Seasonal patterns of growth in Arctic Charr (*Salvelinus alpinus* L.): differences between morphs of Cumberland Sound populations

by

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Abstract

Arctic Charr (*Salvelinus alpinus* L.) are phenotypically variable with multiple life history eco-morphotypes. The mechanism determining life history trajectory remains undiscovered. At maturity, anadromous individuals have greater seasonality in their growth and feeding relative to their resident conspecifics. To determine if lifelong seasonal and annual growth patterns differ between resident and anadromous individuals I measured otolith increment widths with a semi-automated method. I found that there has been a linear increase in growth in Arctic Charr between 1990 and 2015. Additionally, anadromous Arctic Charr have greater growth and seasonality in their growth relative to their resident conspecifics and these patterns are consistent at all ages. Finally, a probable life history trajectory can be assigned to Arctic Charr based on the seasonal growth pattern in the first year of life. In conclusion, further studies examining factors influencing early development are essential to elucidate the mechanism behind life-history trajectory in Arctic Charr.

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Chapter 1 – General introduction

Evolution is understood as being heritable changes in a population through time (Darwin 1859, Stearns and Hoekstra 2005). These heritable changes occur most often in response to the conditions experienced by a population (Darwin 1859, Stearns and Hoekstra 2005). As environmental conditions change it is expected that populations will respond by adapting, hence evolving to adapt to the ever-changing environment (Darwin 1859, Stearns and Hoekstra 2005). The accumulation of these gradual evolutionary changes amount to the entirety of the variation seen within and among every level of biological organization (Darwin 1859, Stearns and Hoekstra 2005). The nature of evolution has been a source of confusion to taxonomists; where should the line be drawn between a sub-species and a species (Darwin 1859, Behnke 1972)? This question has been an important one for the fishes of the genus *Salvelinus*, commonly known as Charrs (Behnke 1972, Balon 1980, Jonsson and Jonsson 2001, Klemetsen 2013, Muir et al. 2016).

Arctic Charr, *Salvelinus alpinus*, are recognized by many biologists as being one of the most diverse vertebrate species on the planet (Jonsson and Jonsson 2001, Klemetsen 2010, 2013) making it a species of interest when studying ecological speciation. The great diversity of the species led to the coining of the term the "Charr problem" commonly used among Arctic Charr biologists (Nilsson and Filipsson 1971, Nordeng 1983, Jonsson and Jonsson 2001, Klemetsen 2010). This phrase refers to the presence of multiple different ecotypes of Arctic Charr found within a single population (Nilson and Filipsson 1971, Nordeng 1983, Jonsson and Jonsson 2001, Klemetsen 2010). This problem has been puzzling Charr biologists for decades now. Throughout history, the Arctic Charr species complex as we known it has been classified as multiple different species with various sub-species (Behnke 1972, Balon 1980, Nordeng 1983),

up to 24 in one reference (Behnke 1972). With the advent of advanced technologies and refined scientific methods, it has been determined that the Arctic Charr species was indeed extremely phenotypically plastic and all morphs should be classified together as a single species (Jonsson and Jonsson 2001, Nordeng 1983).

Per classic evolutionary biology theory, all species should evolve towards a stable equilibrium where fitness, being the survival of an individual's genes in later generations, is maximized (Parker and Maynard Smith 1990, Stearns 2004, Stearns and Hoekstra 2005). This is expected to be species defined by the ever-changing environmental conditions to which each organism is exposed. The combination of all parameters describing this optimal stable equilibrium is known as the species life history (Stearns 2004). Life history refers to the combination of traits that affect the lifetime reproductive fitness of individuals (Stearns 2004). Traits that vary according to life history strategy include, but are not limited to, age and size at maturity, number and size of offspring, number of reproductive events (Stearns 2004). Knowing that species should evolve toward maximizing their reproductive fitness by reaching stable equilibria, one begs the question as to how it is possible for a species, such as Arctic Charr, to have multiple morphs with varying life history strategies that each maintain a relative fitness?

Game theory can be used to examine the variability in the Arctic Charr species' complex and help elucidate an understanding of this diversity. Game theory is a mathematical concept applied in evolutionary biology to model decision making (Maynard Smith and Price 1973, Maynard Smith 1974, Gross and Repka 1998). In biology, the outcome of this decision making may represent, for example any possible life-history characteristic adopted by an individual. Explained concisely game theory encompasses all possible scenarios and models any strategy or combination thereof that have an influence on an individual's fitness (Maynard Smith 1976). An

example used in game theory, or a variation thereof, is that of the hawk and the dove (Maynard Smith 1974). The dove in this scenario represents a subordinate while the hawk is a dominant individual (Maynard Smith 1974). In a situation where resources are limited three scenarios of competition for the resource are possible; two hawks, two doves, and one hawk with one dove (Maynard Smith 1974). Two hawks competing for the resource will result in each hawk receiving part of the resource, however the net gain is less than that received by the resource as both have spent energy while fighting over the resource (Maynard Smith 1974). Two doves will equitably share the resources and avoid energy expenditure by refraining from entering into conflict (Maynard Smith 1974). A hawk in competition with a dove will receive the entire resource while the dove will retreat and receive nothing (Maynard Smith 1974). In these three scenarios, neither the hawk or the dove strategy is an optimal strategy as the result of a conflict depends on the strategy of the competing individual (Maynard Smith 1974). The optimal scenario for a population containing hawks and doves, where individual payoff is maximized, would be to have an equal proportion of hawks and doves (Maynard Smith 1974). In biological game theory, the strategy which is the most profitable even when competing with an individual of an alternate behaviour, and therefore stable under the pressures of natural selection, is known as an Evolutionary Stable Strategy (ESS; Maynard Smith and Price 1973, Maynard Smith 1974).

In populations comprised solely of hawks or of doves the overall energetic gain for a single individual is relatively uniform (Maynard Smith 1974). A lay person might refer to this strategy as one that is "for the greater good of the species". However, we know now that evolution does not work to maximize the fitness of a species, but rather individual fitness (Stearns and Hoekstra 2005). The situation with the greatest net gain to an individual is in the case where a population is made up of equal proportions of hawks and doves (Maynard Smith

1974). Arctic Charr can be thought of as a species that has evolved an ESS that includes both 'hawk' and 'dove' morphs within their populations as a way to maximize each individual's fitness.

Salmonids typically occur in temperate and Arctic regions (Johnson 1980, Johnston 2002, Hendry and Stearns 2004, Thorstad et al. 2011). The marine environment in these regions is often more productive relative to the freshwater systems (Gross 1987, Gross et al. 1988). A strategy that is commonly used in Family Salmonidae to enhance growth is anadromy (Johnston 2002, Hendry et al. 2004, Thorstad et al. 2011). Anadromous fishes of temperate and Arctic regions migrate to the marine environment to exploit the relatively higher productivity and to enhance their growth (Gross 1987, Jonsson and Jonsson 1993, Hendry et al. 2004, Thorstad et al. 2011). All anadromous fishes return to freshwater to spawn after they mature (Johnson 1980, Gross 1987, Gross et al. 1988, Hendry et al. 2004). The frequency of anadromy in fishes generally increases with increasing latitudes as the difference in productivity, where fresh water is less productive than salt water, increases towards the poles (Gross 1987, Gross et al. 1988, Metcalfe and Thorpe 1990).

Arctic Charr (*Salvelinus alpinus* L.) is the freshwater fish species with the northernmost distribution in the world (Johnson 1980, Klemetsen et al. 2003), overcoming the many challenges associated with an Arctic habitat (Jørgensen and Johnsen 2014). The phenotypic plasticity expressed by the species across its circumpolar range is extensive (Klemetsen et al. 2003). Arctic Charr may indeed be the fish species with the greatest phenotypic and ecological variability in the world (Johnson 1980, Klemetsen et al. 2003, Klemetsen 2013). Traits that are known to be variable within the species include: morphology (Klemetsen et al. 1997, Loewen et al. 2009), depth gradient preferences (Knudsen et al. 2007, 2015), diet (Malmquist 1992, Ulrich

2013), size and age at maturity (Gulseth and Nilssen 2001, Loewen et al. 2010), fecundity (Tallman et al. 1996), feeding (Klemetsen et al. 2006) and migratory behaviour (i.e. anadromy or residency; Johnson 1980, Loewen et al. 2010).

Within Canadian Arctic Charr populations, two different migratory types have been observed: resident and anadromous (Johnson 1980, Loewen et al. 2009, 2010). In order to compensate for the limited productivity in the Arctic freshwaters and the limited potential for growth, Arctic Charr may migrate to the sea over the summer to take advantage of the marine environment (Johnson 1980, Gross 1987, Jonsson and Jonsson 1993). Anadromy in Arctic Charr, however, is facultative, as such, migratory and non-migratory Arctic Charr are found living sympatrically within populations (Johnson 1980, Nordeng 1983, Jonsson and Jonsson 1993, Loewen et al. 2009) and are not genetically distinct (Moore et al. 2014).

Differences between resident (i.e. non-migratory) and anadromous (i.e. sea-going) morphs of Arctic Charr are extensive (Jonsson 1980). The most visually striking difference between the two morphs is size (Jonsson 1980). At maturity, anadromous individuals are significantly larger than resident individuals (Johnson 1980, Loewen et al. 2009, 2010). A study on three populations of Arctic Charr from Southern Baffin Island, Nunavut, Canada, found that the mean size range for mature anadromous individuals was 532-641 mm whereas for mature residents, the mean size range was 184-202 mm (Loewen et al. 2010). Not only does size differ between mature individuals, but a study on back-calculated otolith growth demonstrated that resident individuals grow significantly less in the first three years of life relative to their anadromous conspecifics (Grenier 2015). This highlights that growth is an important parameter to consider when trying to understand the factors influencing divergent life histories in Arctic Charr.

Growth in fishes can be studied by analyzing calcified structures that exhibit seasonal growth patterns including scales, fin rays, and otoliths (Pannella 1971). Two traits make otoliths the preferred structure for growth analyses. First, they are metabolically inert (Pannella 1971), thus once the otolith is formed it remains unchanged (Campana and Neilson 1985). Second, otolith growth is continuous making daily, seasonal and annual growth rings that are observable (Pannella 1971). The presence of two seasonal rings, or annuli, is generally observed in species in the northern hemisphere: a lighter coloured one of fast summer growth and a darker annuli of slower winter growth (Pannella 1971). Measuring the width of consecutive winter and summer bands on an otolith has been used to estimate the yearly growth of fish over their lifespan (Tesch 1971).

Growth in anadromous and commercially farmed strains of Arctic Charr has been studied to some extent; whereas studies on growth of resident Arctic Charr are very limited. It is clear that growth in anadromous Arctic Charr is not continuous throughout the year, but happens in two phases (Johnston 2002). In the summer, anadromous Arctic Charr have a large increase in growth associated with seaward migration (Rikardsen et al. 2000, 2003). Following the few weeks at sea, growth in Arctic Charr decreases over the winter period spent in freshwater (Rikardsen et al. 2003); sometimes even to the point of being negative (Johnston 2002, Rikardsen et al. 2003). This seasonal pattern of growth is even seen among Arctic Charr raised in aquaria (Sæther et al. 1996, Tveiten et al. 1996, Johnston 2002). A study examining growth in two morphs (large, littoral spawning, omnivorous morph and small, pelagic spawning, benthivorous morph) of landlocked Arctic Charr in Northern Norway determined that the larger omnivorous morph exhibited a seasonal growth pattern similar to that of anadromous Arctic Charr, while the small benthivorous morph showed relatively constant growth throughout the

year (Knudsen et al. 2015). This suggests that the resident morph may also demonstrate a relatively constant annual growth when compared to their anadromous counterparts.

The comparison of lifelong seasonal growth patterns in sympatric resident and anadromous Arctic Charr, and to my knowledge all facultative migratory salmonids, has not previously been attempted. This research will increase the available knowledge on the different patterns of growth among the many sympatric morphs of Arctic Charr; ultimately leading to a greater understanding of factors influencing growth and an increased understanding of the evolution of life histories in Arctic Charr. This study will also help elucidate the links among growth and life history in Arctic Charr.

The overall objective of this study is to examine and characterize the seasonal patterns of growth among morphs of Canadian wild Arctic Charr. The three specific objectives are as follows:

Objective 1:
To evaluate the accuracy of measurements of seasonal otolith growth band width using two different methods. I hypothesize that there is no difference in the accuracy of seasonal growth band measurements performed with a visual method and via a semi-automated method that involves examining pixel grayscale values (H1). I predict that there will be no statistical difference between the measurements obtained by the manual measurements in ImageJ and the incremental measures provided by an automated pixel colour method.

Objective 2:
To determine the growth patterns of Canadian wild Arctic Charr through time. I hypothesize that the growth patterns in Arctic Charr have changed from 1990 to 2015 (H2). I predict that there will be a significant increase in the amount of growth through time due the increasing mean annual temperature of the Arctic since 1990. I further predict that that there will

be a greater increase in summer growth relative to winter growth due to the earlier thaw and later freezing of sea ice and thus the greater potential for growth in the summer.

To determine if the seasonal patterns of growth differ among various morphs of wild Arctic Charr. I hypothesize that the seasonal patterns in the proportion of annual summer growth will differ between resident and anadromous Arctic Charr individuals (H3) and that these differences will be present in early life (H4). For H3, I predict that anadromous individuals will show greater seasonal variation in their growth (i.e. more summer growth relative to winter growth; Appendix A) while residents will show a more consistent growth throughout the year. For H4, I predict that these differences in seasonal patterns will be present and consistent in the years spent in the natal lake prior to the anadromous individuals' initial migration (i.e. ages 1-4). In other words, I predict that age does not influence the seasonal patterns of growth.

Objective 3:

To determine if it is possible to classify juvenile Arctic Charr as either resident or anadromous according to their juvenile growth patterns (H5). I predict that juveniles that were destined to become anadromous will demonstrate a different growth pattern than individuals that would later adopt a resident life history (both described in Objective 2).

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Chapter 2 – 256 shades of grey; comparison of two methods of seasonal otolith increment measurements and growth in Arctic Charr (*Salvelinus alpinus* L.)

Introduction

Otoliths are found in the inner ear of all teleosts. They are formed by the deposition of a protein matrix imbedded with carbonate crystals (Degens et al. 1969, Pannella 1971). Variability in the deposition pattern of protein and carbonate crystals in the otolith result in the formation of translucent and opaque rings which are commonly referred to as growth increments (Degens et al. 1969, Pannella 1971) or annuli (Campana & Neilson 1985). In temperate and Arctic fishes, annuli are formed due to the seasonally variable rates of deposition of calcium carbonate and other materials. Periods with a fast rate of deposition in the otolith creates annuli rich in inorganic carbonate crystals thus creating opaque growth bands (Pannella 1971, Mugiya et al. 1980). Translucent bands are formed during periods of slower growth and are mainly composed of an organic protein matrix with a lowered concentration of calcium carbonate crystals (Degens et al. 1969, Pannella 1971, Mugiya et al. 1980).

Since their first use in the 19th century otolith growth increments are now widely used in fisheries to infer age and other life cycle events (Riebish 1899). The first description of daily increments in otoliths (Pannella 1971) furthered the use of otoliths in scientific studies. It was noted that the width of the daily increments varies (Gauldie & Radtke 1990); resulting in variation in the formation of other recognizable periodical patterns such as weekly, bi-monthly, monthly, and seasonal (Pannella 1971).

Growth of the otolith is related to somatic growth of the individual fish (Campana & Neilson 1982, 1985, Casselman 1990). However, many studies have indicated the importance of

external factors in the variation of the increment deposition process in otoliths leading to changes in increment width including photoperiod (Tanaka et al. 1981, Schramm 1989), feeding (Neilson & Geen 1982, 1985), life history events (Pannella 1971), stress (Campana 1983), and temperature (Neilson & Geen 1985, Gauldie & Radtke 1990).

Otolith increments are used by biologists for many purposes such as age estimates and growth studies. Otoliths show a seasonal pattern with an opaque ring being deposited in periods of fast growth and a dark, translucent ring of slow growth (Pannella 1971). These seasonal rings are used as a method to estimate age of fish. Measuring the width of annual growth increments, a combination of an opaque and a translucent ring, is regularly used to infer patterns in the annual somatic growth of fishes (Ricker 1971, Francis 1990, Campana 2005). This technique is known as back-calculation (Ricker 1971, Francis 1990, Campana 2005). Although valuable, there are many assumptions and limitations to the back-calculation technique (Ricker 1971, Francis 1990). For example, a direct, linear, relationship between otolith growth and somatic growth is assumed (Ricker 1971, Francis 1990), in reality, otolith radius often changes nonlinearly with body size (Campana 1990).

Identification, enumeration, and measurement of seasonal increments is useful for age and growth estimation, but no studies using seasonal increment widths of otoliths to infer seasonal patterns in the somatic growth of fish exist within the literature. Developing methods to study and estimate seasonal growth patterns of fishes is valuable to the field of conservation and management. This is especially important for species and populations located in areas where other methods, such as a tag and recapture experiment, are logistically difficult or costly. This is the case for many Arctic Charr fisheries of the Canadian Arctic that often have an issue with data deficiency.

