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ARTICLE

Lifelong divergence of growth patterns in Arctic charr life history strategies: implications for sustainable fisheries in a changing climate[1]

Gabrielle Grenier and Ross F. Tallman

Abstract: Arctic charr (*Salvelinus alpinus* Linnaeus, 1758) are phenotypically variable with multiple life history strategies including anadromous and freshwater resident individuals. The mechanism determining life history is believed to be set early in life. Anadromous individuals show greater seasonality in growth and feeding after the first seaward migration relative to resident conspecifics. We used otolith growth increment measurements to estimate lifelong growth patterns for 355 individuals with anadromous or resident life history from four populations within Cumberland Sound, Nunavut. Using a general and a generalized linear model, we discovered a linear increase (estimate = 0.006) in growth for both Arctic charr life histories between 1990 and 2016. Resident Arctic charr have lower annual growth (estimate = −0.176) and show a decrease in the annual proportion of summer growth as they age (estimate = −0.042), whereas their anadromous counterparts maintain a higher seasonality in their growth patterns with age. This suggests that growth is indeed important in life history trajectory for Arctic charr and that seasonal growth patterns differ among life histories. The results highlight the importance of improving our understanding of mechanisms influencing life history trajectory in Arctic charr to ensure sustainability of harvested Arctic charr populations in a changing climate.

Key words: early life, otolith, Arctic charr, seasonal growth, life history strategy.

Résumé : L'omble chevalier (*Salvelinus alpinus* Linnaeus, 1758) est variable sur le plan phénotypique avec de multiples stratégies de cycle biologique, y compris des individus anadromes et résidents en eau douce. On croit que le mécanisme déterminant le cycle biologique est établi tôt dans la vie. Les individus anadromes affichent une plus grande saisonnalité au niveau de la croissance et de l'alimentation après la première migration vers la mer par rapport aux congénères résidents. Nous avons utilisé des mesures de la croissance des otolithes pour estimer les profils de croissance tout au long de la vie de 355 individus ayant des cycles biologiques anadromes ou résidents de quatre populations dans la baie Cumberland, au Nunavut. À l'aide d'un modèle linéaire général et généralisé, nous avons découvert une augmentation linéaire (estimation = 0,006) de la croissance pour les

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deux cycles biologiques de l'omble chevalier entre 1990 et 2016. L'omble chevalier résident montre une croissance annuelle plus faible (estimation = –0,176) et une diminution de la proportion annuelle de la croissance estivale à mesure qu'il vieillit (estimation = –0,042), tandis que ses congénères anadromes maintiennent une plus grande saisonnalité dans leurs modèles de croissance avec l'âge. Cela donne à penser que la croissance est effectivement importante dans la trajectoire du cycle biologique de l'omble chevalier et que les modèles de croissance saisonniers diffèrent d'un cycle biologique à l'autre. Les résultats mettent en évidence l'importance d'améliorer notre compréhension des mécanismes qui influent sur la trajectoire du cycle biologique de l'omble chevalier afin d'assurer la pérennité des populations d'omble chevalier récoltées dans un climat changeant. [Traduit par la Rédaction]

Mots-clés : début de vie, otolithe, omble chevalier, croissance saisonnière, stratégie du cycle biologique.

Introduction

Arctic charr (*Salvelinus alpinus* Linnaeus, 1758) demonstrate great phenotypic plasticity (Johnson 1980; Hindar and Jonsson 1993; Jonsson and Jonsson 2001; Klemetsen et al. 2003; Igoe and Hammar 2004). Among the most striking evidence of phenotypic plasticity in Arctic charr are characteristics related to each individual's migratory behaviour and feeding niche (Hindar and Jonsson 1982; Nordeng 1983; Jonsson and Jonsson 1993; Loewen et al. 2009). Many have speculated that plasticity observed within the Arctic charr species complex is attributable to its habitat at high latitudes where environmental conditions, notably food availability, are seasonally fluctuating (Nordeng 1983; Gross et al. 1988; Jørgensen and Johnsen 2014). Prey availability is restricted in the winter as the productivity of the freshwater environment is limited due to the lack of light and cold temperatures while the marine environment is unavailable (Dempson and Kristofferson 1987). Conversely, in the summer, primary productivity and prey availability increase within freshwater while the ice-free summer also provides marine foraging opportunities for Arctic charr. To thrive in such a variable environment, Arctic charr have evolved in a manner for their biology to be synchronized with the timing of events and the limitations of their habitat (Jørgensen and Johnsen 2014).

Environmental adaptations in Arctic charr can also be variable among individuals (Brännäs 1998). Within individual Arctic charr populations multiple morphs with diverging life history strategies are generally encountered (Hindar and Jonsson 1982; Nordeng 1983; Gulseth and Nilssen 2001; Loewen et al. 2009, 2010). Throughout their range, Arctic charr life histories will include morphs that segregate based on their feeding niche (Hindar and Jonsson 1982; Nordeng 1983; Loewen et al. 2009; Ulrich 2013). The mechanism influencing the phenotype of life history trajectory of Arctic charr is still puzzling to Arctic charr biologists. Many biologists are now highlighting the importance of early development and growth on the life history strategy adopted by Arctic charr (Jonsson and Jonsson 2014; Jørgensen and Johnsen 2014; Knudsen et al. 2015; Woods et al. 2018).

In many instances where divergence in life history strategy is present within Arctic charr the various morphs segregate into genetically distinct populations (Walker et al. 1988; Skúlason et al. 1989; Klemetsen et al. 1997; Adams 1999); therefore, highlighting the importance of genetics in setting an individual's life history strategy. However, previous work on populations of Arctic charr from the Cumberland Sound area has determined that genetics alone are unable to separate individuals by life history (Moore et al. 2014). This suggests that life history morphs are not reproductively isolated and that environmental conditions have a large role to play in the life history trajectory of individual Arctic charr (Ringø 1987; Hindar and Jonsson 1993; Adams 1999). Growth, especially in early life, is highly related to life history traits such as size at maturity and size at age, and therefore, studies examining

growth have the potential to improve our understanding of determinants of life history trajectories (Klemetsen et al. 2002; Knudsen et al. 2015).

