

Effects of temperature on the growth of
Arctic charr *Salvelinus alpinus* in Ungava
and Labrador, Canada

by

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Arctic surface air temperatures have been warming at twice the global rate, making it one of the most susceptible regions to current climate change. Effects on cold-adapted aquatic species, such as the culturally and ecologically important Arctic charr (*Salvelinus alpinus*), are difficult to anticipate and may vary depending on site-specific attributes. Temperature has a direct influence on aspects of species' fitness, including growth, reproduction and, ultimately, survival. Previous research on temperature-growth patterns in Arctic charr has yielded variable results, particularly for studies observing these patterns in the wild. Two field-based studies are presented in this thesis, in an attempt to better understand temperature-growth patterns for wild populations of Arctic charr.

In the first study, individual measurements of annual, or within-season growth were determined from tag-recaptured Arctic charr and examined in relation to summer sea surface temperatures and within-season capture timing in the Ungava and Labrador regions of eastern Canada. Differences in among-year growth were significant for Ungava Bay Arctic charr, with growth being positively correlated with temperature. Growth of Labrador Arctic charr did not vary significantly among years. Regional comparisons demonstrated that Ungava Arctic charr had significantly higher annual growth rates, with differences among years in all regions being positively correlated with temperature. Within-season growth rates of Labrador Arctic charr peaked in June, declined toward August, and were negatively correlated with the length of time spent at sea and mean experienced sea surface temperatures. A quadratic model relating growth rate to temperature best explained the pattern of within-season growth. The higher annual growth of Ungava Bay Arctic charr was attributed to the high sea surface temperatures experienced in 2010-11 and the localized differences in nearshore productivity as compared to Labrador. Results suggest that increases in water temperature may have profound consequences for Arctic charr

growth in the Canadian sub-Arctic, depending on the responses of local marine productivity to those same temperature increases.

In the second study, oxygen stable isotope temperature reconstruction methods were used to estimate mean experienced summer temperatures from growth zones within individual otoliths of Arctic charr sampled from contrasting lake environments. For either lake, otolith-estimated temperatures were not significantly related to back-calculated growth. Significant negative effects on back-calculated growth were observed due to increasing air temperatures in the smaller lake, owing to warmer surface waters and a limited amount of preferred cool-water habitat available. A similar relationship was not observed in the larger lake, indicating that the cooler, deeper lake provides ample preferred cool-water habitat for Arctic charr despite climate warming. In addition, young-of-the-year temperatures negatively related to zone 2 growth for the smaller lake, whereas no significant correlation was found for the larger lake. Results here provide evidence for differing climate-influenced growth outcomes depending on the site-specific fish density: preferred thermal habitat volume ratio as dictated by local attributes including lake morphometry, upstream catchment area and life-history strategy.

Conclusions from this thesis include the increased need for detailed site- and population-specific assessments of the impacts of increasing temperatures on Arctic charr growth. Better understanding of the drivers of temperature-growth relationships in wild Arctic charr populations will facilitate more accurate stock forecasts with the overall goal of sustaining exploited Arctic charr populations as the climate warms and becomes increasingly variable.

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Chapter 1

General Introduction

1.1 An Overview of Climate Change Effects on Arctic Fish

The Arctic is considered to be one of the most at risk regions due to current climate change (ACIA 2005; Anisimov et al. 2007). Arctic surface air temperatures have been warming at twice the global rate and may have some potentially catastrophic effects on cold-adapted resident species (e.g., McDonald et al. 1996; Chu et al. 2005; Sharma et al. 2007). For high-latitude aquatic ecosystems, the possible effects of increasing temperatures may include changes in: seasonal phenologies (e.g., length of the ice-free season), ecosystem productivity, species ranges and distributions, and the frequency and severity of extreme weather events, with the latter holding implications for flow regimes, water levels, and annual water balance (ACIA 2005; Anisimov et al. 2007).

Increasing temperatures will have direct and indirect effects on fish species (Reist et al. 2006a). The importance of temperature for fish physiology and behavior has been well documented in the scientific literature, with temperature known to be an important controlling factor for individual growth, reproduction and survival that may also impact inter-specific interactions such as niche partitioning, competition and predation (e.g., Jobling 1983; Baroudy and Elliott 1994; Anderson et al. 2001; Finstad et al. 2011). A detailed overview of predicted climate change effects on Arctic fish species is found in Reist et al. (2006a; 2006b). Briefly, effects may include: increased growth and overwintering survival, changes in anadromy, increased competition and/or predation from warmer water species, northward or vertical (increased altitude or depth) range expansions where accessibility to new habitat is permitted, longer ice-free seasons, local extinctions or introductions, and the introduction of new diseases. However, accurate species-specific forecasts are difficult to make as climate change will affect both abiotic and biotic processes simultaneously, and will thus depend on how multiple ecosystem levels respond and interact as

climate varies. To predict how increasing temperatures may influence fish population dynamics, base-line monitoring of water temperature and biological data are required. Yet, long-term water temperature datasets in the Arctic are scarce, particularly for freshwater and nearshore marine areas where many fish species congregate (Dempson and Kristofferson 1987; Power et al. 2008).

1.2 Temperature and Growth

As fish are obligate poikilotherms (ectotherms), body temperature is closely linked to fluctuations in ambient water temperature. Metabolic heat produced is quickly lost to the environment and does not aid in internal temperature regulation (Brett 1971). As such, fishes can detect small differences in ambient water temperature ($<0.5^{\circ}\text{C}$) (Murray 1971), and may actively seek temperatures with the maximum physiological benefit for individual fitness (e.g., Brett 1971; Beitinger and Fitzpatrick 1979; Jobling 1981). Body size may affect individual sensitivity to changes in water temperature, with smaller fish being the most susceptible to changes in temperature due to the higher surface area:volume ratio which facilitates more rapid heat exchange with ambient water temperature (e.g., Elliott 1981).

Temperature has direct repercussions for fish growth and survival, and an optimal range of temperatures for maximum growth and critical limits for feeding and survival may be determined in a controlled laboratory setting (e.g., Jobling 1983; Baroudy and Elliott 1994). A non-linear temperature-growth curve is often demonstrated for fish species, with temperature and growth being positively correlated up until an optimal range, after which they are negatively related (Brett 1971). With increasing temperatures below the optimal point both feeding activity and metabolic rate will increase, promoting an increased growth rate (Elliott 1994). Notably, because energy required for metabolic processes also increases with temperature, the optimal temperature for growth is dynamic, and will be adjusted depending on ration availability (e.g., Elliott and Hurley 2000a; Elliott and Hurley 2000b). Thus, where less food is available, the effective optimal temperature for maximum growth will shift downwards.

Evidence of this food-dependent relationship exists for fish species both in the laboratory (e.g., brown trout, *Salmo trutta*, Elliott and Hurley 2000a; Elliott and Hurley 2000b) and in the wild where fish distributions are largely determined by temperature and productivity (Rudstam and Magnuson 1985; Bailey 1989; Welch et al. 1998).

Indirect effects of temperature may also play an important role in determining growth. Where preferred thermal habitat is limited, fish may demonstrate intra- and/or inter-specific interactions resulting in thermal-based advantages for individuals or species (Gilman et al. 2010). The designation of temperature as a resource has prompted the development of the concept of the thermal niche, where temperature is considered a significant additional axis of the overall multidimensional niche (Magnuson et al. 1979). Thus, the availability and abundance of preferred thermal habitat may determine species' realized habitat use and distribution (e.g., Christie and Regier 1988; Perry et al. 2005) either via niche segregation, competition or predator-prey dynamics, with all mechanisms having potential consequences for growth (e.g., Murawski 1993; Anderson et al. 2001; Beaugrand et al. 2003; Finstad et al. 2011).

Given the importance of temperature for fish growth and the determination of habitat use, better understanding of temperature-related effects on all Arctic resident fish species is required to better predict and understand the possible consequences of climate-warming in the Arctic. Key among the fish species for which such information is required are the ecologically and economically important species, such as Arctic charr (*Salvelinus alpinus*).

1.3 Arctic Charr

1.3.1 Ecology and Importance

The Arctic charr has a circumpolar distribution, and is often the only fish species present in high Arctic and alpine lakes (Johnson 1980). Due to its wide distribution and relative abundance in northern regions,

the anadromous Arctic charr fishery is the most important subsistence fishery for Inuit communities in Arctic Canada. For example, nutritional surveys from Nunavik demonstrate that almost 50% of all meat and alternative food products consumed daily are obtained locally, with Arctic charr making up 16-20% of the country food harvest (Blanchet and Rochette 2008). Furthermore, harvest reports from Nunavut (population = 33,322, Nunavut Bureau of Statistics 2011) indicate that there is a mean annual subsistence harvest totaling 198,611 Arctic charr within the territory (Priest and Usher 2004). In addition, commercial Arctic charr fisheries have been operating in Arctic Canada for several decades, with current reports indicating that over 80 waterbodies were open for commercial operations from April 2010 - March 2011 in Nunavut alone (Roux et al. 2011). Aside from its economic value, Arctic charr also has an important ecological value due to its role as a top predator in many high-latitude watersheds (Hammar 1989; Rouse et al. 1997).

The study of Arctic charr life-history reveals its high habitat flexibility and adaptability, evidenced by its wide colonization of post-glacial habitats characterized by low productivity and often harsh environmental conditions (Power et al. 2008). Arctic charr may exist in various life-history forms such as lacustrine, riverine and partially and fully anadromous (Jonsson and Jonsson 2001; Klemetsen et al. 2003a). Furthermore, several sympatric morphotypes of Arctic charr have been found to co-exist in the absence of other species, with the most extreme case being Lake Thingvallavatn, Iceland, where four concurrent resident morphotypes are present (Sandlund et al. 1992).

Anadromy is common throughout much of the Arctic charr's northern range where local marine habitat is accessible (Johnson 1980; Jensen 1981). Anadromous individuals migrate to seawater during the summer for periods ranging from 5-9 weeks (Johnson 1980; Dempson and Kristofferson 1987; Berg and Berg 1989), after which they return to freshwater for spawning and/or overwintering. Age at first migration is highly variable depending on the population (ages 1-8), as is age-at-maturity, fecundity and spawning periodicity (Johnson 1980; Dempson and Kristofferson 1987; Klemetsen et al. 2003a; Power et

al. 2005). Anadromous individuals often exhibit higher growth rates than their local freshwater counterparts (e.g., Rikardsen et al. 2000), a result attributable to the higher quality and quantity of food available in the marine environment.

Although Arctic charr is not considered an at-risk species throughout the majority of its range (IUCN designation = least concern species, IUCN 2011), it is considered vulnerable in many areas, particularly in its southern range where impacts from human development are high. Accordingly, declining Arctic charr populations have been identified in Britain and Ireland (Igoe et al. 2003; Maitland et al. 2007; Winfield et al. 2010) and Iceland (Malmquist et al. 2009). Current threats associated with Arctic charr declines include species introductions, habitat loss and alteration, eutrophication, acidification and climate change (Igoe et al. 2003; Maitland et al. 2007).

1.3.2 Temperature and Growth

The effect of varying temperature on the growth of Arctic charr is well understood in the context of a controlled laboratory setting where ration is unlimited (Jobling 1983; Larsson and Berglund 1998; Larsson et al. 2005). Arctic charr is one of the most cold-adapted members of the salmonid family, with feeding and growth occurring at temperatures as low as 0.2°C (Klemetsen et al. 2003b). Growth is positively correlated with temperature up to an optimum of between 13-18°C, after which it rapidly declines (e.g., Jobling 1983; Larsson and Berglund 1998; Larsson et al. 2005). Further, Arctic charr is one of the least resistant salmonids to high temperatures, with temperatures over 21-22°C suppressing feeding and growth, and those > 22°C affecting survival (Elliott and Elliott 2010). However, comparable research using brown trout has demonstrated the importance of varying ration on the temperature-growth relationship, with the optimal temperature for growth decreasing with ration (Elliott and Hurley 2000b). As current laboratory research studying temperature-growth relationships for Arctic charr has not

systematically varied ration, it is unknown whether optimal temperatures for growth may differ in natural settings where food availability fluctuates.

Studies have indicated that in the wild Arctic charr display preferences for temperatures lower than laboratory reported optima (10.7-11.8°C, Larsson 2005; Rikardsen et al. 2007), despite the availability of warmer water. One explanation is that Arctic charr select temperatures closer to the optimal temperature for growth efficiency (9°C, Larsson and Berglund 2005) as an adaptation for maximizing growth while living in food limited environments. Population-level studies of temperature effects on Arctic charr growth in a natural setting have also reported variable results that differ from controlled laboratory responses, with both positive and negative temperature-growth correlations having been observed (Power et al. 2000; Kristensen et al. 2006; Michaud et al. 2010). Examinations of within-season growth of anadromous Arctic charr have further demonstrated a tendency for high early-season growth that coincides with lower experienced temperatures (Berg and Berg 1989; Rikardsen et al. 2000). Finally, research on conditional inter-specific effects has indicated that Arctic charr may have a growth advantage at lower temperatures in the presence of competitor species such as brown trout (Finstad et al. 2011). Thus, there is an evident discrepancy between laboratory predicted-optima based on juveniles grown in freshwater facilities on full ration, and temperature-growth relationships observed in wild populations that vary in life-history tactics, age (size), and ration opportunity.

One explanation for the discrepancy is that most attempts to examine temperature-growth relationships for Arctic charr have focused on population-level relationships using mean population growth and temperature data (Power et al. 2000; Chavarie et al. 2010; Michaud et al. 2010) that disregards consideration of intra-population variability and does not uniquely link temperature-growth patterns in a manner akin to laboratory studies. Thus, more detailed investigation of individual temperature-growth relationships *in situ* is necessary to facilitate a better understanding of the uncertainties associated with predicting Arctic charr responses to climate warming in natural settings.

1.4 Thesis Overview

Based on the above, the overall goal of this thesis is to improve understanding of temperature-growth patterns in individual wild Arctic charr and to attempt to reconcile differences between previous investigations of the temperature-growth relationship conducted in both laboratory and field settings. Increased knowledge of how Arctic charr growth will respond to temperature variability *in situ* is critical for accurate population- or site-specific forecasts of the likely impacts of climate warming and, ultimately, for abilities to maintain exploited Arctic charr populations in the face of climate change.