Growth is known to be variable among morphs of the same population in many salmonid species including Arctic Charr (Klemetsen et al. 2003, Knudsen et al. 2015). Large anadromous Arctic Charr individuals have a diet that consists primarily of marine origin prey consumed in the summer and demonstrate compensatory growth in the first weeks of their annual marine residence to compensate for the low growth in winter (Rikardsen et al. 2000). Smaller resident Arctic Charr consume prey only from within the freshwater environment and have been observed to have prey in their stomachs throughout the winter period while also demonstrating a more even growth relative to anadromous individuals (Rikardsen et al. 2000). Developing a method that can account for the differences in seasonal growth is important for further improving our management abilities of Arctic Charr populations.

The principle objective of this chapter was to verify visual estimates of seasonal increment widths on cross-sectioned otoliths. Visual estimates were compared to semi-automated seasonal increment width measurements to verify the reproducibility of the visual estimates. I hypothesize that there will be no difference in increment width measurement between the two methods used in this study (H1). Therefore, I propose that measurements of seasonal otolith increments would be a feasible method to infer seasonal patterns in the somatic growth of individual fishes.

Methods

Otoliths for this study were taken from the Freshwater Institute otolith Arctic Charr (*Salvelinus* alpinus L.) archive that were previously cross sectioned for other studies (Fig. 1; Loewen 2008, Loewen et al. 2009, 2010). Below is a brief description of the otolith preparation process. For complete details see Loewen (2008). Otoliths were prepared by embedding in epoxy and then cross sectioned through the nucleus, or 'core region' of the otolith to expose all annuli (Secor et al. 1992). Otolith cross sections were photographed under reflected light using a Leica

DFC 490 digital camera mounted to a Leica M125 stereomicroscope. Sectioned otoliths were put in a depression slide and then covered in water to increase the clarity of the annuli. Magnification of the stereomicroscope was constant (4X) for all images.

ImageJ 1.51k (Rasband 2017) was used to measure width of each seasonal annulus (mm), otolith radius (mm), and greyscale value of each pixel along the otolith radius. Greyscale values range from 0 (black), which is the total absence of brightness, to 255 (white). All images were transformed from their original format to 16-bit images to extract greyscale values. A standardized transect (Fig. 2.1) was drawn with the straight-line tool following the sulcus, extending from the nucleus to the outer edge of the ventral lobe while ensuring that the transect crossed each visible annulus (Campana 1992). The greyscale value of each pixel was determined using the plot profile tool (Fig. 2.2; Takashima et al. 2000). These values were used for the semi-automated method of determining increment width.

Greyscale pixel data were smoothed in R 3.5.0 (R Core Team 2018) with a loess smoother (span =0.09) to reduce the noise in the data created by sub seasonal checks in the annuli (Fig. 2.3). Points of inflection in the data, where subsequent pixels went from dark to light or vice-versa, were determined by computing the difference between successive pixels (Fig. 2.3). Increasing values, under reflected light, indicate pixels that are whiter, therefore indicating an opaque band, whereas decreasing values indicated darker translucent bands. Opaque peaks were determined using the "findpeaks" function in the pracma library (Borchers 2018). The number of peaks to return was set to estimated age of the otolith (2 - 14) and the minimum peak distance was set to 10 to avoid selecting sub-seasonal checks. I determined visually that no subsequent peaks had a distance less than 10 pixels. To determine lowest points, or translucent peaks, the findpeaks function was used in the inverse of the data by specifying to find one peak between

pre-determined opaque peaks. The number of pixels between each opaque and translucent peak were transformed to a distance (mm) by multiplying with the known width of a pixel. These data were then used to compare methods. For the visual method, increment widths (mm) were measured along the standard transect with the use of the IncMeas (Rountrey 2009) plugin by manually placing markers at the start of a new seasonal band.

Measurements were log transformed to satisfy the assumption of normality. In R 3.5.0 (R Core Team 2018), a two-way repeated-measures ANOVA (eq. 1), using the aov function from the R base package, was used to determine the effect of two factors, method and age, on the measured seasonal increment widths. The two methods included a semi-automated method based on pixel greyscale value and a visual method. Repeated measures were used to control for the greater variation among increment widths than between widths measured by the two methods. Repeated measures also controlled for decreasing increment width with age.

$$y_{ij} = \beta_0 + \beta_1 Method_i + \beta_2 Age_j + \alpha_{ij} + e_{ij} \qquad \text{(eq. 1)}$$

In this model:

y_{ij} represents the estimated increment width

β_0 is the constant representing the overall mean of all the increment widths

$\beta_1 Method_i$ represents the effect of method (visual or semi-automated)

$\beta_2 Age_j$ is the effect of the age of the increment (1 to 14)

α_{ij} represents the normally distributed random intercept representing repeated

measures which is described with a mean of 0 and a variance of σ_α^2

e_{ij} represents the normally distributed random error with a mean of zero and

variance of σ^2

Where the subscripts *i* represents the levels of factor method (visual or semi-automated) and *j* the levels of factor age (1 to 14).

Results

A total of 137 Arctic Charr otoliths aged 2 to 14 years were used in this study. The otoliths were collected in 2004 from two waterbodies, Iqalugaarjuit (n=54) and Qasigiat (n=83) in the Cumberland Sound area of Baffin Island, Nunavut, Canada (Fig. 2.4).

Increment width was significantly related to age but not measurement method. Increment width did not differ significantly between semi-automated and visual measurement methods (Fig. 2.5; $F_{(1, 3343)}$ = 2.641, p = 0.104; Table 2.1, 2.2). Age was significantly related to increment width (Fig. 2.5; $F_{(1, 3343)}$ = 298.921, p < 0.001) demonstrating a decrease in increment width with age.

Table 2.1 Summary table of mean value (top) and standard deviation (bottom) of parameters included in the model evaluating the log increment width measured on Arctic Charr (*Salvelinus alpinus* L.) otoliths

	Age													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Visual	-2.82	-3.37	-3.43	-3.52	-3.59	-3.67	-3.58	-3.55	-3.68	-3.70	-3.89	-3.85	-4.26	-4.52
	1.06	0.67	0.60	0.59	0.66	0.58	0.70	0.63	0.62	0.60	0.51	0.55	0.46	0.44
Semi-automatic	-3.07	-3.32	-3.35	-3.42	-3.48	-3.55	-3.51	-3.61	-3.52	-3.57	-3.59	-3.84	-3.83	-3.84
	0.73	0.66	0.59	0.56	0.55	0.44	0.53	0.45	0.45	0.44	0.52	0.47	0.49	0.45

Table 2.2 ANOVA summary table of the model evaluating log increment width measured on Arctic Charr (*Salvelinus alpinus* L.) otoliths

	df	SS	MS	F	p-value
Method	1	1.1	1.13	2.641	0.104
Age	1	127.8	127.80	298.921	<0.001
Residuals	3343	1429	0.43		

Discussion

My results indicated that seasonal increment widths measured by semi-automated and visual methods did not differ significantly. I conclude that width of seasonal increments can be measured, and that opaque and translucent bands are evident enough to visually determine the start of each seasonal increment. Similar results, were obtained in a study examining daily increment patterns, opacity profiles, and traditional reading methods of measuring annual otolith increment in Baltic cod (*Gadus mohua*). It was determined that the estimated width of increments did not differ among methods (Hüssy 2010).

The most common method of studying otolith microstructure has been by visual analysis (Campana 2001, 2005). Visual analysis of otolith microstructure, however, is expensive and time consuming, requires much training and skills, and is susceptible to reader bias (Campana1992, Cardinale 2000). An automated method for analyzing otolith increments would greatly advance the field of otolith microstructure analysis, by being relatively quick, less prone to bias from reader error, and more cost effective (Cardinale et al. 2000, Francis & Campana 2004).

In recent years the body of literature proposing new methods to improve and to automate otolith microstructure analysis has been growing. The methods proposed include the use of otolith weight, various otolith morphometric measurements, and greyscale profiles of otoliths to make age estimates (Ré & Gonçalves 1993, Morales-Nin et al. 1998, Cardinale et al. 2000, Fossen et al. 2003, Francis & Campana 2004, Quintanilla et al. 2014).

The semi-automated method used in this study depended on knowledge of the estimated age of the otolith to return the desired number of peaks corresponding to the opaque zones. Therefore, this method did not remove the requirement of having an experienced reader estimate the age for each otolith. However, the goal was not to estimate age, but rather to measure the

width of seasonal increments. This was accomplished by determining that the logarithm of the measurements obtained by visual and semi-automated methods are not statistically different.

A further improvement to this method could be to process the digitized images prior to extracting the brightness profile of the selected transect representing the otolith radius. Multiple studies using semi-automated methods to measure daily and annual increments have processed images by enhancing the contrast of the image (Campana 1992, Ré & Gonçalves 1993, Morales-Nin et al. 1998), smoothing the image (Takashima et al. 2000) or enhancing the otolith microstructure (Nava et al. 2018). Image processing was not used in this study to avoid altering the image and potentially influencing the increment widths. Smoothing, using a loess smoother, was performed on the raw greyscale value data which provided similar results as if the image was smoothed prior to the extraction of the greyscale values (Takashima et al. 2000).

Although a semi-automated method offers the potential to correct many of the drawbacks of the visual method, it is not without flaws. The semi-automated method provides measurements by examining only a selected transect. By having an experienced reader measure increments along a transect, the reader can make decisions such as whether a ring should be classified as a check or as a true seasonal increment with having the advantage of being able to examine the whole cross section of the otolith. Additionally, otoliths are known to vary among species, populations, and even among different morphs of the same species (Florø-Larson et al. 2016). For the semi-automated method to be of value to fisheries biologists, it will need to provide reliable measurements for a variety types of otoliths and be cost effective. An experienced reader is able to adapt to reading otoliths from different species rendering the visual method invaluable.

The semi-automated method used in this study needs to be further refined if it is going to be promising as an alternative to visual analysis. I determined the feasibility of obtaining seasonal incremental widths from otoliths. Reliability of these measurements remains to be determined as the understanding of factors influencing otolith accretion rates and their chemical composition is still limited. Validating the use of seasonal otolith increment measurements would enhance our management abilities of commercially fished stocks. If growth patterns of fished stocks were to change in a fishery, this method would assist in monitoring these changes over time. Analysis of growth patterns using otoliths also has the benefit of being a natural record of the fish's life. This is especially important in areas, such as the Arctic, where mark-recapture studies are logistically difficult and expensive. Finally, studying seasonal growth estimates of Arctic Charr can help monitoring of changes in the climate of the Arctic. An understanding of differences in seasonal growth patterns of Arctic Charr morphs will improve the ability to understand the influence of climate change on the species.

