

Ecology of Juvenile Arctic charr in 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. I understand that my thesis may be made electronically available to the public.

Abstract

Increases in global temperatures resulting from climate change have raised concern over potential responses of Arctic charr, *Salvelinus alpinus*, a cold-adapted freshwater/anadromous fish species in the salmonid family. While various aspects of adult Arctic charr ecology are well established, juvenile, and in particular, young-of-the-year (YOY) ecology is less well understood. The study of early life stages is important because of implications for subsequent population dynamics as well as their particular sensitivity to climate change. In this thesis, I aimed to broaden the scope of knowledge on juvenile Arctic charr from Canadian populations with a particular emphasis on YOY, and thermal habitat use through four studies.

An intensive study of juvenile Arctic charr from Lake Hazen, Nunavut, demonstrated a preference during the summer for stream environments, particularly those fed by warm upstream ponds. Charr occupying both stream and nearshore lake habitats were found to feed similarly, with chironomids occurring most frequently in diets. Some older stream-dwelling charr preyed on smaller, younger Arctic charr. Preferred stream occupancy is likely mediated by physical barriers created mainly by water velocity, and by distance from the lake, lake-ice dynamics, low water depth, and turbidity. Water velocities and possibly intercohort competition resulted in stream habitat segregation by size, with YOY mainly found in low velocity pools and back eddies adjacent to stream banks, but not in water velocities greater than 0.1m/s. Greatest charr densities in streams were found in small, shallow, slow-flowing side channels, which are highly susceptible to drought.

A discriminant function analysis model based on carbon and nitrogen stable isotope values was used to identify offspring of piscivorous large-form and non-piscivorous small-form Arctic charr morphotypes from Lake Hazen, Nunavut. The adult morphotypes were estimated to contribute approximately equally to the YOY population, however, the morphotype offspring were differentially distributed among sampled nursery sites. Unequal distribution corresponds with prerequisites suggested for the evolution of trophic specialists within a single population that experiences assortative mating based on trophic specialization.

An assessment of growth rates and otolith-inferred metabolic rates obtained from YOY from 23 populations over a 27° latitudinal gradient demonstrated latitudinal variability consistent with countergradient variation where northern populations demonstrated faster growth and higher metabolic rates compared to southern populations. Countergradient variation (CGV) is defined as genetic variation that counteracts the negative influences of the physical environment, minimizing phenotypic variability along a gradient. Otolith-inferred metabolic rates from free-living animals reflect the average daily energy expenditure of the organism, which incorporate the energetic costs of standard metabolic

rate (SMR) and other processes such as feeding, locomotion, thermoregulation, reproduction and growth. As such, variations in otolith-inferred metabolic rates may reflect a combined increase in feeding, activity and SMRs in northern populations. Nevertheless, the phenotypic variation in physiological traits observed here demonstrates the significant adaptability of Arctic charr to different thermal regimes with different growing season lengths.

Otolith-inferred temperatures and fork lengths at capture from YOY from two proximal fluvial and lacustrine sites in Labrador were used to compare growth and thermal habitat use between habitat types. Otolith-inferred temperatures were not significantly correlated with air temperatures, suggestive of behavioural thermoregulation by YOY at both sites. The majority of YOY from Kogluktokoluk Brook (fluvial) were found using temperatures consistent with laboratory determined preferred temperatures for juvenile Arctic charr, whereas most Tom's Pond (lacustrine) YOY were found using temperatures ranging between preferred temperatures and optimal temperatures for growth. Otolith-inferred temperatures were only correlated to fork lengths in Tom's Pond YOY. The lack of correlation in Kogluktokoluk Brook YOY may reflect resource partitioning occurring as a result of territoriality known to occur among stream salmonids. The limited range of temperatures used by fluvial YOY in this study, particularly the lack of cooler temperatures, suggests that fluvial YOY may face barriers to accessing thermal refugia, and as a result may be particularly vulnerable to climate change.

Examining the ecology of juvenile Arctic charr from Canadian populations over a number of spatial scales (i.e. latitudinal, regional and local) highlighted the considerable phenotypic plasticity demonstrated by the species. While physiological plasticity observed over the latitudinal gradient reflected the ability for juvenile Arctic charr to utilize different thermal regimes, the regional comparison between habitat types demonstrated that the ability for juvenile Arctic charr to respond to climate change is likely to vary between habitat types. Further, on a local scale, behavioural plasticity was observed, but was found to be influenced by several regulatory factors.

The study of the ecology of juvenile Arctic charr in this thesis has highlighted various factors affecting juvenile Arctic charr in Canada: temperature, water velocity, cover, maternal influences, habitat type and ration. The relative contributions of these factors as well as others which were not directly testable in this thesis (e.g. variability in standard metabolic rate, the role of genetic adaptation) are likely to vary with latitude, populations and habitat types. Deciphering the relative roles of these factors will allow better predictions of responses to climate change.

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Chapter 1: General Introduction

General context of thesis

The work compiled in this thesis aims to expand the present understanding of the ecology of juvenile Arctic charr, *Salvelinus alpinus*, in Canada. Arctic charr is an important food resource for the Inuit people of Canada providing both social and economic benefit and is often the dominant or only fish species in high latitude lakes. Rising global temperatures, however, are thought to pose a particular risk to Arctic charr, and a contemporary understanding of how Arctic charr relate to their environment may provide insight into how the species may respond to climate change. Developing an understanding of climate change effects on every life history stage is thought to be vital for predicting overall responses (Pörtner & Peck 2010, Russell et al. 2012, Radchuk et al. 2013). Despite the importance of understanding each life history stage and the particular sensitivity of early life history stages to environmental change (Rijnsdorp et al. 2009, Pankhurst & Munday 2011), a relatively modest amount of study has focused on the juvenile life stage of Arctic charr. This thesis consists of a general introduction chapter, four data chapters (Chapters 2 to 5), each written as an independent study, and a general conclusions chapter. At the time of submission, Chapter 2 was published in *Ecology of Freshwater Fish*, and Chapter 3 was published in *Freshwater Biology*.

Arctic charr

Distribution

Arctic charr are the only freshwater/anadromous fish species found in the Arctic with complete circumpolar distribution (Reist et al. 2006a). The native distribution of Arctic charr closely matches the last glaciation in the Holarctic and in early post-glacial times the species likely occurred over most deglaciated areas (Power 2002). Presently, however, Arctic charr are absent from many lakes in the southern extent of that region, likely as a result of increased temperature, eutrophication and competition with complex fish assemblages (Klemetsen et al. 2003). Nevertheless, Arctic charr exhibit the widest natural distribution of all salmonids (Maitland 1995) and in North America presently exist from northern New England (~43°N) to the northern coast of Ellesmere Island, NU (~82°N) (Power et al. 2008).

Polymorphism

Arctic charr demonstrate a high degree of diversity in range, phenotype, size-at-maturity, behaviour, ecology and life-history, and have been suggested to be the most variable vertebrate species (Klemetsen 2010). Arctic charr are considered to be habitat generalists and can occupy marine environments, fluvial environments and all parts of oligotrophic lakes (Klemetsen et al. 2003), although lacustrine

populations predominate the Arctic distributional range. Termed ‘the charr problem’, Arctic charr frequently occur as two or more distinctive morphotypes within the same lake (Johnson 1980, Klemetsen 2010). Typically, distinct sympatric morphotypes include a small epibenthic form that feeds on zoobenthos, and a larger pelagic form that feeds on zooplankton (Power et al. 2008). In high Arctic lakes where Arctic charr are often the only fish, cannibalistic morphotypes are common (e.g. Johnson 1980, Guiguer et al. 2002, Berg et al. 2010). Piscivory, particularly in the form of cannibalism, may also lead to divergent body size (large and small) occurrences (Power et al. 2008). The number of forms which co-exist within a lake is thought to depend on the number of available niches (Klemetsen et al. 2003), although examples of sympatric morphotypes existing within more complex communities of fish exist in both Russia and Canada (Alekseyev et al. 2002, O'Connell & Dempson 2002, Power et al. 2009). Within lakes, inter- and intra-specific competition can give rise to habitat segregation based on morphotype (e.g. Frost 1965, Skúlason et al. 1989) and/or ontogeny (e.g. Klemetsen et al. 1989, Bystrom et al. 2004, Amundsen et al. 2008).

Early life-history stages

The adult life-history stage of Arctic charr has been well studied (e.g. Johnson 1980, Jonsson & Jonsson 2001, Klemetsen et al. 2003, Power et al. 2008), however, juvenile Arctic charr ecology, particularly that of young-of-the-year (YOY), is not similarly understood (Klemetsen et al. 2003). Particularly in North America, early life-history stages of Arctic charr have only been considered in a few populations (Moore & Moore 1974, Johnson 1976, Johnson 1980, Stenzel 1987, Adams et al. 1988, Stenzel et al. 1989, Stenzel & Power 1991, Simon 1995, Gallagher & Dick 2010, Gallagher & Dick 2011, Murdoch & Power 2013). Improving the current understanding of ecology during early life-history stages is vital owing to the broader implications of juvenile success for population sustainability and dynamics (Power 2007). For example, success during early life-history stages can have significant implications for later recruitment success and year class strength (Suda & Kishida 2003, Martino & Houde 2010). In addition, compared with adults, early life-history stages are thought to be more sensitive to environmental fluctuations, and as such are likely to be more sensitive to the broader ecosystem perturbations likely to be associated with climate change (Rijnsdorp et al. 2009, Pankhurst & Munday 2011).

Klemetsen et al. (1989) suggested a model for ontogenetic habitat segregation in Takvatn, Norway, where following emergence from spawning sites, YOY move to the profundal zone where low feeding potential is offset by the benefits of low predation risk. YOY have similarly been observed occupying the profundal zone in other lakes (e.g. Kircheis 1976, Hindar & Jonsson 1982, Simon 1995, Godiksen et al. 2011). However in some populations YOY have been found to remain in the littoral zone during the open water season (e.g. Johnson 1976, Johnson 1980, Stenzel 1987, Sandlund et al. 1988, Stenzel &

Power 1991, Simon 1995, Bystrom et al. 2004, Gallagher & Dick 2010, Godiksen et al. 2011). Only two accounts of pelagic habitat use by YOY Arctic charr have been noted in the literature (Sandlund et al. 1988, Winfield et al. 2002).

While dietary information on YOY is particularly sparse (Klemetsen et al. 2003), accounts that exist point to a benthic-dominated diet. Examples of YOY diet from Nordic lakes have shown YOY to feed on a variety of items including: chironomid larvae and pupae, benthic copepods, benthic cladocerans, ostracods, and other zooplankton, benthic insects and gastropods (Lindström 1955, Hindar & Jonsson 1982, Sparholt 1985, Sandlund et al. 1988, Bystrom et al. 2004). Similar to habitat use, dietary information on YOY from Canada is sparse. Studies on juvenile Arctic charr diet from Canadian populations indicate a dietary predominance of chironomid larvae and pupae and frequent occurrences of other dipteran larvae, Collembola and Acarina (Moore & Moore 1974, Stenzel 1987, Gallagher & Dick 2010).

The thermal requirements of juvenile Arctic charr have been well described by laboratory studies (e.g. Swift 1964, Jobling 1983, Larsson & Berglund 1998, Larsson et al. 2005). The optimal temperature for growth in Arctic charr lies between ~12 and 18°C (Swift 1964, Jobling 1983, Jensen 1985, Larsson & Berglund 1998, Larsson & Berglund 2005) with preferred temperatures ranging from ~9 to 12°C range (Peterson et al. 1979, Larsson 2005, Mortensen et al. 2007). The difference between optimal and preferred temperatures may allow Arctic charr to optimise growth efficiency instead of growth rate, a trait that may be favoured in low productivity environments inhabited by many Arctic charr populations (Larsson 2005). Compared to other fish species, Arctic charr have a relatively small thermal tolerance range (Ficke et al. 2007) and among salmonids, are the most cold tolerant (Peterson et al. 1979, Larsson 2005) as evidenced by a small thermal polygon (Baroudy & Elliott 1994a) and the ability to survive and feed at temperatures close to 0°C (Brännäs & Wiklund 1992).

Climate variability and change

Adaptation to cold environments suggests that Arctic charr may face physiological challenges in warming environments, with climate variability and change having prompted concern regarding the potential impacts of increased global temperatures on Arctic charr (Reist et al. 2006a, Reist et al. 2006b). As a result of climate change, mean global temperatures have increased by approximately 0.6°C in the last century (IPCC 2007), with polar regions having experienced the greatest regional warming (2-3°C since 1950) (ACIA 2005). Mean global temperatures are predicted to rise another 1.1 to 6.4°C by 2100 (IPCC 2007). Arctic freshwater ecosystems are thought to be particularly vulnerable to climate variability and change (ACIA 2005). Increased temperatures are expected to result in a longer ice-free season and increased productivity in freshwater environments (ACIA 2005). The longer ice-free season in the north may result in some initial benefit for resident freshwater fish species, such

as increased survival, abundance and size for early life-history stages. However, as temperatures increase, the distributional range of other fish species may shift northward, thereby increasing the competitive pressures on existing populations of Arctic fish, including Arctic charr (ACIA 2005). More southerly populations of Arctic charr are likely to face temperatures above their thermal optima, resulting in restricted growth and/or reduced survival (Jonsson & Jonsson 2009).

Improved understanding of how Arctic charr ecology and physiology currently vary across the existing distributional range of a species is likely to help improve the ability to more accurately predict the consequences of future climate change for the species. For example, countergradient variation (CGV), defined as genetic variation that counteracts the negative influences of the physical environment, thereby minimizing phenotypic variability along a gradient (Levins 1969, Conover & Present 1990), is thought to have relevance for predicting the response of ectotherms to projected climate warming scenarios (Conover et al. 2009, Baumann & Conover 2011).

Stable isotope applications in ecological studies

Oxygen stable isotopes and otolith thermometry

Recorded environmental temperatures do not always reflect water temperatures experienced by individual fish, owing to behavioural thermoregulation (Lehtonen 1996, Godiksen et al. 2011, Godiksen et al. 2012). Data storage tags can be used to record temperatures experienced by individual fish (e.g. Godo & Michalsen 2000, Rikardsen et al. 2007), but the technique is limited by cost, fish size and having to recapture tagged fish (Brown et al. 1999). In contrast, oxygen stable isotope analysis of biogenic calcium carbonate structures such as otoliths can be used to reconstruct the thermal histories of fish of any size with reasonable accuracy (Power et al. 2012) based on the temperature-dependent relationship between the oxygen stable isotopes in the otolith and inhabited waters at the time of otolith formation (e.g. Devereux 1967, Kalish 1991a).

Otoliths are formed extracellularly within the inner ear from crystallisation of calcium carbonate (largely aragonite) into an organic matrix (Carlstrom 1963, Degens et al. 1969). Otoliths are metabolically inert so that otolith material is not reabsorbed after deposition (Campana & Neilson 1985). Formation occurs continually throughout the lifetime of the fish by the addition of concentric layers of proteins and calcium carbonate about the nucleus (Campana & Neilson 1985).

Temperature reconstructions from otolith oxygen stable isotopes are possible because the otolith is formed close to isotopic equilibrium with the ambient water inhabited by the fish (Kalish 1991a, Iacumin et al. 1992, Thorrold et al. 1997) and the oxygen stable isotope compositions of the otolith and ambient water are offset in a predictable manner based on temperature-dependent fractionation (Sharp 2007). Accordingly, the thermal history experienced by the fish can be inferred if the otolith and water

oxygen stable isotope compositions, and a temperature-dependent fractionation equation are known (Patterson et al. 1993). Several fractionation equations have been published (Patterson et al. 1993, Radtke et al. 1996, Thorrold et al. 1997, Gao 2002, Høie et al. 2004, Storm-Suke et al. 2007, Godiksen et al. 2010). Comparisons of existing equations have demonstrated a high degree of variability in the inferred temperatures when inappropriate equations are used (Høie et al. 2004, Storm-Suke et al. 2007). Given that differences in physiology among fish species may affect the relationship between temperature and oxygen fractionation in the otolith on a species-specific basis (Høie et al. 2004, Rowell et al. 2005, Storm-Suke et al. 2007), it is important to select a fractionation equation estimated for a physiologically similar group of fish (Rowell et al. 2005). In that regard, the genus-specific and species-specific fractionation equations estimated (e.g. Storm-Suke et al. 2007, Godiksen et al. 2010) are of particular relevance for thermal studies in Arctic charr.

Metabolic rate inferred from carbon stable isotopes

The incorporation of some metabolically sourced $\delta^{13}\text{C}$ into biological carbonates was suspected by Keith & Weber (1965) in some taxonomic groups of coral, with Kalish (1991a) later bringing similar notions to otolith science. Since then, it has become more accepted that the carbon composition of biological carbonates (including otoliths) is derived from ambient dissolved inorganic carbon (DIC) and carbon derived from the diet (metabolic carbon) in varying proportions. The proportion of metabolic carbon compared to ambient DIC within the otolith is dependent on the metabolism of the fish. Thus the ratio has been used to infer relative metabolic rate of individual fish (Kalish 1991a, Thorrold et al. 1997, Schwarcz et al. 1998, Weidman & Millner 2000, Wurster & Patterson 2003, Jamieson et al. 2004, Wurster et al. 2005, Shephard et al. 2007). Since otolith $\delta^{13}\text{C}$ values reflect levels of metabolically derived $\delta^{13}\text{C}$ in plasma (Sherwood & Rose 2003) and are metabolically inert once precipitated into the otolith (Campana 1999), the otolith-inferred metabolic rate reflects the average field metabolic rate of the organism over its lifetime. Field metabolic rate refers to the metabolic rate of free-living animals which reflects the average daily energy expenditure of an organism and incorporates the energetic costs of standard metabolic rate (SMR), thermoregulation, locomotion, feeding, reproduction and growth (Nagy 1987).

Trophic and feeding ecology

Stable isotope analysis has become a commonly used and well documented method for quantifying trophic interactions and assessing changing food webs (Kling et al. 1992, Cabana & Rasmussen 1994, Vander Zanden & Rasmussen 1999). The difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between a consumer and its diet has been widely accepted to be in the 0-1‰ and 3-5‰ ranges, respectively (Peterson & Fry 1987). Dietary carbon sources are now commonly traced using $\delta^{13}\text{C}$, whereas $\delta^{15}\text{N}$ lends itself to assessing

trophic positioning in the food web (Peterson & Fry 1987, Kling et al. 1992, Cabana & Rasmussen 1996, Post 2002). Owing to the long term view provided by stable isotope signatures (Peterson & Fry 1987) and that neonate offspring are formed from materials derived from maternal sources rather than food directly consumed by the individual, stable isotope signatures from offspring muscle tissue can be used to infer maternal dietary information and where maternal diets differ significantly the same data can be used to infer juvenile maternal origin (e.g. Vander Zanden et al. 1998, Doucett et al. 1999, McCarthy & Waldron 2000, Charles et al. 2004, Murchie & Power 2004, Curry 2005, Jardine et al. 2008, Godbout et al. 2010).

Research objectives

Various ecological and physiological aspects of adult Arctic charr have been well studied (e.g. Johnson 1980, Jonsson & Jonsson 2001, Klemetsen et al. 2003, Power et al. 2008). However, early life-history stages of Arctic charr, particularly from North American populations have been paid little attention. Since early life-history success has been linked to eventual recruitment success (Suda & Kishida 2003, Martino & Houde 2010) and since individuals in early life-history stages tend to be more sensitive to environmental change (Rijnsdorp et al. 2009, Pankhurst & Munday 2011), the work compiled in this thesis aims to investigate juvenile Arctic charr ecology with a focus on YOY, to broaden the currently limited scope of knowledge on Canadian populations. Owing to the significant influence of temperature on fish physiology and distribution and the predicted increases in temperatures resulting from climate change, an emphasis was placed on investigating thermal habitat use. Diet and physiological variability among individuals and populations were also addressed. The specific objectives of each chapter are outlined below.

Chapter 2: Summer habitat use and feeding of juvenile Arctic charr, *Salvelinus alpinus*, in the Canadian High Arctic

To address the particular lack of information on juvenile Arctic charr in the Canadian High Arctic, chapter 2 assembled and analysed all data available on juvenile Arctic charr from repeated surveys of Lake Hazen, Ellesmere Island, Nunavut (summer 2001, 2007, and 2008) to characterise dietary and habitat use patterns. The study tested the specific hypotheses that: (1) juvenile Arctic charr exhibit preference for stream over nearshore lake habitats; (2) there are significant differences in the diets of juvenile Arctic charr in stream and nearshore lake habitats; and (3) physical features of the stream (e.g. velocity, temperature, and water source) influence stream density of Arctic charr.

Chapter 3: Identification of the maternal source of young-of-the-year Arctic charr in Lake Hazen, Nunavut, Canada

Chapter 3 used stable isotope methods, and the maternal stable isotope information present within offspring somatic tissue, to identify the maternal source (piscivorous large-form morphotype vs. largely non-piscivorous small-form morphotype) of randomly sampled Lake Hazen YOY Arctic charr. Inferred information on maternal source was used to estimate the relative reproductive contribution of each morphotype to the Lake Hazen Arctic charr population as a whole to test the null hypothesis that each morphotype contributes equally to the YOY population.

Chapter 4: Latitudinal compensation in growth and otolith-inferred metabolic rate of Canadian young-of-the-year Arctic charr

Chapter 4 used information on differences in growth and field metabolic rates among YOY Arctic charr sampled over a 27° latitudinal gradient in eastern and central Canada as inferred from stable isotope analyses to test the hypotheses that growth and metabolic rates increase with latitude in a manner consistent with the countergradient variation hypothesis.

Chapter 5: Thermal habitat use and growth in young-of-the-year Arctic charr from two proximal fluvial and lacustrine populations in Labrador, Canada

Chapter 5 used data gathered contemporaneously at two proximal fluvial and lacustrine sites over a number of years to compare growth and thermal habitat use between habitat types. Largely based on the expectation that accessible thermal habitats are restricted for fluvial YOY Arctic charr, the following hypotheses were tested: (1) that thermal habitat used by fluvial individuals are more correlated to air temperatures; and (2) as a consequence, fluvial YOY use warmer habitats than lacustrine fish; (3) that lacustrine fish exhibit greater variability in utilized thermal habitats which is (4) reflected in increased variances in fork lengths among lacustrine individuals. Lastly, the relationship between fork length and otolith-inferred temperature was characterised and the hypothesis that (5) fluvial and lacustrine YOY exhibit similar correlation between fork length and otolith-inferred temperature was tested.

Chapter 2: Summer habitat use and feeding of juvenile Arctic charr, *Salvelinus alpinus*, in the Canadian High Arctic

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Introduction

Arctic charr, *Salvelinus alpinus*, demonstrate a high degree of variability in habitat selection, occupying marine environments, streams, and all parts of oligotrophic lakes, with the most common of these being lacustrine environments (Klemetsen et al. 2003). Within lakes, inter- and intraspecific competition can give rise to habitat segregation based on ontogeny (e.g. Klemetsen et al. 1989, Bystrom et al. 2004, Amundsen et al. 2008). How habitats are divided among life-history stages seems to vary. For example, in Takvatn, Norway, adult Arctic charr mainly occupy the littoral zone and juveniles generally inhabit the profundal zone (Klemetsen et al. 1989). Conversely, Bystrom et al. (2004) found that young-of-the-year (YOY) Arctic charr in three alpine lakes in northern Sweden used nearshore littoral environments. Sandlund et al. (1988) also noted that in Arctic and alpine lakes, juvenile Arctic charr tend to use nearshore environments owing to lower predation risks, possibly related to the absence of competitor species (e.g. brown trout, *Salmo trutta*) that dominate the littoral environments of most European subarctic and temperate lakes where YOY Arctic charr are typically not found.

Similar to other salmonid species, seasonal habitat shifts have been well documented for Arctic charr (e.g. Näslund 1990, Klemetsen et al. 2003, Amundsen et al. 2008). Anadromous individuals undergo seaward migrations with subsequent returns to freshwater environments to spawn or overwinter (Klemetsen et al. 2003). In some instances, juvenile estuarine migrations have been reported (Dempson 1993, Jonsson & Antonsson 2005). Resident and juvenile Arctic charr also make seasonal habitat shifts within freshwater to inhabit more productive waters, find preferred temperatures, avoid predation and/or minimize inter- and intraspecific competition (Näslund 1990, Amundsen et al. 2008, Amundsen & Knudsen 2009). For example, Craig and Poulin (1975) first reported migration of small numbers of 1+ to 3+ year old Arctic charr (subsequently reclassified as Dolly Varden, *Salvelinus malma*, J.D. Reist, personal communication) from a large Arctic river to a small tributary stream in Alaska and attributed the shift to water temperature and the abundance of food items. Gulseth & Nilssen (1999) also observed the migration of immature (2+ to 8+) lake-spawned Arctic charr from Dieset Lake, Svalbard, into an outlet river used by anadromous individuals to access the ocean. Naslund (1990) demonstrated the use of small streams during the migration of a landlocked Arctic charr population between two lakes in northern Sweden.

Only a few accounts of seasonal occupancy of small tributary streams by lacustrine juvenile Arctic charr have been recorded in the literature. Johnson (1980) noted that young lake-spawned Arctic charr occupy streams during the summer. Similarly, Babaluk et al. (2001) observed movement of small lake-spawned Arctic charr into the tributary streams of Lake Hazen. Occupancy of tributary streams by lake-spawned juvenile salmonids was previously described for YOY lake-dwelling brook charr, *Salvelinus fontinalis* (Curry et al. 1993, Curry et al. 1997). For juvenile brook charr, small tributary streams were found to represent important rearing habitat because of the potential fitness advantages conferred by maximizing length gains in cooler stream habitats that better approximated optimal thermal conditions for growth (Curry et al. 1997).

Descriptions of habitat use by YOY and other small juvenile Arctic charr have predominantly come from Scandinavian and other high altitude European lakes where they have been found to primarily use littoral (e.g. Sandlund et al. 1988, Bystrom et al. 2004, Godiksen et al. 2011) or profundal (e.g. Hindar & Jonsson 1982, Klemetsen et al. 1989, Godiksen et al. 2011) environments. Only two accounts of pelagic habitat use by YOY exist (Sandlund et al. 1988, Winfield et al. 2002). In Canada, Johnson (1976) observed juveniles between 30 and 200mm using rocky parts of the shoreline of Keyhole Lake, Victoria Island, Nunavut and using the fine gravel shoreline of Tree River, Nunavut the latter of which he described as being unusual because of minimal protection from predation (Johnson 1980). Similarly, in the Koroc River system, Ungava Bay, Quebec, juvenile Arctic charr were found to use shoreline environments in the river and lake (Stenzel 1987, Stenzel & Power 1991). In contrast, in the Sapukkait River, Ungava Bay, Quebec, YOY and 1+ individuals used both littoral and profundal habitats, but predominantly used the latter (Simon 1995). In a recent study by Gallagher and Dick (2010) on a southern Baffin Island Arctic charr population, most of the juvenile charr obtained during the summer were captured via electrofishing in the littoral zone.

A review by Klemetsen et al. (2003) specifically highlighted the lack of dietary information for YOY Arctic charr. For the most part, whether using littoral or profundal habitats, most dietary accounts of YOY and older juveniles suggest a benthic lifestyle. Examples of YOY diet from Nordic lakes have shown YOY to feed on a variety of items including chironomid larvae and pupae, benthic copepods, benthic cladocerans, ostracods, and other zooplankton, benthic insects and gastropods (Lindström 1955, Hindar & Jonsson 1982, Sparholt 1985, Sandlund et al. 1988, Bystrom et al. 2004). Similar to habitat use, dietary information on YOY from Canada is sparse. In Cumberland Sound, Baffin Island, Nunavut juveniles <50mm collected from tributary rivers fed mainly on chironomid larvae and pupae (Moore & Moore 1974) and in the Koroc River system, young juveniles fed most frequently on chironomids and other dipteran larvae (Stenzel 1987). YOY charr from a southern Baffin Island population fed most frequently on chironomid larvae, Collembola and Acarina (Gallagher & Dick 2010).

Given the limited information about the ecology of juvenile Arctic charr in general, and the particular lack of information on High Arctic juveniles, the overall objective of this study was to assemble and analyse all data available on juvenile Arctic charr from repeated surveys of Lake Hazen, Ellesmere Island, Nunavut (summer 2001, 2007 and 2008) to characterise dietary and habitat use patterns. Specifically, the study aimed to test the hypotheses: (1) that juvenile Arctic charr exhibit preference for stream over nearshore habitats, (2) that there are significant differences in the diets of juvenile Arctic charr in stream and nearshore habitats, and, (3) that physical features of the stream (e.g. velocity, temperature, and water source) influence stream density of Arctic charr.