The effects of temperature on growth will be investigated in two adjacent regions of sub-Arctic Canada in Chapter 2, and then between two adjacent lake populations residing in lakes with differing climatic vulnerabilities (shallow vs. deep) in Chapter 3. Chapter 2 will focus on an anadromous population in southern Ungava Bay (Nepihjee River) and compare it to an anadromous population from Hebron Fiord in northern Labrador. The study utilizes individual growth data collected from Arctic charr tagging experiments and associated sea surface temperatures obtained from extended reconstructed SST data interpolation methods (Smith et al. 2008). The chapter will also compare temperature-growth patterns of annual and within-season growth for Labrador Arctic charr using within season growth data obtained from tagging experiments completed at Nain, Labrador. The working hypotheses of Chapter 2 were that increases in annual temperature would produce increased growth, whereas within-season growth would be negatively correlated with temperature due to the tendency for high early-season growth coinciding with low temperatures.

Chapter 3 focuses on individual thermal regimes and their implications for growth as inferred from an examination of otolith microstructure. Data for the study were obtained from two adjacent lake-dwelling Arctic charr populations residing in southern Ungava lakes with differing vulnerabilities to climate change. Rather than using large-scale temperature data to approximate individual thermal use, oxygen-

stable isotope analysis was employed for calculating individually experienced mean summer temperatures. Corresponding back-calculated growth increments were then calculated from the otolith for growth-temperature comparisons. The main hypothesis for this chapter was that Arctic charr in the smaller, shallower lake would display a negative relationship between back-calculated growth and otolith-estimated temperature due to its enhanced vulnerability, whereas Arctic charr in the larger, deeper lake would demonstrate a positive correlation. In addition, we predicted that increasing air temperatures would have negative and null effects on back-calculated growth for fish obtained from the smaller and larger lakes, respectively, due to the differential impact of warming on the available volume of preferred thermal habitat in either lake.

Chapter 2

Temperature-growth patterns of tagged anadromous Arctic charr

2.1 Introduction

Surface air temperatures in the Arctic have been warming at twice the global rate over the past several decades (ACIA 2005; Solomon *et al.*, 2007), with direct consequences for marine and freshwater environments (Reist *et al.*, 2006a, 2006b; Anisimov *et al.*, 2007). For Arctic fish species in particular, climate change effects are predicted to range from mainly positive to negative depending on species' adaptability, local conditions and the rate and magnitude of the changes in climatic variability (Reist *et al.*, 2006b). Projected increases in temperature may drive multiple ecosystem and species shifts, with predicted outcomes including: increases in species growth or overwintering survival, northward range extensions, increases in competition, changes in anadromous behaviour, and local rapid natural selection or extinction (Reist *et al.*, 2006a, 2006b, and references therein). As a result, major international collaborative efforts have been directed towards increasing understanding of potential climatic effects on species and ecosystems in the north, (e.g., Arctic Climate Impact Assessment (2005), Intergovernmental Panel on Climate Change, Fourth Assessment Report: Climate Change 2007 (Pachauri and Reisinger, 2007)). These projects underline the importance of understanding how species will adapt to climate change in order to aid the management of populations facing an uncertain and increasingly variable climate.

The Arctic charr *Salvelinus alpinus* is a cold-adapted species that is widely distributed across northern regions (Johnson, 1980) and forecasted to be significantly affected by climate change (Lehtonen, 1996, 1998). Arctic charr is heavily depended on by northern communities particularly for subsistence use, but also for commercial purposes in some locales (Dempson, 1995; Priest and Usher, 2004; Roux *et al.*, 2011). Growth pattern differences among Arctic charr have been previously attributed to varying life-history strategies (Naslund *et al.*, 1993; Rikardsen *et al.*, 2000; Power *et al.*, 2005), environmental

conditions (Power *et al.*, 2000; Kristensen *et al.*, 2006; Michaud *et al.*, 2010), inter-specific interactions (Fraser and Power, 1989), and local resource availability (Dempson *et al.*, 2002, 2008). The influence of temperature on attributes such as growth has also been demonstrated in the wild for many other fish species, including Atlantic salmon *Salmo salar* (Power, 1981; Scarnecchia, 1984), Atlantic herring *Clupea harengus harengus* (Anthony and Fogarty, 1985), Atlantic cod *Gadus morhua* (Brander, 1995; Dutil *et al.*, 1999; Drinkwater, 2005; Arnason *et al.*, 2009) and some Pacific salmon species (Beamish, 1993; Beamish *et al.*, 1997) and is well understood in the context of aquaculture settings where ration and photoperiod covariates can be experimentally controlled (e.g., Johnston, 2002).

The influence of temperature on Arctic charr growth in particular has been well documented by laboratory research (Jobling, 1983; Larsson and Berglund, 1998; Larsson *et al.*, 2005). Experiments with juvenile Arctic charr in freshwater facilities have shown that growth occurs just above freezing, increasing to an optimum at temperatures between 13-18°C, after which it rapidly declines (Jobling, 1983; Larsson and Berglund, 1998; Larsson *et al.*, 2005). Reported upper thresholds for growth vary from 20-23°C, making Arctic charr one of the least resistant salmonids to high temperatures (Baroudy and Elliott, 1994; Larsson *et al.*, 2005). However, such studies have been conducted under unlimited food conditions and comparable research with food supply variability has documented how the capacity for growth at a given temperature may be limited by ration (Elliott, 1994; Elliott and Hurley, 2000a, 2000b).

In contrast to laboratory-based findings, field-based studies have suggested lower optimal temperatures for Arctic charr growth. For example, Berg and Berg (1989) observed that marine growth and temperature were inversely correlated because of an apparent adaptation to low temperature growth, even under conditions of ration constancy. Other studies have shown Arctic charr to prefer water temperatures of around 11°C, notably lower than laboratory reported optima (Larsson, 2005; Rikardsen *et al.*, 2007). Results have led to the suggestion that wild Arctic charr select temperatures closer to their optimal growth efficiency point (9°C) as an adaptation to living in food variable environments where individuals risk

achieving a reduced scope for growth if they remain at more metabolically expensive temperatures during periods of food shortages (Elliott, 1994; Larsson and Berglund, 1998; Larsson *et al.*, 2005).

As the majority of studies investigating temperature-growth relationships in Arctic charr have been limited to laboratory situations, similar work in the natural environment where food availability fluctuates is generally lacking. Exceptions include some North American studies that examined the variable consequences for growth of local environmental variation, including temperature (Power *et al.*, 2000; Chavarie *et al.*, 2010; Michaud *et al.*, 2010). A limitation of such studies was that they were completed using population-level data, inferring population somatic growth rates from size-at-age averages that disregard intra-population growth variability, and none utilized individual temperature data (Power *et al.*, 2000; Kristensen *et al.*, 2006; Michaud *et al.*, 2010). To overcome these limitations, individual measurements of annual or within-season growth in this study were determined from tag-recaptured Arctic charr and examined in relation to summer sea surface temperature and within-season capture timing. Based on laboratory and existing field-based studies (e.g., Jobling, 1983; Berg and Berg, 1989; Larsson and Berglund, 1998; Rikardsen *et al.*, 2000; Larsson *et al.*, 2005), it was hypothesized that: [1] annual averages for individual fish would reflect a positive correlation between temperature and growth and [2] patterns of within season growth would not be correlated with average experienced temperature as a result of the tendency for early season, low temperature growth (e.g., Berg and Berg, 1989).

2.2 Materials and Methods

2.2.1 Study Sites and Sampling Procedures

Tagging experiments were carried out in the adjacent regions of northern Québec and Labrador in north-eastern Canada (Figure 2.1) during two different time periods. Specifically, anadromous Arctic charr were captured on their upstream migration from the sea, measured for fork-length (mm or cm), tagged and released in either the Nepihjee River, near Dry Bay, Ungava Bay, Québec (58°32'N, 68°15'W) in

2009-10, or the Ikarut River, Hebron Fiord, Labrador (58°12'N, 62°31'W) in 1981-84. Notably, the Dry Bay Arctic charr population is an introduced anadromous population that has been supported over the period 2000-2009 by 0+ hatchery stocking. Hatchery eggs were obtained from Arctic charr in the Finger Lakes (58°34'N, 70°00'W) (e.g., Murdoch et al., in review). Carlin tags were used at Hebron, whereas passive integrated transponder (PIT) tags were employed at Dry Bay. Recaptures were obtained one year later at both sites (Dry Bay: n=122 for 2010-2011; Hebron Fiord: n=72 for 1982-1985) during the return upstream migration where length data were again recorded and used for growth analyses.

Within-season growth data were obtained from Arctic charr tagging experiments carried out during the spring near the village of Nain, Labrador (56°32'N, 61°48'W). Experiments took place in three adjacent bays including Nain Bay, Tikkoatokak Bay, and Webb Bay, hereafter referred to as the Nain stock complex (Dempson and Kristofferson 1987). Individual Arctic charr were angled or gillnetted at river mouths in the nearshore marine environment during ice break-up (May-June), measured (mm), and subsequently recaptured from the commercial fishery at sea later in the season (n=742 recaptures, 1979-1987).

2.2.2 Measuring Growth

For the Dry Bay-Hebron comparisons, individual annual absolute growth was calculated as:

$$\Delta L = L_{\text{recap}} - L_{\text{tag}} \quad (1)$$

For the Nain stock complex, individual within-season growth rates were calculated as:

$$G = \frac{L_{\text{recap}} - L_{\text{tag}}}{\text{days free}} \quad (2)$$

ΔL is the annual absolute growth (mm), G is the individual within-season growth rate (mm/day), L_{recap} is length at recapture (mm), L_{tag} is length at tag release (mm), and days free is the total number of days

between tagging and recapture within a growing season. Fish lengths used for analyses were between 300-550mm (Hebron and Dry Bay) and 350-660mm (Nain).

2.2.3 Temperature Data

Sea surface temperature data (SST) were obtained from the National Oceanic and Atmospheric Administration (NOAA) website (<http://www.esrl.noaa.gov/psd/data/gridded/>), using the NOAA Extended Reconstructed Sea Surface Temperature (SST) V3b dataset. The dataset provides monthly SST data on a 2°x2° grid with temporal coverage from 1854 to the present. Long-term monthly means measured from 1971-2000 were also obtained to assess temperature anomalies, but were not used in growth-temperature analyses.

Mean summer SSTs were computed as weighted averages of relevant data for the period May 15 - August 15 for Hebron Arctic charr (Dempson, 1995; Power et al., 2000), and June 1 - August 31 for Dry Bay Arctic charr (Boivin, 1994; Nunavik Research Centre unpubl. data), with chosen periods being reflective of the general period when the fish are in the marine environment in each region. For within-season growth-temperature analyses, individual mean temperatures were calculated using weighted averages computed for the calendar dates between tagging and re-capture as follows:

$$\text{Individual mean temperature} = [(days\ at\ sea\ in\ May \times May\ SST) + (days\ at\ sea\ in\ June \times June\ SST) \dots + (days\ at\ sea\ in\ September \times September\ SST)] / \text{total number of days at sea} \quad (3)$$

The NOAA SST data were compared with local temperature data recorded in nearshore marine areas proximate to the experimental tagging sites. Temperature data collected from fixed water column temperature recorders in nearshore areas may be more reflective of the thermal regimes experienced by Arctic charr than the NOAA-derived data as Arctic charr are often known to reside close to shore during the period of marine residency (Dempson and Kristofferson, 1987). In addition, as the NOAA data encompasses a larger off-shore area the data may not appropriately reflect local-scale temperature

fluctuations. However, as nearshore temperature logger data were not consistently recorded by site or year, the logger data could not be used for growth-temperature analyses. To investigate potential biases in the temperature data, linear regression was used to test for significant linear relationships between the NOAA and logger data recorded near Nain, Labrador, and to determine whether regression intercepts and slopes, respectively, deviated significantly from zero and unity (Zar, 2010). Regression analyses supported the supposition that the relationship between the data sets was not significantly different from a 1:1 line (t -test $P \geq 0.13$ for slope = 1 test; t -test $P \geq 0.08$ for intercept = 0 test), thereby validating the use of NOAA data as a proxy for nearshore water column temperatures in Labrador. Similar analyses were not made for Hebron or Dry Bay owing to the paucity of annual water column temperature data collected at either site.

Logger temperature data used in the comparative analysis discussed above were collected from thermographs deployed during summer months near Nain, in Tikkoatokak Bay and Loon Bay (outer Nain Bay) in July-August, 1985-2007. Thermographs were deployed at depths of 3-5m. Temperature data from Tikoatokak Bay and Loon Bay were averaged prior to comparison with NOAA data for the region.

2.2.4 Statistical Analyses

Annual growth (ΔL) data were examined by analysis of covariance (ANCOVA), with length-at-tagging used as the covariate. Annual growth was analyzed by year and site, with all years of growth pooled within sites for the between-site comparisons. Tests for heterogeneity of slopes among years for each site were examined by fitting a model with an interaction between each factor variable and covariate. Where the interaction term was found to be non-significant, it was subsequently removed from further analyses. Finally, multiple regression methods were used to determine correlations between within- and among-site ΔL means with mean summer SST data, using initial length as an additional independent variable.

For the within-season growth rate (G) analysis of spring-tagged Nain Arctic charr, data were pooled among years and G was \log_{10} transformed to stabilize the data variance (Zar, 2010). A preliminary analysis found that length at tagging contributed little (5%) to the within-season variation in growth rate and it was not included in subsequent analyses as a covariate.