One of the main adaptations of Arctic charr is their ability to exploit a diversity of feeding niches (Jørgensen and Johnsen 2014). Larger Arctic charr generally exploit food available in the water column and the limnetic zone, whereas smaller Arctic charr rely heavily upon the benthos as their main prey source region (Hindar and Jonsson 1982; Fraser et al. 2008; Garduño-Paz and Adams 2010). Life history strategy also influences feeding niche with anadromous individuals having a diet consisting mainly of marine origin (Swanson et al. 2011), whereas freshwater residents feed exclusively in the freshwater (Moore and Moore 1974).

Energy storage, in the form of lipid reserves, and growth are also known to differ between Arctic charr life histories. Anadromous individuals demonstrate substantial seasonal variability in food consumption (Damsgård et al. 1999; Rikardsen et al. 2000), growth, metabolism, and storage of their lipids (Jørgensen et al. 1997). Anadromous individuals gorge themselves with marine prey over the summer and produce extensive energy stores in lipid form resulting in fish of large size (Jørgensen et al. 1997; Rikardsen et al. 2000). Subsequently, lipid reserves in Arctic charr are depleted during spawning and the overwinter fast in freshwater (Jørgensen et al. 1997; Finstad et al. 2003). In contrast, the smaller-sized morph is unable to have lipids stores of the same extent as their anadromous counterparts (Finstad et al. 2006). Voluntary fasting over the winter period is seen in most Arctic charr individuals held in aquaculture even when fed in excess, whereas a small proportion of individuals are observed to continue feeding over the winter season (Jørgensen et al. 2013). It might be reasonable to speculate that winter feeding individuals in aquaria, along with wild freshwater residents, must continue to forage over the winter period to sustain their metabolic needs. The difference in metabolism between resident and anadromous morphs may result in the large differences in the overall growth pattern seen between the life histories (Griffiths 1994).

Climate change is predicted to be greatest in the Arctic environment (Post et al. 2009). Large shifts in the temperatures and climate of the Arctic have already been recorded (Post et al. 2009; Collins et al. 2013). Predictive modelling expects the warming trend of the Arctic to continue and at a disproportionately larger rate than Earth's other regions (Collins et al. 2013). With the advent of all the environmental changes in the Arctic, one wonders how Arctic charr, whose biology is intimately tied to the environment, might respond. An understanding of factors influencing life history strategy in Arctic charr will enhance our abilities to sustainably manage Arctic charr populations in changing climates.

In this study, we use otolith growth patterns to reflect the overall patterns of growth in Arctic charr, with the assumption that seasonal increments in otoliths have a consistent growth pattern relative to the seasonal pattern of somatic growth. The purpose is to examine annual and seasonal growth patterns in Arctic charr through time and also comparatively between anadromous and freshwater resident life histories.

Materials and methods

Study sites

The sites selected are all located in Southern Baffin Island, Nunavut, surrounding Cumberland Sound (Fig. 1). In terms of environmental variables, the lakes are expected to be relatively similar as they are all located within Cumberland Sound and at similar latitudes. All these lakes have been studied as potential sites for emerging Arctic charr fisheries and, thus, are predicted to hold Arctic charr populations large enough for sustainable harvest. Two of the four lakes, Ikpit and Qasigiat, have the potential for marine water to inundate the freshwater environment and, thus, could show greater growth in the

Fig. 1. Map of the four lakes in the Cumberland Sound Region of Baffin Island, Nunavut, Canada where anadromous and resident Arctic charr were collected and sampled in 2004, 2011, 2016, and 2017. Map prepared using the ggmap package v2.7.900 (Kahle and Wickham 2013) in R with maps queried from Google, TerraMetrics using the get_map function. Permission is not required to use the information in this map as presented here.
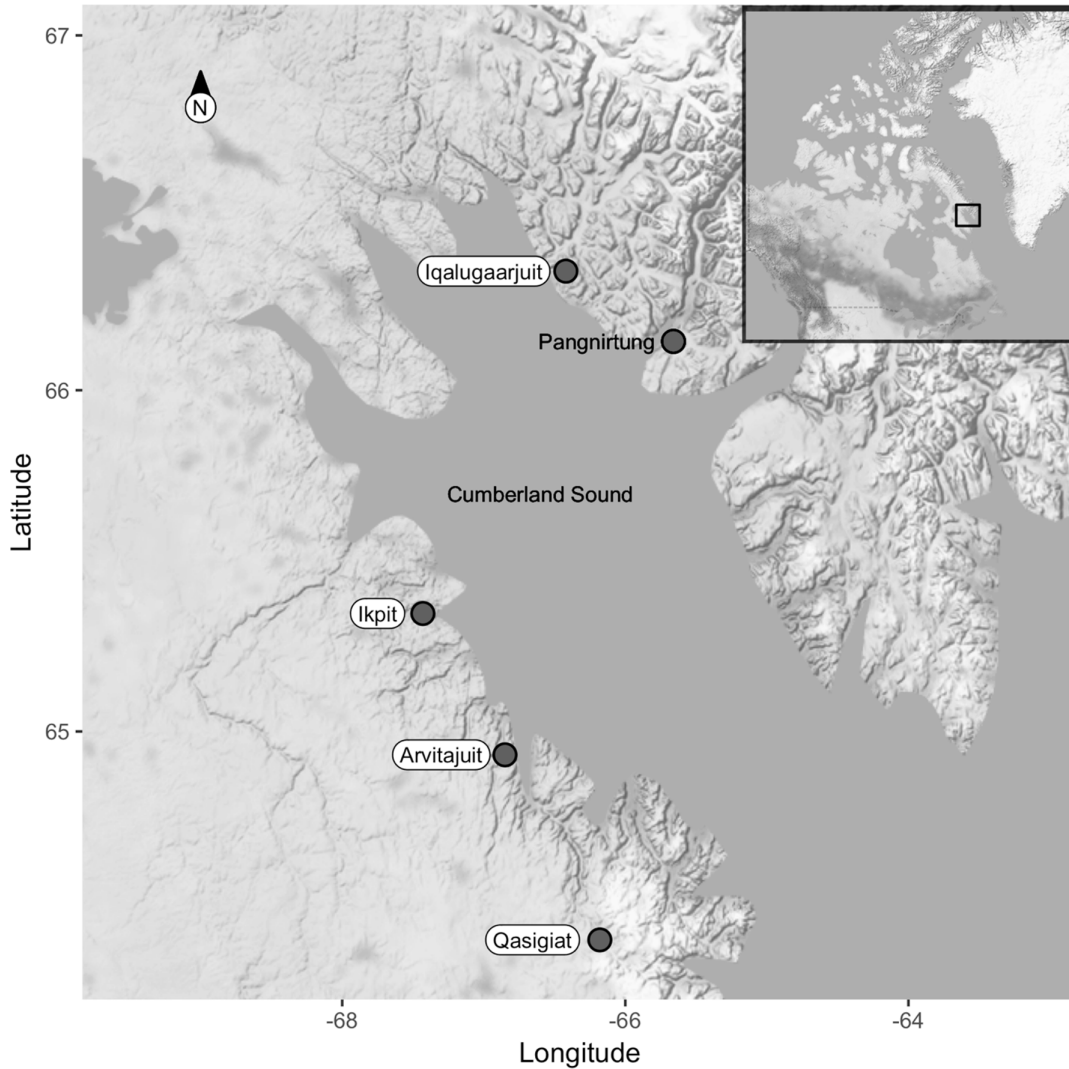
juvenile phase and at older ages for resident individuals relative to other lakes (Loewen et al. 2010). It is expected that the differences in growth between resident and anadromous individuals will be consistent among lakes (Loewen et al. 2010). Two sites were selected based on the availability of archived otoliths to be able to assess changes in growth pattern through time. Iqalugaarjuit Lake and Qasigiat Lake are known to contain both resident and anadromous Arctic charr and have previously been studied and described by Tracey Loewen (2008; Loewen et al. 2010, 2009) and Kendra Ulrich (2013). The following is a summary of their descriptions.

