The Effects of Climate Change on Growth and Thermal Habitat Use of Cumberland Sound Arctic Charr (*Salvelinus alpinus*)

By

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Abstract

The Arctic is warming at an unprecedented rate and experiencing longer growing seasons, greater rainfall, and less snowfall. Cold-adapted ectotherms, such as Arctic charr, *Salvelinus alpinus*, are likely to experience growth changes. Anadromous Arctic charr (charr, hereafter) are of great importance for northern communities, providing income from commercial fisheries and food security from subsistence harvest. While warming may initially increase the growth of charr, temperatures exceeding the optimum for growth can lead to metabolic stress, slowed growth, and higher mortality. This thesis examines whether annual growth and thermal habitat use have changed in three charr stocks from Cumberland Sound, Nunavut, with climate change between 1984 and 2013. In Chapter 2, I examined age-specific growth using otolith radius and annulus lengths. Trend analyses indicated significant growth increases in ages 1-6 and 8. Mixed modelling revealed growing degree days (GDD=°C*Day, base 4°C) positively influenced growth, while annual precipitation (mm) had an overall negative effect. Variation in growth between stocks was most pronounced in ages 1-6, coinciding with the pre-migratory period. These results suggest that charr experienced the most growth increases prior to their first migrations. Chapter 3 explored whether growth changes resulted from longer growing seasons or warmer conditions supporting higher metabolic rates. I used otolith-derived $\delta^{18}O$ to estimate summer experienced temperatures between 1987 and 2013. Using a mixed model, I found no significant relationships between summer experienced temperatures and the climate variables (GDD and annual precipitation). Experienced temperatures decreased with age in each stock, indicating the presence of distinct thermal habitats and thus, thermal stratification. To control for behavioural thermoregulation, I ran a linear regression to investigate changes in experienced temperatures in ovo from 1987 to 2008. Unexpectedly, the results suggest experienced temperatures in ovo have decreased over the time period. However, it is hypothesized that the cooler temperatures are likely a reflection of changing isotopic compositions of the study lakes in response to climate change. Overall, the results suggests that increases in growth are likely driven by longer growing seasons rather than rising temperatures, as evidence of thermal stratification and a disconnect between experienced temperatures and climate variables was found.

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1. General Introduction

1.1 Climate Change Impacts

As of 2020, average global surface temperatures have increased by ~1.1°C since the late 1800s, due to industrialization and its associated greenhouse gas emissions (IPCC, 2023). However, the Arctic has seen nearly 3 times the global rate of warming (AMAP, 2021). As a result, freeze-ups on rivers occur later and ice melts earlier (AMAP, 2021). Similar trends are seen in the extent of sea ice, in addition to it becoming thinner (AMAP, 2021). This trend has been exacerbated by the increase in rainfall from October to May and a decline in snow cover (AMAP, 2021).

The Intergovernmental Panel on Climate Change (IPCC, 2023) states that observed changes in ecosystem structure in Arctic freshwater and ocean ecosystems are medium and high to very high, respectively. This may be attributed to comparatively more components in the Arctic marine, rather than the Arctic freshwater ecosystems (IPCC, 2023). In addition, many species that make up marine ecosystems have already been impacted by climate change as they rely on the presence of sea ice. These species include marine mammals, polar bears (*Ursus maritimus*), fish, and birds (Michel et al., 2012). However, these impacts do not always manifest negatively. While polar bear numbers may suffer from sea ice loss, increased primary production due to warmer temperatures may benefit marine fishes, demonstrating the array of impacts within the same ecosystem.

1.2 Ectotherms and Their Environment

Unlike endotherms, ectotherms rely on the temperature of their environment to regulate physiological rates. In general, warmer temperatures support faster metabolic rates, allowing for increased growth, as long as energy intake persists (Beuvard et al., 2022; Kristensen et al., 2006;

Larsson & Berglund, 2005). Ectotherms can alter their physiology to some extent to cope with changing temperatures (Seebacher et al., 2015). However, this ability diminishes with accelerated warming (Seebacher et al., 2015).

Since growth is a metabolic process and the metabolism of ectotherms is highly dependent on environmental conditions, energetic trade-offs are an important factor to consider in climate change. In energetic trade-off models for fish, it is assumed that a fixed amount of energy is allocated between metabolic processes such as growth, reproduction, and maintenance (Rosenfeld et al., 2020). However, that allocation of energy changes with environmental conditions. Therefore, when temperatures become too high (i.e., above optimum temperature), more energy may be diverted from growth and allocated towards maintenance in response to cardiovascular stress and other aspects of active metabolism (Gilbert et al., 2020). Numerous studies have found that the growth rate of fish will increase with temperature up to a critical point, where their physiology (e.g., cardiac performance) can no longer support their increased metabolic needs (e.g., Das et al., 2005; Gilbert et al., 2020; Khieokhajonkhet et al., 2022).

However, fish have options to avoid warming conditions. Behavioural thermoregulation allows ectotherms to maintain their body temperature within an optimum range (Barton et al., 2014). Fish can achieve this via horizontal (range shifts) and vertical movements (deepening). Range shifts have been well documented in many species, shifting poleward with progressive warming (e.g., Hastings et al., 2020; Melbourne-Thomas et al., 2022; Rose, 2005). Ramalho et al. (2023) found that ectotherms, especially, responded to climate change via range shifts compared to endotherms. Deepening, or seeking thermal refuge at depth, has also been documented with climate warming (Chaikin & Belmaker, 2023; Dulvy et al., 2008; Iglesias et al., 2024). Chaikin and Belmaker (2023) noted that cold-water species were more likely to move to greater depths than warm-water species in response to climate change. This behaviour has been described by Dulvy et al. (2008) to be analogous to the poleward migrations of terrestrial organisms. That said, declining abundance has been associated with both range shifts and deepening, suggesting the strategies are insufficient in mitigating the negative impacts of climate change on their own (Chaikin et al., 2024; Chaikin & Belmaker, 2023).

1.3 Arctic Charr as a Model Species

Arctic charr (*Salvelinus alpinus*) may be the best model species for investigating the effects climate change will have on fish and other ectothermic species. In the rapidly warming Arctic, Arctic charr is typically the only fish in freshwater systems (Skulason & Smith, 1995). This makes them an excellent species for investigating climate change impacts in their natural environment, without the added complexity of interspecific competition. Arctic charr is generally described as a cold-adapted species, with an upper thermal limit of 21°C. Due to their circumpolar distribution, there is no opportunity for poleward range shifts, as is the case for species at lower latitudes. These constraints restrict Arctic charr to their current habitat range, forcing the species to endure changes in their environment with limited ability to adapt to climate change.

With that said, Arctic charr is a highly diverse species. Since it is typically the sole species in the freshwater system, it is thought to differentiate into ecotypes to take advantage of the different ecological niches (Skulason & Smith, 1995). There are three ecotypes in Canada: anadromous, resident, and landlocked (Johnson, 1980). As the name implies, landlocked populations occupy lakes with impassable barriers to the marine environment. Anadromous and resident, on the other hand, occupy freshwater environments with access to the sea. However, while anadromous individuals reach much larger sizes and migrate to the sea to exploit marine feeding opportunities during the summer, residents remain small and live exclusively in the freshwater environment. While these two ecotypes are not genetically distinct, it is unknown why this differentiation in life history occurs, but is thought to be attributed to phenotypic plasticity (Loewen et al., 2010; Moore et al., 2014). A large sex bias toward resident males has been observed (Loewen et al., 2010; Moore et al., 2014). One possible explanation for this bias is that anadromy evolved to enable females to take advantage of the abundant food resources at sea, thereby supporting increased egg production (Grainger, 1953; Loewen et al., 2010; Moore et al., 2014). This strategy may also be linked to alternative mating tactics, where resident males remain small, as reproduction is less costly for them. By staying small, they can sneak in and fertilize the eggs of anadromous females (Brattli et al., 2018; Moore et al., 2014; Sigurjónsdóttir & Gunnarsson, 1989). With this extensive life history variation, different ecotypes will probably respond to climate change differently, making the species fascinating and complex to study.

Beyond the research potential, Arctic charr have long been a species of commercial, subsistence, and more recently, recreational importance across northern Canada (Babaluk et al., 2010; Roux et al., 2011). For Nunavut residents, Arctic charr, along with other country foods, is an essential part of food security (Kenny et al., 2018) since market foods are so expensive (Beaumier et al., 2015; Myers et al., 2005). For this reason, it is important to understand how climate change is affecting this species to preserve food security and economic benefits.

1.4 Otoliths as Lifelong Records

Otoliths are calcium carbonate structures found in the inner ear of bony fish (Degens et al., 1969). Three pairs of otoliths exist: the asteriscus, lapillus, and sagitta (Popper & Lu, 2000). The sagitta (referred to as otolith hereafter) is typically larger than the other two, making it the most commonly used pair of otoliths for research (Radtke & Shafer, 1992). Otoliths have been used to estimate age since as early as 1899 when Reibisch published on the topic (Jackson, 2007).

The process of otolith development also allows them to be used as an indicator of growth and environmental conditions. Calcium carbonate is continuously laid down on the surface of the otolith as ions become available in the endolymph from food items via blood plasma (Campana & Neilson, 1985; Friedrich, 2009). In periods of high feeding, layers become thicker and appear more opaque; this is the summer band. Less feeding occurs over the winter, resulting in a thin and translucent winter band. The difference in opacity between summer and winter bands is attributed to varying mineral composition, crystalline structure, and frequency of deposition (Wright et al., 2002). These annuli, or annual growth rings, can be compared to tree rings and are proportionate to fish growth (Vigliola & Meekan, 2009). The measurement of consecutive annuli, or back-calculation of fish growth, allows for an expanded dataset of length-at-age measurements across each individual's lifetime. For example, the dataset used in the current study was derived from only 594 otoliths but includes more than 8000 length-at-age estimates. Otoliths are considered the preferred structure for estimating age and growth as they are metabolically inert and do not undergo resorption (Campana & Neilson, 1985; Campana & Thorrold, 2001).

Various trace elements and isotopes deposited onto the calcium carbonate structure of otoliths can be measured to infer changes in life history and environmental conditions across a lifetime (Campana, 1999; Campana & Neilson, 1985). Otolith microchemistry has been used to infer anadromous migrations and habitat use (Franco et al., 2019; Lin et al., 2011; Tran et al., 2019), experienced temperatures (Higuchi et al., 2019; Willmes et al., 2019), stock differentiation (Campana, 1999; Secor & Zdanowicz, 1998), and natal origins (Carlson et al., 2016; Stewart et al., 2021), among other life history questions. Oxygen isotopes are used to infer experienced temperatures, providing important context to changes in growth (i.e., metabolic changes). Oxygen isotopes and temperature have an inverse relationship, meaning higher temperatures correspond to lower oxygen isotope values (Elsdon & Gillanders, 2002). However, salinity also influences oxygen isotopes, resulting in higher oxygen isotope values with increasing salinity (Elsdon & Gillanders, 2002).

1.5 Data Chapters

My thesis aims to describe the effects of climate change on the growth and thermal habitat use of Arctic charr. In Chapter 2, I investigated changes to the growth of Arctic charr in response to climate change, using age-specific otolith annulus lengths (ages 2-10) and age-1 radius lengths, and atmospheric climate variables. Using trend analyses, I identified the nature of age-specific growth across a period spanning from 1984 to 2013. I ran mixed-effect models to describe age-specific growth relative to climate change (annual precipitation and growing degree days) and location. The results of Chapter 2 indicated significant changes in growth relative to climate variables. Since fish can move within their heterogeneous environment, it was not possible to determine whether changes to growth occurred due to increased feeding opportunities resulting from longer growing seasons, or altered metabolic rates from changes to the thermal habitat. Chapter 3 aims to clarify this question by investigating changes to summer thermal habitat use in response to climate change, using otolith-estimated experienced temperatures. Temperatures were estimated using otolith $\delta^{18}O$ sampled from summer growth bands with a species-specific fractionation equation (Godiksen et al., 2010). Using a generalized linear mixed model, I identified the relationship between climate variables (GDD and annual precipitation) and thermal habitat use across ages and locations in the freshwater environment. With a simple linear regression on nucleus experienced temperatures, I identified how experienced temperatures have changed in the littoral zone during egg development from 1987 to 2008. In Chapter 4, I brought the findings of both chapters together, identifying knowledge gaps and future research priorities.

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2. The Influence of Climate Change on the Growth of Arctic Charr

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Author Contributions: The topic of this chapter was conceptualized with the help of R. Tallman and M. Docker. I developed the methodology, analyzed the data, interpreted the results, created the visualizations and wrote this chapter. R. Tallman and M. Docker aided in the final revisions.

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Abstract

As a result of climate change, both annual precipitation and annual mean temperature have increased substantially in the Arctic. As a cold-adapted ectotherm, Arctic charr (*Salvelinus alpinus*) is likely to be impacted by such changes. Initial warming may increase the growth of Arctic charr. In the longer term, temperatures exceeding its optimum are expected to suppress growth and induce physiological stress such as arrhythmia. I assessed Arctic charr growth from 1984 to 2013 in relation to climate change in three stocks around Cumberland Sound using back-calculation techniques to estimate otolith radius and annulus lengths. The findings of the mixed effect models suggest that increasing growing degree days (GDD, base 4°C) resulted in greater growth, while greater annual precipitation (mm) led to less growth. Overall, the influence of GDD on growth decreased with increasing age, likely reflecting shallow habitat use of younger age classes. Annual precipitation, however, had a greater influence on the growth of ages 2 and 6-10, with negligible effects on ages 3-5. The variable effect of annual precipitation across ages is thought to be linked to the insulating properties of snow, which prolong ice cover, insulating shallow juvenile habitats from warming and restricting marine migration in older ages. Variation in growth between lakes was only found in ages 1-6, suggesting growth was most affected prior to the first marine migration while occupying the freshwater environment. Overall, the results suggest Arctic charr in Cumberland Sound have indeed experienced changes in growth with climate change.

2.1 Introduction

Arctic charr (*Salvelinus alpinus*), charr hereafter, is a highly diverse species with a circumpolar distribution (Weinstein et al., 2024). It is a slow-growing and relatively long-lived species, due to its high latitude range, where average water temperatures are low and the growing season is short (Grainger, 1953; Johnson, 1980). Anadromous individuals migrate to sea during the summer months to feed, returning to freshwater lakes in the fall to spawn and overwinter (Grainger, 1953). Much of their growth occurs during this intense feeding period between ice-off and spawning (Grainger, 1953). After spawning, anadromous charr overwinter in freshwater lakes due to poor tolerance of the sub-zero marine temperatures, where they are thought to remain fairly dormant to conserve energy (Finstad et al., 1989; Mulder et al., 2018b; Wandsvik & Jobling, 1982).

Anadromous charr reach a greater maximum length than their resident counterparts (Loewen et al., 2010; Tallman et al., 1996; Young et al., 2021), likely resulting from increased food availability at sea (Näslund, 1990). As a result, anadromous charr are of commercial and subsistence importance across northern Canada (Babaluk et al., 2010; Roux et al., 2011). These fisheries are an essential ecosystem service in terms of economy, culture, and food security for Inuit and northern communities across Canada (Falardeau et al., 2022; Kenny et al., 2018; Kuhnleini & Soueida, 1992; Myers et al., 2005).