Figures
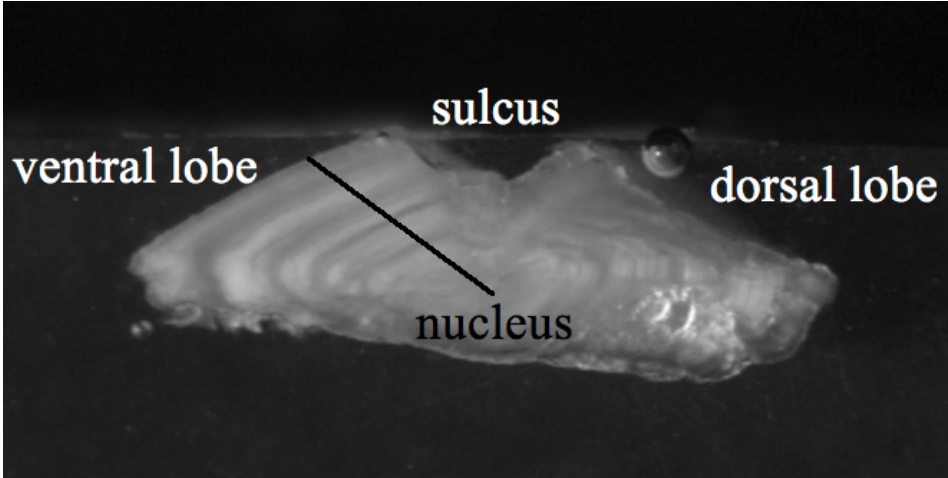
Fig. 2.1 Arctic Charr (*Salvelinus alpinus* L.) otolith cross section aged 4+ with a standard transect (black line) used for increment and pixel grey value measurements
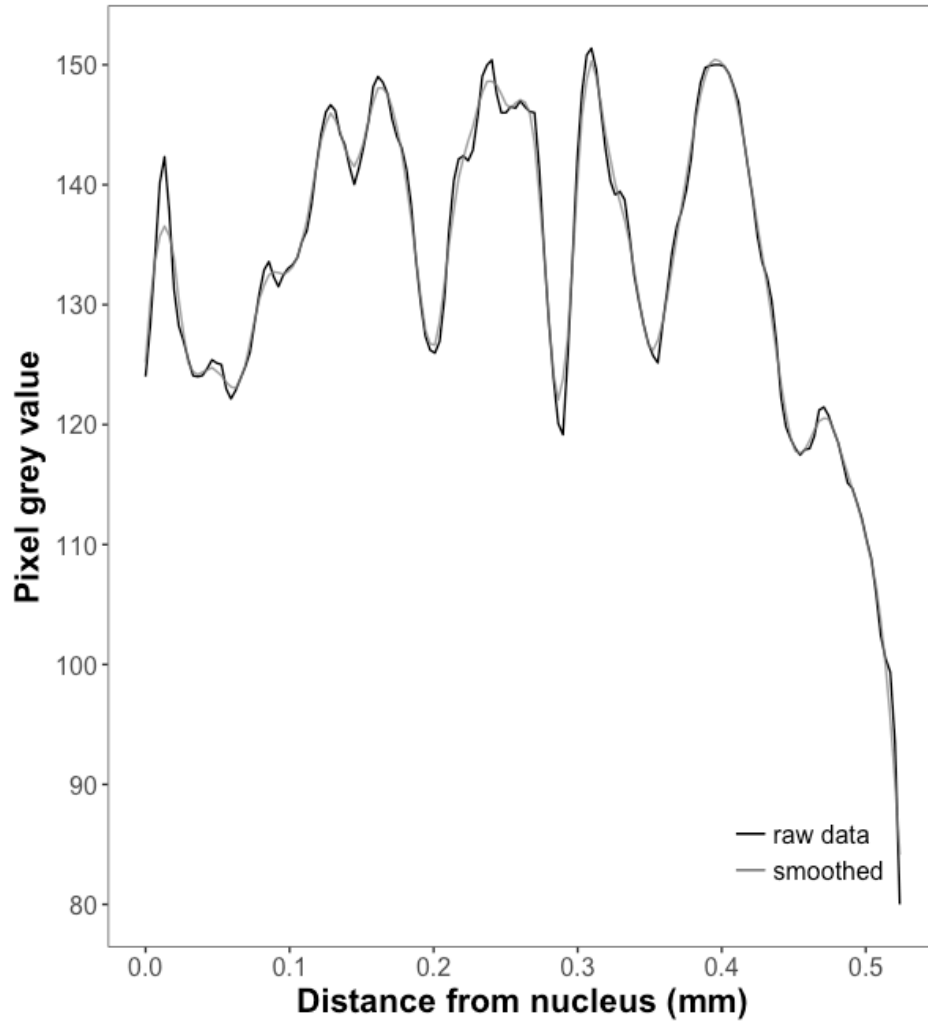
Fig. 2.2 Pixel grey value profile plot of raw pixel data and smoothed data measured along standard transect of the Arctic Charr (*Salvelinus alpinus* L.) otolith shown in Fig. 2.1
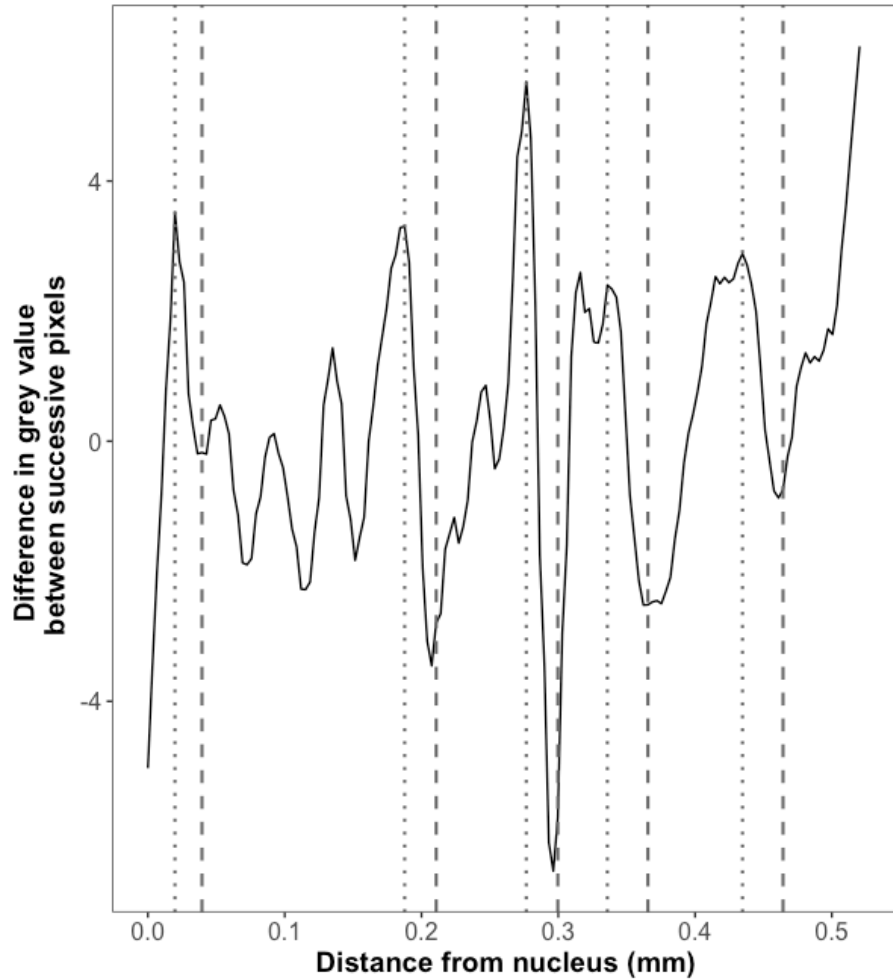
Fig. 2.3 Points of inflection in the difference in grey value of successive pixels along the standard transect on the Arctic Charr (*Salvelinus alpinus* L.) otolith shown in Fig. 1 determining the end of an opaque band (peak, dotted line) and the end of a translucent band (valley, dashed line)
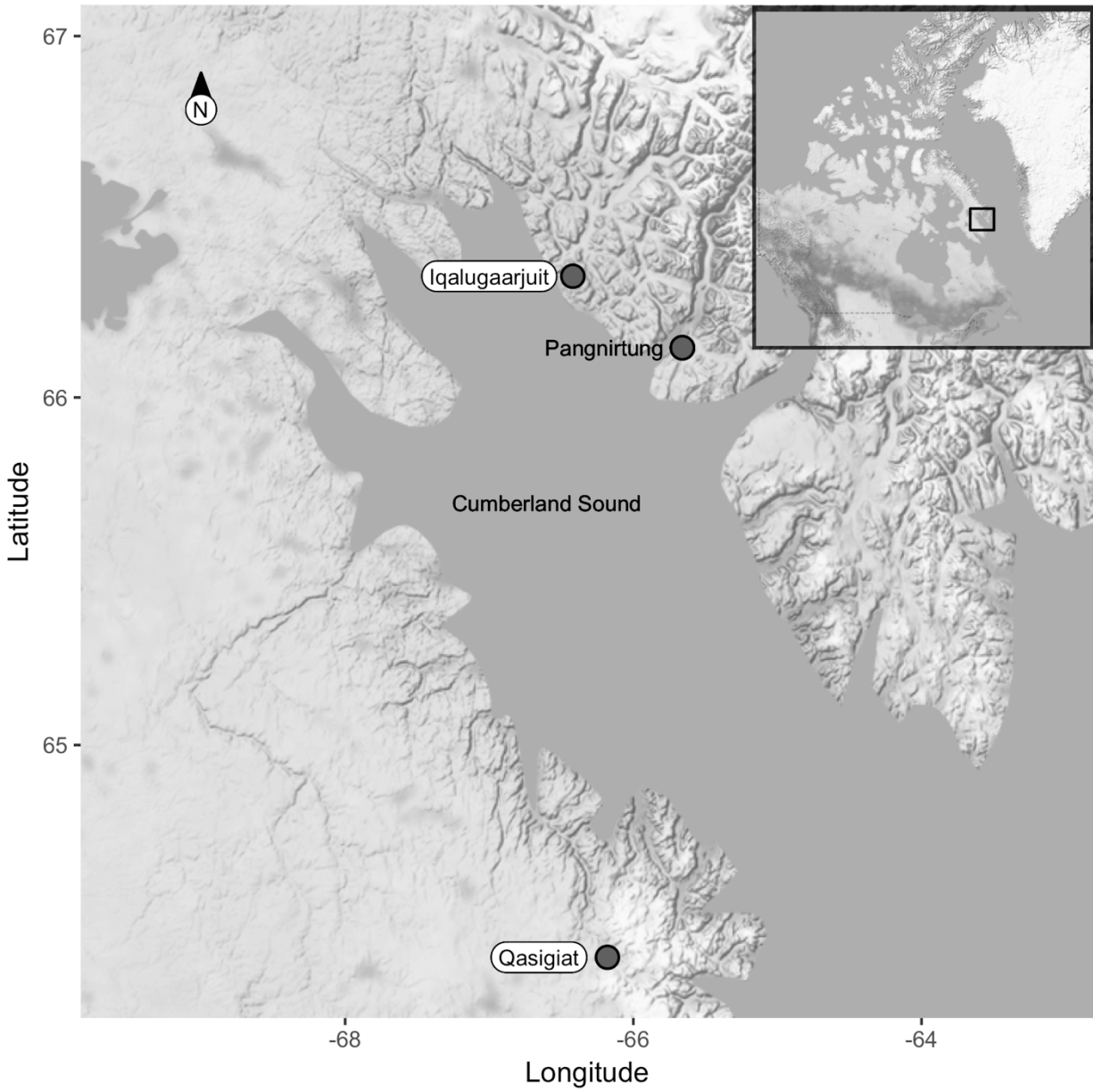
Fig. 2.4 Map of the two lakes of the Cumberland Sound region of Baffin Island, Nunavut where Arctic Charr (*Salvelinus alpinus* L.) were collected and sampled for otoliths used in this study
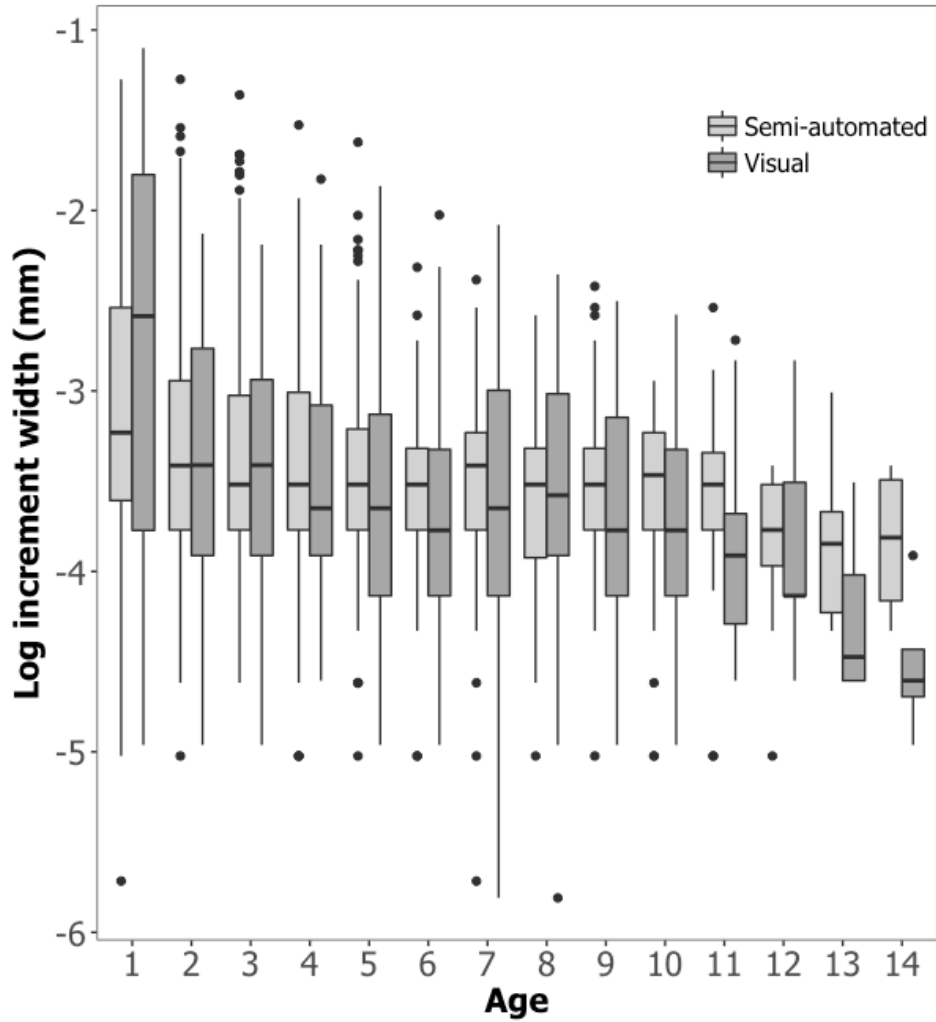
Fig. 2.5 Boxplot of the log of the increment width (mm) measured by the semi-automated and visual methods for every age of the Arctic Charr (*Salvelinus alpinus* L.) otoliths (n=137) used in the study, edge of boxes represents the first and third quartiles and the whiskers represent 1.5 of the interquartile range

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Chapter 3 – Growth in wild Arctic Charr
Introduction

Arctic Charr 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 seen within the Arctic Charr species' complex is attributable to its habitat at high latitudes (Nordeng 1983, Gross et al. 1988, Jørgensen and Johnsen 2014).

The environmental conditions experienced by Arctic Charr are extremely variable throughout the year throughout its circumpolar distribution (Johnson 1980, Dempson and Kristofferson 1987, Gross et al. 1988, Jørgensen and Johnsen 2014). One of the main seasonally fluctuating variables directly affecting Arctic Charr is food availability (Gross et al. 1988). In winter, when light is absent and ice cover is thick, prey availability is greatly restricted as the productivity of the freshwater environment is limited and the marine environment is unavailable (Dempson and Kristoffersen 1987). When summer approaches, sunlight gradually increases. Consequently, there is an increase in primary productivity. Access to the marine environment becomes available as the ice breaks up providing an increase in available food for Arctic Charr. To thrive in such a variable environment, Arctic Charr have adapted their biology to coincide with the timing of events and the limitations of their habitat (Jørgensen and Johnsen 2014).

Adaptations in Arctic Charr are variable among individuals (Brännäs 1998). Within a single Arctic Charr population 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 morphs will include those that segregate based on their feeding niche (Hindar and Jonsson 1982, Nordeng 1983, Loewen et al. 2009, Ulrich 2013). The mechanism influencing the life-history trajectory of Arctic Charr is still puzzling to Arctic Charr biologists. However, a number of studies 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).

Previous work on populations of Arctic Charr from the Cumberland Sound area of Baffin Island has determined that genetics alone is unable to separate individuals by morph type (Moore et al. 2014). This suggests that 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).

One of the main adaptations in 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 while smaller Arctic Charr rely heavily upon the benthos as their main prey source (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) while freshwater residents feed exclusively in freshwater habitat (Moore and Moore 1974).

Energy storage, in the form of lipid reserves, is also known to differ between Arctic Charr morphs. Anadromous individuals demonstrate substantial seasonal variability in food consumption (Damsgård et al. 1999, Rikardsen et al. 2000), 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 are depleted during spawning and their 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 due to their limited size (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, while a small proportion of individuals are observed to continue feeding over the winter season (Jørgensen et al. 2013). I speculate that individuals feeding throughout the winter, along with wild residents, must continue to forage over the winter period in order 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 morphs (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 (Collins et al. 2013, Post et al. 2009). Predictive modelling projects the warming trend of the Arctic will continue and at a disproportionately larger rate than the 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, is going to respond.

There are two likely scenarios when examining the balance between sympatric resident and anadromous Arctic Charr. Both of these scenarios are based on our current understanding of Arctic Charr life-history trajectory. One hypothesis is related to growth (Hindar and Jonsson 1993). In many salmonids with a dichotomy of possible life-histories, the slow growing individuals will migrate to the relatively more productive marine environment where they grow

extensively to increase body size and thus increase its overall fitness (Metcalfe and Thorpe 1992, Metcalfe and Monaghan 2001). Faster growing individuals, that are able to mobilize enough energy in the freshwater environment to reach a threshold (Jonsson and Jonsson 2001), will mature earlier in life and at a smaller size relative to their anadromous counterparts (Thorpe 1989, Svenning et al. 1992). Alternatively, it is proposed that slow growing individuals will remain in the freshwater (Strand and Heggberget 1994, Jonsson and Jonsson 2001). This theory relies on the fact that the freshwater environment is less productive than the marine environment towards the poles (Gross 1988). Slower growing individuals are able to garner enough nutrients from the environment to sustain their metabolism and growth (Svenning 1992, Jonsson and Jonsson 2001). For faster growing and larger individuals it is advantageous to migrate to the relatively more productive sea water to maintain their growth and condition (Svenning 1992, Rikardsen and Elliott 2000, Jonsson and Jonsson 2001). If the first hypothesis presented is correct, a warming of the Arctic where the freshwater environment has a productivity rivaling that of the marine environment, there would be less advantage for individual Arctic Charr to adopt the anadromous life history which would theoretically result in an increase in the prevalence of the smaller resident form. Rather than seeing an increase in the resident life history one could also see a shift towards a higher proportion of anadromous Arctic Charr in the case where the second hypothesis is true. An increase in understanding the potential implications of Arctic climate change on Arctic Charr populations is vital in the management and sustainability of the Arctic Charr fisheries of the Canadian Arctic.

In this chapter, I propose to use otoliths to describe the overall patterns of growth in Arctic Charr given that seasonal increments have a consistent growth pattern relative to the seasonal pattern of somatic growth. I predict that annual growth in Arctic Charr has increased

through time (H2) due to the increase in temperature of the Arctic environment and therefore greater growth season (Arrigo et al. 2008). I also predict that within this increase in growth, a greater increase will be seen in the summer (opaque band) relative to the winter (translucent band) likely related to the earlier thaw and later freeze up of the sea ice (Stirling and Parkinson 2006) creating a greater potential for summer growth (Arrigo et al. 2008) in Arctic Charr.

This chapter will also examine the seasonal growth of the different morphs of Arctic Charr encountered in the study lakes (Fig 3.1). I hypothesize that the growth patterns in Arctic Charr differ between resident and anadromous individuals (H3). I predict that greater seasonal variation in growth patterns will be correlated with an anadromous life history (i.e. more summer growth relative to winter growth within a year.) I further predict that seasonal growth patterns of mature individuals will be consistent with their juvenile growth (H4) (i.e. that anadromous and resident individuals will demonstrate differential growth patterns at all ages).

Methods

Study sites

The sites selected are all located in Southern Baffin Island, Nunavut, surrounding Cumberland Sound (Fig. 3.2). Two sites were selected based on the availability of archived otoliths for assessing changes in growth pattern through time. Iqaluggarjuit Lake (PG082) and Qasigiat Lake (PG015) are known to contain both resident and anadromous Arctic Charr and have previously been studied and described by Tracey Loewen (2008, Loewen et al. 2009, 2010) and Kendra Ulrich (2013). The following is a summary of their descriptions.

Iqaluggarjuit 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 logistic 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 (> 21m) 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 the 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, Arvituajuit (PG013; Fig. 3.3) and Ikpit (PG041; Fig. 3.4), were also 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.

Arvituajuit (Fig 3.3) is known to contain both resident and anadromous (Fig 3.1) Arctic Charr individuals as 2 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 is formed of a larger upper lake and two successive lower basins (Fig 3.4). 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 spring tide, it is possible for the marine

water the overflow and inundate the freshwater environment of the lowest basin. The edges of the basin slope gradually. The water in the lower basin is clear, of a blue colour, and considered 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 2016, 72 and 60 Arctic Charr were collected from the freshwater in Arvitajuit and Ikpit respectively. Fish were photographed and their fork length (mm) and weight (g) were measured in the field. For larger individuals, complete biological, morphometric, and meristic data were collected and sagittal otoliths extracted in the field to allow for the carcass to be returned to the community of Pangnirtung for consumption. Smaller individuals were frozen and shipped to Winnipeg to collect biological, morphometric, and meristic data and to extract sagittal otoliths. A subsample of 50 Arctic Charr collected for the fisheries independent stock assessment program by Fisheries and Oceans Canada were photographed and morphometric and meristic data were collected in addition to the standard biological data collected for the program. In 2017, 68 and 49 Arctic Charr were collected from the freshwater in Arvitajuit and Ikpit, respectively. These fish were photographed and their fork length (mm) and weight (g) were measured in the field. The suspected morph type of each fish was assessed visually when characteristics were sufficiently evident. Fish were then frozen and shipped to Winnipeg to collect complete meristic and morphometric data and to extract sagittal otoliths.

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 by AAE Tech Services (Winnipeg, MB.)

