Changes in the biological characteristics of Canadian Arctic charr (*Salvelinus alpinus*) populations in response to climate-induced environmental variation

By

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Authors'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.

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Abstract

The thesis includes two studies of Arctic charr, *Salvelinus alpinus*, responses to climate variation. In the first chapter, site-specific data from a fishery on the Hornaday River, Northwest Territories (NWT), are used to make inferences about the environmental drivers of observed variation in the mean biological characteristics of the catch. Mean length and weight characteristics of subsistence-fished Arctic charr available from 15 years of monitoring on the Hornaday River, were significantly influenced by among-year differences in local summer temperature and/or precipitation patterns. Environmental influences on mean length were age-specific, with temperature being the most important influence on younger (age-5) fish and precipitation being the most important influence on older (age-8) fish. Mean weight was positively influenced by precipitation only. Significant models of length-temperature relationships further indicated that larger mean sizes occurred in years when average summer air temperatures ranged from 6.7-7.1°C. The effects of precipitation on nutrient exports to the nearshore marine area appear to trigger many of the observed correlations. Overall, results suggest that the large-scale environmental changes predicted by climate change scenarios will hold significant implications for Arctic charr from the Hornaday River, with population-specific effects likely to be exhibited in other northern Arctic charr populations.

The second chapter uses archival biological data on 67 anadromous and lacustrine charr populations from eastern North America to assess variation within and among populations of Arctic charr as a function of latitude. Eastern North America was defined to include areas east of 80° W, including: Maine, the Canadian Maritime Provinces, insular Newfoundland, Labrador, Québec, and the eastern Arctic Islands of Baffin, Devon

and Ellesmere. Obtained population data sets contained individual observations on age, length, weight, sex and fecundity of Arctic charr from as many age-classes as possible and included sufficient life-history information to permit grouping populations to life-history types: dwarf lacustrine, normal lacustrine and anadromous. Data were used to determine the significance of latitudinal clines in the biological responses as explanations of variation in age-specific biological characteristics (length and growth rate) among populations and life-history-types. The presence of a gradient in temperature and growing season length across latitudes was significantly related to a latitudinal compensation in the growth rate of all age-classes of normal and dwarf lacustrine Arctic charr populations. No decrease in dwarf length-at-age along the gradient was noted, whereas normal lacustrine length-at-age in the younger ages (age-4 to age-6) declined along the gradient. Results provide evidence of the applicability of the countergradient hypothesis as an explanation of among population differences in length-at-age for normal and dwarf lacustrine Arctic charr. Only weak evidence of the applicability of the countergradient hypothesis to anadromous Arctic charr populations was found. Although a decrease in length-at-age for all age-classes was observed along the gradient, only four age-classes (age-10 to age-13) showed a significant increase in growth rate with an increase in latitude. The similarity of the marine thermal environment across the latitudinal gradient is argued to account for the differential response of anadromous Arctic charr in comparison to lacustrine populations.

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Chapter 1 General Introduction

Concerns about global warming have grown in recent years, especially in northern areas where climate change now looms as an important and real issue. The climate in the Arctic has experienced rapid and drastic shifts that have produced notable changes in the physical phenologies of the seasons. Together with the Antarctic, the Arctic has experienced the greatest documented regional warming in recent decades and projections suggest a continuation of the strong warming trend (ACIA, 2004). Over the next century additional increases of 3.7°C are projected for continental areas of North America north of 60° and increases of up to 5°C are predicted for the Canadian Arctic Archipelago (ACIA, 2004). Accordingly, northern regions are predicted to experience the earliest and most extreme impacts of the global climate warming trend.

Climate change has been identified as an important source of aquatic disturbance on a global scale and cold water ecosystems are particularly at risk (McCarthy *et al.*, 2001). Climate-drivers and environmental factors expected to have the maximum direct effects on aquatic ecosystems include: temperature change, sea-level rise, availability of water from precipitation and/or run-off, wind patterns and storm frequency (Kennedy *et al.*, 2002). A general synthesis of the potential impacts of climate change on Arctic estuarine ecosystems, including bottom-up and top-down effects is given in the Arctic Climate Impact Assessment (2004). In particular, an increase in open water areas combined with more mixing caused by wind is expected to result in greater nutrient availability in many water bodies. Additionally, an increase in open water areas and more seasonal light penetration may lead to higher primary production and increases in UV radiation exposure. Along coastal regions, storms and increased open water areas are

likely to augment coastal erosion, sediment loading, nutrient inputs, and mixing, leading to probable increases in primary production, especially late in the season (Darnaude *et al.*, 2004). Increases in basin rainfall may further expedite the export of carbon to the nearshore areas. The resulting increases in primary production in nearshore areas may favour Arctic estuarine organisms over longer seasonal periods. However, the consequences of climate change on Arctic estuarine ecosystems may also be negative. Possible decreases in ice cover may drive declines in ice-associated algal production and negatively impact pelagic and benthic communities, with potential negative cascade effects on higher trophic level consumers (Carmack & MacDonald, 2002).

Similar impacts are predicted for key freshwater habitats. Rouse *et al.* (1997) describes many of the more important impacts and changes. Briefly, predicted increases in evaporation during the ice-free period and a shift in the vegetation from non-transpiring lichens and mosses to vascular plants are likely to result in a negative annual water balance. Changes in water balance may modify river flows, reduce migratory channel availability and alter anadromous fish run times. Increases in temperature will reduce the water storage potential of peatland and permafrost thawing will increase terrain slumping, leading to modifications in drainage patterns, sediment transport and deposition via runoff. The potential climate changes as described above are likely to have major consequences for Arctic aquatic biota. First, aquatic biota will experience direct physiological effects of temperature increases via changes in metabolism and growth (Reist *et al.*, 2006). Second order, indirect effects (e.g., primary productivity driven impacts on ration and growth) are expected to follow and should have repercussions for population dynamics (e.g., increased competition between species, southern species'

range extension) (Minns & Moore, 1992; Reist *et al*., 2006). The migratory behaviour of some species may integrate impacts across several ecosystems resulting in multi-scale effects on both species and communities (ACIA, 2004).

One of the aquatic biota of concern in Arctic regions is Arctic charr, *Salvelinus alpinus*. Known to be sensitive to minor environmental changes (Langeland, 1995), Arctic charr will likely be one of the first northern species to react and be threatened by climate change (Lehtonen, 1998). As a result of its ubiquity in the Arctic, Arctic charr has an important economic value in the north, and forms the basis of many important subsistence and commercial fisheries. In addition, Arctic charr is a key species in northern aquatic ecosystems and has important ecological value because the Arctic food chains are rather simple, usually ending in Arctic charr as the top predator (Rouse *et al*., 1997; Hammar, 1999). Although there has been increased interest shown in the fate of Arctic ecosystems in the face of climate change, Arctic charr remain as a species about which little is known about how population characteristics (mean length, weight, etc.) covary with the environment (ACIA, 2004).

1.1 Thesis Overview

In the absence of existing information on the probable biological effects of climate change on key Arctic species, such as Arctic charr, possible climate change effects need to be evaluated and quantified (ACIA, 2004). Knowledge of existing spatial and temporal patterns of Arctic charr biological characteristic variation provide one possible means of predicting future impacts. Accordingly, here research focussed on documenting past patterns of spatial and temporal variation in Arctic charr biological

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characteristics in relation to the environment was carried out. Specifically, the research focused on the study of temporal variation in the biological characteristics of a single Arctic charr population from the Hornaday River and on the spatial variation among populations of Arctic charr along a latitudinal gradient in eastern North America. The specific aims of the research were:

I) To understand the pattern of correlation observed between key environmental factors (e.g., temperature, precipitation, etc.) and the biological characteristics (e.g., length, weight) of Hornaday River (69˚21'N, 123˚42'W) Arctic charr;

II) To understand possible connections between observed latitudinal zoogeographic variation in Arctic charr population characteristics (e.g., size-at-age) among populations of eastern North America Arctic charr along a latitudinal gradient from Maine (USA) to Ellesmere Island (Nunavut).

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Chapter 2 Influences of environmental variation on anadromous Arctic charr from the Hornaday River, NWT

2.1 Introduction

The Arctic charr, *Salvelinus alpinus* (L.), is a Holarctic species common in most of the high Arctic (Hammar, 1985). The species has a circumpolar distribution with a latitudinal range in North America extending from Ellesmere Island (84°N) in the north to northern New England (43°N) in the south. Throughout much of the range, but particularly in northern Canada, the species is of economic importance and forms the basis of community subsistence and/or commercial fisheries. Many of these fisheries are routinely monitored by government agencies in conjunction with local fishers and long-term datasets on the biological characteristics of the catch (mean age, length and weight) useful for management purposes have been compiled. In the face of increasing concerns about the impacts of northern development and/or climate change (e.g., ACIA, 2004), these monitoring databases now provide the only biological references against which the implications of large scale anthropogenic impacts on Arctic charr may be gauged. Among the more important of the possible impacts is climate change, which has the potential to significantly alter northern aquatic ecosystems (ACIA, 2004).

Variations in life-history tactics for many fish are related across spatial gradients to environmental conditions, including climate (Mann *et al.*, 1984), with differential responses to overall environmental conditions being seen as a strategy to perpetuate animal genomes (Venne & Magnan, 1989). Arctic charr, in particular, are among the species known to be strongly influenced by climate variation (Power *et al.*, 2000; Power *et al.*, 2005) and have flexible life-history strategies adapted to local environmental

conditions (Klemetsen *et al.*, 2003). Thus, much of the observed biological variation (e.g., size) within and among Arctic charr populations has been explained by direct environmental influences, phenotypic plasticity and/or genetic adaptations to local environments (Adams & Huntingford, 2002; Klemetsen *et al.*, 2003).