Pangnirtung, Nunavut, is one such community that has long relied on charr stocks in the Cumberland Sound region for subsistence. The hamlet is located on Baffin Island on the North side of Cumberland Sound. The average annual temperature and precipitation in Pangnirtung have both increased since 1950. Temperature and precipitation are also projected to continue increasing to 2095 for both low and high carbon climate scenarios (RCP 4.5 and 8.5, respectively) according to climate modelling in the Climate Atlas of Canada (2019). The high carbon scenario (RCP 8.5) can be considered the ‘business as usual’ outcome of climate change, where measures are not taken to decrease carbon emissions (IPCC, 2023). The low carbon scenario (RCP 4.5) in this case is referred to as an intermediate climate change scenario according to the IPCC (2023), where some measures are being taken to reduce carbon emissions.

Annual precipitation and air temperature have both been found to affect charr growth (Hesthagen et al., 2004; Kristensen et al., 2006; Murdoch et al., 2015). The most notable of the two factors is temperature, whether it be of air or water, as the Arctic continues to warm at an accelerated rate (AMAP, 2021). Much of the research on climate and growth in charr focuses on identifying thermal limits and optimum temperatures for growth (e.g., Beuvard et al., 2022; Gilbert et al., 2020; Lyytikäinen et al., 2002). An upper thermal limit of 21°C is consistently documented in the literature and characterized by reduced growth, increased mortality and arrhythmia (Beuvard et al., 2022; Gilbert et al., 2020; Larsson & Berglund, 2005). However, optimum temperatures for growth are not always consistent across the literature, possibly due to differing methods (i.e., laboratory vs. field-based) or varying thermal tolerance between populations. The optimum temperature for growth has been reported anywhere from 10.3 to 16.3°C (Beuvard et al., 2022; Larsson & Berglund, 2005; Lyytikäinen et al., 2002). These studies suggest that the growth of charr may increase with rising temperatures, until an optimum temperature is reached, after which point, the growth rate is expected to decline. Despite a handful of experimental studies, there are limited studies investigating the relationships between climate and growth in natural settings. This is an important factor, as wild charr live in complex, heterogenous systems and can behaviourally thermoregulate by moving to different thermal habitats. In addition, the application of these thermal limits and optimums for inferring climate-driven changes to growth is difficult without long-term water temperature datasets. Air temperature records, on the other hand, are widely available for much of the planet, including remote regions of the Arctic. Based on the climate changes already seen in the Arctic, charr may have already been experiencing impacts. If not, it is probable in the future as climate change continues.

A commonly used method for estimating age-specific annual growth of fish is measuring annual growth bands, or annuli, of otoliths. This method is based upon the assumption of a proportionate relationship between fork length and otolith length in charr (Svenning et al., 1992). Otoliths are calcified structures found in the inner ear of bony fishes, aiding in balance and orientation (Campana, 1999; Pannella, 1971). One annulus is comprised of a translucent winter band and an opaque summer band, together representing 1 year of growth. For that reason, measurements from the nucleus to the end of each annulus can be used as a proxy for length-at-age and the measurements of individual annuli a proxy for annual growth.

The objective of this study is to investigate the growth of Cumberland Sound Arctic Charr relative to climate change between 1984 and 2013 by (1) determining which climatic factors influence growth during this period, and (2) determining the nature of variation in growth between lakes and age classes. I predicted that (1) temperature and precipitation would have significant positive influences on growth, and (2) growth has increased over time in all three lakes, with differences in growth between lakes attributed to early life habitat variation.

2.2 Materials & Methods

2.2.1 Study Area

Cumberland Sound is located on the southeastern coast of Baffin Island, Nunavut. The Sound is 300 km long and averages 65 km wide (Roux et al., 2019; Tallman & Marcoux, 2021). Its water originates from both Arctic and North Atlantic water masses (McMeans et al., 2012). Depth ranges from 200 m to 1000 m (Tallman & Marcoux, 2021). The steep sides of the Sound (> 2125 m) are lined with deep fiords, connecting the marine environment to freshwater river and lake systems (Roux et al., 2019; Tallman & Marcoux, 2021). Three of these lakes, located along the south side of Cumberland Sound, were selected for this study: Kipisa (PG004), Iqaluit (PG001), and Qasigiat (PG015; Fig. 2.1). DFO waterbody codes are included in parentheses for consistency across the literature, since common lake names vary in the region. Qasigiat Lake (64°62′N, 66°31′W) is unusual in that it has a very short river connecting the marine environment to the lake. At high tide, there is virtually no separation between the two environments, leading to an inflow of saltwater into the lake (T. Loewen, personal communication, 29 November 2023). Iqaluit Lake (65°2’N, 67°7’W) is a large, deep lake, connected to the marine environment via a 1.3-km-long river (Martin et al., 2023). Kipisa Lake (66°52’N, 67°85’W) is the largest of the three lakes in terms of surface area and has the longest river (approximately 6.4 km) connecting the lake to the marine environment.

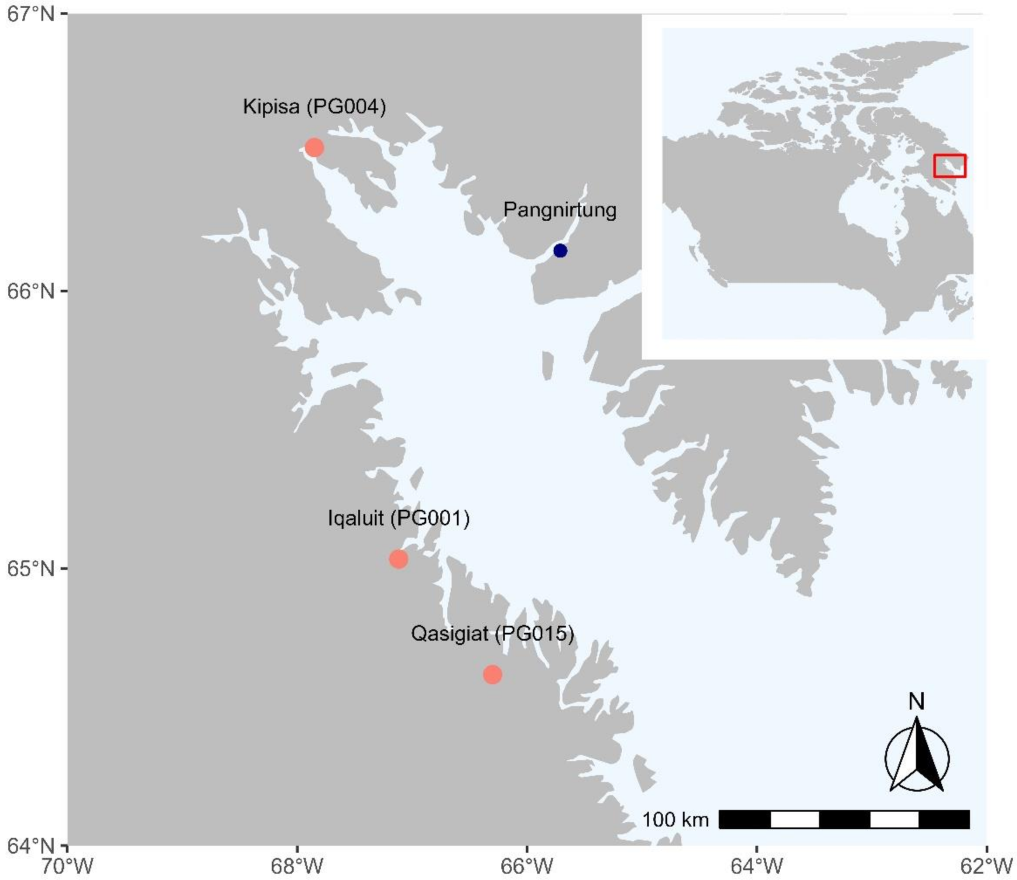

Figure 2.1. Map of Cumberland Sound, showing the nearest community, Pangnirtung, and the three study lakes: Kipisa (PG004), Iqaluit (PG001), and Qasigiat (PG015). The inset map shows the location of Cumberland Sound in Canada.

2.2.2 Data Collection

2.2.2.1 Biological and Otolith Growth Data

Sectioned otoliths were used to examine annual growth over individual lifespans. Archived otoliths from 594 individuals were selected from the three lakes in two different sample years to create a time series of growth radii and annuli (Kipisa – 2002 & 2011; Iqaluit – 2001 & 2013; Qasigiat – 2003 & 2011). These otoliths were collected as part of stock assessment initiatives.

All fish were caught in gill nets of various mesh sizes. For Iqaluit 2001 and Kipisa 2002, mesh sizes of 139.7-mm were used. In Qasigiat 2003, a combination of 139.7-mm mesh and multi-mesh (38-120 mm) nets were used. In 2011, Qasigiat was sampled with 38.1-mm mesh and multi mesh nets. The remainder of the sampling (Kipisa 2011 and Iqaluit 2013) was done using multi-mesh nets. Sampling occurred in freshwater at Iqaluit Lake in 2013 and Qasigiat in 2003 and 2011, when anadromous charr had returned to the lake for spawning and overwintering. Marine sampling took place at Iqaluit Lake in 2001 and Kipisa in 2002 and 2011, during marine residency. Fish were dissected on-site to record sex, maturity, fork length, and weight. At this time, sagittal otoliths were collected for age estimation.

When left and right otoliths were available, both were examined in a shallow dish of water under a Leica M125 microscope at 10x magnification for initial screening of otolith quality. Otoliths were rejected when crystallization was observed. The otoliths in the best condition or with a flat or wide peak on the dorsal lobe were selected for embedding. Flat or wide peaks on the dorsal lobe are a prime location for sectioning, as there is a lower margin of error in the placement of the saw blade, resulting in better sections with easy-to-distinguish annuli. Debris was cleaned from the otolith using precision forceps under the microscope, and a lateral grind was performed to improve the clarity of the nucleus and first annulus. A two-part epoxy was mixed and poured onto a labelled strip of Parafilm® before the otolith was placed into the epoxy, sulcus side up. The epoxy was then left to cure in a fume hood for at least two days before sectioning. Once cured, the sectioning plane was marked under a microscope with a micrometre eyepiece using an Ultra Fine Tip Sharpie®. A true transverse section was generally used, although a slight anterior or posterior rotation was also used in some cases to achieve a better section. Sectioning was accomplished using a Buehler IsoMet™ Low-Speed Saw with a single saddle chuck set at a speed of 10. Two diamond wafering blades separated by a thin plastic spacer were used to cut a thin section from the embedded otolith.

Sections were then photographed using a Leica M125 microscope fitted with a Leica Flexacam C3, with a magnification that allowed the ventral lobe and nucleus to fill most of the frame. A 1-mm scale bar was added at the time of image capture to account for different levels of magnification. The RFishBC package (v0.2.4; Ogle, 2022) was used to measure the distance between each annulus (annulus lengths; mm). Measurements were taken along a transect close to the ventral edge of the sulcus, extending from the nucleus to the edge of the otolith. This region was selected for measurements due to the consistent spacing and clarity of annuli. Annulus lengths are used as a proxy for annual growth. I was not able to identify the margin between annulus 1 and the nucleus, meaning the first year of growth could not be isolated from larval growth. Subsequently, age-1 radius length (mm) will be used to assess growth in the first year.

2.2.2.2 Climate and Geographic Data

Overall, the Canadian Arctic is a data-limited region due to the high costs associated with Arctic travel and poor weather conditions, making it difficult to obtain long-term water temperature datasets. However, studies have found that climate warming directly resulted in lake warming, and data derived from air temperatures can be used as a surrogate for water temperature in freshwater systems (Johnson et al., 2014; Kirillin, 2010; Mooij et al., 2008). As such, growing degree days (GDD; °C·Day) derived from air temperature are used as a surrogate for water temperature data.

Growing degree days is a popular metric for describing growth in relation to temperature in ectotherms, such as fish (Neuheimer & Taggart, 2007). The Climate Atlas of Canada (2019) describes growing degree days as the "annual sum of the number of degrees Celsius that each day's mean temperature is above a specified threshold temperature" (eq. 1; Anandhi, 2016). Thus, GDD effectively combines time and temperature into a single metric, which has been shown to better describe growth in fish than temperature alone (Honsey et al., 2019; Neuheimer & Taggart, 2007). Growth in Arctic charr slows drastically or even stops during winter months while overwintering in freshwater lakes (Mulder et al., 2018b). Water temperatures during this time are typically 0.2-2°C (Klemetsen et al., 2003; Mulder et al., 2018a). Because maximum heart rate drops rapidly below 4°C, likely indicative of a slowing metabolism like that seen during overwintering, a standard base temperature of 4°C was selected for the calculation of GDD:

$$\sum \frac{Daily\ High\ Temperature - Daily\ Low\ Temperature}{2} - Base\ Temperature \qquad \textbf{(Equation 1)}$$

Climate data (historical GDD and annual precipitation) used in this study were extracted from the Climate Atlas of Canada (2019). The Climate Atlas of Canada (2019) is an extensive collection of historical climate variables (11 variables for hot weather, 9 variables for cold weather, 3 variables for temperature, 7 variables for precipitation, and 8 variables for agriculture) and their associated future projections under two climate scenarios (RCP 4.5 and 8.5), covering all of Canada. The interactive map allows users to select areas of interest and explore their climate data.

Annual precipitation (mm) and GDD (base of 4°C; °C·Day) were extracted from 10-km^2 map cells from the Climate Atlas of Canada for the general areas of the three lakes, for the year of each otolith radius formation (Climate Atlas of Canada, 2019). Historical climate data (1950-2013) used in the atlas are provided by Natural Resources Canada (McKenney et al., 2011).

The surface area (km^2) of the three lakes was estimated using the polygon measurement tool in ArcGIS Online (ESRI, 2023). This tool allows the user to trace the perimeter of an object in satellite images to acquire its area. Nõges (2009) found that lakes with larger surface areas tend to be deeper than those with smaller surface areas, validating its use as a proxy for lake size.

2.2.3 Statistical Analyses

Because of the nature of back-calculated datasets, the number of observations declines with increasing age. As such, only ages for which there are at least 25 observations per location were analyzed, resulting in the exclusion of ages 11-20. Moreover, focusing on younger age classes reduces the likelihood of errors in identifying annuli, as growth slows with age, resulting in smaller annuli that may become difficult to distinguish. The analyses to follow examine ages 1-10 only. In addition, measurements of annuli formed during the year of capture were excluded from analysis, as they are considered incomplete when sampling occurs during the summer. The resulting dataset includes 3783 annulus measurements (ages 2-10) and 542 age-1 radius measurements from 542 individuals.

2.2.3.1 Trend Analysis

Trends in mean otolith measurements-at-age for ages 1-10 were detected using two methods with the notrend_test() function from the funtimes package in R; a sieve-bootstrap student's t-test for linear trends and a sieve-bootstrap Mann-Kendall test for monotonic trends (Lyubchich et al., 2023). The purpose of this analysis is to establish whether mean otolith measurements have increased significantly between 1984 and 2013 and to determine which age classes are affected.

2.2.3.2 Model Development

All statistical analyses were done using R Statistical Software (v4.3.1; R Core Team, 2023). The data were compiled into a single dataset, which was then split into a training data set (70%) for model development and a test data set (30%) to cross-validate the model. The training dataset is used to develop the growth models, which were then applied to the test dataset to rule out overfitting and ensure model robustness. A series of model validation plots (distribution of residuals, variance of residuals, and residuals plotted against covariates) were produced to confirm that the model assumptions were met. The simulateResiduals() function from DHARMa was also applied to the models to detect potential issues in dispersion and heteroskedasticity (Hartig, 2024). Data exploration was conducted on the entire dataset following the protocol described by Zuur et al. (2010).