Methods

Site description

All samples were collected from within the Lake Hazen drainage basin. Lake Hazen (81°50'N, 70°25'W) is a large (537.5km²) lake located at the north end of Ellesmere Island in Quttinirpaaq National Park, Nunavut (Fig. 2.1) with a recorded maximum depth of 267m (G. Köck, University of Innsbruck, Innsbruck, Austria, pers. comm.). The area is part of an Arctic oasis formed by a protective ridge of mountains to the north that is noted for stable summer temperatures and higher than average biological richness in comparison to other high Arctic biomes (Oliver et al. 1964, France 1993). The lake is extremely oligotrophic, contains no aquatic macrophytes, has low zooplankton productivity (McLaren 1964) and 34 known species of benthic invertebrates (Oliver 1963). Arctic charr is the only fish species in the lake, with the populations consisting of two morphologically distinct forms (Reist et al. 1995) that represent a resource polymorphism (Guiguer et al. 2002, Arbour et al. 2011). Current knowledge suggests that there is no anadromous component to the lake's Arctic charr population (Babaluk et al. 1997, Babaluk et al. 2001). Along the north shore of the lake, streams are fed by glaciers or small upland ponds. On the south shore of the lake, dry stream channels and small streams fed by melting permafrost predominate (Fig. 2.1).

Habitat selection

Preferences for habitat type were estimated using Manly's standardized selection index (Manly et al. 1993) based on August 2007 captures. Arctic charr were captured with 15cm diameter, 75cm long Y-shaped funnel nets (1mm mesh) with 1m wings. The funnel nets were placed randomly at the mouths of small tributary streams and in nearshore habitats (depth ≤ 1m) of Lake Hazen (Fig. 2.1). At each site, water source (glacial or non-glacial runoff), and net set and retrieval water temperatures were recorded. Sixty-seven net sets were deployed for approximately 24 hour intervals over the period of a week. Charr caught in each trap were counted and measured for fork length (FL, mm).

For the habitat preference index calculation, each net was assumed to effectively sample an equivalent area. Proportion of habitat types available for use by Arctic charr thus equalled the proportion of net sets in a given habitat type. Data on the proportion of habitat types available and the proportion of fish captured in each habitat type were used to determine relative preferences for each habitat type following procedures outlined in Manly et al. (1993). A G-test was used to test the null hypothesis that habitats were chosen randomly (Manly et al. 1993). A t-test (not assuming equal variances) was used to test for differences between lake and stream habitats based on average water temperature measurements determined from temperatures taken at net deployment and retrieval. A Welch's ANOVA and the Games-Howell multiple comparison test were used to assess differences among lake and stream-mouth trap set temperatures when subdivided by water source. Data normality and variance homogeneity were assessed prior to all statistical analyses. The maximal Type I error in all statistical analyses was set at $\alpha = 0.05$.

Stream vs. nearshore lake juvenile ecology

In 2001, Arctic charr were collected from nearshore lake habitat approximately 0.5km southwest of Hazen Camp (Fig. 2.1) using an electrofisher and dip net. Electrofishing was carried out from the shore to waters of 1m-depth. All charr were measured for fork length, frozen on-site and shipped to Fisheries and Oceans Canada, Winnipeg, Manitoba for age determination and gut content analyses. In 2008, juveniles were randomly selected from those obtained during stream density estimate surveys (see below) and retained for stomach content analysis and carbon and nitrogen stable isotope analysis (SIA). All charr were frozen on site and shipped to the University of Waterloo, Waterloo, Ontario for subsequent analyses. Otoliths were collected and ages were determined using the whole otolith method. Otolith ages were verified by length-frequency distribution analysis. Stomachs were removed and prey items were identified to at least subclass, with the exception of Ostracoda, and recorded for prey presence or absence. Prey item categories included: chironomid larvae, chironomid pupae, Copepoda, Acarina, Cladocera, Ostracoda, Diptera (non-chironomid), Trichoptera, and terrestrial arthropods (Collembola, Hymenoptera and Arachnida).

In order to compare diets for Arctic charr from stream and lake shore habitats, YOY were analysed separately from older fish (1+ to 3+ years). Multi-way contingency tables were used to test the independence of three categorical variables using hierarchical log-linear analysis. The three categorical variables involved were water body (stream vs. lake), prey item, and fish age. Chi-square tests were used to test for statistical significance in all two-way contingency tables (Zar 2010). Post-hoc tests to determine which specific prey items differed between stream and lake fish were carried out as described in Cortés (1997), whereby the main source of variability (the prey item with the largest χ^2 column total) was removed from the χ^2 test and the data re-analysed until the overall χ^2 result was not significant.

Stream density estimates & diet

Stream density estimates were mainly obtained in August 2008, with the exception of two density estimates obtained in August 2007. Sampling sites were selected based on accessibility and suitability (Fig. 2.1). Henrietta Nesmith Stream, Ptarmigan Creek and Blister Creek are fed by Bridge Glacier melt water, and Cuesta Creek and Mesa Creek are fed by runoff from the Garfield Range glaciers. The latter streams are also influenced by inputs from small tundra lakes. Muskox Creek is fed by a small upland pond. At the time of sampling, Traverse River, located on the southeast shore of Lake Hazen, was fed largely by permafrost seeps occurring both above and within the sampled reach.

The three-pass Zippin method for estimating population size (Seber & LeCren 1967, Seber & Whale 1970) was completed at the selected tributary stream sites using a Smith-Root LR-24 electro-fisher (Smith-Root Inc., Vancouver, Washington, USA). Sampling occurred in the first 100m of well-defined channels immediately above the shore and barrier nets were used to enclose the selected area. Stream characteristics recorded included area sampled (m^2) and water temperature. Twenty random water velocity measurements were taken 1cm above the substrate proximate to observed fish holding stations in pools using a Marsh-McBirney Flow-mate 2000 (Hach Company Inc., Loveland, Colorado, USA). A similar set of velocity measurements were taken randomly from riffle areas where fish were generally not captured or observed. Owing to shallow water and the low number of pool sites at Henrietta Nesmith Stream, only two pool-related measurements were obtained for that site. Water samples were obtained from each sample site and analysed for a standard suite of nutrients (see Babaluk et al. 2009) at Fisheries and Oceans Canada's Freshwater Institute Analytical Water Chemistry Laboratory in Winnipeg following methods described in Stainton et al. (1977).

In August 2007, density estimates were obtained from the 100m reach closest to the lake shore (Muskox Creek 2007 – lower) and another 100m reach upstream (Muskox Creek 2007 – upper). In August 2008, two population estimates were obtained from the same lower reach of Muskox Creek twelve days apart (Muskox Creek 2008 – early, late). Two density estimates were obtained at Ptarmigan Creek, Cuesta Creek and Traverse River. At the first two sites, smaller side channels were sampled in addition to the main channel (Ptarmigan Creek – side and Cuesta Creek – side, respectively). At Traverse River, a second channel (Traverse River B) was sampled in addition to the main channel (Traverse River A), however, unlike the side channels indicated above, Traverse River B had an independent connection to the lake.

The constant catchability assumption of the three-pass Zippin method was verified using a χ^2 goodness of fit test (Seber 1992) and fish density in streams was calculated by dividing estimated population size (\hat{N}) by the area sampled. Fish density estimates were related to stream characteristics such as water temperature, water velocity and water chemistry using linear regression.

Horn's index of dietary overlap (Horn 1966) was used to assess similarity in the frequency of prey occurrence among age-classes and stream sites as follows:

$$R_0 = \frac{\sum (P_{ij} + P_{ik}) \log(P_{ij} + P_{ik}) - \sum P_{ij} \log P_{ij} - \sum P_{ik} \log P_{ik}}{2 \log 2}$$

where P_{ij} and P_{ik} are the proportions of prey item i consumed by individuals in categories j and k (age class or site). Levins's standardized niche breadth (Levins 1968) was assessed to compare the diversity of prey items used by each age-class within the streams as follows:

$$B_A = \frac{1}{\sum p_j^2} - 1$$

where p_j is the fraction of items in the diet that are of food category j (estimated by the number of individuals found using food category j /total number of individuals sampled; Krebs 1989) and n is the total number of food categories. In both Horn's and Levins's indices, the percent of frequency of occurrence was standardized by dividing by the sum of the frequencies of occurrence of all food categories, such that $\sum P_i$ and $\sum p_j = 1.0$, respectively.

Zooplankton samples analysed for stable isotopes were obtained from horizontal tows carried out in an offshore region of Lake Hazen near Hazen Camp using a boat. Chironomid larvae and pupae samples analysed for stable isotopes were obtained from juvenile Arctic charr stomach contents from several Lake Hazen nearshore and stream sites. The use of stomach and gut contents has been suggested as a useful source of recent prey isotope signatures in trophic studies (Tieszen et al. 1983, Peterson 1999). However, caution in determining the isotopic values of prey items from gut contents has been suggested owing to the potential impacts of digestive fractionation on isotopic ratios (Guelinckx et al. 2008a) and potential contamination from digestive tract material (Ponsard & Averbuch 1999). Nevertheless, the influence of digestion on stable isotope signatures of ingested prey items was considered negligible in Arctic charr dietary studies from Loch Ness (Grey et al. 2002) and was also found to be less likely for prey items obtained from the stomach rather than the hindgut (Guelinckx et al. 2008a). With that in mind, only foregut prey items with minimal evidence of digestion were selected for SIA in this study. To further minimize the influence of digestive tract material on prey stable isotope values, all stomach-derived prey items were rinsed with deionised water prior to analysis.

Fish and prey samples were analysed for carbon and nitrogen stable isotope signatures at the Environmental Isotope Laboratory, University of Waterloo, on a Delta Plus continuous flow isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an analytical precision of $\pm 0.2\%$ ($\delta^{13}\text{C}$) and $\pm 0.3\%$ ($\delta^{15}\text{N}$). Precision was established through repeat analysis of International Atomic Energy

Agency CH6, N1 and N2 standards. Study measurement variability was additionally assessed by the repeat analysis of one in ten samples. For fish greater than 80mm, dorsal muscle tissue was used, otherwise whole fish samples (minus head, fins and gut) were analysed. All analytical results are quoted in standard delta (δ) notation as parts per mil (‰) with respect to the relevant international standard (e.g. Clark and Fritz 1997). The international standards included are Peedee Belemnite limestone ($\delta^{13}\text{C}$) (Craig 1957) and atmospheric nitrogen gas ($\delta^{15}\text{N}$) (Mariotti 1983).

General linear models and the Games-Howell multiple comparison tests were used to assess variances in the stable isotope signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) across stream sites and age-classes. YOY data were excluded from these analyses owing to the likely inclusion of maternal source signatures within their tissues (e.g. Doucett et al. 1999). Simple comparisons between data sets were completed with two-sample t-tests appropriately adjusted for the homogeneity of variance assumption (Zar 2010).

Results

Habitat selection

Mean water temperatures were significantly higher in stream-mouth sites relative to nearshore lake sites (t-test: $t=-4.756$, $df=47$, $p<0.001$). Preference indices varied significantly between habitat types (nearshore lake vs. stream-mouth; G-test: $X^2=11.408$, $df=1$, $p<0.001$) indicating a relative preference for stream mouth environments (Table 2.1). When classification of stream water source was included in the analysis, non-glacial stream-mouth water temperatures were found to be significantly higher than glacial and non-glacial-influenced lake shore temperatures, and glacial-fed stream-mouth water temperatures were found to be significantly higher than non-glacial lake shore temperatures (Welch's ANOVA: $F_{3,26.7}=8.20$, $p<0.001$; Games-Howell: $p<0.05$). No other differences were significant. Significant differences in preference indices existed between habitats divided by water source (G-test: $X^2=16.719$, $df=3$, $p<0.001$; Table 2.1) with a relative preference existing for non-glacial-fed streams. No significant differences were found among the remaining habitat types.

Stream vs. lake juvenile ecology

All Arctic charr collected from the nearshore environment ranged in fork length between 26 and 94mm and age-classes from 0+ to 3+ years, with the distribution of the 138 (105 electrofished, 33 trapped) individual charr collected being heavily skewed toward YOY (Fig. 2.2; $FL<41\text{mm}$). In 2008, all streams contained only immature fish (Fig. 2.2; $FL=29-204\text{mm}$; $\text{Age}=0+-7+$). Most charr using the streams were between 40 and 70mm, mainly aged 1+ and 2+ (Fig. 2.2). In 2007, one 232mm fish was caught at Muskox Creek, however, this fish was not retained owing to collection permit restrictions, and its age and maturity were not determined.

Diets of all nearshore charr had a high percent occurrence of chironomid larvae and pupae (82 and 61%, respectively), moderate occurrences of Copepoda (47%) and Acarina (21%), and few occurrences of Cladocera (6%), Ostracoda (1.9%) and Trichoptera (1.9%). Chironomid larvae and pupae occurred in most stream fish diets (76 and 58%, respectively) and were the only prey items that occurred in all streams and in all age-classes. Copepoda, non-chironomid Diptera, terrestrial arthropods and Acarina were also contained in stomachs at most sites. Fish remains were found in two individuals – a 4+ fish from Ptarmigan Creek – main (FL=124mm) and a 7+ fish at Muskox Creek (FL=174mm).

A three-way log-linear analysis comparing diet between stream and nearshore lake fish for individuals aged 1+ to 3+ produced a final model that retained only two of the possible two-way interactions: water body x age ($\chi^2(2)=11.800$, $p<0.003$), and water body x prey ($\chi^2(6)=18.635$, $p<0.005$). Post hoc tests determined that stream fish had significantly fewer occurrences of Cladocera relative to nearshore lake fish ($\chi^2(5)=13.650$, $p<0.02$; Fig. 2.3B). No significant differences were found between stream and lake fish diets in the frequency of chironomid larvae and pupae, Copepoda, terrestrial arthropod and Acarina occurrences ($\chi^2(4)=7.498$, $p>0.05$). Stream YOY had significantly more occurrences of terrestrial insects and chironomid pupae relative to nearshore lake YOY ($\chi^2(4)=18.342$, $p<0.003$, Fig. 2.3A). No significant differences were found between stream and lake fish diets in the frequency of chironomid larvae, Copepoda and Acarina occurrences ($\chi^2(3)=6.396$, $p>0.05$). Empty stomachs occurred in 5.6% of 1+ to 3+ aged charr and 9.8% of similarly aged stream charr (Fig. 2.3B). No empty stomachs were found in stream or lake shore YOY (Fig. 2.3A).

Because of low sample numbers of the older age-classes in the streams, all fish between 4+ and 7+ were combined ($n=9$) for subsequent analyses of the stable isotope and stomach content data and denoted as $\geq 4+$. When examined by age rather than site, higher percent occurrences of terrestrial arthropods were found in older fish. YOY and 1+ fish contained no non-chironomid Diptera and the dipteran percent occurrence increased with age (between 2+ and $\geq 4+$). Levins's measure of niche breadth indicated that niche breadth increased notably at age 2+ and 3+ and remained more or less constant thereafter (Fig. 2.4).

Pair-wise comparisons of stream diet based on stomach content analysis between age-classes illustrated high dietary similarity ($R_0 \geq 0.78$) between all age-classes. Higher similarities occurred between closer age-classes and the lowest overlap occurred between 0+ and $\geq 4+$ fish. Similarly, when compared among sites, all pair-wise comparisons showed overlap ranging from 0.6 to 1.0.

Stable isotope signatures obtained from fish from tributary streams in 2008, excluding YOY, varied between -31.17 and -21.04‰ in $\delta^{13}\text{C}$ and 5.94 and 11.47‰ in $\delta^{15}\text{N}$ (Table 2.2, Fig. 2.5). Analyses of variance indicated significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by site (Welch's ANOVA: $\delta^{13}\text{C}$: $F_{9,27}=7.60$, $p<0.001$; $\delta^{15}\text{N}$: $F_{9,28}=15.24$, $p<0.001$) but not age (Table 2.3) for tributary streams sampled in 2008. A

Games-Howell multiple comparison test indicated 11 combinations of site pairs that were significantly different in $\delta^{13}\text{C}$, however, the results showed no clear pattern. Ptarmigan Creek – side channel $\delta^{15}\text{N}$ was found to be significantly lower than Cuesta Creek (main and side), Muskox Creek 2008 – early, and Traverse River A and B (Games-Howell $p < 0.05$). No other significant differences were found. In the single instance of temporal sampling, no significant isotopic differences were found between the early and late sampling events at Muskox Creek in 2008 (t-test: $\delta^{13}\text{C}$: $t = 0.459$, $df = 10$, $p > 0.05$; $\delta^{15}\text{N}$: $t = 1.113$, $df = 10$, $p > 0.05$). Zooplankton samples obtained from horizontal tows in Lake Hazen had mean stable isotope signatures of -36.77 ± 1.64 ($\delta^{13}\text{C}$) and 5.22 ± 0.58 ($\delta^{15}\text{N}$). Mean $\delta^{13}\text{C}$ signatures of chironomids obtained from juvenile charr stomach contents were found to be -27.88 ± 4.41 (pupae) and -29.47 ± 1.64 (larvae) and related $\delta^{15}\text{N}$ signatures were 4.81 ± 1.72 (pupae) and 3.83 ± 1.34 (larvae). Mean $\delta^{13}\text{C}$ signatures of chironomids obtained from adult charr stomach contents were found to be -18.29 ± 2.39 (pupae) and -23.79 ± 0.17 (larvae) and related $\delta^{15}\text{N}$ signatures were 3.90 ± 1.02 (pupae) and 6.74 ± 0.35 (larvae).

Stream density estimates

Arctic charr density estimates obtained at each stream site varied between 0.08 charr/m² at Traverse River A and 3.3 fish/m² at Ptarmigan Creek – side channel (Fig. 2.6). A density estimate was not obtainable from Blister Creek because of low catch numbers ($n = 4$). The highest density estimates were obtained from the side channels of larger stream systems (Cuesta and Ptarmigan creeks). Spatial and temporal variability in fish density was evident in the multiple sampling events at Muskox Creek, with density declining as distance from the lake shore increased and density increasing between the first sampling event when ice jamming occurred at the mouth of the creek and the second sampling event once ice had cleared from the lake (Fig. 2.6).

Charr were found mainly in pool habitats where water velocities ranged from 0.01 to 0.30 m/s (median = 0.04 m/s, Fig. 2.7A), rather than in riffle habitat where substrate velocities ranged from 0.12 to 1.39 m/s (median = 0.46 m/s). A significant positive correlation was found between mean fork length and mean pool velocity available at each site (Fig. 2.7B; $r^2 = 0.61$, $p < 0.008$). No significant relationships were found between fish density estimates and stream temperature, water source or water chemistry measurements including a suite of measured nutrients.

Discussion

This study demonstrated preferential use of tributary streams by juvenile Arctic charr. Despite the preference exhibited for stream habitat, charr diets were found to be similar in both stream and lake shore environments. Among streams, charr densities were found to differ, although differences could not be correlated with any of the examined physical features or differences among the streams.

Despite higher temperatures in streams relative to the lake shore, and that water temperature and aquatic primary productivity are tightly linked in the High Arctic (Michelutti et al. 2005), the diets of similarly aged charr were comparable between stream and lake shore habitats. In both habitats, diet was dominated by chironomid larvae and pupae. The dominance of chironomids in the diet of Arctic charr has been observed previously in juveniles and small-form charr obtained from Lake Hazen (Guiguer et al. 2002) and juveniles from rivers feeding Cumberland Sound (Moore & Moore 1974). Juveniles in the Koroc River system, Ungava Bay, Quebec were similarly found to depend mainly on chironomids and other dipteran larvae (Stenzel 1987) and temporal analysis of YOY charr diet from Scandinavian lakes has demonstrated the dominance of chironomids during part of the summer when the chironomids are most abundant (Sandlund et al. 1988, Næsje 1995, Bystrom et al. 2004). That chironomids were frequently observed in the diets of both stream and lake-dwelling juveniles in this study likely reflects the predominance of their availability relative to other prey items in the habitats occupied by juvenile Arctic charr during our sampling period. Although comparisons between lake and stream diets involved comparing samples from different years, the stable physical environment and simple biological community (Oliver 1963, McLaren 1964) within Lake Hazen suggests little year-to-year variability in the prey resources available to Arctic charr. Owing to the limited time spent in the streams between ice-melt and capture dates, stable isotope signatures of the stream-dwelling fish reflected a mix of stream and lake feeding. As a result, stomach contents provide a better reflection of stream-specific differences for juveniles in the High Arctic. Nevertheless, stable isotope signatures supported the high frequency of chironomids (Fig. 2.5) in the diets of juvenile Arctic charr.

Within stream environments high overlap in diet was found among age-classes, suggesting the occurrence of intraspecific competition (Amundsen et al. 2001), with stronger competition occurring between adjacent age-classes. Diets of older stream charr comprised a greater variety of prey items including the increased incorporation of non-chironomid Diptera, terrestrial insects and Arctic charr. The restricted diet of younger fish may relate to size-restricted prey choice and foraging ability (Amundsen et al. 2001) or intraspecific competition (Bohlin 1977), although the smallest individuals were not found in the higher velocity stream habitats typically associated with increased prey densities (Bremset & Berg 1999).

Arctic charr remains were found in the stomachs of 22% of fish $\geq 4+$ in the streams, with the smallest cannibalistic individual being 4+ and 124mm. A switch to cannibalism in many Arctic charr populations has been suggested to be size-limited and to occur at a threshold size ranging from 150mm based on stomach contents (Svenning et al. 2007, Berg et al. 2010) to 400mm based on SIA (Guiguer et al. 2002). Hobson and Welch (1995) also indicated 400mm as the threshold for the switch to heavy reliance on cannibalism based on SIA, but noted evidence of partial cannibalism in intermediate sized

fish (120–365mm). Despite the evidence of cannibalism here, $\delta^{15}\text{N}$ signatures for stream captured Arctic charr were generally reflective of a minimal reliance on fish as a prey item. Thus, cannibalism among juvenile charr is likely a marginal or opportunistic feeding tactic, possibly related to the small size of fish using the streams and the decreased aggression associated with exercise necessary to maintain station in flowing water (Christiansen & Jobling 1990). Nevertheless, for some individuals, stream occupancy may provide an opportunity for early piscivory which has not been observed previously within Lake Hazen.

While use of lotic environments by lake-spawned juvenile Arctic charr has been noted previously (Johnson 1980, Näslund et al. 1993, Gulseth & Nilssen 1999), this study presents the first report of YOY migration through, or occupation of, streams. Näslund et al. (1993) suspected that YOY were incapable of swimming upstream via a 5km creek with a water velocity of 0.5m/s. Similarly, the significant positive correlation between mean fork length and mean pool velocity demonstrated here, suggests that access to tributary streams is restricted based on individual size (fork length) and related swimming ability. Arctic charr critical swimming speed (CSS) varies with temperature (Beamish 1980) and diet (Pettersson et al. 2010) and CSS estimates range from 2.1 to 4.3 body lengths/s. Based on that CSS range, YOY in Lake Hazen tributary streams (FL=29-43mm) would have maximum swimming abilities ranging from 0.06 to 0.18m/s (Fig. 2.7A). Lower CSS estimates are more realistic in the High Arctic, which is characterised by low temperature and low productivity systems. Even if upper end CSS values are assumed, stream environments represent challenging environments for YOY charr and water velocity is most likely the key factor limiting stream use by YOY. At each stream site, smaller individuals were found only in low velocity pools, or in eddies adjacent to stream banks. No YOY were found using habitat with velocities greater than 0.1m/s.

Habitat segregation in stream-dwelling salmonids is common and YOY are often found using habitat closer to the shore where shallower and slow-flowing water predominates (Bohlin 1977, Bremset & Berg 1999). Although segregation may occur as a result of competitive displacement (Bohlin 1977) or YOY preference for marginal habitat (Nislow et al. 2000), our results suggest that in High Arctic streams, physical barriers created by flow velocities effectively separate fish by size into distinctive habitat types. Thus, under climate warming scenarios, predicted changes in the pattern of stream flow may hold significant consequences for stream occupancy either as a result of increased competition where flows decline, or as a result of increased physical barriers where flows increase. In particular, for pond-fed streams the former scenario is more likely (Smol & Douglas 2007), whereas for glacier-supported streams the latter is more likely.

The mean density of charr occupying sampled tributary streams in 2008 (0.90 fish/m²) was lower than densities found in the surf zone of Thingvallavatn (mean density=1.83-4.70 fish/m²) (Sandlund et

al. 1988), but higher than densities found in the nearshore areas of a northern Swedish lake (<0.05 fish/m²) (Bystrom et al. 2006) or the nearshore areas of Alik Lake, Ungava Bay, Quebec (density range = 0.01-0.08 fish/m²) (Stenzel & Power 1991). In our study, the highest densities were found in the side channels of larger stream systems (Ptarmigan Creek, Cuesta Creek) and likely reflect the higher proportion of low velocity habitat available relative to the main channels. Side channels are sustained by high flows in the main channel and may be susceptible to drought under low flow conditions (Milner et al. 2009). Reduction of marginal flow environments has been found to increase competition among age-classes within streams (Bohlin 1977), suggesting that variable availability may be linked to eventual year-class success.

Despite the importance of temperature (Näslund 1991) and substrate type (Erkinaro 1995) to salmonids, charr density was not detectably related to either factor. Additionally, differences in water velocity, source, chemistry and prey composition could not explain differences in measured densities. It is likely that physical factors influencing stream accessibility impacted relative occupancy rates and obscured potential relationships between density and environmental factors. For example, distance from the lake, as observed in Muskox Creek in 2007, low water depth at the mouth of Traverse River A and high sediment loads observed at Blister Creek, may all act as physical barriers to stream use. In addition, access to Muskox Creek during the first sampling event in 2008 was hindered by large amounts of canded ice at the stream mouth and likely contributed to the observed temporal variability in the stream resident density. Similarly, Curry et al. (1997) demonstrated that dispersal of YOY brook charr upstream varied annually according to habitat accessibility.

L'Abée-Lund et al. (1993) demonstrated that differences in the distribution of juvenile Arctic charr between habitats may occur as a trade-off between food availability and predation risk. In contrast, our results suggest that the presence of physical barriers contribute to a higher proportion of YOY occupying the nearshore environment rather than stream environments preferred by juvenile Arctic charr. Preference for stream environments was not attributable to differences in feeding, however, streams provided water temperatures closer to optimal thermal conditions for growth (Larsson 2005) and contained more structurally complex substrates. Lewin et al. (2004) demonstrated that juvenile fish distributions are controlled by habitat structure complexity rather than food biomass and several studies have demonstrated the importance of cover to salmonids (e.g. Cunjak & Power 1986, Gibson & Erkinaro 2009). When accessible, stream habitats may be preferred in comparison to the structurally sparse nearshore environment that is associated with increased avian predation risks (e.g. Gibson et al. 1993) and/or cannibalistic adult Arctic charr that congregate at stream inlets (Babaluk et al. 2001).

Stream environments represent only a small proportion of available habitat relative to the area contributed by the nearshore lake environment (Lake Hazen circumference: ~185km). As such, the

importance of the nearshore environments to the juvenile population of Lake Hazen should not be underestimated. Additionally, the potential use of other habitat in the lake such as pelagic and profundal zones was not determined. Deep-set traps were deployed and were unsuccessful, but efforts made were low relative to the size of the lake.

It is likely that the amount of usable stream environment varies annually depending on snow pack, glacial melt and associated sediment load, and lake-ice dynamics. Unless supported by significant glaciers or upstream storage in lakes and ponds, summer flow in many High Arctic streams occurs only periodically (Prowse et al. 2006). Reduced snow pack and loss of permafrost will increase the likelihood of desiccation of small ponds and the streams they support (Prowse et al. 2006). Indeed, as a consequence of climate change, once permanent Arctic water bodies have become ephemeral (Smol & Douglas 2007). Within the Lake Hazen watershed, there is evidence of several intermittently flowing river systems along the southeast shore which are not supported by glaciers. To the southeast of Lake Hazen, reduced flow on a small creek feeding Craig Lake caused juvenile Arctic charr to be stranded in the remnant pools (R.N. Sinnatamby, unpublished data). Glacial environments are among the most susceptible to climate change and variability as illustrated by accelerated shrinking of ice sheets over the last few decades (Milner et al. 2009). Consequently, the predicted continued warming in the Arctic will likely increase glacial runoff. If increased melt water is associated with greater sediment load and higher velocities, more water may not benefit juvenile Arctic charr using the streams. Until conditions stabilize, a warming climate may not be favourable to the productivity of Arctic charr juveniles in Lake Hazen.