The relationship between individual within-season growth rates and temperature was investigated in two ways. First, linear regression evaluated the consistency of an overall effect of experienced temperatures on individual growth rates, with G estimated as a quadratic function of SST and the resulting regression assessed for statistical adequacy (Zar, 2010). An alternative analysis sorted individuals into temperature groupings (e.g. intervals of 0.5°C over the range of $1\text{-}4^{\circ}\text{C}$) reflective of the estimated temperatures those individuals had experienced while in the marine environment. All individuals having experienced temperatures $\leq 1^{\circ}\text{C}$ were grouped in a single category to ensure a minimum group size of $n=30$. Individual growth rate data (G) were then analysed using ANOVA, followed by Tukey's post-hoc HSD test to examine for significant among-group differences. Temperature-grouped growth data were also modelled as a quadratic function of SST, with the resulting regression model assessed for statistical adequacy (Zar, 2010).

To investigate differences in within-season growth rate (G) throughout the season, individuals were partitioned into five capture intervals (late June, early July, late July, early August, and late August). Differences in within-season growth rates among capture timing intervals were evaluated using ANOVA, followed by the Tukey's post-hoc HSD test. Individually experienced temperatures were assessed for significant differences among capture timing periods using Welch's ANOVA, to account for unequal variances, followed by a post-hoc Games-Howell test to determine significant differences among the groups (Myers and Well, 2003). To assess the correlation between within-season G and experienced temperatures by capture timing period a linear regression was performed.

All statistical testing was performed using SPSS version 17 (IBM Corp., New York, USA 2008) with significance levels set to $\alpha = 0.05$.

2.3 Results

2.3.1 Regional Annual Growth

Mean annual Arctic charr growth (ΔL) varied between a low of 13.2mm \pm 3.55(SE) in 1985 to a high of 22.1mm \pm 2.62(SE) in 1982 at Hebron Bay (Figure 2.2). Considerably higher growth was observed at Dry Bay, 91.3mm \pm 1.18(SE) and 86.4mm \pm 1.77(SE) in 2010 and 2011, respectively. Within sites, there were no significant differences in mean ΔL by year for Hebron Arctic charr (ANCOVA, $r^2 = 0.24$, year: $F_{3,67} = 1.54$, $P = 0.21$), but there were for Dry Bay Arctic charr (ANCOVA, $r^2 = 0.34$, year: $F_{1,119} = 5.25$, $P = 0.02$). Further, there was a significant difference in mean annual growth by site (Figure 2.2; ANCOVA, $r^2 = 0.91$, site: $F_{1,191} = 1450.03$, $P < 0.01$). Interaction terms (Site or Year x initial length) were not significant for any of the analyses ($P > 0.05$) reported above and were not included in subsequent statistical analyses.

The years 1982-1985 in the Hebron region experienced mean SSTs ranging from 0.8-1.7°C (Figure 2.2) based on the NOAA-derived data. These temperatures were all below the long-term SST summer mean (1971-2000) for the region (1.9°C). In contrast, the long-term SST summer mean (1971-2000) for the Dry Bay region was 1.5°C, much lower than the mean summer SSTs of 3.1-3.5°C (Figure 2.2) observed in 2010 and 2011. Mean ΔL was not related with mean SST over the four year study period at Hebron (Table 2.1, multiple regression, $P = 0.82$). In contrast, mean ΔL was correlated with mean SST for the two years at Dry Bay (multiple regression, $P = 0.02$), with SST explaining 21% of the variation in annual growth. When data from both sites were grouped there was a significant relationship between mean ΔL and mean SST (multiple regression, $P < 0.01$), with temperature accounting for 92% of the observed growth variability.

2.3.2 Within-Season Growth

Individual within-season growth rates of Nain Arctic charr were significantly related to mean summer temperature (Table 2.2), although temperature explained < 2% of the variation in growth. When fish were grouped by 0.5°C temperature class-intervals, a significant decline in growth rate was observed (Figure 2.3) as temperature increased above the 1-2°C range (ANOVA, $F_{(6,717)} = 3.00$, $P = 0.01$; Tukey HSD test, $P < 0.02$), with the quadratic growth-temperature relationship explaining 91.8% of the variation in the data. Estimated thermal growth optima for the individual and grouped data, was 1.6 and 1.8°C, respectively.

Within-season growth rates of Nain Arctic charr differed significantly when sorted by capture date (ANOVA, $F_{(4,725)} = 4.69$, $P < 0.01$), with post-hoc tests indicating that Arctic charr caught in June grew significantly faster than those caught in August (Figure 2.4; Tukey HSD test, $P \leq 0.01$). In contrast, the SST's associated with seasonal capture dates rose steadily over the June to August period (see Figure 2.4; Welch's ANOVA, $F_{(4,272)} = 185.52$, $P < 0.01$; Games-Howell test, $P < 0.01$ for all comparisons), with individuals caught in June experiencing the lowest temperatures (1.4°C) and individuals caught in late August experiencing significantly higher temperatures (3.3°C). Regression of mean individual growth rate (mm/day), MIGR, on mean experienced sea surface temperatures, MESST for common periods of capture indicated a significant inverse relationship (see Figure 2.4) ($\log_{10} \text{MIGR} = -0.28 - 0.07 \text{MESST} (\text{°C})$, $r^2 = 0.91$, $F_{1,3} = 31.39$, $P = 0.01$).

2.4 Discussion

The effects of sea surface temperature and days at sea variably influenced the *in-situ* marine growth of anadromous Arctic charr. Growth-temperature comparisons between Hebron Fiord, Labrador, and Dry Bay, Ungava Bay, yielded evidence of conditional temperature effects, with individual annual incremental growth increasing as a function of experienced temperature when comparing between sites and among years at Dry Bay, but not among years at Hebron. At Nain, increases in mean SST did not

demonstrate a significant positive relationship with growth. Instead, increases in SST associated with longer seasonal marine residency were correlated with lower mean growth as a result of the observed inverse relationship between growth rate and the length of marine residency. Data, therefore, provided partial support for the annual growth-temperature hypothesis and substantiated the within season growth hypothesis.

2.4.1 Regional Differences in Growth

Differences in the realized rates of growth between Hebron and Dry Bay and their contrasting responses to increasing temperatures may have been related to differences in regional food availability. Ration (local productivity) is a major factor influencing growth-temperature relationships in fish, as has been demonstrated in laboratory studies for brown trout (Elliott, 1994). Where ration is limited, the realized scope for growth is reduced and subsequent increases in temperature will further reduce achievable growth as metabolic maintenance demands rise with temperature (Elliott, 1994). The null effect of the increases in temperature on the growth of Hebron Arctic charr, therefore, is suggestive of food limitations where increases in temperature are not matched by proportionate increases in energy availability.

Particularly as reported temperature-growth relationships for salmonids suggest the most responsive range for growth comes at the lower end of the temperature range (e.g., Brett *et al.*, 1969; Elliott, 1994; Larsson *et al.*, 2005). In contrast, a very small increase in temperature (0.44°C) at Dry Bay yielded a significant response in growth, and is suggestive of sufficient local food availability for Arctic charr to have taken advantage of the increasing scope for growth as temperatures rose. Further reinforcing the notion are the demonstrated marine productivity differences between sites. In Ungava Bay productivity measured as chlorophyll *a* ranges between 1-1.5mg m⁻³ (median 1.4mg m⁻³) and exceeds values typically observed along the Labrador coast (0.4-0.6mg m⁻³) (Witman *et al.*, 2008; Frajka-Williams and Rhines, 2010). The combined site-specific differences in productivity, temperature and observed growth thus suggest a scenario where temperature driven increases in metabolic demand are met with sufficient surplus energy

availability to realize more of the temperature dependent scope for growth (Elliott, 1994) in Ungava Arctic charr than in Hebron Arctic charr.

The sensitivity of Labrador Arctic charr to variation in ration, but not temperature, has been noted elsewhere. Changes in Arctic charr diet associated with the reduced availability of preferred fish prey and the use of lower quality invertebrate prey have been correlated with the declining body weight of the Nain stock complex Arctic charr in the early 1990s (Dempson *et al.*, 2002, 2008). And while long-term studies of mean population biological characteristics have noted significant relationships between environmental variability and mean size-at-age (Power *et al.*, 2000; Michaud *et al.*, 2010), cohort-based studies have also noted the lack of a growth response to increases in experienced lifetime temperatures by Labrador Arctic charr (Michaud *et al.*, 2010).

Differences in regional productivity leading to the differing growth responses may be explained by contrasting oceanographic conditions which have created highly productive conditions in southern Ungava Bay by comparison with the northern Labrador Sea. Dry Bay receives a large volume of freshwater from the Koksoak River and its southern tributaries (discharge: 59.79km³/year, drainage area: 110 136 km²) (Dery *et al.*, 2005). The high productivity of the Koksoak River is exemplified by its considerable subsistence fishery, where important harvested species include *S. salar*, brook trout *Salvelinus fontinalis*, lake whitefish *Coregonus clupeaformis* and round whitefish *Prosopium cylindraceum* (Doidge and Gordon, 1999). In contrast, Hebron is a cold fiord that maintains a high Arctic marine environment in deeper waters even during the summer and fall (Nutt and Coachman, 1956). The Hebron Fiord also has a much smaller catchment area, consisting principally of the Ikarut River watershed and three additional unnamed rivers with a total drainage area of 4072km² (Anderson, 1985). All entering rivers flow easterly or northeasterly to the Labrador Sea over Arctic cordillera landforms characterized by low biological productivity (Natural Resources Canada, 2007). The extent of freshwater discharge into estuaries has been associated with high productivity elsewhere in the Arctic, with large

estuaries considered hotspots for local marine life (Heiskanen and Keck, 1996; Bousein and Stein, 2000; Carmack *et al.*, 2004). Furthermore, surface water nutrient concentrations are known to be high in regions with strong tidal mixing, such as Ungava, with chlorophyll *a* data corroborating the suggested increased biological productivity proximate to the region (Drinkwater and Jones, 1987).

Although differences in regional productivity can explain observed regional differences in Arctic charr growth, diverse reproductive tactics resulting in variations in egg size, egg number, age-at-maturity or spawning periodicity may also hold consequences for the surplus energy available for somatic growth. While evidence for trade-offs between egg number and size have been found in some populations of anadromous Arctic charr, no compelling evidence exists to suggest a pervasive effect of egg size or egg number when comparing among populations (Power *et al.*, 2005). Furthermore, studies of latitudinal variation in fecundity among Arctic charr that included populations from Ungava and the Labrador coast noted that size adjusted mean fecundity varies significantly in anadromous populations, with Ungava (George River) Arctic charr being among the highest.

A comparison of mean age-at-maturity supports the notion that Ungava Arctic charr may allocate relatively more energy to reproduction, with Hebron Arctic charr reaching maturity by age 8.8 (DFO, unpubl. data) in comparison to ages 5 and 7.6, respectively, for George River (Gillis *et al.*, 1982) and Sapukkait (Boivin, 1994) origin Ungava Arctic charr. Offsetting differences, however, are apparent when considering annual spawning frequency, with a low percentage of reproductively ready females recorded in Ungava populations, 7.7-28.6% in the George River and 5-23% at Sapukkait, (Gillis *et al.*, 1982; Boivin, 1994) as compared to a high percentage in Labrador populations, 60-70% in the Fraser River (Dempson and Green, 1985; Dempson, 1995). Thus, while Ungava individuals mature at a younger age, and produce marginally more eggs (size adjusted mean fecundity, respectively, for George River and Hebron is 2726 and 2449 eggs/female, DFO, unpubl. data; Grainger, 1953), the significantly lower

percentage of reproductively ready Ungava females implies a reduced spawning frequency that contributes to explaining the large differences in annual growth seen in the two regions.

Differential growth may also be further influenced by inherent genetic differences between the studied populations. Nilsson (1994) demonstrated that length, weight and condition of Arctic charr were heritable and noted selection for enhanced growth was possible. Indeed, heritability of growth rates have been documented for other salmonid species, including: *S. salar* (Gunnes and Gjedrem, 1978; Heggberget *et al.*, 1986), coho salmon *Oncorhynchus kisutch*, (Silverstein and Hershberger, 1995), and rainbow trout *Salmo gairdneri* (Ayles and Baker, 1983).

2.4.2 Within-Season Growth

The pattern of higher within-season growth at lower temperatures accords with field-based observations of early season feeding along the Labrador coast, with estimated optima not inconsistent with water temperatures (1-2°C) that prevail on early season entry into the marine environment (Dempson, personal communication). In Labrador, Arctic charr migrate at first ice-out (May and early June) and immediately commence feeding, with return migrations beginning during the latter half of July (Dempson and Green, 1987). Increased early season growth coinciding with generally colder and earlier seasonal temperatures may be related to an energetics-based advantage resulting from the increased productivity and decreased temperatures existing at the beginning of the growing season. The spring bloom in the north Labrador Sea starts in mid-April when thermal stratification has not yet been established, implying the general unavailability of warmer surface layer waters (Wu *et al.*, 2008), and coincides with the return of Arctic charr to the marine environment. The combination of conditions may offer individuals preferential feeding opportunities via physiological and/or competitive advantages, particularly as low temperatures have been shown to trigger competitive release for Arctic charr in other environments (Hammar, 1998).

The pattern of enhanced early season growth rates has also been demonstrated elsewhere for anadromous Arctic charr (Berg and Berg, 1989; Rikardsen *et al.*, 2000), and may be explained by compensatory growth following restricted feeding in the winter, and/or by the heightened growth efficiency of Arctic charr at lower temperatures (e.g., Larsson and Berglund, 2005). The accelerated increase of growth due to increased food availability following a period of restriction, growth compensation, has been demonstrated in laboratory Arctic charr where individuals alternately food deprived and satiated attained similar body weights to those having constant access to food (Jobling *et al.*, 1993).

Alternatively, seasonal downward averaging of growth may be related to the averaging effect of body-size changes on the computed growth rate implicit in the nature of asymptotic seasonal growth functions (e.g., von Bertalanffy) believed to prevail among fish (Jobling, 2002). With increasing body size, the scope for growth generally declines (Brett, 1979). Thus, the larger sizes associated with spending longer periods of time in the marine environment will effectively have lower realized growth rates because of the declining rate of change in body size that occurs as the seasonal growth asymptote is approached, with the downward averaging effect occurring independently of any physiological-based mechanism that may similarly lower growth over time (Power and Attrill, 2007).