Annulus lengths for age-1 were not taken due to difficulty determining the boundary between the nucleus and the first annulus. For that reason, only radial measurements are taken for age-1 (i.e., from the centre of the nucleus to the end of age-1 growth). Since younger age classes are thought to be disproportionately affected by climate change due to their shallow habitats, age-1 radial lengths were modelled separately to not overlook such a vulnerable age class. The development of both models was done following the protocol described in Zuur and Ieno (2016). This protocol involves determining the dependency structure of the data, presenting and fitting the model, model validation, interpretation of numerical outputs, and visualizing the model (Zuur & Ieno, 2016).

2.2.3.3 Annulus Length Model

A mixed effect model was used to account for the repeated measurements of each individual, individual variation in growth, temporal autocorrelation, and similarities in growth during the same year. Sample ID and year were included as random intercepts to account for this dependency structure. An overparameterized model was fitted using the mgcv package (Wood, 2011). A reduced model was reached by backward stepwise selection, where predictors are sequentially dropped and compared to the full model by likelihood ratio tests (LRT) using the mgcv package (Wood, 2011). Terms were removed from the final model when LRT indicated no improvement in fit with the additional parameter.

2.2.3.4 Age-1 Radius Model

A random intercept of year is necessary for modelling age-1 radius length to account for cohort effects. As such, an overparameterized mixed effect model was fitted using the glmmTMB package (Brooks et al., 2017). Backward stepwise selection was used to reduce the model using LRT in base R, dropping terms that do not significantly improve the model fit (R Core Team, 2023).

2.3 Results

2.3.1 Trend Analysis

Of the 10 age classes, only ages 1-6 and 8 were found to have significant trends in mean otolith measurements over time (Fig. 2.2). The trends in ages 1-6 were all found to be linear. Ages 1-3, 5 and 8 were also found to have significant monotonic trends in mean otolith measurement. No trends were detected in ages 7 and 9-10. Overall, it appears that the magnitude of the positive trend decreases with age.

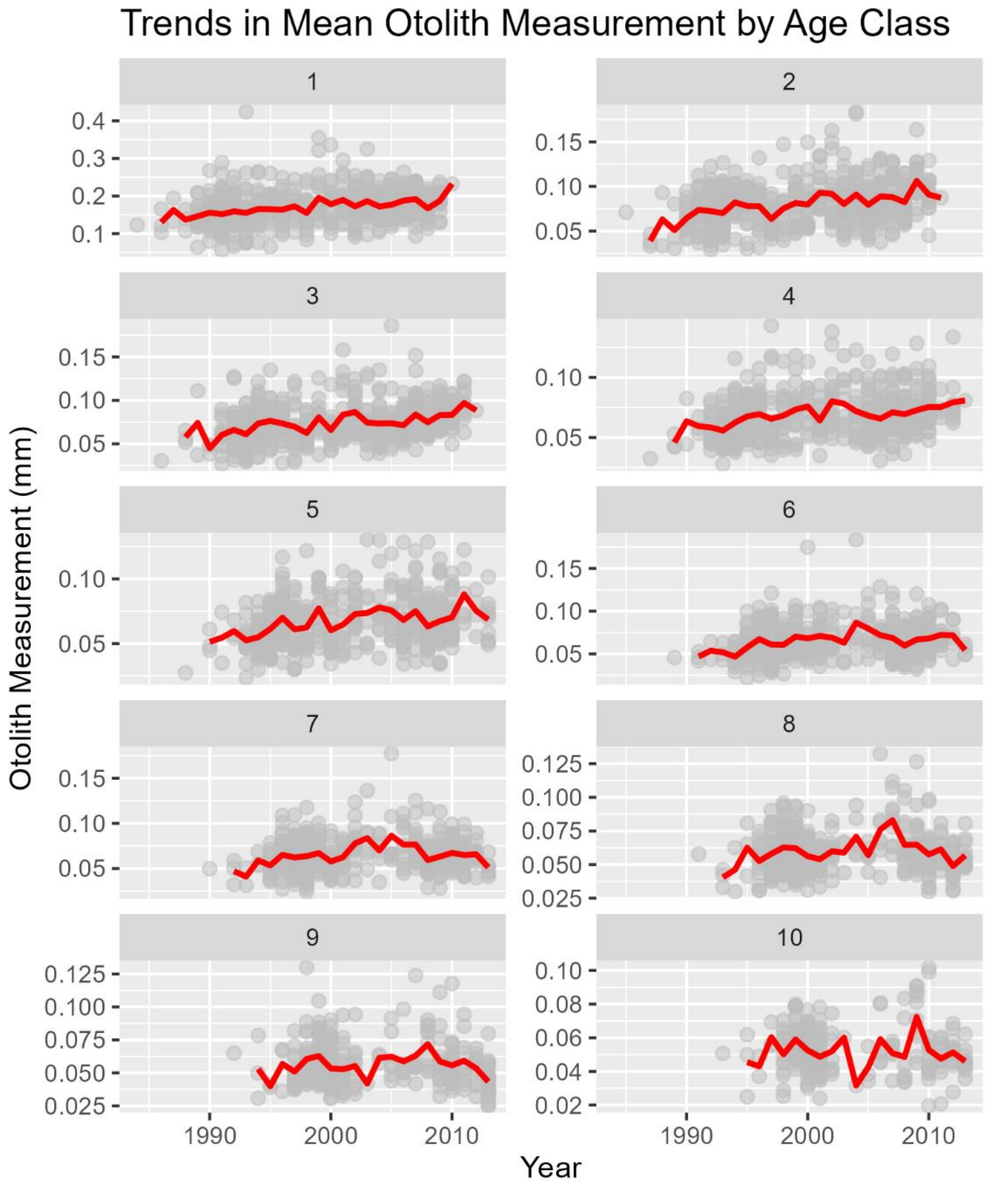

Figure 2.2. Mean otolith growth-at-age over time showing the observed increase in mean otolith measurements across age classes. The grey points represent observed otolith measurements. The red lines represent the trends in mean otolith measurement over time. Significant trends were detected in ages 1-6 and 8 only. Note that for age-1, radius length is used while the remaining age classes are investigated using annulus lengths.

2.3.2 Annulus Length Model

A Cleveland dot plot revealed a single outlier with an annulus length of 0. It was removed, as it was determined to be a measurement error. A histogram of annulus lengths indicated they have a right-skewed distribution, suggesting a gamma distribution may better describe the positive non-zero data, compared to a Gaussian distribution. The relationships between the response and predictors were visually assessed using ggplot scatterplots with gam-smoothed curves (Wickham, 2016). Non-linearity was found in GDD, annual precipitation, year, and age, leading to the choice of a generalized additive mixed model (GAMM).

Three interactions were found using coplots in base R (R Core Team, 2023). Larger annulus lengths were associated with high growing degree days in young ages (<5 years). Large annulus lengths were also associated with less annual precipitation in ages 2 and 3. Finally, age-specific annulus lengths differed between lakes. Variance inflation factors (VIF) revealed that location and surface area are aliased, resulting in surface area being dropped from the model. All other covariates had VIF values below 2.

From backward stepwise selection, only sex was dropped from the model, as it did not improve the model fit. The interaction between age and location was also found to have an insignificant contribution to fit, however, it was retained as it allows for variation we would expect to see between younger age classes across locations. Thus, the reduced model is as follows:

$$Annulus\ Length_{ijk} \sim Gamma(\mu_{ijk})$$

$$\log\left(\mu_{ijk}\right) = s\left(Annual\ Precipitation_{ijk}\right) + s\left(GDD_{ijk}\right) + s\left(Age_{ijk}\right) + Location_{ijk} + ti\left(GDD_{ijk} \times Age_{ijk}\right) + ti\left(Annual\ Precipitation_{ijk} \times Age_{ijk}\right) + s\left(Age_{ijk} \times Location_{ijk}\right) + Sample\ ID_j + Year_k \qquad \textbf{(Model 2.1)}$$

Where $\textit{Annulus Length}_{ijk}$ (continuous; mm) is the i^{th} otolith annulus length from $\textit{Sample ID}_j$ in $\textit{Year}_k$. Three thin-plate splines were included in the model: s($\textit{Annual precipitation}_{ijk}$) (continuous; mm) is the annual precipitation of the i^{th} annulus length from $\textit{Sample ID}_j$ in $\textit{Year}_k$; s($\textit{GDD}_{ijk}$) (continuous; °C*Day) is the corresponding growing degree days with a base of 4°C; and s($\textit{Age}_{ijk}$) (continuous; years) is the corresponding age of the individual at annulus measurement in $\textit{Year}_k$. $\textit{Location}_{ijk}$ (3 level factor; Kipisa, Iqaluit, or Qasigiat) is the presumed natal lake of the i^{th} annulus length from $\textit{Sample ID}_j$ in $\textit{Year}_k$. The tensor product interactions, ti($\textit{GDD}_{ijk}\ x\ \textit{Age}_{ijk}$) and ti($\textit{Annual Precipitation}_{ijk}\ x\ \textit{Age}_{ijk}$), represent the disproportionate effects of GDD and Annual Precipitation on younger ages. The smoothed interaction, s($\textit{Age}_{ijk}\ x\ \textit{Location}_{ijk}$), allows for variation in annulus lengths-at-age between locations. $\textit{Sample ID}_j$ and $\textit{Year}_k$ are the random intercepts, assumed to follow normal distributions with mean 0 and variance σ^2.

No significant issues were detected during model validation, allowing for interpretation of the effects of each variable on otolith annulus length. All variables were found to be significant at the 5% level (p-value < 0.05; Table 2.1), except for Location Kipisa. Of the three locations, Qasigiat has the largest annulus lengths, at 0.052 mm greater than Iqaluit and 0.035 mm greater than Kipisa. The estimated degrees of freedom (EDF) in Table 2.1 describe the non-linearity of the smooth terms and interactions. When EDF is equal to 1, the term is linear. The larger the EDF, the more non-linear the term. 20.4% of the deviance was explained by the model.

Table 2.1. Table of Model 2.1 summary statistics

Parametric coefficients				
	Estimate	Standard Error	t value	p-value
(Intercept)	-2.710	0.008	-320.275	<0.001
Location Kipisa	-0.014	0.012	-1.185	0.236
Location Qasigiat	0.050	0.014	3.700	<0.001
Approximate significance of smooth terms				
	Edf	Reference df	F	p-value
S(precipitation)	4.776	5.810	7.018	<0.001
S(GDD)	6.074	7.175	6.813	<0.001
S(age)	3.722	4.536	34.514	<0.001
ti(GDD, age)	6.793	8.341	4.949	<0.001
s(age): Iqaluit	0.003	0.005	0.004	0.996
s(age): Kipisa	3.785	4.612	6.577	<0.001
s(age): Qasigiat	1.006	1.012	6.751	0.009
ti(precipication, age)	8.591	11.020	3.267	<0.001

To visualize the effects of GDD and annual precipitation independently, I created plots as follows: a new dataset was made where GDD and Age varied from the observed minimums to maximums while holding precipitation constant at its mean observed value (304.88mm). This new dataset was then applied to model 2.1 using the mgcv package to predict annulus lengths and standard errors for each age across the range of GDD values (Wood, 2011). Results were then plotted in Figure 2.3. GDD was found to have an overall positive effect on annulus length across all ages.

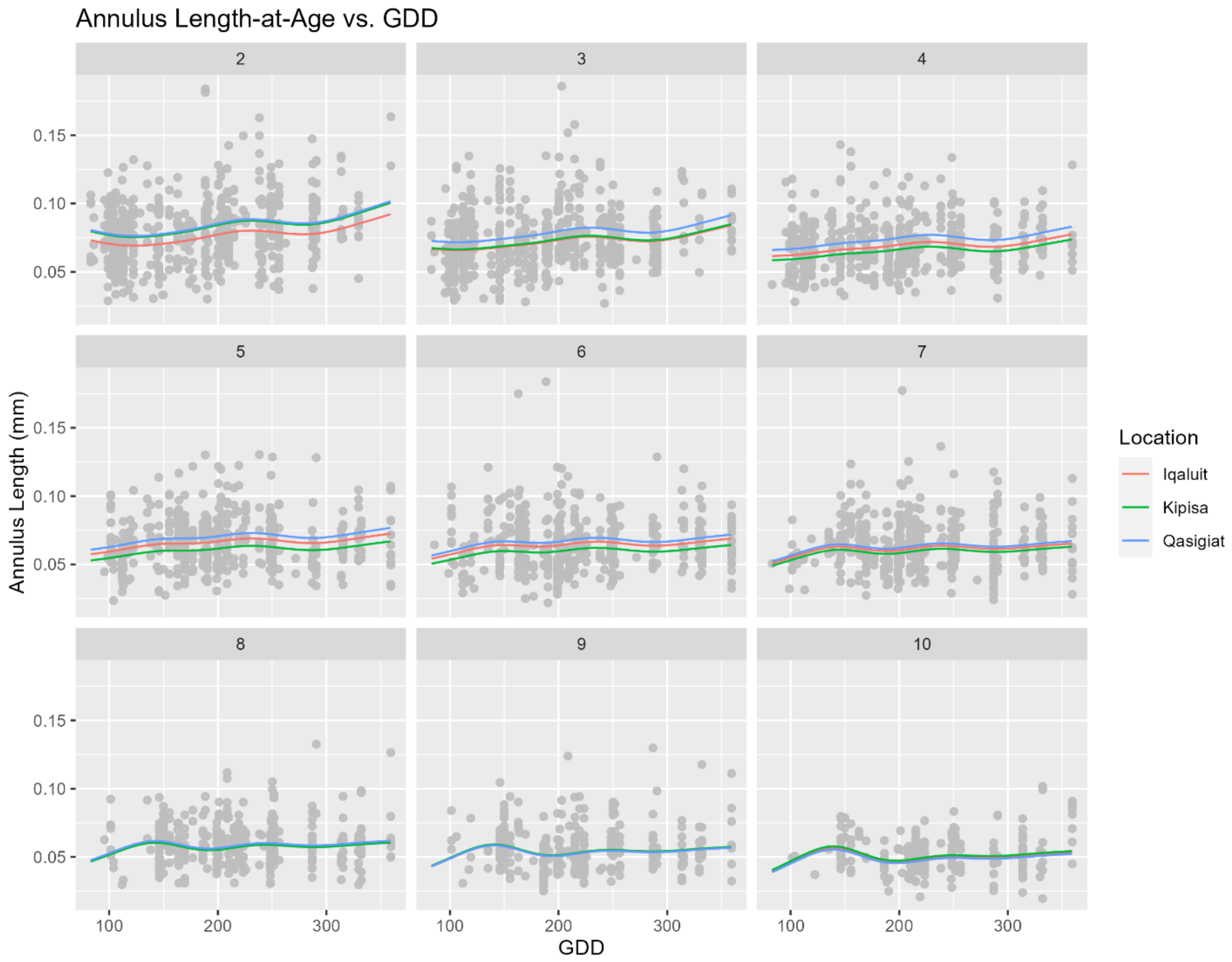

Figure 2.3. A series of plots demonstrating the effect of GDD on annulus length across ages 2-10. Predicted annulus length is represented by a red line for Iqaluit, green for Kipisa, and blue for Qasigiat. The grey points are the observed annulus lengths across all locations.