All 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 (4X) was kept constant for all images.

Measurements of growth increments were made on the photographs of all otoliths in ImageJ (Rasband 2017) following a standard linear transect extending from the nucleus and the edge of the otolith's ventral lobe following the sulcus resulting in a transect of approximately 45º to 50º angle from the longest axis between the nucleus and the edge of the otolith's ventral lobe (Fig. 3.5). 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. 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.

Statistical analyses – growth in Arctic Charr over time

A linear mixed effect model (eq. 2) fit by restricted maximum likelihood was built in R 3.5.0 (R Core Team 2018) with the lmer function from the lme4 package (Bates et al. 2015) to examine the annual otolith growth (mm) of Arctic Charr over time (H1). Otolith growth

increment measurements were log transformed to satisfy the assumptions of normality and homogeneity of variance of the model which were verified visually (Fig. 3.6). The fit of the model was then checked with residual plots prior to interpretation of results (Fig. 3.7) The predictor variables included in the model were year of growth (H1, 1990-2015), life history (resident, anadromous, or unknown), sex (male, female, or unknown), growth increment (age of growth 1-15), and lake (Arvitajuit, Ikpit, Iqalugaarjuit, Qasigiat) with fish ID nested within lake. ID was set as a random variable to correct for the repeated measures performed on each individual. Polynomial contrasts were added to the factor year to include the possible non-linear effect of year on growth. Sex was excluded from the predictor variables for the final model as it was determined using a likelihood ratio test (p=0.298) to not have a significant effect on annual growth. The final model selected had a lower AIC value (AIC=1327.940) than the model that included the variable sex (AIC=1340.177). Model p-values and degrees of freedom were estimated with t-tests using Satterthwaite's method from the package LmerTest (Kuznetsova et al. 2018).

The linear model was as follows:

$$y_{ij} = \beta_0 + \beta_1 Year_{ij} + \beta_2 Lake_{ij} + \beta_3 Increment_{ij} + \beta_4 Life\ history_{ij} + \alpha_{ij} + \varepsilon_{ij} \quad \text{(eq. 2)}$$

In this model:

y_{ij} represents the increment width from the jth level of factor ID within the ith factor lake

β_0 is the intercept of the model

$\beta_{1-n} X_{ij}$ is the linear effect of each factor in the model

α_{ij} represents the random effect as a normally distributed described with a mean of 0 and a variance of σ_α^2

ε_{ij} represents the normally distributed random error with a mean of zero and variance of σ^2

Statistical analyses – seasonal growth in morphs of Arctic Charr

A generalized linear mixed effects model (eq. 3) was fit using restricted maximum likelihood in R 3.5.0 (R Core Team 2018) using the glmmTMB function from the glmmTMB package (Magnusson et al. 2018) with the summer proportional growth data to examine the effect of Arctic Charr life-history on otolith growth seasonality (H3) and to test the consistency of seasonal otolith growth patterns with age in Arctic Charr (H4). 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 shape 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 (eq. 4) proposed by Ferrari and Cribari-Neto (2004) was used for this study.

$$f(y; \mu, \phi) = \frac{\Gamma(\phi)}{\Gamma(\mu\phi)\Gamma((1-\mu)\phi)} y^{\mu\phi-1}(1-y)^{(1-\mu)\phi-1}, 0 < y < 1 \qquad \text{(eq. 3)}$$

Where $0 < \mu < 1$ and $\phi > 0$

Simply the beta distribution can be written as:

$$y \sim B(\mu, \phi)$$

Where:

$$E(y) = \mu$$

$$VAR(y) = \mu(1-\mu)/(1+\phi)$$

Factors included in the linear predictor (η, eq.4) for the model were year of growth (1990-2015), life history (anadromous, resident, or unknown), growth increment (i.e. age of

growth, 1-15), sex (male and female), and lake (Arvitajuit, Ikpit, Iqalugaarjuit, Qasigiat) with

fish ID nested within lake. A random effect was added to ID to correct for the repeated measures

performed on individuals. Sex was removed from the final model as it did not help explain the

variation in the data which was determined using a likelihood ratio test (p=0.109). Additionally,

the final model was selected as it had a lower AIC value (AIC=-7738.3) than the model

including sex (AIC=-7737.9).

    The model was as follows:

$$\eta_{ij} = \beta_0 + \beta_1 Year_{ij} + \beta_2 Lake_{ij} + \beta_3 Increment_{ij} + \beta_4 Life\ history_{ij} + \alpha_{ij} + \varepsilon_{ij} \quad \text{(eq. 4)}$$

    In this model:

η_{ij} represents the increment width from the jth level of factor ID within the ith

factor lake

β_0 is the intercept of the model

$\beta_{1-n} X_{ij}$ is the linear effect of each factor in the model

α_i represents the random effect as normally distributed described with a mean of

0 and a variance of σ_α^2

ε_{ij} represents the normally distributed random error with a mean of zero and

variance of σ^2

Finally, the function used to link the beta distribution to the linear predictor was a logit link

function (eq. 5).

$$g(\mu_{ij}) = \log\left\{\frac{\eta_{ij}}{(1 - \eta_{ij})}\right\} \qquad \text{(eq. 5)}$$

The fit of the model was then checked with residual plots prior to the interpretation of the results (Fig. 3.8).

Results

A total of 500 Arctic Charr otoliths were used in this study (Table 3.1). Age estimates from otoliths ranged from 1 to 16 with an average age of 6+ years and modal age of 5+ years. 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 0.01mm and 0.36mm with average growth increment width of 0.086mm. The proportional summer growth data ranged from 0.33 to 0.98 and the mean was 0.767.

Table 3.1 Metadata on otoliths used to fit the models evaluating the effects of various factors on the annual and seasonal growth in Arctic Charr

Lake	Sample year	Life history	Number of samples	Total samples
Qasigiat	2004	Anadromous	91	102
		Resident	11	
	2011	Anadromous	30	116
		Resident	20	
		Unknown	66	
Iqalugaarjuit	2004	Anadromous	27	68
		Resident	41	
	2011	Anadromous	14	69
		Resident	11	
		Unknown	44	
Ikpit	2016	Anadromous	32	69
		Resident	6	
		Unknown	31	
Arvitajuit	2016	Anadromous	33	76
		Resident	5	
		Unknown	38	

Annual growth in Arctic Charr over time

Results from the first model examining annual Arctic Charr otolith growth demonstrated that year does have a significant effect on annual growth with a linear increase in annual otolith

growth through time (p<0.001; Table 3.2; Fig. 3.9) spanning the years 1999 to 2015. Otolith

growth differed significantly between anadromous and resident individuals (p<0.001; Table 3.2;

Fig. 3.9) and between anadromous and individuals with an unknown life history (p<0.001; Table

3.2; Fig. 3.9) with both life history types having lower annual otolith growth relative to

anadromous individuals. Lake had a significant effect on annual otolith growth with Qasigiat and

Iqalugaarjuit having greater growth than Ikpit and Arvitajuit (p<0.001; Table 3.2; Fig. 3.9).

Finally, there was a significant linear trend with growth increments becoming smaller with age

(p<0.001; Table 3.2; Fig. 3.9)

Table 3.2 Terms (β_n) included in the final model assessing the effect of factors on the annual growth of Arctic Charr. Significant terms are indicated with *

Fixed effects	Estimate	Standard error	df	t-value	Pr(>|t|)	
Intercept	-2.991	0.036	846	-83.054	<0.001	*
Year.L	0.533	0.091	587	5.840	<0.001	*
Year.Q	-0.119	0.050	3362	-2.400	0.016	*
Year.C	0.025	0.037	3206	-0.682	0.495	
Qasigiat	0.101	0.028	570	3.616	<0.001	*
Ikpit	-0.014	0.025	463	-0.574	0.566	
Iqalugaarjuit	0.100	0.030	588	3.323	<0.001	*
Increment.L	-1.642	0.139	3364	-11.791	<0.001	*
Increment.Q	0.442	0.141	3186	3.149	0.002	*
Increment.C	-0.370	0.131	3133	-2.828	0.005	*
Increment^4	0.303	0.117	3087	2.577	0.010	*
Increment^5	-0.240	0.106	3051	-2.265	0.024	*
Increment^6	0.143	0.096	3038	1.485	0.138	
Increment^7	-0.142	0.085	3040	-1.669	0.095	
Increment^8	0.027	0.071	3043	0.374	0.709	
Increment^9	-0.056	0.058	3040	-0.972	0.331	
Increment^{10}	0.007	0.046	3032	0.151	0.880	
Increment^{11}	0.026	0.037	3016	0.708	0.479	
Increment^{12}	0.035	0.019	3007	1.100	0.271	
Increment^{13}	-0.005	0.027	3003	-0.196	0.844	
Increment^{14}	0.045	0.024	2997	1.909	0.056	

Increment[15]	-0.003	0.021	2986	-0.158	0.875	
Resident	-0.172	0.020	500	-8.698	<0.001	*
Unknown	-0.101	0.025	563	-4.120	<0.001	*
Random effects		Variance	Std. Dev.			
Lake:ID	Intercept	0.010	0.982			
Residual		0.076	0.275			

Seasonal growth in morphs of Arctic Charr

Results from the sec

ond model examining proportion of seasonal growth in morphs of Arctic Charr

demonstrate that life history has a significant effect on the proportion of summer growth with

resident and individuals of unknown life history having a lower proportion of summer growth

when compared to anadromous individuals (p=0.009 and p=0.044 respectively; Table 3.3; Fig.

3.10, 3.11). Increment age did not have a significant linear effect on the proportion of summer

otolith growth (p=0.080; Table 3.3; Fig. 3.10, 3.11). Year did not have a significant linear

influence on otolith growth (p=0.279; Table 3.3, Fig. 3.10, 3.11). Lake had a significant effect

with Qasigiat (p<0.001; Table 3.3; Fig. 3.10, 3.11) and Iqalugaarjuit (p=0.035; Table 3.3; Fig.

3.10, 3.11) having a lesser proportion of summer otolith growth relative to Arvitajuit and Ikpit.

Table 3.3 Terms (β_n) included in the final model assessing the effect of factors on the proportion of summer growth of Arctic Charr. Significant terms are indicated with *

Fixed effects	Estimates	Standard error	z-value	Pr(>|z|)	
Intercept	1.262	0.065	19.526	<0.001	*
Year.L	0.189	0.175	1.082	0.279	
Year.Q	-0.145	0.120	-1.211	0.226	
Year.C	-0.255	0.114	-2.236	0.025	*
Year[4]	-0.035	0.108	-0.325	0.745	
Year[5]	0.047	0.103	0.457	0.648	
Year[6]	0.155	0.097	1.604	0.109	
Year[7]	-0.164	0.091	-1.811	0.070	
Year[8]	0.045	0.084	0.535	0.593	
Year[9]	-0.171	0.080	-2.141	0.032	
Year[10]	0.059	0.075	0.784	0.433	

Year[11]	0.012	0.071	0.164	0.870	
Year[12]	-0.012	0.067	-0.178	0.859	
Year[13]	0.028	0.064	0.431	0.666	
Year[14]	0.065	0.060	1.088	0.277	
Year[15]	-0.074	0.056	-1.324	0.186	
Year[16]	-0.039	0.053	-0.734	0.463	
Year[17]	-0.033	0.050	-0.669	0.504	
Year[18]	-0.073	0.046	-1.568	0.117	
Year[19]	0.122	0.043	2.858	0.004	*
Year[20]	-0.086	0.040	-2.144	0.032	*
Year[21]	0.005	0.037	0.137	0.891	
Year[22]	0.004	0.037	0.110	0.912	
Year[23]	0.066	0.037	1.797	0.072	
Year[24]	-0.014	0.030	-0.457	0.648	
Year[25]	-0.051	0.036	-1.417	0.157	
Qasigiat	-0.273	0.050	-5.472	<0.001	*
Ikpit	0.002	0.045	0.055	0.956	
Iqalugaarjuit	-0.113	0.054	-2.106	0.035	*
Increment.L	-0.440	0.252	-1.748	0.080	
Increment.Q	1.109	0.263	4.217	<0.001	*
Increment.C	0.179	0.250	0.717	0.473	
Increment[4]	0.789	0.221	3.563	<0.001	*
Increment[5]	0.265	0.189	1.399	0.162	
Increment[6]	0.502	0.159	3.158	0.002	*
Increment[7]	0.113	0.131	0.866	0.386	
Increment[8]	0.170	0.105	1.621	0.105	
Increment[9]	0.015	0.083	0.176	0.860	
Increment[10]	0.054	0.065	0.830	0.406	
Increment[11]	0.019	0.053	0.361	0.718	
Increment[12]	-0.016	0.046	-0.345	0.730	
Increment[13]	-0.058	0.040	-1.465	0.143	
Increment[14]	0.019	0.035	0.533	0.594	
Increment[15]	-0.045	0.031	-1.452	0.147	
Resident	-0.088	0.034	-8.698	0.009	*
Unknown	-0.085	0.042	-4.120	0.044	*

Random effects		variance	Std. Dev.	
ID:Lake	Intercept	0.035	0.187	
Lake	Intercept	$1.043e^{-11}$	$3.230e^{-6}$	

Discussion

The results of this chapter indicate that there has been a significant linear increase in annual growth of wild Arctic Charr in the Cumberland Sound area of Baffin Island, Nunavut, Canada from 1990 to 2015. This is consistent with my 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 (Collins et al. 2013, Post et al. 2009). This is supported by predictive modelling used on two populations of Arctic Charr which indicated that an increase in growth and consumption would be likely if the current warming trends persist (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 area between the years 1989 to 2009 (Grenier 2015).

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. An increase in Arctic Charr growth potential could be interpreted as a reason to increase commercial catch quotas. 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 changes. As mentioned in the introduction, two alternative scenarios have been proposed to explain the effect of 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 1988, Rikardsen and Elliott 2000) as their comparatively reduced metabolic needs are able to be fully met in the freshwater environment (Svenning 1992, Jonsson and Jonsson 2001). 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 anadromous Arctic Charr.

The results of this study suggest that individuals with greater growth 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 are those with the greatest growth (Thorpe 1989, Svenning et al. 1992).

I 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 trajectories 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* L.), 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 to the freshwater environment is influenced by latitude where the marine environment is increasingly productive towards the poles (Gross 1988). The populations in this study are located on the fringe of the Arctic Circle and are well within the July 10°C mean isotherm. Freshwater environments in the study area are suspected to have a lower productivity relative to the marine environment as per Gross' (1988) report. This provides further evidence to suggest that Arctic Charr in the studied populations follow a life history trajectory 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 trajectory 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. Further studies examining the relationship among environmental productivity, growth, and life history trajectory in Arctic Charr is essential for the continued management of exploitation of Arctic Charr.

An increase in growth season and temperature related to Arctic climate change may also have a large effect on Arctic Charr populations by changing the food-web dynamics. Temperate species may increase their northern range and invade Arctic Charr habitat. Evidence for a shift in

prey availability has already been documented in Cumberland Sound, Nunavut with capelin (*Mallotus villosus*) being a recent invader (Marcoux et al. 2012). A dietary shift in Cumberland Sound Arctic Charr towards a higher proportion of capelin in the diet has been recorded in areas where capelin was previously absent (Ulrich 2013). Increase in prey availability, especially quality prey items such as capelin (Lawson et al. 1998), could result in an increase in growth in Arctic Charr (Ulrich 2013). Changes in food web dynamics due to increasing invaders could negatively influence Arctic Charr populations by the means of changing competition and predation risk which are not independent of one another (Persson et al. 2013). It is recorded that when competitors are present, Arctic Charr feeding niche is compressed (Sandlund et al. 2016) and that juvenile Arctic charr are at increased risk of predation (Langeland et al. 1991, L'Abbé-Lund et al. 1992). However, predicting the effects of climate change on biotic interactions within an environment can be troublesome (Ulvan et al. 2012).

Life history was found to significantly influence the growth patterns in Arctic Charr otoliths. Resident individuals exhibit significantly lower annual growth and proportional summer growth relative to anadromous individuals. One of the distinguishing features between resident and anadromous individuals is the resident's smaller size, therefore it is no surprise that residents exhibit lower annual growth. What is interesting, however, is the divergence in seasonal otolith incremental pattern within the annual growth between life histories. Based on the knowledge of anadromous seasonal feeding and fasting habits it is no surprise that anadromous Arctic charr exhibit great seasonality in their otolith growth as they have extremely seasonal feeding 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).

Age of the increment did not have an effect on the seasonal pattern of growth in the otoliths while increment age is related to a decrease in annual growth as was expected (Forseth et al. 1994). This suggests that the divergence between resident and anadromous individuals happens within the first year of growth. The results presented here are in agreeance that an individual Arctic Charr's life history trajectory is highly influenced by the growth in the early stage of life (Rikardsen and Elliott 2000) and that there is consistency in growth trajectories (Björklund et al. 2003).