Temperature optima for Arctic charr growth have been commonly recorded in the range of 13-18°C by laboratory studies (Jobling, 1983; Larsson and Berglund, 1998; Larsson *et al.*, 2005). However, laboratory derived temperature optima are typically estimated for juvenile Arctic charr reared in freshwater aquaria and may not be directly applicable to the description of growth in adult Arctic charr residing at sea. Direct application of laboratory optima to Arctic charr *in-situ* has proven a difficult task, with evidence for lower thermal preferences existing in the literature (Larsson, 2005; Rikardsen *et al.*, 2007). For example, research investigating temperature preferences of adult anadromous Arctic charr in north Norway indicated use of shallow water areas with a mean temperature 10.6°C, despite the

availability of warmer (12-15°C) water (Rikardsen *et al.*, 2007). Thus, the influence of food availability, as well as growth timing, may be crucial in explaining differences in field reported growth-temperature relationships, as has been illustrated by the regional comparison of annual growth between Hebron Fiord and Dry Bay.

The apparent dichotomy between growth-temperature correlations observed at inter-annual and intra-annual temporal scales, as found here, relate to (i) the pattern of differences in site-specific productivity and environmental variation that drive among-site or among-year differences in growth and (ii) the timing match between early season growth compensation in Arctic charr and the energy available from the spring productivity bloom that varies the within season opportunity for growth. Differences in productivity between sites set the potential for growth by controlling the physical and biotic factors determining ultimate energy availability, with inter-annual variation in environmental conditions causing fluctuations about the mean. Thus comparisons between sites can yield significant differences in growth because of one environment being better endowed with the resources necessary for growth, although such comparisons may be confounded by year-to-year temperature variability driving the physiological abilities of fish to exploit resources for growth gains. The timing of natural growth compensation that occurs after the prolonged period of winter fasting twins with spring productivity blooms to facilitate individuals achieving high early season growth that declines as individuals grow. Thus, the annual increment attained will increase as increases in temperature and time allow, provided sufficient ration is available, yet the within-season rate of gain decreases, yielding the apparently anomalous negative correlation between measured growth rate and temperature. Improved description of population-specific growth and temperature relationships as well as information on local prey availability, therefore, are necessary for determining accurate portrayals of this complex relationship, especially as Arctic charr are considered vulnerable to possible climate change effects (Reist *et al.*, 2006a, 2006b). Results here suggest that future increases in water temperature may have profound consequences for Arctic charr growth

depending on local productivity and/or any shifts in key seasonal phenologies such as the timing of spring blooms. Furthermore, the study of specific mechanisms driving growth in natural environments is critical for the development of management strategies for sustaining Arctic charr population levels as climate varies.

2.5 Figures and Tables



Figure 2.1 Map of Ungava and Labrador including the three field sites, Dry Bay in Ungava and Hebron Fiord and Nain Bay in Labrador.

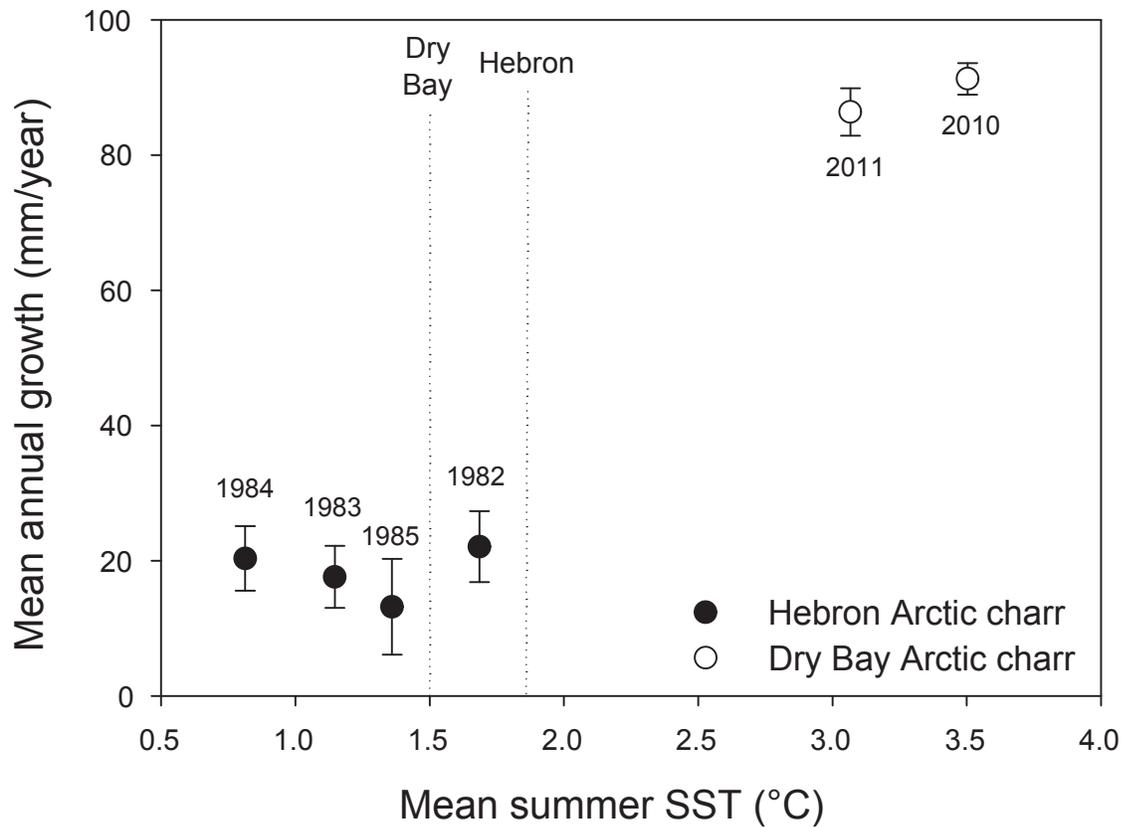


Figure 2.2 Mean summer sea surface temperatures (SST) and length-adjusted mean annual growth $\pm 95\%$ confidence intervals of Arctic charr in Hebron Fiord, Labrador and Dry Bay, Ungava Bay. Mean growth is adjusted to site-specific mean lengths of 418mm for Hebron Arctic charr and 376mm for Dry Bay Arctic charr. Years for which the growth rates are relevant are given above or below each point. Long-term summer means (1971-2000) for each region are plotted with dotted lines.

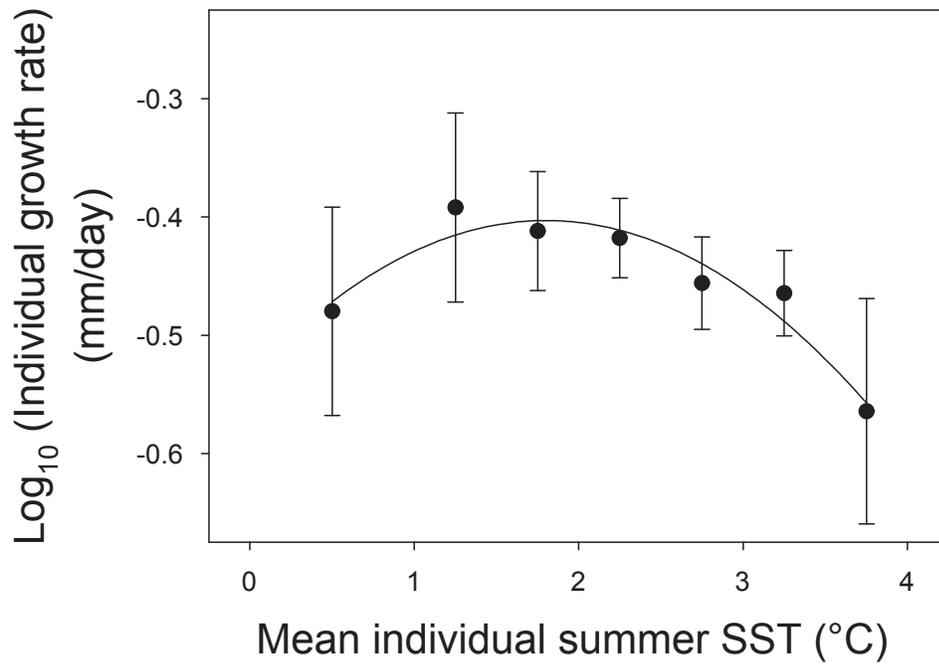


Figure 2.3 Individual within-season growth rates and mean experienced summer sea surface temperatures (SST) partitioned into temperature intervals. Data are plotted as means and associated 95% confidence intervals. The solid line plots the quadratic model reported in Table 2.2.

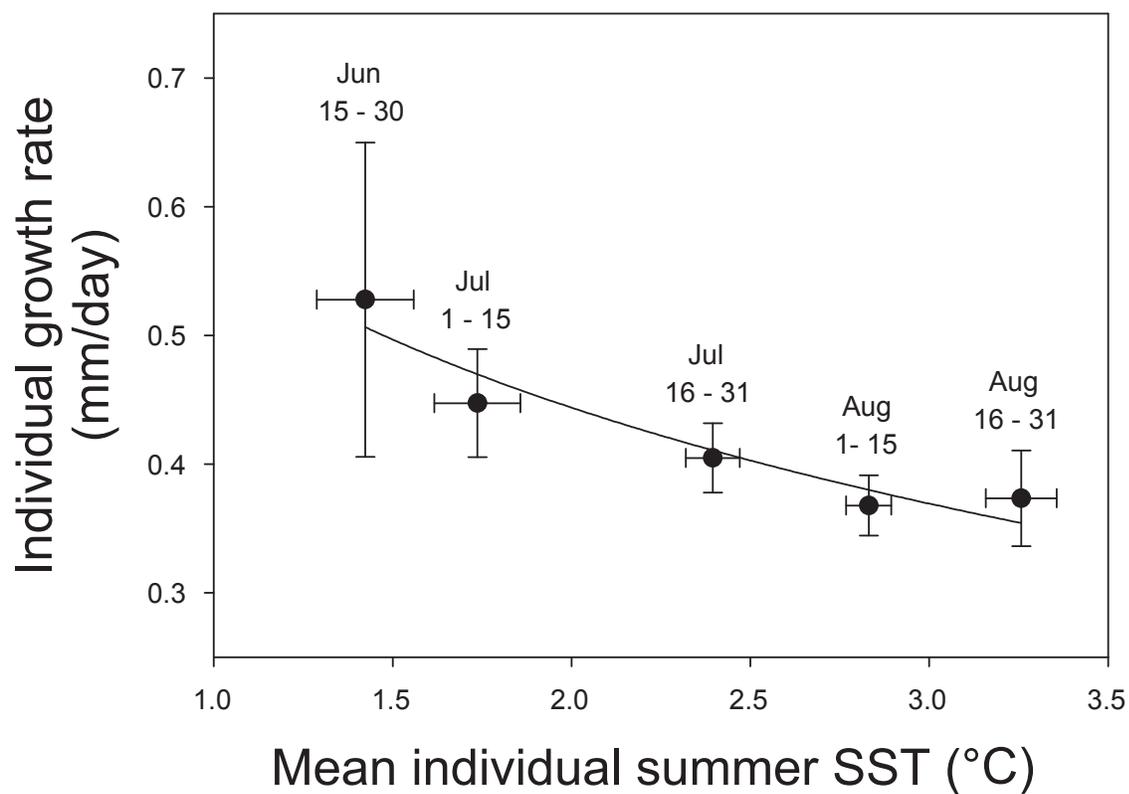


Figure 2.4 Mean within-season growth rates as a function of mean experienced summer SST for common periods of capture starting in June and ending in August. Data are plotted as means with associated 95% confidence intervals. The solid line plots the regression line relating the two variables ($r^2 = 0.91$).

Table 2.1 Multiple linear regression results for models relating covariates temperature and initial length to annual growth (mm/year). Values reported include covariate coefficients, *P*- values, and partial correlation coefficients, in addition to overall model r^2 , regression *F* statistics and *P*- values.

Model	Site	Covariates	Coefficient	<i>P</i> - value	Partial correlation	r^2	Regression <i>F</i>	<i>P</i> - value
Within sites by year	Hebron					0.19	$F_{2,69} = 7.89$	0.82
		Length	-3.93	< 0.01	-0.43			
		temperature	0.23	0.82	0.03			
	Dry Bay						0.34	$F_{2,119} = 30.87$
length		-7.81	< 0.01	-0.58				
		temperature	2.29	0.02	0.21			
All sites and years combined	Hebron and Dry Bay					0.88	$F_{2,191} = 685.89$	< 0.01
		Length	-7.96	< 0.01	-0.50			
		temperature	32.03	< 0.01	0.92			

Table 2.2 Quadratic regression coefficient estimates for models relating temperature to within season growth measured as \log_{10} (growth rate (mm/day)) for individuals and temperature grouped means. The grouped data model combines growth rate data by 0.5°C temperature increments and uses the resulting means for both temperature and growth. Also given are model r^2 , regression F statistics and overall regression P - value.

Model	Coefficient	P - value	r^2	Regression F	P - value
Individual Data			0.02	$F_{2,727} = 5.64$	< 0.01
Intercept	-0.48	< 0.01			
Temperature	0.08	0.08			
Temperature ²	-0.02	0.02			
Grouped Data			0.92	$F_{2,4} = 22.63$	< 0.01
Intercept	-0.54	< 0.01			
Temperature	0.15	0.01			
Temperature ²	-0.04	< 0.01			

Chapter 3

Individual thermal habitat use and growth of two contrasting Arctic charr populations

3.1 Introduction

The climate risks facing Arctic species are predicted to be highly variable and will be difficult to anticipate for many species as a result of the complex interactions between abiotic and biotic processes (Reist et al. 2006a; Reist et al. 2006b). The unpredictability will be further heightened by the lack of long-term physio-chemical data available for Arctic regions, precluding the creation of reliable benchmarks for change (Power et al. 2008). Among the physio-chemical environmental variables that are particularly important in the climate change context is temperature. Temperature has an important influence on all aspects of aquatic physiology, affecting growth, reproduction and survival and playing a key role in delimiting habitat use and distribution (e.g., Christie and Regier 1988; Perry et al. 2005). Through its physiologically mediated effects on growth and habitat use, temperature ultimately influences species' fitness. Accordingly, improved understanding of temperature-growth relationships are required for many Arctic species if the possible effects of a warming climate are to be anticipated and mitigated.

