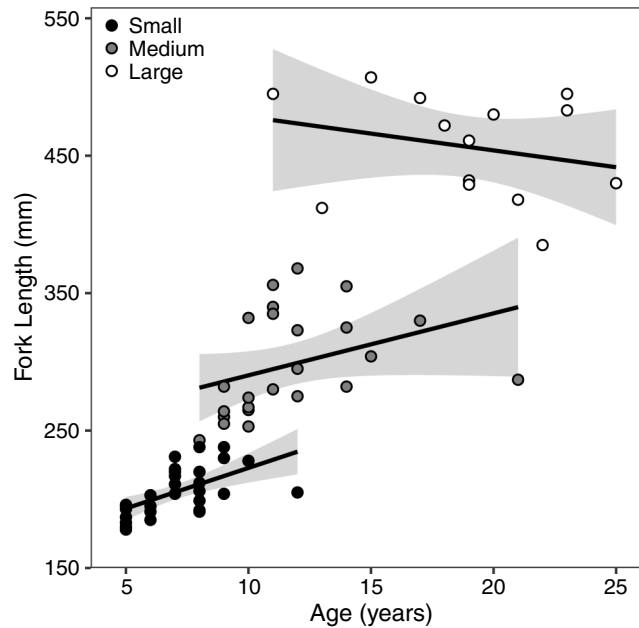
Growth

Gompertz model parameter estimates and associated confidence intervals were $L_{\infty} = 678.7$ (652.2–711.4), $g = 0.37$ (0.31–0.44) and $t^* = 5.34$ (5.01–5.63) for 409 anadromous Arctic charr and $L_{\infty} = 503.7$ (434.9–692.5), $g = 0.13$ (0.07–0.19), and $t^* = 5.70$ (4.42–8.99) for 69 landlocked Arctic charr (Fig. 3). The most parsimonious significant growth model had different L_{∞} and g parameters, but not t^* parameter, among populations ($p < 0.001$). Thus, L_{∞} and g , but not t^* , differed between anadromous and landlocked Arctic charr, with both L_{∞} and g higher for anadromous Arctic charr. All anadromous Arctic charr were longer than landlocked Arctic charr of the same age after age 7 (Fig. 4). For landlocked Arctic charr, FL did not increase significantly for “small” fish ($p = 0.060$), did increase significantly for “medium” fish ($p = 0.029$), and did not increase significantly for “large” fish ($p = 0.227$; Fig. 5).

Condition

All interaction terms with \log_e FL in the \log_e weight – \log_e FL linear model were not significant ($p > 0.560$); thus, the slope of the \log_e weight – \log_e FL relationship did not differ

Fig. 5. Length-at-age with fitted linear relationships for three size classes of landlocked Arctic charr. Note that the relationship is not significant for the “small” and “large” fish, but is significant for “medium” fish.