Population trait correlations with environmental conditions (e.g., growth rate, Hestagen *et al.*, 2004), suggest variations in annual weather patterns associated with climate change may hold significant consequences for Arctic charr populations throughout the north. Climate change has been identified as an important source of aquatic disturbance on a global scale (McCarthy *et al.*, 2001) with Arctic ecosystems being among those seen as particularly at risk (ACIA, 2004). Temperature change, sea-level rise, local hydrology, wind, storm pattern and frequency, length of the ice-free season and annual water balance are among the environmental conditions likely to be significantly affected by climate change (Kennedy *et al.*, 2002) and will have impacts, both direct and indirect, on all stream, lake, estuarine and marine ecosystems used by Arctic charr. Climate-driven cumulative effects resulting from changes to adjacent terrestrial ecosystems and cascade effects resulting from changes at lower trophic levels are also likely to significantly affect Arctic charr (ACIA, 2004).

The nature and magnitude of climate-related impacts are not directly quantifiable for most Arctic charr populations, particularly those that form the basis of many community food fisheries (ACIA, 2004). By combining existing monitoring data with environmental information (e.g., temperature, precipitation), however, it is possible to describe past relationships between climate and Arctic charr biological responses to climate-driven environmental variation, and to use the relationships that exist as a proxy

for predicting possible climate change effects on Arctic charr (e.g., Power & Power, 1994; Power *et al*., 2000). Accordingly, in this study, available monitoring data (15 years) for Arctic charr captured near the mouth of the Hornaday River were used to investigate linkages between measured population characteristics (e.g., age-specific length and weight) and climate-driven environmental variation and to comment on possible climate change related impacts on Arctic charr populations in the western Canadian Arctic.

2.2 Material and methods

Study area

The data for this study were collected from the Hornaday River (69˚21'N, 123˚42'W) which empties into Darnley Bay in the Amusden Gulf region of the Arctic Ocean. The river varies in width (40-100m) and depth (≤ 0.5-3m) along its 260km length. Approximately 45km upstream from the sea, a 20m waterfall, La Roncière Falls, forms an impassable barrier to fish migration. The lower reaches of the river are the focus of an annual subsistence fishery for the nearby community of Paulatuk (69° 21' N, 124°4'W).

Biological data

Fisheries and Oceans Canada, in conjunction with local fishers, monitored the catch on the Hornaday in 1979, 1981 and 1990-2003, and collected biological data (length (mm), weight (g), sex, and age) for a sub-sample of all fish captured. In 1979 and 1981, commercial harvesting was allowed, although catches did not exceed 6795kg. In

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1987, the fishery was closed to all but subsistence use, with annual catches in the 1990-2003 period varying between 1492 and 3850kg.

Variation in net size and, in some instances capture technique, required that all available data be filtered to produce a standardized sample. Therefore, analysis was restricted to the catch obtained from common gear type and size, 4 to 5.5 inch (stretched measure) multi-mesh gillnets. Data were further filtered to restrict analysis to specimens captured in a common period (mid-July to early September) coincident with standardized Fisheries and Oceans Canada monitoring practices for other Arctic rivers (e.g., Cambridge Bay system). Finally, fish younger than five years and older than eight years were excluded from the analysis due to insufficient annual sample sizes (<10/year), with an annual sample size of 10 being chosen to ensure the statistical sufficiency of estimated means and selected statistical testing procedures (e.g., Zar, 1999). For age-five samples, the years 1992-1994, 1998 and 2002-2003 were thus excluded as a result of the above sample size criterion.

Environmental data

Meteorological data for the years 1970 to 2003 were obtained from diverse sources for latitudinal and longitudinal co-ordinates as close to the Hornaday River mouth as possible. Monthly sea surface temperatures (°C) were obtained from the Hadley Centre for Climate Prediction (U.K., Met Office, http://hadobs.metoffice.com,15 July 2005). Data represent one degree latitude and longitude grid interpolations derived using a two-stage estimation procedure that combines general circulation model predictions with actual gridded observations to restore local climate detail (Rayner *et al.*,

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2003). The monthly air temperature (°C) and monthly precipitation (mm) from 1970 to

2000 were obtained from the Center for Climatic Research, Department of Geography,

University of Delaware (http://climate.geog.udel.edu/~climate/index.shtml, 18 July

2005). Data represent 0.5 degree latitude and longitude interpolations from a general

circulation model simulation of historical meteorological station data. Precipitation and

temperature data for 2001-2003 were obtained from the station records for the Paulatuk

area (69°21'N, 124°4'W) from Environment Canada. The monthly ice cover (km^2)

records were obtained from the National Snow and Ice Center (USA,

http://nsidc.org/data/smmr_ssmi_ancillary/area_extent.html#nsidc, 20 July 2005) and are

available only from 1978 to 2003. Ice data cover the Arctic Ocean and include the total

ice-covered area and sea-ice extent in the Arctic Ocean basin. The Arctic oscillation

index (AOI) values were obtained from the Climate Prediction Center, a division of the

National Oceanic and Atmospheric Administration (NOAA). Values of AOI portray

teleconnection patterns in atmospheric circulation using monthly mean 1000-hPa height

anomalies poleward of 20° latitude for the Northern Hemisphere

(http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/history/method.s

html, 21 July 2005).

To represent the potential opportunity for growth, an index of cumulative degree-

days referenced to critical growing temperatures for Arctic charr was constructed.

Degree-days were computed on a daily basis as the excess of mean daily air temperature

(°C) over a minimum bound of water temperature for growth (2.57°C) established from

a multiple population study (Larsson *et al.*, 2005) and summed over the growing season

(June to August) to estimate a cumulative total. When daily mean temperature was

<2.57°C, degree-days were set to zero. Specifically, cumulative degree-days were computed as (Larsson *et al.*, 2005):

$$\text{Cumulative degree-days} = \sum_{i=x}^{n} (\text{daily temperature} - 2.57°C) * M$$

Where n is equal to number of days for which cumulative degree-days were computed and M is an index variable set equal to one if mean daily temperature $\geq 2.57°C$, or zero otherwise.

Meteorological data were also used to compute seasonal averages (winter and summer) for each year and lags in seasonal averages for up to seven years. Winter was defined as the January to March period. Winter averages for precipitation, AOI, and ice cover were computed for use in statistical analysis. Summer was defined as the June to August period. Summer averages for sea surface temperature, air temperature, precipitation, AOI, summer degree-days, and ice cover were computed for use in statistical analysis.

All meteorological variable lags refer to the number of years between the date of fish capture and the period for which the relevant meteorological data were collected (Power *et al.*, 2000). Because the maximum fish age included in the analysis was eight, the maximum possible lag in environmental influences relevant for fish length or weight was seven. Consideration of environmental lags was included to allow for the possible affect of environmental influences on early juvenile lifestages (1+).

Statistical analysis

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All biological and meteorological data were examined for temporal trends by regressing variable data against an index of time. Where significant trends existed, the residuals from the trend regression were used to form a detrended data series for further statistical analysis (e.g., Abraham & Ledolter, 1983). To avoid possible spurious correlation between biological and environmental variables, biological rationalizations were used to select an *a priori* set of environmental variables for inclusion in candidate regression models relating variations in Arctic charr biological data to environmental influences. Biological and environmental data were then used to estimate regression models of the form (Power *et al.*, 2000):

$$D_t = a_0 + a_1 X_{1t} + a_2 X_{2t} + ... + a_k X_{kt} + e_t$$

Where D_t and $X_{1t}, X_{2t}, ..., X_{kt}$, respectively, were the biological response of Arctic charr (length or weight) and the associated explanatory environmental variable (e.g., temperature, precipitation) values at time t; $a_0, a_1...a_k$ were the estimated regression parameters; and, e_t was the normally and independently distributed error term. Forward selection step-wise regression was employed to determine which of the *a priori* environmental variables best explained biological data (Draper & Smith, 1981; Dunn & Clark, 1987). Coefficient significance was judged at $\alpha=0.05$ level using Student's t-test (two tailed) and standardized regression coefficients were used to rank selected independent variables in order of explanatory importance in the regression (e.g., Cox, 1987). An $\alpha=0.05$ threshold was also used to define the variable F-to-enter and F-to-exit values used in the step-wise regression technique (Draper & Smith, 1981). Sensitivity tests on variable selection were performed by varying the F-to-enter and exit criteria in the step-wise regression procedure (Draper & Smith, 1981).

Age-specific models of the relationship between length and temperature were estimated from mean length-at-age and summer air temperature data to determine whether significant relationships existed. A non-linear model of the form:

$$\text{Mean length-at-age (cm)} = b_0 + b_1 T + b_2 T^2$$

was estimated, where T= mean summer air temperature (°C) and b_0, b_1, and b_2 are the estimated model coefficients. The model has a single optimum defined by its estimated coefficients at $T = b_1/2b_2$ (Ratkowsky, 1990) that can be used to infer optimum temperatures from field data (e.g., Magnuson *et al.*, 1979). Age-specific optimum temperature values were then tested for significant differences using a t-statistic based test. All pairwise comparison significance levels were Bonferroni adjusted.

2.3 Results

No significant temporal trends (all regression *P*-values >0.05) were found for any of the examined environmental variable datasets (Fig. 2.1). Significant temporal trends (Table 2.1) were found in age-specific annual mean lengths and weights (all regression *P*-values <0.05), thus all biological data were detrended for subsequent regression analyses (Fig. 2.2 and 2.3).

After data filtering (see methods), sufficient data existed to model variability in Arctic charr biological characteristics (length and weight) at ages 5 through 8. Significant correlations were found only for cotemporaneous biological and environmental data. No significant associations were found for biological and lagged (1 through 7 years)

environmental data (all regression *P*-values >0.05).