Table 2.1. Habitat types, number of trap sets, number of Arctic charr captured, mean water temperatures \pm standard deviation (SD), and selection index values by habitat type: proportion of total fish using habitat i (o_i), proportion of habitat i that is available relative to all habitat types (P_i), Manly's standardized selection index (B_i). Significant preference as determined by statistical testing is indicated by an asterisk (*).

| Habitat type | Number of trap sets | Number of Arctic charr | Mean temperature ($^{\circ}$ C) \pm SD | Selection index variables | | |
|------------------------|---------------------|------------------------|---|---------------------------|-------|--------|
| | | | | o_i | P_i | B_i |
| Lake | 39 | 33 | 6.69 \pm 1.47 | 0.398 | 0.582 | 0.322 |
| Stream | 28 | 50 | 8.83 \pm 2.02 | 0.602 | 0.418 | 0.678* |
| Lake | | | | | | |
| glacial-influenced | 10 | 5 | 7.23 \pm 1.29 | 0.060 | 0.149 | 0.105 |
| non-glacial-influenced | 29 | 28 | 6.52 \pm 1.52 | 0.337 | 0.433 | 0.202 |
| Stream | | | | | | |
| glacial-influenced | 10 | 12 | 7.89 \pm 1.04 | 0.145 | 0.149 | 0.251 |
| non-glacial-influenced | 18 | 38 | 9.37 \pm 2.25 | 0.458 | 0.269 | 0.442* |

Table 2.2. Sample location, date, and fork lengths for all Arctic charr captured during density estimates and number of fish obtained during 3-pass Zippin methods by site. Mean and standard deviation (SD) values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for sub-sampled individuals at each stream site excluding YOY (n=10).

| Location | Sample date (mm/dd/yy) | Number of fish | Fork length (mm) | | | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ |
|---------------------------|---------------------------|-------------------|------------------|-----|-----|-----------------------|-----------------------|
| | | | mean | min | max | ‰ (\pm SD) | ‰ (\pm SD) |
| Henrietta Nesmith Stream | 8/5/2008 | 100 | 51.6 | 29 | 204 | -25.91 (2.93) | 9.16 (2.31) |
| Ptarmigan Creek – main | 8/11/2008 | 137 | 71.7 | 47 | 194 | -26.93 (1.42) | 6.86 (1.54) |
| Ptarmigan Creek – side | 8/11/2008 | 102 | 55.7 | 34 | 97 | -27.28 (1.12) | 6.86 (1.02) |
| Muskox Creek 2007 – lower | 8/4/2007 | 52 | 66.5 | 32 | 232 | n/a | n/a |
| Muskox Creek 2007 – upper | 8/4/2007 | 21 | 67.4 | 57 | 78 | n/a | n/a |
| Muskox Creek 2008 – early | 8/1/2008 | 19 | 65 | 46 | 115 | -23.17 (1.38) | 7.71 (0.68) |
| Muskox Creek 2008 – late | 8/12/2008 | 61 | 57 | 29 | 115 | -23.05 (2.34) | 7.55 (1.04) |
| Cuesta Creek – main | 8/9/2008 | 33 | 75.1 | 49 | 183 | -27.74 (1.83) | 8.51 (0.90) |
| Cuesta Creek – side | 8/9/2008 | 24 | 54.4 | 42 | 84 | -24.67 (1.23) | 8.11 (1.06) |
| Mesa Creek | 8/7/2008 | 44 | 66.2 | 51 | 104 | -25.87 (0.66) | 8.41 (1.76) |
| Traverse River A | 8/4/2008 | 13 | 83.4 | 51 | 163 | -25.93 (1.82) | 8.26 (0.37) |
| Traverse River B | 8/4/2008 | 13 | 66.6 | 49 | 102 | -27.96 (1.57) | 8.13 (0.42) |

Table 2.3. Analysis of variance results comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation across stream sites and age-classes including degrees of freedom (df), type IV sum of squares (SS), F and p values.

| Isotope | Model r^2 | Source of variation | df | Type IV SS | F | p |
|-----------------------|----------------|------------------------|----|---------------|-------|--------|
| $\delta^{13}\text{C}$ | 0.63 | Stream | 9 | 11.501 | 4.183 | <0.001 |
| | | Age | 3 | 3.974 | 1.449 | >0.05 |
| | | Stream x Age | 17 | 3.128 | 1.140 | >0.05 |
| $\delta^{15}\text{N}$ | 0.51 | Stream | 9 | 3.448 | 4.759 | <0.001 |
| | | Age | 3 | 0.646 | 0.776 | >0.05 |
| | | Stream x Age | 17 | 1.132 | 1.474 | >0.05 |

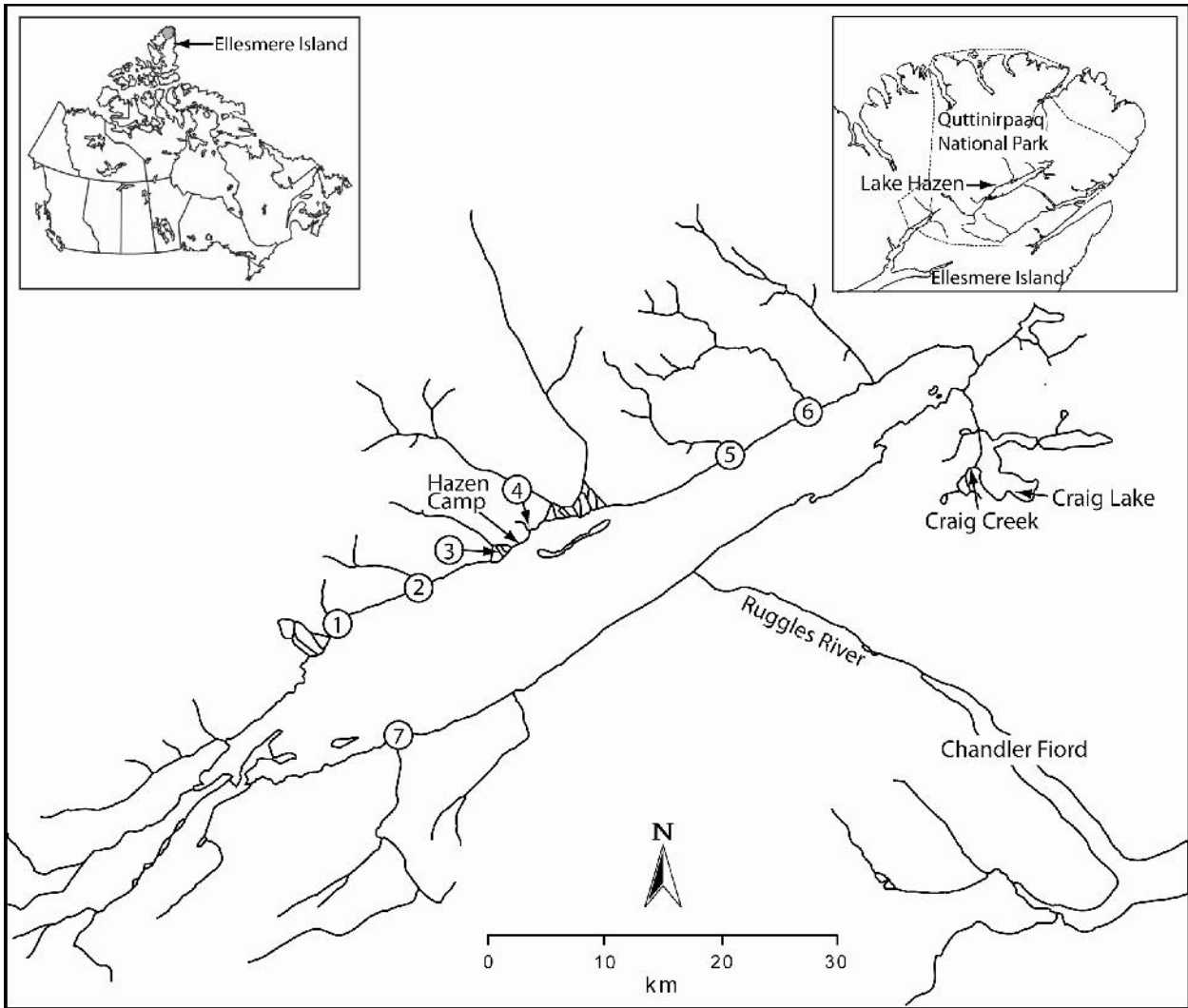


Figure 2.1. Map of Lake Hazen area indicating sampled stream sites: 1. Henrietta Nesmith Stream, 2. Ptarmigan Creek, 3. Blister Creek, 4. Muskox Creek, 5. Cuesta Creek, 6. Mesa Creek, 7. Traverse River.

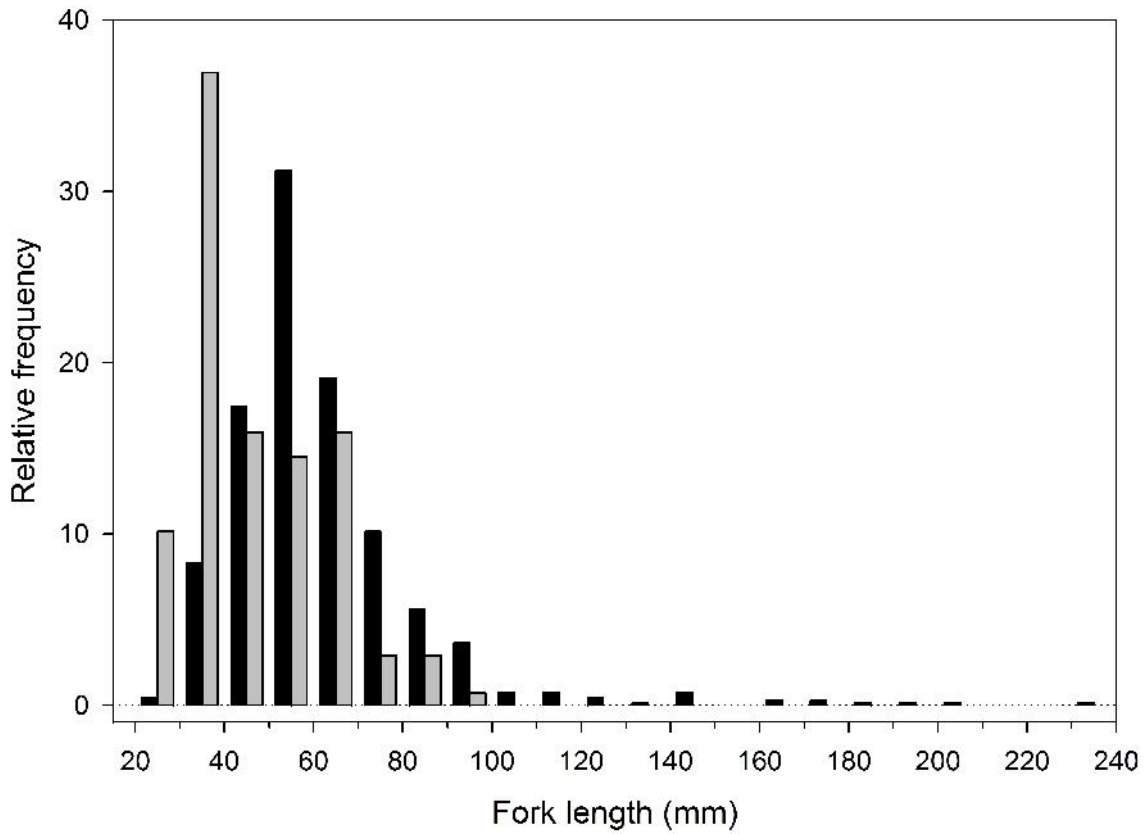


Figure 2.2. Relative length frequency distributions of Arctic charr from Lake Hazen tributary streams (black) and the nearshore habitat (grey) captured by electrofishing and funnel net traps.

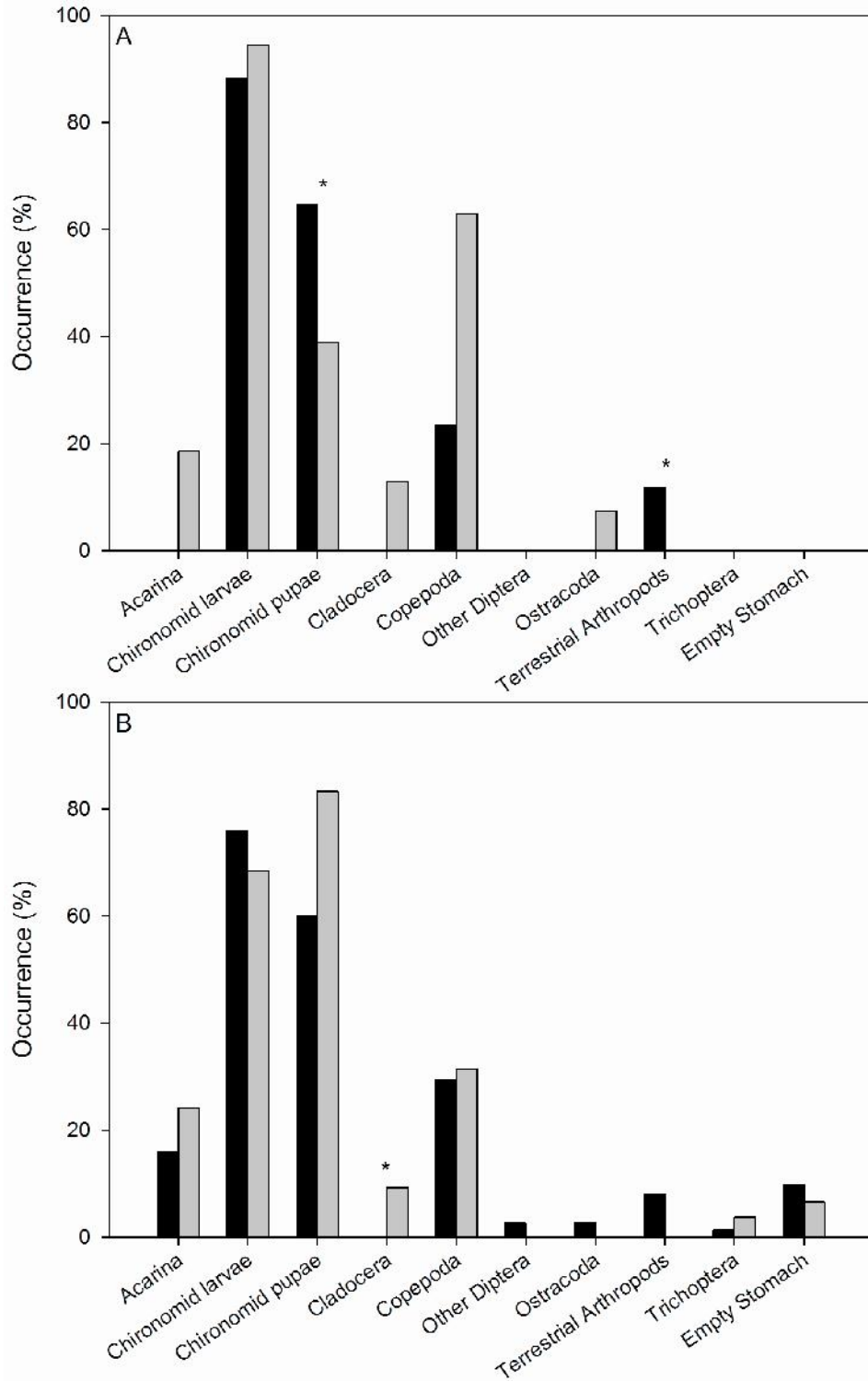


Figure 2.3. Percent occurrences of dietary items from stomachs of YOY Arctic charr (A) and charr aged 1+ to 3+ (B) obtained from Lake Hazen tributary streams (black) and lake shore (grey) captured by electrofishing. Asterisks indicate prey item occurrences that were significantly different between stream and lake shore fish.

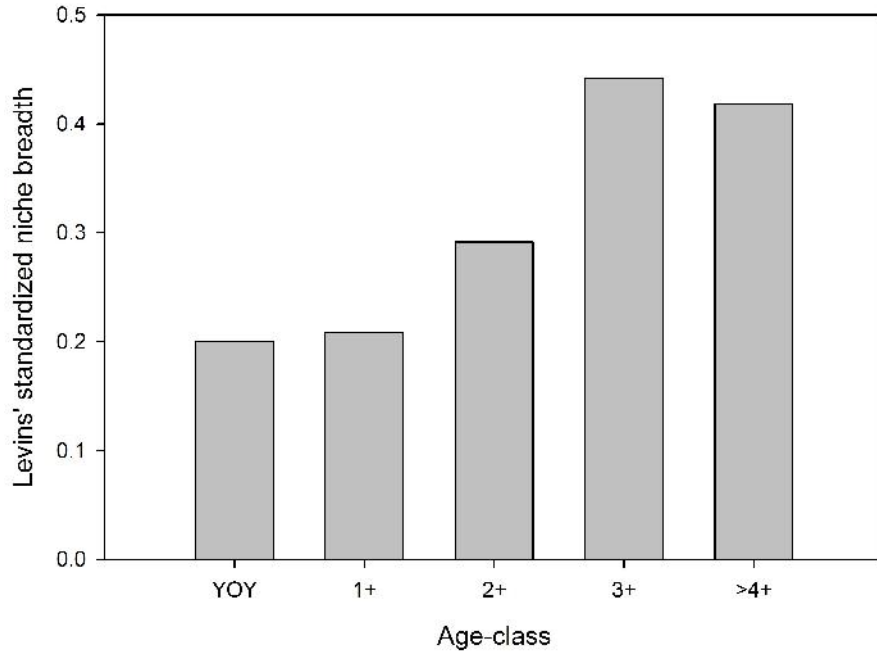


Figure 2.4. Levins' standardized niche breadth (B_A) in stream-captured Arctic charr by age-class.

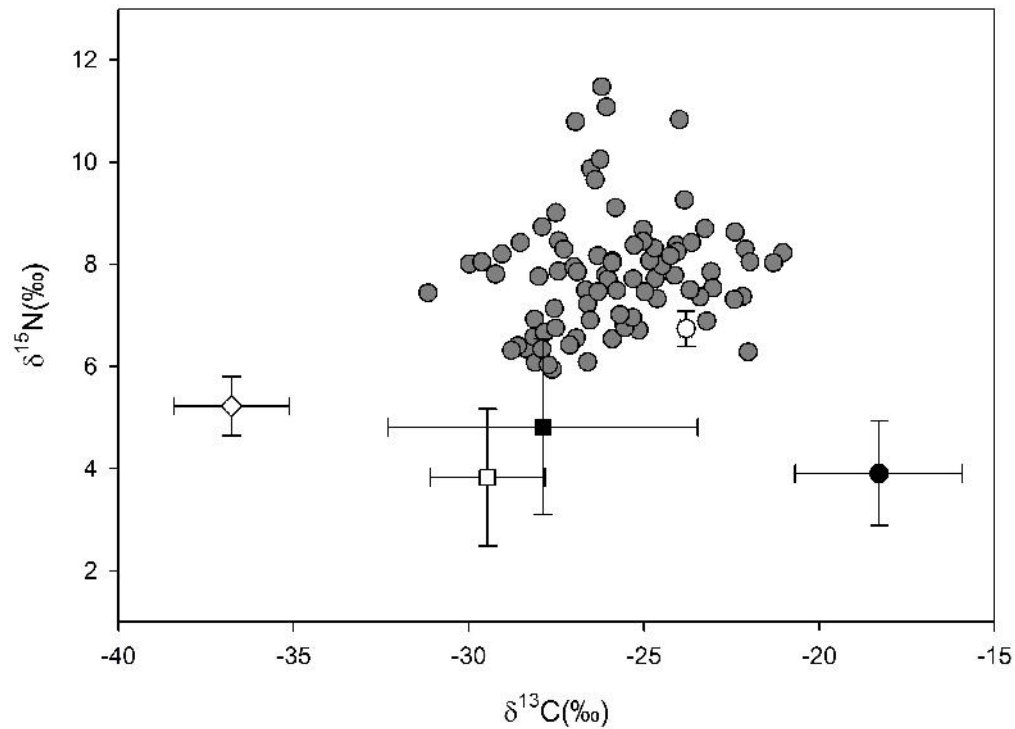


Figure 2.5. Nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotopes of individual Arctic charr retained from stream sampling (excluding YOY) in 2008 (\bullet). Mean and standard deviation $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotopes of chironomid larvae (\square) and pupae (\blacksquare) obtained from gut contents of stream-dwelling juveniles, chironomid larvae (\circ) and pupae (\bullet) obtained from gut contents of lake-dwelling adults, and zooplankton (\diamond) obtained from horizontal tows within Lake Hazen.

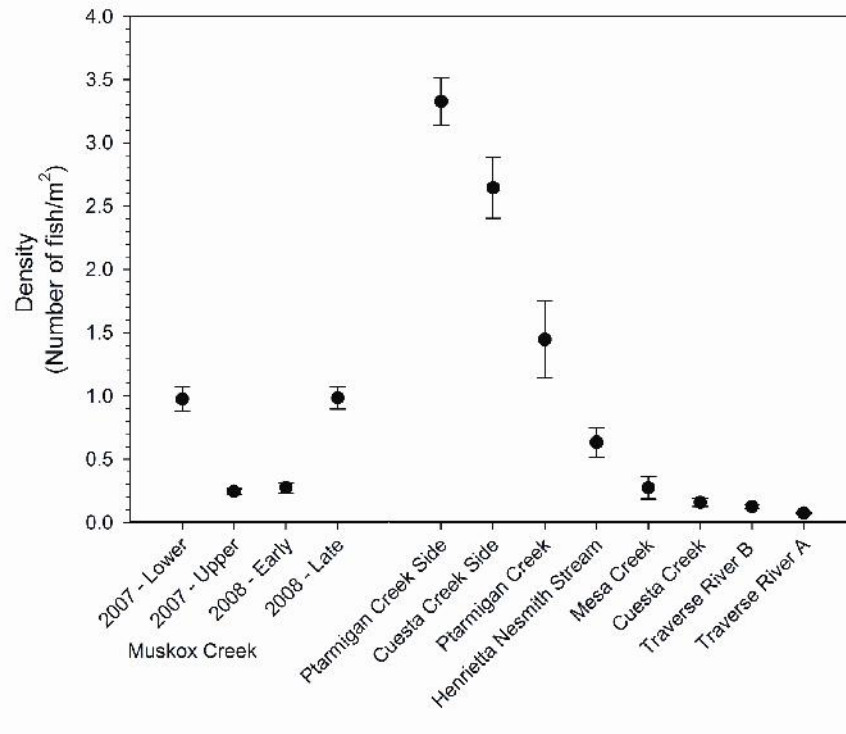


Figure 2.6. Arctic charr density estimates in each tributary stream. Vertical bars indicate 90% confidence intervals.

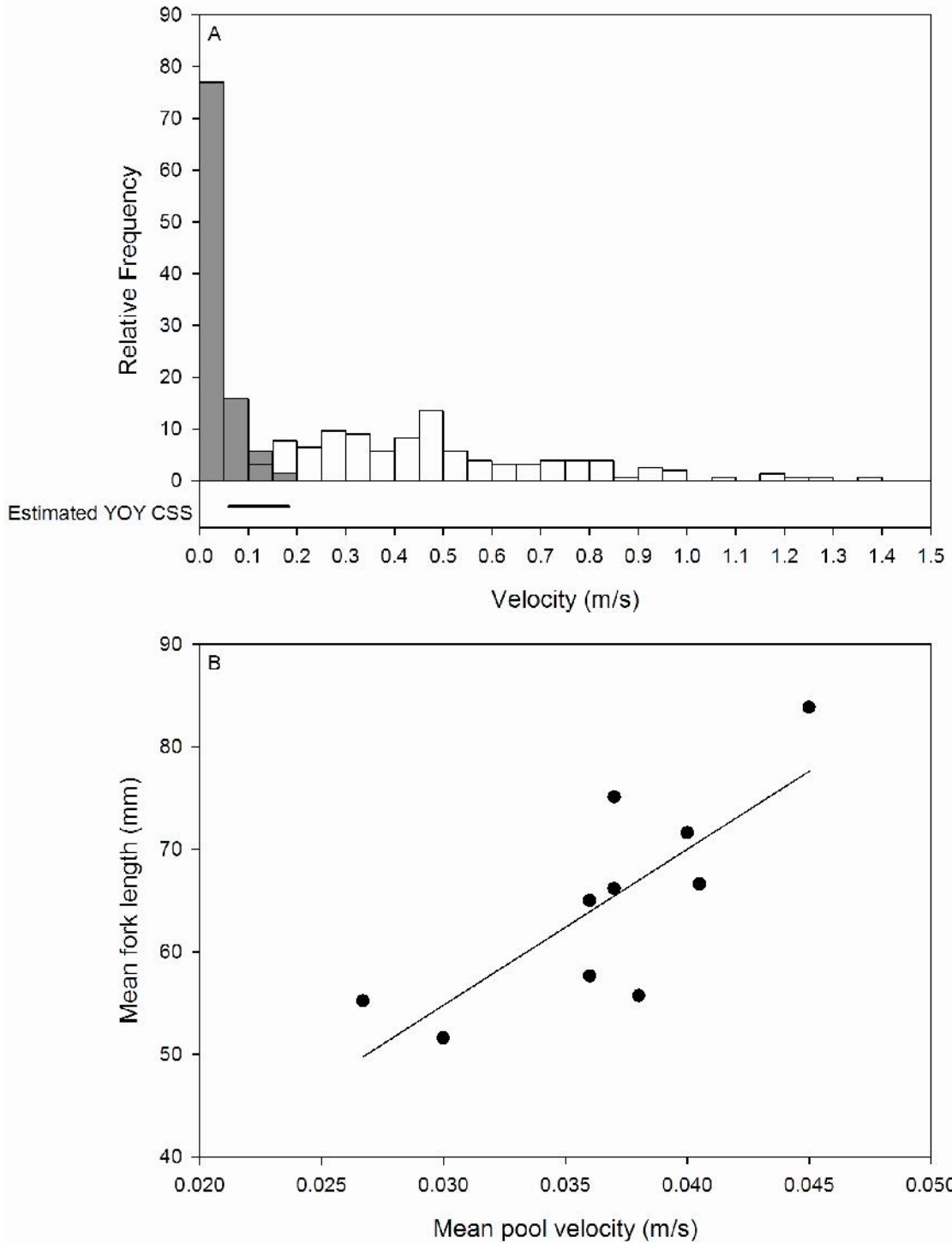


Figure 2.7. (A) Relative frequency distribution of substrate velocities in pool sites where Arctic char were generally found (grey) and riffle sites where fish were generally not found (white). Solid line indicates estimated critical swimming speed (CSS) values for YOY based on the range of critical swimming speed estimates in the literature (2.1–4.3 body lengths) (Beamish 1980, Petterson et al. 2010); (B) Mean fork length versus mean velocity measured in pools at each site except for Muskox Creek 2008 - late ($y=1522.55x+9.09$, $r^2=0.61$, $p<0.008$).

Chapter 3: Identification of the maternal source of young-of-the-year Arctic charr in Lake Hazen, Canada

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Introduction

Following a switch in diet, organism tissues undergo isotopic turnover whereby the stable isotope ratios of the tissues shift from ratios reflecting the earlier diet to equilibrate with those of the new diet (Fry & Arnold 1982). Isotopic turnover is mediated by the dilution of existing tissue with the addition of newly accrued tissue (somatic growth) and the replacement of existing tissue with material synthesized from the new diet (metabolism) (Fry & Arnold 1982, Hesslein et al. 1993, Guelinckx et al. 2007). For fast-growing poikilotherms, isotopic turnover occurs predominantly due to tissue anabolism, and metabolic tissue replacement is negligible (e.g. Hesslein et al. 1993, Jardine et al. 2004, Trueman et al. 2005).

The rate of isotopic turnover influences the length of time between a diet switch and the achievement of isotopic equilibration with the new diet, and has been found to vary with species (Tieszen et al. 1983), tissue type (Guelinckx et al. 2007, Buchheister & Latour 2010), temperature (Bosley et al. 2002, Witting et al. 2004) and diet quality (Haramis et al. 2001, Mirón et al. 2006). During the time lag between a diet switch and equilibration, organism tissues provide valuable information, which in juvenile fish has been used to estimate larval settlement rates (Herzka et al. 2002) and estuarine residency times (Hoffman et al. 2007), to identify ontogenetic habitat shifts and diet transitions (reviewed by Herzka 2005) and to elucidate patterns in fish recruitment dynamics (Guelinckx et al. 2008b).