Iqalugaarjuit Lake is connected to the marine environment of Shark Fjord via a short river of approximately 0.64 km at low tide. This lake is made up of a larger shallow upper

lake (1–2 m deep) and a smaller deeper lower basin (15–20 m deep). These two basins are joined by a shallow stream. For logistical reasons, fish were only sampled from the lower basin. The edges of the lake are gradually sloped. This lake is eutrophic and brown in colour.

Qasigiat is a very deep lake (>21 m) with steep fjord-like edges. The lake is joined to the marine environment of Ptarmigan Fjord via two short rivers (0.11 and 0.39 km). During the highest tides, it is possible for salt water to enter the freshwater due to the proximity of the lake to the marine environment. This lake is blue in colour and oligotrophic (Loewen 2008; Ulrich 2013).

Two other lakes, Arvitajuit and Ikpit, have also been sampled for resident and anadromous Arctic charr in the summers of 2016 and 2017 in conjunction with the annual fisheries independent data collection for stock assessments purposes performed by Fisheries and Oceans Canada.

Arvitajuit is known to contain both resident and anadromous Arctic charr individuals as two small maturing resident individuals were captured in the 2014 stock assessment field collection. This lake is horseshoe-shaped with steep rock edges and a large sandbar in its middle. This lake is connected to the marine environment by a short river (0.45 km). The lake is blue-green in colour with clear water and is oligotrophic.

Community members of Pangnirtung reported that Ikpit contains both resident and anadromous Arctic charr. This was confirmed by the capture of small mature individuals with typical resident physical traits in the freshwater of Ikpit during the field sampling season of 2016. The lake consists of a larger upper lake and two successive lower basins. For logistical reasons and ease of access only the second, lowest basin was sampled. The lake's lower basin spills over a rocky wall directly into the marine environment at high tide and onto a long tidal flat (0.9–1.4 km) during low tide. During the highest of high tides, it is possible for the marine water to overflow into the freshwater environment of the lowest basin. The edges of the basin slope gradually. The water in the lower basin is clear and is of a blue colour, the basin is oligotrophic.

Data collection

All samples were collected with the use of multimesh (38–140 mm stretched mesh) and 38 mm stretched mesh gillnets. For a complete description of data collected from Iqalugaarjuit and Qasigiat in 2004 refer to Loewen (2008) and in 2011 to Ulrich (2013). In late August 2016, 72 and 60 Arctic charr were collected from the freshwater in Arvitajuit and Ikpit, respectively, and an additional 68 and 49 were collected in 2017. Animal use protocols (FWI-ACC-2016-038 and FWI-ACC-2017-045) were approved by the Freshwater Institute Animal Care Committee and collection of fish were performed under Licence to Fish for Scientific Purposes (No. S-16/17-1008-NU, No. S-16/17-1030-NU, and No. S-17/18-1026-NU) granted by Fisheries and Oceans Canada. Fish were photographed, and their fork length (mm) and weight (g) were measured in the field. For larger individuals, complete biological data (i.e., fork length, weight, sex, maturity, and tissue samples) were collected, and sagittal otoliths extracted in the field. Smaller individuals were measured and weighed in the field then frozen and shipped to Winnipeg, Canada to collect information on sex and maturity, and to extract sagittal otoliths. Anadromous individuals were collected from the marine environment near the entrance to Arvitajuit and Ikpit. Anadromous individuals consisted of a random subsample of 50 Arctic charr from both population collected in 2016 for the fisheries independent stock assessment program by Fisheries and Oceans Canada. Anadromous samples in 2017 are relatively limited compared with other years as there was no collection for the fisheries independent stock assessment program in the studied lakes for that year, and thus sampling was limited to the freshwater.

In all years of sampling, the suspected life history trajectory of each fish was assessed visually and recorded in the field when characteristics were sufficiently evident. The characteristics used to classify morphs included: eye size, where resident individuals have a proportionally larger eye relative to the anadromous counterparts; fin length, which is proportionally longer in resident individuals; head shape, where the resident morph typically has a blunt snout; and colouration, where resident individuals have tones of yellow-brown colouration along with the retention of parr marks relative to the more silvery juvenile anadromous morph (Loewen et al. 2009). Upon dissection gonads of all fish were also inspected to assign sex and maturity status as fish were collected prior to their spawning season in the fall. Fish life history classifications based on visual characteristics were confirmed with all small maturing individuals having been assigned as a suspected resident. Individuals with an undetermined life history, typically because life history types are virtually undistinguishable while in the juvenile stage, were removed from the study ($n = 164$), which represents 31.6% of the otoliths considered for the study ($n = 519$).