At age-5 detrended mean length (cm) data were modelled only as a positive function of mean summer sea-surface temperature (°C) (Table 2.2). At age-6 and age-7, fluctuations in mean length covaried positively with July-August precipitation and negatively with cumulative summer degree-days. At age-8, detrended mean lengths correlated positively only with total August precipitation. Estimated models explained between 54 (age-5) and 79 (age-8) percent of the observed variation in detrended mean lengths. Standardized regression coefficients showed approximately equal influence of temperature and precipitation variables on year-to-year fluctuations in age-6 mean lengths and greater influence of precipitation on year-to-year fluctuations in age-7 mean lengths. Fluctuations in all age-specific detrended mean weight (g) data (ages 5 to 8) were modelled as a positive function of August precipitation (cm) (Table 2.3), with estimated models explaining between 37 (age-7) and 59 (age-5) percent of the observed variation in the detrended mean weight data.

Regression diagnostic tests (homogeneity of variance, normality, autocorrelation) confirmed the statistical adequacy of all estimated trend and detrended mean length and weight models (Tables 2.1, 2.2, 2.3) at the $\forall$=0.05 level of significance. Sensitivity tests performed on the detrended mean length and weight models by varying the *F*-to-enter and exit criteria for variable selection during step-wise regression did not add explanatory variables to the models and confirmed model robustness.

Statistically significant quadratic relationships relating length-at-age to mean summer air temperature were estimated for all considered age-classes (all slope coefficient p≤0.05). Model explanatory power declined with age from r^2=0.82 at age-5 to

0.37 at age-8. Estimated optimum temperatures (Fig. 2.4) varied between 6.7 and 7.1 ºC but did not differ significantly (all pairwise comparisons $P \geq 0.40$).

2.4 Discussion

Environmental influences on long-term phenological patterns in Arctic charr (Berg, 1995) and their biological characteristics (Power *et al.*, 2000) have been reported previously. The findings of this study generally concur with those of earlier studies in noting significant associations between stock mean length and weight characteristics and local environmental variation (e.g., temperature and precipitation). Differences in long-term rates of climate change in the eastern and western Canadian Arctic, particularly over recent years (ACIA, 2004), may account for observed differences in the responses of eastern and western Arctic charr stocks to local environmental variation. Whereas Arctic charr from the Nain stock complex were influenced by both past and concurrent environmental conditions (Power *et al.*, 2000), Arctic charr from the Hornaday River were influenced exclusively by concurrent conditions. These discrepancies suggest possible genetic or developmental differences in Hornaday Arctic charr.

Developmental rates (e.g., growth and maturation) in salmonids are known to be phenotypic and operate under environmental control (Thorpe, 1987; Elliott, 1994; Rikardsen and Elliott, 2000). Genetic variations, however, may also influence differences in physiological responses to environment. For example, mitochondrial DNA studies have partitioned Arctic charr in the Hornaday and Nain areas into different Arctic and Atlantic lineages (Brunner *et al.*, 2001). In addition, there are numerous additional examples in the literature to support the conclusion that Arctic charr have flexible life-

history patterns adapted closely to local conditions (Rikardsen and Elliott, 2000).

Age-specific differences in the importance of environmental influences on mean length were also found in this study, suggesting that the importance of increasing length varied by life-period. With the onset of maturation at age-7, the influence of temperature on length decreased, presumably as a result of the implications for fitness of diverting surplus energy to gonad formation (e.g., Wootton, 1990). In contrast, weight was influenced only by precipitation, implying no age-specific interactions between increases in body mass and the environment.

To avoid problems with possible spurious correlation, biological rationalizations were used here to select the *a priori* set of variables considered for inclusion in regression models. Selections were based on literature reported relationships between life-history traits (e.g., growth, age at first migration) and environmental factors such as air temperature, sea surface temperature, precipitation and ice cover demonstrated for Arctic charr and other salmonid species (Baker, 1983, Adkison *et al*., 1996, Elliott *et al*., 1998, Friedland *et al*., 2000, Power *et al*., 2000; Ojanguren *et al*., 2001, Cavalli *et al*., 2002, Svenning & Gullestad, 2002, Larsson & Berglund, 2005, Kristensen *et al*., 2006). Data-based inferences of the implications of climate for fish require long time series (Walters & Collie, 1988) with data collected on time scales appropriate for the organism under study (Power *et al*., 2000). Studies should also focus on an understanding of variation about long-term trends rather than the trend itself (Power *et al*., 2000). Because long-term trends reflecting exploitation (e.g., Dempson, 1995), or the influence of large-scale environmental forcing variables (e.g., Beamish, 1993), were not the aim of this study, the data were detrended to remove the possible confounding influences. Detrending ensured

that any trend patterns did not obscure the short-term effects of environmental variables most likely to be correlated with patterns of variation about the trend (Brown & Rothery, 1993; Abraham & Ledolter, 1983) and is consistent with other biologically based studies of environmental influences (e.g., Power, 1981; Bradford, 1999; Power *et al.*, 2000). Nevertheless, correlations between environmental variables and stock biological characteristics do not imply causation unless plausible explanations of observed associations can be offered and supported by independent study.

Length models

Temperature and precipitation affected Arctic charr mean length-at-age differentially for the studied age-classes, with temperature decreasing in importance as an explanation of year-to-year variation as fish matured. At age-8 (i.e., mean age at maturation), precipitation alone affected mean length-at-age. The importance of precipitation for Arctic charr mean length-at-age is derived from the importance of run-off for nearshore ecosystems. Physical oceanography is affected largely by run-off and nutrient-rich upwellings of deep oceanic waters (Tully & Dodimead 1957, Beamish, 1993). Increased rainfall will affect runoff to estuaries and increase nutrient concentrations (Meyer & Likens, 1979; Meyer & Tate, 1983, Allan, 1995) and redistribution, with consequences for local primary production (Dame & Gardner, 1993; Kennedy *et al.*, 2002; Torres *et al.*, 2003). As a result, terrestrial matter has been shown to contribute to Baltic planktonic foodwebs (Rolff & Elmgren, 2000) and high river discharge can have a strong positive effect on the production of coastal fisheries (Loneragan & Bunn, 1999). In the context of the Hornaday River system, permafrost

minimizes groundwater flows such that rain events have the potential to cause pulses of high water flows in the river and its tributaries (DFO, 1999). In the summer period, nearshore primary production could be limited by low freshwater flows to Darnley Bay such that increased rainfall would drive both increased freshwater discharge and maintain the nutrient levels within the bay important for primary production. As a result, Arctic charr would have access to higher quantities of food and greater amounts of energy available for tissue anabolism (Adkison *et al.*, 1996).

Below the age of maturation, temperature (mean sea surface temperature or total summer degree-days >2.57 °C) variably affected mean length-at-age. Among age-5 fish, increases in sea surface temperature positively influenced mean length-at-age, probably as a result of maintaining temperatures at, or close, to the laboratory determined optimal range for growth, 12-16 °C (Johnson, 1980; Baker, 1983), for longer periods of time. Growth, however, is a complex phenomenon dependent on both temperature and ration (e.g., Elliott, 1994). Without suitable net addition of nutrients, rises in temperature may reduce increases in length as a result of increased metabolic costs. Such negative effects on size were observed among age-6 and age-7 fish, where increases in summer degree-days were associated with reductions in mean length-at-age. The near zero correlation between summer precipitation and degree-day totals (r=-0.02) suggests that increased metabolic demands associated with increasing temperature (degree-days) were not associated with sufficient precipitation-driven increases in nutrient availability to meet the growth potential of higher temperatures.

Field-based relationships between growth and temperature for Arctic charr have been reported elsewhere. Power *et al.* (2000) noted the importance of temperature for

determining mean size-at-catch in the Nain mixed-stock fishery. Hesthagen *et al*. (2004) demonstrated the strength of temperature-growth relationships can vary as a function of age. Results suggest age-specific physiological demands will induce diverse age-specific reactions to common environmental stimuli as was seen here, with the onset of maturation holding significant implications for responses to environmental variation. Among Atlantic salmon, the majority of feeding-derived energy the year before maturation is allocated to lipid storage, rather than protein elaboration (Thorpe, 1987). Rikardsen and Elliott (2000) have similarly argued that Arctic charr maturation is associated with higher lipid allocation tendencies. These results would suggest a pattern of decreasing age-related importance of temperature as a determinant of size and increasing age-related importance of precipitation-driven nutrient availability sufficient to fuel growth and maturation. Such a pattern of age-related changes in the importance of environmental variables would also agree with the marked change observed in the effect of environmental variation at the mean onset of maturation (i.e., age-8) in the Hornaday Arctic charr.

Computed average temperatures for optimal mean sizes at all ages yielded values considerably below the often quoted 12-16 °C range (e.g., Johnson, 1980). Under natural conditions, where feeding is restricted, the best growth rates will be observed at temperatures lower than those typically reported from laboratory experiments (Elliott, 1994; Jobling, 1994). For example in detailed experiments with brown trout (*Salmo trutta*), Elliott (1994) demonstrated significant reductions in both the temperature range over which growth occurs and the optimum temperature for maximum growth associated with ration reductions, with the optimum temperature for growth for a 50g brown trout

being reduced from 13 °C at maximum ration to 5 °C at 500 cal d^{-1}. Values computed

here on the basis of field observations from the Hornaday River system, therefore, yield

plausible values within the range of reduced optimal growth temperatures observed for

other salmonid species under the assumption of ration restrictions.

Coupled with the negative relationship between temperature and growth found in

reported multiple regression models, the optimal temperature-size models suggest a

plausible mechanism for the reductions in size associated with warmer thermal regimes.