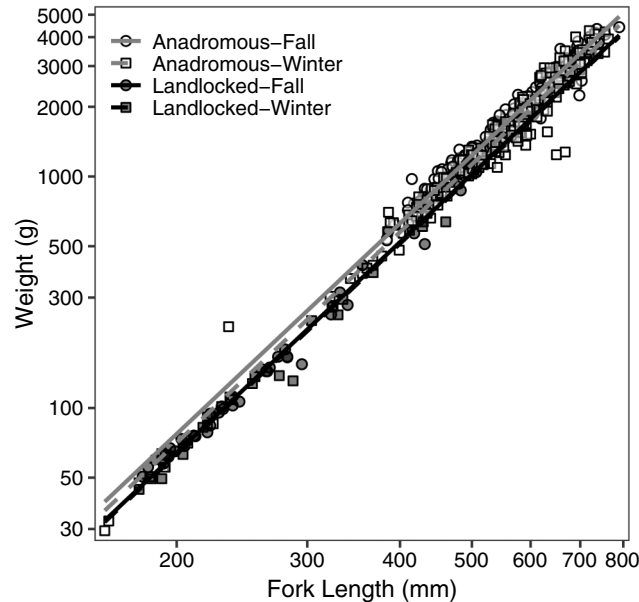


among all season–population combinations (Fig. 6). The slope of the \log_e weight – \log_e FL relationship was significant ($p < 0.001$). The season–population interaction term was significant ($p = 0.002$), which indicates that the intercept of the \log_e weight – \log_e FL relationship differed among season–population combinations but not consistently between seasons or between populations. The intercepts, and thus the mean \log_e weight at each \log_e FL, differed between all season–population combinations ($p < 0.001$), with the exception of between landlocked Arctic charr captured in fall and winter ($p = 0.953$). The predicted mean weight at each FL of anadromous fish captured in the fall was 1.09 (95% CI: 1.06–1.13) times greater than the predicted mean weight for anadromous fish captured in the winter, 1.21 (95% CI: 1.13–1.29) times greater than the predicted mean weight for landlocked fish captured in the fall, and 1.22 (95% CI: 1.14–1.32) times greater than the predicted mean weight for landlocked fish captured in the winter. The predicted mean weight at each FL for anadromous fish captured in the winter was 1.10 (95% CI: 1.04–1.18) times greater than the predicted mean weight for landlocked fish in the fall and 1.12 (95% CI: 1.04–1.21) times greater than for landlocked fish in the winter.

Morphometrics

Morphological differences were identified between the anadromous and landlocked populations. As expected, each morphometric measure was significantly related to FL ($p < 0.001$; Fig. 7). After accounting for the size effect, upper jaw length ($p < 0.001$), pectoral fin length ($p < 0.001$), pelvic fin length ($p < 0.001$), and eye diameter ($p < 0.001$) all differed between anadromous and landlocked populations, but body depth ($p = 0.344$), caudal peduncle width ($p = 0.791$), snout length ($p = 0.558$), and fork depth ($p = 0.0054$) did not differ between populations. Examination of the GAM smoothers (Fig. 7) suggests that landlocked fish had larger eye diameters at all FL, and larger upper jaw lengths, pectoral fin lengths, and pelvic fin lengths at FL larger than approximately 350 mm or 375 mm.

Fig. 6. Linear regression model fit for weight–length relationship for anadromous and landlocked Arctic charr in fall and winter. Note the natural log scale for both axes and that the regression line for Landlocked-Winter is completely obscured by the regression line for Landlocked-Fall.



Diet

Stomachs of all anadromous Arctic charr were empty, except for one fish suspected to have scavenged Arctic charr flesh. Conversely, stomach contents from 33 landlocked Arctic charr (48% of fish sampled) across all seasons contained prey. Prey diversity was limited to invertebrates of Culicidae (mosquito pupae and egg sacks) and Chironomidae (midge larvae), and fish of Gasterosteidae (sticklebacks) and juvenile Arctic charr. In the fall, 57% of landlocked fish sampled had food in their stomachs, with the majority (79%) containing invertebrates (Culicidae) and the remaining containing fish (sticklebacks). In winter, prey was found in the stomachs of nine landlocked Arctic charr, which consisted primarily (78%) of fish, with all but one fish having juvenile Arctic charr, with the remaining containing Chironomidae. Across all seasons, landlocked Arctic charr stomachs contained either fish or invertebrates, with only a single stomach found to contain both fish and invertebrates. Invertebrates were the main prey type found in the stomachs of “small” Arctic charr in both fall and winter (93% and 67%, respectively). Stomach contents of “medium” and “large” landlocked Arctic charr varied by season, with stomachs of fish sampled in the fall containing equal proportions of fish (primarily sticklebacks) and invertebrates (Culiciadae). Stomachs from “medium” and “large” landlocked Arctic charr sampled in winter contained only fish, primarily juvenile Arctic charr. The \log_e length of prey increased with \log_e FL of Arctic charr ($p < 0.001$; Fig. 8). The probability of piscivory increased with FL of Arctic charr ($p = 0.003$; Fig. 9), with the estimated FL for 50% probability of piscivory being 322 mm.

Discussion

To our knowledge, this is the first study that directly compares growth, seasonal condition, and morphology of allopatric Arctic charr populations with anadromous and landlocked life histories in the Canadian Arctic. Our findings show distinct differences

Fig. 7. Morphometric variables (see Fig. 2 for definitions) versus fork length for anadromous and landlocked Arctic charr populations with general additive models (GAM) for each population. All relationships were significantly positive. There was no significant difference in GAM between anadromous and landlocked populations for (A) body depth, (B) caudal peduncle width, (C) snout length, and (D) fork depth, but did differ significantly for (E) upper jaw length, (F) pectoral fin length, (G) pelvic fin length, and (H) eye diameter.