Few studies have focussed on examining the feeding habits of resident individuals living in sympatry with anadromous individuals. Divergent patterns of growth between morphs have been found in multiple studies examining growth in Arctic Charr (Rikardsen et al. 2000, Loewen et al. 2010, Knundsen et al. 2015). Resident Arctic Charr had a consistent degree of stomach fullness during summer whereas first-time migrants demonstrated a decrease in stomach fullness throughout the summer (Rikardsen et al. 2000). It was also noted that resident individuals had a more consistent growth pattern relative to the first-time migrants that exhibited fast compensatory growth upon their arrival to the marine environment (Rikardsen et al. 2000). These results are consistent with the findings of this study.

The intrinsic mechanism influencing the divergence of growth patterns between sympatric morphs of Arctic Charr has yet to be determined. Genetic studies have 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 set within the first year of growth. For the sake of conservation and the field of evolutionary

biology, further studies are warranted to determine a solution to the problem of trajectory of life histories in Arctic Charr.

Figures

Fig. 3.1 Picture of mature male anadromous and resident (inset) Arctic Charr (*Salvelinus alpinus* L.) from Arvitajuit collected in 2016
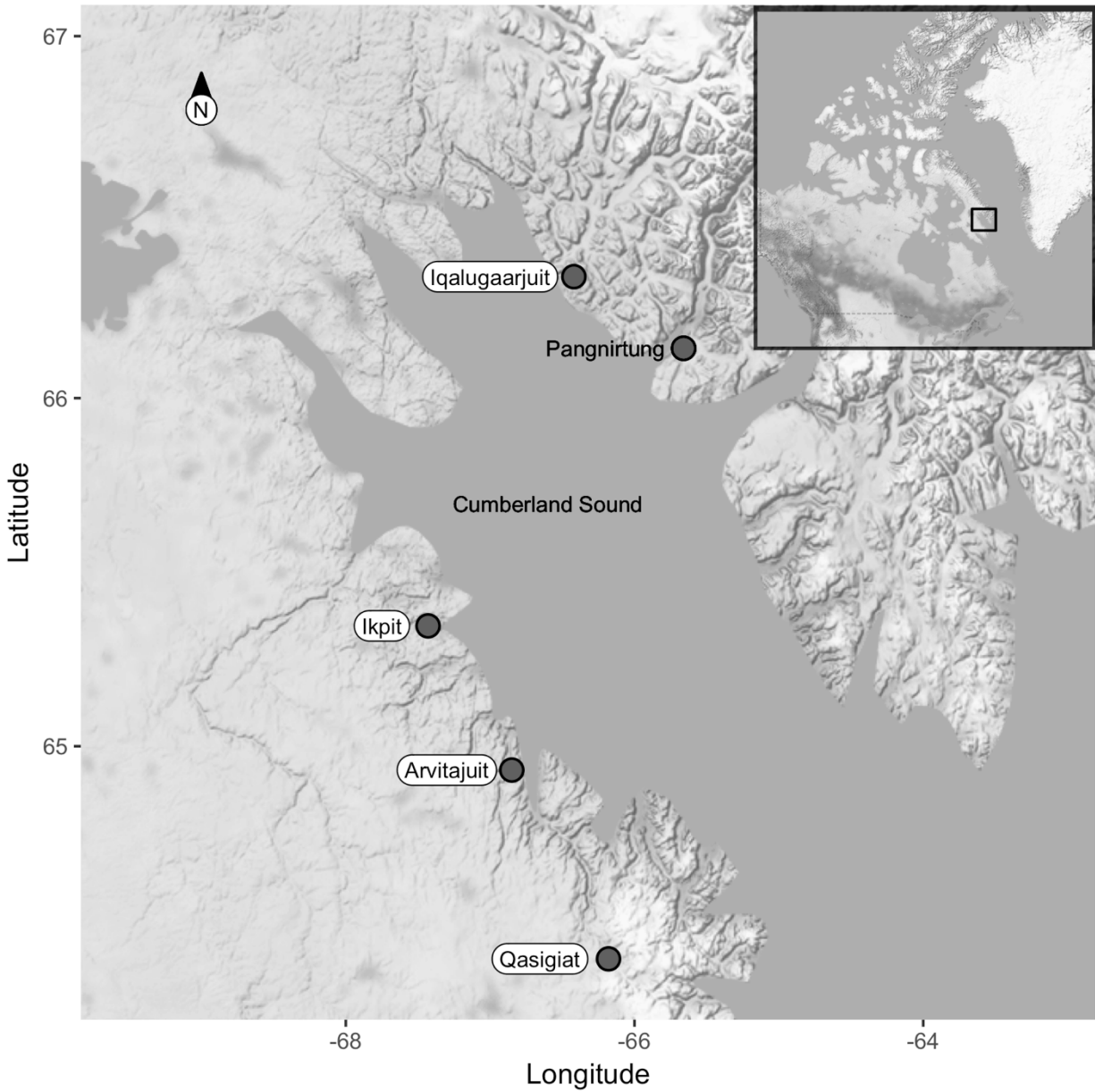
Fig. 3.2 Map of the four lakes in the Cumberland Sound Region of Baffin Island, Nunavut, where Arctic Charr (*Salvelinus alpinus* L.) were collected and sampled in 2004, 2011, 2016, and 2017
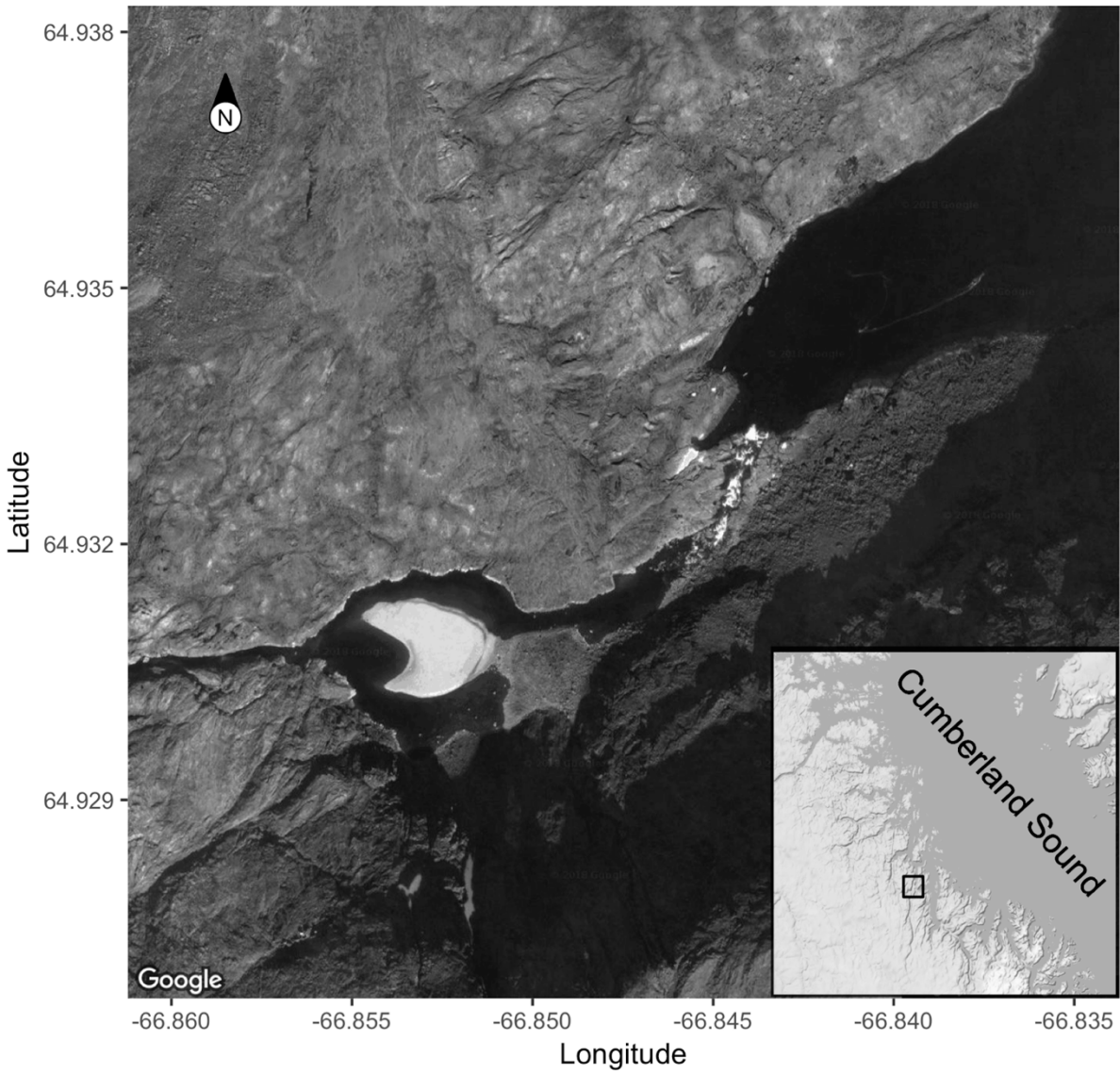
Fig. 3.3 Map of Arvitajuit Lake from the Cumberland Sound Region of Baffin Island, Nunavut, where Arctic Charr (*Salvelinus alpinus* L.) were collected and sampled in 2016 and 2017
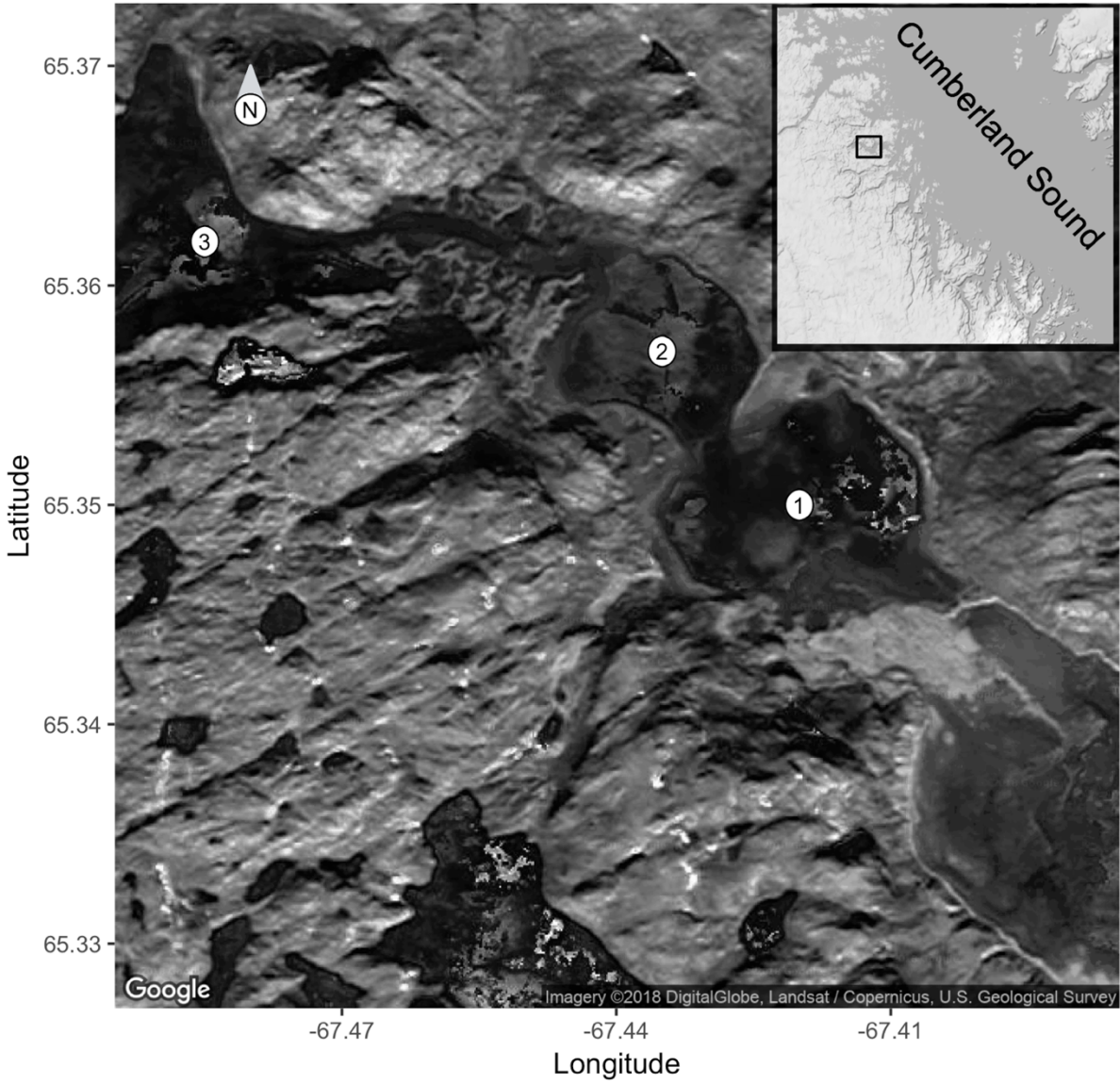