Similarly, lags in achieving isotopic equilibrium have been noted at the onset of exogenous feeding (Vander Zanden et al. 1998, Doucett et al. 1999, Murchie & Power 2004). Fish eggs and newly hatched embryos are formed from materials derived from maternal sources rather than from food directly consumed by the individual. As such, neonate offspring have been found to reflect the stable isotope signatures of the maternal parent in a number of organisms (e.g. Hobson et al. 2004, Ducatez et al. 2008, Matich et al. 2010) including multiple fish species (e.g. Vander Zanden et al. 1998, Doucett et al. 1999, Murchie & Power 2004, Godbout et al. 2010). Once individuals begin to feed exogenously, offspring tissues begin to increasingly reflect the stable isotope values of the diet, and the maternal signature is eventually lost because of isotopic turnover, primarily isotopic growth dilution (Doucett et al. 1999). The maternal stable isotope signal within offspring tissue has been used to classify the source of salmonid progeny (Doucett et al. 1999, McCarthy & Waldron 2000, Charles et al. 2004, Curry 2005,

Jardine et al. 2008, Godbout et al. 2010) and estimate the relative contributions of different life-history strategies (i.e. anadromous vs. resident) to the annual pool of juveniles produced by a population (Charles et al. 2004, Curry 2005, Jardine et al. 2008, Godbout et al. 2010).

In Arctic charr, *Salvelinus alpinus*, differentiation by life-history type and morphotype is common, with numerous examples reported in the literature (e.g. Frost 1965, Jonsson et al. 1988, O'Connell & Dempson 2002, Power et al. 2009), including the population in Lake Hazen, Ellesmere Island, Nunavut. While the Lake Hazen population does not contain anadromous individuals (Babaluk et al. 1997), the population does consist of two distinctive morphotypes that differ in length-age relationships, colouration, meristic characteristics (Reist et al. 1995) and feeding ecologies reflected in significantly different stable isotope values (Guiguer et al. 2002). While both morphotypes were found to feed on chironomids, the large-form morphotype has a heavier reliance on fish relative to the small-form morphotype (Guiguer et al. 2002). Since the large-form morphotype occupies a higher trophic level than the small-form, the large-form morphotype typically has higher nitrogen stable isotope values compared to the small-form (Peterson & Fry 1987, Guiguer et al. 2002). Additionally, differences in carbon stable isotope values have been reported to reflect differences in dietary sources between the two morphotypes, specifically that the small-form morphotype has a greater reliance on benthic sources (Guiguer et al. 2002).

Although Lake Hazen Arctic charr have been studied sporadically since the 1950s, little is known about relative morphotype abundances or the relative reproductive importance of each morphotype. Here, we employ stable isotope methods, and the maternal stable isotope information in offspring somatic tissue, to identify the maternal source (piscivorous large-form morphotype vs. largely non-piscivorous small-form morphotype) of randomly sampled Lake Hazen young-of-the-year (YOY) Arctic charr. We further use inferred information on maternal source to estimate the relative reproductive contribution of each morphotype to the Lake Hazen Arctic charr population as a whole and test the null hypothesis that each morphotype contributes equally to the YOY population.

Methods

All samples were collected from Lake Hazen (81°50'N, 70°25'W), a large (537.5km²), oligotrophic (McLaren 1964) lake located at the north end of Ellesmere Island in Quttinirpaaq National Park, Nunavut (Fig. 3.1). The lake is the focal point of an Arctic oasis noted for stable summer temperatures and higher than average biological richness in comparison to other high Arctic biomes (Oliver et al. 1964, France 1993). Juvenile Arctic charr (including YOY and older juveniles) are found primarily along the lake shore with higher concentrations at, or near, tributary streams (Sinnatamby et al. 2012). Along the northwest shore of the lake, streams are fed by glaciers or small upland ponds. In contrast, on the southeast shore of the lake, dry stream channels and small, low-flow streams fed by melting

permafrost predominate, with the result that preferred juvenile habitat is sparse along the south-eastern shores of the lake (Sinnatamby et al. 2012).

Young-of-the-year Arctic charr were collected by electrofishing identified lake shore and tributary stream nursery areas from late July to mid-August in 2007 and 2008 (Fig. 3.1). In 2007, sampling was confined to Blister Creek, Hazen Camp, Skeleton Creek and Muskox Creek, and in 2008 sampling was extended to include additional sampling sites (Fig. 3.1). Data for adult Arctic charr from Lake Hazen were compiled from sampling that occurred in 1992, 2007 and 2008 to ensure sufficient sample sizes of each morphotype. Data for adult fish caught in 1992 were obtained from Guiguer et al. (2002), and data for adult fish caught in 2007 and 2008 were obtained from a parallel sampling program studying adult Arctic charr feeding ecology in the lake (J.D. Reist & W.K. Michaud, unpublished data). Adult samples were originally obtained using multi-mesh Lundgren multifilament benthic nets set under the ice and angling through the ice in June 1992 and in the open water in August 2007 and 2008 (e.g. Reist et al. 1995, Guiguer et al. 2002). Fork lengths (FL, mm) of all captured YOY were measured in the field and individuals were frozen and shipped to the University of Waterloo, Waterloo, Ontario for further analysis.

For stable isotope analyses, YOY samples with fins, head and gut removed were dried in a laboratory convection oven (50°C) and ground. All YOY individuals (n=135) were analysed for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes. Stable isotope analyses for adult fish were obtained using dorsal muscle excised posterior to the dorsal fin from frozen samples following methods described in Guiguer et al. (2002). Potential YOY prey items were obtained and analysed for carbon and nitrogen stable isotopes as a means of identifying endpoints of YOY tissue stable isotope values following isotopic turnover. Chironomid larvae were obtained from the stomach contents of older juvenile Arctic charr caught at or near YOY sample sites and were dried, ground and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Owing to the potential alteration of prey stable isotope values from digestive fractionation (Guelinckx et al. 2008a) and/or inclusion of digestive tract material (Ponsard & Averbuch 1999), only prey items obtained from the stomach with minimal evidence of digestion were selected and rinsed with deionised water prior to analysis. Zooplankton samples were obtained from horizontal tows taken from Lake Hazen in 2007 and 2008.

All stable isotope analyses were performed at the Environmental Isotope Laboratory, University of Waterloo. Contemporary sample (2007 and 2008) carbon and nitrogen stable isotope analyses were performed on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan/Bremen - Germany) coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108 - Italy). Internal laboratory standards, calibrated against International Atomic Energy Agency standards CH6 for $\delta^{13}\text{C}$ and N1 and N2 for $\delta^{15}\text{N}$ were analysed contemporaneously with samples with a precision of

$\pm 0.2\text{‰}$ for carbon and $\pm 0.3\text{‰}$ for nitrogen. Stable isotope values for 1992 adult samples were similarly obtained, as described in Guiguer et al. (2002). Machine analytical variability was assessed with a repeat analysis of one in ten samples protocol.

A discriminant function analysis (DFA) was completed using SPSS 17 on the pooled stable isotope data for all adult Arctic charr with prior probabilities based on equal group sizes. Data were assessed with ANOVA for temporal differences by comparing contemporary (2007 and 2008) with 1992 adult sample data. ANOVA indicated no significant differences in $\delta^{15}\text{N}$ (Small-form: $F_{1,68}=0.053$, $p>0.05$; Large-form: $F_{1,41}=1.446$, $p>0.05$), and small differences in $\delta^{13}\text{C}$ (Small-form: $F_{1,68}=8.422$, $p=0.005$, mean difference= 0.9‰ ; Large-form: $F_{1,41}=11.496$, $p=0.002$, mean difference= 0.9‰) relative to the separation between forms of at least 1.5‰ . Adult sample data were pooled for the DFA. Individuals were divided into piscivorous and non-piscivorous groups based on morphological characteristics and stable isotope values, with the piscivorous grouping corresponding to large-form individuals, and the non-piscivorous grouping corresponding to small-form and other individuals as described in the literature (Reist et al. 1995, Guiguer et al. 2002). A leave-one-out classification was completed on the adult data to cross-validate results. The resulting discriminant function was then applied to the YOY stable isotope data to classify individuals into one of the two origin groups, piscivorous progeny or non-piscivorous progeny.

Studies on a related charr species (brook charr, *Salvelinus fontinalis*) have suggested that the maternal isotopic signal is retained in offspring to lengths of 30 to 35mm (Doucett et al. 1999, Jardine et al. 2008). Since no YOY above 34mm were found to have $\delta^{15}\text{N}$ values exceeding the minimum value consistent with persistent adult piscivory (11‰ , see Fig. 3.2), a maximum FL of 34mm was selected as the cut-off for maternal source classification. Given the arbitrary nature of the cut-off fork length selection, a sensitivity analysis was run to determine the impact of cut-off choice on the conclusions regarding the resulting percent contribution estimates of each maternal morphotype to the YOY population within the lake. The analysis was run by varying the maximum FL criterion from 32 to 36mm for samples obtained in 2008, when the majority of YOY were caught.

Owing to differences in fishing effort expended at each nursery site within and between years, the number of YOY captured was adjusted by effort and is expressed in terms of catch per unit effort (number per ten minutes of electrofishing effort). The percent contribution of each morphotype to the YOY pool was calculated as the mean of fishing effort-adjusted numbers for cut-off lengths between 32 and 36mm. Chi-squared goodness-of-fit analysis was used to test whether the resulting proportion of YOY by source indicated equal contributions by each morphotype. A 2x2 contingency table and Pearson's chi-squared test were used to compare relative contributions of each morphotype to the YOY population with adult Arctic charr morphotype abundances estimated directly from sampling in 2001

(J.D. Reist, unpublished data). Adult Arctic charr morphotype abundance estimates were based on gillnet sets carried out between July 31 and August 6 2001. As the number of YOY sampled in 2007 was both low and spatially restricted, 2007 data were not included in analyses aimed at estimating the percent contribution by morphotype to the YOY population within the lake. Data were retained, however, for use in characterizing the degree of inter-annual variation observed in the distribution of progeny along a portion of the northwest shore of the lake. A 2x8 contingency table and Fisher's exact test were used to compare the relative proportion of the YOY population contributed by each morphotype at each nursery site. Fisher's exact test was conducted using R Statistical Computing Environment (version 2.10.1, R Development Core Team 2007).

Linear regression was used to assess the statistical significance of relationships between the stable isotope data and FL for the identified progeny of piscivorous and non-piscivorous females. ANCOVA was used to compare growth dilution slopes between identified progeny groups for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Field 2005). To compare growth dilution slopes between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each identified progeny group, ANCOVA was applied to square root-transformed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data to remove heteroscedasticity. Where slopes were not significantly different, Fisher's LSD post-hoc test was used to compare intercepts. Two-sample t-tests were used to assess the significance of differences in FL and the stable isotope values between YOY origin groups, and the stable isotope values of piscivorous and non-piscivorous adults.

Results

Young-of-the-year Arctic charr were captured at eight of ten sampled sites, largely at or near streams located on the northwest shore of Lake Hazen. Sampling at sites located on the south-eastern shore of the lake yielded few juveniles and no YOY, probably because of dramatic reductions in stream flow in both years (Sinnatamby et al. 2012) as evidenced by dry stream beds (e.g. Cobb River, Fig. 3.1). In 2007, 26 YOY were obtained from 4 sites between Blister Creek and Muskox Creek and in 2008, 109 YOY were obtained from all 8 sites sampled along the northwest shore of Lake Hazen (Table 3.1, Fig. 3.1)

A DFA based on the stable isotope values of 113 adult Arctic charr from Lake Hazen determined the combination of stable isotope values that best discriminated between piscivorous and non-piscivorous adults (Wilks' $\lambda=0.056$, $\chi^2=317.41$, $p<0.001$) as follows:

$$\text{Score 1} = 1.028 * \delta^{15}\text{N} - 0.542 * \delta^{13}\text{C} \quad \text{Eq. 1}$$

The leave-one-out cross validation method employed by SPSS indicated that 100% of the adult cases were correctly classified by the discriminant function.

Sensitivity analysis of the pre-selected 34mm fork length cut-off for inclusion of YOY in the classification analysis indicated a 5.8% variation (maximum-minimum) in the percent contribution of each morphotype. Classification of the previously ungrouped YOY individuals indicated that 43.1 and 56.9% (± 2.4) of the YOY pool were contributed by piscivorous and non-piscivorous females, respectively (Fig. 3.2, Table 3.2), with the proportions not differing significantly from hypothetical equal contributions by each morphotype ($\chi^2_1=0.065$, $p>0.05$). The proportion of YOY contributed by each morphotype was also not significantly different from the proportion of piscivorous (41%) to non-piscivorous (59%) adult Arctic charr estimated from a single random sample obtained in 2001 (J.D. Reist, unpublished data; $\chi^2_1=0.11$, $p>0.05$). In 2007 and 2008, non-piscivorous origin YOY were found at all sampled nursery sites along the northwest shore of the lake (Fig. 3.1). Piscivorous origin YOY were found in the highest proportions at Henrietta Nesmith Stream (73%) and Cuesta Creek (70%) in 2008, and Blister Creek (50%) in 2007, but made up less than half of the YOY population at the other sampled sites. In addition, progeny of piscivorous fish were missing entirely from Hazen Camp, Skeleton Creek and Muskox Creek in both 2007 and 2008. Similarly, the distribution of the morphotype progeny was found to be significantly different among sites (Fisher's exact test: $p=0.018$).

Significant differences were found between stable isotope values for piscivorous and non-piscivorous adults, with piscivorous adults having significantly lower carbon (mean difference=2.3‰) and higher nitrogen (mean difference=3.9‰) values than non-piscivorous adults ($\delta^{13}\text{C}$: $t=9.43$, $df=111$, $p<0.001$; $\delta^{15}\text{N}$: $t=-37.17$, $df=111$, $p<0.001$). Piscivorous origin YOY had significantly higher $\delta^{15}\text{N}$ (3.4‰) relative to non-piscivorous origin YOY, but there was no significant difference in $\delta^{13}\text{C}$ ($\delta^{15}\text{N}$: $t=12.09$, $df=69$, $p<0.001$, $\delta^{13}\text{C}$: $t=-0.53$, $df=69$, $p>0.05$). No significant differences were found in mean fork lengths of the progeny groups ($t=0.07$, $df=69$, $p>0.05$).

Significant negative linear relationships were found for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with FL for both piscivorous ($\delta^{13}\text{C}$: $r^2=0.25$, $df=26$, $p<0.007$; $\delta^{15}\text{N}$: $r^2=0.25$, $df=26$, $p<0.008$; Fig. 3.3) and non-piscivorous origin YOY ($\delta^{13}\text{C}$: $r^2=0.18$, $df=41$, $p<0.005$; $\delta^{15}\text{N}$: $r^2=0.09$, $df=41$, $p=0.05$). The slope of the relationship between stable isotope values and FL describes the isotopic growth dilution rate (Doucett et al. 1999). A common carbon growth dilution slope (slope=-0.390, $F_{(1,67)}=0.25$, $p>0.05$) and intercept ($F_{(1,68)}=0.38$, $p>0.05$) applied to both YOY origin groups. Although a common nitrogen growth dilution slope model was appropriate (slope=-0.224, $F_{(1,67)}=0.86$, $p>0.05$), significant differences existed between the intercepts of the origin group models ($F_{(1,68)}=166.04$, $p<0.001$, difference=3.4‰). The $\delta^{13}\text{C}$ growth dilution rate differed significantly from the $\delta^{15}\text{N}$ rate for both origin groups (piscivorous origin: $F_{(1,60)}=11.74$, $p<0.001$; non-piscivorous origin: $F_{(1,82)}=12.69$, $p<0.001$), with the carbon isotope signature being diluted faster than that of nitrogen as the fish grow.

Discussion

Differences in the stable isotope signatures of potential parent populations of Arctic charr and lags in attaining isotopic equilibration between YOY tissue and diet associated with the switch to exogenous feeding facilitated identification of the maternal source in randomly sampled YOY from Lake Hazen. The two morphotypes were found to contribute approximately equally to the pool of offspring produced. Although the relative contribution to the YOY pool by each morphotype was similar, differences in the spatial distribution of the progeny were evident. Young-of-the-year offspring of the larger piscivorous morphotype dominated at the sample sites along the northern and southern ends of the western shore, while juveniles of non-piscivorous morphotype origin dominated at sites located near Hazen camp in the lee of the main offshore island located in the lake.

Stable isotope values discriminated between piscivorous and non-piscivorous adult Arctic charr from Lake Hazen with a discriminant function that depended predominantly on the $\delta^{15}\text{N}$ values of the analysed individuals, as indicated by standardized canonical scores (Eq. 1). Similar to other applications of stable isotopes as ecological tracers (e.g. Gao & Beamish 1999, Dempson & Power 2004, Herzka 2005), the utility of the DFA method relies on the existence of appropriate separation among groups. Of the two elements employed here, $\delta^{15}\text{N}$ indicates trophic positioning in the food web, whereas $\delta^{13}\text{C}$ is used to identify carbon sources and/or the degree of pelagic or benthic food chain coupling (Peterson & Fry 1987). In differentiating between the juveniles of the two sympatric morphotypes of Lake Hazen, the trophic information provided by $\delta^{15}\text{N}$ proved the most valuable since the large piscivorous morphotype occupies a higher trophic level than the non-piscivorous small morphotype (Guiguer et al. 2002). Although Guiguer et al. (2002) distinguished between large-form and small-form morphotype diet sources using $\delta^{13}\text{C}$, carbon stable isotope information was less useful in quantitatively distinguishing between the progeny of the two morphotypes. The limited usefulness of $\delta^{13}\text{C}$ seen here may result from the relatively small difference between $\delta^{13}\text{C}$ values of morphotype adults combined with potentially increased variation among individuals at the egg stage (McCarthy & Waldron 2000), and a faster turnover rate in carbon relative to nitrogen (e.g. MacAvoy et al. 2001, Tarboush et al. 2006, this study). Further, the size at which fish can be sampled in the open water season in Lake Hazen is likely to have contributed to the difficulty in distinguishing between morphotype offspring using $\delta^{13}\text{C}$.

Isotopic growth dilution, which was apparent in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from YOY muscle tissue, occurred at the same rate for YOY from both maternal sources ($\delta^{13}\text{C}=0.390 \pm 0.14\%/mm$, $\delta^{15}\text{N}=0.224 \pm 0.08\%/mm$). Carbon and nitrogen isotope growth dilution rates for Lake Hazen YOY were found to be within the range of previously reported isotope growth dilution rates for yellow perch, *Perca*

flavescens, ($\delta^{13}\text{C}$: $<0.091\text{‰}/\text{mm}$, $\delta^{15}\text{N}$: $<0.215\text{‰}/\text{mm}$; Murchie & Power 2004), smallmouth bass, *Micropterus dolomieu*, ($\delta^{13}\text{C}$: $0.106\text{‰}/\text{mm}$, $\delta^{15}\text{N}$: $0.566\text{‰}/\text{mm}$; Vander Zanden et al. 1998) and brook charr ($\delta^{13}\text{C}$: $0.480\text{‰}/\text{mm}$, $\delta^{15}\text{N}$: $0.640\text{‰}/\text{mm}$; Doucett et al. 1999). Murchie & Power (2004) suggested that differences in isotopic growth rates among species may relate to autoecological species-specific differences or geographical differences between studies. If species-specific differences exerted the dominant control on isotopic growth dilution, Arctic charr dilution rates would be expected to be most similar to brook charr. This comparison suggests that any species-specific differences in dilution rates may be overshadowed by other factors such as temperature, diet and separation of start and endpoints in the diet switch (i.e. adult signature and new diet signatures, respectively).

An estimate of the Lake Hazen adult Arctic charr population made in 2001 indicated a ratio of 41% piscivorous to 59% non-piscivorous adult charr based on random sampling (J.D. Reist, unpublished data). The relative occurrence of piscivorous and non-piscivorous origin YOY estimated in this study (44% piscivorous, 56% non-piscivorous) suggests a more or less proportional contribution of the adult forms to the juvenile population. The apparent equiproportional importance of the two morphotypes in Lake Hazen contrasts with studies of other populations where the large, cannibalistic form tends to occur in relatively lower numbers in comparison to the smaller morphotype (e.g. Finstad et al. 2001, Berg et al. 2010). Typically there is a large difference in the relative biomass of each morphotype, with the smaller morphotype accounting for a significantly larger proportion of total adult biomass (Table 3.3). In contrast, Lake Hazen morphotype biomass estimates, based on the estimated abundance (J.D. Reist, unpublished data) and mean weight reported in Guiguer et al. (2002), suggest a more equal importance of Arctic charr morphotypes in Lake Hazen.

Unlike the Arctic charr populations of Lake Øvre Skarddørsjø and Lake Trestikkelen, the Lake Hazen morphotypes do not differ greatly in fork length (Reist et al. 1995), and the larger morphotype does not prey on the smaller morphotype adults (Guiguer et al. 2002). Where large cannibalistic Arctic charr are found to prey on adults of the smaller morphotype, Eltonian pyramid theory (Elton 1927) suggests that the higher trophic level occupants will contain fewer individuals (relatively lower abundance or biomass) than its prey source, as has been noted for the Arctic charr populations of Gander Lake (O'Connell & Dempson 2002). The Eltonian relationship is also demonstrated by the Arctic charr populations of Lake Øvre Skarddørsjø and Lake Trestikkelen (Finstad et al. 2001, Berg et al. 2010). In Lake Hazen, however, the large-form morphotype preys selectively on juveniles only (Guiguer et al. 2002) because smaller morphotype adults are too large for consumption because of gape limitations (Amundsen 1994). The lack of trophic connectivity between the Hazen morphotypes, therefore, does not fit the classic Eltonian pyramid model and may explain the differences in relative

abundances and biomass of Arctic charr in Lake Hazen as compared to other study sites (e.g. Finstad et al. 2001, Berg et al. 2010).

Although the two morphotypes appear to contribute approximately equally to the YOY pool, the two offspring groups were differentially distributed among sampled nursery sites. The unevenness of the distribution between progeny types accords with prerequisites suggested for the evolution of trophic specialists within a single population that experiences size-assortative mating based on trophic specialisation (Wimberger 1994, Jonsson & Jonsson 2001). Moreover, asymmetric distribution of progeny suggests that spawning sites may be non-randomly distributed between the morphotypes, given that offspring distribution is largely determined by redd distribution (Einum & Nislow 2005, Einum et al. 2008, Hudy et al. 2010).

Differentiation into morphotypes is a common phenomenon in Arctic charr populations (Jonsson & Jonsson 2001). In considering various sympatric Arctic charr morphotype pairs from Iceland, Gislason et al. (1999) suggested that resource-based phenotypic segregation in Arctic charr morphotype pairs ranges from very low to complete and noted a positive correlation between morphological differentiation and genetic differentiation (and reproductive isolation). Differential use of available spawning areas and noted morphological variation (Reist et al. 1995), taken together with the relatively equal importance of each morphotype to YOY production and available genetic evidence (Arbour et al. 2011), suggests that the Lake Hazen morphotype pairing is in the initial stages of the morphological and genetic segregation continuum proposed by Gislason et al. (1999), with the evidence of differential use of spawning areas pointing to a mechanism through which divergence may continue to occur.

Since sampling was limited to the nearshore environment, it is not known whether morphotype contributions to the offspring pool vary in other habitats in the lake, such as pelagic or profundal. Only two accounts of pelagic use by YOY have been noted in the literature (Sandlund et al. 1988, Winfield et al. 2002). In lakes where cannibalism is known to occur, juvenile use of the pelagic zone is associated with a higher risk of predation (Andersson & Persson 2005). Deep-set traps were deployed and were unsuccessful, although we recognize that relative efforts in a lake of the size of Lake Hazen were incomplete. Nevertheless, occupation of profundal and sublittoral zones has been noted in YOY Arctic charr in temperate lakes (Kircheis 1976, Svårdson 1976) and in older juveniles (≥ 1 year old) in Scandinavia (Klemetsen et al. 1989) where juvenile Arctic charr might retreat to less favourable regions of the lake in response to interspecific competition. Sandlund et al. (1988), however, suggested that the absence of interspecific competition, as in high Arctic lakes where Arctic charr are often the only fish species, may provide the opportunity for young Arctic charr to utilize the more productive littoral zone. In Lake Hazen, the nearshore environment has been found to be an important nursery habitat for Arctic charr, particularly those areas adjacent to warm stream inlets (Sinnatamby et al. 2012).

While previous studies have utilized the intrinsic differences in stable isotope signatures present between marine and freshwater environments, along with the maternal signature retained within the tissue of YOY to estimate the proportions of anadromous vs. resident salmonid YOY (Charles et al. 2004, Curry 2005, Jardine et al. 2008, Godbout et al. 2010), this study represents the first application of this method to estimating relative contributions of multiple freshwater-resident morphotypes to a YOY population. This method provides a rapid and cost-effective means (Vinson & Budy 2011) for obtaining quick assessments of the relative contributions to the YOY populations of morphotypes with distinctive feeding patterns on both spatial and temporal scales. It is also amenable to use in deciphering the relative reproductive contributions of any identifiable ecological groups that can be separated using stable isotope values such as benthic and pelagic feeding morphotypes, or individuals originating from environments differing significantly in biogeochemical influences.