All otoliths used in this study were cross sectioned. Most archived otoliths were previously prepared for analysis for earlier studies (Loewen 2008; Loewen et al. 2009, 2010). Otoliths were prepared following the embed-section method. Otoliths were embedded in epoxy and then cross sectioned through the nucleus, or "core region" of the otolith, representing the period before hatch. Cross sectioning was performed using a Buehler Isomet Low Speed saw with a Buehler Diamond Wafering blade and resulted in a 0.5 mm thick section, as to include all annuli. All newly cross-sectioned otoliths (2011, 2016, and 2017 samples) were prepared and aged by AAE Tech Services (Winnipeg, Manitoba, Canada).

All otolith cross-sections were aged by multiple readers as is customary. The ages were further corroborated when photographed as otoliths that did not get re-aged accurately at the time of photographing were discarded from the study. Otolith cross-sections were photographed under reflected light using a Leica DFC 490 digital camera mounted to a Leica M125 stereomicroscope. Sectioned otoliths were immersed under water in a depression slide. Magnification (4×) was kept constant for all images.

Measurements of growth increments were made on the photographs of all otoliths in ImageJ (Schneider et al. 2012) following a standard linear transect extending from the nucleus to the edge of the otolith's ventral lobe following the sulcus resulting in a transect of approximately 45° to 50° angle from the longest axis between the nucleus and the edge of the otolith's ventral lobe. A validation study was performed on a subset of otoliths, and it was determined that measurements obtained by the reader did not differ from measurements obtained by a semi-automated method (G. Grenier, unpublished data, 2018). A single reader, therefore, performed all measurements to ensure consistency among samples. The width of each translucent and opaque band was measured (mm) along with the total length of the transect using the IncMeas (Rountrey 2009) plugin. All measurements were performed without the knowledge of the individual's fork length, weight, sex, or life history. For the analyses using annual growth, measurements of opaque bands were combined with the subsequent translucent band to provide estimates of annual otolith increment width (mm). For the analyses of seasonal growth, the measurement of the opaque band was divided by the total annual measurement to provide an estimate of the proportion of summer annual growth. Growth for the year of sampling was incomplete, and therefore, excluded from the analyses.

Statistical analyses — growth in Arctic charr over time

A linear mixed effect model fit by restricted maximum likelihood was built in R 3.5.0 (R Core Team 2018) with the lmer function from the lme4 package v.1.1-17 (Bates et al. 2015) to examine the annual otolith growth (mm) of Arctic charr over time. Otolith growth

increment measurements were log-transformed to satisfy the assumptions of normality and homogeneity of variance of the model, which were verified visually. The fit of the model was then checked with residual plots prior to interpretation of results. The predictor variables included in the model were year of growth (1990–2015) and growth increment (age of growth 1–15) as continuous variables, life history (resident or anadromous), sex (male or female), and lake (Arvitajuit, Ikpit, Iqalugaarjuit, or Qasigiat) with fish ID nested within lake. ID was set as a random variable to correct for the repeated measures performed on each individual. Following parsimony, sex was excluded from the predictor variables in the final model after showing a nonsignificant effect on annual growth. *P*-values and degree of freedom were estimated using Satterthwaite's method from the package LmerTest v.3.0-1 (Kuznetsova et al. 2017).

Statistical analyses — seasonal growth in morphs of Arctic charr

A generalized linear mixed effects model was fit using restricted maximum likelihood in R 3.5.0 (R Development Core Team 2018) using the glmmTMB function from the glmmTMB package v.0.2.2.0 (Brooks et al. 2017) with the summer proportional growth data to examine the effect of Arctic charr life history on otolith growth seasonality and to test the consistency of seasonal otolith growth patterns with age in Arctic charr. The model used a Beta distribution as the summer proportional growth data is bound between 0 and 1. Beta distributions can take multiple shapes ranging from J to U specified by two parameters, μ and ϕ, where μ is the mean of the response variable, and ϕ is the precision factor (Ferrari and Cribari-Neto 2004). The beta distribution notation proposed by Ferrari and Cribari-Neto (2004) is used for this study.

The linear predictor for the model included year of growth (1990–2015) and growth increment (i.e., age of growth, 1–15) as continuous variables, life history (anadromous or resident), growth increment (i.e., age of growth, 1–15), sex (male or female), and lake (Arvitajuit, Ikpit, Iqalugaarjuit, or Qasigiat) with fish ID nested within lake. A random effect "fish ID" was added to correct for the repeated measures performed on individuals. An interaction term between growth increment age and life history was added to the model as data exploration suggested that there might be a difference in the effect of age between life histories while also being suggested from the literature (Klemetsen et al. 2002; Knudsen et al. 2015). Year and sex were removed from the model as likelihood ratio tests determined that they did not help explain a significant part of the variance in seasonal growth. The fit of the model was then checked with residual plots prior to the analysis of the results.

Results

Samples

A total of 355 Arctic charr otoliths were used in this study (Table 1). Anadromous Arctic charr among all lakes had a mean size range of 461–612 mm. Resident individuals were relatively smaller with a mean size range of 140–210 mm among all lakes. Age estimates from otoliths ranged from 1 to 16 years with an average age of 6+ years and modal age of 5+ years (Table 2). A total of 3397 annual otolith growth estimates and proportional summer growth estimates were made. Otolith growth increment data spanned the years 1990 to 2015. The data for annual growth increments ranged from 0.01 to 0.36 mm with an average growth increment width of 0.086 mm. The proportional summer growth data ranged from 0.33 to 0.98 and the mean was 0.767.

Annual growth in Arctic charr over time

Annual otolith increment growth did not differ between males and females (likelihood ratio test χ^2 (1) = 0.080, p = 0.779). Results from the first model examining annual Arctic

Table 1. Metadata on source of otoliths used to fit the models evaluating the effects of age, year, location, and sex on the annual and seasonal growth in anadromous and resident Arctic charr from the Cumberland Sound area of Nunavut, Canada.