Fig. 3.4 Map of Ikpit Lake from the Cumberland Sound Region of Baffin Island, Nunavut, where Arctic Charr (*Salvelinus alpinus* L.) were collected and sampled in 2016 and 2017: *1* Lower basin where collections were made, *2* Middle basin, *3* Upper basin
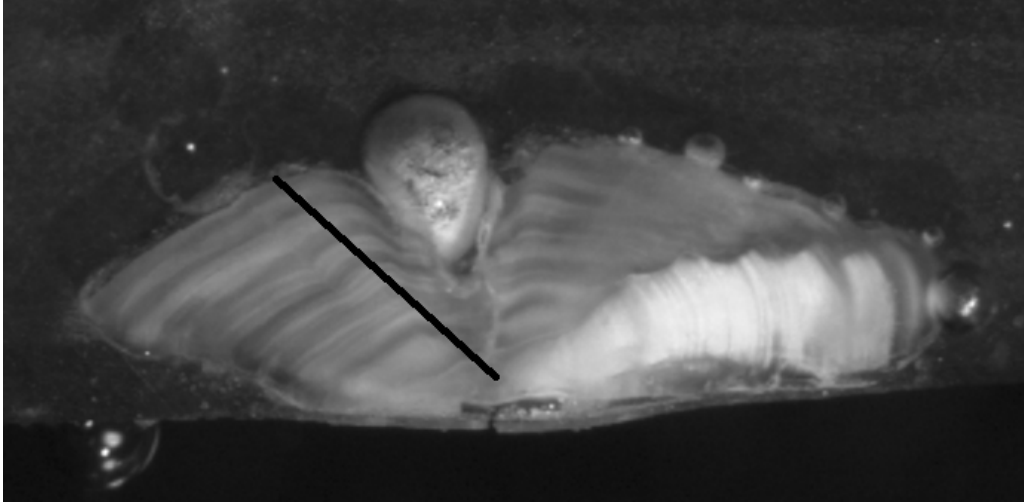
Fig. 3.5 Cross section of an Arctic Charr (*Salvelinus alpinus* L.) otolith with the standard transect (black line) used to measure annual and seasonal increment widths
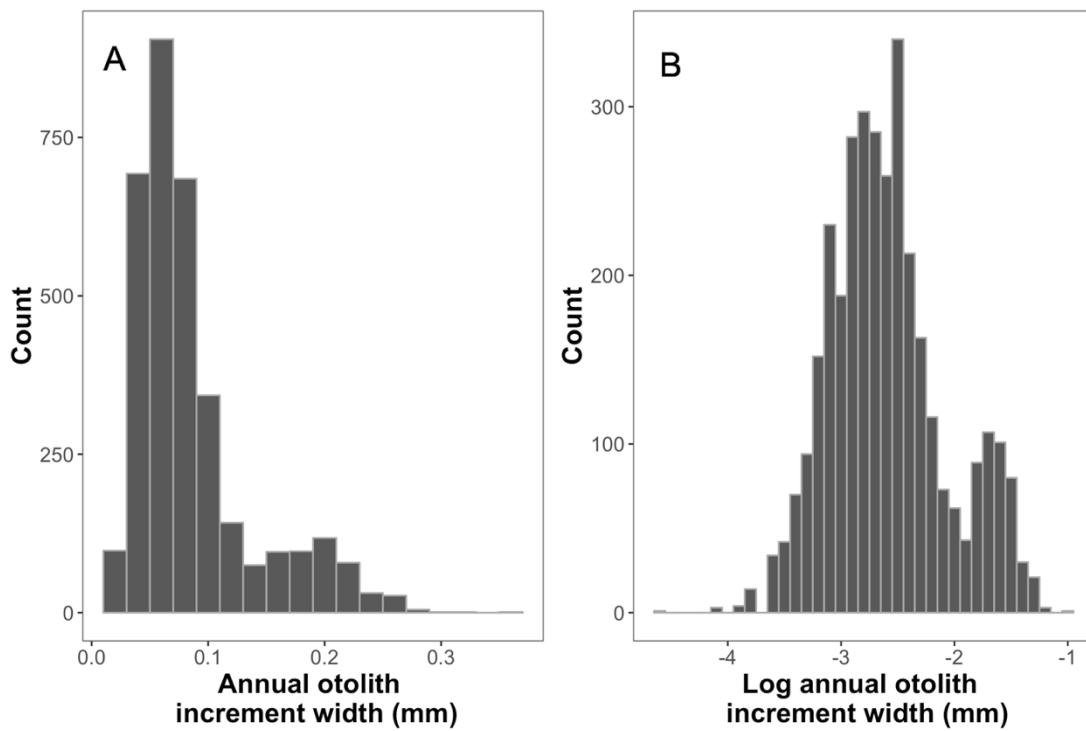
Fig. 3.6 Visual verification of normality and homogeneity of variance assumptions for modelling. *A* histogram of raw data, *B* histogram of log data
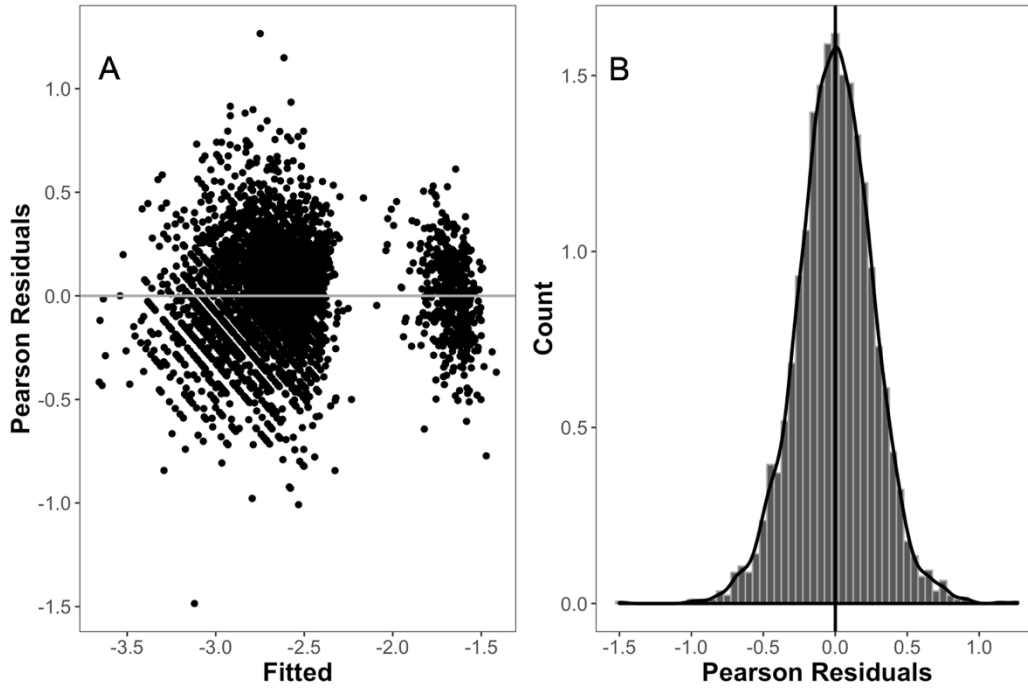
Fig. 3.7 *A* Pearson residuals vs fitted model value for verification of fit of best model, *B* distribution of Pearson residual
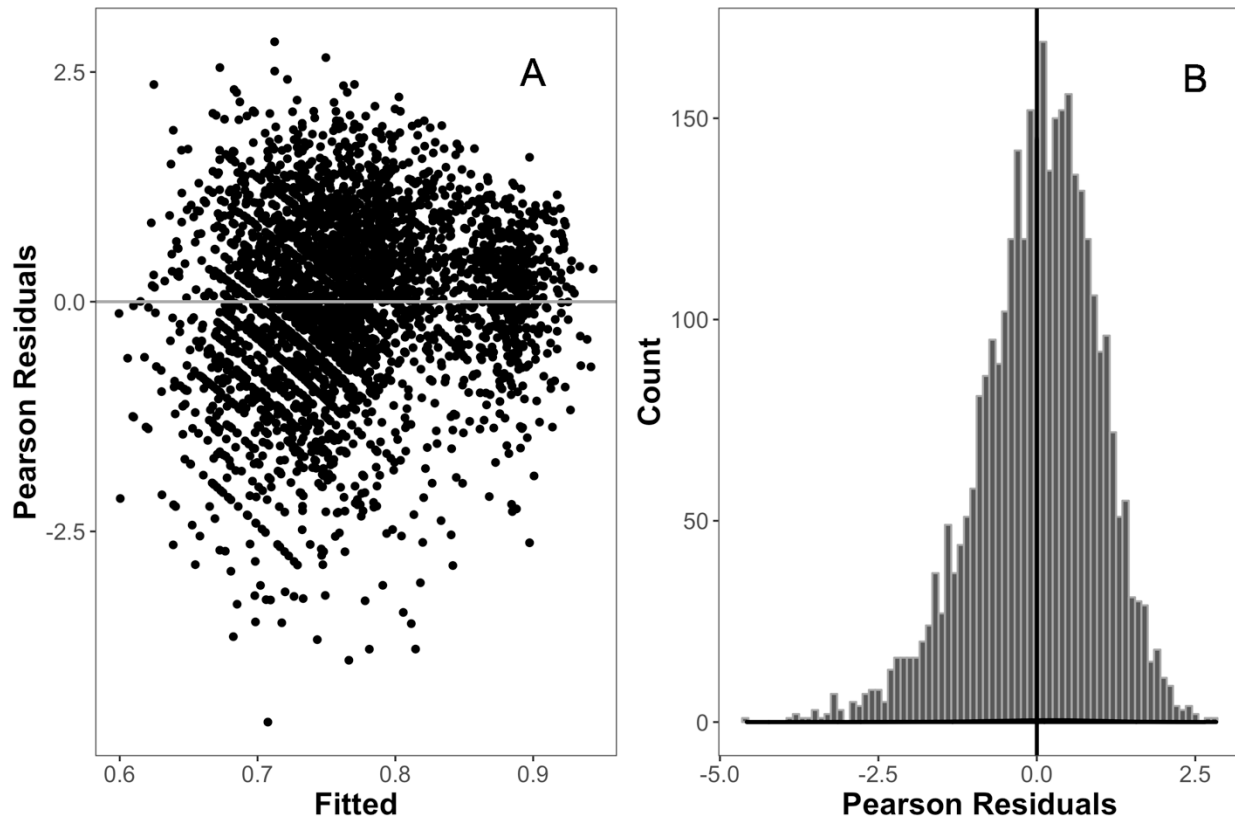
Fig. 3.8 Residual plots used to check assumptions of model assessing effects of factors on proportion of summer growth in Arctic Charr (*Salvelinus alpinus* L.)
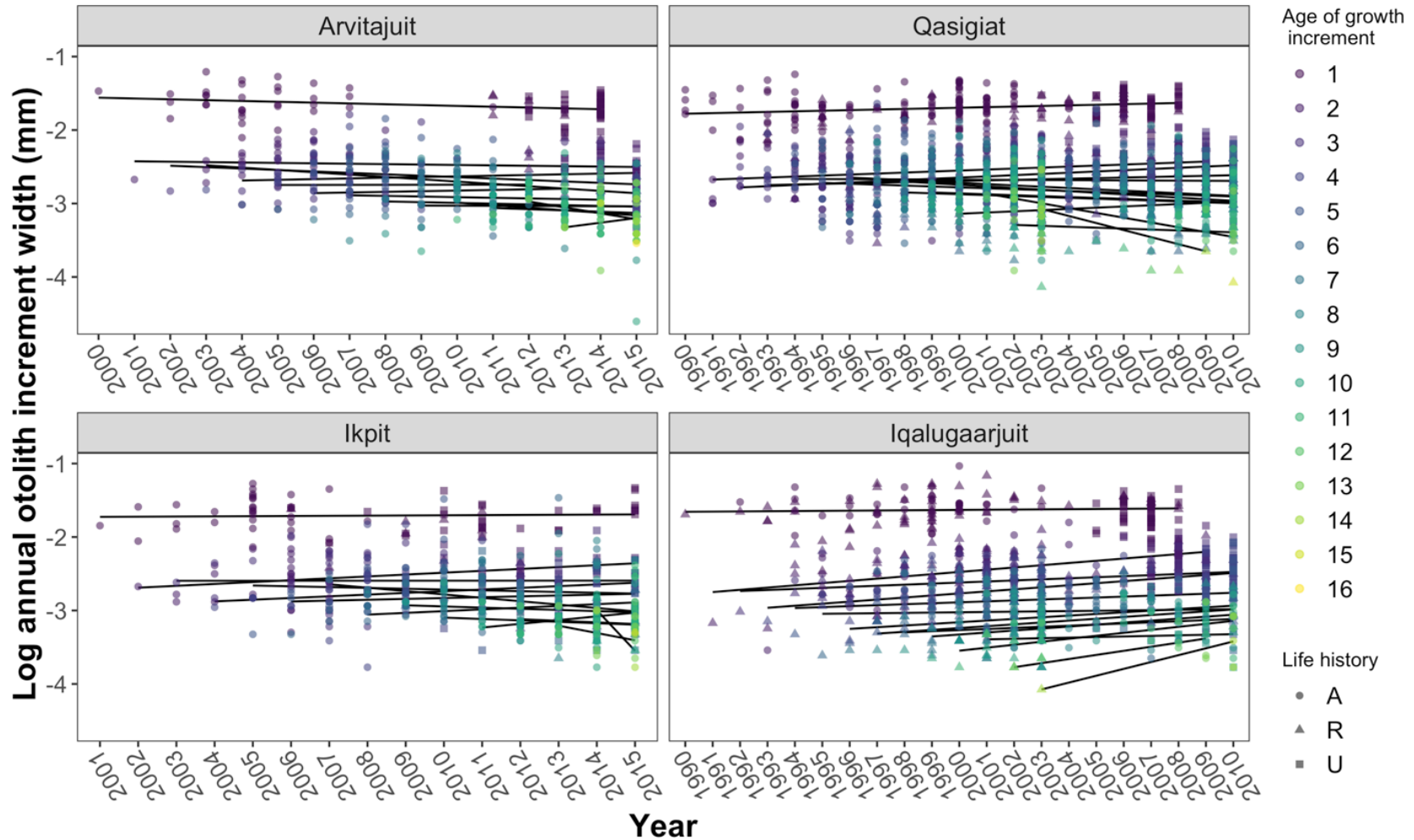
Fig. 3.9 Model estimate for the log of the annual otolith increment (mm) width plotted by year, lake, age of growth increment, and life history type (A=anadromous, R=resident, U=unknown) for Arctic Charr (*Salvelinus alpinus* L) with mean model estimate plotted for each age (line)
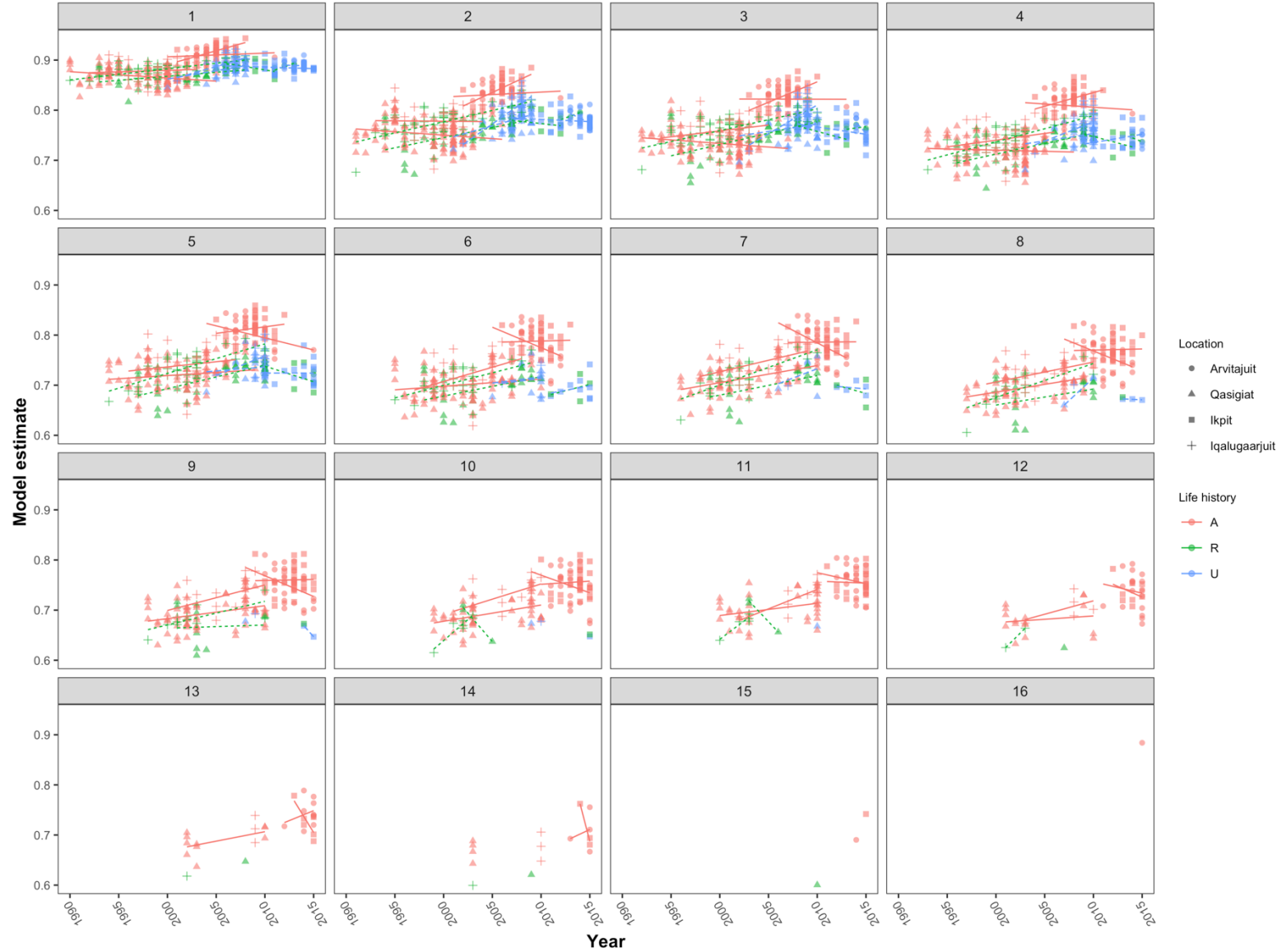
Fig. 3.10 Predicted model estimates for the annual proportion of summer growth plotted by year, age of growth increment, lake, and life history type (A=anadromous, R=resident, U=unknown) for Arctic Charr (*Salvelinus alpinus* L.)
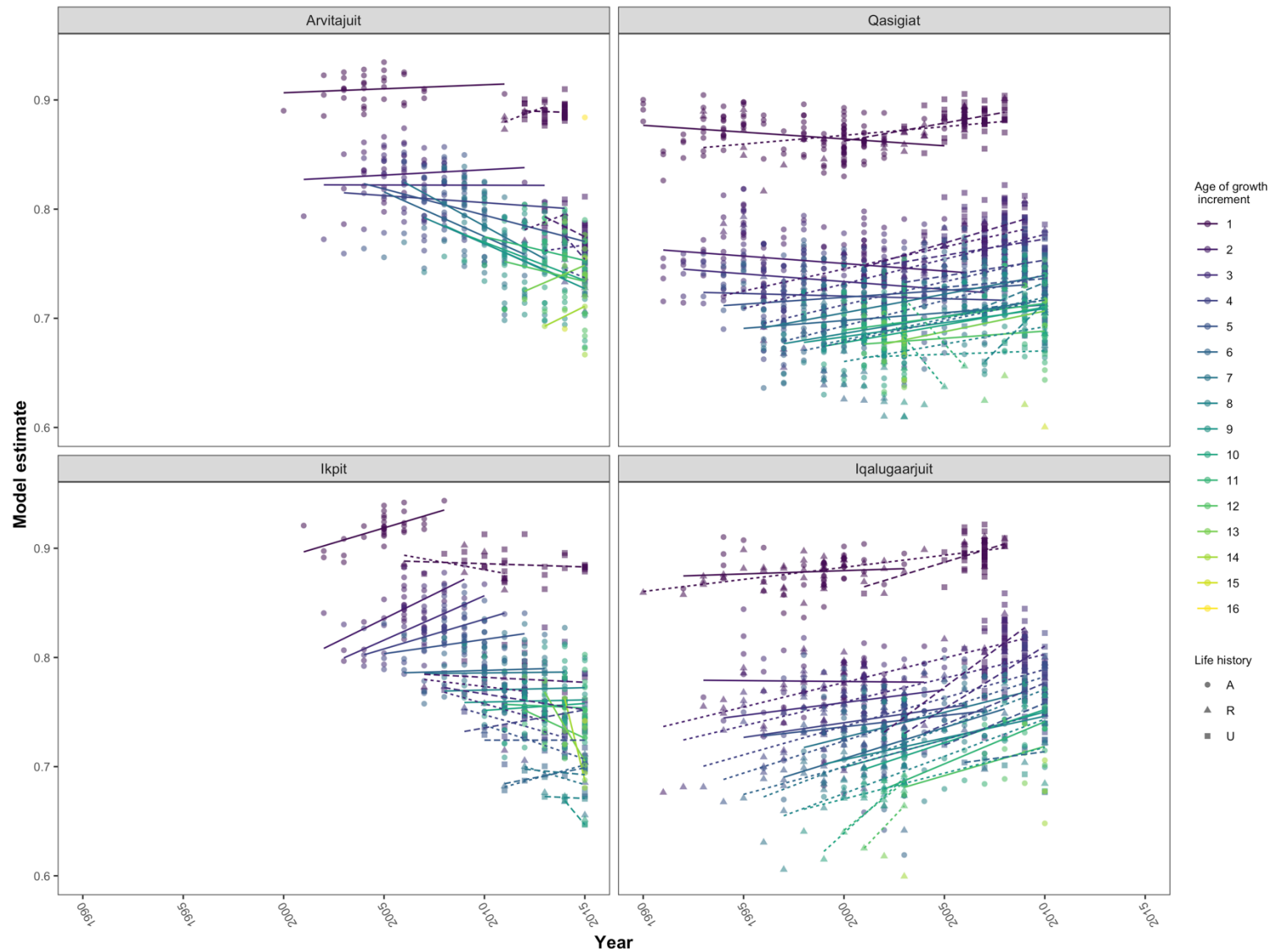
Fig. 3.11 Predicted model estimates for the annual proportion of summer growth plotted by year, lake, age of growth increment, and life history type (A=anadromous, R=resident, U=unknown) for Arctic Char (*Salvelinus alpinus* L.)