Table 3.1. Number of young-of-the-year Arctic charr obtained by site in 2007 and 2008. Numbers are not standardized by fishing effort. n/a indicates when sampling was not conducted.

| Site | Number of YOY obtained | |
|--------------------------|------------------------|------|
| | 2007 | 2008 |
| Henrietta Nesmith Stream | n/a | 25 |
| Ptarmigan Creek | n/a | 19 |
| Blister Creek | 10 | 15 |
| Hazen Camp | 9 | 4 |
| Skeleton Creek | 5 | 5 |
| Muskox Creek | 2 | 8 |
| Cuesta Creek | n/a | 18 |
| Muskox Creek | n/a | 15 |
| Sailor Creek | n/a | 0 |
| Traverse River | n/a | 0 |

Table 3.2. Mean and (standard deviation) of fork length (mm) and stable isotope values (‰) of adult charr used to estimate the discriminant function and YOY individuals successfully classified into trophic morphotypes. Number of individuals classified as offspring of each morphotype – not standardized by fishing effort.

| Morphotype | n | Fork length | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ |
|-----------------|----|--------------|-----------------------|-----------------------|
| Adult | | | | |
| Piscivorous | 43 | 519.6 (71.3) | -21.1 (1.0) | 13.7 (0.5) |
| Non-piscivorous | 70 | 282.6 (82.1) | -18.8 (1.4) | 9.8 (0.6) |
| 2007 YOY | | | | |
| Piscivorous | 4 | 32.8 (1.0) | -23.2 (1.3) | 13.5 (0.2) |
| Non-piscivorous | 13 | 31.9 (2.1) | -24.8 (1.8) | 8.6 (1.6) |
| 2008 YOY | | | | |
| Piscivorous | 28 | 30.7 (2.5) | -23.8 (1.9) | 12.3 (1.1) |
| Non-piscivorous | 43 | 30.7 (2.8) | -23.6 (2.0) | 8.9 (1.2) |

Table 3.3. Minimum, maximum and median fork length, and biomass by morphotype of Arctic charr reported in literature studies. Ratio of large/small morphotype is based on median fork length values and biomass values of the larger morphotype divided by that of the small morphotype. The biomass ratio of Lake Hazen morphotypes are based on estimated abundances (J.D. Reist, unpublished data) and mean weight of each morphotype reported by Guiguer et al. (2002).

| Site & Morphotype | Fork length (mm) | | | Biomass (kg/ha) | Ratio of large/small morphotype | | |
|---|------------------|-----|--------|--------------------|---------------------------------|---------|--|
| | min | max | median | | Fork length | Biomass | |
| <i>Lake Øvre Skarddørsjø, Norway¹</i> | | | | | | | |
| Large | 250 | 600 | 425 | 0.62 | 4.05 | 0.08 | |
| Small | 60 | 150 | 105 | 7.93 | 0.25 | 12.79 | |
| <i>Lake Trestikkelen, Bear Island²</i> | | | | | | | |
| Large | 150 | 500 | 325 | 2.00 | 3.11 | 0.20 | |
| Small | 60 | 149 | 105 | 10.10 | 0.32 | 5.05 | |
| <i>Lake Hazen, Nunavut, Canada³</i> | | | | | | | |
| Large | 394 | 642 | 518 | - | 1.48 | 2.11 | |
| Small | 292 | 409 | 351 | - | 0.71 | 0.47 | |

¹Finstad et al. 2001

²Berg et al. 2010

³Guiguer et al. 2002

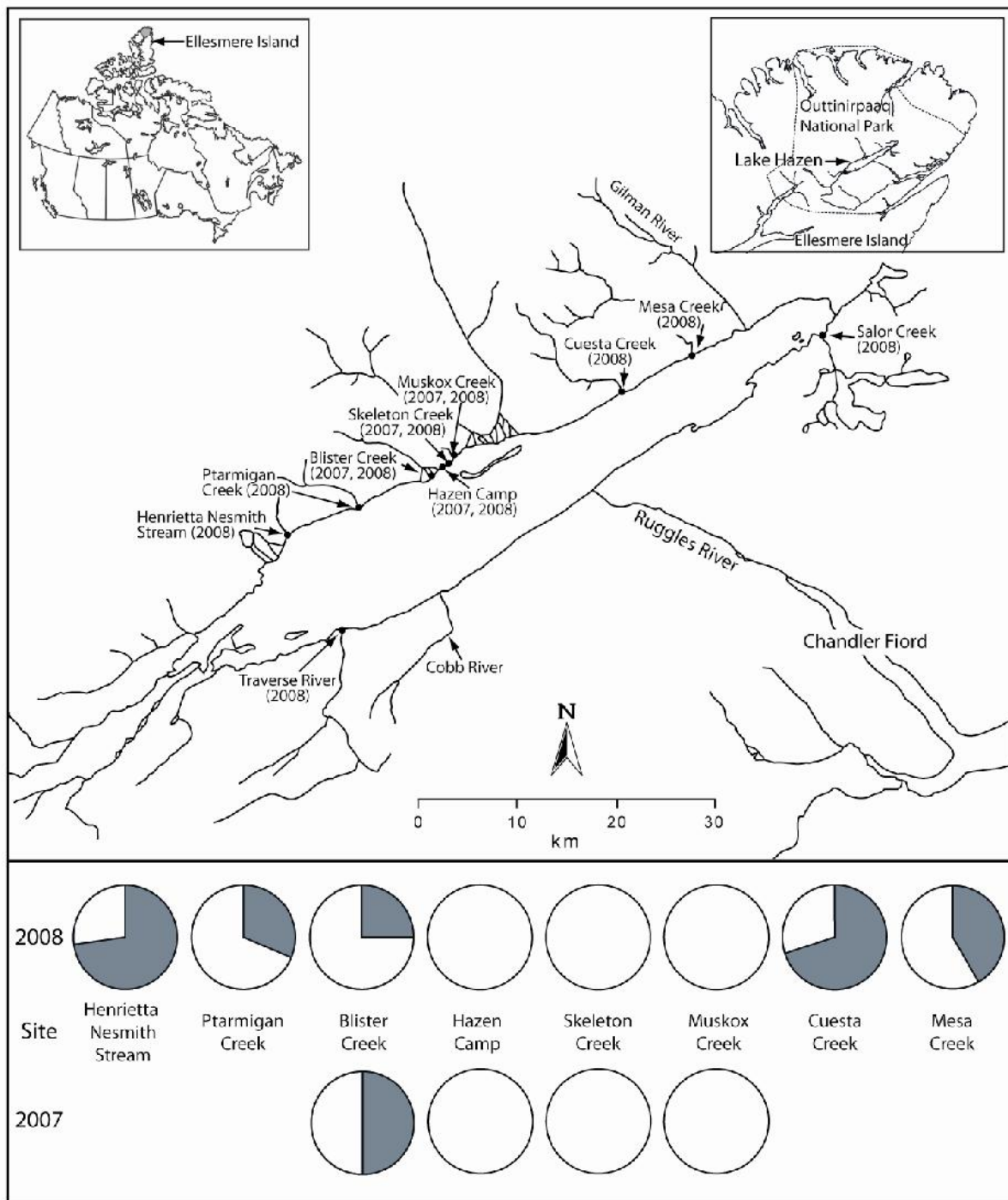


Figure 3.1. Map of Lake Hazen indicating sampled nursery sites (●) and year of sampling. Stream and nearshore lake habitats were sampled at each site. Pie charts on lower panel indicate proportions of YOY classified by maternal origin (piscivorous origin – grey, non-piscivorous origin – white) for each site and sample year.

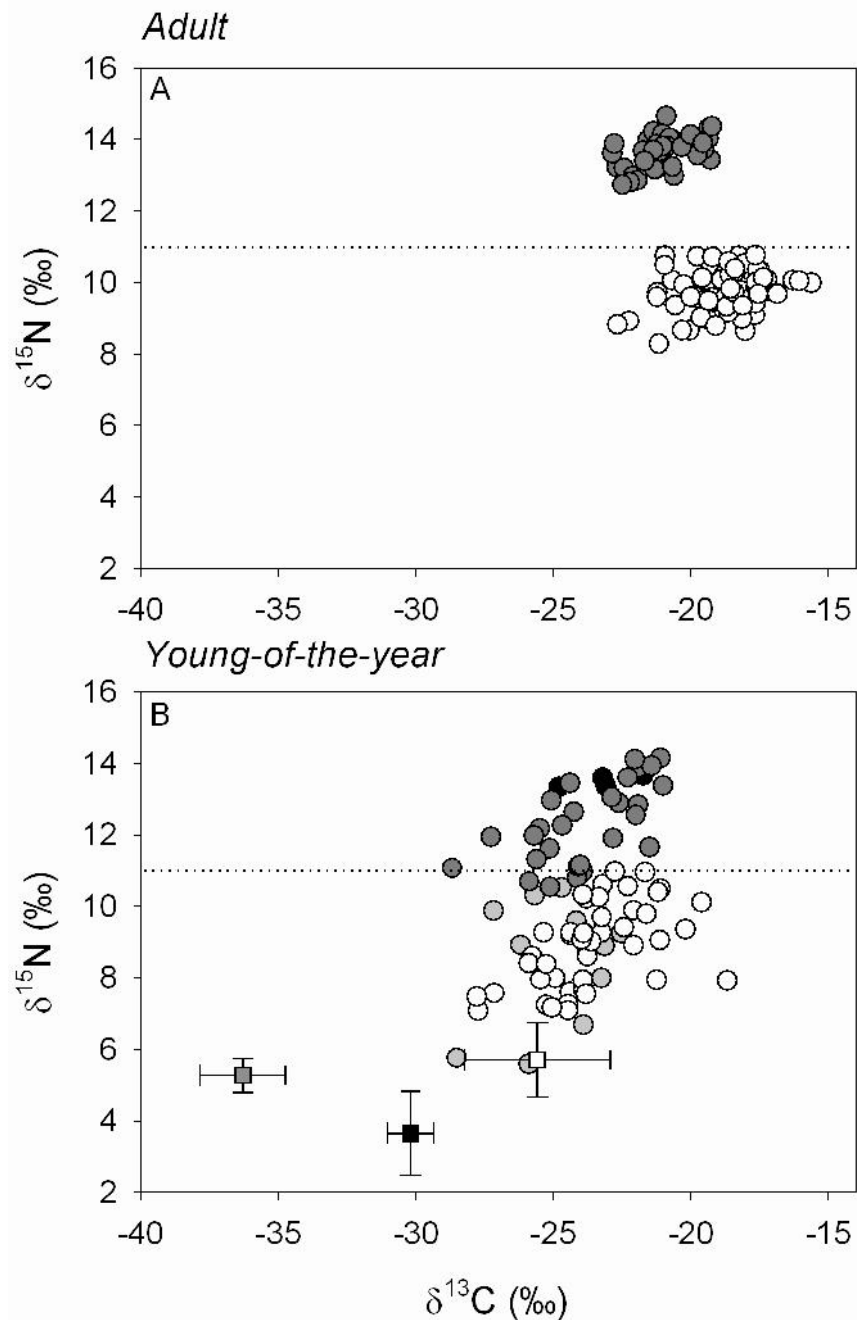


Figure 3.2. Carbon and nitrogen stable isotope cross-plots. Panel A depicts large-form piscivorous (●) and small-form non-piscivorous (○) adult morphotypes. Panel B depicts YOY of piscivorous large-form morphotype origin from 2007 (●) and 2008 (○) and YOY of non-piscivorous small-form morphotype origin from 2007 (○) and 2008 (○). Mean zooplankton (■), chironomid larvae (■) and chironomid pupae (□) stable isotope values are also plotted along with standard deviations indicated as error bars. The dotted line represents the $\delta^{15}\text{N}$ value above which all adults were considered to be piscivorous.

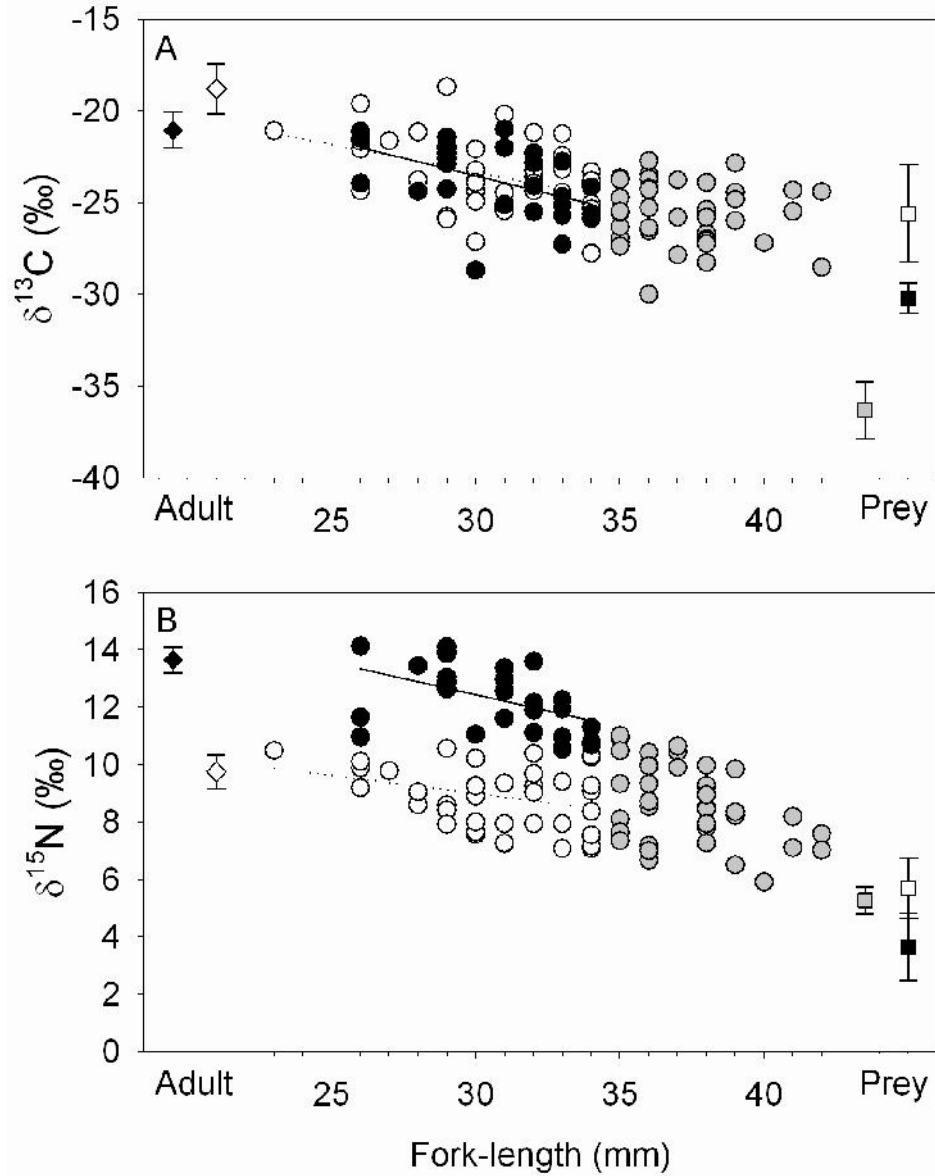


Figure 3.3. (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ vs. fork length for piscivorous origin (\bullet), non-piscivorous origin (\circ) and unclassified (\odot) YOY obtained in 2008. Lines denote significant linear relationships: solid – piscivorous origin; dashed – non-piscivorous origin. Mean stable isotope values are also provided for piscivorous (\blacklozenge) and non-piscivorous (\diamond) Arctic charr adults and potential prey items: zooplankton (\square), and chironomid larvae (\blacksquare) and pupae (\square). Error bars denote standard deviation.

Chapter 4: Latitudinal variation in growth and otolith-inferred metabolic rates of Canadian young-of-the-year Arctic charr

Introduction

Approximately 99 freshwater and/or anadromous fish species are found in the Arctic (Reist et al. 2006a). Of them, Arctic charr, *Salvelinus alpinus*, is the only species with complete circumpolar distribution (Reist et al. 2006a). Consistent with its northerly distribution, Arctic charr are among the most cold-adapted freshwater and/or anadromous fish species in the world (Johnson 1980, Baroudy & Elliott 1994a). In light of their strong association with cold environments, climate variability and change have prompted concern regarding potential impacts of increased global temperatures on Arctic charr (Reist et al. 2006a, Reist et al. 2006b). As a result of climate change, mean global temperatures have increased by approximately 0.6°C in the last century, and are predicted to rise another 1.1 to 6.4°C by 2100 (IPCC 2007). Several studies have aimed to understand the potential impact of rising temperatures on northern fish species, including Arctic charr (Lehtonen 1998, Power et al. 2000, Reist et al. 2006a, Winfield et al. 2008, Graham & Harrod 2009, Michaud et al. 2010, Finstad & Hein 2012), and have suggested that rapid increases in temperature will have significant, albeit varied impacts on Arctic fish populations (Reist et al. 2006a).

Despite their association with cold environments, Arctic charr exhibit the widest natural distribution of all salmonids (Maitland 1995), extending from northern New England (43°N) to the north coast of Ellesmere Island (83°N) in North America (Power et al. 2008). Understanding whether and how Arctic charr populations vary along a latitudinal gradient will be vital to predicting their responses to climate change (Reist et al. 2006a, Reist et al. 2006b). Characterising the phenotypic and/or genotypic variability exhibited by Arctic charr over its geographic range may help to illustrate the adaptive capacity of the species and ultimately improve our understanding of its sensitivity to climate change (Williams et al. 2008).

Environmental change has been suggested to have four possible outcomes for a species: (1) extinction or extirpation, (2) a shift in the distributional range, (3) genetic adaptation and/or (4) phenotypic plasticity (Fuller et al. 2010). Presently, the extent to which phenotypic plasticity contributes to species niche utilization and geographic distribution is not well understood (Ellers & Stuefer 2010, Fuller et al. 2010), even though phenotypic plasticity is thought to be the first likely response of an individual organism to environmental change (Bradshaw & Holzapfel 2008), and is considered to be more important than genetic adaptation in terms of short-term responses to climate change (Williams et al. 2008). The study of physiological traits over large geographic scales (i.e. macrophysiology) may illustrate the physiological capacity of a species to respond to climate change

(Chown & Gaston 2008, Williams et al. 2008) and may, by analogy, allow inference of likely responses to temporal climate change (Baumann & Conover 2011).

Countergradient variation (CGV), defined as genetic variation that counteracts the negative influences of the physical environment (e.g. lower temperature, shorter growth seasons and lower food supply), has been used to explain the phenotypic similarity often observed in traits across a latitudinal cline (Conover & Schultz 1995) and is most commonly seen in physiological traits such as growth, metabolism, activity, and digestion (Conover et al. 2009). The CGV growth rate hypothesis states that at similar temperatures individuals from high latitude environments will grow faster than conspecifics from low latitude environments (Levins 1969). CGV in growth rate has been demonstrated in several taxa, but is most commonly observed in fish (Conover et al. 2009). Despite increasing numbers of examples of CGV (Conover et al. 2009), overall support for the CGV growth rate hypothesis remains uncertain and has been mixed in salmonid species (e.g. Jensen et al. 2000, Jonsson et al. 2001, Finstad et al. 2004, Nicola & Almodóvar 2004, Forseth et al. 2009, Parra et al. 2009, Logez & Pont 2011). Chavarie et al. (2010) demonstrated growth patterns consistent with CGV in Arctic charr aged 6-12 years from 'normal' lacustrine populations in eastern North America. The authors, however, found rather ambivalent support for the hypothesis in anadromous populations and no support for CGV in relictual 'dwarf' lacustrine populations.

Countergradient variation in growth rate is thought to be an adaptation among high latitude populations for an elevated growth rate during the shorter annual period of high temperatures (Conover & Present 1990). Evidence of CGV in growth rate can be demonstrated using common garden experiments (e.g. Conover & Present 1990, Nieceza et al. 1994b), as well as field-based studies on natural populations if environmental differences among sites can be accounted for (Conover et al. 2006). To assess CGV in growth rate in natural populations, previous studies have used a thermal opportunity for growth (TOG) metric based on air temperature data to account for environmental differences among sites (Power & McKinley 1997, Chavarie et al. 2010, Rypel 2012). In the place of air temperatures, otolith-inferred temperatures (e.g. Devereux 1967, Patterson et al. 1993, Høie et al. 2004, Godiksen et al. 2011) may be more representative of temperatures experienced by the fish.

Broad-scale studies have also been conducted on metabolic rates (e.g. Scholander et al. 1953, Bullock 1955, Wohlschlag 1960, Lindgren & Laurila 2009, Buckley et al. 2012), which have been suggested as the key determinant for the rate of resource uptake, and subsequent energy allocation to survival, growth and reproduction (Brown et al. 2004). Physiologists typically measure standard metabolic rate (SMR), the metabolic rate of an inactive organism in the laboratory, whereas, field metabolic rates, the metabolic rate of free-living animals, reflects the average daily energy expenditure of an organism and incorporates the energetic costs of SMR, thermoregulation, locomotion, feeding,

reproduction and growth (Nagy 1987). Owing to the kinetic effect of temperature on metabolic rate (Brown et al. 2004), metabolic rates of ectotherms would be expected to increase with temperature (Buckley et al. 2012). The heavily debated metabolic cold adaptation (MCA) hypothesis (Scholander et al. 1953, Bullock 1955, Wohlschlag 1960), however, suggests higher metabolic rates may be found in organisms from cold environments. The MCA hypothesis is an example of CGV and states that at like temperatures the SMR of ectotherms from colder climates will exceed that of related species from warmer climates. Support for the MCA hypothesis in studies of fish is mixed (e.g. Wohlschlag 1960, Holeton 1974, Steffensen 2002, Schaefer & Walters 2010, White et al. 2012), however, Álvarez et al. (2006) demonstrated microgeographic variation in SMR in brown trout, *Salmo trutta*, consistent with the MCA hypothesis.

Otolith carbon is derived from isotopically distinct sources: ambient dissolved inorganic carbon (DIC) and diet (Mulcahy et al. 1979, Kalish 1991a, Thorrold et al. 1997, Weidman & Millner 2000). Since the relative proportion of carbon derived from the two sources is dependent on individual metabolic rate, otolith carbon stable isotope ($\delta^{13}\text{C}$) values can be used to infer relative metabolic rates (e.g. Schwarcz et al. 1998, Wurster & Patterson 2003, Wurster et al. 2005, Shephard et al. 2007). Since otolith $\delta^{13}\text{C}$ values reflect levels of metabolically derived $\delta^{13}\text{C}$ in plasma (Sherwood & Rose 2003) and are metabolically inert once precipitated into the otolith (Campana 1999), the otolith-inferred metabolic rate reflects the average field metabolic rate of the organism over its lifetime.

Here, we use information on differences in growth rate and field metabolic rates among young-of-the-year (YOY) Arctic charr sampled over a 27° latitudinal gradient in eastern and central Canada as inferred from stable isotope analyses to test the hypotheses that growth and metabolic rates increase with latitude in a manner consistent with the countergradient variation hypothesis.

Methods

Samples of young-of-the-year Arctic charr were obtained either directly by authors or in conjunction with other sampling programs from 23 sites across a latitudinal gradient between 56 and 83°N in eastern and central Canada (Fig. 4.1, Table 4.1). Sampling occurred between July 20 and August 22 over a four year period and included both freshwater resident and anadromous populations (Table 4.2). Samples were captured using electrofishers and/or dipnets in nearshore freshwater environments in water depths of <1m. Individual age was confirmed using otolith aging techniques (Baker & Timmons 1991). Since ambient water $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ data are required to calculate individually experienced temperatures and relative metabolic rates, respectively, water samples were obtained for $\delta^{18}\text{O}$ analysis (50mL) and $\delta^{13}\text{C}_{\text{DIC}}$ analysis (250 mL), coincident with fish sampling, where feasible.

All water samples were shipped to the University of Waterloo Environmental Isotope Lab (UW-EIL) for analyses. Water $\delta^{18}\text{O}$ values were determined following procedures outlined in Epstein and Mayeda (1953) and Fritz et al. (1987) using an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, U.K.). Results were corrected based on EIL-12 (sealed container of laboratory water) calibrated to the international reference materials for VSMOW (Vienna Standard Mean Ocean Water) and SLAP (Standard Light Antarctic Precipitation) from the International Atomic Energy Agency (IAEA). Measured $\delta^{18}\text{O}$ isotope ratios were converted from VSMOW to VPDB (Vienna Peedee Belemnite) following (Coplen et al. 1983):

$$\delta^{18}\text{O}_{\text{Water(VPDB)}} = 0.97002 \times \delta^{18}\text{O}_{\text{Water(VSMOW)}} - 29.98$$

where $\delta^{18}\text{O}_{\text{Water (VPDB)}}$ is the water $\delta^{18}\text{O}$ expressed with respect to VPDB and $\delta^{18}\text{O}_{\text{Water (VSMOW)}}$ is the water $\delta^{18}\text{O}$ reported with respect to the international reporting scale for water (VSMOW). $\delta^{13}\text{C}_{\text{DIC}}$ values were determined following procedures described in McCrea (1950) using a Gilson 222XL auto-sampler coupled to a MicroGas-IsoPrime Mass Spectrometer (GV Instruments/Micromass, Manchester, U.K.) with an analytical precision of $\pm 0.2\%$.

All sampled YOY Arctic charr were frozen and shipped back to a laboratory for processing. In most cases, YOY Arctic charr fork lengths (FL, mm) were measured in the field prior to freezing. In instances when samples were obtained indirectly through collaborative sampling and field FL measurements were not taken, a linear regression relationship estimated from available field and thawed laboratory measurements was used to estimate field FLs. In the lab, sagittal otoliths were removed from the fish, cleaned with distilled water and dried at ambient room temperature ($\sim 21^\circ\text{C}$). Whole otoliths were placed in small reaction glass vials and heated to 350°C for one hour to remove potential organic contamination under a continuous flow of purified helium (Epstein et al. 1953, Guiguer et al. 2003). Vials were flushed with injected purified helium for 30 seconds immediately following roasting. Phosphoric acid was added to each sample by injection and samples were warmed to 90°C for 1 hour prior to analysis. At the UW-EIL, evolved CO_2 gas from acid digestion was drawn off and auto-injected into an IsoPrime mass spectrometer (GV Instruments/Micromass, U.K.) with an analytical precision of $\approx 0.2\%$. Machine accuracy during analysis was assessed with the analysis of commercially available international calcite standards NBS-18 (Carbonite CaCO_3 : $\delta^{13}\text{C}_{\text{VPDB}} = -5.01\%$, $\delta^{18}\text{O}_{\text{VPDB}} = -23.00\%$), NBS-19 (TS-limestone CaCO_3 : $\delta^{13}\text{C}_{\text{VPDB}} = 1.95\%$, $\delta^{18}\text{O}_{\text{VPDB}} = -2.20\%$), EIL-21 (Pine Point CaCO_3 : $\delta^{13}\text{C}_{\text{PDB}} = -0.19$, $\delta^{18}\text{O}_{\text{PDB}} = -15.68$) and EIL-23 (Fisher CaCO_3 : $\delta^{13}\text{C}_{\text{PDB}} = -3.42$, $\delta^{18}\text{O}_{\text{PDB}} = -13.45$) with this set of laboratory standards being analysed before and after sample batches of 5 to 12 otoliths. Otolith $\delta^{18}\text{O}$ values were converted to temperature estimates based on a species-specific fractionation equation developed for Arctic charr by Godiksen et al. (2010) as follows:

$$1000 \ln \alpha = -89.90(1000TK^{-1})^2 - 617.19(1000TK^{-1}) + 1089.24$$

where

$$\ln \alpha = \frac{\delta^{18}\text{O}_{\text{otolith(VPDB)}} + 1000}{\delta^{18}\text{O}_{\text{water(VPDB)}} + 1000}$$

and TK is temperature (°K).

Fish tissue samples were analysed whole (minus head and fins) for carbon stable isotope values at the UW-EIL, on a Delta Plus continuous flow isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an analytical precision of $\pm 0.2\%$. Precision was established through repeat analysis of the IAEA CH6 standard. Study measurement variability was additionally assessed by the repeat analysis of one in ten samples. All analytical results are quoted in standard delta (δ) notation as parts per mil (‰) with respect to VPDB (Craig 1957).

Since otolith $\delta^{13}\text{C}$ may include metabolically and environmentally derived carbon, isotope mixing models developed to estimate the percent of otolith $\delta^{13}\text{C}$ derived from metabolic sources were applied to the obtained stable isotope data (Kalish 1991a, McConnaughey et al. 1997). The percentage of metabolic carbon in the otolith is thought to reflect individual metabolic rate where a higher metabolic rate results in a higher percent of metabolically derived carbon (Wurster & Patterson 2003). As such, the percent of metabolic otolith carbon may be used as an index of individual metabolic rate. For sites where water $\delta^{13}\text{C}_{\text{DIC}}$ samples were collected, a mixing model developed by McConnaughey et al. (1997) was used to estimate the percent of metabolically derived carbon (%M) in the otolith as:

$$\%M = \frac{(\delta^{13}\text{C}_o - \varepsilon_{\text{ar-HCO}_3^-}) - \delta^{13}\text{C}_{\text{DIC}}}{\delta^{13}\text{C}_M - \delta^{13}\text{C}_{\text{DIC}}}$$

where $\delta^{13}\text{C}_o$ is the isotopic composition of the otolith, $\varepsilon_{\text{ar-HCO}_3^-}$ is the fractionation factor between aragonite and bicarbonate, $\delta^{13}\text{C}_M$ is the isotope composition of metabolically derived carbon and $\delta^{13}\text{C}_{\text{DIC}}$ is the isotope value for ambient water. Romanek et al. (1992) estimated $\varepsilon_{\text{ar-HCO}_3^-}$ to equal 2.7.

In the absence of direct isotope measurements for metabolically derived carbon, $\delta^{13}\text{C}$ from the whole fish, minus head and fins, was used (e.g. Kalish 1991b, McConnaughey et al. 1997, Gillikin et al. 2009).

To compare growth rate over the sampled latitudinal gradient, fork lengths were standardized by the thermal opportunity for growth (Conover 1990, Power & McKinley 1997) at each site. TOG was defined here as mean otolith-inferred temperature multiplied by the number of days between the beginning of the growing season and capture date (hereafter termed days used). This method of

estimating growth rate presumes a linear relationship between temperature and growth, which has been demonstrated in Arctic charr at temperatures up to approximately 15°C (Larsson et al. 2005) and applies to this study where individually experienced temperatures were all found to be <14.7°C. To determine the beginning of the growing season date, mean daily air temperatures were obtained from compiled airport weather station data (www.tutiempo.net, www.wunderground.com). Missing daily temperature data were linearly interpolated from existing data. An 11-point smoothing function was applied to the data and the beginning of the growing season was defined as the date when smoothed air temperatures reached and remained consistently above zero. A lower limit of 0°C was used to define TOG owing to evidence that charr can feed and grow at temperatures close to zero (Brännäs & Wiklund 1992, Larsson et al. 2005). Growth rate was then estimated for each individual as FL divided by the TOG (mm/TOG). FL was not standardized by length at emergence since egg diameter, which has been linked to length at emergence (e.g. Baroudy & Elliott 1994b), does not vary with latitude among populations for Arctic charr in North America (Power et al. 2005).

Linear regression was used to assess relationships between mean growth rate and latitude, and mean %M and latitude. Kogluhtokoluk Brook and Torr Bay Brook, the only riverine sites for which $\delta^{13}\text{C}_{\text{DIC}}$ was measured, were excluded from analyses involving %M owing to expected differences in the metabolic rates of lacustrine and riverine individuals (Graham 1949, Facey & Grossman 1990). Multiple regression was used to assess the relationship between %M and latitude while controlling for variations in growth rate among sites, with partial correlation used to calculate the amount of explained variation between %M and latitude while controlling for growth rate (Field 2005). Data normality and variance homogeneity were assessed prior to all statistical analyses using standardized testing procedures (Zar 2010). The maximal Type I error in all statistical analyses was set at $\alpha=0.05$. All statistical analyses were conducted using SPSS version 17.

Results

Mean growth rates ranged between 0.032mm/TOG at Tom's Pond (56° 42'N), Labrador, and 0.292mm/TOG at Clements Markham Lake (82° 37'N), Ellesmere Island (Table 4.2). A significant positive linear relationship was demonstrated between mean growth rate and latitude ($F_{1,21}=27.341$, $p<0.001$) in which 56.6% of the variance in mean growth rate was explained by latitude (Fig. 4.2).