Among the Arctic aquatic species for which better *in situ* temperature-growth relationships are required is Arctic charr, (*Salvelinus alpinus*). Arctic charr are considered to be one of the most cold-adapted fish species (Johnson 1980) and have a measured temperature polygon area that is amongst the lowest recorded for salmonids (Baroudy and Elliott 1994). Arctic charr growth and feeding can occur at temperatures as low as 0.2°C (Klemetsen et al. 2003), although laboratory-based experiments indicate optimal temperatures for growth of between 13-18°C (Jobling 1983; Larsson and Berglund 1998; Larsson et al. 2005). In the wild, Arctic charr appear to prefer cooler temperatures (11°C, Larsson 2005; Rikardsen et al. 2007), which more closely match their optimal temperature for growth efficiency (9°C, Larsson and Berglund 1998; Larsson and Berglund 2005).

The results of laboratory-based studies suggest reduced growth may occur in Arctic charr as climates warm, with the most vulnerable populations being located at the southern edge of the distributional range, particularly those residing in small, shallow, low altitude lakes that lack a cool hypolimnetic refuge (Lehtonen 1998). For example, the Arctic charr population in shallow Lake Ellioavatn, Iceland, has drastically declined owing to significant warming (Malmquist et al. 2009), and declining Arctic charr abundance has been linked with watersheds vulnerable to climate change in the UK (Winfield et al. 2010).

Studies of wild populations, however, have reported variable temperature-growth responses indicative of the possible influence of food availability on growth (e.g., Berg and Berg 1989; Power et al. 2000; Kristensen et al. 2006; Michaud et al. 2010; Godiksen et al. 2011). Thus, climate-driven increases in temperature may have positive or negative consequences for Arctic charr growth that depend on the match between local food availability and the temperature-dependent scope for growth (Elliott 1994). Evidence of varied temperature-driven impacts on growth already exists for some Arctic charr populations in Greenland (Kristensen et al. 2006) and Labrador, Canada (Power et al. 2000; Michaud et al. 2010).

The absence of consistent long-term water temperature data from northern watersheds has hampered abilities to study temperature-growth relationships in Arctic charr under a variety of conditions. Use of oxygen isotope-based ($\delta^{18}\text{O}$) methods to reconstruct the thermal histories of individual fish from the otolith, however, provides one means of directly linking observed fish growth to temperature (e.g., Guiguer et al. 2003; Rowell et al. 2005; Høie and Folkvord 2006; Godiksen et al. 2011; Godiksen et al. 2012). A further advantage of thermal reconstructions is that they overcome the need for extensive monitoring of thermally heterogeneous habitat caused by fish movement within the water column. Temperatures recorded by the otolith represent a mean of all temperatures experienced by the fish during

the period of otolith formation as a result of the precipitation of otolith aragonite close to oxygen isotope equilibrium with ambient water via temperature-dependent hydrolysis reactions (Campana 1999).

To overcome the lack of temperature data available for studying *in-situ* temperature-growth relationships in Arctic charr, this study uses stable isotope temperature reconstructions in concert with otolith back-calculations of growth patterns from two adjacent populations of Arctic charr residing in lakes with differing climactic vulnerabilities. Specifically, we analyze the correlations between varying air and experienced water temperatures on individual growth outcomes while investigating the following hypotheses: (i) otolith-estimated temperature and back-calculated growth are positively and negatively correlated for fish obtained from the larger and smaller lakes, respectively, with young-of-the-year temperature effects extending to the subsequent year of growth, and (ii) increasing air temperatures will have null and negative effects on back-calculated growth for fish obtained from the larger and smaller lakes, respectively, as a result of the differential impact of air temperatures on the available volume of preferred thermal habitat in the smaller and larger lakes.

3.2 Materials and Methods

3.2.1 Study Sites and Sampling Procedures

Anadromous and lacustrine Arctic charr samples were obtained from the Nepihjee River watershed, located immediately to the northwest of the community of Kuujjuaq in the Ungava Bay region of Nunavik, Québec, Canada (Figure 3.1). Sampling sites within the watershed included: Lake Tasiapik (58°31'N, 68°21'W), the Nepihjee River (58°32'N, 68°17'W) and Lake Qamutissait (58°24'N 68°23'W). Lake Tasiapik is a small (0.3km²), shallow (<10m), inland lake supporting a simple fish community consisting of lake trout (*Salvelinus namaycush*), lacustrine Arctic charr and three-spine sticklebacks (*Gasterosteus aculeatus*). Tasiapik connects to the Nepihjee River via a single small tributary, however, the low discharge and high gradient (>10%) of the outlet stream act as barriers for returning adult

migrants, effectively rendering the resident population landlocked. Lake Qamutissait is a medium (12.6km²), shallow (≤ 20 m), oligotrophic lake located approximately 12km from the marine waters of Ungava Bay and is the most easily accessed lake for anadromous Arctic charr seeking overwintering, spawning or juvenile rearing habitat. In addition to Arctic charr, Lake Qamutissait contains lake trout, brook charr (*S. fontinalis*), burbot (*Lota lota*), round whitefish (*Prosopium cylindraceum*), longnose sucker (*Catostomus catostomus*), slimy sculpin (*Cottus cognatus*), northern lake chub (*Couesius plumbeus*), three-spine and nine-spine sticklebacks (*Pungitius pungitius*), and cisco (*Coregonus artedii*).

In 2009 and 2010 anadromous Arctic charr (n=43) were collected from the Nepihjee River and Lake Qamutissait, and lacustrine Arctic charr (n=56) were obtained from Lake Tasiapik. The Lake Qamutissait Arctic charr population is an introduced anadromous population that has been supported over the period 2000-2009 by 0+ hatchery stocking (e.g., Murdoch et al., in review), with eggs obtained from Arctic charr in the Finger Lakes (58°34'N, 70°00'W). Fish were captured during the upstream fall migration in the Nepihjee River using a fyke trap net, with a smaller sub-set captured from Lake Qamutissait by angling during the winter by local residents. The anadromous Arctic charr overwinter in Lake Qamutissait, but rear during the juvenile phase within the lake. Lacustrine Arctic charr were collected via multi-mesh Lundgren benthic gillnets (10-60mm mesh) and electrofishing at Lake Tasiapik in July and August. Fork-length (mm) was recorded for each individual fish and sagittal otoliths were removed, cleaned, air dried and stored in separate wax-paper envelopes for later analysis. Coincident with fish sampling, water samples (30mL) were collected at multiple depths (0.5-7m) from Lake Tasiapik (2009-2010) and at a subsurface (<1m) depth from Lake Qamutissait (2009) for oxygen stable isotope analysis. Water bottles were covered with aluminum foil and stored at room temperature until analyzed.

Temperature loggers (Onset HOBO Pro v2 Water Temperature Data Logger) were set in Lake Tasiapik during July and August of 2009 and 2010. In both years, a temperature logger was anchored in a representative mean lake depth of 2m, with an additional logger added in 2010 to the deepest point of the

lake (~7.5m) as a gauge for determining the extent of temperature stratification. The size of Lake Qamutissait precluded complete monitoring of the lake, particularly as the range of habitats occupied by Arctic charr was unknown. Accordingly, an index of Lake Qamutissait water temperatures was obtained by monitoring Nepihjee River water temperatures, (using an Onset HOBO U20 Water Level Data Logger), proximate to the location of the fish trap at an approximate depth of 1m. Temperatures were recorded at half hour intervals in Lake Tasiapik and at 4h intervals at the Nepihjee River site.

3.2.2 Otolith Growth Measurements

Sampled otoliths were glued to a glass slide, sulcus-side down, using Original Lepage epoxy glue (Henkel Consumer Adhesives Inc., Avon, OH, USA), and polished with 5-30 μ silicon carbide paper (3M Company, St. Paul, MN, USA) until all growth zones were revealed and a flat surface was obtained. Otoliths were then immersed in distilled water and photographed using a stereo-microscope and camera apparatus (DS-Fi1; Nikon Instruments Europe B.V., Kingston, Surrey, England). Otolith radii were measured using Image-Pro 6.0 (Media Cybernetics Ltd., Bethesda, MD, USA) along the clearest and longest possible ventral axis.

The first annual growth zone (0+) was measured from the centre of the nucleus to the end of the first otolith opaque section and, therefore, included the larval stage. Subsequent annual freshwater growth zones were designated as zone 2, zone 3, and so on. Due to the extremely narrow translucent (winter) zones observed in otoliths used in this study, no attempt was made to quantify winter growth. To avoid confounding analyses, growth zones within the otoliths from Nepihjee captured fish associated with marine residency and feeding were identified and removed from the zone 3 dataset. Information obtained from the otolith with respect to the relative size of incremental growth zones was used to identify putative marine-deposited zones, with marine growth classification cross-checked against available isotope data as a confirmation.

Owing to problems with the clarity of zonation caused by irregular crystal formation along the ventral axes of some otoliths, measurements were taken on an adjacent axis offset by 45° and measurements were later proportionally scaled to represent the longest ventral axis. To verify the accuracy of the scaling method, measurements from otoliths for which both axes were clearly visible were taken and the differences between the corresponding proportionally scaled and longest axis measurements were computed. The resulting estimation errors (scaled – actual measure) were then statistically assessed for bias following methods outlined in Power (1993). Differences were not significantly different from zero (one-sample t-test, $t_{75}=0.36$, $P=0.72$), with the mean percent error relative to the longest possible ventral axis measurements being 0.2 ± 0.4 (Std error) for $n=76$ measurements from 20 otoliths.

A modified-Fry back-calculation model was chosen to account for the significant non-linear relationship observed between fish length-at-capture and otolith ventral radii measurements (Vigliola et al. 2000; Wilson et al. 2009). For Lake Tasiapik, the biological intercept used in the model was the smallest young-of-the-year collected (length=27mm), whereas hatchery reared young-of-the-year data (length=17mm) from fish used to stock Lake Qamutissait was used for the growth model for Nepihjee River captured fish. Estimation procedures followed Vigliola et al. (2000) with the exception of the use of the Levenberg-Marquardt algorithm in place of the Quasi-Newton method.

To calculate annual growth, the difference between back-calculated length-at-age x and $x+1$ was used:

$$G_x = L_{x+1} - L_x \quad (1)$$

where G_x is annual back-calculated growth at age x , L_x is back-calculated length-at-age x and L_{x+1} is back-calculated length-at-age $x+1$.

3.2.3 Otolith-Estimated Temperatures

Samples for stable isotope analysis were taken from within each summer growth zone using a New Wave Merchantek Micro Mill (ESI Ltd, Portland, Oregon). Approximately 7 holes were drilled per sample to a

100 μ depth using the edge of a 200 μ diameter scribbler point dental drill tip made of tungsten carbide (Brasseler USA, Savannah, GA, USA). Drilled samples were collected via a vacuum stylus which concentrated sample material on a previously roasted quartz fiber filter (QMA 4.7cm, Whatman plc., Maidstone, Kent, UK). Analysis of all samples followed procedures described in depth elsewhere (e.g., Guiguer et al. 2003; Storm-Suke et al. 2007; Godiksen et al. 2010). Briefly, filters and samples were roasted at 350°C for one hour under a constant flow of helium to remove all organic compounds (Guiguer et al. 2003) and then treated with 100% phosphoric acid, also under a constant flow of helium. Vials containing the acid-reacted samples were heated to 90°C for 1h and the evolved CO₂ gas was collected and auto-injected into a Micromass IsoPrime stable isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, UK) with an analytical precision of $\pm 0.2\%$ (Guiguer et al. 2003) at the Environmental Isotope Laboratory, University of Waterloo, Canada.

Analytical accuracy was gauged using standardized calcite substances IAEA-CO-1 (Carrara marble CaCO₃: $\delta^{13}\text{C}_{\text{PDB}} = +2.49\%$, $\delta^{18}\text{O}_{\text{PDB}} = -2.40\%$), IAEA-CO-8 (Carbonatite CaCO₃: $\delta^{13}\text{C}_{\text{PDB}} = -5.76\%$, $\delta^{18}\text{O}_{\text{PDB}} = -22.70\%$), and EIL-21 (Pine Point CaCO₃: $\delta^{13}\text{C}_{\text{PDB}} = -0.19$, $\delta^{18}\text{O}_{\text{PDB}} = -15.68$) analyzed in sets of n=6 before and after every 21 otolith samples (Godiksen et al. 2010). Stable isotope values reported here are expressed in standard delta (δ) notation with respect to the international standard of carbonate rock from the Peedee Belemnite formation ($\delta^{13}\text{C}$, Craig 1957).

Water sample $\delta^{18}\text{O}$ values were determined by extracting CO₂ using an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, U.K.) determined following procedures outlined in Epstein & Mayeda (1953) and Fritz et al. (1987). Results were standard corrected based on EIL-12 (sealed container of laboratory water) and standard light Antarctic precipitation (SLAP) from the International Atomic Energy Agency (IAEA). All isotopic values for water samples were converted from the Vienna standard mean ocean water scale (VSMOW) to the PDB-scale following Clark & Fritz (1997). Otolith oxygen isotope values were then combined with water $\delta^{18}\text{O}$ values and converted

to temperature (°C) estimates using a literature-derived fractionation equation. Given that differences in physiology among fish species may affect the relationship between temperature and oxygen fractionation in otoliths on a species-specific basis (Høie et al. 2004; Rowell et al. 2005; Storm-Suke et al. 2007) the species-specific fractionation equation developed for Arctic charr by Godiksen et al. (2010) was used:

$$1000\ln\alpha = -41.14 + \frac{20.43}{T} \quad (2)$$

where $\ln\alpha$ is the otolith-water fractionation factor and T is temperature ($10^3/^\circ\text{K}$)(e.g., Storm-Suke et al. 2007; Godiksen et al. 2010).