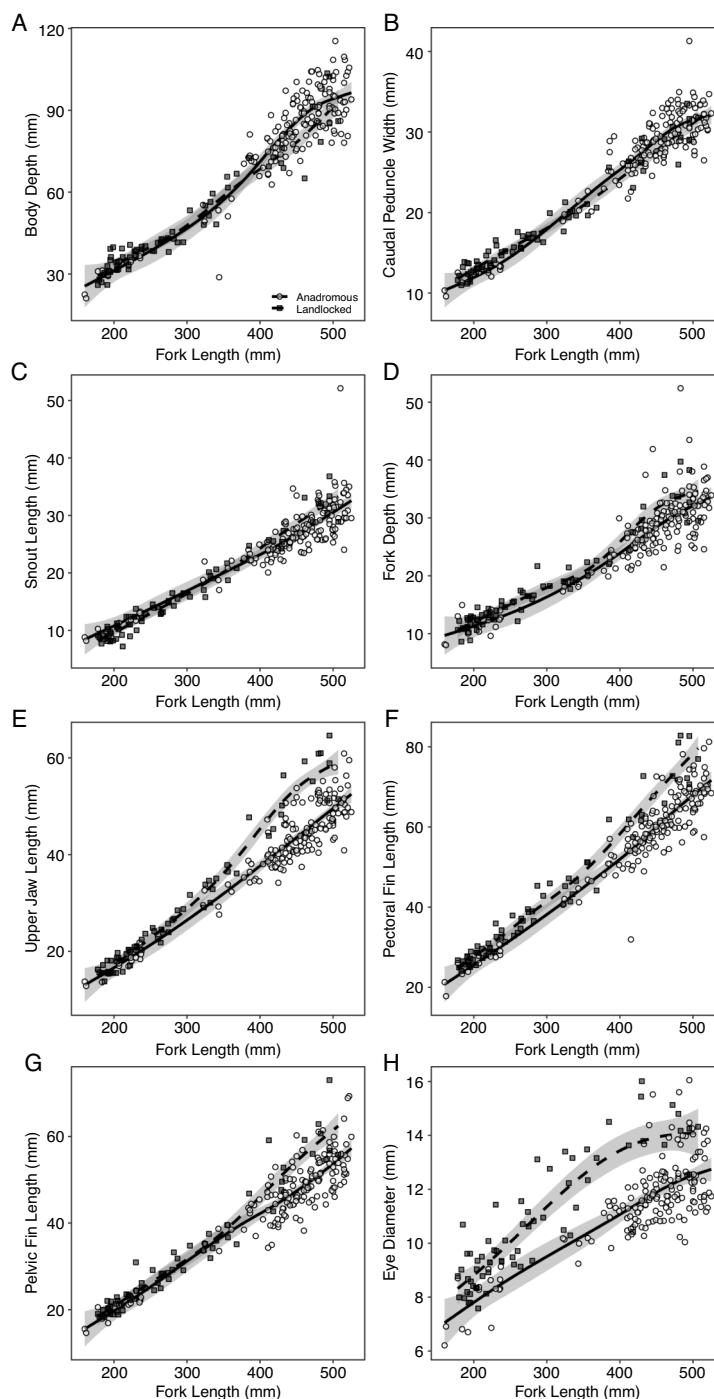


Fig. 8. The linear regression model fit for length of prey consumed and fork length of landlocked Arctic charr. Note the natural log scale for both axes.