Lake	Sample year	Life history	Number of samples	Total samples
Qasigiat	2004	Anadromous	91	102
		Resident	11	
	2011	Anadromous	30	50
		Resident	20	
Iqalugaarjuit	2004	Anadromous	27	68
		Resident	41	
	2011	Anadromous	14	25
		Resident	11	
Ikpit	2016	Anadromous	32	38
		Resident	6	
	2017	Anadromous	1	4
		Resident	3	
Arvitajuit	2016	Anadromous	33	38
		Resident	5	
	2017	Anadromous	30	30

Table 2. Range and mean with standard error otolith age, annual growth increment width (mm), and proportional summer growth estimates for anadromous and resident Arctic charr individuals from four lakes located in Cumberland Sound, Nunavut, Canada.

	Age (years)		Annual growth (mm)		Proportional growth	
Life history	Range	Mean ± standard error	Range	Mean ± standard error	Range	Mean ± standard error
Anadromous	2–16	9 ± 3	0.010–0.356	0.082 ± 0.049	0.226–0.975	0.767 ± 0.107
Resident	2–15	6 ± 2	0.016–0.312	0.081 ± 0.053	0.410–0.983	0.754 ± 0.107

Table 3. Terms (β_n) included in the final model assessing the effect of factors on the annual growth of Arctic charr.

Fixed effects	Estimate	Standard error	df	t value	Pr(>|t|)
Intercept	−14.848	4.520	374	−3.285	0.001*
Year	0.006	0.002	375	2838	0.005*
Qasigiat	0.046	0.030	305	1.518	0.130
Ikpit	−0.025	0.028	265	−0.914	0.361
Iqalugaarjuit	0.014	0.034	309	0.416	0.678
Increment	−0.114	0.003	765	−41.333	<0.001*
Resident	−0.176	0.021	401	−8.371	<0.001*
Random effects		**Variance**	**Std. dev.**		
Lake:ID	Intercept	0.004	0.063	—	—
Residual	—	0.141	0.375	—	—

Note: The results presented here are using anadromous life history and Arvitajuit as reference groups. Individual ID is a random factor nested within their respective lake. Significant terms are indicated with *.

charr otolith growth demonstrated that the amount of otolith growth within a year has increased through time ($p = 0.005$; Table 3; Fig. 2) spanning the years 1999–2016. Otolith growth differed between anadromous and resident individuals with anadromous individuals exhibiting larger annual otolith growth increments ($p < 0.001$; Table 3; Fig. 2). Lake had a marginal effect on annual otolith growth with only Qasigiat demonstrating greater

Fig. 2. Scatter plots of mean annual otolith increment width (mm) for all lakes combined plotted against year for anadromous (black circles, solid line) and resident (grey triangles, dashed line) Arctic charr. Increments older than 10 years of age are not shown in figure as residents had fewer than five individuals. Error bars represent standard deviation of the mean.
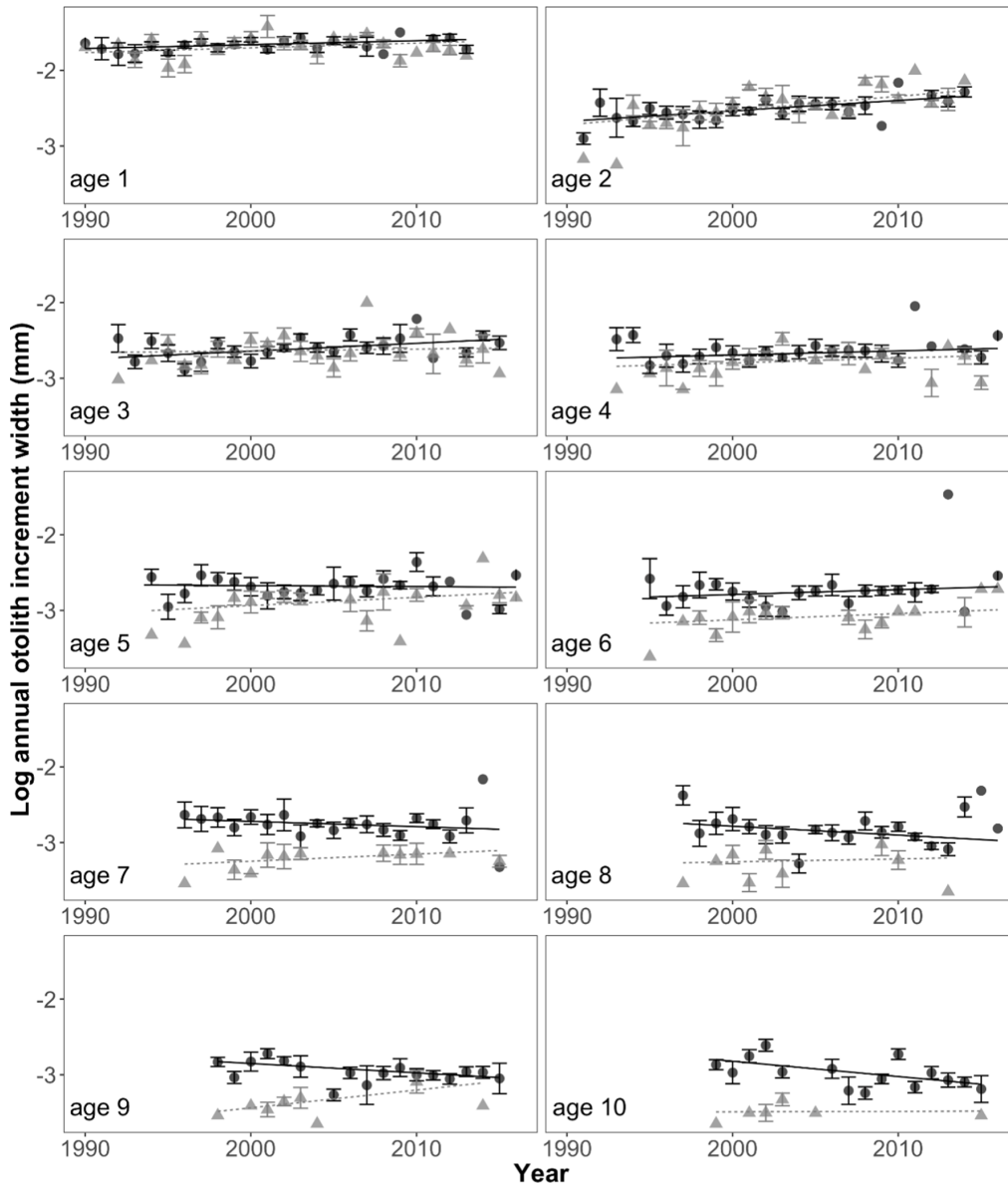
growth than Ikpit ($p < 0.001$; Table 3; Fig. 2). Finally, there was a trend of the otolith growth increments becoming smaller as the fish ages ($p < 0.001$; Table 3; Fig. 2).