3.2.4 Statistical Analyses

All statistical testing was performed using SPSS version 17 (IBM Corp., New York, USA 2008) with significance levels set to $\alpha = 0.05$. Individual otolith-estimated temperatures were analyzed by growth zone within and between sites using the following statistical tests as necessary: ANOVA, Levene's test of equal variances, Tukey's post-hoc HSD test or an independent two sample t-test adjusted for assumptions regarding the variance (Zar 2010). Back-calculated growth was similarly assessed by growth zone between sites. To test hypotheses relating to relationships between air and monitored water temperatures, Pearson's correlation analysis was performed (Zar 2010).

Growth-temperature hypotheses were assessed within separate growth zones using linear regressions of back-calculated growth versus either otolith-estimated or summer air temperatures. Analyses were completed only for growth zones with $n \geq 10$ data points to avoid statistical issues associated with small sample biases (e.g., Zar 2010). Mean summer air temperatures used in the analyses were obtained for Kuujjuaq, which is proximate (38-47km) to both lakes, from the National Climate Data and Information Archive provided by Environment Canada (<http://www.weatheroffice.gc.ca>), and were computed as averaged daily mean temperatures from June 1 – August 31 for the corresponding year.

3.3 Results

3.3.1 Back-Calculated Length

Back-calculated annual growth was determined for 318 annual growth zones using 96 otoliths (44 from the Nepihjee River population and 52 from Lake Tasiapik). Non-linear modified-Fry back calculation models explained 96.6-98.2% of the variability (Table 3.1), with length at otolith formation estimated as 10.39mm and 16.75mm for Qamutissait and Tasiapik Arctic charr, respectively.

Back-calculated growth was high for zone 1 for both sites, after which growth decreased slightly before increasing steadily to highs in zones 3 and 5 for Qamutissait and Tasiapik Arctic charr, respectively (Figure 3.2a). Qamutissait growth was very high for zone 1 ($86.7\text{mm} \pm 13.6(\text{SD})$) as a result of the probable hatchery origin for the majority of individuals analyzed and lower thereafter. Back-calculated growth was significantly higher for Qamutissait Arctic charr for zones 1-3 as compared to Tasiapik Arctic charr (T-test, $T \geq 4.93$, $df \geq 66$, $P < 0.01$), and significantly more variable (Levene's $F \geq 8.00$, $df \geq 82$, $P \leq 0.01$).

3.3.2 Otolith-Estimated Temperatures

Temperature estimations were made for 189 summer growth zones using 72 otoliths (30 from the Nepihjee River population and 42 from Lake Tasiapik). An additional 5 samples obtained from Nepihjee otoliths demonstrated a saltwater influence, and were omitted from further analysis. The ages of individuals analyzed ranged from 2-17 for Tasiapik Arctic charr and from 4-10 for Nepihjee Arctic charr. For Arctic charr from Lake Tasiapik, temperature data for 5 summer growth zones was obtained in comparison to 3 zones for Qamutissait Arctic charr, after which marine migration dominated as a life-history tactic.

Otolith-estimated water temperatures for Tasiapik Arctic charr varied between 6.2–19.8°C with a mean temperature of 13.1°C for all zones combined. Among the zones, the first summer growth zone had the highest mean temperature (14.9°C), after which mean temperatures generally declined as the zone

index increased (Figure 3.2b). Otolith-estimated mean water temperatures for the zones differed significantly (ANOVA, $F_{4,114}=5.57$ $P=0.00$), with zone 1 being warmer than zones 3, 4 and 5 (Tukey test $P<0.04$). Lake Qamutissait Arctic charr summer growth zone temperatures ranged from 0.1 - 17.4°C with a mean temperature of 9.9°C. Notably, zone 1 reflects a combination of hatchery experienced temperatures and temperatures experienced after release in the Nepihjee watershed. Mean temperatures for zones 1-3 remained steady between 9-11°C. Within Qamutissait Arctic charr no significant among-zone temperature differences were found (zones 1-3: ANOVA, $F_{2,67}=0.52$ $P=0.60$). Tasiapik Arctic charr experienced significantly higher temperatures than Qamutissait Arctic charr for zones 1-3 (T-test, $T\geq 2.31$, $df\geq 36$, $P\leq 0.03$). Qamutissait otolith-estimated temperatures were significantly more variable than Tasiapik otolith-estimated temperatures for zones 1 and 2 (Levene's $F\geq 5.19$, $df\geq 46$, $P\leq 0.03$), but not for zone 3 (Levene's $F=2.24$, $df=45$, $P=0.14$).

3.3.3 Air-Water Temperature Comparisons

Average monitored Lake Tasiapik water temperatures (2m depth) for the period of July 24 – September 8 in 2009 and 2010 measured 12.2°C and 14.6°C, respectively (Figure 3.3). An additional temperature logger deployed during 2010 at the deepest point of the lake (~7.5m) had a mean temperature of 10.2°C and remained within a 1.8°C interval throughout the entire monitored period. For the same time interval, the average Nepihjee River water temperature (at 1m depth) was significantly lower than the mean temperature in Lake Tasiapik (at 2m depth) in 2009 (11.7°C, Paired t-test $t=5.57$, $df=56$, $p<0.01$), however, similar means were recorded in 2010 (14.4°C, Paired t-test $t=0.96$, $df=47$, $p=0.34$; Figure 3.3). Air temperatures for the corresponding time period were significantly colder than shallow water temperatures in either watershed for both years of monitoring (Paired t-tests $t\geq 2.82$, $df\geq 47$, $P<0.01$), being 11.0°C for 2009 and 13.0°C for 2010 (Figure 3.3), although significant correlations were found between monitored water and air temperatures for Lake Tasiapik (2m depth: Pearson's $R\geq 0.77$, $df\geq 46$, $P=0.00$ and

7.5m depth: Pearson's $R=0.35$, $df=46$, $P=0.01$), and for the Nepihjee River (Pearson's $R\geq 0.84$, $df=58$, $P=0.00$).

3.3.4 Air and Otolith-Estimated Temperature Effects on Back-Calculated Growth

Otolith-estimated temperatures were not significantly correlated with back-calculated growth for Tasiapik Arctic charr in any zone (Figure 3.4a; Linear regressions, $R^2\leq 0.19$, $df\geq 1,8$, $P\geq 0.14$). However, there were significant negative relationships between air temperature and back-calculated growth for zones 3-5 in Lake Tasiapik (Figure 3.4b; Linear regressions, $df\geq 1,11$, $P\leq 0.02$), with air temperature explaining 19-43% of the observed variation in back-calculated growth. In contrast, air temperatures experienced by zones 1, 2 and 6 from Lake Tasiapik were not significantly related to back-calculated growth (Linear regressions, $R^2\leq 0.15$, $df\geq 1,9$, $P\geq 0.11$). Back-calculated growth was not correlated with otolith-estimated temperatures for Qamutissait Arctic charr in any of the zones examined (Figure 3.5a; Linear regressions, $R^2\leq 0.11$, $df\geq 1,15$, $P\geq 0.13$). Similarly, there were no correlations between back-calculated growth and air temperature for any of the examined growth zones (Figure 3.5b; Linear regressions, $R^2\leq 0.01$, $df\geq 1,35$, $P\geq 0.52$).

3.3.5 Young-Of-The-Year Temperature Effects on Subsequent Back-Calculated Growth

Tasiapik zone 1 temperatures were significantly negatively correlated with zone 2 back-calculated growth, with otolith-estimated temperatures in zone 1 explaining 33% of the observed variation of back-calculated growth in zone 2 (Figure 3.6a; Linear regression, $df=1,21$, $P<0.01$). A similar relationship was not found for Lake Qamutissait (Figure 3.6b; Linear regression, $R^2=0.11$, $df=1,25$, $P=0.09$).

3.4 Discussion

Data derived from the study of fish thermal habitat use and back-calculated growth provided no support for suggested relationships between otolith-estimated temperature and back-calculated growth, with similar variability in growth increments at all temperatures in each studied growth zone being observed.

Young-of-the-year in the smaller of the two lakes, however, tended to grow less in the second summer when having experienced elevated temperatures in the first summer. As hypothesized, increasing air temperatures were found to have variable influences on growth, with age-dependent effects being observed in the smaller, shallower of the study lakes and no effects being observed in the larger, deeper of the study lakes.

Contrasting lake morphometry is likely responsible for the increased sensitivity of fish from the smaller Lake Tasiapik to warmer air temperatures when compared to Arctic charr residing in Lake Qamutissait. Lake Tasiapik is notably shallower, with a smaller area, and has no surface water inputs following the spring melt. During the ice-free season the majority of the lake is warm and relatively isothermal, with thermal stratification likely occurring only in a singular region within the south basin where it is deep enough (>6m) to permit stratification (Wetzel 2001). In comparison, the increased size, depth and positioning of Lake Qamutissait relative to its large upstream catchment (area > 115km²) facilitates the maintenance of overall cooler water temperatures. As climate warming has been shown to increase epilimnetic temperatures, in addition to the overall length, stability and intensity of thermal stratification (e.g., Schindler et al. 1990; Hondzo and Stefan 1991; Stefan et al. 1993; De Stasio Jr. et al. 1996), years with increasing air temperatures are likely to have a direct impact on the surface waters of both lakes. Arctic charr not restricted to marginal lake habitat areas may behaviourally thermoregulate to avoid increasing littoral zone temperatures by retreating to deeper cooler waters earlier in the summer to avoid thermal stress and/or increase their realized growth increment if food is limiting (e.g., Brett 1971; Magnuson et al. 1979; Baroudy and Elliott 1994; Elliott and Hurley 2000). The availability of a hypolimnetic refuge would be particularly important for Lake Tasiapik Arctic charr, as surface waters may approach or exceed literature reported thermal preferences or critical limits for growth or survival (e.g., Baroudy and Elliott 1994; Larsson and Berglund 1998; Larsson et al. 2005; Larsson 2005; Rikardsen et al. 2007). And where lake morphometry is associated with a small hypolimnion, the

movement of fish to the hypolimnion is likely to increase fish densities and lower individual ration and growth if profundal foraging opportunities are limited.

Evidence of an earlier and warmer stratification pattern due to climate warming has been correlated with a reduction in preferred thermal habitat volume for other cold-water fish species (e.g., Schindler et al. 1990; De Stasio Jr. et al. 1996; Mackenzie-Grieve and Post 2006; Plumb and Blanchfield 2009), with associated decreases in growth being attributed to the reduction of shallow water habitat usage where feeding opportunities are typically greater (King et al. 1999). While data presented here suggest sensitivity to climate warming in small lakes even within the bounds of current temperature variability, larger lakes are likely to remain unaffected, particularly if like Lake Qamutissait they enjoy the advantage of larger, deeper lakes as upstream thermal buffers. In turn, resident fish species are less likely to be restricted to remaining in deep-water habitat as littoral forage zones are less likely to exceed thermal preferences (e.g., Larsson 2005; Rikardsen et al. 2007). Thus, where a large volume of deep cooler water is available, the comparison of data from lakes Qamutissait and Tasiapik suggest Arctic charr can or will select thermal habitats to avoid the immediate negative effects of increasing surface water temperatures. Similarly, Arctic charr in the deep Lake Windermere did not experience any negative effects from documented rising surface water temperatures, presumably due to the stable depth of the 16°C isotherm marking the upper limit for vertical fish migrations in the lake (Jones et al. 2008). Results thus provide corroborating evidence for literature predictions regarding the likely complexity of climate-warming impacts on Arctic charr populations and the varying degrees of population-specific vulnerability (e.g., Lehtonen 1998; Graham and Harrod 2009).

Contrasting life-history strategy opportunities and differences in the relative densities of juvenile Arctic charr may have contributed to climate-driven inter-specific interactions that enhanced the effect of warming temperatures on Arctic charr in Lake Tasiapik. For example, in warmer years Lake Tasiapik Arctic charr may experience amplified interactions with lake trout as preferred cool-water habitat is

increasingly limited for both species (e.g., Coutant 1987). Lower juvenile densities associated with the recent establishment of the Arctic charr population in Lake Qamutissait (e.g., Murdoch et al. 2012, in review) and opportunities for anadromy beginning at age 4 that release older fish from freshwater competition (e.g., Rikardsen et al. 2003), may combine to reduce both the intra-specific competition for food and space that may drive reduced growth in warmer years.

Lake trout has been previously shown to influence the diet, growth rate, survival and longevity of Arctic charr by means of interactive segregation or competition (Fraser and Power 1984; Fraser and Power 1989). Furthermore, other studies have noted the unaggressive behaviour and the tendency of Arctic charr to avoid inter-specific interactions by shifting their habitat use in the presence of other species (e.g., Johnson 1980; Langeland et al. 1991). Available thermal data for Arctic charr and lake trout demonstrates a great similarity (preferred temperatures: 8-12°C for lake trout, e.g., Ferguson 1958; Coutant 1977; Olson et al. 1988; 11-12°C for Arctic charr, e.g., Larsson 2005; Rikardsen et al. 2007) and thus a high potential for thermal resource competition where habitat is limiting. Increasing temperatures have also been shown to trigger conditional species interactions between Arctic charr and brown trout (Finstad et al. 2011), and between Dolly Varden charr (*Salvelinus malma*) and white-spotted charr (*Salvelinus leucomaenis*) (Taniguchi and Nakano 2000), with differing behavioural tactics, lake size and productivity all contributing to climate-driven outcomes.

The lagged effect of higher temperatures on subsequent seasonal growth suggests resilience to temperature-induced impacts in Arctic charr may be low, particularly among juveniles. Temperatures experienced by young-of-the-year fish may have a significant influence on end of summer body condition with cascading effects for winter survival (McDonald et al. 1996), and subsequent summer growth. Thus, increasing thermal stress on young-of-the-year may decrease end of season body condition and lipid accumulation, which would in turn decrease the probability of winter survival and/or result in poor spring condition for surviving individuals (e.g., Post and Evans 1989; Johnson and Evans 1991; Schultz and

Conover 1997; Sogard and Olla 2000). Reduced body condition at the beginning of the second summer would require that initial energy intake be allocated to existing body tissue repair and maintenance prior to the beginning of seasonal somatic growth (Jobling 1994), an effect likely to result in a smaller overall growth increment for that season. While evidence of growth compensatory tactics do exist for Arctic charr following short periods of time in resource limitation in the laboratory (Jobling et al. 1993), it is unknown if such mechanisms act after extended periods of fasting, particularly after the lengthy period of fasting associated with over-wintering. Studies of seasonal growth variability in brown trout (Swift 1955) have noted seasonal peaks of growth in spring and fall triggered by changes in photo-period and reliant on accumulated lipid reserves that suggest reduced spring condition would be consistent with subsequent reduced seasonal growth.