There was also a significant positive relationship between mean %M (the percent of metabolically derived carbon within the otolith) and latitude, where 53.5% of the variation was explained ($F_{1,12}=13.799$, $p<0.01$, Fig. 4.3). Once mean growth rate was controlled for in the regression, the significant positive relationship between %M and latitude was maintained ($r^2=0.47$, $p<0.02$, Table 4.3, Fig. 4.4).

Discussion

Inferred growth and metabolic rates of young-of-the-year Arctic charr sampled across a $\sim 27^\circ$ latitudinal gradient in eastern and central Canada demonstrated patterns consistent with countergradient variation. Once standardized by the thermal opportunity for growth based on mean otolith-inferred temperature experienced at each site, YOY Arctic charr from northern populations had a higher growth rate (mm/TOG) than southern conspecifics. Similarly, metabolic rates inferred from the percent of metabolic carbon found within the otolith were higher in YOY Arctic charr from northern populations relative to those from southern populations.

Mean growth rate was significantly and positively related to latitude, with latitude explaining 56.6% of the observed variability in growth rate among sites. The latitudinal compensation in growth rate, demonstrated here, is consistent with the CGV hypothesis for growth rate (Levins 1969) and contributes to the growing body of literature which has demonstrated faster growth in populations from harsher climates (e.g. Conover & Present 1990, Nicieza et al. 1994b, Conover et al. 2009, Rypel 2012), including that for Arctic charr (Chavarie et al. 2010).

Despite the growing empirical support for the CGV hypothesis (Conover et al. 2009), its validity and ubiquity continues to be questioned (Clarke 1993), and its applicability with respect to salmonids remains uncertain. Whereas the prevalence of CGV in growth rate among lacustrine and juvenile anadromous Arctic charr (Chavarie et al. 2010) was noted in eastern Canada, studies on juvenile brown trout have largely failed to demonstrate CGV in growth rate (Blanck & Lamouroux 2007, Parra et al. 2009, Logez & Pont 2011). As the studies on brown trout did not standardize fork length measurements by the length of growing season to adjust for the effect of differences in the opportunity for growth (Conover 1990, Power & McKinley 1997), evidence of growth compensation across latitude may have been obscured within data sets that essentially compare the effect of differing growing season lengths on growth rate. Jensen et al. (2000) and Nicola and Almodóvar (2004), however, observed that mean annual growth rates for populations resident in colder regions were higher than predicted, and suggested that growth compensation may occur in these populations. In Atlantic salmon, *Salmo salar*, Jonsson et al. (2001) did not find evidence to support CGV in growth rate, but noted that feeding efficiencies were higher in individuals from more hostile environments. In contrast, Nicieza et al. (1994a, 1994b) demonstrated CGV in both growth and digestive rates in salmon. Potential reasons for contrasting evidence with respect to CGV have been suggested in previous studies. Chavarie et al. (2010) noted that most instances of weak or absent evidence of CGV have resulted from assessments of European populations. Since North America is characterised by a steeper latitudinal gradient in temperature and growing season length it is more likely to result in pronounced variations in growth patterns consistent with CGV. Likewise, Rypel (2012) demonstrated strong correlations between growth rate, climate and

latitude among North American populations of northern pike, *Esox lucius*, whereas similar relationships were noticeably weaker among Eurasian populations.

Unlike studies that evaluate CGV in growth rate using common garden experiments, the methods used here facilitated the comparison of growth rate variation in natural populations. Fuller et al. (2010) illustrated that the potential ecological effects of climate change can only be predicted once physiology at the organism level is understood within its natural habitat. Although common garden experiments should be used to confirm the presence of a genetic component in CGV (Conover et al. 2006), the practicalities of experimental logistics limit the application of the approach when attempting to test CGV using a large number of populations from across a large latitudinal range as was done here. Further, Finstad and Jonsson (2012) related incubation temperature to later growth performance in Atlantic salmon and speculated that their findings may have implications for common garden experiments attempting to assess CGV in growth. Specifically, the authors suggested that unless the parents of study individuals were also raised in common conditions, embryos originating from cold environments may experience experimental temperatures as being elevated compared to their natal environment, resulting in elevated growth rates and vice versa for embryos that originate from warm natal environments (Finstad & Jonsson 2012).

Similar to the latitudinal patterns observed in growth rate, YOY Arctic charr in this study from northern populations were found to have higher otolith-inferred field metabolic rates relative to southern conspecifics. Once the effect of growth rate was removed, latitude accounted for 48.6% of the remaining variation in metabolic rate in a pattern consistent with the metabolic cold adaptation hypothesis. Otolith-inferred metabolic rates only partially reflect SMR, however, and are influenced by other processes typically performed by free-living organisms, such as thermoregulation, locomotion, feeding, aggression, reproduction and growth (Nagy 1987). The observed latitudinal patterns in otolith-inferred metabolic rates may also reflect increased food consumption (Beamish 1974), higher activity levels (Facey & Grossman 1990) and/or higher SMRs in high latitude populations. Nevertheless, the higher growth rates observed in the north reflect a surplus of seasonal energy available to northern YOY relative to those from southern populations. Although northern lakes are less productive (e.g. Shortreed & Stockner 1986, ACIA 2005), the large pulse of productivity that occurs in the Arctic summer as a consequence of continuous daylight and warm temperatures (ACIA 2005) may result in larger amounts of available energy per individual fish during the limited open water season, and may provide the opportunity for higher relative consumption during that time (Jørgensen et al. 1993). Chavarie et al. (2010), however, suggested that differences in food alone are unlikely to result in the observed countergradient in growth rate for Arctic charr.

Previous studies have linked increased growth rate achieved by northern populations to increased consumption and growth efficiency in Atlantic silversides (*Menidia menidia*) (Present & Conover 1992) and among tadpoles of the common frog (*Rana temporaria*) (Lindgren & Laurila 2005). Higher growth and metabolic rates observed in northern Arctic charr may similarly reflect increased foraging as has been noted among northern populations of the common frog tadpole (Lindgren & Laurila 2010) and Japanese rice fish (*Oryzias latipes*) (Suzuki et al. 2010). Higher foraging rates and slower swimming speeds resulting from increased consumption, however, have been linked to increased predation risk with the result that northern conspecifics were more heavily predated in common garden experimentation (Lankford et al. 2001, Suzuki et al. 2010). Since predation has been found to suppress fast growth rates (Biro et al. 2006), latitudinal variation in predation pressures may play a role in the evolution of countergradient variation in growth rate (Suzuki et al. 2010).

The possibility that higher SMRs in high latitude populations contribute to the observed pattern in otolith-inferred metabolic rates can not be dismissed. Among salmonids, inter-individual variation in SMR has been well established (Metcalf et al. 1992, Cutts et al. 2002b, Finstad et al. 2007), with variation known to hold implications for life-history strategy, reproduction, social status and growth (Jonsson & Jonsson 1993, Metcalf et al. 1995, Forseth et al. 1999). Since high SMRs in salmonids have been linked to rapid growth and social dominance (e.g. Metcalf et al. 1995, Forseth et al. 1999, McCarthy 2001, Cutts et al. 2002a, Lahti et al. 2002, Álvarez et al. 2006), high SMRs in northern populations may have additional implications for climate change responses. Millidine et al. (2009) demonstrated that Atlantic salmon juveniles with higher SMRs are able to extract and assimilate more nutrients, and process meals faster. Faster processing and assimilation times associated with higher metabolic rates may be well suited to take advantage of the large pulse of summer Arctic productivity (ACIA 2005).

The phenotypic variation in growth and field metabolic rates observed in YOY Arctic charr across eastern and central Canada demonstrate the significant ability of the species to utilize different thermal regimes with different growing season lengths. Questions remain as to how Arctic charr may ultimately respond to the rate of temperature change associated with climate warming (e.g. Reist et al. 2006a, Reist et al. 2006b, Finstad & Hein 2012). Nevertheless, the marked phenotypic variation exhibited by the species suggests that phenotypic plasticity is likely to play a key role in defining Arctic charr responses to climate change and may ultimately facilitate genetic adaptation by buffering populations against immediate negative consequences of environmental change (Fuller et al. 2010, Fierst 2011). The capacity for phenotypic plasticity, however, is not unlimited. Arctic charr populations from the southern extent of the range will face significant risks associated with rising temperatures and are more

likely to face local extirpation if they are unable to behaviourally thermoregulate and utilize cooler waters in hypolimnia, where available (e.g. Lehtonen 1996, Murdoch & Power 2013).

The genetic component potentially underlying the phenotypic patterns observed in this study could not be verified or quantified using the field-based assessment employed here. In assessing the vulnerability of a species to climate change effects, the difficulty in separating genetic from phenotypic components has been identified as a challenge (Williams et al. 2008). Nevertheless, the implications of countergradient variation are thought to have relevance in predicting the response of organisms to projected climate warming scenarios (Conover et al. 2009). In response to rising global temperatures, northward migrations of species have already been demonstrated (Nye et al. 2009), and are predicted to persist (Reist et al. 2006a). Similarly, based on CGV theory, Baumann and Conover (2011) have predicted a poleward migration of genotypes under climate warming scenarios. Understanding the specific contributions of phenotypic plasticity and genetic variability to the observed latitudinal compensation gradient will be critical to more accurately predicting the responses of Arctic charr to climate change on various time scales, and facilitating the adaptive and sustainable management of Arctic charr in many parts of its current geographic range.

Table 4.1. Sampled sites, corresponding map code, and latitude and longitude coordinates, by region.

| Site | Map Code | Latitude (°N) | Longitude (°W) |
|---|----------|---------------|----------------|
| <i>Labrador, NL</i> | | | |
| Kogluktokoluk Brook | 1 | 56°17' | 62°09' |
| Tom's Pond | 2 | 56°42' | 61°38' |
| Ikarut River | 3 | 58°09' | 63°03' |
| Torr Bay Brook | 4 | 58°27' | 62°49' |
| Southwest Arm Brook | 5 | 58°28' | 63°35' |
| North Arm Brook | 6 | 58°34' | 63°29' |
| <i>Baffin Island South, NU</i> | | | |
| Katuqa, Pritzler Harbour | 7 | 62°18' | 67°34' |
| Qinngu, Blandford Bay | 8 | 63°33' | 71°15' |
| Qasigiat, Ptarmigan Fiord | 9 | 64°38' | 66°19' |
| <i>Kent Peninsula Area, NU</i> | | | |
| Louis Lake | 10 | 68°04' | 107°14' |
| <i>Baffin Island North, NU</i> | | | |
| Pond Inlet Lake 1 – informal name | 11 | 72°36' | 77°58' |
| <i>Cornwallis Island, NU</i> | | | |
| Resolute Lake | 12 | 74°41' | 94°53' |
| Char Lake | 13 | 74°42' | 94°53' |
| Small Lake | 14 | 74°46' | 95°03' |
| North Lake | 15 | 74°46' | 95°05' |
| Amituk Lake | 16 | 75°03' | 93°53' |
| <i>Quttinirpaaq National Park, Ellesmere Island, NU</i> | | | |
| Lake E | 17 | 81°49' | 69°27' |
| Lake Hazen | 18 | 81°49' | 71°19' |
| Lake G | 19 | 81°49' | 69°16' |
| Craig Lake | 20 | 81°52' | 68°51' |
| Lake C | 21 | 82°05' | 68°24' |
| Lake D | 22 | 82°06' | 67°31' |
| Clements Markham Lake | 23 | 82°37' | 68°60' |

Table 4.2. Mean and (standard deviations) of fork length, otolith-inferred temperature, percent of metabolically derived otolith carbon (%M) and growth rate at each site. Year, sample size (n) and days used are also noted. Days used refers to the number of days between the beginning of the growing season and capture date. TOG refers to the thermal opportunity for growth, which is estimated as mean otolith-inferred temperature multiplied by the number of days used.

| Site | Year | n | Mean FL mm (±SD) | Mean otolith-inferred temperature °C (±SD) | Mean %M (±SD) | Days used | Mean growth rate mm/TOG (±SD) |
|---------------------------------------|------|----|---------------------|---|------------------|--------------|----------------------------------|
| <i>Labrador, NL</i> | | | | | | | |
| Kogluktokoluk Brook | 2008 | 7 | 46.2 (5.1) | 11.3 (1.5) | 36.4 (4.2) | 116 | 0.035 (0.004) |
| Tom's Pond | 2008 | 6 | 40.3 (4.8) | 11.5 (2.2) | 15.7 (4.0) | 108 | 0.032 (0.004) |
| Ikarut River | 2009 | 10 | 28.8 (2.8) | 8.2 (2.8) | n/a | 60 | 0.059 (0.006) |
| Torr Bay Brook | 2008 | 9 | 35.5 (3.0) | 8.4 (0.8) | 33.1 (3.6) | 93 | 0.045 (0.004) |
| Southwest Arm Brook | 2007 | 8 | 39.8 (5.7) | 6.4 (2.9) | n/a | 61 | 0.102 (0.015) |
| North Arm Brook | 2008 | 9 | 31.2 (4.3) | 4.8 (1.9) | n/a | 59 | 0.110 (0.015) |
| <i>Baffin Island South, NU</i> | | | | | | | |
| Katuqa, Pritzler Harbour | 2007 | 8 | 29.9 (4.7) | 3.7 (0.8) | n/a | 75 | 0.109 (0.017) |
| Qinngu, Blandford Bay | 2007 | 10 | 34.7 (3.5) | 5.1 (2.5) | n/a | 72 | 0.096 (0.010) |
| Qasigiat, Ptarmigan Fiord | 2007 | 10 | 30.5 (2.7) | 2.8 (0.7) | n/a | 58 | 0.186 (0.016) |
| <i>Kent Peninsula Area, NU</i> | | | | | | | |
| Louis Lake | 2008 | 10 | 31.6 (3.8) | 2.9 (1.1) | 19.4 (6.4) | 51-54 | 0.078 (0.010) |
| <i>Baffin Island South, NU</i> | | | | | | | |
| Pond Inlet Lake 1 | 2010 | 10 | 34.8 (4.4) | 7.3 (1.5) | n/a | 61 | 0.203 (0.023) |
| <i>Cornwallis Island NU</i> | | | | | | | |
| Resolute Lake | 2008 | 5 | 27.3 (1.2) | 2.5 (1.1) | 21.0 (3.4) | 41 | 0.272 (0.012) |
| Char Lake | 2008 | 8 | 29.1 (2.3) | 4.0 (1.1) | 35.3 (2.9) | 44 | 0.166 (0.013) |
| Small Lake | 2008 | 4 | 26.5 (1.1) | 4.4 (2.9) | 21.3 (2.0) | 45 | 0.134 (0.005) |
| North Lake | 2008 | 7 | 22.6 (1.9) | 2.3 (1.5) | 27.7 (2.5) | 45 | 0.222 (0.019) |
| Amituk Lake | 2008 | 7 | 28.2 (1.8) | 2.7 (1.6) | 39.4 (3.8) | 46 | 0.226 (0.014) |
| <i>Quttinirpaaq National Park, NU</i> | | | | | | | |
| Lake E | 2007 | 9 | 40.2 (2.3) | 5.8 (2.0) | 39.2 (3.7) | 44 | 0.158 (0.009) |
| Lake Hazen | 2007 | 8 | 34.6 (5.5) | 4.9 (0.9) | 34.4 (7.9) | 41-51 | 0.158 (0.012) |
| Lake G | 2007 | 5 | 30.6 (2.9) | 4.2 (1.1) | 35.7 (3.6) | 42 | 0.172 (0.016) |
| Craig Lake | 2008 | 11 | 39.5 (2.1) | 4.7 (1.4) | 41.3 (5.6) | 52 | 0.161 (0.009) |
| Lake C | 2008 | 10 | 39.0 (3.6) | 2.7 (0.4) | 37.5 (2.4) | 51 | 0.283 (0.026) |
| Lake D | 2007 | 7 | 26.7 (5.1) | 2.6 (6.9) | 24.9 (6.9) | 43 | 0.236 (0.045) |
| Clements Markham Lake | 2008 | 8 | 39.8 (4.7) | 0.9 (0.9) | 45.1 (3.7) | 54 | 0.292 (0.034) |

Table 4.3. Regression results for the model relating mean %M to mean growth rate and latitude. Partial correlation coefficients measure the strength of association between mean %M and the listed explanatory variables when the effect of the other variable has been controlled for in the analysis.

| | Unstandardized coefficients | | t-statistic | p | Partial correlation |
|-------------|-----------------------------|----------------|-------------|-------|---------------------|
| | B | Standard error | | | |
| Constant | -42.638 | 21.449 | -1.988 | >0.05 | |
| Growth rate | -10.150 | 33.819 | -0.300 | >0.05 | -0.090 |
| Latitude | 0.990 | 0.318 | 3.110 | 0.01 | 0.684 |

$r^2=0.539$, $F_{2,11}=6.421$, $p<0.02$

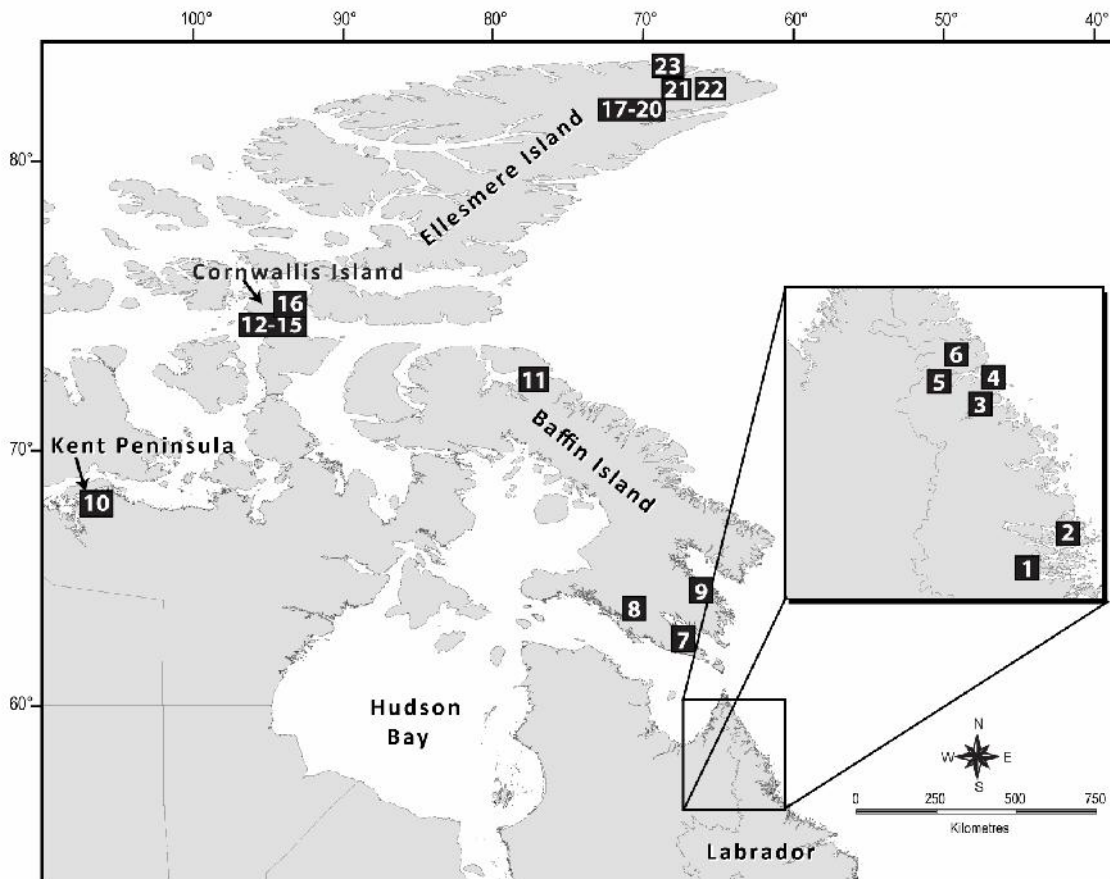


Figure 4.1. Map of sampling site locations. Numbers correspond to the map code as described in Table 4.1.

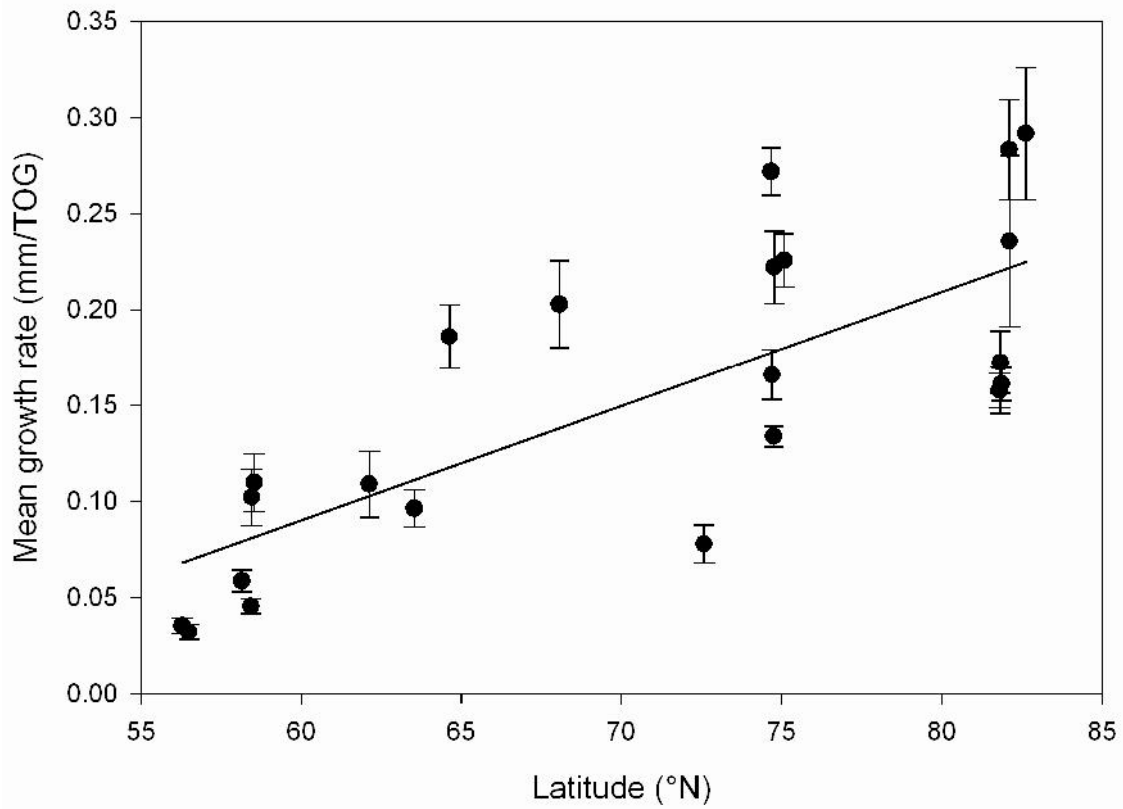


Figure 4.2. Mean growth rate vs. latitude for sampled YOY Arctic charr, *Salvelinus alpinus*, ($r^2=0.57$). Error bars represent the standard deviations. The solid line depicts the estimated linear relationship between the plotted variables.

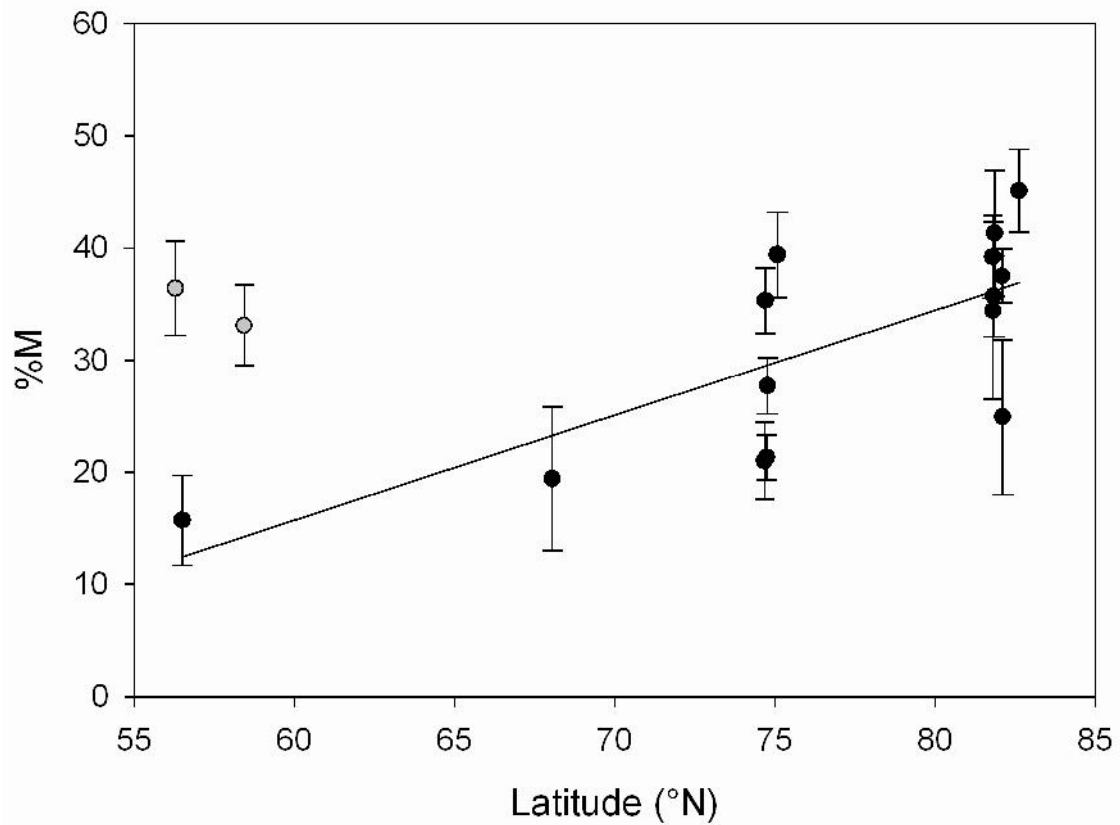


Figure 4.3. Mean percent of metabolically derived carbon (%M) vs. latitude for sampled YOY Arctic charr ($r^2=0.53$). Error bars represent standard deviations. The solid line depicts the estimated linear relationship between the plotted variables. Data for the Kogluktokoluk Brook and Torr Bay Brook riverine sites, excluded from the regression analysis are plotted in grey (see methods).

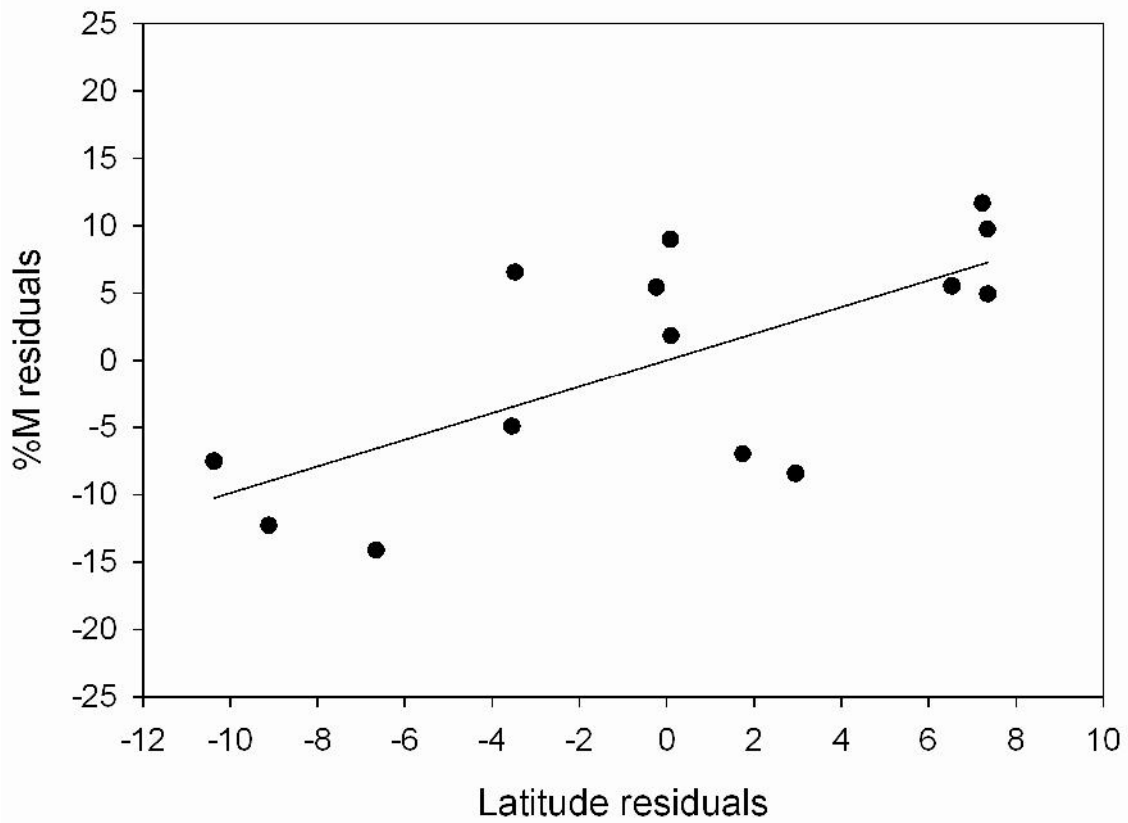


Figure 4.4. Partial regression plot depicting the relationship between mean %M and latitude for sampled Arctic charr ($r^2=0.47$) once the effect of growth rate was removed. %M residuals and latitude residuals are the residuals resulting from simple linear regression analysis with each variable regressed against mean growth rate (Moya-Larano & Corcobado 2008).