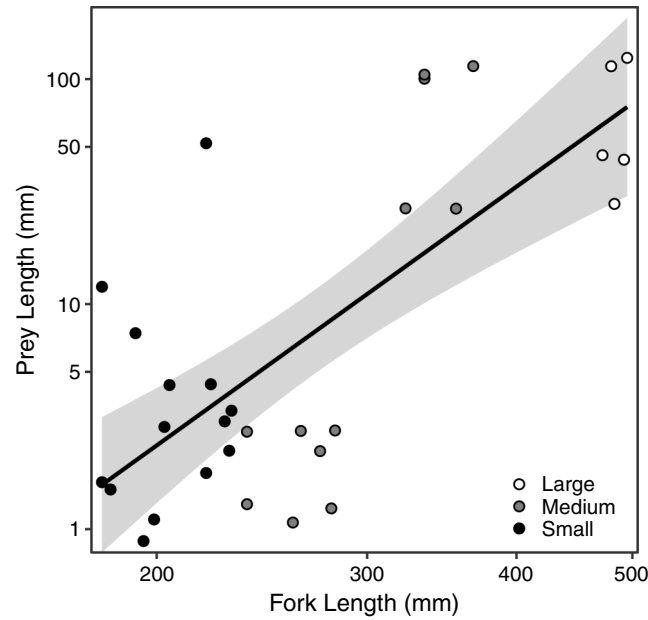
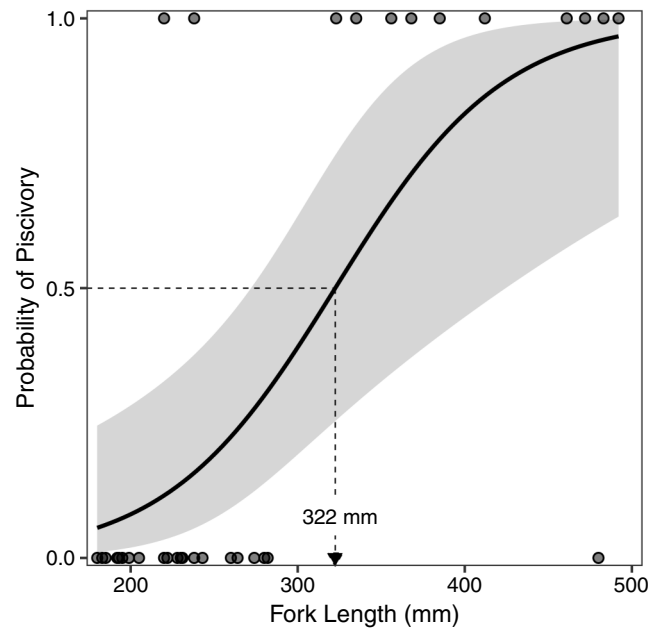


Fig. 9. The logistic regression fit for probability of piscivory on fork length of landlocked Arctic charr. The fork length where the probability of piscivory was predicted to be 0.50 mm is marked at 322 mm.



between these Arctic charr populations, with anadromous Arctic charr achieving higher growth rates and condition than their landlocked counterparts. The impact of marine feeding and differences in growth between anadromous and freshwater resident Arctic charr populations is well documented (Johnson 1980; Jonsson and Jonsson 1993; Kristoffersen 1994; Rikardsen et al. 2000), with high growth rates of anadromous Arctic charr obtained at sea during periods of marine feeding (Chapman et al. 2012) where weight can double (Gulseth and Nilssen 2001). In a separate study of anadromous Arctic charr from PG027 in Cumberland Sound, Young and Tallman (2021) postulated that anadromous Arctic Charr from PG027 experienced a rapid increase in growth with their first trip to sea, which occurred at approximately age 6 for most fish. In this study, the growth curve of PG027 Arctic charr had an inflection point at 5.34 years old, which indicates an increased growth rate near this age. This increased growth rate is dramatic as the mean length of anadromous fish is twice that of landlocked fish by age 10. This difference in mean length is maintained as mean asymptotic length differed between the anadromous and landlocked populations. Although the growth results presented here cannot substantiate the age at first migration for PG027 Arctic charr estimated by Young and Tallman (2021), these results indicate that an anadromous life history positively affects the growth of Arctic charr.

Life-history-associated diet and seasonal feeding strategies are suspected to be the primary influences leading to the observed differences in condition and growth between these populations of anadromous and landlocked Arctic charr. Arctic charr with anadromous life histories have been documented to adopt feeding strategies that focus on the accumulation of lipid reserves during periods of high food availability (summer fattening) and then mobilizing those lipid reserves during periods of low food availability (winter emaciation; Vijayan et al. 2006). This behaviour is exemplified in Arctic anadromous fishes due to the short period of marine feeding in summer (35–45 days) wherein body mass may double and lipid stores increase dramatically (Jørgensen et al. 1997), followed by a freshwater residency for the remainder of the year where lipid reserves are mobilized to cope with energy demands (Aas-Hansen et al. 2005; Jobling et al. 1998; Jørgensen et al. 1997). The diet of anadromous Arctic charr could not be formally assessed in this study due to a lack of stomach contents obtained from anadromous fish, but information gathered from local traditional Inuit knowledge (Pangnirtung Hunters and Trappers Organization, personal communication, 2011), regional fisheries managers (Z. Martin, Fisheries and Oceans Canada, personal communication, 2011), and Moore and Moore (1974) suggest that anadromous Arctic charr in Cumberland Sound feed only in the marine environment during a short summer window and cease to actively feed while overwintering in freshwater lakes.