Past the optimum, increases in temperature will invariably be associated with reductions

in size as a result of increased metabolic demands. Ration-restricted growth optima

predict potentially serious effects associated with climate-induced increases in average

nearshore temperatures, unless such changes are accompanied by sufficient increases in

available energy.

Weight models

Age-specific mean weight models were driven exclusively by August

precipitation. Increased precipitation exports more nutrients to the nearshore marine

system and drives primary production. Precipitation-driven changes in the flow regimes

of freshwater input from rivers may have positive or negative consequences for nearshore

marine residents depending on when the hydrological fluxes occur in the context of

species life-history events (Jager *et al*., 1997; Clark *et al*., 2001; O'Neal, 2002). Changes

in tributary river hydrology will induce variability within the physical environment with

consequences for the availability, quality, size and spatial distribution of prey items for

fish (Loneragan & Bunn, 1999; ACIA, 2004). Variations in prey resources will ultimately

be reflected in coastal fisheries (Salen-Picard *et al.*, 2002; Darnaude *et al.*, 2004), including in the mean biological characteristics of the catch. For example, declines in the mean weight of Arctic charr from Nain Labrador were correlated with the average quantity of capelin (*Mallotus villosus*) found in the stomachs (Dempson *et al.*, 2002).

Although Arctic charr have been shown to decrease specific growth rate with the length of time spent at sea (Berg & Berg, 1989; Rikardsen *et al.*, 2000), overall fish size must still increase. Furthermore, salmonid fish have been shown to exhibit pulsed growth with peaks of maximum growth occurring in spring and autumn (Swift, 1955). Reduced growth rates in mid-summer appear to be associated with increased activity levels and may be temperature mediated (Swift 1955). During late summer when the rate of supply of metabolites from the gut must be maximized to facilitate both gonad maturation and growth, growth can only be maintained if sufficient nutrients can be obtained. Thus, August precipitation may play an important role in determining eventual Arctic charr weights through its effect on the quality and quantity of basal food chain nutrients that allow nearshore Arctic charr to consume greater quantities and/or quality of food for longer periods of time.

Findings from this study, interpreted in the context of life-history strategies and requirements for the species, indicate clear environmental effects on the biological characteristics of Hornaday River Arctic charr. Temperature and precipitation are the most important environmental influences on Arctic charr as a result of their respective effects on fish metabolism and opportunity for acquiring surplus energy for growth. Climate change will affect both environmental variables. Changes in environmental variables will have varying impacts on different populations of Arctic charr that depend

on the magnitude and variety of trophic impacts that occur (ACIA, 2004), and the specifics of population adaptation to existing environmental conditions. Arctic charr, in particular, are known to be sensitive to minor changes in inhabited biotic and abiotic environments (Langeland, 1995) and, therefore, are likely to show substantive variation in age-specific mean length and weight as a result of climate-induced environmental variation. To understand and maintain sustainable fisheries for Arctic charr, appropriate management regimes must be developed to account for the effects of climate variation and change. Well designed management regimes will rely on the availability of suitable long-term data. As this study has highlighted, there is value in long-term fisheries data and we would encourage the extension of programmes in the Arctic to acquire matching fishery and environmental data to better understand the course of climate change effects on Arctic charr and other key northern fishery resources.

2.5 Acknowledgements

2.7 References

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Table 2.1. Trend model coefficient estimates for age-specific Hornaday Arctic charr mean length and weight characteristics.

	Length				Weight			
	Age 5	Age 6	Age 7	Age 8	Age 5	Age 6	Age 7	Age 8
Intercept	-1217.80	-6903.36	2818.65	-2756.32	-1.08×10^{-5}	-7304.90	-45236.90	-46959.40
Slope	6.42	3.73	1.70	1.80	54.84	40.23	23.86	24.96
P-value	<0.01	<0.01	0.02	0.03	<0.01	<0.01	0.03	0.04
r^2	0.85	0.52	0.32	0.29	0.80	0.56	0.29	0.27

Table 2.2. Age-specific model coefficient estimates explaining the variation in detrended mean length data for the Hornaday River Arctic charr fishery data (1979, 1981 and 1990-2003).

Variable	Age 5			Age 6			Age 7			Age 8		
	b_j	β_j	P	b_j	β_j	P	b_j	β_j	P	b_j	β_j	P
SST	12.54		0.02									
SUD				-0.10	-0.52	<0.01	-0.05	-0.39	<0.01			
PJULAUG				1.06	0.53	<0.01	0.85	0.62	0.05			
PAU										0.93		<0.01
Intercept	-37.16		0.02	10.66		0.02	-4.93		0.60	38.50		<0.01
r^2	0.54			0.63			0.60			0.79		

The b_j's are the estimated regression coefficients. P gives the associated coefficient p-value. The β_j's are the standardized regression coefficients that facilitate ranking of explanatory variables in terms of their relative importance for explaining variations in the modelled dependent variable, with larger values indicating greater influence on the dependant variable. SST = average sea surface temperature (°C); SUD = cumulative summer degree-days (>2.57°C); PJULAUG = total July and August precipitation (mm); PAU=total August precipitation (mm).

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Table 2.3. Age-specific model coefficient estimates explaining the variation in detrended mean weight data for the Hornaday River Arctic charr fishery data (1979, 1981 and 1990-2003).

Variable	Age 5		Age 6		Age 7		Age 8	
	b_j	P	b_j	P	b_j	P	b_j	P
PAU	9.99	<0.01	10.30	<0.01	8.23	0.01	9.83	<0.01
Intercept	-458.52	0.02	-395.02	<0.01	-318.71	0.02	-421.58	<0.01
r^2	0.59		0.56		0.37		0.53	

The b_j are the estimated regression coefficients. P gives the associated coefficient p-value. PAU= total August precipitation (mm).