The same method was used to isolate the effects of annual precipitation by holding GDD constant at its mean value (210.59°C*Day). Figure 2.4 indicates that precipitation has a negative effect on annulus length for age classes 2 and 7-10. The most pronounced negative effect of precipitation is seen at age-2. For ages 3-6, annual precipitation seems to have a marginal effect on annulus length.

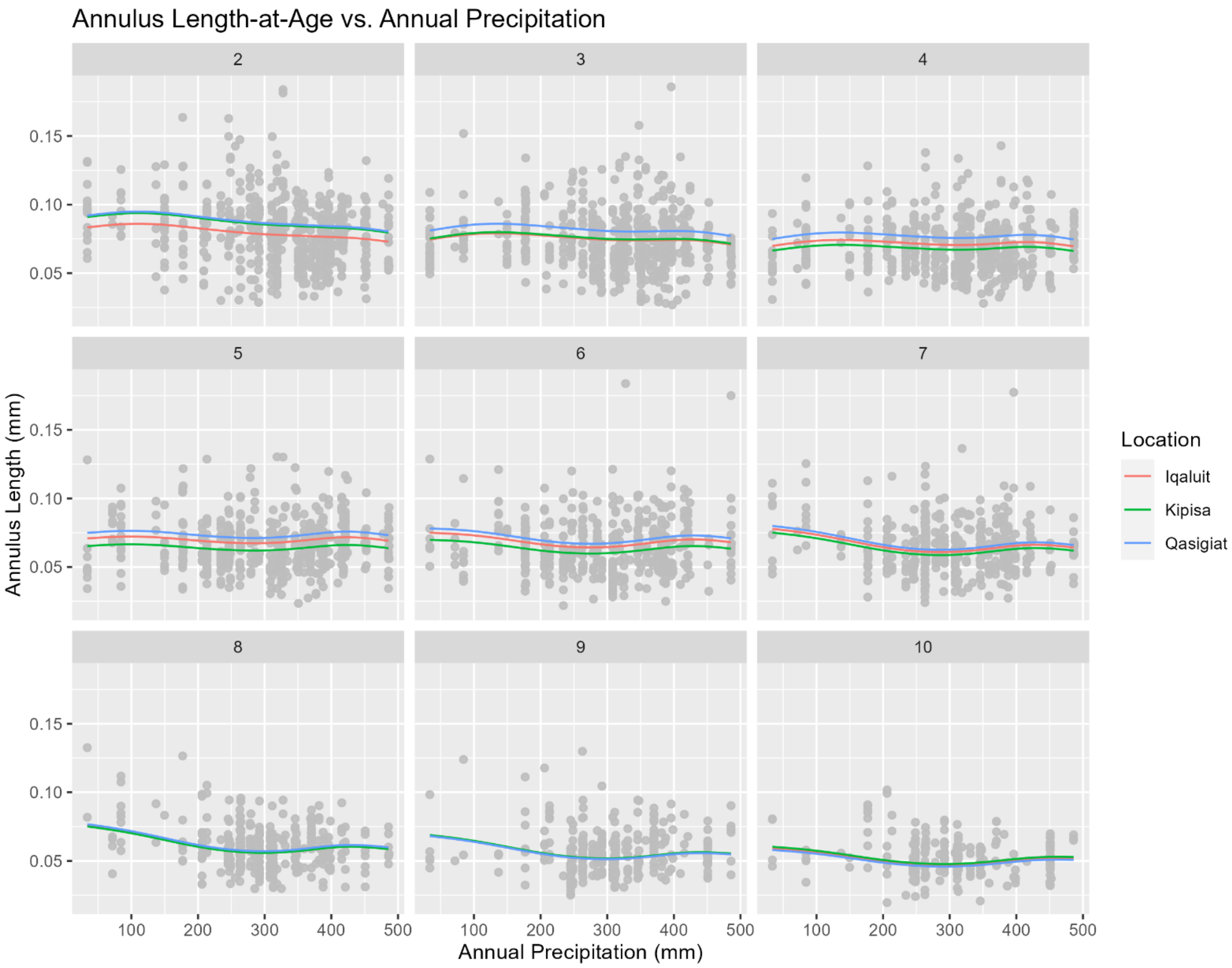

Figure 2.4. A series of plots demonstrating the effect of annual precipitation on annulus length across ages 2-10. Predicted annulus length is represented by a red line for Iqaluit, green for Kipisa, and blue for Qasigiat. The grey points are the observed annulus lengths across all locations.

2.3.3 Age-1 Radius Length Model

No outliers were found within the age-1 radius lengths. The radius lengths were found to be normally distributed, suggesting that a typical Gaussian distribution fit the data. Relationships between the response and each covariate were found to be linear. Year was included as a random intercept to account for variation between cohorts, resulting in the use of a linear mixed model. No biologically relevant interactions were found. Backward stepwise selection indicated that none of the variables should be dropped from the model. The following model was produced based on data exploration to describe age-1 radius length:

$$Age1\ Radius_{ij} \sim N(\mu_{ij}, \sigma)$$

(Model 2.2)

$$Age1\ Radius\ _{ij} \sim GDD_{ij} + Annual\ Precipitation_{ij} + Location_{ij} + Year_j$$

Where $Age1\ Radius_{ij}$ (continuous; mm) is the age-1 radius length for the i^{th} observation of $Year_j$, GDD_{ij} (continuous; °C*Day), $Annual\ Precipitation_{ij}$ (continuous; mm), and $Location_{ij}$ (3-level factor) are the corresponding GDD, annual precipitation, and location of the i^{th} observation of $Year_j$. $Year_j$ is the random intercept, assumed to be normally distributed with mean 0 and variance σ^2.

No significant issues were detected during the model validation or cross-validation process. GDD and Location Kipisa are the only variables found to be statistically significant (p-value < 0.05; Table 2.2). Similar to annulus lengths for ages 2-10, GDD has a positive influence on age-1 radial length, while annual precipitation shows a small negative influence (Figures 2.5 & 2.6). Age-1 radial lengths in Kipisa are found to be 0.022mm larger than in Iqaluit and 0.017mm larger than in Qasigiat. Nakagawa's R^2 was calculated using the performance package and found to be 0.210 for the conditional model and 0.125 for the marginal (Lüdecke et al., 2021).

Table 2.2. Table of Model 2.2 summary statistics

Summary Statistics				
	Estimate	Std. Error	z value	p-value
Intercept	0.1543	0.020	7.672	<0.001
GDD	0.0001	0.00006	2.164	0.03
Location Kipisa	0.022	0.005	4.352	<0.001
Location Qasigiat	0.005	0.006	0.861	0.38
Annual Precipitation	-0.00005	0.00004	-1.468	0.142

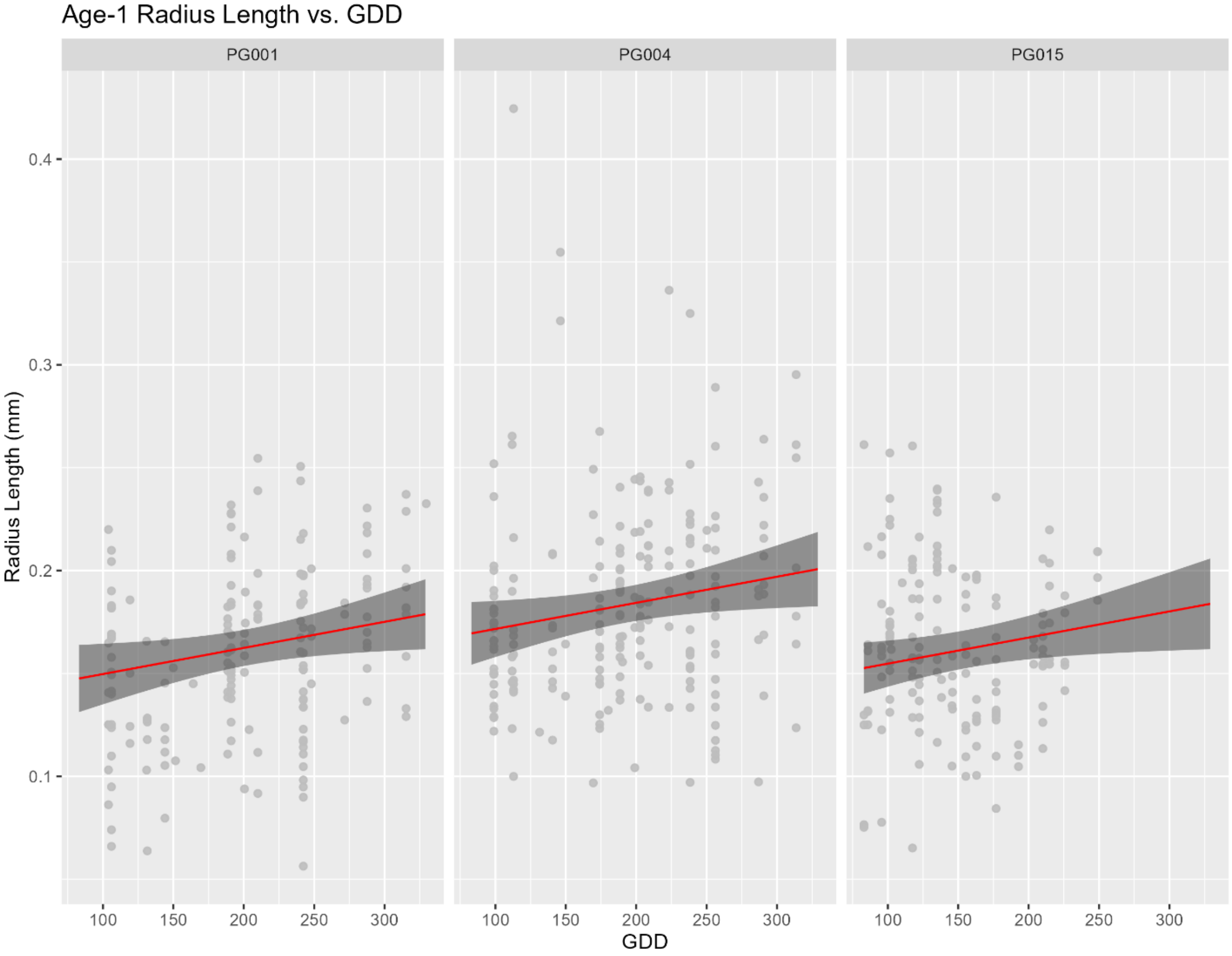

Figure 2.5. Plot showing the effect of GDD and location on age-1 radius length. The grey shadow represents the 95% confidence interval around the predicted age-1 radius length, represented by the red line. The grey points are the observed age-1 radius lengths.

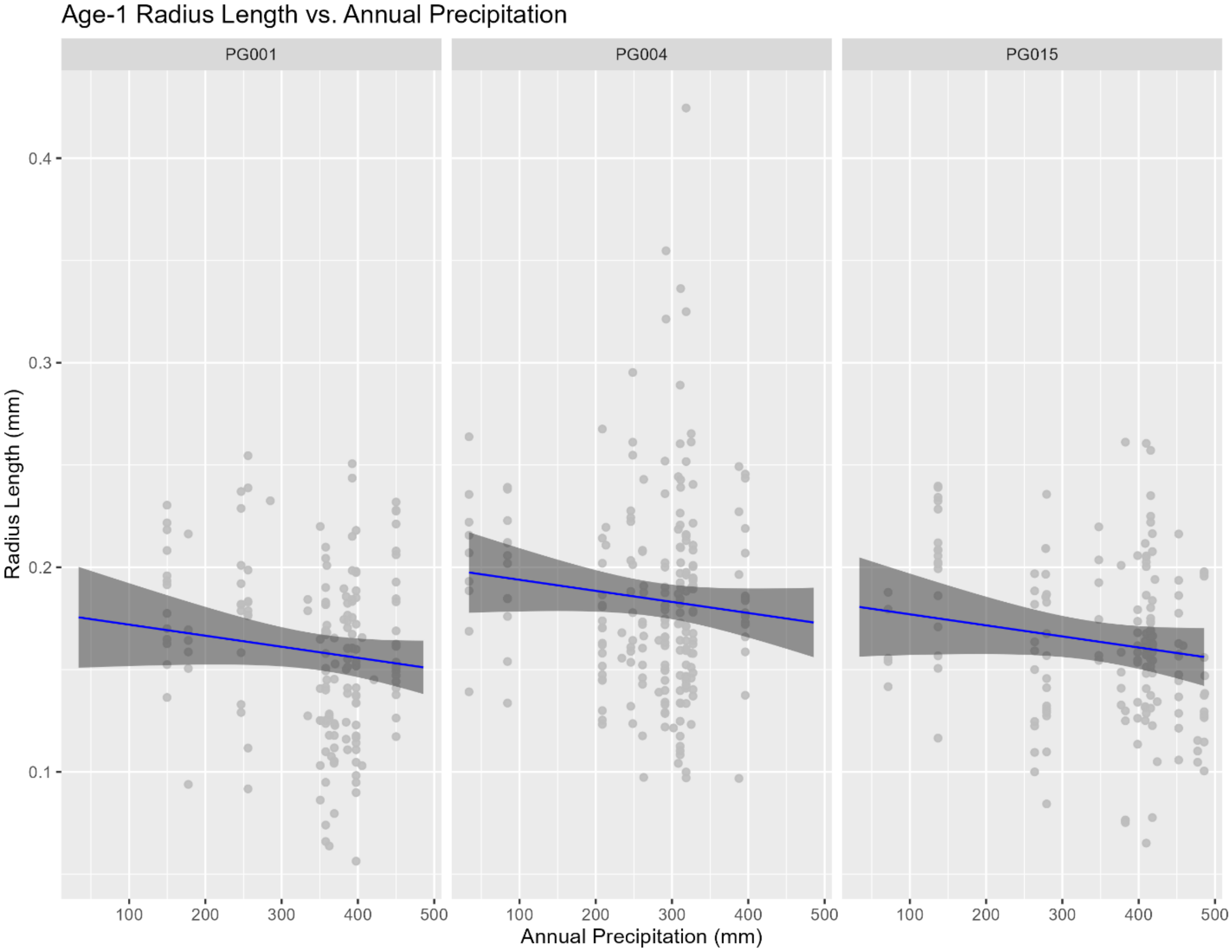

Figure 2.6. Plot showing the effect of annual precipitation and location on age-1 radius length. The grey shadow represents the 95% confidence interval around the predicted age-1 radius length, represented by the blue line. The grey points are the observed age-1 radius lengths.

2.4 Discussion

The main goal of this study was to determine whether the growth of Arctic charr has changed in response to climate change between 1984 and 2013. As anticipated, I found that otolith radius and annulus lengths (and, by inference, charr growth) have increased significantly across age classes (1-10) in concert with increases in GDD. However, annual precipitation had an overall negative effect on ages 2 and 6-10, and virtually no effect on ages 3-5. Trend analyses indicate that significant increases in otolith measurements have occurred in ages 1-6 and 8 during the time period.