The feeding strategy of anadromous Arctic charr contrasts with that of landlocked Arctic charr, where feeding appeared to take place continuously throughout the year, including the prevalence of cannibalism in the winter. With resources in high-latitude lacustrine environments being less diverse and abundant than those of the marine environment (Gulseth and Nilssen 2001), the landlocked strategy of feeding continually throughout the year as opposed to a single annual period of intense feeding provides the opportunity for maintaining stable condition, as indicated by the lack of a difference in weight–length relationships of landlocked Arctic charr between seasons. Although landlocked Arctic charr were found to feed more intensely in the fall than in the winter, the majority of the diet in fall was invertebrates, whereas fish were almost all of the food consumed in the winter. This suggests a trade-off with the seasonal opportunistic feeding strategies of large landlocked Arctic charr that influences condition; i.e., eating a large amount of low-lipid prey in the fall is balanced by eating lesser amounts of higher-lipid prey in the winter (Imrie 2012). However, despite continuous feeding by landlocked Arctic charr throughout

the year, the condition of anadromous Arctic charr surpassed that of landlocked Arctic charr, even during a suspected extended period of winter starvation, which emphasizes the benefits of a seasonal marine diet to freshwater fishes in Arctic environments.

As generalist feeders, Arctic charr display a high degree of dietary variability, much of which is associated with morphological variation (Reist et al. 2013). Morphological characters associated directly with feeding and prey capture are deemed the most important to the feeding ecology of fishes (Ward-Campbell and Beamish 2004). These include features commonly associated with maneuverability and facilitation of the capture of prey (Ward-Campbell and Beamish 2004; Kimirei et al. 2013), such as length of paired fins (Loewen et al. 2009) and mouth gape (Keeley and Grant 2001). Landlocked Arctic charr had larger eye diameters than anadromous fish at all sizes and longer pectoral fin, pelvic fin, and upper jaw lengths at fork lengths longer than approximately 350 mm or 375 mm. These characters have been found to be important in other studies with Arctic charr. Adams et al. (1998) found that piscivorous Arctic charr had larger eye diameters and more elongate upper jaws than sympatric planktivorous and benthivorous morphotypes in Loch Rannoch, Scotland. The larger eyes of landlocked Arctic charr are likely related to feeding in a freshwater environment as large eye diameters are thought to maximize predation in limnetic environments (Barton 2007). Pectoral fin length has been shown to be a significant morphological character for locomotor ability in salmonids (Robinson and Parsons 2002; Andersson 2003; Drucker and Lauder 2003; Peres-Neto and Magnan 2004; Loewen et al. 2009) responding to environmental constraints, such as water velocity (Grünbaum et al. 2007; Peres-Neto and Magnan 2004). Pectoral fin length has been identified as a morphological character differentiating lake-resident and anadromous Arctic charr populations in Cumberland Sound, where (Loewen et al. 2009) found that lake-resident fish had longer overall pectoral fins, assumed to be adapted to improve short, fast swimming maneuvers in slow flowing lacustrine environments to increase predator avoidance and prey capture.

Indications of dietary–morphological adaptations were observed in the landlocked Arctic charr population. “Small” landlocked Arctic charr had shorter overall fork lengths, a younger and narrower age range, as well as a predominance of invertebrates in the stomachs in both sampling seasons. “Medium” landlocked Arctic charr were more variable in length-at-age and seasonal diet, with a prevalence of both fish and invertebrates found in the stomachs in both seasons. “Large” landlocked Arctic charr displayed a broader range of age classes and fed exclusively on fish in both seasons. Upper jaw length and pelvic and pectoral fin lengths increased in size relative to fork length after 350 mm for landlocked Arctic charr. These morphological characters are important for the capture and acquisition of prey and are likely related to the ontogenetic shift to piscivory in landlocked Arctic charr at 322 mm, or within the “medium” size category. Piscivory is a feeding strategy often adopted by fishes in low-productivity lacustrine environments as an important means of attaining and optimizing growth (Kerr 1979; Reist et al. 2013), with salmonids being shown to become predominantly piscivorous at 310 mm FL (Keeley and Grant 2001). The shift to a predominantly piscivorous diet in larger (>350 mm) landlocked individuals is likely related to the facultative (secondary) piscivorous nature of Arctic charr, as facultative species become piscivorous at larger sizes than primarily piscivorous species (L’Abée-Lund et al. 1992). Thus, we postulate that landlocked Arctic charr categorized as “small” have a primarily invertebrate-based diet and those categorized as “medium” are in the process of becoming piscivorous, feeding on both invertebrates and fish. By 350 mm, landlocked Arctic charr have likely experienced dietary–morphological adaptations in paired fins and upper jaw lengths to facilitate a primarily piscivorous diet.