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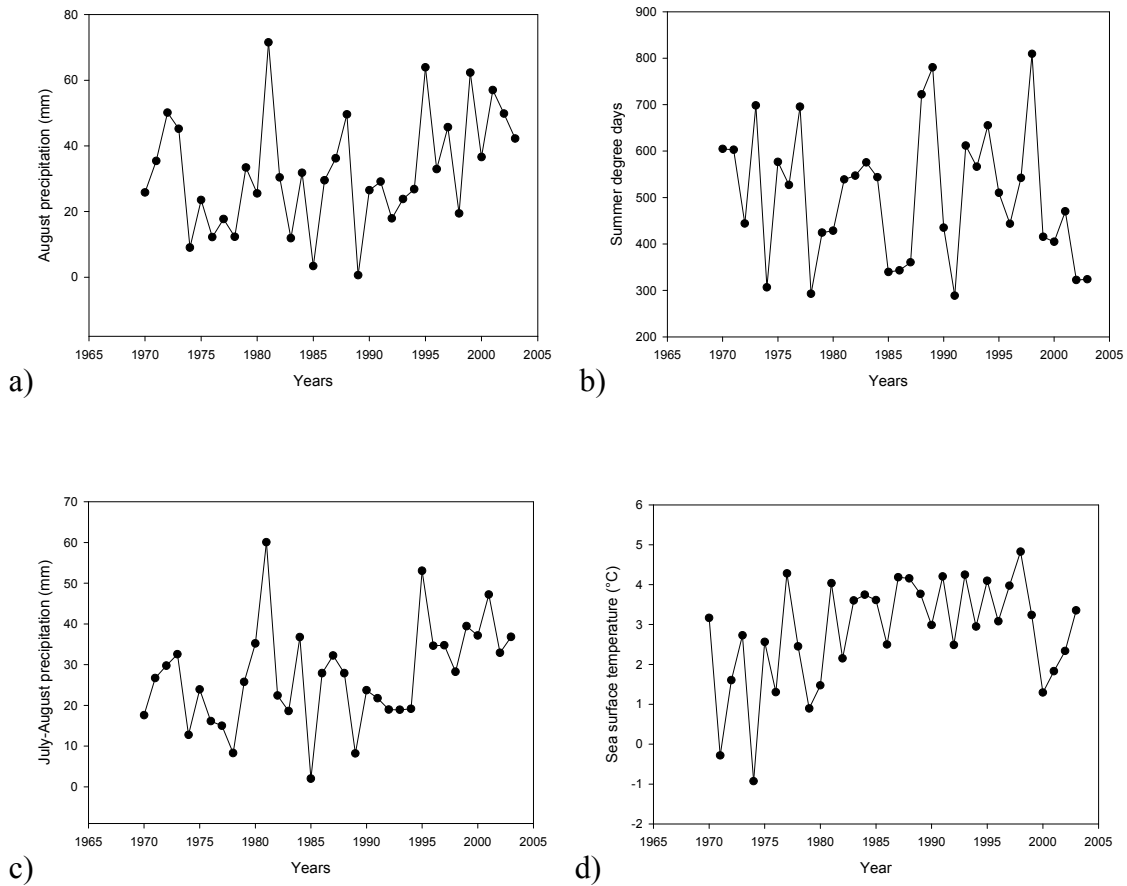
Fig. 2.1. Meteorological data for the Hornaday River (69˚21'N, 123˚42'W) area from 1970 to 2003 used to estimate multiple regression models explaining the variation in the mean length and weight characteristics of Hornaday River Arctic charr. Panel (a) plots of total August precipitation (mm). Panel (b) plots of cumulative summer (June-August) degree-days (>2.57°C). Panel (c) plots of total July-August precipitation (mm) and panel (d) plots of average summer (June-August) sea surface temperature (°C).
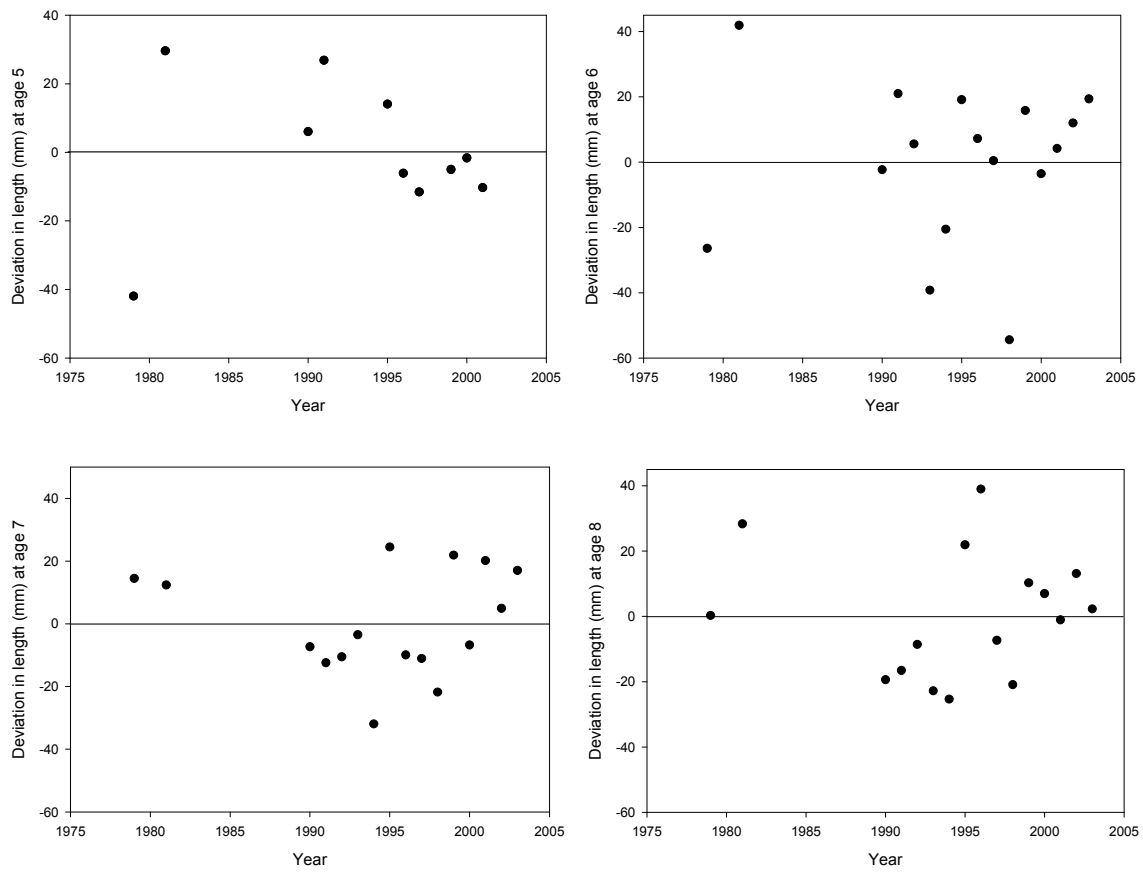
Fig. 2.2. Detrended mean length for each age class of Hornaday Arctic charr from 1979, 1981 and 1990 to 2003. Detrended data are the residuals from the time-trend regression for the biological variable versus the year of catch.
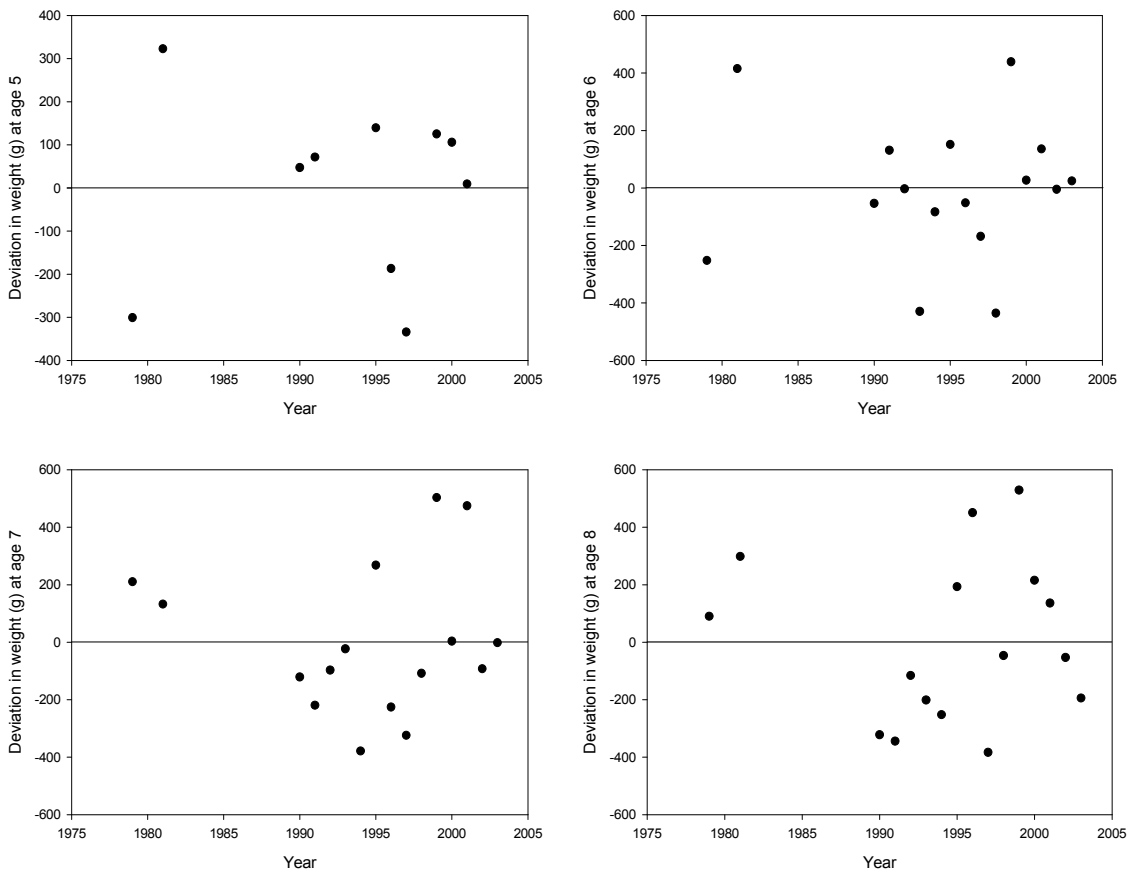
Fig. 2.3. Detrended mean weight for each age class of Hornaday Arctic charr from 1979, 1981 and 1990 to 2003. Detrended data are the residuals from the time-trend regression for the biological variable versus the year of catch.
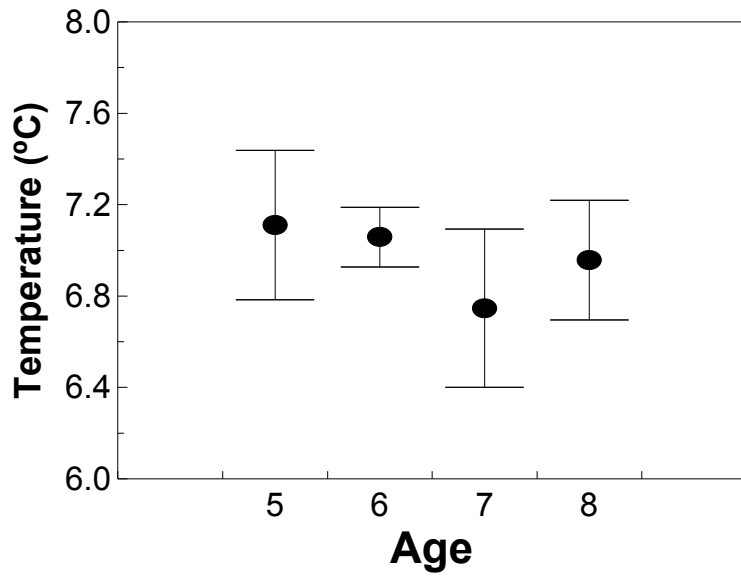
Fig. 2.4. Age-specific optimal temperatures for Hornaday River Arctic charr as estimated from quadratic models relating length-at-age to mean summer temperature (ºC). Mean estimated optima plotted as solid circles (●) plus or minus standard error. All pairwise comparison P-values from t-tests for significant differences between means were ≥ 0.40.

Chapter 3 Latitudinal variation in growth among Arctic charr in eastern North America.

3.1 Introduction

Arctic charr, *Salvelinus alpinus,* is adapted to cold-water habitats throughout its

Holarctic distribution (Hammar, 1999). In eastern North America, Arctic charr are widely

distributed at latitudes ranging from approximately 43°N in Maine to 84°N on Ellesmere

Island, Nunavut. Along the latitudinal gradient, Arctic charr inhabit a graded series of

environments that differ in annual temperatures and growing season lengths. Temperature

and growing season length combine to have a pervasive controlling effect on fish growth

rate and food consumption, with lower temperature and shorter summer seasons generally

reducing growth (Wootton, 1998). Thus in high-latitude environments, individuals

experiencing low temperatures and shorter growing seasons ought to exhibit both lower

growth rates and smaller size-at-age than individuals at lower latitudes. However, a

number of species-specific studies of geographic variation in size-at-age and growth rate

have demonstrated latitudinal compensation gradients resulting in better growth

performance in northern fish compared to southern fish (Conover & Present, 1990;

Present & Conover, 1992; Schultz *et al*., 1996; Billerbeck *et al*., 2000).