The three interaction terms considered for Model 1 are a reflection of age-specific habitat use. Juvenile charr tend to occupy warm shallow habitats (Larsson, 2005), which are more strongly influenced by the climate (i.e., GDD and annual precipitation) than deeper habitats (Kirillin, 2010; Mooij et al., 2008). Thus, we would expect to find disproportionately larger climate change impacts on younger age classes. In addition, though poorly described, it is thought that the three study lakes differ in their morphometry. For instance, we know Qasigiat and Iqaluit are quite deep and that Qasigiat has limited littoral habitat (Loewen, 2008; Martin et al., 2023), but the variability in such habitats between the lakes is not documented. As such, we should expect the extent and quality of age-specific habitats to be different in each lake.

My findings of increased growth with GDD are consistent with the results of similar studies of Arctic charr in Norway and Greenland (Kotowych et al., 2023; Kristensen et al., 2006; Svenning et al., 2024). Svenning et al. (2024) found that young-of-the-year Arctic charr growth in Svalbard was positively correlated with summer air temperature. This is consistent with my finding of a positive correlation between GDD and annulus length (ages 2-10) and age-1 radius, respectively, as winter temperatures below the base temperature of 4°C would not contribute to cumulative GDD and, therefore, growth. Kotowych et al. (2023) also reported juvenile Arctic charr (ages 1-4) growth increased by 6.8-12.6% with water temperatures (modelled from air temperature) over a similar time period (1986-2016).

As previously mentioned, the growth of Arctic charr is expected to increase with temperature up to an optimum (10.3-16.3°C; Beuvard et al., 2022; Larsson & Berglund, 2005; Lyytikäinen et al., 2002). However, growth is only enhanced by temperatures if food availability is not limited.

When food availability is insufficient, metabolic needs cannot be met while maintaining growth at high temperatures, leading to diversions of energy from growth (and possibly reproduction) to support metabolism (Gilbert et al., 2020). Kristensen et al. (2006) studied the effects of temperature increases on the growth of landlocked Arctic charr. Despite similar warming trends, one population showed increased growth, while in the other, growth was suppressed (Kristensen et al., 2006). The latter habitat was described as poor with limited food availability, demonstrating energetic diversions from growth towards metabolic needs when temperatures rise and energy intake is insufficient (Kristensen et al., 2006). My current findings did not indicate such trade-offs, suggesting the study lakes are sufficiently productive to support enhanced growth prior to first migration.

Precipitation has varying effects on the growth of Arctic charr, depending on the season and type of precipitation. In the current study, I found annual precipitation had an overall negative influence on growth in ages 1-2 and 6-10. A similar result was found by Kristensen et al. (2006) in a landlocked population of charr, where mean annual precipitation had a negative effect on growth. Svenning et al. (2024) found that greater snow depth (i.e., higher winter precipitation) had a negative influence on growth due to its insulating properties, delaying ice melt. However, Chavarie et al. (2019) reported increased growth in older age classes with spring precipitation only, likely resulting from related increases in estuarine productivity and thus, feeding opportunities. Because annual precipitation was used, it is difficult to infer whether the relationships seen here are due to the influence of rain or snow.

However, greater snowfall could very well be an explanation for the more pronounced effects on growth in ages 1-2 and 6-10. For instance, a large proportion of growth occurs at the commencement of anadromy at ~6 years of age for nearby lakes (Loewen, 2016; Young et al., 2021). If the snow cover is deep, the ice is insulated and can persist longer. This could then result in delayed migration, possibly explaining the greater decline in growth with precipitation for ages 6-10. Hammer et al. (2022) found that Arctic charr migration occurred just before the ice breaks up, probably to maximize feeding opportunities by being in the marine environment before the initial pulse of productivity. Age-1 and -2 growth show similar trends, which again may be related to snow accumulation, which shortens the growing season (Svenning et al., 2024). For ages 3-5, annual precipitation seems to have marginal effects on growth, perhaps reflecting their movements within the lake prior to first migration. Dubos et al. (2022) found that juveniles greater than 1 year of age had no habitat preference within the freshwater environment, and they were much more mobile than their younger conspecifics. In addition, the risk of predation generally decreases with size, so smaller individuals (thus, younger) may restrict habitat use to shallow areas (Byström et al., 2004).

The models reveal variations in growth between locations in ages 1-6. In addition, the trend analyses indicate significant increases in growth mostly in these age classes. As previously mentioned, the mean age at first migration is ~6 years in Cumberland Sound (Loewen, 2016; Young et al., 2021). The variation seen in growth between locations is likely a reflection of the habitat variation and food availability of the lakes, as older age classes do not appear to have this same variation. For ages 2-6, charr in Qasigiat appear to have greater growth than those in the other two locations. Qasigiat is somewhat unique in comparison to Iqaluit and Kipisa, as it is often inundated with saltwater due to its proximity to the marine environment. It has a limited littoral habitat due to its steep edges, reaching depths greater than 21 m and it is thought that rearing occurs in shallow off-shoot ponds that surround the lake (Loewen, 2008). Martin and Tallman (2013) reported that charr in this system appears to reach an asymptotic length of ~600 mm around 10 years of age. Other stocks in Cumberland Sound do not appear to share this characteristic (Harris & Tallman, 2010; Martin & Tallman, 2013). One possible explanation for the greater observed growth in Qasigiat is that the inflow of marine water may carry nutrients that could support greater juvenile growth. Alternatively, Gilbert et al. (2022) found that Arctic charr behaviourally thermoregulate by moving to cooler thermal zones in a body of water to support metabolic processes. We know Qasigiat is deep (>21 m), suggesting it may have more extensive thermal stratification than the two other lakes. As such, Qasigiat charr may be able to maximize growth by moving to different thermal zones within the water column.

Kipisa was found to have greater age-1 radial lengths than Iqaluit and Qasigiat. These measurements not only include age-1 growth but also larval growth, as it includes the nucleus. This stock is quite distinguishable as Kipisa charr tend to have deeper bodies, smaller heads, and lighter body colour in comparison to other Cumberland Sound stocks (DFO, 2005). Studies have found that larger females are able to produce larger eggs with greater yolk sac content than smaller females (Eiríksson et al., 1999; Leblanc et al., 2016). These larger eggs then go on to produce larger embryos. Thus, the larger age-1 radius in Kipisa may be attributed to larger embryos due to a maternal effect. However, egg size has also been attributed to spawning habitat. Alternatively, Beck (2019) found that anadromous charr spawning in rivers produced smaller eggs than those that spawned in lakes. Takatsu et al. (2023) also found this to be true with charr in Greenland, although not statistically significant. While it is hypothesized that Kipisa charr spawns in the river above the lake, the spawning sites of most stocks in the area are not well studied.

Growth of ages 7-10 does not appear to vary between lakes. This pattern is likely linked to both a reduced growth rate and abundant and likely similar resource availability in the marine environment. Between the ages of 8 and 13, Arctic charr in these stocks begin to spawn (DFO, 2005; Martin et al., 2023; Martin & Tallman, 2013). As a result, energy is likely to be diverted from somatic growth towards reproduction, depressing the growth rate. In addition, this age range is also exploiting the rich marine environment. All three of the stocks studied here migrate to Cumberland Sound, where we can presume resource availability and environmental conditions are more similar than those of the freshwater lakes. In addition to food availability, we know the temperature of the marine environment remains fairly stable and is not as influenced by atmospheric temperature as smaller bodies of water. Each of these aspects would contribute to more homogeneity of growth between stocks.

2.5 Conclusion

I have found that Cumberland Sound Arctic charr has been experiencing changes in growth since at least 1984, in concert with climate change-associated increases in GDD and annual precipitation. Qasigiat Arctic charr were found to have significantly larger annulus lengths in ages 2-6 in comparison to Iqaluit and Kipisa. These differences are thought to be attributed to differences in lake habitats and presumed extensive thermal stratification resulting in maximized growth. In contrast, Kipisa was found to have greater age-1 radial lengths than the other lakes, hypothesized to be related to a maternal effect, thus producing larger embryos. GDD was found to have a positive influence on growth in ages 1-2 and 7-10, while annual precipitation had a negative effect in these same ages. These patterns are thought to be tied to the shallow nature of habitats occupied by younger ages and impediments to migration for older ages. The results of the models and trend analyses point to a disproportionate effect of climate change on individuals before their first migration. Whether these changes are due to warmer water temperatures or longer growing seasons remains unclear and necessitates further research.

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3. Estimated Temperatures Experienced by Cumberland Sound Arctic Charr in a Changing Climate

Abstract

The previous chapter found that three Arctic Charr stocks in the Cumberland Sound region of Nunavut were significantly affected by climate change (i.e., growing degree days and annual precipitation) from 1984 to 2013. Using otolith annulus (ages 2-10) and radius (age-1) lengths, it was determined that there had been significant increases in annual growth across the time series and age classes. However, I can not infer whether these findings are the result of warmer lake conditions or longer growing seasons. In an attempt to answer that question, this chapter investigates whether temperatures experienced by Arctic charr, estimated from otolith $\delta^{18}O$, follow climate patterns. Experienced summer temperatures in freshwater were modelled with growing degree days and annual precipitation. We found that neither of the climate variables had a significant effect on experienced temperature. Age and location were found to have the most significant effect on experienced summer temperatures in the freshwater environment. To further investigate changes to lake temperature without the added complexity of behavioural thermoregulation, I also used a simple linear model to investigate changes in experienced temperatures in ovo from 1987 to 2008, which suggests that Arctic charr in ovo experienced significantly cooler temperatures over the time period. However, it is hypothesized that the declining experienced temperatures are not a reflection of cooler lake temperatures, but of changing isotopic composition in the lakes over time. Together, these findings suggest that the increase in growth related to climate variables is likely not due to warmer lake conditions, but rather a longer growing season.

3.1 Introduction

Arctic charr (*Salvelinus alpinus*; charr, hereafter) are the northernmost freshwater fish with a circumpolar distribution (Klemetsen et al., 2003). They are a cold-adapted species, occupying water as cold as 1°C (Brännäs, 1992). Three different ecotypes of charr exist: anadromous, freshwater resident, and landlocked. Anadromous individuals migrate to sea to feed during the ice-free season, returning to freshwater in autumn to over-winter (Grainger, 1953). These anadromous Arctic charr are larger than their resident and landlocked counterparts, thus are favoured among northern communities for commercial and subsistence harvest. However, climate change has warmed the Arctic at an accelerated rate, putting this species of importance at risk. The effects of climate change have been well documented and reported via the Intergovernmental Panel on Climate Change (IPCC). Temperatures and precipitation have increased substantially, resulting in longer ice-free seasons (IPCC, 2023), extending the growing season for Arctic charr and allowing for greater warming of their habitat.

Because fish are ectotherms, their metabolic rate is dependent on the temperatures experienced in their environment. Metabolic rate increases with temperature, allowing fish to increase their growth rate as long as food availability persists (Beuvard et al., 2022; Larsson & Berglund, 2005; Lyytikäinen et al., 2002). With that said, there is a critical point at which rising temperatures result in metabolic stress and a decrease in growth rate (Beuvard et al., 2022; Gilbert et al., 2020; Larsson & Berglund, 2005). The energetic costs of maintenance during these times of heat stress are likely to result in less growth due to the allocation of energy towards life-sustaining metabolic processes. Thus, lake temperature is a main predictor of growth rate.

Lake temperature regimes differ between shallow and deep lakes (Kirillin, 2010; Mooij et al., 2008). Studies have linked growth rate and mortality in charr to lake depths, likely resulting from differing experienced temperatures. One study found that charr occupying a large, deep lake showed no significant relationship between growth, age or temperature, but did note negative impacts on growth in a smaller lake related to increased air temperatures (Murdoch & Power, 2013). In another study, Kristensen et al. (2006) were unable to catch any charr under the age of 5+ years in a shallow lake (7-metre maximum depth), suggesting that the increasing water temperatures may have impacted breeding success.

$\delta^{18}O$ is a stable isotope incorporated into the otolith that can be used to infer both the salinity and temperatures experienced by fish over their lifetime (Elsdon & Gillanders, 2002). Temperature and $\delta^{18}O$ have an inverse relationship, meaning that as temperature increases, $\delta^{18}O$ decreases (Elsdon & Gillanders, 2002). In studies, otolith-derived $\delta^{18}O$ is most often used as an indicator of environmental temperature when paired with a fractionation equation (e.g., Godiksen et al., 2010; Sinnatamby et al., 2013). A fractionation equation allows $\delta^{18}O$ to be converted to temperature data through the relationship between ambient $\delta^{18}O$ and its incorporation into mineral structures, such as the otolith (Morissette et al., 2023). Godiksen et al. (2010) published a polynomial species-specific fractionation equation for charr via an experimental approach. This equation has since been used in many studies to reconstruct the thermal habitat use of young-of-the-year and juvenile charr in freshwater environments (e.g., Godiksen et al., 2011, 2012; Sinnatamby et al., 2013).

In the previous chapter, I found that annual growth increased across age classes (ages 1-10) from 1984 to 2013, which was significantly related to an increase in growing degree days and annual precipitation over the time period. However, we can not say with certainty whether this trend was the result of warmer lake conditions or longer growing seasons. This study aims to delve deeper into the results from Chapter 2 to understand the effects of climate on the thermal habitat use of charr. Here, I investigate whether charr in Cumberland Sound experienced warmer conditions over the period of 1989 to 2013, by modelling experienced summer temperatures against annual precipitation (mm), growing degree days (GDD; °C*Day), location and age. In addition, in ovo temperatures estimated from $\delta^{18}O$ sampled from the nucleus were modelled with year of formation as a way to infer changes to lake temperatures in spawning areas over the time period. During this stage of development, the added complexity of behavioural thermoregulation is removed as it is assumed here that spawning occurs at similar depths from year to year.

Depths of the lakes around Cumberland Sound are, for the most part, unknown, but we expect at least the upper part of the water column to follow air temperature trends. Consequently, I predict that (1) charr in the Cumberland Sound region have experienced warmer lake conditions, supporting a higher metabolic rate, thus increasing annual growth. (2) I expect to find significant differences in experienced summer temperatures between locations, due to differing lake characteristics such as depth or thermal stratification. (3) Precipitation has also influenced experienced summer temperatures, as spawning charr have been observed moving to deeper waters during rainstorms (personal observation). (4) Experienced temperatures are significantly different between locations and age classes due to differences in lake and river morphology, and different thermal requirements with age. (5) Experienced temperatures in ovo will reflect changes in lake temperature related to climate change. This is the first study, to our knowledge, examining charr experienced summer temperatures to infer the effects of climate change on thermal habitat use on Baffin Island, Nunavut and the first to examine such a large range in age classes.

3.2 Materials & Methods

3.2.1 Study Area

Cumberland Sound is located on the southeastern coast of Baffin Island, Nunavut. The Sound is 300 km long and averages 65 km wide (Roux et al., 2019; Tallman & Marcoux, 2021). Its water originates from both Arctic and North Atlantic water masses (McMeans et al., 2012). Depth ranges from 200 m to 1000 m (Tallman & Marcoux, 2021). The steep sides of the Sound (> 2125 m) are lined with deep fiords, connecting the marine environment to freshwater river and lake systems (Roux et al., 2019; Tallman & Marcoux, 2021). Three of these lakes, located along the south side of Cumberland Sound, were selected for this study; Kipisa (PG004), Iqaluit (PG001) and Qasigiat (PG015; Fig. 1). DFO waterbody codes are included in parentheses for consistency across the literature, since common lake names vary in the region. Qasigiat Lake (64°62′N, 66°31′W) is unique in that it has a very short river connecting the marine environment to the lake, with depths greater than 21 m and limited littoral habitat (Loewen, 2008). At high tide, there is virtually no separation between the two environments, leading to an inflow of saltwater into the lake (T. Loewen, personal communication, 29 November 2023). Iqaluit Lake (65°2’N, 67°7’W) is a large, deep lake, connected to the marine environment via a 1.3-km-long river (Martin et al., 2023). Kipisa Lake (66°52’N, 67°85’W) is the largest of the three lakes in terms of surface area and has the longest river (approximately 6.4km) connecting the lake to the marine environment.