Seasonal growth in morphs of Arctic charr

During model construction, it was determined that the proportion of otolith summer growth was not influenced by year (likelihood ratio test χ^2 (1) = 2.533, $p = 0.111$) and did not differ between males and females (likelihood ratio test χ^2 (1) = 0.1718, $p = 0.679$). Results

Table 4. Terms (β_n) included in the final model assessing the effect of factors on the proportion of summer growth of Arctic charr.

Fixed effects	Estimates	Standard error	z value	$\Pr(>|z|)$
Intercept	1.859	0.034	55.10	<0.001*
Qasigiat	−0.451	0.034	−13.09	<0.001*
Ikpit	0.007	0.045	0.16	0.871
Iqalugaarjuit	−0.317	0.041	−7.79	<0.001*
Increment	−0.073	0.003	−23.51	<0.001*
Resident	0.119	0.047	2.54	0.011*
Increment:Resident	−0.042	0.008	−5.37	<0.001*
Random effects		**Variance**	**Std. dev.**	
ID:Lake	Intercept	0.022	0.147	—
Lake	Intercept	$2.353e^{-10}$	$3.230e^{-5}$	—

Note: The results presented here are using anadromous life history and Arvitajuit as reference groups. Individual ID is a random factor nested within their respective lake. Significant terms are indicated with *.

Fig. 3. Scatter plots of mean proportion of summer otolith growth for (*a*) Arvitajuit, (*b*) Qasigiat, (*c*) Ikpit, and (*d*) Iqalugaarjuit plotted against increment age for anadromous (black circles, solid line) and resident (grey triangles, dashed line) Arctic charr. Error bars represent standard deviation of the mean.
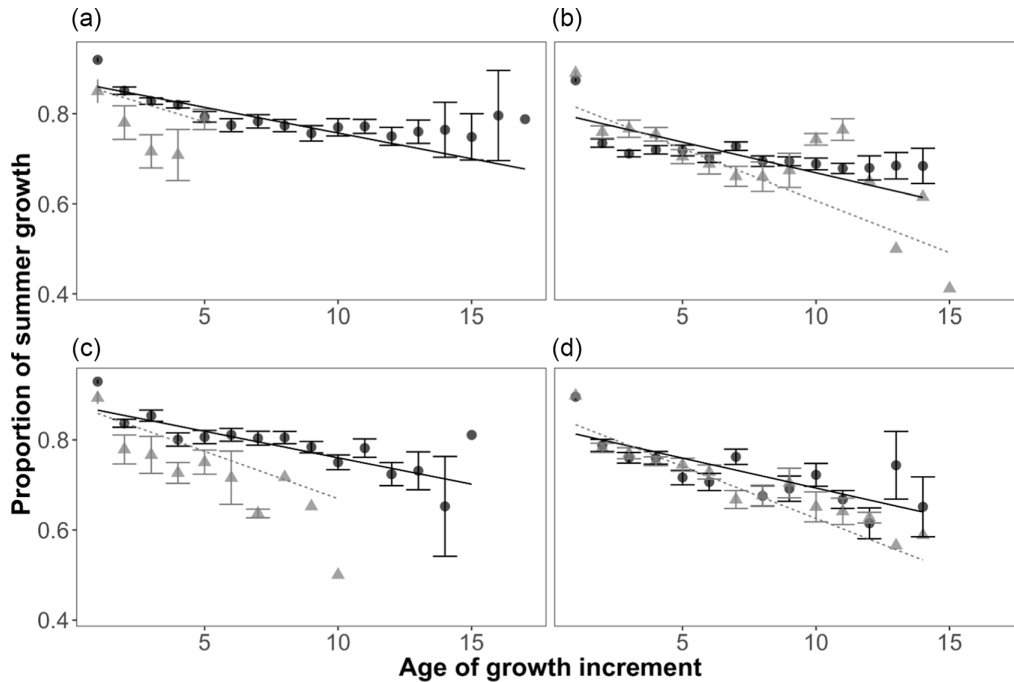
from the second model examining proportion of seasonal growth in both life histories of Arctic charr demonstrate that the proportion of otolith summer growth decreases with increment age ($p < 0.001$; Table 4; Fig. 3), and, thus, otolith growth becomes more even between seasons with age. Life history affects the proportion of summer growth with resident individuals having a larger proportion of summer growth when compared with anadromous individuals ($p = 0.011$; Table 4; Fig. 3). However, the interaction term between growth increment and life history demonstrates that negative effect of increment age on