3.5 Conclusions

Study findings have revealed how two contrasting Arctic charr populations with differing life-history strategies and preferred thermal habitat availability can display strikingly different growth patterns as temperatures increase. The negative effects observed among Lake Tasiapik Arctic charr stemmed from the lake's physical vulnerability to climate change and the limited availability of cool-water habitat.

Contrasting impacts observed among Lake Qamutissait Arctic charr indicate the outcomes will be extremely variable, even within the same watershed. Although climate change has been predicted to have its greatest impacts on populations resident in small, shallow lakes situated along the southern margin of the distributional range, lakes at high latitudes are as likely to be similarly impacted. The eventual effects of increasing temperatures on Arctic charr will operate through a variety of complex mechanisms, and will depend on many mitigating factors including: life-history, interspecific effects, lake morphometry and productivity (Reist et al. 2006b; Finstad et al. 2011), as demonstrated by the variable population-specific findings from this study. Thus, results here further underline the necessity for increasing understanding of how Arctic charr in different populations will respond to temperature

variability so that accurate stock-specific forecasts can be made and strategies for mitigating impacts can be designed to ensure the continued sustainability of the species throughout the majority of its existing distributional range.

3.6 Figures and Tables



Figure 3.1 Map of the downstream portion of the Nepihjee watershed, including Lake Qamutissait, Nepihjee River and adjacent Lake Tasiapik. All lakes drain into Dry Bay, Ungava Bay (DMTI Spatial Inc. 2010).

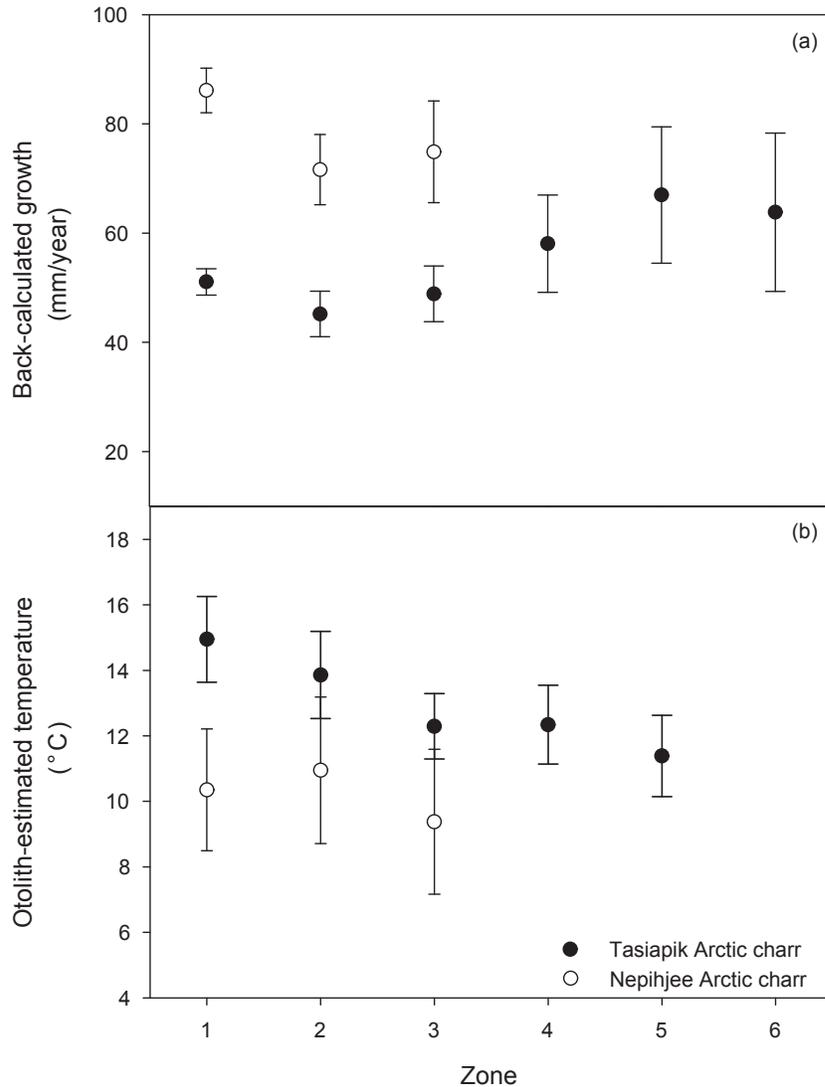


Figure 3.2 (a) Back-calculated growth by annual growth zone and (b) otolith-estimated temperatures by summer growth zone for Arctic charr in Lake Tasiapik and Lake Qamutissait. A total of 3 zones are plotted for Lake Qamutissait Arctic charr, whereas for Lake Tasiapik Arctic charr there are 5 and 6 zones plotted for otolith-estimated temperatures and back-calculated growth, respectively. Qamutissait Arctic charr were of hatchery origin and thus zone 1 is a combination of hatchery and natural thermal conditions, whereas Qamutissait zones 2+ represent natural thermal conditions exclusively. Data are plotted as means and associated 95% confidence intervals.

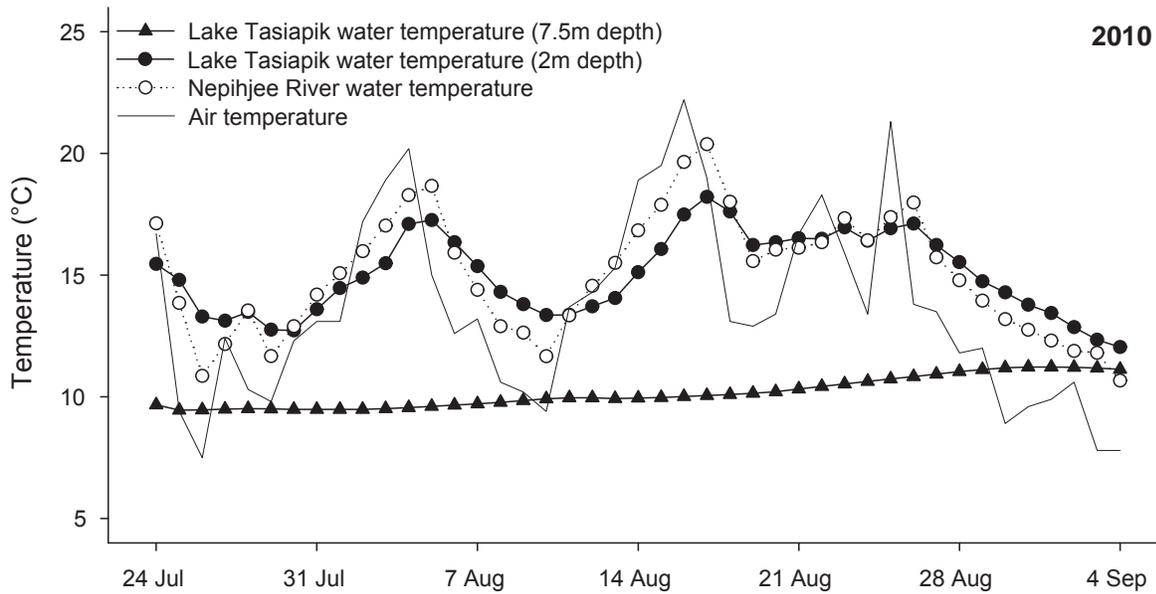
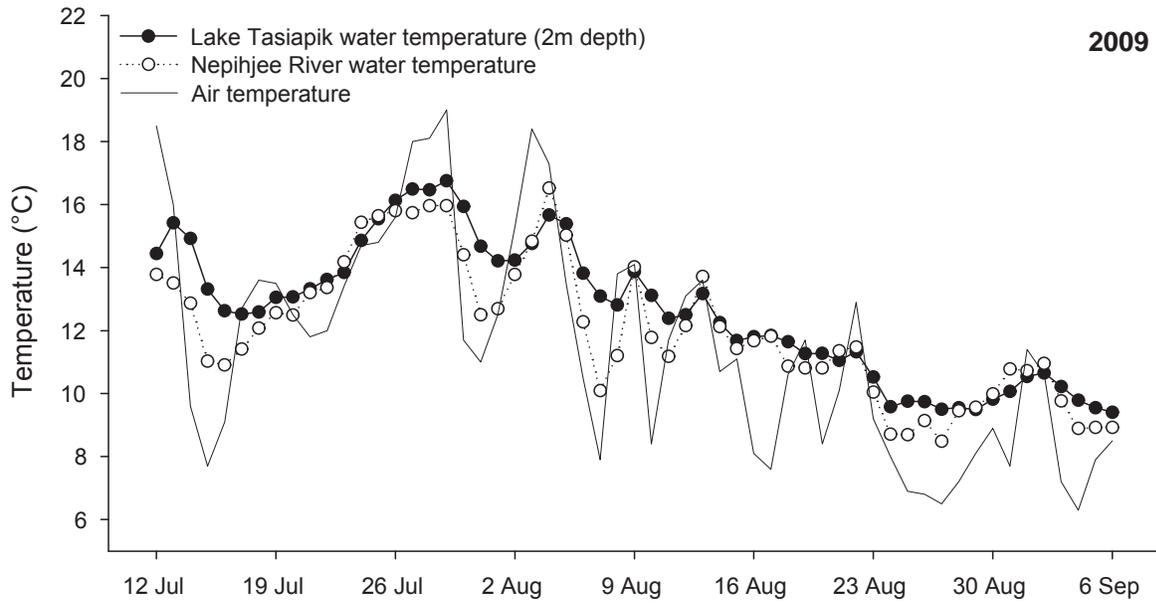


Figure 3.3 Daily water temperatures from Lake Tasiapik and the Nepihjee River in relation to local air temperature data for years 2009 and 2010.

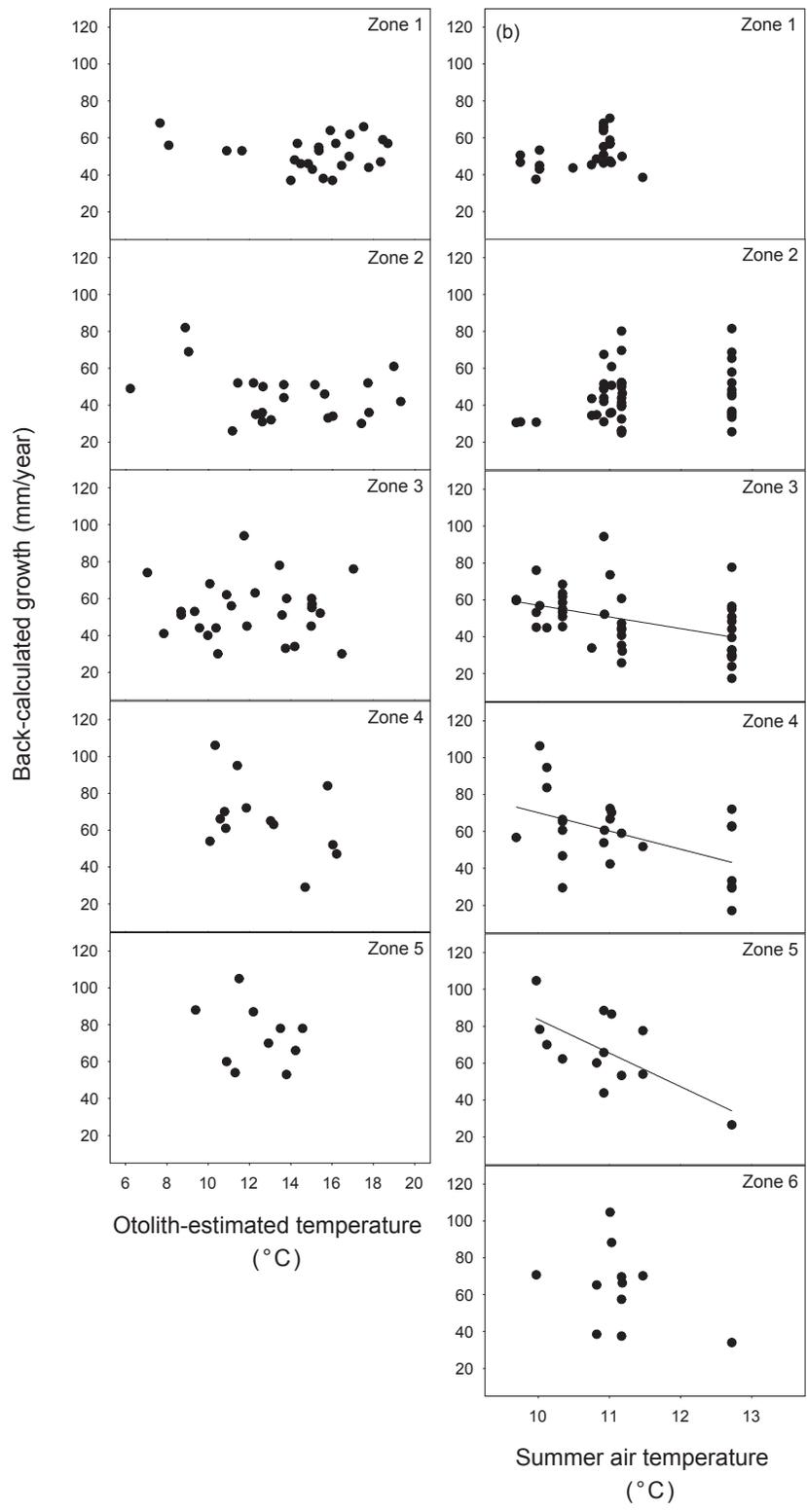


Figure 3.4 Lake Tasiapik Arctic charr back-calculated zone growth and (a) related otolith-estimated temperatures and (b) summer air temperatures. Linear regression lines are included for significant relationships only.