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Chapter 4 – Classification of juvenile Arctic Charr
Introduction

Divergent life history strategies between individuals of a single population have evolved within multiple salmonids (Thorpe et al. 1982, Klemetsen et al. 2003, Hendry and Stearns 2004). Life history strategies involve trade-offs among growth, survival, and reproduction (Stearns 2004). In Arctic Charr, the differences in growth between resident and anadromous individuals is extreme, where anadromous individuals have greater growth relative to residents (Forseth et al. 1994). This divergence in growth is related to other trade-offs such as age at maturity (Forseth et al. 1994, Rikardsen and Elliott 2000) and body condition (Boivin and Power 1990, Finstad et al. 2003, 2006). There is extensive literature describing differences between life history morphs in Arctic Charr and other salmonids (Elliott 1976, Nordeng 1983, Letcher and Griest 2003), however the mechanism controlling life history trajectory in Arctic Charr is poorly understood (Jonsson and Jonsson 2001).

Many articles in the Arctic Charr literature mention a 'shift' in life history strategy (Langeland et al. 1991, Jonsson and Jonsson 1993, Finstad et al. 2006) implying that individuals are not different at early stages and adopt their life history later in life (Balon 1980). One of the predominant hypotheses is that Arctic Charr life history is largely mediated by the environmental conditions (Hindar and Jonsson 1993, Jonsson and Jonsson 2001). Following this hypothesis, researchers have been increasingly examining patterns in the early life and development of Arctic Charr to try and elucidate the mechanism behind the divergence of life history (Björklund et al. 2003, Knudsen et al. 2015, Wood et al. 2018). Results of studies examining early development of Arctic Charr are suggesting that the 'shift' in life history strategy happens very early in the development of individual Arctic Charr (Knudsen et al. 2015, Wood et al. 2018).

Results from Chapter 3, examining annual and seasonal growth patterns in resident and anadromous Arctic Charr, are consistent with the hypothesis that the 'shift' in life history trajectory happens early in life. My findings in Chapter 3 suggest that the divergence in growth patterns is present within the first year of life while both morphs are still inhabiting the freshwater environment.

Visually distinguishing resident and anadromous individuals in juvenile Arctic Charr is difficult (Balon 1980, Loewen et al. 2010) owing to their sympatric origins and to the juvenile like characteristics (e.g. parr marks) of resident individuals. I propose that individuals of an unknown life history can be identified based on their seasonal growth patterns. The objective of this chapter is to use seasonal growth patterns of the first year of growth measured from otolith cross sections of resident and anadromous individuals to assign a probable life history to juveniles of an unknown life history.

Methods

Data used in chapter 3 were used to perform the analyses for this chapter. Refer to methods of chapter 3 for complete details on the lakes and data collection. A generalized linear model using a binomial distribution (eq. 6) and the logit link (eq. 7) was used to model the effect of seasonal growth pattern in terms of proportional summer growth the first year of growth on the life history trajectory in Arctic Charr (eq. 8). This model was constructed using a randomly selected sub-sample of samples that had previously been identified as anadromous or resident Arctic Charr (Fig. 3.1).

$$RA \sim B(n, \pi) \qquad \text{(eq. 6)}$$

Where:

n = number of samples

π = probability that an individual is classed as anadromous (i.e. value of 1)

$$E(RA) = \pi$$

$$VAR(RA) = \pi(1 - \pi)$$

$$g(\mu_i) = \log \left\{ \frac{\pi(\eta_i)}{1 - \pi(\eta_i)} \right\} \qquad \text{(eq. 7)}$$

The linear predictor of the model was as follows:

$$\eta_i = \beta_0 + \beta_1 Growth_i + \beta_2 Lake_i + \beta_3 Year_i + \varepsilon_i \qquad \text{(eq. 8)}$$

In this model:

η_i represents the life history, either anadromous or resident of the ith individual

β_0 is the intercept of the model

$\beta_1 Growth_i$ is the linear effect of proportional summer growth of the ith individual

$\beta_2 Lake_i$ is the linear effect of lake of the ith individual

$\beta_3 Year_i$ is the linear effect of growth of the ith individual

ε_{ij} represents the normally distributed random error with a mean of zero and

variance of σ^2

The predictive ability of the model was then tested by assessing its ability to correctly assign life history to the sub-sample that was not used to construct the model. Individuals were assigned as anadromous when the probability of anadromy predicted by the model was greater or equal to 0.5 and as a resident if the probability fell below the threshold value. The model accurately predicted the correct classification in 92.39% ($\pm 4.11\%, \alpha = 0.05$; Table 4.1; Fig. 4.1) of known cases. Samples that had an unknown classification were assessed using the logistic

regression model to predict their probable life history trajectory based on the seasonal growth of their first year.

Table 4.1 Error matrix of true life history and predicted life history for Arctic Charr classified using logistic regression.

		True	
		Resident	Anadromous
Predicted	Resident	36	6
	Anadromous	8	134

Results

A total of 428 Arctic Charr otoliths were used (Table 4.2). The mean proportion of summer growth in the first year of growth for anadromous individuals was 0.9152, for residents 0.8942, and for unknown individuals 0.8956 (Fig. 4.2). Age estimates of otoliths ranged from 1 to 16 and the mean age for anadromous, resident, and unknown individuals was 10, 6, and 4, respectively. The data spanned the years 1997 to 2015. The final model terms are presented in Table 4.3.

Table 4.2 Metadata on Arctic Charr otoliths used to fit and test the logistic regression model and used in the classification of unknown life history types

Lake	Sample year	Life history	Number of samples	Total samples
Qasigiat	2011	Anadromous	30	116
		Resident	20	
		Unknown	66	
Iqalugaarjuit	2011	Anadromous	14	69
		Resident	11	
		Unknown	44	
Ikpit	2016	Anadromous	32	69
		Resident	6	
		Unknown	31	
	2017	Anadromous	1	40
		Resident	3	
		Unknown	36	

Arvitajuit	2016	Anadromous	33	76
		Resident	5	
		Unknown	38	
	2017	Anadromous	30	58
		Resident	0	
		Unknown	28	

Table 4.3 Terms (β_n) included in the logistic regression model for assignment of probable life history trajectory of juvenile Arctic Charr. Significant terms are indicated with *

Effects	Estimates	Standard error	z-value	Pr(>|z|)	
Intercept	20.2553	49215.0206	0.000	0.9997	
Growth	33.2452	14.3544	2.316	0.0206	*
Qasigiat	-72.4040	9962.3735	-0.007	0.9942	
Ikpit	-32.8946	7113.6491	-0.005	0.9963	
Arvitajuit	-75.1602	9962.3734	-0.008	0.9940	
Year 1997	47.8006	54552.9337	0.001	0.9993	
Year 1998	44.6255	58848.9039	0.001	0.9994	
Year 1999	46.7087	57903.1199	0.001	0.9994	
Year 2000	45.8976	49291.0676	0.001	0.9993	
Year 2001	46.0023	52254.4651	0.001	0.9993	
Year 2002	23.4919	48196.1530	0.000	0.9996	
Year 2003	24.1205	48196.1531	0.001	0.9996	
Year 2004	20.6437	48196.1531	0.000	0.9997	
Year 2005	22.8764	48196.1531	0.000	0.9996	
Year 2006	2.1584	48515.6571	0.000	1.0000	
Year 2007	3.2015	48796.8353	0.000	0.9999	
Year 2008	0.5032	54672.4431	0.000	1.0000	
Year 2009	- 33.9700	48957.2994	-0.001	0.9994	
Year 2010	-40.0613	68515.5618	-0.001	0.9995	
Year 2011	-49.0902	49215.0186	-0.001	0.9992	
Year 2012	-48.5821	49215.0186	-0.001	0.9992	
Year 2013	-48.5026	49215.0186	-0.001	0.9992	

Proportion of summer growth in the first year of life differed between resident and anadromous individuals (p=0.0206; Table 4.3). This significant difference in proportional summer growth allowed us to use the logistic regression model to assign probable life history to individuals that had previously not been identified as either resident or anadromous. From the 243 unknown individuals 220 were identified as anadromous and 23 were identified as residents.

The average proportional summer growth of the newly classified anadromous and resident samples was 0.9041 and 0.8139, respectively (Fig 4.3).

Discussion

The results of this chapter indicate that there is a significantly different pattern of seasonal growth between resident and anadromous Arctic Charr. The pattern is discernible in the first year of growth. Resident individuals demonstrate relatively more consistency in their growth rate throughout the year while anadromous individual show greater seasonality in their annual growth pattern. This is consistent with examples in Arctic Charr literature (Forseth et al.1994, Rikardsen and Elliott 2000).

The findings of this study can have interesting applications in fisheries science. When performing ecological modeling of populations in fisheries it is often important to have a sample representing each life stage of the fish population in question. When studying Arctic Charr populations, it is important to consider their divergent life histories. However, it is not possible to identify the life history trajectory of individuals in the juvenile stage (Balon 1980, Loewen et al. 2010). This limits the use of the juvenile category in ecological modelling for Arctic Charr. This study proposes a means by which to assign a life history to individuals that could previously not be identified as belonging to resident or anadromous Arctic Charr morphs.

Studies applying the back-calculation technique on anadromous and resident Arctic Charr or other salmonids could use the method proposed in this chapter to model the growth of both life histories with classified juvenile samples. A study examining growth in anadromous and resident Arctic Charr discarded all their juvenile samples as they could not be assigned a life history and used only mature individuals (Loewen et al. 2010). Using an analysis of the seasonal growth pattern of juvenile samples could provide an alternative to visual classification and

consequently improve studies examining divergent patterns in anadromous and resident Arctic Charr.

If one chooses to assign a probable life history trajectory to a juvenile Arctic Charr, they must however be aware that the logistic regression method used here does not assign an absolute grouping but assigns a probability that an individual belongs to resident or anadromous groupings. Logistic regression is indeed not a classifier, but, when setting a threshold it can be used as a way to assign probable groupings to individuals. In logistic regression, each sample is assigned a probability of belonging in either group which ranges between zero and one based on the supplied values of the fixed terms. With probability values near the extremes (i.e. close to zero or to one), one can be confident in the grouping of samples. The challenge arises when an individual is assigned an intermediate value between zero and one, as the probability of it belonging to either group is low. When interpreting results that have been classified using logistic regression for grouping resident and anadromous Arctic Charr, one must remember that the classification is not absolute but rather probable and to interpret results accordingly.

Growth rate in fishes is highly correlated to metabolism as larger bodies are more energetically costly in maintenance, swimming, and feeding (Elliott 1976, Forseth et al. 1994, Finstad et al. 2006). The presence of divergent seasonal growth patterns in the first year of growth in morphs of Arctic Charr suggests that metabolic differences exist between resident and anadromous individuals early on in life. Divergent growth patterns in the first year of growth were seen in two morphs of Arctic Charr with an omnivorous morph showing greater seasonality in growth rate relative to a benthivorous morph (Knudsen et al. 2015). Additionally, feeding behaviour was noticed to differ between morphs with the omnivorous morph having a period of fasting over the winter period where the benthivorous individuals did not show a period of

fasting (Knudsen et al. 2015). These findings indicate that indeed, metabolism within the first year may contribute to life history trajectory in Arctic Charr.

In addition to exhibiting different growth and feeding patterns, Arctic Charr individuals with divergent life histories demonstrate different energy storage and lipid metabolism (Rikardsen and Elliott 2000, Finstad et al. 2003). Anadromous individuals show much seasonality in their lipid metabolism and body condition with a decline in lipid reserves and body condition occurring over the period of winter fast (Boivin and Power, 1989). A population of Arctic Charr parr with a higher lipid content had an earlier maturation, a lower degree of anadromy, and a slower growth rate (Rikardsen and Elliott 2000).

A relationship between sexual maturation and lipid dynamics exists in Arctic Charr. A study examining the relationship between energy gain, which is dependent on body size, and maturation determined that small and large individuals matured once they were near the maximum energy gain of their size class (Finstad et al. 2006). This same study also found that immature Arctic Charr of the small size class that were near the maximum energy gain had low lipid reserves and a high growth rate. They propose that those individuals were initiating a niche shift from feeding on small invertebrate prey to a more profitable cannibalistic diet (Finstad et al. 2006).

Future work in life history trajectory and plasticity in Arctic Charr should consider early metabolism and factors that can influence the metabolism in Arctic Charr. For instance, hormones such as ghrelin and leptin that are known to influence the metabolism of lipid in mammals (Denver et al. 2011, Sato et al. 2012) have been found in fishes (Kurokawa et al. 2005, Unniapan and Peter 2005). For hibernating mammals who demonstrate seasonality in their feeding behaviour and their metabolism, ghrelin is essential in the regulation of feeding before

hibernation to increase fat deposition, while leptin is related to the catabolism of the lipid reserves over the winter hibernation (Nieminen et al. 2002, Healy et al. 2010, Gardi et al. 2011). Leptin and ghrelin are determined to have similar effects in the regulation of feeding and lipid metabolism in fishes (Volkoff et al. 2003, Riley et al. 2005, Unniapan and Peter 2005, Murashita et al. 2008, 2011, Kling et al. 2009) as seen in mammals. Patterns in leptin levels have been observed salmonids in relationship to seasonality (Trombley et al. 2012) and fasting (Johansson et al. 2016). Ultimately, there is great potential to make interesting discoveries if one chooses to study life history trajectory of Arctic Charr.

In conclusion, I have determined that it is possible to assign probable life history for juvenile Arctic Charr using growth pattern in the first year which was previously not possible (Balon 1980, Loewen et al. 2010). Awareness that the method used here assigns a probability of anadromy and not absolute classification is critical if one is to use this method to classify juvenile Arctic Charr as resident or anadromous. Finally, the results of this study suggest that the divergence in life history trajectory happens early on in the development of Arctic Charr. A possible avenue examining lipid dynamics in Arctic Charr in relation to life history trajectory is discussed. Studying life history trajectory in Arctic Charr has the potential to elucidate what is known as the 'charr problem' and even possibly the process of ecological speciation.