Fig. 4. Scatter plots of proportion of summer otolith growth data used in this study plotted against increment age for (a) anadromous and (b) resident Arctic charr with loess line showing the moving average with age representing the general growth trajectory with age.
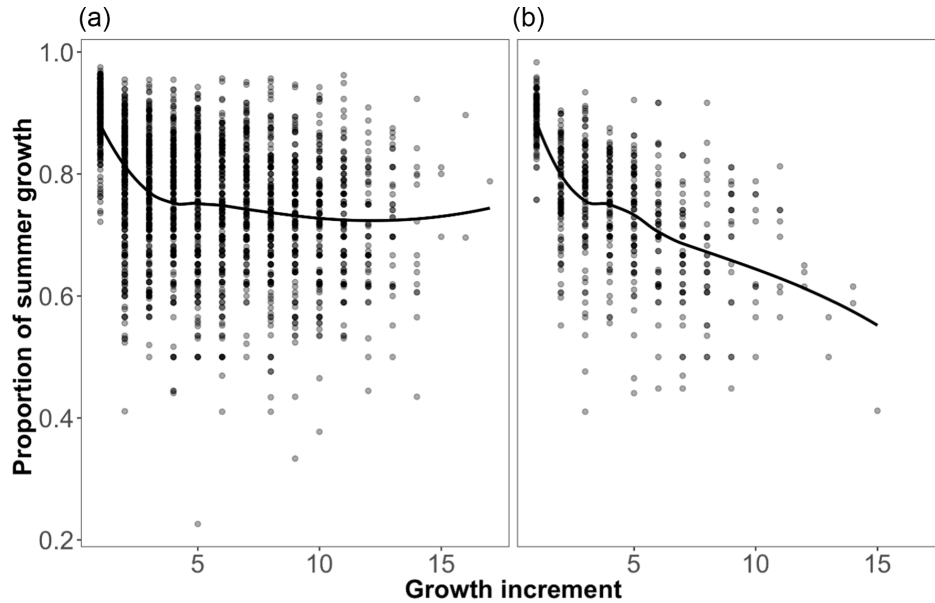
proportional seasonal growth was more pronounced in resident individuals than in anadromous individuals ($p < 0.001$; Table 4; Fig. 3). When examining the data, we notice that this interaction results in resident individuals having a lower proportion of summer growth relative to anadromous individuals at older ages (Fig. 4). Plotting of the data shows that the proportional summer growth declines with age in a manner visually resembling a negative logarithmic function with anadromous individuals seemingly arriving at an asymptote, whereas resident individuals maintain a decline with age (Fig. 4). The proportion of summer growth was smallest in Qasigiat, intermediate in Iqalugaarjuit, and highest in Ikpit and Arvitajuit ($p < 0.001$; Table 4; Fig. 3).

Discussion and conclusion

Growth increased through time in wild freshwater resident and anadromous Arctic charr in the Cumberland Sound area of Baffin Island, Nunavut, Canada from 1990 to 2016. This is consistent with the hypothesis that Arctic charr would exhibit greater growth, likely related to the symptoms of climate change in the Arctic, including a longer growth season (Arrigo et al. 2008) and an increase in temperature (Post et al. 2009; Collins et al. 2013). Although the effect of temperature on growth was not tested here, some information on temperature data was available from a Canadian weather station (Climate ID 2403049) located in the community of Pangnirtung, Nunavut. Information for mean annual temperature was rather limited, but it was possible to reconstruct the mean July temperature recordings spanning the years 1996–2016, excluding 2005, 2011, 2013, 2014, 2015, due to incomplete data, and demonstrates a trend of increased temperature with time (Supplementary Fig. S1[1]). The relationship between growth and temperature is well

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[1]Supplementary material is available with the article at https://doi.org/10.1139/as-2019-0032.

established in fishes; an increase in temperature is related to an increased growth in Arctic charr when temperatures do not exceed the optimum temperature (Jobling 1983; Larsson and Berglund 2005). Predictive modelling used on two populations of Arctic charr had indicated that if the current warming trends persist an increase in growth and consumption would be likely (Budy and Luecke 2014). These results also align with a back-calculation study that detected patterns of increased annual growth in other populations of Arctic charr in the Cumberland Sound area between the years 1989 and 2009 (Grenier 2015). Overall, the results demonstrate an increase in annual growth over time, which may be related to climate-change-induced increased temperatures in the area (Supplementary Fig. S1[1]).

An increase in growth potential for Arctic charr in the Canadian Arctic could be seen as an advantage to many; especially to local Inuit who rely on the "country food" for subsistence and to those involved in the commercial Arctic charr fisheries (Kristofferson and Berkes 2005). An increase in Arctic charr growth potential and thus yield could be interpreted as a reason to sustainably increase commercial catch quotas (Day and Harris 2013; Tallman et al. 2019). However, our understanding of the effect of early growth and development on the life history trajectory of Arctic charr is still limited leading to very little predictability on how population dynamics will truly be affected by such environmental changes. Two alternative scenarios are plausible to explain the effect of early growth on life history trajectory in Arctic charr. The first states that slower growing individuals will adopt an anadromous life history to "catch-up" to faster growing individuals in the population and, therefore, have an overall reproductive fitness comparable with faster growing individuals that remain in freshwater (Metcalfe and Thorpe 1992; Metcalfe and Monaghan 2001) and mature at an earlier age (Thorpe 1989; Svenning et al. 1992). The alternative is that slower growing individuals are able to remain in the relatively less productive freshwater environment as residents (Gross et al. 1988; Rikardsen and Elliott 2000) as their comparatively reduced nutritional needs are able to be fully met in the freshwater environment (Svenning et al. 1992; Jonsson and Jonsson 2001). Evidence for both of these scenarios exist within the literature; therefore, it is probable that enhanced early growth affects life history strategy differently among populations. Changes in the proportion of individuals adopting divergent life history strategies would have large implications for our current management of Arctic charr fisheries. Depending on which of these scenarios are true for Arctic charr life history trajectory one can predict that climate change may result in either a decrease or an increase in the proportion of commercially valuable larger anadromous Arctic charr and that these results are likely to vary among populations. An understanding of population-specific growth and life history dynamics are critical for a continued sustainable fishing practice.

The lakes used in this study are part of exploratory fisheries program in Cumberland Sound, and thus long-term data on the populations is not available to examine any changes in proportion of individuals adopting each life history in relation to climate or fishing pressure. Fishing in these lakes is mainly for subsistence and fishing for profit is limited. Subsistence fishing by local Inuit is unreported but is not considered to be at a harvest rate greater than 1%–2% of the stock. These stocks are fished under exploratory licences, also. During the exploratory fisheries phase, commercial fishing is allowed in each lake for a period of five years where a fisheries independent survey is also performed to monitor population parameters (VanGerwen-Toyne and Tallman 2011; VanGerwen-Toyne et al. 2014). Preliminary assessments of the impact of the exploratory fisheries indicate that there is fishing pressure of a less than 5% harvest rate and minimal impact on the populations. For the purpose of this study, we assume that the harvest impacts among the studied lakes would be similar to those reported in the preliminary assessments. As of yet, none of the

lakes studied have gone from being in the exploratory phase to being assessed a commercial quota for continued fishing and, therefore, rarely have data for the period outside the five year assessment phase.