Chapter 5: Thermal habitat use and growth in young-of-the-year Arctic charr from proximal fluvial and lacustrine populations in Labrador, Canada

Introduction

Body size has broad implications for individual fish and aggregate population dynamics, affecting survival, reproduction, swimming and foraging ability, and predation risk (Beamish 1980, Quinn & Peterson 1996, Bystrom et al. 2004, Power et al. 2005, Bystrom et al. 2006). Since fish are ectotherms, growth is highly dependant on environmental temperatures as a consequence of direct physiological effects (Elliott 1976, Brett 1979) and indirect effects on habitat productivity and prey availability (Vikebø et al. 2005, Handeland et al. 2008, Michaud et al. 2010, Beaugrand & Reid 2012). The pervasive influence of temperature on growth has contributed to growing concern over the potential impacts of climate warming on fish (Reist et al. 2006a, Reist et al. 2006b). Many of the expected effects of climate change have already been observed, including: changes in species distributions and abundances, phenology, individual growth, and reproductive success (Parmesan & Yohe 2003, Root et al. 2003, Jonsson & Jonsson 2004, Condron et al. 2005, Parmesan 2006, Post & Forchhammer 2008, Sheridan & Bickford 2011, Almodóvar et al. 2012, Todd et al. 2012).

The strong association of Arctic charr, *Salvelinus alpinus*, with cold water environments has prompted particular interest in how they may respond to predicted increases in temperature (Power et al. 2000, Reist et al. 2006a, Reist et al. 2006b, IPCC 2007, Graham & Harrod 2009, Michaud et al. 2010, Finstad & Hein 2012), particularly at the southern edge of the distributional range where they are thought to be most at risk (Lehtonen 1998, Winfield et al. 2008). Early life-history stages are thought to be particularly sensitive to climate change (Rijnsdorp et al. 2009, Pankhurst & Munday 2011), the effects of which are likely to have consequence for subsequent population dynamics, affecting year class strength and recruitment success (Suda & Kishida 2003, Power 2007, Martino & Houde 2010).

Arctic charr are habitat generalists that can occupy marine, fluvial and all parts of lacustrine environments depending on the presence of predators or competitors (Klemetsen et al. 2003). For some salmonids, however, habitat type may have implications for attained body size and condition (e.g. Dempson et al. 2004). Despite the variety of habitat types occupied by Arctic charr populations (Power et al. 2008) and differences in predicted hydroecological responses to climate change in fluvial vs. lacustrine environments (Allan et al. 2005, Prowse et al. 2006), little attention has been given to determining whether fluvial and lacustrine Arctic charr populations may respond differently to climate change effects.

Young-of-the-year (YOY) salmonids, including Arctic charr, inhabiting fluvial habitats typically occupy nearshore areas, characterised by shallow, low velocity waters (Bohlin 1977, Bremset & Berg

1999, Sinnatamby et al. 2012). Flow velocities likely act as a physical deterrent to YOY owing to size-related swimming ability (Beamish 1980), and combine with intercohort competition (Bohlin 1977, Sinnatamby et al. 2012) to largely restrict YOY Arctic charr to the nearshore environment (Sinnatamby et al. 2012). Lacustrine-dwelling YOY Arctic charr, on the other hand, have demonstrated wider use of available habitats (Godiksen et al. 2011, Godiksen et al. 2012, Murdoch & Power 2013), although they are largely thought to preferentially occupy nearshore areas unless deterred by predation or competition pressures (Klemetsen et al. 2003, Bystrom et al. 2004, Godiksen et al. 2012).

Laboratory studies on juvenile Arctic charr have determined optimal temperatures for growth (~12-18°C) and preferred temperatures (~9-12°C) (Swift 1964, Peterson et al. 1979, Jobling 1983, Jensen 1985, Larsson & Berglund 1998, Larsson 2005, Larsson & Berglund 2005, Mortensen et al. 2007). Temperatures experienced by fish in the wild, however, have proven to be variable and differ from laboratory determined values, with Arctic charr using and growing at temperatures lower than laboratory estimated optima (Berg & Berg 1989, Rikardsen et al. 2007). Estimating temperatures experienced by fish in the wild can pose several challenges. Where thermal water monitoring is feasible, recorded environmental temperatures may not accurately reflect individually experienced temperatures owing to spatial thermal heterogeneity and behavioural thermoregulation (Lehtonen 1996, Godiksen et al. 2011, Godiksen et al. 2012, Murdoch & Power 2013). Although data storage tags can be used to record temperatures experienced by individual fish (e.g. Godo & Michalsen 2000, Rikardsen et al. 2007), the technique is often limited by cost, fish size, and the necessity of retrieving tags to acquire data.

Oxygen stable isotope analysis of biogenic calcium carbonate structures such as otoliths, however, can be used to reconstruct organism thermal histories with reasonable accuracy (Campana 1999). Otoliths form continually through out the life of a fish (Campana & Neilson 1985). Oxygen stable isotopes in otolith aragonite are deposited in equilibrium with the oxygen stable isotope ratio ($\delta^{18}\text{O}$) of the waters in which the fish lived at the time of otolith formation and are thereafter metabolically inert (e.g. Devereux 1967, Kalish 1991a, Iacumin et al. 1992, Thorrold et al. 1997). Since the water $\delta^{18}\text{O}$ ratio and fractionation during deposition into the otolith vary predictably with temperature, the thermal history of individual fish may be reconstructed provided that the relationship between otolith and water $\delta^{18}\text{O}$ ratios is known (Sharp 2007). Equations relating the relationship are termed fractionation equations (Patterson et al. 1993) and have been estimated for a number of fish species (e.g. Radtke et al. 1996, Thorrold et al. 1997, Gao 2002, Høie et al. 2004, Storm-Suke et al. 2007), including Arctic charr (Godiksen et al. 2010).

Here, we present a comparative study of growth and thermal habitat use in YOY Arctic charr from two proximal fluvial and lacustrine populations in Labrador, Canada. Specifically we use data gathered

contemporaneously at both sites over a number of years to compare growth and thermal habitat use between habitat types (fluvial vs. lacustrine). Largely based on the expectation that accessible thermal habitats are restricted for fluvial YOY Arctic charr, we test the hypotheses that: (1) thermal habitat used by fluvial individuals will be more correlated to air temperatures; (2) as a consequence fluvial YOY will use warmer habitats than lacustrine fish; (3) lacustrine fish will exhibit greater variability in utilized thermal habitats which will be (4) reflected in increased variances in fork lengths among lacustrine individuals. Lastly, we characterise the relationships between fork length and otolith-inferred temperatures, and hypothesize that (5) fluvial and lacustrine YOY will exhibit similar correlation between fork length and otolith-inferred temperature.

Site description

Fluvial and lacustrine assemblages of YOY Arctic charr were sampled, respectively from Kogluktokoluk Brook (56°17'N, 62°09'W) and Tom's Pond (56°42'N, 61°38'W, non-gazetted name). Sites are located in the Nain region of Labrador ~54km apart. Kogluktokoluk Brook flows easterly into the northwest end of Voisey Bay ~35km south of Nain Bay. The Kogluktokoluk Brook system contains two large lakes and 18 tributaries with a total drainage area of 1095km² (Anderson 1985). A large tributary, Ikadlivik Brook, flows into Kogluktokoluk Brook ~5km upstream from its mouth and is believed to contain most of the suitable over wintering habitat in the Kogluktokoluk Brook system (Beddow et al. 1998). Arctic charr are the dominant species in Kogluktokoluk Brook. Other fish species reported include: three-spine stickleback (*Gasterosteus aculeatus*), nine-spine stickleback (*Pungitius pungitius*), Atlantic salmon (*Salmo salar*), brook charr (*S. fontinalis*), lake trout (*S. namaycush*) and round whitefish (*Prosopium cylindraceum*). Tom's Pond is located on the Itilialuk Peninsula on the southwest side of South Aulatsivik Island near Webb's Bay, ~16km north of Nain. Tom's Pond has a surface area of ~1.1km² and is connected to the sea via a small southward flowing stream ~200m in length. Other fish species found in Tom's Pond include: brook charr and three-spine stickleback.

Methods

Young-of-the-year Arctic charr were collected from the nearshore areas of Tom's Pond and Kogluktokoluk Brook, at the confluence of Ikadlivik Brook, or occasionally within Ikadlivik Brook, using an electrofisher and/or dipnet in water depths of <1m by the Department of Fisheries and Oceans. Specimens were collected at Tom's Pond and Kogluktokoluk Brook between 2004 and 2008. Eight sampling events were conducted at each site so that both sites were sampled contemporaneously (≤eight days apart, Table 2.1). Coincident with the fish collection, water samples were also obtained for δ¹⁸O analysis (50mL). Fish were measured for fork length (FL, mm) in the field, frozen and shipped to the laboratory.

All water samples were shipped to the University of Waterloo Environmental Isotope Lab (UW-EIL) for analysis. Water $\delta^{18}\text{O}$ values were determined following procedures outlined in Epstein and Mayeda (1953) and Fritz et al. (1987) using an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, U.K.). Results were corrected based on EIL-12 (sealed container of laboratory water) calibrated to the international reference materials for VSMOW (Vienna Standard Mean Ocean Water) and SLAP (Standard Light Antarctic Precipitation) from the International Atomic Energy Agency (IAEA). Measured $\delta^{18}\text{O}$ isotope ratios were converted from VSMOW to VPDB (Vienna Peedee Belemnite) following (Coplen et al. 1983):

$$\delta^{18}\text{O}_{\text{Water(VPDB)}} = 0.97002 \times \delta^{18}\text{O}_{\text{Water(VSMOW)}} - 29.98$$

where $\delta^{18}\text{O}_{\text{Water(VPDB)}}$ is the water $\delta^{18}\text{O}$ expressed with respect to VPDB and $\delta^{18}\text{O}_{\text{Water(VSMOW)}}$ is the water $\delta^{18}\text{O}$ reported with respect to the international reporting scale for water (VSMOW). $\delta^{13}\text{C}_{\text{DIC}}$ values were determined following procedures described in McCrea (1950) using a Gilson 222XL auto-sampler linked to a MicroGas-IsoPrime Mass Spectrometer (Micromass UK Limited, U.K.).

In the lab, sagittal otoliths were removed, washed in distilled water, and dried at ambient air temperatures. Whole otoliths were placed in small reaction glass vials and heated to 350°C for one hour to remove potential organic contamination under a continuous flow of purified helium (Epstein et al. 1953, Guiguer et al. 2003). Vials were flushed with purified helium injected into the vial for 30 seconds immediately following roasting. Phosphoric acid was added to each sample by injection and samples were warmed to 90°C for 1 hour prior to analysis. At the UW-EIL, evolved CO_2 gas from acid digestion was drawn off and auto-injected into an IsoPrime mass spectrometer (GV Instruments/Micromass, U.K.) with an analytical precision of $\approx 0.2\text{‰}$ (Storm-Suke et al. 2007). Machine accuracy during analysis was assessed with the analysis of commercially available international calcite standards NBS-18 (Carbonitite CaCO_3 : $\delta^{13}\text{C}_{\text{VPDB}} = -5.01\text{‰}$, $\delta^{18}\text{O}_{\text{VPDB}} = -23.00\text{‰}$), NBS-19 (TS-limestone CaCO_3 : $\delta^{13}\text{C}_{\text{VPDB}} = 1.95\text{‰}$, $\delta^{18}\text{O}_{\text{VPDB}} = -2.20\text{‰}$), EIL-21 (Pine Point CaCO_3 : $\delta^{13}\text{C}_{\text{PDB}} = -0.19$, $\delta^{18}\text{O}_{\text{PDB}} = -15.68$) and EIL-23 (Fisher CaCO_3 : $\delta^{13}\text{C}_{\text{PDB}} = -3.42$, $\delta^{18}\text{O}_{\text{PDB}} = -13.45$) with this set of laboratory standards being analysed before and after sample batches of 5 to 12 otoliths. Otolith $\delta^{18}\text{O}$ values were converted to temperature ($^{\circ}\text{C}$) estimates based on a species-specific fractionation equation developed for Arctic charr by Godiksen et al. (2010) as follows:

$$1000 \ln \alpha = 20.43(1000\text{TK}^{-1}) + 41.14$$

where

$$\ln \alpha = \frac{\delta^{18}\text{O}_{\text{otolith(VPDB)}} + 1000}{\delta^{18}\text{O}_{\text{water(VPDB)}} + 1000}$$

and TK is temperature (°K) converted to °C as $TK-237.15$. Mean air temperature corresponding to the estimated period of growth for fish captured during each sampling event was estimated by averaging mean daily air temperature data obtained from the Nain, Labrador airport weather station (CYDP, compiled at wunderground.com) between April 1 and the date of capture for each sampling event.

Linear regression was used to assess the relationship between mean otolith-inferred temperatures and mean air temperature for each site. Levene's test was used to compare variances in otolith-inferred temperatures and FLs for data compiled from all sampling events (Field 2005). Independent t-tests, accounting for heteroscedasticity when necessary, were used to compare mean otolith-inferred temperatures between sites (sampling events compiled) and between sampling event pairs, where sites were sampled ≤ 8 days apart (Zar 2010). Multiple regression analyses were employed to assess the relationship between FL and otolith-inferred temperature, while controlling for day of the year of capture (DYC). Partial correlation was used to quantify the amount of variability in FL that is explained by otolith-inferred temperature, while controlling for DYC (Field 2005). Data normality and variance homogeneity were assessed prior to all statistical testing. Maximal Type I error in all statistical analyses was set at $\alpha = 0.05$, and analyses were conducted using SPSS version 17.

Results

From eight paired sampling events conducted at both sites, otolith-inferred temperatures were obtained for 80 YOY Arctic charr from Tom's Pond and 74 YOY Arctic charr from Kogluktokoluk Brook. No significant relationship was found to exist between mean otolith-inferred temperature and mean air temperature for either site (Tom's Pond: $r^2=0.016$, $F_{1,6}=0.099$, $p>0.05$; Kogluktokoluk Brook $r^2=0.006$, $F_{1,6}=0.038$, $p>0.05$; Fig. 5.1).

Otolith-inferred temperatures from YOY Arctic charr obtained from Tom's Pond ranged from 4.0 to 18.6°C, with 50% of individuals occupying habitat with temperatures between 9.6 and 14.7°C (Fig. 5.2). Otolith-inferred temperatures from YOY Arctic charr obtained from Kogluktokoluk Brook ranged from 6.5 to 15.1°C, with 50% of YOY occupying thermal habitat defined by 9.9 and 12.5°C. A significantly larger variance was found in Tom's Pond otolith-inferred temperature data (Levene: $F=14.337$, $p<0.001$, Fig. 5.2), although no significant difference in mean temperatures were found to exist overall between sites (t -statistic= -1.956, $df=137.618$, $p>0.05$, Fig. 5.2). Pair-wise comparisons of sampling events demonstrated significant differences in mean otolith-inferred temperatures at three of eight contemporaneous sampling events (Table 5.2), however, there was no consistent tendency for fish from the fluvial or lacustrine site to use warmer temperatures, with Tom's Pond YOY higher in August 2006 and 2008 and Kogluktokoluk Brook YOY higher in July 2008. There were no significant differences in mean temperatures experienced in Kogluktokoluk Brook vs. Tom's Pond in the remaining five comparisons (Table 5.2). A significantly larger variance was found among

Kogluktokoluk Brook YOY Arctic charr FLs relative to those from Tom's Pond (Levene: $F=5.254$, $p<0.03$, Fig. 5.2).

When differences in sampling dates embodied in the DYC measure were accounted for in the statistical analysis, FL and otolith-inferred temperature were significantly and positively related in YOY obtained from Tom's Pond, but not from Kogluktokoluk Brook (Table 5.3, Fig. 5.3). Partial correlation coefficients indicated that 9.5% ($r=0.309$) of the variation in Tom's Pond YOY fork length was explained by otolith-inferred temperatures whereas only 2.2% ($r=0.147$) was explained in Kogluktokoluk Brook.

Discussion

Contrary to the stated hypotheses, otolith-inferred temperatures from young-of-the-year Arctic charr obtained from Tom's Pond and Kogluktokoluk Brook, Labrador did not correlate with mean air temperatures characterizing the estimated period of growth, and fluvial YOY were not found to use consistently warmer temperatures than those used by lacustrine YOY. Lacustrine YOY did reflect greater variation in experienced temperatures in accordance with our hypothesis, however, this was not reflected in fork length variation. Rather, fluvial YOY demonstrated increased variation in fork length at capture. Despite the similarity in experienced water temperatures for YOY from the two sites, fork length was only significantly related to otolith-inferred temperatures in YOY Arctic charr from Tom's Pond.

That experienced temperatures did not correlate with environmental air temperatures suggests that YOY Arctic charr from both sites were not exclusively using shallow nearshore habitat. The lack of correlation may indicate behavioural thermoregulation in which fish select habitat with more favourable temperatures (e.g. Murdoch & Power 2013). Indeed, the majority of YOY Arctic charr sampled from Kogluktokoluk Brook were found to use temperatures similar to preferred temperatures determined using laboratory studies on juvenile Arctic charr ($\sim 9-12^{\circ}\text{C}$, Peterson et al. 1979, Larsson 2005, Mortensen et al. 2007, this study: $9.8-12.5^{\circ}\text{C}$, see Fig. 5.2). On the other hand, the majority of YOY Arctic charr from Tom's Pond were found using temperatures comprising experimentally determined preferred temperatures and optimal temperatures for growth ($\sim 12-18^{\circ}\text{C}$, Swift 1964, Jobling 1983, Jensen 1985, Larsson & Berglund 1998, Larsson & Berglund 2005, this study= $9.6-14.7^{\circ}\text{C}$). Preferred temperatures have been suggested to optimize food conversion efficiency, whereas optimal temperatures for growth allow for higher growth rates but assume unlimited ration (Larsson 2005, Larsson & Berglund 2005, Mortensen et al. 2007).

Although behavioural thermoregulation was expected among Tom's Pond YOY, the evidence of thermoregulation in Kogluktokoluk Brook YOY was surprising. While Godiksen et al. (2011, 2012) demonstrated broad variation in thermal habitat use by Dieset Lake YOY Arctic charr, it has been

suggested that movement of YOY Arctic charr within fluvial environments may be restricted by water velocity and intercohort competition (Sinnatamby et al. 2012), with subsequent implications for their ability to behaviourally thermoregulate outside of shallow nearshore habitat. Breau et al. (2007) demonstrated that YOY Atlantic salmon continued to maintain position and forage even during periods of high temperature despite a tendency for older juveniles to aggregate in cooler habitat. However, YOY Arctic charr are not as physiologically tolerant to high temperatures (Elliott & Elliott 2010) and stream-dwelling Arctic charr in Iceland have demonstrated higher forage mobility than Atlantic salmon (Tunney & Steingrímsson 2012). As such, it is feasible that if opportunities exist, YOY Arctic charr may seek cooler habitat during high temperature events, particularly if intercohort competition is reduced by temperature driven changes in the distribution of older juveniles (e.g. Breau et al. 2007). Although cooler temperatures may be accompanied by increased energy costs to maintain position, the ability to maximize growth efficiency by using preferred temperature habitat may offset those costs and provide a net fitness benefit.

Otolith-inferred temperatures from Tom's Pond YOY reflect the use of a wider range of thermal habitats than Kogluktokoluk Brook YOY. The use of cooler temperatures by some Tom's Pond YOY likely reflects the ability of Tom's Pond YOY to access deeper areas of the lake. Godiksen et al. (2011, 2012) found similar evidence of use of cooler temperatures, and suggested profundal habitat use by YOY. Habitat selection theory states that animals will choose habitat to maximize their fitness (Kramer et al. 1997). Thus, the use of higher temperatures by some Tom's Pond YOY suggests they may be able to obtain sufficient ration within the shallow, nearshore margins of the lake to offset the added metabolic costs of higher temperatures, thereby taking advantage of water temperatures in the optimal growth range. Indeed, it has been suggested that the shallow margins of lakes provide favourable microhabitats characterised by warmer water temperatures and wind and surface currents that concentrate organic material along the shore (Power 2002). Conversely, in streams, where prey density is largely associated with flow velocity (Everest & Chapman 1972), low-flow nearshore habitats are likely to be associated with low prey availability, however, in Kogluktokoluk Brook YOY Arctic charr were often found in nearshore, back eddies, where more organic matter was generally present.

Since mean temperatures experienced by YOY Arctic charr from both populations were largely near or below the optimal temperatures for growth for Arctic charr recorded in the laboratory (e.g. Larsson & Berglund 1998), it was expected that temperatures would be positively related to fork length. While a positive correlation was observed in the present study for Tom's Pond YOY, it was not observed for Kogluktokoluk Brook YOY. Even among Tom's Pond YOY, otolith-inferred temperatures accounted for only 9.5% of the observed variation in fork length. Murdoch & Power (2013) similarly observed a distinctive lack of correlation between apparent habitat temperatures and growth ($r^2 \leq 0.19$ for

all tested relationships) for two Quebec populations, as did Godiksen et al. (2011) for YOY from Dieset Lake, Svalbard ($r^2=0.13$), with the latter study suggesting that the unexplained variation in size may be related to individual differences in length at hatch (Baroudy & Elliott 1994b) or ration (Elliott 1994). Additionally, since a high standard metabolic rate can result in reduced growth if metabolic demands can not be met, or enhanced growth when resources are abundant (Forseth et al. 1999, Millidine et al. 2009, Biro & Stamps 2010), variation in standard metabolic rates are likely to contribute to variability in fork lengths. Variability in energy allocation strategy among individuals (Post & Parkinson 2001) may also contribute to variability in fork length. A trade-off is thought to exist between somatic growth optimization, which maximizes fork length attained during the first growing season, and energy storage optimization, which maximizes lipid storage for winter (Post & Parkinson 2001). Within populations, individual variation in lipid storage has been found to be high in juvenile Atlantic salmon (Berg et al. 2006, Næsje et al. 2006, Berg et al. 2009).

The observed difference in correlation between fork length and otolith-inferred temperature between sites, as well as the higher fork length variability observed in Kogluktokoluk Brook may be explained by the differences in foraging tactics usually employed between salmonids using different habitats (e.g. Biro et al. 1997, Tunney & Steingrímsson 2012). Stream salmonids are generally found to use a sit-and-wait foraging tactic (also called stayers), where they occupy a relatively small amount of space, wait for drifting prey to approach, and ambush their prey (Grant & Noakes 1987). As such, faster current is associated with the benefit of delivering more drift per unit time (Everest & Chapman 1972), but with the added energetic cost of maintaining position (e.g. Fausch 1984). Consequently, positions that maximize drift, while minimizing swimming costs are preferred and tend to be occupied by dominant individuals or species (Fausch & White 1981, Fausch 1984, Hughes 1992). Thus, subordinates are often shunted to higher velocity waters that lack cover and have greater energy occupancy costs, are found using low velocity habitats with associated reduced drift feeding opportunities, or are required to use non-territorial tactics that increase energy expenditure (Fausch 1984, Metcalfe 1986, Nakano 1995). Further, since food is delivered via water current, individuals positioned further forward in the stream encounter food first and exhibit feeding benefits related to their position, while others may suffer the consequences of shadow competition (Hughes 1992, Elliott 2002). Territoriality and dominance hierarchies established by stream salmonids determine positions acquired by individuals and have been found to result in unequal resource partitioning (Nakano 1995) which would have direct consequences for somatic growth.

On the other hand, lake-dwelling salmonids are found primarily using non-territorial cruising forage tactics (also called movers), where individuals swim around more, presumably to increase the likelihood of encountering prey (Gerritsen & Strickler 1977), and attack prey while swimming (Grant &

Noakes 1987). The reduced territoriality and aggression in lacustrine salmonids (Biro et al. 1997) would suggest that a more even distribution of food resources may be expected among individuals, and is likely to contribute to the reduced variability in fork length achieved by lake-dwelling YOY in this study. A gradient in foraging techniques has been identified and linked to water velocity within and among salmonid species (Biro et al. 1997, Nakano et al. 1999, Steingrímsson & Grant 2011, Tunney & Steingrímsson 2012). The difference in experienced water velocities between the two habitat types examined in this study, therefore, may be a key determinant of the observed differences in fork length variability. In addition, the greater variability in feeding tactics associated with stream feeding may obscure the relationship between temperature and growth normally expected within the range of temperatures observed in this study.

Understanding of contemporary relationships between experienced temperatures and achieved fork lengths may provide insight into possible population-specific responses to climate change. As long as summer temperatures remain within or near the optimal temperatures for growth, and ration levels can meet metabolic demands, high temperatures will likely result in increased growth in young-of-the-year Arctic charr, as demonstrated in this study. However, as temperatures continue to rise, Arctic charr population responses are likely to vary depending on habitat type (e.g. Murdoch & Power 2013). It has been suggested that Arctic charr populations inhabiting low latitude lakes without a hypolimnion face the greatest risk from climate change effects (Lehtonen 1996). Observed differences in behavioural thermoregulation between fluvial and lacustrine YOY, demonstrated here, also highlight the increased risk posed to fluvial YOY Arctic charr by climate change.