Figures
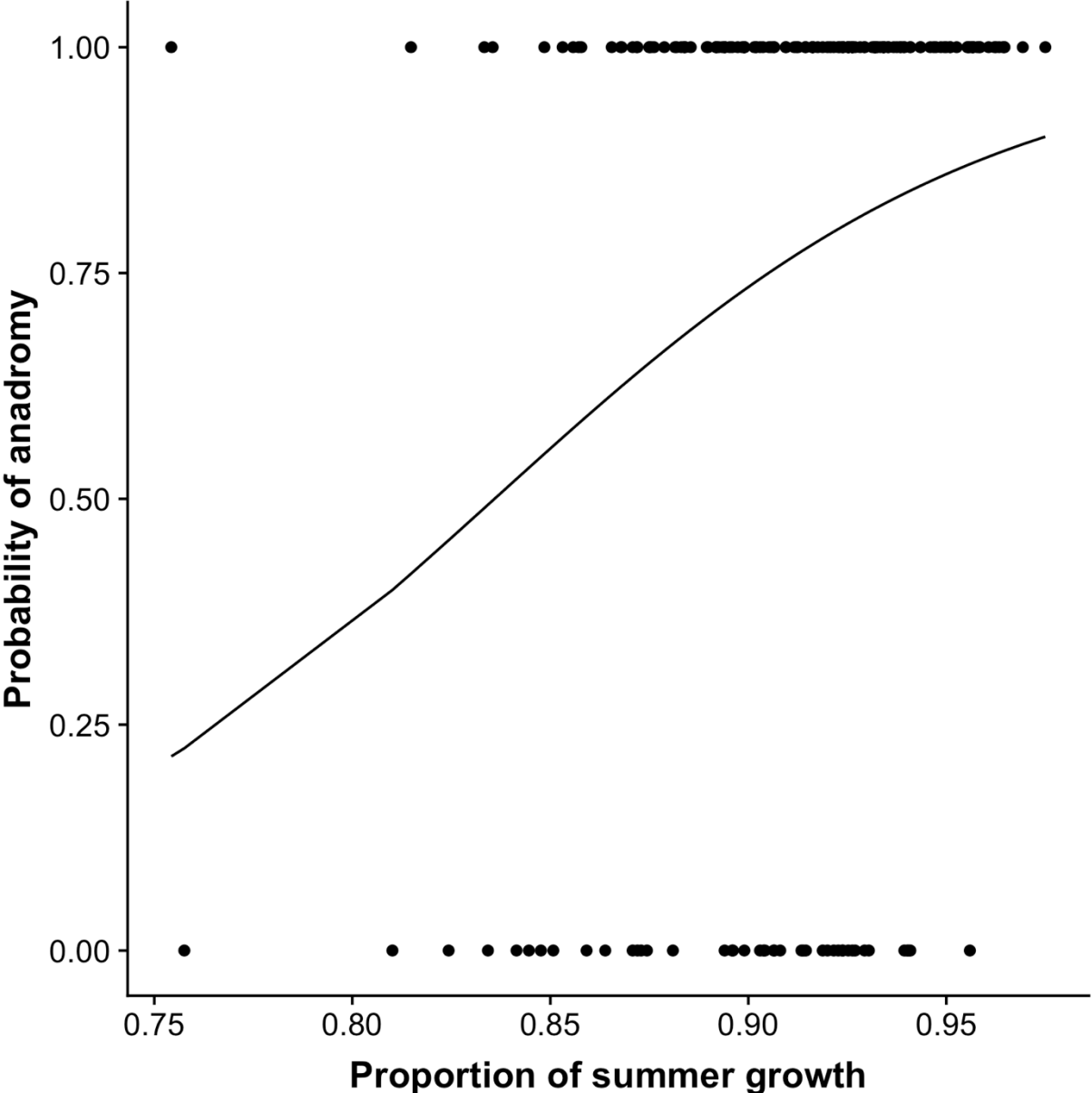
Fig. 4.1 Fitted values (solid line) from the logistic model of the proportional summer growth data in the first year of growth in anadromous and resident Arctic Charr (*Salvelinus alpinus* L.). The dots are the observed values with 1 being anadromous (n= 140) and 0 resident (n=44)
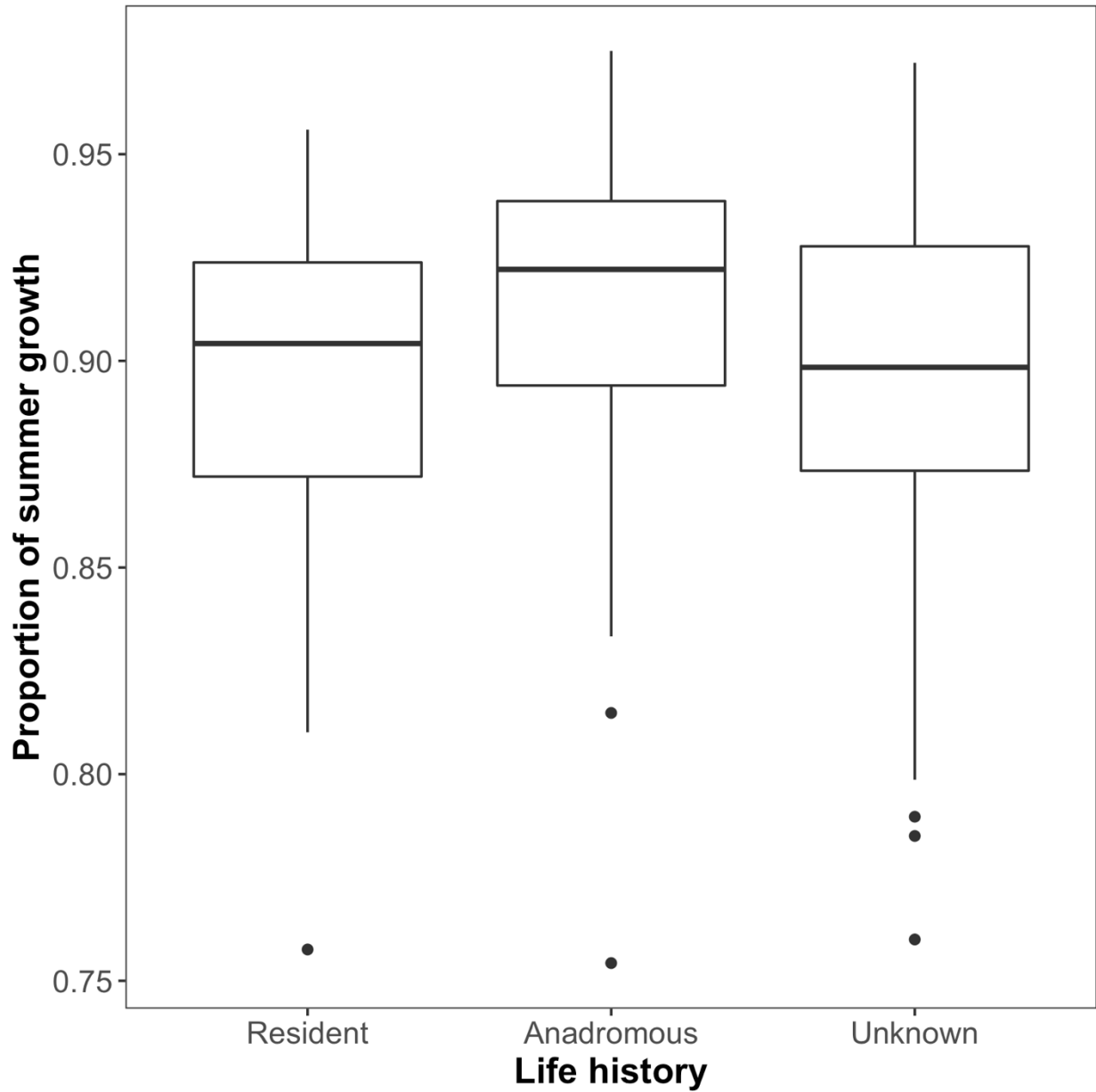
Fig. 4.2 Boxplot of proportion of summer growth of all data used to fit and test the logistic regression model and used in the classification of Arctic Charr (*Salvelinus alpinus* L.) of unknown life history types, edge of boxes represents the first and third quartiles and the whiskers represent 1.5 of the interquartile range
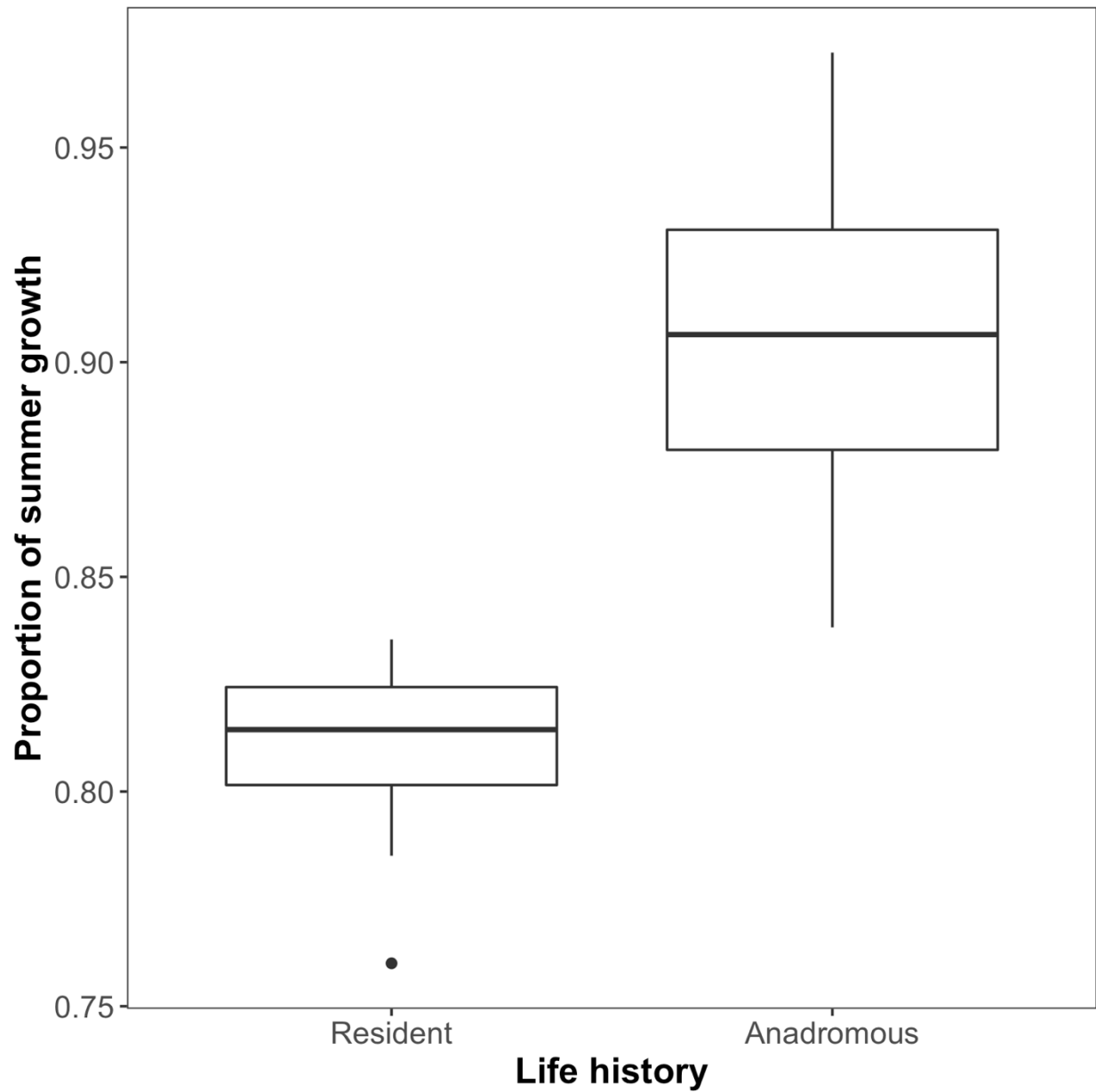
Fig. 4.3 Boxplot of proportion of summer growth Arctic Charr (*Salvelinus alpinus* L.) individuals of an unknown life history assigned a probable resident (n=23) or anadromous (n=220) life history type using the logistic regression model, edge of boxes represents the first and third quartiles and the whiskers represent 1.5 of the interquartile range

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Chapter 5 – Summary and general conclusions

Arctic Charr is a species of great interest to biologists who study the evolution of life history trajectories owing to the species' extreme phenotypic plasticity exhibited throughout their distribution (Nordeng 1983, Jonsson and Jonsson 2001, Klemetsen 2010). With access to the sea, Arctic Charr generally exhibit a minimum of two migratory types (Johnson 1980, Dempson and Kristofferson 1987, Loewen et al. 2010). The two common migratory types of Arctic Charr include a sea-going anadromous morph and a non-migratory freshwater resident morph (Johnson 1980, Dempson and Kristofferson, Loewen et al. 2009). Anadromous Arctic Charr will exploit the marine environment during the summer where feeding and growth are increased relative to the winter period in freshwater where anadromous individuals fast and enter a state of quiescence (Johnson 1980, Rikardsen et al. 2000). It is suggested that non-migratory individuals that remain in the freshwater habitat show less extreme seasonality in their growth and hypothesised that feeding is more consistent throughout the year relative to their anadromous conspecifics (Rikardsen et al. 2000). The purpose of this study was to examine growth patterns in Arctic Charr otoliths from four populations of Cumberland Sound and to relate otolith growth patterns to life history trajectory.

Otoliths, calcified structure exhibiting seasonal growth rings, were used to estimate life-long growth patterns of Arctic Charr. Incremental growth patterns in otoliths were assumed to be representative of somatic growth patterns in Arctic Charr. A new semi-automated method of measuring otolith incremental width was developed to estimate seasonal growth patterns in otoliths. It was determined that the results from the semi-automated method were as reliable as the traditional visual increment measurement method. The seasonal otolith incremental widths measurement method was then used to collect data for the remainder of the thesis. We assume

that the relative pattern of otolith growth and somatic growth will be related as both growth metrics are influenced by metabolism. A future study verifying the relationship between seasonal somatic growth and otolith growth is still required to validate this method.

Growth patterns in anadromous and resident Arctic Charr were assessed on an annual and seasonal scale. An increase in annual growth has occurred for anadromous and resident Arctic Charr spanning the years 1990 and 2015. This increase is suspected to be related to the increase in temperature, growing season, and other variables symptomatic of climate change, however this was not tested explicitly in this study. Anadromous Arctic Charr exhibited greater annual growth throughout their life relative to their non-anadromous conspecifics. This suggests that Arctic Charr populations of the Eastern Canadian Arctic may be sensitive to climate change. Arctic Charr is relied upon for subsistence by Inuit. It is also fished commercially in many communities across the Canadian Arctic. The effect of climate change on populations of Arctic Charr must be studies in greater depths to ensure the persistence of the species. This study further highlights the importance of using a cautious and conservative approach when modelling and estimating harvest rules for Arctic Charr fisheries.

Seasonal growth patterns were different between resident and anadromous individuals. Residents had a relatively more consistent growth pattern throughout a year while anadromous individuals exhibited a greater proportion of summer growth within a year. Patterns were consistent with life history at all ages. This suggests that life history trajectory is indeed set very early on in the life of Arctic Charr highlighting that the field of study of Arctic Charr life history trajectory should investigate early ontogeny.

Growth in fishes has a strong correlation with feeding. The divergence of seasonal patterns of growth between resident and anadromous morphs is easily explained by the

seasonality in the feeding. Anadromous Arctic Charr show seasonality in their feeding with hyperphagia in the summer and a voluntary fast in the winter (Knudsen et al. 2015). Their growth is therefore greater in summer relative to the winter. Resident individuals show greater consistency in their growth and are hypothesized to have a more consistent feeding pattern relative to anadromous individuals. Metabolism links the growth and feeding of individuals. Further work examining differences in the metabolism of anadromous and resident individuals are needed to further our understanding of life history trajectory. For example, timing of first exogenous feeding can occur while juveniles are still extracting nutrients from their yolk sac or it can happen after yolk sac reserves have been depleted (Wallace and Aasjord 1984). Growth in Arctic Charr is known to be influenced by the relationship between the state of the yolk sac and timing of exogenous feeding (Wallace and Aasjord 1984). Individuals feeding only once the yolk sac was exhausted had the lowest growth compared to individuals that started feeding while still extracting nutrients from the yolk sac (Wallace and Aasjord 1984). There is still much to discover when it comes to life history trajectory in Arctic Charr.

Estimates of various population parameters require samples of all age classes. Different morphs of Arctic Charr should be managed as different species (Jonsson and Jonsson 2001). For Arctic Charr it is not possible to segregate anadromous and resident individuals at the juvenile stage (Balon 1980, Loewen et al. 2010). I demonstrate that it is possible to assign a probable life history trajectory to juveniles using seasonal growth pattern in the first year of growth. The significance of the ability to be able to discriminate between anadromous and resident juveniles will provide additional information for population modelling. For example, the relative abundance of anadromous and resident individuals is variable among populations (Johnson 1980, Svenning et al. 1992). Without estimates on the proportion of resident and anadromous

individuals within the juvenile age class, it is then difficult to estimate further parameters for both morphs. Mortality rate could very likely differ between resident and anadromous individuals at early ages owing to their divergence in size and thus vulnerability to predation. Without a baseline proportion of juvenile anadromous and resident individuals estimating this mortality rate relies on many assumptions. Classifying juveniles using seasonal patterns of growth offers a solution to this current gap in Arctic Charr fisheries sciences.

Finally, this thesis is focused on growth patterns in anadromous and resident Arctic Charr. Divergences in the growth patterns of the sympatric morphs of Arctic Charr are highlighted and their potential implications are discussed in relation to the 'charr problem'. Studying early development and divergence in Arctic Charr seems a promising avenue to get at the root of the 'charr problem'. A greater understanding of ecological divergence in Arctic Charr morphs may also help with our understanding of the overall process of speciation.

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