The results of this study suggest that individuals with greater growth, including in early life, adopt the anadromous life history. This is consistent with the previous findings that Arctic charr individuals that exhibit greater growth in the first three years of life adopt an anadromous life history later in life (Grenier 2015). Many studies have, however, highlighted that individuals from partially migratory salmonid populations adopting the freshwater resident life history strategy and investing in early maturation are those with the greatest growth (Dellefors and Faremo 1988; Thorpe 1989; Svenning et al. 1992; Thériault and Dodson 2003; Berejikian et al. 2011; Gallagher et al. 2019). Furthermore, when examining the predicted effect of climate change scenarios, with increase in temperature and environmental productivity, it was determined that it is likely that the prevalence of anadromy in Arctic charr would be reduced (Finstad and Hein 2012).

Studies examining conditions experienced in early life in relation to polymorphism in salmonids demonstrate that, indeed, early life is important to an individual's life history strategy. Morphological changes were observed in juvenile Arctic charr reared at different temperatures where a generation of plankton feeding Arctic charr reared in elevated temperatures developed head morphology analogous to a benthic feeding morph (Hooker et al. 2020). In addition to temperature, environmental productivity may also influence life history strategy in salmonids (Finstad and Hein 2012). Finally, available food resources during early development may also direct the life history strategy and morph type in Arctic charr (Adams et al. 2003).

We speculate, along with others (Forseth et al. 1994; Jonsson and Jonsson 2001), that there may be a threshold in environment productivity and the balance between possible life history strategies of Arctic charr. Environments that have a productivity above the threshold would be able to support the early maturation and rapid development of fast growers making it an advantageous overall reproductive strategy. In Atlantic salmon (*Salmo salar* Linnaeus, 1758), growth was determined to be related primarily to maturation and secondarily to smoltification, where fast growers matured before smoltification could occur, thus forgoing migration (Thorpe et al. 1982), highlighting the importance of maturation in salmonids. Where environments that have a productivity below the proposed threshold, fast growers are unable to garner enough resources to build lipid and energy reserves for an early maturation and must, therefore, exploit the marine environment to reach a body condition allowing for maturation and, thus, enhance their reproductive fitness (reviewed by Finstad et al. 2006). Similarly, fast growing Arctic charr individuals were found to shift their dietary niche from less to more efficient prey sources (e.g., small vs. large; Hart and Connellan 1984) at shorter lengths and younger ages to sustain their metabolic needs (Forseth et al. 1994). Once fast growers shift to a more efficient feeding niche, slow growers can take advantage of the relatively less efficient niche vacated by migrating fast growers. Exploiting this environmental niche, although less energetically efficient, allows sufficient resources for sexual maturation of slower growing individuals (Persson 1985). Fitness of slower growing and smaller individuals can be maximized by adopting alternative mating strategies (e.g., sneaking or satellite behaviour) as is frequently seen in many salmonid species (Jonsson and Hindar 1982; Myers and Hutchings 1987; Foote 1988).

The gradient in relative productivity of the marine environment compared with the freshwater environment is influenced by latitude where the marine environment is increasingly productive towards the poles (Gross et al. 1988). The populations in this study are located on the fringe of the Arctic Circle (66°33 N) and are located North of the July 10 °C mean isotherm (Fig. 1). Freshwater environments in the study area are suspected

to have a lower productivity relative to the marine environment (Gross et al. 1988). This provides further evidence to suggest that Arctic charr in the studied populations follow a life history strategy where fast-growing individuals migrate to the marine environment to enhance their growth and overall reproductive fitness. In the case where an environmental threshold affects life history strategy in Arctic charr one would hypothesize that an increase in freshwater productivity related to climate change would increase the number of individuals that are able to reach a mature status as residents. Environmental variations related to climate change have been documented to affect sockeye salmon (*Oncorhynchus nerka* Walbaum, 1792) life history traits and are having implications in management and conservation (Marschall 2019). Further studies examining the relationship among ecological and environmental variables and life history strategy in Arctic charr are essential for the continued management of Arctic charr exploitation.

Life history was found to significantly influence the growth patterns in Arctic charr otoliths. Resident individuals exhibit significantly lower annual growth relative to anadromous individuals, whereas residents also show a more pronounced decrease in the proportion of summer growth with age in comparison with their anadromous counterparts. One of the distinguishing features between resident and anadromous individuals is the resident's smaller size (Loewen et al. 2010); therefore, it is no surprise that residents exhibit lower annual growth. It is also well known that age is related to a decrease in annual growth (Forseth et al. 1994).What is interesting, however, is the divergence in seasonal otolith incremental pattern within the annual growth between life histories. It is not surprising that anadromous Arctic charr exhibit great seasonality in their otolith growth as they have extremely seasonal feeding and fasting behaviours (Rikardsen et al. 2000) and that faster growth in Arctic charr is related to a shift towards a more productive niche (i.e., the marine environment for anadromous; Forseth et al. 1994). The results of our work highlight that anadromy is an effective behaviour to maintaining growth at older ages. However, resident individuals, although they, on average, have better growth performance in their first summer relative to anadromous young-of-year individuals, have a pronounced decrease in growth performance within the freshwater environment as they age. This would suggest that resident individuals develop from individuals who are better at exploiting the freshwater environment already in their first year of life, but that this ability may be reduced as the fish grows.

The intrinsic mechanism influencing the divergence of growth patterns between sympatric morphs of Arctic charr has yet to be determined. Genetic studies have yet been unable to account for the extreme variation in growth patterns seen among sympatric Arctic charr morphs suggesting that environment and development have a large role in the life history trajectory of individual Arctic charr. This study suggests that the life history trajectory of Arctic charr is already set within the first year of growth. For the sake of sustainable management, conservation, and evolutionary biology, further studies are warranted to determine a solution to the problem of life history trajectories in Arctic charr.

Acknowledgements

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