Diet and niche shifts throughout ontogeny are commonly observed in high-latitude freshwater fishes for the purpose of maximizing growth and fitness (Eloranta et al. 2010). Both anadromous and landlocked Arctic charr appeared to experience a shift in diet around 240 mm FL, but the effects and subsequent benefits of this ontogenetic shift experienced by each population appear to differ. The shift for anadromous Arctic charr was more extreme, shifting from freshwater feeding to a seasonal marine-based diet during a narrow length-at-age window. The increase in length-at-age ranges between “small” and “large” anadromous Arctic charr suggests a drastic increase in growth once marine feeding has been adopted, which is not surprising given that the marine environment offers rich feeding opportunities that surpass those in high-latitude freshwater lakes (Chapman et al. 2012). The distinct age ranges associated with the two size classes of anadromous Arctic charr suggest that age plays an influencing role on the timing of the ontogenetic shift in diet, given that all “small” anadromous Arctic charr were 4–6 years old. This is supported by Loewen (2016), who estimated the age at first migration of anadromous Arctic charr populations in Nunavut to be 5–7 years old.

Variability in age ranges of “medium” landlocked Arctic charr suggests a lack of uniformity at the population level in the timing of the ontogenetic shift in diet, likely related to the fact that the shift is gradual and largely dependent on an individual’s ability to take advantage of seasonal opportunistic feeding events at certain points in ontogeny. Our findings suggest that the introduction of fish into the diet of landlocked Arctic charr takes place within the age and size range of the “medium” size category, likely beginning around 240 mm FL and at approximately 9 years old. We further speculate that once fish enter the diet, “medium” landlocked Arctic charr will continue to opportunistically feed on invertebrates until a primarily piscivorous diet and associated dietary–morphological adaptations are achieved at approximately 350 mm FL. The older ages of “large” landlocked Arctic charr suggests that a primarily piscivorous diet likely isn’t fully adopted until at least 15 years of age, inferring that the shift in diet may take place over the course of several years.

Conclusions

This research demonstrates notable differences in growth, seasonal condition, and morphology between two allopatric populations of Arctic charr in the Canadian Arctic with contrasting life histories. Our results suggest that these differences are likely related to ontogenetic shifts in diet, with a shift to marine feeding for the anadromous population and a shift to piscivory for the landlocked population. These diet shifts appear to influence growth and condition of these high-latitude Arctic charr populations, with anadromous Arctic charr having much higher growth rates and higher condition than landlocked Arctic charr. Morphological differences between life histories manifested most predominantly in larger eye diameter, longer paired fins, and longer upper jaw lengths at FL longer than approximately 350 mm or 375 mm of landlocked Arctic charr and were assumed to be attributable to efficiencies required for piscivorous feeding in a freshwater environment and is suggestive of an ontogenetic shift to a primarily piscivorous diet in larger individuals. The suspected shift in diet for anadromous Arctic charr was apparent earlier in ontogeny than that of landlocked Arctic charr, allowing anadromous Arctic charr to achieve larger overall size at age.

In summary, these findings emphasize the benefits that marine feeding can have for freshwater fishes in Arctic environments, conveying the necessity of adaptation of strategies such as ontogenetic diet shifts to optimize growth and condition in fishes inhabiting low-production lacustrine habitats. Our findings suggest that the dietary–morphological variation experienced by plastic, high-latitude salmonids such as landlocked

Arctic charr can manifest in the form of adaptations that optimize capture of new prey items at different points in ontogeny. Further research into the ontogenetic dietary–morphological variation within high-latitude salmonid populations with differing life histories is warranted to substantiate these findings.

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