3.2.2 Data Collection

3.2.2.1 Otolith Preparation

A subset of 36 otoliths used in Chapter 2 was selected from the three lakes in two different years to create a time series of annuli (Table 3.1). These otoliths were collected as part of stock assessment initiatives (DFO, 2005, 2013, 2023).

Table 3.1. Number of otoliths and sample points by location and sample year.

Sample year	Location	Otolith Sample Size	Sample Points
2001	PG001	5	41
2002	PG004	5	30
2003	PG015	7	198
2011	PG004	6	79
2011	PG015	6	122
2013	PG001	7	199

When left and right otoliths were available, both were examined in a shallow dish of water under a Leica M125 microscope at 10x magnification for initial screening of otolith quality. Otoliths were rejected when crystallization was observed. The otoliths in the best condition (i.e., with fewer cracks and chipping) or with a flat or wide peak on the dorsal lobe were selected for embedding. Flat or wide peaks on the dorsal lobe are a prime location for sectioning as there is a lower margin of error in the placement of the saw blade, resulting in better sections with easy-to-distinguish annuli. Debris was cleaned from the otolith using precision forceps under the microscope, and a lateral grind was performed to improve the clarity of the nucleus and first annulus. A two-part epoxy was mixed and poured onto a labelled silicone ice cube tray before the otolith was placed into the epoxy, sulcus side up. The epoxy was then left to cure in a fume hood for at least two days prior to sectioning. Once cured, the epoxy was polished to improve visibility of the nucleus. The sectioning plane was then marked under a microscope with a micrometre eyepiece using an Ultra Fine Tip Sharpie®. A true transverse section was generally used, although a slight anterior or posterior rotation was also used in some cases to achieve a better section (Gallagher et al., 2016). Sectioning was accomplished using a Buehler IsoMet™ Low Speed Saw with a single saddle chuck set at a speed of 10. Two diamond wafering blades separated by a thin plastic spacer were used to cut a thin section from the embedded otolith. The back of the section was marked with a Sharpie® before excess epoxy was trimmed using an ultrasonic cutter.

3.2.2.2 Oxygen Isotope Extraction

Otoliths embedded within individual epoxy blocks and roughly sectioned were arrayed on adhesive tape and cast together in epoxy along with centrally-located calcite reference material (RM) into a 25 mm diameter mount (M1806). The mount was ground and polished with diamond compounds to achieve a uniformly flat surface. Polarized incident light microscope images were acquired for each specimen. After cleaning with soap and de-ionized water, the mount was coated with Au prior to SIMS analysis.

Oxygen isotope ratios ($^{18}O/^{16}O$) were determined using the IMS-1280 multi-collector ion microprobe at CCIM. Primary beam conditions included the use of 20 keV $^{133}Cs^{+}$ ions focused to form a probe with diameter of 20 µm and beam current ~ 2.0 nA. The primary beam was rastered for 30 s prior to analysis to clean the surface of Au and contaminants and implant Cs. The normal incidence electron gun was utilized for charge compensation. Negative secondary ions were extracted through 10 kV potential into the secondary column (Transfer section). Conditions for the Transfer section included an entrance slit width of 122 µm, field aperture of 5 x 5 mm, and a field aperture-to-sample magnification of 100 x. Automated tuning of the secondary ions in the Transfer section preceded each analysis. The energy slit was fully open. Both $^{16}O^{-}$ and $^{18}O^{-}$ were analyzed simultaneously in Faraday cups (L'2 using 10^{10} Ω amplifier, and H'2 with 10^{12} Ω) at mass resolutions of 2000 and 2275, respectively. Mean count rates for $^{16}O^{-}$ and $^{18}O^{-}$ were typically 2.0 x 10^{9} and 4 x 10^{6} counts/s, respectively, determined over a 60 s counting interval. Total spot-to-spot time was 200 s. Typical spot depths after completion are < 1 µm. The analytical sequence interspersed analyses of unknowns with in-house end-member calcite reference material (CCIM sample S0161 with $\delta^{18}O_{VSMOW}$ = +25.33 ‰, $\delta^{18}O_{VPDB}$ = -5.42 ‰; R. Stern, unpublished data) in a 5:1 ratio. Instrumental mass fractionation (IMF) for $^{18}O^{-}/^{16}O^{-}$ was determined for each of three analytical sessions from utilizing all the replicate analyses of S0161 calcite, for which the standard deviations were 0.17‰, 0.09 ‰, and 0.12 ‰. Individual spot uncertainty in $\delta^{18}O$ for unknowns is ±0.25 ‰ – 0.35 (2σ). The calcite-calibrated data for unknowns were bias corrected by -0.95 ‰ to account for the difference in mass fractionation between calcite and the aragonite matrix of the otoliths, determined by separate calibration within CCIM. Sample points were placed along a transect running along the sulcus on the ventral lobe of the otolith (Fig. 3.1). Sample points were positioned so that they only included material formed during one season. Some larger growth zones had several sample points to account for the entirety of that season's $\delta^{18}O$. As a result, sample points within a single summer growth zone were averaged to achieve average summer $\delta^{18}O$ values. Of the averaged $\delta^{18}O$ values, only those which represented at least 60% coverage of the summer growth zone from ages 1-10 were kept for analysis. The same averaging was done for δ^{18}O data points originating from the nucleus.

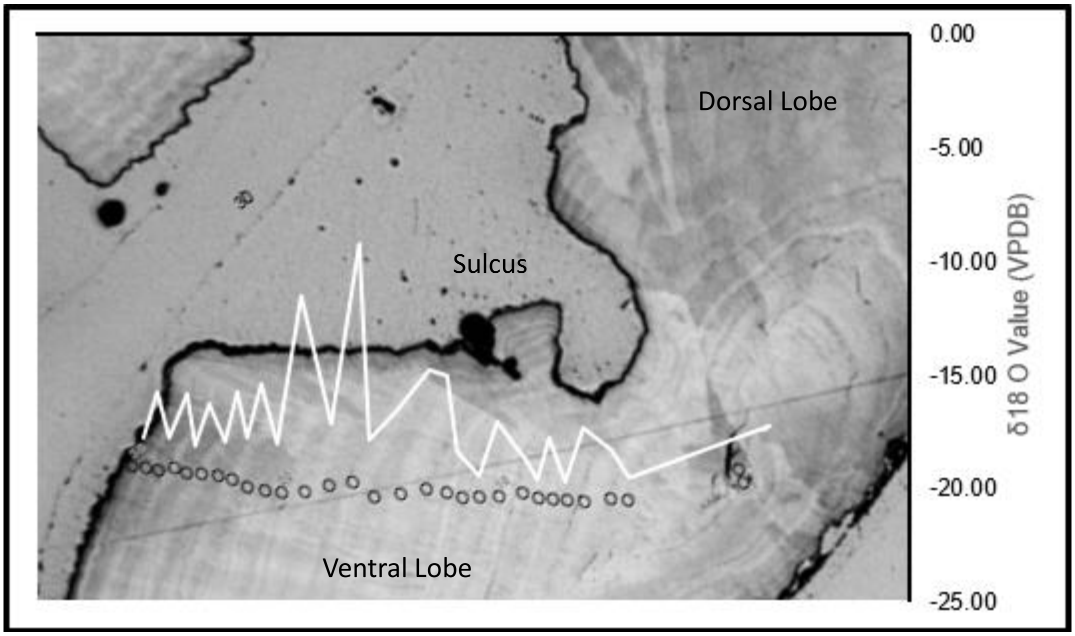

Figure 3.1. Example of the sample point placement and δ^{18}O value (VPDB) fluctuation from nucleus to edge of otolith (right to left; PG001 2013 #41).

3.2.2.3 Climate Data

Annual precipitation (mm) and GDD (°C*Day) were extracted from 10 km^2 map cells from the Climate Atlas of Canada for the general area of the three lakes, for the year of each otolith annulus formation (Climate Atlas of Canada, 2019). Historical climate data (1950-2013) used in the atlas are provided by Natural Resources Canada (McKenney et al., 2011).

3.2.3 Statistical Analyses

3.2.3.1 Temperature Estimation

Average summer experienced temperatures were estimated using the averaged δ^{18}O values in conjunction with a polynomial species-specific fractionation equation for Arctic charr (Godiksen et al., 2010). In order to use this fractionation equation, a δ^{18}O value of the lake water at the time of fish sampling is required. However, water samples are not routinely collected for stock assessment purposes. In this case, a δ^{18}O value was drawn from the data used by Gorbey et al. (2022) and used as a surrogate. The lake was selected as it was samples during the time period (1994), is in relatively close proximity to the study lakes (30-196 km), is relatively close to the coast of Cumberland Sound (6.7km), is classified as a flow-through lake and has the lowest elevation (85 metres above sea level) of the nearby sampled lakes. The δ^{18}O value of the surrogate lake was converted from VSMOW (Vienna standard mean ocean water) to VPBD (Vienna PeeDee Belemnite):

$$\delta^{18}O_{water\ (VPDB)} = -29.98 + 0.97002 * \delta^{18}O_{water(VSMOW)} \qquad \text{(Eq. 3.1)}$$

where $\delta^{18}O_{\text{water (VPDB)}}$ is the δ^{18}O of the water with respect to the reference standard for calcium carbonate and $\delta^{18}O_{\text{water (VSMOW)}}$ is the δ^{18}O of the water with respect to the reference standard for water.

Otolith fractionation factors are then computed from the VPDB standardized δ^{18}O values of the water and the otoliths:

$$\alpha = (\delta^{18}O_{\text{otolith}(VPDB)} + 1000)/(\delta^{18}O_{\text{water}(VPDB)} + 1000) \qquad \text{(Eq. 3.2)}$$

Experienced temperatures are then estimated using the fractionation factors and the polynomial fractionation equation for Arctic charr, developed by Godiksen et al. (2010):

$$1000 \ln \alpha = 89.9/T^2 - 617.19/T + 1089.24 \qquad \text{(Eq. 3.3)}$$

where 1000lnα is the natural log-transformed fractionation factor, T is temperature (10^3/Kelvin), and 89.9, -617.19, and 1089.24 are the empirical constants determined by Godiksen et al. (2010). Estimated temperatures were then converted to Celsius:

$$°C = T \times 10^3 - 273.15 \qquad \text{(Eq. 3.4)}$$

3.2.3.2 Model Development

All statistical analyses were performed using R Statistical Software (v4.3.1; R Core Team, 2023). Estimated experienced temperatures and the climate data were compiled so that each experienced temperature was associated with the annual precipitation and GDD of the year of annulus formation. Following the protocol described by Zuur et al. (2010), a thorough exploration of the data was conducted prior to model development. Experienced temperatures associated with the nucleus were separated from the rest of the data for analysis, as nucleus experienced temperatures do not correspond to summer temperatures, but rather the temperatures experienced from fertilization to hatch (fall to spring). The larger age 1-10 dataset was randomly split into a training data set (70% of the data) and test data set (30%). The training data set was used to develop the model, and the test data set was used to assess the models' ability to generalize unseen data. With the nucleus dataset being quite small, the dataset was not split into training and test data sets. Instead, k-fold cross-validation (k=5) was used to validate model performance. To assess whether model assumptions are met, a series of validation plots were produced from the model residuals to ensure normal distribution, homoscedastic variance, and independence from covariates. To further detect potential issues in dispersion and heteroskedasticity, the simulateResiduals() function from 'DHARMa' was applied to the models (Hartig, 2024). Both models are built following the protocol outlined in Zuur and Ieno (2016) by identifying the data's dependency structure, presenting and fitting the model, model validation, interpretation of numerical outputs, and model visualization.

3.2.3.3 Experienced Temperature Model

To investigate the influence of location, climate and age on experienced temperatures, a mixed effect model was used to account for the repeated measures on a single individual, individual variation in experienced temperatures, temporal autocorrelation, and similarities in experienced temperatures of the same year. Due to this dependency structure, Sample ID and Year were included as random intercepts in the mixed effect model.

3.2.3.4 In Ovo Temperature Model

Due to the small sample size of nucleus experienced temperatures, experienced temperatures in ovo was regressed on year alone. This model functions as a control for behavioural thermoregulation, and a clue as to whether lake temperatures have changed over the time period.

3.3 Results

3.3.1 Temperature Estimation

Since the structure of the polynomial fractionation equation is a quadratic formula, two possible estimated temperatures were found for each of 196 observations from ages 1-10 and 28 nucleus observations. The most likely temperatures originated from the positive discriminants and were easily identified, as they were always within a reasonable range of temperatures (2-18°C) expected in the Arctic and for the species' biology. The alternative root always exceeded temperatures of 18°C.

3.3.2 Experienced Temperature Model

Cleveland dot plots did not indicate any outliers in the data. A histogram of experienced temperatures closely resembled a normal distribution, suggesting that a typical Gaussian distribution should be adequate. It was determined that there are no problems with collinearity in the variables, based on Pearson's correlation coefficients (<0.6) and variance inflation factors (<2). All relationships between experienced temperatures and the variables were found to be linear upon visual assessment using scatterplots fitted with gam-smoothed curves in 'ggplot2' (Wickham, 2016; Zuur et al., 2010). One biologically relevant interaction was found between location and age by plotting experienced temperature over age and applying linear relationships by location in 'ggplot2' (Wickham, 2016). This interaction seems to reflect variability in age-specific thermal habitat between the lakes. Kipisa had less overall variation in experienced temperatures across ages. Younger age classes in Iqaluit and Qasigiat appear to have experienced warmer conditions than Kipisa. Some temporal autocorrelation was detected using the acf function in 'base R', due to the nature of time series data (R Core Team, 2023).

Based on these findings, the proposed model is a GLMM (generalized linear mixed effect model) with a Gaussian distribution and identity link, suitable for describing linear relationships between variables and a response which follows a normal distribution:

$$Experienced\ Temperature_{ijk} = GDD_{ijk} + Annual\ Precipitation_{ijk} +$$

$$Age_{ijk} + Location_{ijk} + Age_{ijk} \times Location_{ijk} + Sample\ ID_j + Year_k \quad \textbf{(Model 3.1)}$$

where *Experienced Temperature*$_{ijk}$ (continuous; °C) is the i^{th} experienced temperature from *Sample ID*$_{j}$ in *Year*$_{k}$. Four fixed effects are included: *GDD*$_{ijk}$ (continuous; °C*Day) is the corresponding GDD, *Annual Precipitation*$_{ijk}$ (continuous; mm) is the corresponding annual precipitation, *Age*$_{ijk}$ (continuous; years) is the age of *Sample ID*$_{j}$ in *Year*$_{k}$, and *Location*$_{ijk}$ (3-level factor; Iqaluit, Kipisa, or Qasigiat) is the presumed natal lake. The interaction term Age$_{\text{ijk}}$ x Location$_{\text{ijk}}$ represents the variation in age-specific thermal habitat use between lakes. *Sample ID*$_{j}$ and *Year*$_{k}$ are the random intercepts, assumed to follow a normal distribution with mean 0 and variance σ^2.