Table 5.1. Year, day of the year of capture (DYC), sample size (n), mean fork length (mm) and mean otolith-inferred temperature of YOY Arctic charr sampled from Kogluktokoluk Brook and Tom's Pond, Labrador. Standard deviations (SD) are presented in brackets where noted. Mean air temperatures from Nain, Labrador, averaged between April 1st and the capture date, are also presented.

| Site | Year | DYC | n | Mean FL (±SD) | Mean otolith- inferred temperature °C (±SD) | Mean air temperature (°C) |
|--------------------------------------|------|-----|----|------------------|--|---------------------------------|
| <i>Tom's Pond, Labrador</i> | | | | | | |
| | 2004 | 237 | 8 | 37.4 (0.9) | 10.4 (2.8) | 5.3 |
| | 2005 | 239 | 5 | 37.2 (0.8) | 6.8 (1.9) | 6.6 |
| | 2006 | 202 | 9 | 35.9 (3.4) | 11.7 (2.5) | 6.1 |
| | 2006 | 233 | 10 | 39.9 (2.4) | 15.0 (0.9) | 7.3 |
| | 2007 | 219 | 14 | 33.2 (2.8) | 12.4 (2.5) | 3.7 |
| | 2008 | 198 | 15 | 31.6 (2.4) | 10.0 (2.6) | 3.5 |
| | 2008 | 227 | 8 | 40.4 (5.0) | 12.7 (2.2) | 5.1 |
| | 2008 | 241 | 11 | 38.1 (4.0) | 14.7 (2.5) | 5.7 |
| <i>Kogluktokoluk Brook, Labrador</i> | | | | | | |
| | 2004 | 232 | 8 | 36.1 (3.6) | 10.0 (1.4) | 5.0 |
| | 2005 | 238 | 5 | 39.1 (1.1) | 8.6 (1.6) | 6.6 |
| | 2006 | 203 | 9 | 36.2 (4.0) | 11.4 (2.8) | 6.2 |
| | 2006 | 233 | 11 | 39.9 (5.6) | 12.7 (1.5) | 7.3 |
| | 2007 | 213 | 9 | 35.3 (2.1) | 10.5 (2.4) | 3.2 |
| | 2008 | 205 | 15 | 36.8 (4.3) | 11.9 (1.9) | 4.1 |
| | 2008 | 235 | 7 | 46.2 (5.1) | 11.7 (1.1) | 5.5 |
| | 2008 | 248 | 11 | 45.5 (7.1) | 10.7 (1.4) | 6.0 |

Table 5.2. Year, day of the year of capture (DYC), pair-wise comparisons of otolith-inferred temperature (°C) estimates for Tom's Pond (TP) and Kogluktokoluk Brook (KB) YOY Arctic charr. Mean temperature differences are presented as Tom's Pond minus Kogluktokoluk Brook values.

| Year | DYC | | t-statistic | df | p | Mean difference |
|------|-----|-----|-------------|-------|--------|--------------------|
| | TP | KB | | | | |
| 2004 | 237 | 232 | -0.330 | 10.11 | >0.05 | -0.37 |
| 2005 | 239 | 238 | 1.54 | 8 | >0.05 | -1.75 |
| 2006 | 202 | 203 | -0.25 | 16 | >0.05 | 0.32 |
| 2006 | 233 | 233 | -4.22 | 18 | <0.001 | 2.26 |
| 2007 | 219 | 213 | -1.85 | 21 | >0.05 | 1.92 |
| 2008 | 198 | 205 | 2.31 | 28 | 0.03 | -1.92 |
| 2008 | 227 | 235 | -1.08 | 13 | >0.05 | 0.99 |
| 2008 | 241 | 248 | -4.64 | 16.17 | <0.001 | 4.00 |

Table 5.3. Regression results for models relating YOY fork length to the day of the year of capture (DYC) and otolith-inferred temperature for Tom's Pond and Kogluktokoluk Brook YOY Arctic charr. Unstandardized coefficients (B), standard error, t-statistics and p-values are given. Partial correlation coefficients measure the strength of association between YOY fork length and the listed explanatory variable when the effect of the second variable has been controlled for in the analysis.

| | B | Standard error | t-statistic | p | Partial correlation |
|--|--------|----------------|-------------|--------|---------------------|
| <i>Tom's Pond^a</i> | | | | | |
| Constant | 3.732 | 5.320 | 0.701 | >0.05 | |
| DYC | 0.126 | 0.025 | 5.101 | <0.001 | 0.503 |
| Otolith-inferred temperature | 0.364 | 0.128 | 2.850 | 0.006 | 0.309 |
| <i>Kogluktokoluk Brook^b</i> | | | | | |
| Constant | -8.181 | 9.392 | -0.871 | >0.05 | |
| DYC | 0.193 | 0.037 | 5.232 | <0.001 | 0.528 |
| Otolith-inferred temperature | 0.368 | 0.294 | 0.215 | >0.05 | 0.147 |

^a $r^2=0.366$, $F_{2,77}=22.253$, $p<0.001$

^b $r^2=0.280$, $F_{2,71}=13.781$, $p<0.001$

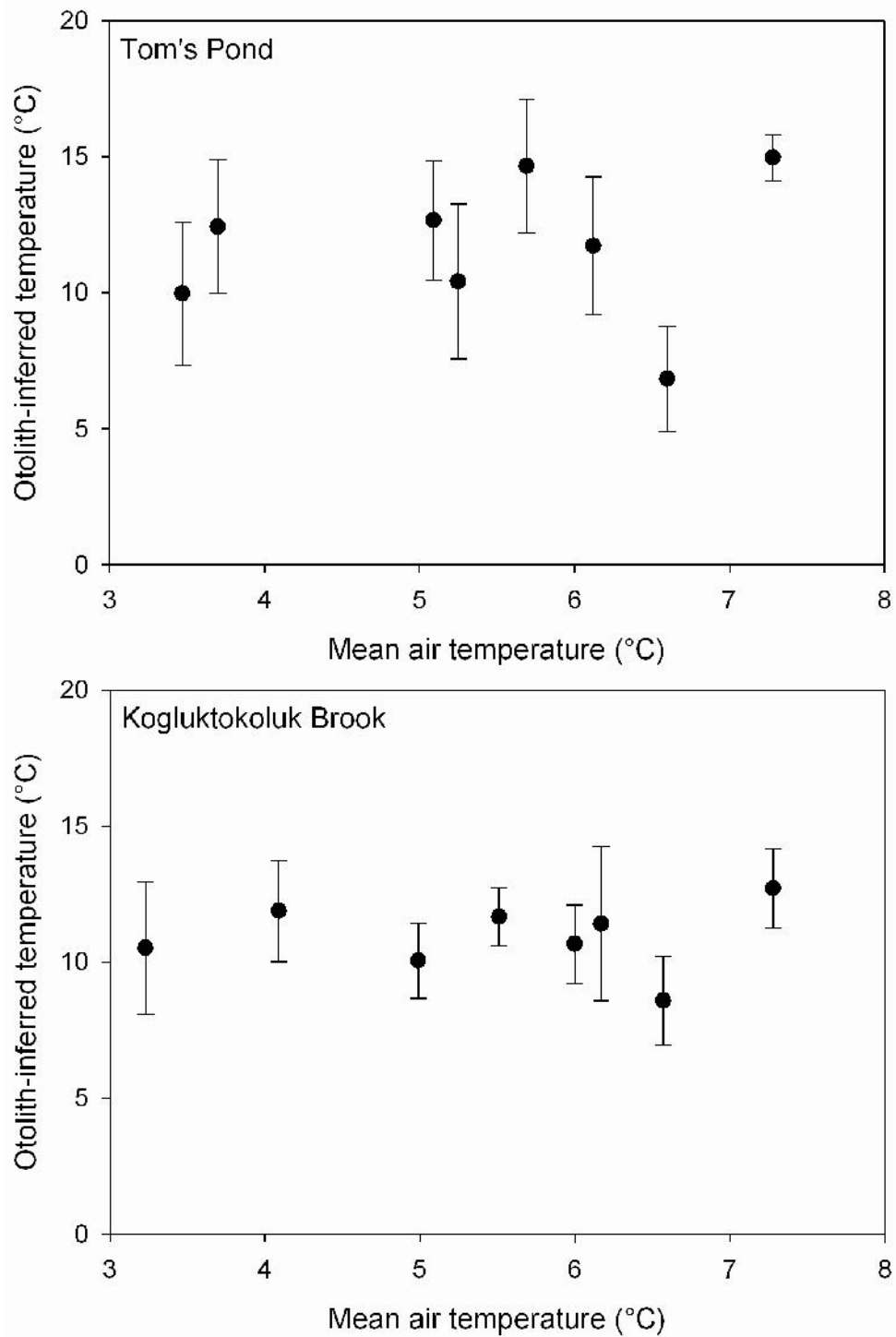


Figure 5.1. Mean otolith-inferred temperature vs. mean air temperature from Nain, Labrador. Mean air temperature data are averaged between April 1st and the date of capture.

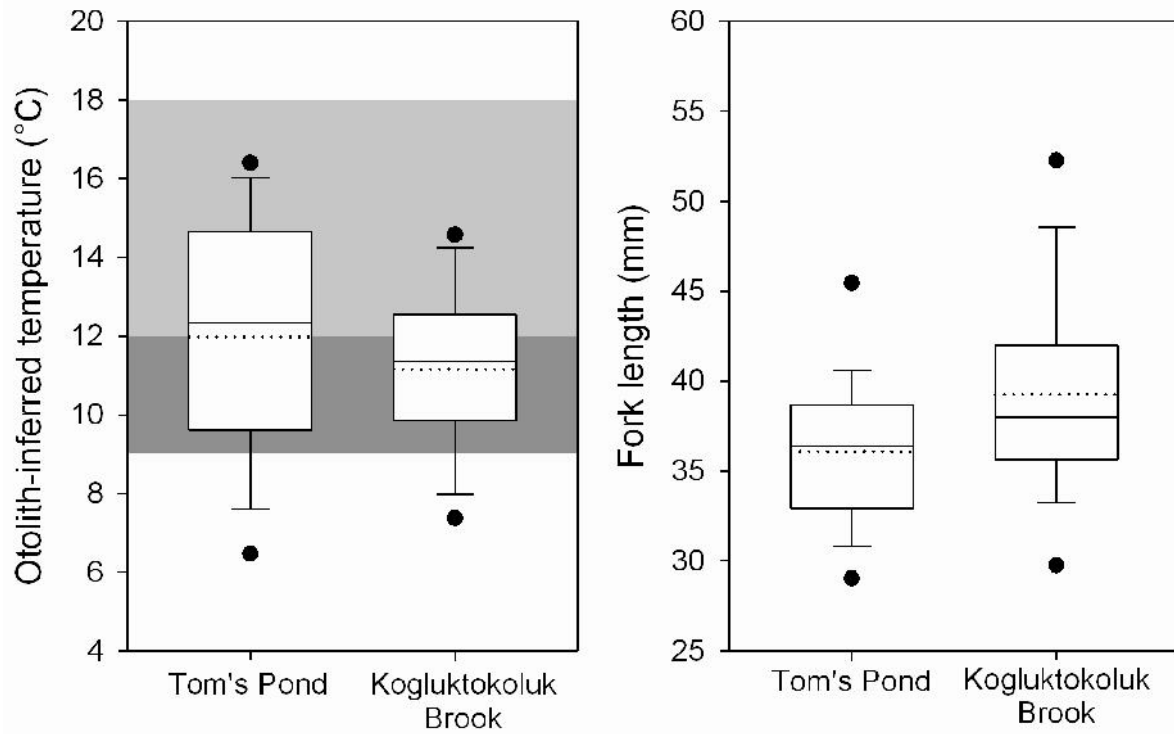


Figure 5.2. Box plots displaying otolith-inferred temperatures (left) and fork lengths (right) from YOY Arctic charr obtained from Tom's Pond and Kogluktokoluk Brook from all sampling events. Dots indicate 5th and 95th percentiles. Lines indicate median (solid) and mean (dotted) values. Shaded areas on left panel indicate laboratory defined optimal temperature for growth (light grey) and preferred temperature (dark grey) (Swift 1964, Jobling 1983, Jensen 1985, Larsson & Berglund 1998, Larsson 2005, Mortensen et al. 2007).

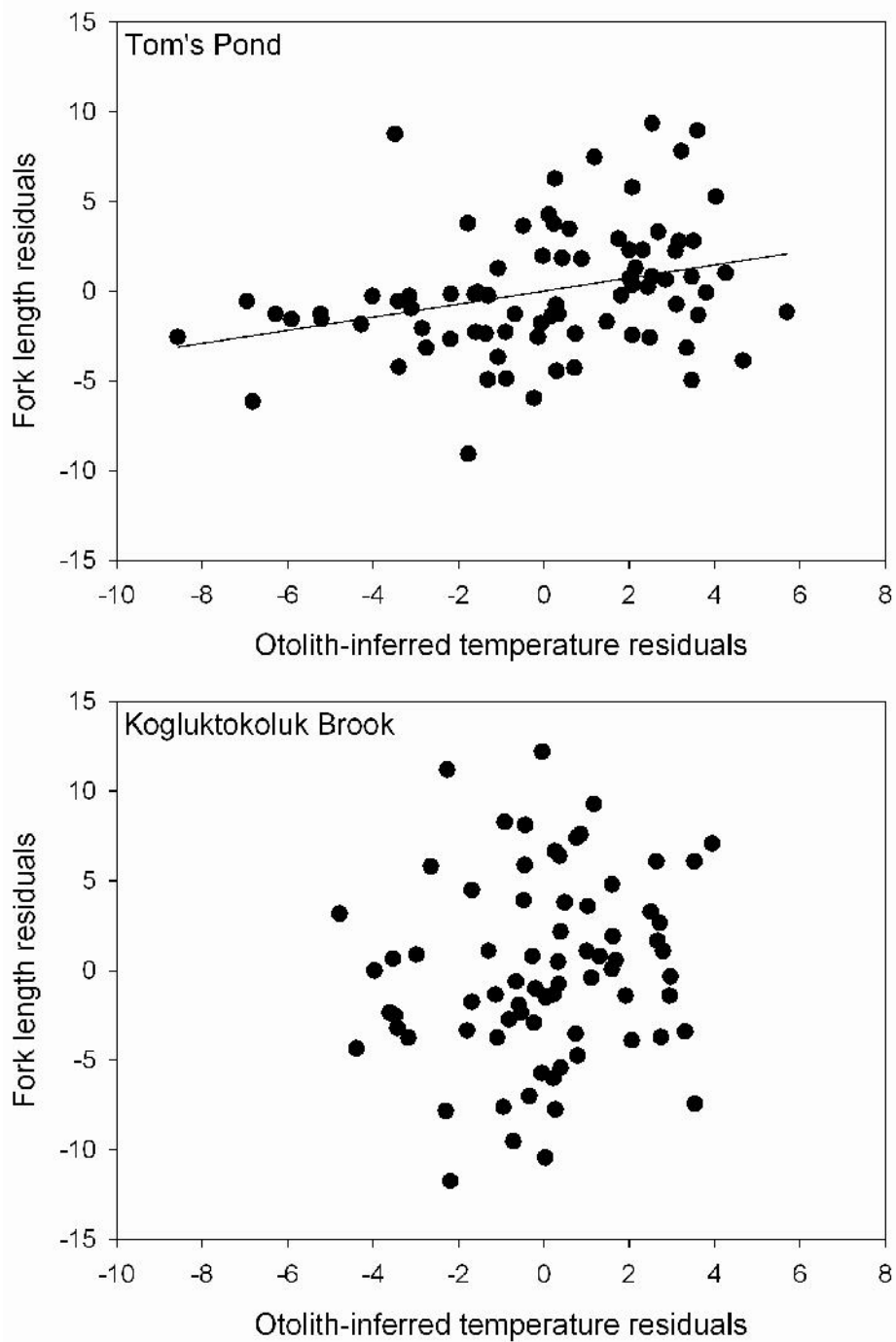


Figure 5.3. Partial regression plots depicting the relationship between fork length vs. otolith-inferred temperature once DYC was controlled, for Tom's Pond (upper panel) and Kogluktokoluk Brook (lower panel) YOY Arctic charr. Fork length residuals and otolith-inferred residuals are the residuals resulting from linear regression analyses with each variable regressed against DYC. Lines indicate significant linear relationships between fork length and otolith-inferred temperature, once DYC was controlled for, when present.

Chapter 6: General Conclusions

Synopsis

The study of early life-history stages of fish is essential to understanding the ecology of a species owing to its effects on subsequent population dynamics (Power 2007). Further, investigations of early life-history stages are particularly relevant in view of climate change owing to the increased sensitivity of juveniles to environmental fluctuations (Rijnsdorp et al. 2009, Pankhurst & Munday 2011). Finally, information on early life-history stages is often a key missing link in fisheries research (de Lafontaine et al. 1992), with implications for restricting the predictive power of fisheries models. Accordingly, the work compiled in this thesis investigated juvenile Arctic charr ecology, particularly focusing on young-of-the-year (YOY) from Canadian Arctic charr populations. The thesis comprises four studies which aimed to address different aspects of juvenile ecology over a number of spatial scales.

Juvenile Arctic charr were found to prefer stream environments within the Lake Hazen watershed, with a particular preference for warmer streams fed by upland ponds (Chapter 2). Since feeding did not differ significantly between stream and lake shore environments, it was believed that stream habitats were preferred by juvenile Arctic charr because they provided temperatures closer to optimal temperatures for growth and were more structurally complex, possibly providing increased cover from predators. Within the Lake Hazen watershed, occupation of fluvial habitats is limited to the open water season when the streams inhabited by juvenile Arctic charr are accessible. Migrations to streams were found to be restricted by physical barriers, such as water velocity, distance from the lake shore, water levels, glacial melt and sediment load, and lake ice dynamics. For YOY in particular, water velocity was thought to be the main deterrent from stream use. The relatively few YOY that were found using stream environments were found in slower water in ephemeral pools or along stream banks, and were thought to be largely restricted to those marginal habitats by size-based limitations on swimming ability, and/or intercohort competition.

Chapter 3 demonstrated a method to identify and quantify offspring of two freshwater Arctic charr morphotypes within Lake Hazen. The small non-piscivorous morphotype and the large piscivorous morphotype were found to contribute approximately equally to the YOY population of Lake Hazen. Offspring of the two morphotypes, however, were found to be differentially distributed among sampled nursery sites. Since offspring distribution is generally determined by redd distribution (Einum & Nislow 2005, Einum et al. 2008, Hudy et al. 2010), differences in the distribution of YOY by maternal source likely reflects differences in the spatial distribution of morphotypes at spawning. Despite differential distribution among offspring, YOY from both morphotypes were found to feed similarly and did not differ significantly in fork length.

Growth rates and otolith-inferred metabolic rates of YOY Arctic charr sampled from populations over a 27° latitudinal range in eastern and central Canada demonstrated patterns consistent with countergradient variation (Chapter 4). Higher otolith-inferred metabolic rates found in northern populations may reflect increased consumption, higher activity levels and/or higher intrinsic standard metabolic rates (SMR). The higher growth rates observed in the north likely reflect a surplus of seasonal energy available to northern YOY as a consequence of continuous daylight and warm temperatures (ACIA 2005). However, it is unlikely that differences in food alone resulted in the observed countergradient in growth rate for Arctic charr (Chavarie et al. 2010). Variations in food conversion efficiency and predation pressures have been suggested as potential drivers in CGV patterns (e.g. Present & Conover 1992, Lindgren & Laurila 2005, Suzuki et al. 2010). As well, intrinsic variability in SMR may play a role in observed differences in growth and has been suggested to be potentially advantageous in highly seasonal environments found at high latitudes (Burton et al. 2011). The phenotypic variation in growth and field metabolic rates observed in YOY Arctic charr across eastern and central Canada demonstrates the significant adaptability of the species to different thermal regimes with different growing season lengths. The marked phenotypic variation exhibited by the species suggests that phenotypic plasticity is likely to play a key role in defining Arctic charr responses to climate change.

A comparison between fork length at capture and otolith-inferred temperatures from YOY Arctic charr from two proximal fluvial and lacustrine sites in Labrador, Canada suggested that behavioural thermoregulation may be occurring in YOY from both populations (Chapter 5). Temperatures preferentially used by lacustrine YOY were broader, ranging from experimentally defined preferred temperatures to the optimal temperatures for growth, whereas, fluvial YOY Arctic charr largely occupied temperatures around the preferred temperature range (Swift 1964, Peterson et al. 1979, Jobling 1983, Jensen 1985, Larsson & Berglund 1998, Larsson 2005, Larsson & Berglund 2005, Mortensen et al. 2007). The difference suggests that fluvial YOY may be more food limited within nearshore habitats relative to lacustrine YOY and are unable to obtain sufficient ration to support increased metabolic demands at optimal temperatures for growth. Lacustrine YOY also demonstrated increased use of cooler temperatures, likely reflecting offshore/profundal habitat occupancy by some lacustrine YOY. Fluvial YOY, on the other hand, exhibited limited use of cooler habitat likely owing to water velocity barriers and intercohort competition (Chapter 1). Despite the broad range of experienced temperatures by lacustrine YOY, fluvial YOY demonstrated a wider fork length range. A wider fork length range combined with a weaker relationship between fork length and otolith-inferred temperature among fluvial Arctic charr may be explained by an increase in variability in resource acquisition stemming from the role of dominance and territoriality in foraging in streams.

Synthesis

Phenotypic plasticity is thought to be more important than genetic adaptation for short-term responses to climate change (Williams et al. 2008). Through examining various aspects of juvenile Arctic charr ecology, this thesis illustrates phenotypic plasticity exhibited by Canadian juvenile Arctic charr over three different spatial scales: latitudinal, regional (between sites), and local (within a site). At a latitudinal scale, YOY Arctic charr expressed a notable amount of phenotypic plasticity (i.e. physiological), demonstrating a remarkable ability to utilize different thermal regimes (Chapter 4). The observed capacity for phenotypic plasticity is thought to lend itself well to coping with environmental fluctuations caused by climate change (Fuller et al. 2010, Fierst 2011). At a regional level, however, differences in demonstrated phenotypic plasticity (i.e. behavioural) between proximal fluvial and lacustrine sites indicated that habitat type is likely to impact the ability for juvenile Arctic charr to respond successfully to climate change (Chapter 5). Murdoch & Power (2013) demonstrated the effect of lake morphometry on the ability for juvenile Arctic charr to behaviourally thermoregulate, and in Chapter 5 a similar limitation on behavioural thermoregulation in stream YOY Arctic charr was observed. At a local scale, phenotypic plasticity (i.e. behavioural) was observed among juvenile Arctic charr from Lake Hazen, but was found to be influenced by several regulatory factors (e.g. stream accessibility, intercohort competition, etc.) (Chapter 2).

The study of Canadian juvenile Arctic charr using populations from different ends of the latitudinal range, and occupying different habitats types provided insight into various drivers currently affecting juvenile Arctic charr success in Canada. Each of the potential factors is discussed separately below:

1. Temperature

As suggested above by the pervasiveness of behavioural thermoregulation, water temperatures emerged as a factor of importance. At both the northern (Lake Hazen, Chapter 2) and southern (Tom's Pond and Kogluktokoluk Brook, Chapter 5) parts of the latitudinal range studied in this thesis, juvenile Arctic charr demonstrated a tendency to access or maintain position in habitat with temperatures close to preferred or optimal temperatures for growth (Swift 1964, Peterson et al. 1979, Jobling 1983, Jensen 1985, Larsson & Berglund 1998, Larsson 2005, Larsson & Berglund 2005, Mortensen et al. 2007). As environmental temperatures continue to rise, the ability to find favourable water temperatures will become even more vital to juvenile Arctic charr and is likely to affect the amount and location of usable habitat, particularly in southern populations.

2. Water Velocity

Access to favourable temperatures, however, may be confounded by water velocity, which is thought to have important implications for YOY Arctic charr owing to size-based swimming limitations (Beamish 1980). In Lake Hazen, water velocity acted as a barrier to stream access

(Chapter 2). Stream-dwelling YOY from Lake Hazen, as well as Kogluktokoluk Brook were largely restricted to nearshore habitat, presumably owing to a combination of water velocity and intercohort competition (Chapter 2, Chapter 5). Marginalization of stream-dwelling YOY salmonids has been noted previously (Bohlin 1977, Bremset & Berg 1999). Further, water velocity plays a role in stream foraging techniques (Tunney & Steingrímsson 2012) and is likely to affect resource partitioning in streams with subsequent impact on the variability in attained fork length among juveniles (Chapter 5).

3. Cover

In Lake Hazen, use of streams by lake-spawned juveniles was thought to provide the benefit of temperatures closer to thermal optima and increased cover as a result of increased structural and substrate complexity (Chapter 2). Cover has been noted to be of importance to juvenile salmonids (e.g. Cunjak & Power 1986, Adams et al. 1988, Holierhoek & Power 1995, Gibson & Erkinaro 2009), however, it is likely to be even more vital to high Arctic juveniles owing to constant daylight and an absence of riparian and submerged macrophytic vegetation. On the other hand, juvenile Arctic charr from populations from further south have been found to hide during the day and forage by night (Adams et al. 1988, Holierhoek & Power 1995). Within the nearshore habitat of Lake Hazen large numbers of juveniles were commonly found over gravel or small cobble substrate. However, where gravel or cobble substrate was not present, juvenile Arctic charr exhibited shoaling behaviour (personal observation), as has been previously noted (Moore 1975). Alternatively, individuals would remain still presumably as an attempt to avoid notice by predators (e.g. Holierhoek & Power 1995), although the tactic only seemed effective for the smallest YOY (personal observation). Where silt substrate was prevalent, some juvenile Arctic charr demonstrated fossorial behaviour (personal observation), which was previously demonstrated in northern Quebec (Simon 1995). Each of the tactics described above are likely efforts to avoid predation (Holierhoek & Power 1995).

4. Maternal influences

It is likely that maternal influences also play a role in the success of YOY Arctic charr. In Lake Hazen, where two morphotypes cohabit the lake, the identification of YOY Arctic charr as originating from either small-form or large-form maternal adults indicated unequal distribution of YOY among nursery habitat (Chapter 3). Given the limited dispersal of YOY from redds (Einum & Nislow 2005, Einum et al. 2008, Hudy et al. 2010), it is likely that the uneven distribution of YOY reflects a similar uneven distribution of spawning sites between morphotypes. Spawning locations may have consequences with respect to access to quality nursery sites. Indeed, relatively low numbers of juveniles were found using nearshore habitat and streams between Hazen Camp and

Muskox Creek, in the lee of John's island in Lake Hazen, an area that was not inhabited by offspring of the large-form morphotype.

5. Habitat type

The use of different habitat types may have consequences for juvenile Arctic charr success, as well as their capacity for coping with climate change. Common to the intensive studies carried out at the two extremes of the latitudinal range covered in this thesis (Lake Hazen & Labrador), fluvial habitats and the juveniles that occupy them were identified as being the most at risk to climate change effects (Chapter 2, Chapter 5). In the Lake Hazen watershed, preferred streams tended to be those fed by upland ponds. Those small ponds, however, are thought to be at considerable risk of desiccation as a result of climate change (Prowse et al. 2006), and several dry stream beds along the south east shore of Lake Hazen were evidence of reduced flow for streams not supported by glaciers (Chapter 2). For glacier-fed streams, increased glacial melt was suggested to be associated with increased velocity and accompanying sediment load, to the likely detriment of juvenile inhabitants of those streams. Within the streams, the small side channels that were preferred by the smaller juveniles are at particular risk for drought (Milner et al. 2009). In Kogluktokoluk Brook, the limited use of cooler temperatures attributed to a water velocity barrier and intercohort competition suggests that as environmental temperatures rise, the ability of fluvial YOY Arctic charr to access habitat with favourable temperatures will decline (Chapter 5).

6. Ration

Ration is known to play a vital role in organism growth rate and survival (e.g. Elliott 1975, Storebakken & Austreng 1987). The diet analysis of Lake Hazen juveniles, as well as findings of increased growth rates in high latitude YOY, however, both point to sufficient ration being available for YOY in the north (Chapter 2, Chapter 4). Sufficient ration for northern juvenile Arctic charr is not surprising given that sampling occurred coincident with the pulse of productivity which occurs in the high Arctic as a consequence of constant daylight and warm temperatures (ACIA 2005). In the south, there was no indication that ration was limited for Tom's Pond YOY as they were able to use optimal temperatures for growth, which requires more energy to offset increasing metabolic costs. Only among Kogluktokoluk Brook YOY was ration suggested to be a limiting factor (Chapter 5). As temperatures rise, the ability for YOY Arctic charr to acquire sufficient energy to offset metabolic costs is expected to become increasingly difficult, particularly in the south.

Based on findings from the studies in this thesis, it is concluded that overall, juvenile Arctic charr from Canadian populations display strong potential to cope with predicted climatic changes in the near term. However, the population-specific ability to adapt will vary with several factors, primary among

these being the ability to continue to access favourable habitats. As the amount and accessibility of favourable habitat may vary with latitude, habitat type and competitive pressures, the resulting adaptive capacity of juveniles is likewise expected to vary. Accordingly, continuing to build a strong understanding of the factors currently affecting growth and survival will improve our ability to predict responses to climate change.

Future Directions

The studies on juvenile Arctic charr ecology in eastern and central Canada included in this thesis have highlighted several areas of research that require further investigation.

- Intrinsic differences in metabolic rates have been well established among salmonid individuals (Burton et al. 2011), and may play a role in latitudinal variations in growth and field metabolic rate observed in this thesis (Chapter 4). However, the inability to quantify the various components of field metabolic rate to isolate potential patterns in SMR limited the ability to directly test the hypothesis of metabolic cold adaptation. Development of laboratory based models that estimate the proportion of various components of field metabolic rate based on known temperature, ration and activity levels may help to elucidate this ratio and increase our abilities to interpret otolith-inferred metabolic rates from natural environments.
- Although phenotypic plasticity is considered more important with respect to short-term responses to climate change than genetic adaptation, phenotypic variability may have an underlying genetic component. Understanding the relative roles of phenotypic plasticity and genetic variability in the observed phenotypic variability in YOY Arctic charr across the latitudinal gradient will be critical to more accurately predicting the responses of Arctic charr to climate change.
- The studies compiled in this thesis focused on the nearshore habitat use of juveniles. It is believed that in the absence of interspecific predation risk, juvenile Arctic charr prefer the nearshore littoral zone where productivity tends to be high (Klemetsen et al. 1992, Simon 1995, Power 2002, Power et al. 2008). However, recent otolith thermometry studies on juvenile Arctic charr have noted more profundal habitat use by juveniles than previously expected (Godiksen et al. 2011, Godiksen et al. 2012, Murdoch & Power 2013) and with increasing environmental temperatures use of profundal habitat may become more common. Elucidating the relative roles of factors which may effect the current determination of profundal vs. littoral occupation by juvenile Arctic charr within and among populations (e.g. interspecific competition, predation risk, temperature, juvenile density and prey availability) may further our understanding of how juvenile Arctic charr will respond to direct and indirect consequences of climate change.

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