Two hypotheses have been proposed to explain the occurrence of such gradients,

with both enjoying empirical support from ectothermic species (Yamahira & Conover,

2002). The thermal adaptation hypothesis suggests that growth rates are maximized at the

temperature most commonly experienced by fish in their native environments

(Levington, 1983). Individuals from high latitudes will, therefore, have a reaction norm

for growth at lower temperatures than individuals from lower latitudes. Such growth

responses to temperature imply local adaptations that evolve via genotypic responses to

the environment to maximize fitness for native environments, and consequent reductions in fitness of those individuals elsewhere.

In contrast, the countergradient hypothesis focuses on latitudinal differences in seasonality, rather than average temperature. Individuals from higher latitudes are hypothesised to grow better as a result of having a higher capacity for growth than conspecifics from lower latitudes (Conover, 1990). Countergradient theory predicts patterns in genetic or phenotypic variation that are inversely related to the prevailing environmental gradient, with evolved genetic capacities for growth in northern populations offsetting, or compensating, for the effect of reduced growing season length (Conover & Present, 1990).

Support for the countergradient hypothesis is equivocal at best. For example, Conover and co-workers have reported pervasive evidence for the hypothesis (e.g., Conover, 1990; Present & Conover, 1992; Conover *et al*., 1997; Yamahira & Conover, 2002), whereas others have argued no compensation gradient can be found (e.g., Otterlei, 1999) or that the geographic variation that does exist is more related to environmental variability than any intrinsic differences in growth capacity among populations (e.g., Jensen *et al*., 2000). Studies of salmonid species have been particularly non-supportive. In brown trout (*Salmo trutta*), geographic variation in growth rates was related to local environmental differences (Jensen *et al*., 2000). In sockeye salmon (*Oncorhynchus nerka*), the influence of any countergradient effect was masked by the influence of prey resource availability and temperature (Edmunston & Mazumder, 2001). Among Norwegian Atlantic salmon (*Salmo salar*), no clear pattern in growth in relation to latitudinal compensation was found (Jonsson *et al*., 2001). Studies of thermal adaptation

in Arctic charr have also found no support for the premise of differential genetic capacities based on growth experiments with populations from Scandinavia and Britain (Larsson *et al*., 2005).

Few true comparative studies of geographic variation in populations of Arctic charr exist. A number of studies provide anecdotal support for the countergradient explanation of observed latitudinal variation in size-at-age characteristics (e.g., Venne & Magnan, 1989; Tallman & Saurette, 1996). Evidence of latitudinal variation in population characteristics when coupled with the wide distribution of Arctic charr at Arctic and temperate latitudes in eastern North America suggests possible local adaptability within the species, and raises obvious questions about the underlying causes of reported variation in size-at-age among populations (e.g., Johnson, 1980; Klemetsen *et al*., 2003).

Here we examine variations in characteristic size-at-age among populations of eastern North America Arctic charr along a 36° latitudinal gradient from Maine, USA, at the south, to Ellesmere Island, Nunavut, at the north. Specifically, we aim to document patterns of variation in size-at-age among both lacustrine and anadromous populations of Arctic charr and to test the applicability of the countergradient hypothesis as an explanation of differences in seasonally adjusted growth rates observed among populations.

3.2 Material and methods

Biological data (length, age and sex) on 67 Arctic charr populations located in eastern North America, principally Canada, were obtained from varying sources including DFO (Department of Fisheries and Oceans), personal archival and published

data (e.g., Grainger, 1953; Rombough *et al*. 1978). In this study, eastern North America was defined to include Maine, Québec, insular Newfoundland, Labrador and the eastern portion of the Canadian Arctic archipelago (Baffin and Ellesmere islands). Thus the analysis that follows uses only information for populations located east of $80\degree$ W to avoid the possible confounding effects of any longitudinal gradient.

Data included in the study consisted of observations on three life-history types: anadromous, normal lacustrine and dwarf lacustrine Arctic charr. Dwarf lacustrine populations of Arctic charr were defined as populations in which maximal observed fork-length did not exceed 22 cm (e.g., Parker & Johnson, 1991; Power *et al*., 2005). Normal lacustrine populations consisted of those populations where the length of >50% of mature individuals exceeded 25 cm. Where lacustrine morphotypes potentially occurred in sympatry, additional life-history, morphological or meristic data were used to confirm morphotype classifications (e.g., Reist *et al*, 1995; O'Connell & Dempson, 2002). Anadromous Arctic charr were defined as populations known to use near-shore marine areas for summer feeding.

The majority of the data (n= 67 populations) included in this study consisted of individual specimen observations of fork-length (cm), mass (g) and age (years) obtained from summer or early autumn sampling programmes that used multi-meshed gillnets, typically in the range 38-114 mm, or weirs to monitor and sample the studied population (e.g., Power *et al*., 2005). The numbers of individuals sampled in each age-class varied by population. To avoid problems associated with the use of single observations, population age-class data were included only if the study dataset contained information on at least five specimens in each age-class. Population age-class weighted means were

computed from available individual data and age-class analysis was completed only if at least five populations could be included in the analysis. For anadromous Arctic charr, application of the above criteria permitted the use of data for age-classes four to 15. For normal lacustrine populations, age-classes three to 12 and three to 16 were included, respectively, in the study for length and growth rate analyses. For dwarf lacustrine populations age-classes three to six were included. The locations of all study populations are shown in Figure 3.1.

To account for the differences in the opportunity for growth among populations, an index of the thermal opportunity for growth (TOG) was calculated from available air temperature data. TOG was defined as the cumulative number of degree-days >0°C and calculated on the basis of literature that indicated Arctic charr can survive and feed at 0°C (Johnson, 1980; Brännäs & Wiklund, 1992; Baroudy & Elliott, 1994; Larsson *et al*., 2005). Degree-days >0°C were cumulated over the life of individual fish to estimate growing season thermal opportunities for growth at age (e.g., age-1, age-2) and a cumulative life-time total. Cumulative degree-day data were then combined with fish length information to estimate growth rate (cm/cumulative degree-day >0°C) as a function of growth opportunity as represented by TOG (e.g., Conover, 1990; Power & McKinley, 1997) for fish.

Air temperatures used in the analyses were obtained from the Center for Climatic Research, Department of Geography, University of Delaware (http://climate.geog.udel.edu/~climate/index.shtml). Data are gridded one degree latitude by one degree longitude spacings starting, respectively, at the prime meridian and the equator. Data represent spatial monthly means interpolated from a two-stage estimation

procedure that combines general circulation model predictions with actual gridded observations to restore local climate detail (Rayner *et al*., 2003). The data for the grid containing latitudinal and longitudinal co-ordinates of a given Arctic charr population were used to represent prevailing meteorological conditions for the population. In some circumstances, correction for altitude was required where, for example, coastal anadromous populations were located in data grids largely dominated by upland or glacial terrain. In such instances, Environment Canada data (http://www.ec.gc.ca/) or data from the nearest adjacent sea-level grid were used to represent the prevailing meteorological conditions for the population.

To determine if length-at-age (cm) and/or age-specific growth rates (cm/cumulative degree-day>0°C) differed among populations, one-way analysis of variance (ANOVA) was used to test the null hypothesis of a common mean (H_o: $\mu_1 = \mu_2 = \mu_3 = \ldots \mu_n$) for all populations within a morphotype. Homogeneity of variance among populations for each ANOVA was verified with Levene's test. If there was heterogeneity of variance among populations, a Welch test was used to confirm the difference between means (Zar, 1999). To determine the explanatory power of latitude as a determinant of observed variations in length-at-age and/or growth rate (i.e., test the countergradient hypothesis) weighted least squares regression models relating length-at-age or age-specific growth rates (cm/cumulative degree-day>0°C) to latitude were estimated using the number of individuals in each population as a weighting factor. Finally, an average growth rate (cm/cumulative degree-day>0°C) for the population that included information on all age-classes was computed and the data for all populations within a morphotype regressed against latitude. Regression residuals tests (normality and

homoscedascity) were used to validate obtained regression models. ANOVA and regression analyses were repeated for each morphotype classification (anadromous, normal lacustrine and dwarf lacustrine). Finally, the variances in length-at-age and age-specific growth rate within morphotypes sampled in similar five degree latitude intervals were compared among morphotypes using Levene's F-test. A significance level of $\alpha=0.05$ was used in all statistical procedures.

3.3 Results

Among the 67 populations for which detailed biological data (length, weight and age) could be obtained, length-at-age and age-specific growth rates varied widely. No evidence was found to support the null hypothesis of common length-at-age or age-specific growth among studied populations (Table 3.1 and 3.2) for all morphotype classifications. Homogeneity of variance within morphotype classifications differed among populations (Levene's $p<0.05$). The Welch test confirmed that length-at age and growth rate means differed significantly among populations of each morphotype (all $p<0.02$). Variability in age-specific length and growth rates did differ in some cases among morphotypes sampled at common five degree latitude grid, with normal lacustrine populations tending to show less variability than anadromous populations but greater variability than lacustrine dwarf populations (Table 3.3).

Weighted least squares regressions of length-at-age or age-specific growth rates on latitude yielded varying results (e.g., Fig. 3.2 and Fig. 3.3). Among anadromous populations there was a general tendency for length-at-age to decline as a function of latitude for age-classes four to 11 (all slopes $p<0.01$). The r^2 values of the age-specific

regressions declined with increasing age ($r = 0.74$) and there were significant differences between the mean explanatory power of the relationships for younger (ages 4-8) and older (age 9-11) fish ($t=5.02$, df=5, $p=0.002$). No relationship was found for age-classes 12-15 (all slopes $p>0.05$). Among lacustrine fish, a significant negative relationship between length-at-age and latitude was found for normal charr for age-classes 4-6 only (slope $p<0.01$), with all other lacustrine age-classes, either for dwarf or normal charr, showing no significant change in length-at-age as a function of latitude (slope $p>0.05$). The explanatory power of the normal lacustrine latitudinal relationship was significantly lower ($t=11.12$, df=3, $p=0.008$) on average (0.227) when compared to similar age-classes of anadromous fish (0.543).