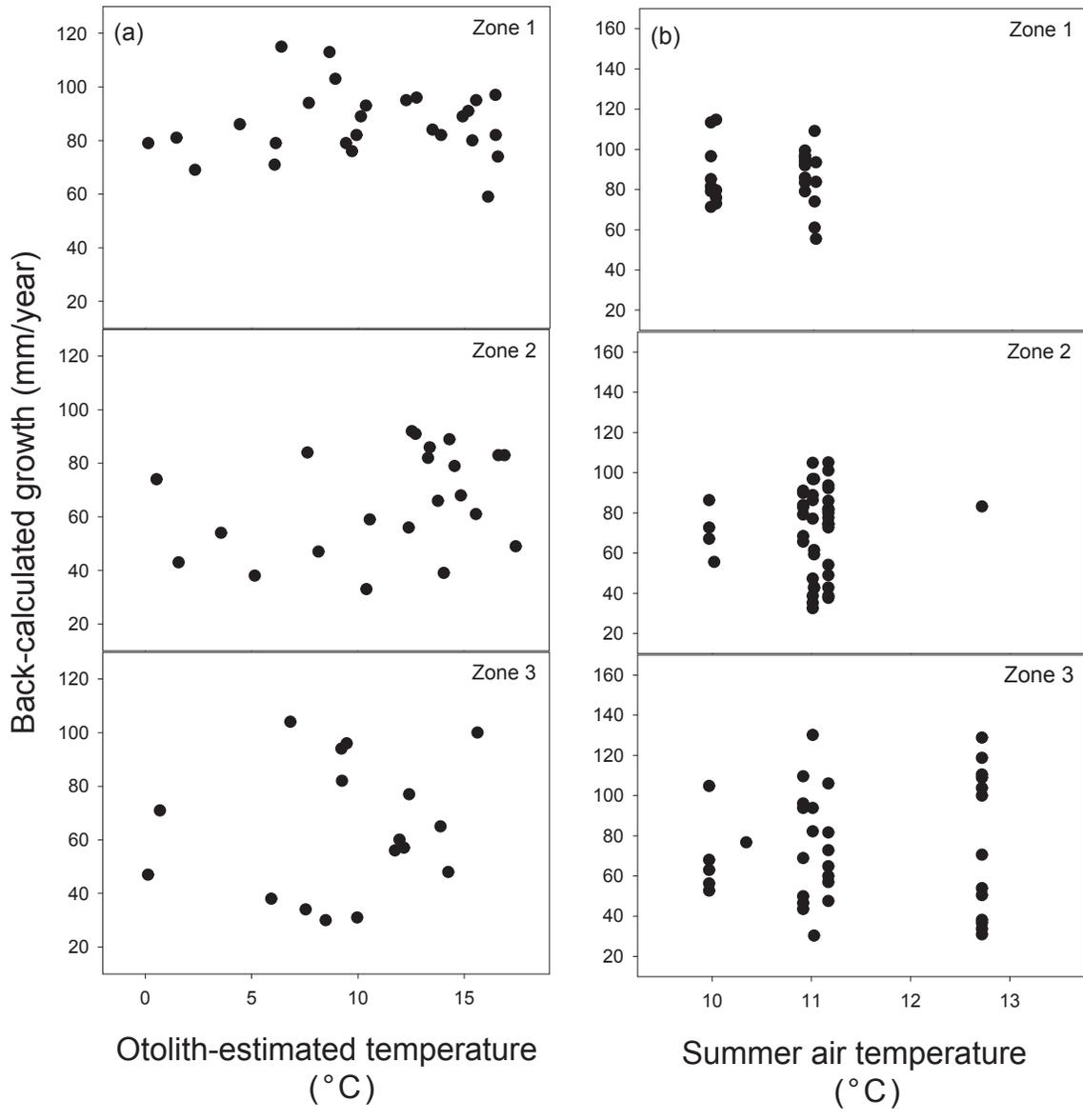


Figure 3.5 Lake Qamutissait Arctic charr back-calculated zone growth and (a) related otolith-estimated temperatures and (b) summer air temperatures. No significant relationships occur.

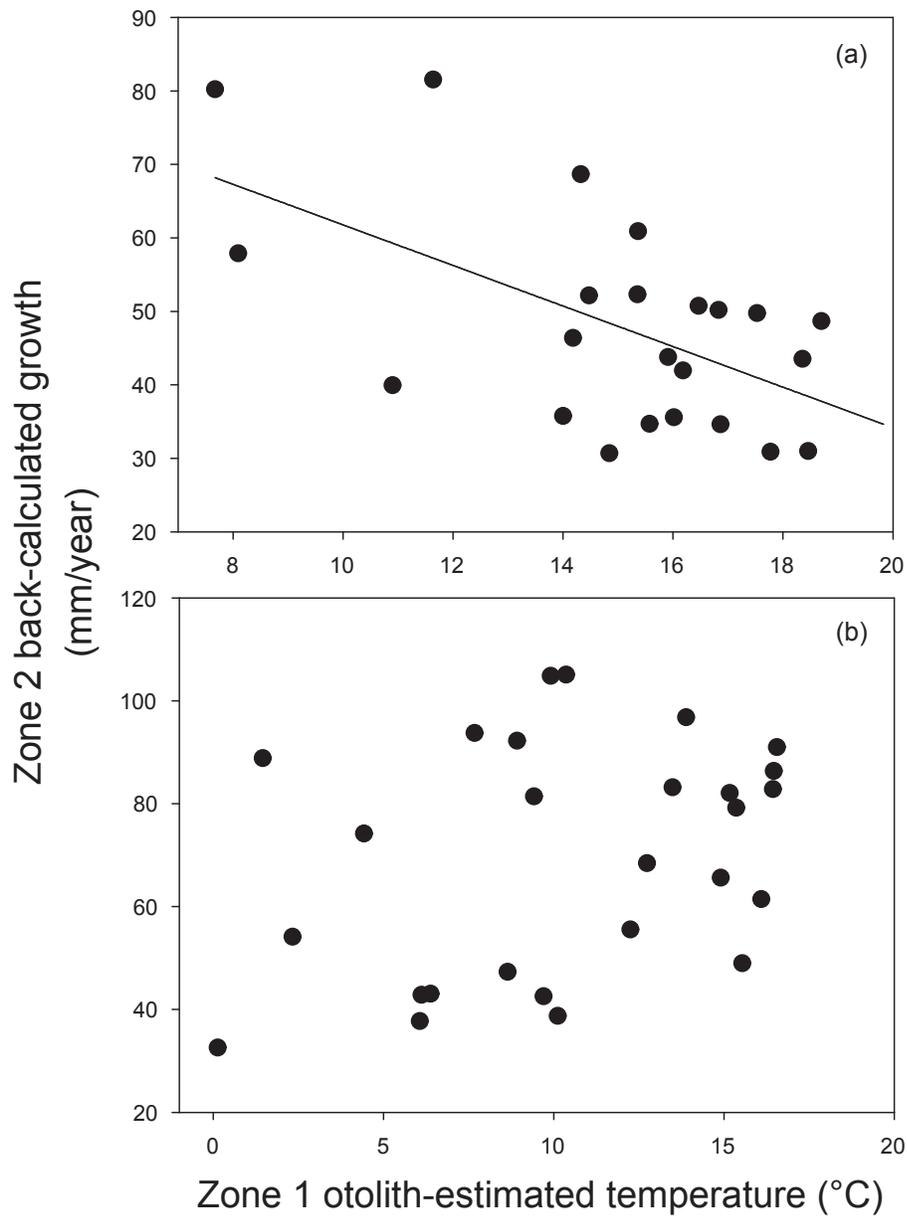


Figure 3.6 (a) Lake Tasiapik and (b) Lake Qamutissait zone 1 (young-of-the-year) otolith-estimated temperatures and associated zone 2 back-calculated zone growth. The linear regression line indicates a significant trend.

Table 3.1 Summary of modified-fry back-calculation model estimation results. Two non-linear regressions per site were analyzed, one with fish length (L) as the dependent variable and otolith radius (R) as the independent variable, and vice versa. Overall regression significance (P), estimated coefficients, b and c, and *p*- values are also given.

Site	Regression	n	r^2	Regression <i>p</i> - value	b	c	Coefficient <i>p</i> - value
Tasiapik	L on R	71	0.97	< 0.01	0.00196	1.64	≤ 0.04
	R on L	71	0.97	< 0.01	0.00013	-0.50	≤ 0.01
Nepihjee	L on R	68	0.97	< 0.01	0.01550	1.38	≤ 0.12
	R on L	68	0.98	< 0.01	0.00090	-0.57	≤ 0.06

Chapter 4

General Conclusions and Future Considerations

Comparisons of Arctic charr temperature and growth using data obtained from different regions and watersheds with differing climate vulnerabilities reveal evidence of population-specific effects resulting from increasing temperatures. Study findings, therefore, accord with the variable predictions that have been made for Arctic charr in the face of climate change (e.g., Reist et al. 2006a; Graham and Harrod 2009). Specifically, cooler waters with an ample food supply are expected to demonstrate positive growth changes whereas warmer and more vulnerable waters with limited ration availability should demonstrate negative growth impacts due to warming temperatures. The dichotomous result helps to explain the discord between laboratory-estimated growth optima and research conducted on wild Arctic charr temperature-growth relationships by underlining the consequences of local food availability, environmental conditions and within-season growth timing for realized growth, with differing conditions capable of producing different responses to the same apparent environmental driver – increasing temperature. Thus, the laboratory predicted thermal growth performance curves for Arctic charr remain applicable for wild populations in many instances, although the realized optimum will vary depending on the local food supply. Previous observations of both positive and negative temperature-growth relationships observed when studying wild Arctic charr (Power et al. 2000; Kristensen et al. 2006; Michaud et al. 2010), therefore, may have resulted from shifts in the optimal temperature for growth driven by local variations in feeding resources and/or water temperatures that placed local populations on either the increasing, stable (optimal), or decreasing portion of ration-adjusted temperature-growth curves and yielded positive, null or negative correlations, respectively.

The additional confusion arising from the dichotomy between annual and within-season temperature-growth patterns further demonstrates the complexity of the temperature-growth relationship in natural

settings. While other studies have also reported high early seasonal growth that may be attributed in part to temperature (Berg and Berg 1989; Rikardsen et al. 2000), it is unknown what the relative influences of temperature, seasonal growth compensation and abundant early season food availability are in determining growth seasonal timing. Annual and within-season observations of temperature-growth patterns may appear decidedly contradictory, however, it is still expected that increasing mean annual temperatures will have a positive effect on early seasonal growth, provided there is sufficient food to meet increased energetic demands. Stated otherwise, warmer May-June temperatures will allow a greater scope for growth when fish have more food available and may be experiencing rapid growth connected with seasonal compensatory growth mechanisms (e.g., Jobling et al. 1993; Rikardsen et al. 2000).

Research here provides strong evidence for the roles of local food availability, seasonal growth timing and watershed vulnerability in determining growth outcomes as temperatures increase. Based on the results obtained in this study, future fisheries management and research scenarios should include consideration of the following:

1. The use of local productivity (e.g., chlorophyll *a*) measurements taken prior to, (as reconnaissance surveying for determining population vulnerability to climate change), or concurrently with fish sampling.
2. A greater focus on monitoring Arctic charr populations at risk, particularly freshwater populations residing in climate-vulnerable watersheds (small, shallow lakes at low altitudes and/or latitudes), especially those co-occurring with closely related dominant fish species such as lake trout, brook trout or brown trout which may be expected to be competitively superior under most climate change scenarios.
3. Conduct of laboratory research on Arctic charr comparable to the work completed for brown trout where temperature-growth relationships were determined with varying ration (Elliott and Hurley

2000a; Elliott and Hurley 2000b). Results may be used as a proxy for predicting how changes in temperature will affect growth in the wild where local productivity information is available.

Furthermore, where water temperature data is also available, results of such work may be used to better identify at-risk populations of Arctic charr.

4. Further study of the relative influences of low temperatures, food availability and growth compensation for determining high early-seasonal growth patterns. This may be investigated in a controlled laboratory experiment, or in the wild using regions with differing but seasonally consistent food supplies, to determine if optimal growth occurs later in the season at higher temperatures where more food is available.

Finally, as differing methodologies were employed here for measuring individual temperature and growth patterns, suggestions for future research to improve the accuracy of inferences of temperature-growth relationships include:

1. The greater use of methods which estimate individual thermal regimes and do not rely on stationary temperature loggers (e.g., otolith reconstruction methods, individual data loggers). However, concurrent use of temperature loggers will provide additional verification of the accuracy of otolith temperature reconstruction methods.
2. The employment of long-term temperature data loggers in lakes and nearshore areas as a means for identifying climatically vulnerable regions which are most in need of future monitoring.
3. The development of otolith microchemistry procedures to allow temperature estimation of fish which experience a large range of salinities for the estimation of experienced marine temperatures.
4. The increased emphasis on long-term fish tagging experiments to obtain the most accurate growth measurements possible, as was done in the 1980s in Labrador by Fisheries and Oceans Canada

(DFO). Furthermore, otoliths may be extracted from long-term recaptures and used for temperature reconstruction.

The Arctic charr is a complex, cold-adapted species which will be both positively and negatively affected by climate change dependent on local conditions. Northern communities have been experiencing rapid growth over the past few decades (e.g., Duhaime 2008), greatly increasing the demand for highly valued subsistence foods such as Arctic charr. Evidence presented here demonstrates the need for obtaining local population-specific biological data on Arctic charr in concurrence with local environmental and productivity measurements for the creation of accurate Arctic charr climate-induced population forecasts. In particular, such data is most needed for exploited and climatically-vulnerable Arctic charr populations which northern indigenous people rely upon for their personal health and livelihood, if we are to maintain sustainable Arctic charr populations as the climate varies.

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