Model validation did not reveal any significant issues in the model's fit. Of the variables, Age, Location Kipisa, and the interaction term between Location and Age for Kipisa and Qasigiat were found to be significant at the 5% level (p-value < 0.05; Table 3.2). Of the three locations, Kipisa appears to experience the coldest temperatures, while Qasigiat and Iqaluit are not significantly different from one another. As expected, experienced temperature decreases with age.

Table 3.2. Table of model 3.1 summary statistics

	Estimate	Std. Error	Z value	P value
Intercept	13.250	2.192	6.044	<0.001
Annual Precipitation	0.001	0.003	0.475	0.635
GDD	-0.002	0.006	-0.317	0.751
Age	-0.659	0.141	-4.682	<0.001
Location PG004	-3.215	1.401	-2.294	0.022
Location PG015	-1.409	1.455	-0.968	0.333
Age : Location PG004	0.399	0.185	2.154	0.031
Age : Location PG015	0.376	0.184	2.046	0.041

The effects of location and age on experienced temperatures were visualized (fig. 3.2) using the following methods. A simulated data set was created, which allowed age to vary from 1-10 for each location while holding the climate variables constant at their mean observed values (annual precipitation = 307.116mm; GDD = 203.363°C*Day). Experienced temperatures were then predicted from the simulated dataset using Model 1 with the predict function in 'base R' (R Core Team, 2023). The resulting predicted experienced temperatures were then plotted with the observed data in Figure 2.

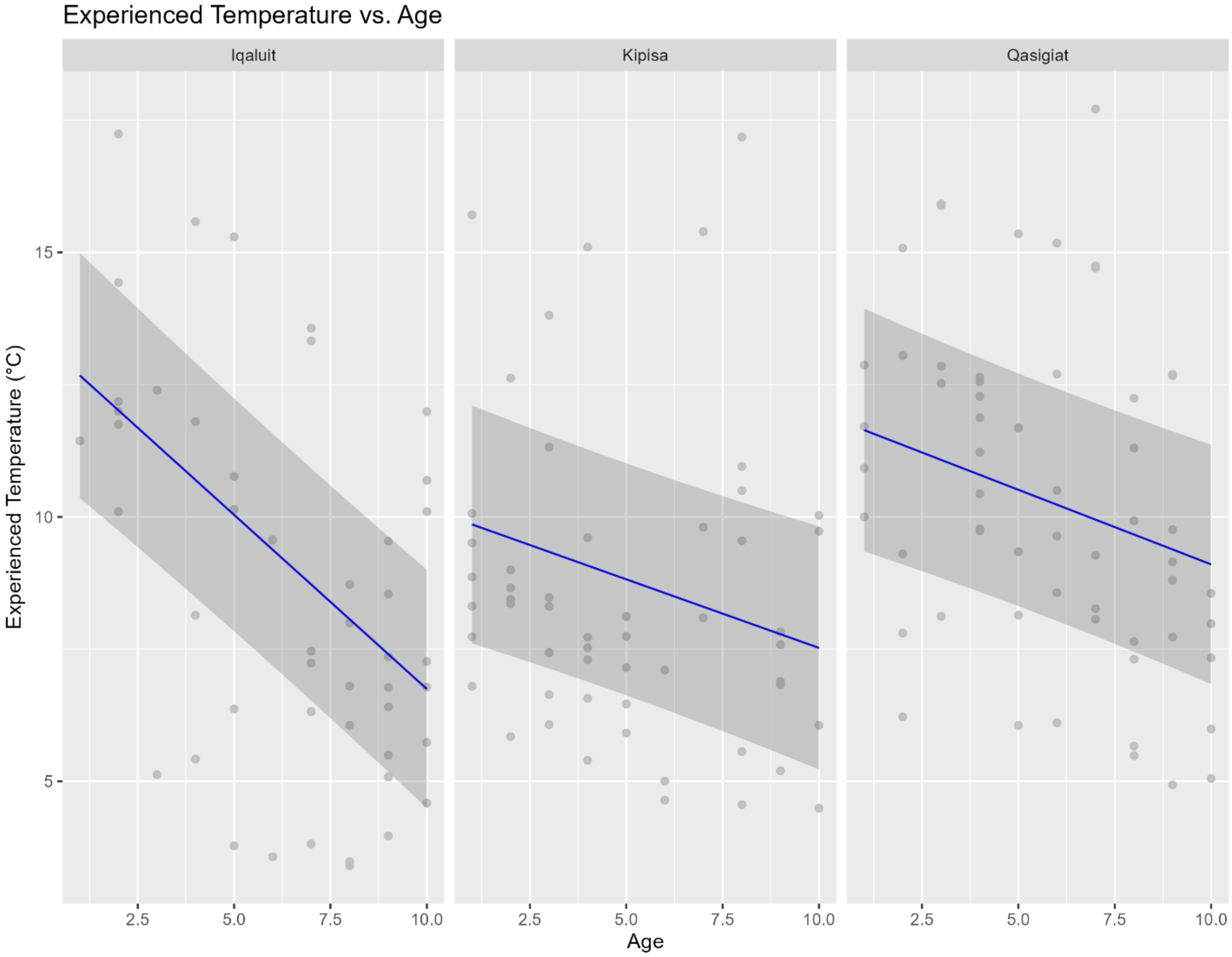

Figure 3.2. A plot showing the effect of age and location on experienced temperature. The predicted experienced temperatures and 95% confidence interval are represented by the blue

lines and grey shaded areas, respectively. The observed experienced temperatures are represented by the grey points.

3.3.3 In Ovo Temperature Model

Experienced temperatures in ovo were found to be normally distributed. The relationship between experienced temperature in ovo and year is linear. Therefore, a simple linear model was used to describe the relationship.

No significant issues were detected during model validation. The k-fold cross-validation output indicated a relatively good model fit and performance with RMSE (root mean squared error) of 2.32°C, MAE (maximum absolute error) of 2.03°C, and an R2 of 0.28. Year was found to have a significant negative influence on experienced temperature in ovo at the 5% level ($p < 0.05$; Table 3.3; Figure 3.3). The model's R2 was found to be 0.17.

Table 3.3. In ovo temperature model summary statistics

	Estimate	Standard Error	T value	P value
Intercept	352.260	145.90	2.41	0.023
Year	-0.172	0.07	-2.36	0.026

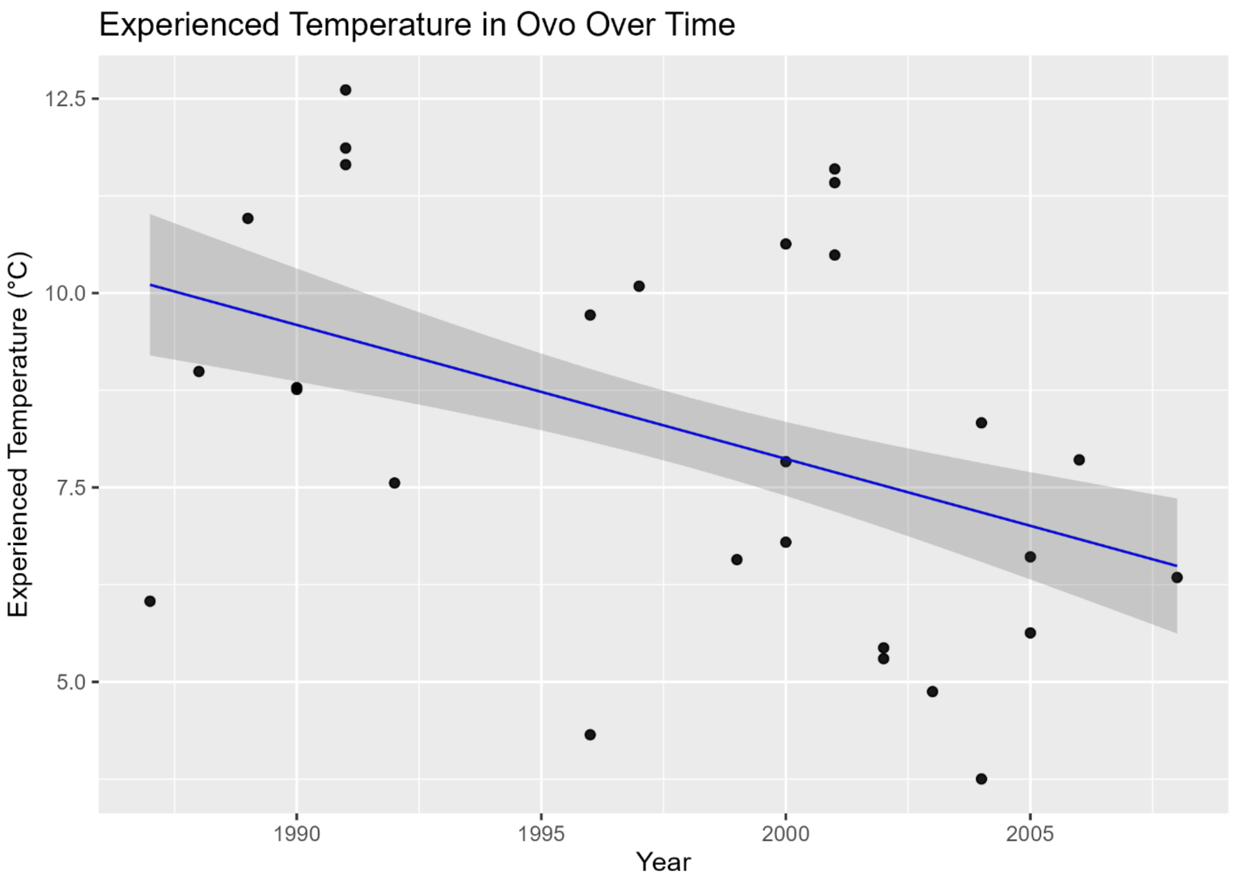

Figure 3.3. Plot showing the relationship between experienced temperature in ovo over the study period. The observed data is represented by the black points. The predicted experienced temperature and 95% confidence interval are represented by the blue line and grey shaded area, respectively. $y = -0.172x + 352.260$

3.4 Discussion

The goal of this chapter was to determine whether experienced temperatures follow trends in GDD and annual precipitation. Contrary to my hypothesis, no significant relationship was found between the climatic variables and experienced temperatures in ages 1-10. In corroboration with this finding, Godiksen et al. (2012) also noted a lack of relationship between experienced temperatures and air temperatures from 1985 to 2005 in juvenile Svalbard charr. Rather, I found age and location accounted for most of the variation in experienced temperatures. These results suggest that during this time period, the extent of thermal stratification in the lakes allowed for variation in age-specific experienced temperatures between lakes, thus reflecting the extent of thermal stratification and shallow juvenile habitats.

Experienced temperatures were found to decrease with increasing age, which is consistent with the idea of ontogenetic shifts in preferred temperatures (e.g., Coutant, 1977; Mccauley & Huggins, 1979; Morita et al., 2010). Godiksen et al. (2012) investigated thermal habitat use in ages 1-4, finding a similar trend of decreasing experienced temperatures with age. Larsson (2005) found that charr had a preference for cooler temperatures with increasing age than what would be considered optimal for growth due to the metabolic trade-off between growth and reproduction at maturity. It has also been hypothesized that preferred temperatures are those that are optimal for growth efficiency rather than growth itself (Larsson & Berglund, 1998, 2005).

In comparison to Iqaluit and Qasigiat, Kipisa charr experienced a narrower range of temperatures from age 1-10, with cooler experienced temperatures early in life, suggesting a cooler juvenile habitat. Qasigiat is described as having very limited littoral habitat, with a deep region (>21 m). Thus, it is hypothesized that rearing occurs in shallow offshoot ponds (Loewen, 2008), where temperatures may be warmer than littoral juvenile habitats in other lakes. Iqaluit lake charr have the greatest range in experienced temperatures, suggesting it may have the most extensive thermal stratification of the study lakes. Iqaluit Lake has been described as being a deep lake (Martin et al., 2023), but whether it is deeper than Qasigiat remains unknown. In Chapter 2, I hypothesized that the larger age-1 radial lengths from Kipisa may be due to a maternal effect. However, when considered with the current findings, it is possible that the cooler juvenile temperatures experienced in Kipisa are more favourable for growth than the warmer conditions of Qasigiat and Iqaluit (i.e., temperatures in Qasigiat and Iqaluit Lake are more metabolically demanding than Kipisa). These findings are consistent with those of Murdoch and Power (2013), where age-specific experienced temperatures were lower in the deeper of their two study lakes. Further, they found that growth-at-age was greater in the deeper lake, possibly owing to the availability of cooler habitats (Murdoch & Power, 2013).

Charr spawning site depth is dependent on the population and varies greatly across its geographic range. For instance, landlocked populations in Europe have been reported to spawn at various depths, depending on the ecotype. Some of these redds have been found in shallow littoral habitats (Low et al., 2011; Skúlason et al., 1989), while others are found at great depths (Klemetsen et al., 1997). River spawning charr tend to construct redds at depths of only 0.5 to 1.5 m (Dempson & Green, 1985). While the exact spawning sites in these study lakes are unknown, Moore (1975) studied spawning sites of two anadromous stocks in the Cumberland Sound region, finding redds between 1 and 11 m of depth. With that said, I assumed here that spawning sites have remained consistent over the time period. Since embryos are immobile, experienced temperatures in ovo were estimated from $\delta^{18}O$ signatures originating from the nucleus to assess changes to lake temperature without the added complexity of behavioural thermoregulation post-hatch. I found that experienced temperatures in ovo have decreased significantly from 1987 to 2008, suggesting lake temperatures at spawning sites have gotten cooler. These results were not expected. I expected that one of two results would be found: spawning site temperatures have (1) gotten warmer, or (2) remained stable. To my knowledge, no studies have found decreasing experienced temperatures (in ovo or otherwise) with climate change. To follow, I propose three hypotheses that may explain such decreases in temperature.

The initial thought was that lake water may be getting colder below the thermocline, due to a high influx of cold meltwater. However, Lake Hazen has received an immense influx of glacial meltwater since 2007 (Lehnherr et al., 2018; Michelutti et al., 2020; St. Pierre et al., 2019), and there is no evidence of this resulting in a cooling trend at depth. In fact, St. Pierre et al. (2019) noted that the temperature of the meltwater warmed by 7°C by the time it reached the lake. In addition, Smol et al. (2005) studied diatom communities in several Arctic lakes, some of which are on Baffin Island. They found that diatom community composition has changed, with declining numbers of benthic taxa typically associated with colder temperatures (Smol et al., 2005). To my knowledge, only one study has found cooling lake bottom temperatures in Pielinen Lake, Finland (Kraemer et al., 2015). Even so, another study noted that a lake of similar size and within 100km of Pielinen found warming trends at depth (Noori et al., 2022). Noori et al. (2022) suggest the discrepancy in bottom temperature trends could be due to the shorter time span investigated for Lake Pielinen (30 years) compared to Lake Kallavesi (56 years).