Age-specific growth rates varied with latitude only for anadromous fish aged 10 to 13, and were not significantly correlated with latitude in any of the younger or older age-classes (all slopes $p>0.05$). Among normal lacustrine fish, age-specific growth rates were correlated with latitude in all age-classes, three to 16 (all slopes $p\leq0.013$). Similarly in dwarf lacustrine Arctic charr populations, growth rates were significantly correlated with latitude (all slope $p\leq0.01$) for all studied age-classes (three to six). Among anadromous Arctic charr, latitude explained an average only 42% of the variation in observed growth rates. Among lacustrine charr populations latitude explained, respectively, 89 and 81% of the variation among dwarf and normal populations (Fig. 3.4). Among normal lacustrine populations, the explanatory power of the latitudinal relationship differed significantly between immature (ages 3-8) and mature (ages 9-16) fish ($t=5.31$, df=12, $p<0.001$).

3.4 Discussion

The results of this study provide strong evidence for latitudinal compensation in the growth of lacustrine morphotypes and limited evidence of the applicability of the countergradient hypothesis for anadromous populations of Arctic charr in eastern North America. Growth rates increased in all age-classes of normal and dwarf lacustrine Arctic charr as latitude increased. Less consistent results were found for anadromous Arctic charr where higher growth rates were observed in the age-classes of many northern populations. The positive correlation between growth rate (cm/cumulative degree-day>0°C) and latitude found in this study indicates that northern Arctic charr grow faster than their conspecifics from the south. According to the countergradient hypothesis, genetic effects can act to counteract the environmental gradients which influence the general zoogeographic patterns of growth seen in a species, since shorter growing seasons and lower temperatures should reduce the size of northern fish (Shultz *et al.*, 1996). In this study, increased growth rates partially offset body size differences along the gradient at younger ages, and in some instances totally offset the differences in body size that would be predicted by the environmental gradient.

Many studies have tested the Conover countergradient hypothesis for latitudinal variation in biological characteristics as it applies to fish and a growing body of literature has found support for the hypothesis (e.g., see Table 3.6). The empirical support for the countergradient hypothesis summarized in Table 3.6 demonstrates a widespread phenomenon, especially in North America, and illustrates geographic variation in growth is an important descriptor of differences among populations. Differences in growth rates

also hold likely consequences for differences in age-at-maturity given documented documented trade-offs between growth and maturation (e.g., Wootton, 1998).

Most studies with no evidence of countergradient effects on fish growth included study sites in Europe (e.g., see Table 3.7). The discrepancy between geographic regions concerning the applicability of the countergradient hypothesis may be related to differences in latitudinal temperature gradients in North America and Europe (Fig. 3.5), with the more pronounced temperature gradient in North America meeting the precondition for the development of geographic variation in biological characteristics (Conover & Schultz, 1995). The greater differences in temperature along the gradient in eastern North America may explain the strength of the observed latitudinal-related growth differences in eastern North America and contrast with the limited thermal variability observed in Scandinavia (Fig. 3.5) and the associated lack of evidence for latitudinal clines in growth rates (e.g., Jensen *et al*., 2000; Jonsson *et al*., 2001).

The potential for geographic differentiation is great on the east coast of North America since steep latitudinal gradients occur in a number of environmental variables (e.g., temperature, ice-free season) critical to species' success (Schultz *et al*., 1996). Given the notably high phenotypic variability in Arctic charr (Klemetsen *et al*., 2003), exaggerated differences in selective pressure along a given latitudinal gradient are more likely to elicit measurable differences in fitness-related measures such as growth rate. Therefore, both geographic location and the environmental gradient will act to determine the local selective pressures on the fish which in turn, influence the expression of compensatory responses such as growth rate measured in countergradient studies.

Similarly, differences between anadromous and lacustrine Arctic charr growth

rates along the studied gradient may be related to broad scale differences in the

environmental influences on coastal and freshwater habitats. The observed consistency

in sea surface temperature (T° range along a Y° gradient) in the nearshore marine habitats

used by anadromous Arctic charr may explain the lack of evidence for a latitudinal cline

in growth rate (Fig. 3.5). The broad effect of prevailing maritime currents is dampened

variation and fewer extreme temperatures in maritime climate zones (Belk *et al*., 2005).

Thus, eastern North American anadromous populations using thermal environments

influenced by the Labrador Current will experience little difference in thermal habitat as

a function of latitude. The constancy of selective pressures along the gradient, therefore,

correlates well with the lack of differences in observed growth rates, except at younger

ages (<age 4) where growth is dominated more by differences in freshwater habitats.

Further diluting the effect of any differences in selective pressure that might occur among

anadromous populations is the migratory exchange known to occur among assemblages

of Arctic charr (e.g., Dempson & Kristoffersen, 1987). By comparison, in isolated

lacustrine populations, where differences in thermal selection pressures among

populations are maintained over the entire life-history, latitudinally based differences in

growth rate are more likely to be observed.

In addition to more uniform temperatures, food availability is another factor likely

to contribute to stable environments for anadromous Arctic charr. Feeding conditions in

the ocean are more favourable than in freshwater systems and the abundance of food

enhances the thermal stability of the marine environment (Gross, 1987; Gross *et al*.,

1988). More uniform thermal regimes may, therefore, act in conjunction with non-

restricted feeding opportunities to buffer differences in growth opportunity and reduce

the variability of growth rates among anadromous Arctic charr populations along the

latitudinal gradient. Similar lacustrine and anadromous population differences along

latitudinal gradients have been observed in the study of other biological attributes in

Arctic charr. For example, Power *et al*. (2005) observed a lower among-population

variability in the fecundity of anadromous compared to lacustrine Arctic charr along a

latitudinal gradient in eastern North America.

The Conover hypothesis excludes age as a factor since the majority early

countergradient studies were conducted on immature fish (Conover, 1990; Present &

Conover, 1992; Schultz *et al*., 1996; Conover *et al*., 1997; Yamahira & Conover, 2002).

However, differences in reproductive investment associated with maturity have been

observed to affect the strength of association between fish biological characteristics (e.g.,

length, weight) and latitude (Power & McKinley, 1997). In this study, higher growth

rates were preserved as fish aged but there were notable decreases in the size differences

between northern and southern populations within a morph. The decline in the correlation

between length-at-age and latitude in older fish may be consequence of age-at-maturity.

If maturity occurs at younger ages in southern populations (e.g., Tallamn & Saurette,

1996), the trade-off between somatic growth and gonad development will imply

reductions in growth at maturity and act to decouple the growth rate response from the

environmental gradient. For example, in salmonids in the year before maturation the

majority of feeding-derived energy is allocated to lipid storage rather than protein

elaboration (Thorpe, 1987). Consequently, the increase in length (growth) is slower for

maturing salmonids than non-maturing salmonids (Hestagen *et al*., 2004). Earlier

maturation of dwarf and normal lacustrine and anadromous Arctic charr at low latitudes may, therefore, effectively counterbalance the effect of shorter growing seasons at higher latitudes on length, with energy surplus to maintenance being increasingly diverted to reproduction rather than growth.

In summary, results of analyses here show that the length-at-age and growth rate of eastern North American Arctic charr varied among populations distributed along a latitude gradient from Maine to Ellesmere Island. Overall, the study supported the countergradient hypothesis for lacustrine morphotypes, where northern populations compensated for shorter growing seasons with higher growth rates. Anadromous populations exhibited less evidence in favour of the countergradient hypothesis, with only four age-classes showing higher growth rates with increased latitude. Morphotype-specific responses along the described thermal gradients for lacustrine and anadromous Arctic charr suggest that a minimum temperature gradient may be needed before a latitudinal compensation in growth rates is observed. Accordingly, studies testing the countergradient hypothesis should take into consideration the extent of thermal differences along the tested gradient when assessing the applicability of the hypothesis to a species of concern.

3.5 Acknowledgements

3.7 References

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Table 3.1 Analysis of variance results relating age-specific growth rate (cm/cumulative degree-days >0C°) to latitude for all morphotypes of Arctic charr. Abbreviations: df, F and P, respectively, define the ANOVA degrees of freedom, computed F statistic and associated P-value.

Age	Anadromous			Normal lacustrine			Dwarf lacustrine		
	df	F	P	df	F	P	df	F	P
3				12	589.61	<0.01	6	1192.22	<0.01
4	5	33.61	<0.01	16	441.58	<0.01	7	3178.45	<0.01
5	11	81.26	<0.01	16	169.95	<0.01	5	1517.54	<0.01
6	17	121.71	<0.01	15	161.09	<0.01	6	179.67	<0.01
7	18	180.34	<0.01	11	191.87	<0.01			
8	20	229.30	<0.01	6	112.50	<0.01			
9	19	177.87	<0.01	7	724.91	<0.01			
10	18	186.93	<0.01	9	286.10	<0.01			
11	17	143.78	<0.01	5	157.41	<0.01			
12	17	233.84	<0.01	5	47.95	<0.01			
13	14	117.59	<0.01						
14	12	112.06	<0.01						
15	8	89.71	<0.01						

Table 3.2 Analysis of variance results relating age-specific length (cm) to latitude for all morphotypes of Arctic charr. Abbreviations: df, F and P, respectively, define the ANOVA degrees of freedom, computed F statistic and associated P-value.