Another hypothesis is that lake water is warming, but the trend could be explained by higher survival rates of cooler redds. The egg stage is the most vulnerable to warm temperatures, and several studies have found higher mortality in charr as incubation temperatures rise (de March, 1995; Elliott & Elliott, 2010; Koops & Tallman, 2004). de March (1995) found a significant decrease in hatch rate of Arctic charr eggs from 3°C to 6°C. Conversely, Bebak et al. (2000) found that hatching success was high (<90%) for temperatures between 6.5°C and 12°C, but survival to 90 days-post-hatch decreased at temperatures above 11.5°C. Koops and Tallman (2004) found that the highest survival of charr eggs was typically between 4.89°C and 3.54°C across its longitudinal range. With thermoclines becoming steeper and deeper with climate change (Kraemer et al., 2015), warm temperatures may be reaching greater depths. As mentioned prior, research suggests redds are built in relatively shallow water between 1 and 11m in depth on Baffin Island (Moore, 1975). If the redds were typically below the thermocline early on in the time period, and the thermocline is getting deeper, some of the shallower redds may be experiencing warmer conditions, resulting in higher mortality. As a consequence, the results here may not be representative of cooler temperatures, but rather greater survival of individuals originating from cooler redds. However, studies suggest that when temperatures are too high, Arctic charr delay spawning (Gillet, 1991; Jobling et al., 1995) to ensure favourable conditions for incubation, making the argument for poor survival unlikely.

The final and most probable hypothesis is that the isotopic composition of the lakes has changed over the time period in response to climate change. Since $\delta^{18}O$ has an inverse relationship with temperature, $\delta^{18}O$ enrichment in lakes would result in cooler estimated temperatures. When estimating experienced temperatures from otoliths, water samples are typically collected in concert with fish sampling (e.g., Godiksen et al., 2011, 2012; Murdoch & Power, 2013), reducing estimation errors. However, the otoliths used in the current study were collected for stock assessment efforts, where water sampling is not required. Subsequently, a surrogate water $\delta^{18}O$ value from 1994 was found in Gorbey et al. (2022) from a nearby lake and used to estimate temperatures across the time series (1989-2013). Water $\delta^{18}O$ values are crucial for estimating temperatures, as the proportion of $\delta^{18}O$ from the environment that is incorporated into the otolith is dependent on temperature. Thus, if the environment has a higher concentration of $\delta^{18}O$, the otolith will reflect this. As such, temperatures may be underestimated in later years if the $\delta^{18}O$ of the lakes has increased. Cluett and Thomas (2020) explain that in general, the concentration of $\delta^{18}O$ in lakes is influenced by two processes: inflow and evaporation, typically one more dominant than the other. Lakes in areas of high precipitation are likely primarily influenced by precipitation, whereas those in dry areas are more influenced by evaporation (Cluett & Thomas, 2020). For instance, in regions with low summer precipitation, such as inland Greenland, lakes were found to be more sensitive to evaporative enrichment, where lighter isotopes are preferentially removed via evaporation (Cluett & Thomas, 2020; Gorbey et al., 2022). In contrast, coastal Greenlandic lakes were more sensitive to precipitation, due to higher humidity and precipitation (Cluett & Thomas, 2020; Gorbey et al., 2022). Gorbey et al. (2022) found that in general, Baffin Island lake $\delta^{18}O$ values fell along the local meteoric water lines, meaning the isotopic compositions closely match those of local precipitation. Another factor that influences lake water isotopes is water residence times (Gorbey et al., 2022). This is the time it takes for the water in a lake to be replaced and is typically shorter in flow-through lakes, such as those in the current study, than in closed systems (Gorbey et al., 2022). Lakes with short residence times, like those on Baffin Island, tend to be more representative of seasonal rather than annual precipitation (Gorbey et al., 2022). Akers et al. (2024) investigated temporal changes in lake isotopes in Greenland and found greater evaporative enrichment across most of their 20 study lakes in 2019 compared to 2018. 2019 was a particularly hot and dry summer and had a longer ice-free season, making conditions more favourable for evaporation (Akers et al., 2024). While evaporation seems to have less of an influence on Baffin Island (Gorbey et al., 2022), the longer ice-free seasons, higher summer precipitation and short residence times in the area point towards $\delta^{18}O$ enrichment, regardless of the dominant process, and a reflection of summer climate trends. Additional lake $\delta^{18}O$ values across the time period would be necessary for estimating more accurate estimated experienced temperatures and to rule out $\delta^{18}O$ enrichment of the study lakes.

Caution should be used when interpreting any of the results from this chapter, as the estimated temperatures themselves and/or relationship to climate variables may be inaccurate. Based on these hypotheses and the support (or lack thereof) from the literature, it is unlikely that water temperatures have been getting cooler as suggested by the in ovo temperature model. Most probably, surface waters have increased in temperature, but temperatures at depth have remained cool.

3.5 Conclusion

No significant relationship was found between climate variables and GDD in Model 3.1. However, the estimated temperatures from otolith $\delta^{18}O$ may be erroneous due to the use of a surrogate $\delta^{18}O$ for a nearby lake from a single year early on in the 30-year time period. Likewise, the decreasing experienced temperatures in ovo may not be representative of the true change in temperature occurring at spawning sites. In consequence, drawing conclusions from these results should be done with caution, as the effects of climate variables and time on experienced temperatures may be capturing changes in lake isotopic composition resulting from climate change. With that said, the effects of age class and location likely are capturing true effects. In all lakes, experienced temperatures were found to decrease with age, consistent with ontogenetic shifts in habitat use and metabolic needs. The range in experienced temperatures, however, differed between locations, suggesting varying extents of thermal stratification and juvenile habitat. From these findings, it can be assumed that the increases in growth found in Chapter 2 are likely the result of longer growing seasons. However, it cannot be ruled out that the metabolic rates of younger age classes are increasing due to warming shallow habitats. Future research efforts should be focused on gleaning more information about the habitats of Cumberland Sound Arctic charr. Specifically, there is a lack of information on lake morphometry, thermal regimes, and the locations and extent of critical spawning and juvenile habitats in the region. Without this information, it is quite difficult to assess the species' risk to climate change.

3.6 References

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4. Conclusion

4.1 Overview

Climate change is occurring at an unprecedented rate in the Arctic (AMAP, 2021). As a result, the Arctic is experiencing warmer temperatures, more rainfall, less snowfall, and longer ice-free seasons (AMAP, 2021). Physiological rates of ectotherms are closely linked to environmental temperatures, putting cold-adapted species like Arctic charr at risk of climate-related impacts. Initial warming may lead to increased growth rates, but once temperatures exceed the optimum for growth, it is expected that the growth rate will decline as energy is diverted towards maintaining and supporting critical bodily functions. Arctic charr (charr, hereafter) is an ideal model species for investigating the impacts of climate change on ectotherms as they are cold-adapted, live in environments highly impacted by warming, are unable to expand their range, and are typically the sole fish species in the freshwater environment. Thus, the response of charr to climate change can be studied without the added complexities of interspecific competition and range expansion.

In Chapter 2, I investigated changes in age-specific growth of three Cumberland Sound charr stocks relative to climate change between 1984 and 2013. Otolith growth measurements were taken from 594 otoliths and used as a proxy for age-specific growth via annulus lengths (ages 2-10) and age-1 radius lengths. I performed a trend analysis on age-specific growth to establish how and whether growth has changed over the time period. I found significant increasing trends only in ages 1-6 and 8, suggesting the pre-migratory age classes restricted to the freshwater environment may be the most vulnerable to climate change. A generalized additive mixed model was used to describe growth changes in ages 2-10 in relation to growing degree days

(GDD=°C*Day, base 4°C) and annual precipitation (mm). Age-1 radius, however, was modelled using a generalized linear mixed-effect model. Both models indicated that growth had a positive relationship with GDD and a negative relationship with annual precipitation. GDD had the most prominent effect in ages 1-6, coinciding with pre-migratory ages. Annual precipitation had a more variable effect across ages, primarily affecting ages 2 and 6-10 with marginal effects on ages 3-5. Growth between stocks varied the most for ages 1-6, with Qasigiat having the largest annulus lengths (ages 2-6) and Kipisa having the largest age-1 radius lengths. This variation is likely due to differences in lake habitats such as maximum depth, extent of thermal stratification, and quality of the juvenile habitat.

Chapter 3 aimed to determine whether the changes in growth described in Chapter 2 were related to warmer temperatures raising metabolic rates, or greater feeding opportunities related to longer growing seasons. From a subset of 36 otoliths used in Chapter 2, I estimated age-specific experienced summer temperatures from otolith $\delta^{18}O$ and a species-specific fractionation equation (Godiksen et al., 2010). I used a generalized linear mixed model to investigate the relationship between otolith-estimated summer temperatures and the aforementioned climate variables (GDD and annual precipitation) across age classes. I found no relationship between experienced temperatures and the climate variables, suggesting experienced temperatures were independent of the climate. However, significant differences in age-specific experienced temperatures were found between stocks. Since charr live in heterogeneous environments and are motile, I performed a linear regression between experienced temperatures in ovo (i.e., derived from the nucleus) and year (1987-2008) to investigate changes in littoral temperatures and as a way to control for behavioural thermoregulation. I anticipated finding either increasing or stable temperatures over the time period. However, I instead found that otolith-estimated temperatures in ovo had decreased between 1987 and 2008. I could not find any evidence in the literature to support cooling lake temperatures or incubation temperatures with Arctic warming. Instead, I believe what is seen here is progressive $\delta^{18}O$ enrichment of the study lakes, allowing for higher levels of $\delta^{18}O$ in the otolith, which appear as cooler temperatures when only one $\delta^{18}O$ value is used for temperature estimation across a long time period. While caution should be taken when interpreting the result of Chapter 3 due to suspected inaccuracies of the temperature estimations, I believe it is highly unlikely that the study lakes are warming to great depths. Rather, it is more likely that surface waters are warming while cool habitats persist at depth. This is supported by my finding of decreasing experienced summer temperatures with age, consistent with the idea of ontogenetic shifts in preferred temperatures (e.g., Coutant 1977; Mccauley and Huggins 1979; Morita et al. 2010).

When considering the findings from both chapters together, I hypothesize that the increased growth seen in ages 1-6 across the time period was likely a combined effect of increased metabolic rates from warmer conditions and longer growing seasons. Particularly, the youngest age-classes may be experiencing increased growth due to the warming conditions of shallow juvenile habitats, while the older age classes are more probably experiencing greater growth due to longer growing seasons, which allows for longer periods of feeding before winter dormancy. This is based on the idea that habitat selection is determined by both the risk of predation and food availability (Damsgård & Ugedal, 1997). For example, younger and smaller individuals may endure warming conditions to avoid predation in deeper and cooler habitats. However, as individuals get larger, their risk of predation decreases, allowing them to move more freely throughout the water column. Overall, my findings suggest that charr in Cumberland Sound have indeed experienced increases in growth in relation to climate change. However, increased growth was primarily found in pre-migratory ages (1-6), suggesting disproportionate effects of climate change on the freshwater environment.

4.2 Limitations

While my study provides valuable findings, it does not come without limitations. In Chapter 2, I was able to detect positive trends in age-specific growth, but it is unclear what that trend translates to in terms of growth in body length. This could have been achieved with the use of a back-calculated growth model, however, I lacked the necessary data to apply such a model. Studies have also found uncoupling between otolith and somatic growth in salmonids (Morrison et al., 2019; Wright et al., 1990). The nature of this phenomenon can go two ways: somatic growth halts while the otolith growth continues (Wright et al., 1990), or somatic growth increases at a greater rate than otolith growth (Morrison et al., 2019). Thereby, it is difficult to interpret the extent growth has increased.

As mentioned in Chapter 3, limitations also arose in the otolith-estimated temperature analysis. I employed a species-specific fractionation equation (Godiksen et al., 2010) to convert otolith $\delta^{18}O$ values from summer growth bands to temperature data using a $\delta^{18}O$ water value sampled in 1994 from a nearby lake. However, the literature suggests $\delta^{18}O$ enrichment is occurring in Arctic lakes (Akers et al., 2024; Cluett & Thomas, 2020; Gorbey et al., 2022). Thus, there is a high probability for spatiotemporal variation in $\delta^{18}O$ water values, introducing error to the fractionation equation. With that in mind, it is not likely that water temperatures have gotten cooler over time, but that $\delta^{18}O$ enrichment of the lakes is occurring. While it is difficult to draw strong conclusions from the results of Chapter 3, it is apparent that there is a gradient in experienced temperatures across ages in each lake. This finding is consistent with the idea of ontogenetic shifts in temperature preference and suggests some extent of thermal stratification within the study lakes. Additional water $\delta^{18}O$ values would be required across the time period to account for isotopic enrichment. It may also be possible to estimate the change in water $\delta^{18}O$ across the period if we can determine the rate of enrichment. However, I have yet to find information in the literature that would allow for such estimations.

4.3 Significance

To my knowledge, this is the first study to describe climate-induced changes to Arctic charr growth relative to thermal habitat use on Baffin Island. The results of my thesis demonstrate the ability of ectotherms to adapt to a changing climate via physiological (Seebacher et al., 2015) and behavioural changes (Barton et al., 2014). The lack of a relationship between GDD and otolith-estimated experienced temperature is suggestive of behavioural thermoregulation. If Arctic charr continued to occupy the same depths and habitats, there would likely be changes in experienced temperature with warming. As a result, some extent of deepening is likely occurring within the study lakes. However, I suspect that the decreasing experienced temperatures in ovo over time are a reflection of $\delta^{18}O$ enrichment of the study lakes with climate change.

Arctic charr are an invaluable resource to Inuit communities, providing a reliable source of income via commercial fisheries and food security via subsistence harvest. My findings underline the importance of long-term growth studies in the management of fisheries in a changing climate. For example, while I found significant increases in growth, the assessments of these stocks found none (DFO, 2005, 2013, 2023). These assessments only use around 5 years of data, which is likely too short a time period to detect changes in growth. In addition, sampling typically targets migratory charr in the marine environment, with subsequent analyses looking at length- and age-at-capture. Thus, the assessments effectively missed the changes in the growth of pre-migratory charr. By using otolith growth measurements, I was able to take a deeper look into growth across the lifespan of the sampled individuals. It is critical to understand the bigger picture, rather than only studying the fishable stock to identify vulnerable age classes. My results suggest climate change has had a disproportionate effect on the freshwater environment, which may mean pre-migratory individuals are most vulnerable. If temperatures become too warm, juvenile mortality may increase, resulting in later recruitment failures.

4.4 Future Directions

The findings of my thesis also highlight critical knowledge gaps in the habitats and life history of Cumberland Sound Arctic charr. Future research should be directed toward closing knowledge gaps related to lake characteristics, including bathymetry, thermal regime, and identification of spawning sites. Each of these pieces of information would provide critical insight into the results found in my thesis. Bathymetric and thermal regime data could be used to determine the extent of thermal stratification (i.e., thermal refugia) and whether seasonal mixing is occurring. The location of spawning sites is also largely unknown around Cumberland Sound. Critical habitats such as spawning sites should be the focus of conservation and management efforts, as the egg stage is the most vulnerable developmental stage to warming. Timing of ice break-up, migration, and spawning should also be examined to determine if Arctic charr is indeed occupying the marine habitats for longer periods.

The literature suggests $\delta^{18}O$ enrichment is occurring in the Arctic, however, I could not find any long-term studies to infer the rate of enrichment. In order to use otolith-estimated temperatures for long-term studies, routine water sampling for $\delta^{18}O$ should be implemented in coincidence with fish sampling. Water sampling for isotopic composition is relatively cost-effective, as only 50 ml of water is required (Godiksen et al., 2011), and the analysis itself is only around $30 (CAD) per sample (MIRF, 2020).

4.5 References

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