Age	Anadromous			Normal lacustrine			Dwarf lacustrine		
	df	F	P	df	F	P	df	F	P
3				12	94.75	<0.01	6	115.28	<0.01
4	5	19.44	<0.01	16	219.12	<0.01	7	256.29	<0.01
5	11	24.65	<0.01	16	208.64	<0.01	5	293.05	<0.01
6	17	39.63	<0.01	15	85.35	<0.01	6	55.29	<0.01
7	18	59.13	<0.01	11	124.09	<0.01			
8	20	43.52	<0.01	6	165.58	<0.01			
9	19	47.71	<0.01	7	155.89	<0.01			
10	18	53.37	<0.01	9	61.45	<0.01			
11	17	41.84	<0.01	5	213.72	<0.01			
12	17	48.69	<0.01	5	46.27	<0.01			
13	14	30.17	<0.01						
14	12	40.57	<0.01						
15	8	14.94	<0.01						

Table. 3.3. Morphotype-specific variances in age-specific length measured among populations within 5° segments of the studied latitudinal range. DW, NO and AN, respectively, denote dwarf lacustrine, normal lacustrine and anadromous group variances. Asterisks indicate non-significant differences, Levene's test P>0.05, between tested morphotypes.

Age	45-50°N		55-60°N		60-65°N		65-70°N		70-75°N		75-80°N	
	DW	NO	AN	NO	AN	NO	AN	NO	AN	NO	AN	NO
3	7.34	5.88			11.35*	11.93*	26.46	0.53				
4	10.29*	7.16*			17.57	26.78	31.91	1.49				
5	15.30	16.64			33.66	32.51	98.66	28.06	15.26*	10.49*	20.72	0.68
6	15.85	67.67	44.14	5.95	33.89*	47.18*			10.32	23.33	18.09	0.38
7	9.99	83.61	27.98	11.78	36.48	18.92	87.78	3.26	60.32	0.25	11.19*	6.87*
8					35.97*	23.39*			55.81	0.455	25.62*	14.03*
9					43.35	21.46			30.22	0.61		
10					47.26*	29.89*	39.12*	34.72*	34.12	0.79		
11					56.44*	13.57*			41.24	2.85		
12									29.12	1.44		

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Table 3.4 Regression coefficients from weighted least squares models relating length-at-age to latitude for anadromous and normal lacustrine Arctic charr. All models were statistically significant (regression P<0.05). All non-reported age-classes or morphotypes showed no significant correlation between length-at-age and latitude (regression P>0.05).

Age	Anadromous				Normal lacustrine			
	Populations	intercept	slope	r^2	Populations	intercept	slope	r^2
4	7	61.84	-0.64	0.60	19	37.22	-0.35	0.26
5	14	78.95	-0.85	0.45	21	42.26	-0.38	0.19
6	20	116.74	-1.37	0.58	19	47.50	-0.41	0.23
7	22	120.76	-1.37	0.60				
8	25	119.47	-1.26	0.57				
9	24	98.56	-0.86	0.36				
10	23	108.33	-0.96	0.39				
11	21	102.40	-0.81	0.31				

Table 3.5 Weighted least squares regression models relating age-specific growth rates (cm/cumulative degree-days >0C°) to latitude for all morphotypes of Arctic charr. All reported models were sognofocant (regression P<0.013). Non-reported age-classes showed no significant correlation between growth rates and latitude (regression P>0.05).

Age	Anadromous				Normal lacustrine				Dwarf lacustrine			
	Populations	intercept	slope	r^2	Populations	intercept	slope	r^2	Populations	intercept	slope	r^2
3					14	-0.012	$2.80*10^{-4}$	0.79	6	-0.019	$4.26*10^{-4}$	0.92
4					19	-0.013	$2.93*10^{-4}$	0.72	7	-0.017	$3.77*10^{-4}$	0.86
5					21	0.015	$3.55*10^{-4}$	0.65	5	-0.016	$3.61*10^{-4}$	0.87
6					19	-0.015	$3.49*10^{-4}$	0.76	7	-0.015	$3.40*10^{-4}$	0.89
7					17	-0.016	$3.67*10^{-4}$	0.71				
8					10	-0.015	$3.46*10^{-4}$	0.72				
9					12	-0.019	$4.25*10^{-4}$	0.94				
10	23	-0.0094	$2.89*10^{-4}$	0.32	13	-0.017	$3.89*10^{-4}$	0.87				
11	21	-0.013	$3.82*10^{-4}$	0.43	9	0.013	$3.24*10^{-4}$	0.87				
12	21	-0.016	$3.94*10^{-4}$	0.46	9	-0.015	$3.38*10^{-4}$	0.89				
13	18	-0.016	$3.79*10^{-4}$	0.48	6	-0.022	$4.54*10^{-4}$	0.83				
14					9	-0.028	$3.86*10^{-4}$	0.81				
15					4	-0.034	$6.28*10^{-4}$	0.96				
16					6	-0.026	$4.78*10^{-4}$	0.82				

Table 3.6 Studies of fish species where variations in growth rates were found to correlate with latitude as predicted by the countergradient hypothesis.

Study	Species	Approximate latitude range
Conover & Present (1990)	*Menidia menidia*	30° N to 46° N
Conover (1990)	*Alosa apidissima*	29° N to 46° N
	Morone saxatilis	
	Fundulus heteroclitus	
Williamson & Carmichael (1990)	*Micropterus salmoides*	24° to ?
Present & Conover (1992)	*Menidia menidia*	46° N to 30° N
Malloy & Targett (1994)	*Paralichthys dentatus*	34° N to 38 ° N
Nicieza *et al*. (1994)	*Salmo salar*	43° N to 58° N
Lobon-Cerviá et al.(1996)	*Leuciscus leuciscus* (L.)	51° N to 66° N
Schultz *et al*. (1996)	*Fundulus heteroclitus*	37° N to 44° N
Conover *et al*. (1997)	*Morone saxatilis*	33 ° N to 45 ° N
DiMichele & Westerman (1997)	*Fundulus heteroclitus*	29° N to 41° N
Power & McKinley (1997)	*Acipenser fulvescens*	43° N to 54° N
Brown *et al*. (1998)	*Morone saxatilis*	30° N to 41° N
Arendt & Wilson (1999)	*Lepomis gibbosus*	39° N to 42° N
	Lepomis macrochirus	
Billerbeck *et al*. (2000)	*Menidia menidia*	33° N to 44° N
Imsland *et al*. (2000b)	*Scophthalmus maximus*	45° N to 59° N
Imsland *et al* (2000a)	*Hippoglossus hippoglossus*	45° N to 66° N
Jonassen *et al*.(2000)	*Hippoglossus hippoglossus*	45° N to 66° N
Purchase & Brown (2000)	*Gadus morhua*	42° N to 45° N
Secor *et al*. (2000)	*Morone saxatilis*	33° N to 38° N
Billerbeck *et al*. (2001)	*Menidia menidia*	33° N to 44° N
Imsland *et al*. (2001a)	*Scophthalmus maximus*	45° N to 59° N
Imsland *et al*. (2001b)	*Scophthalmus maximus*	45° N to 59° N
Lankford *et al*. (2001)	*Menidia menidia*	33° N to 44° N
Pegg & Pierce (2001)	*Notropis atherinoides*	38° N to 49° N
Braaten & Guy (2002)	*Ictalurus punctatus*	38° N to 49° N
	Notropis atherinoides	
	Apoldinotus grunniens	
	Carpiodes carpio	
	Stizostedion canadense	
Munch & Conover (2002)	*Menidia menidia*	46° N to 30° N
Yamahira & Conover (2002)	*Menidia menidia*	24° N to 44° N
	Menidia peninsulae	
Galarowicz & Wahl (2003)	*Stizostedion vitreum*	34° N to 51° N
Heibo *et al*. (2005)	*Perca fluviatilis*	40° N to 67° N
Marcil *et al*. (2005)	*Gadus morhua*	43° N to 48° N
Alvarez *et al*. (2006)	*Salmo trutta*	Along 43° N

Table 3.7 Empirical studies of fish species where variations in growth rates did not correlate with latitude as predicted by the countergradient hypothesis.

| Study	Species	Latitude range	Summary Comments
Gudkov (1996)	*Salvelinus malma*	59° N to 63° N	Anadromous *Salvelinus malma* has fairly similar growth rate.
Oliveira (1999)	*Anguilla rostrata*	32 ° N to 47° N	The growth potentials of all eels are equal and are a result of the habitat's growth conditions.
Otterlei *et al.* (1999)	*Gadus morhua*	60° N to 68° N	Neither temperature adaptation across latitudes nor countergradient latitudinal variation in growth capacity of the two larval stocks was indicated.
Jensen *et al.* (2000)	*Salmo trutta*	61° N to 70° N	The present study shows that most of the variation in growth of brown trout in Europe can be related to environment variability.
Edmundson & Mazumder (2001)	*Oncorhynchus nerka*	55° N to 65° N	If there is countergradient variation in the growth of sockeye salmon smolts, the data suggest that it is heavily masked by the influence of food resource and temperature.
Jonsson *et al.* (2001)	*Salmo salar*	59° N to 70° N	There was no clear pattern in growth performance either in relation to latitude or temperature regime.
Pegg & Pierce (2001)	*Ictalurus punctatus* *Apoldinotus grunniens* *Carpiodes carpio* *Stizostedion canadense*	38° N to 49° N	Some evidence of a correlation between growth and latitudinal was found, albeit at a more regional scale in four of five species studied.
Belk *et al.* (2005)	*Snyderichthys copei*	38° N to 41° N	The data suggest the possibility that each might exhibit intrinsic growth rates that are adapted to local temperature regimes.
Larsson *et al.* (2005)	*Salvelinus alpinus*	54° N to 70° N	No significant correlation between growth rate and length of the growth season in this European study
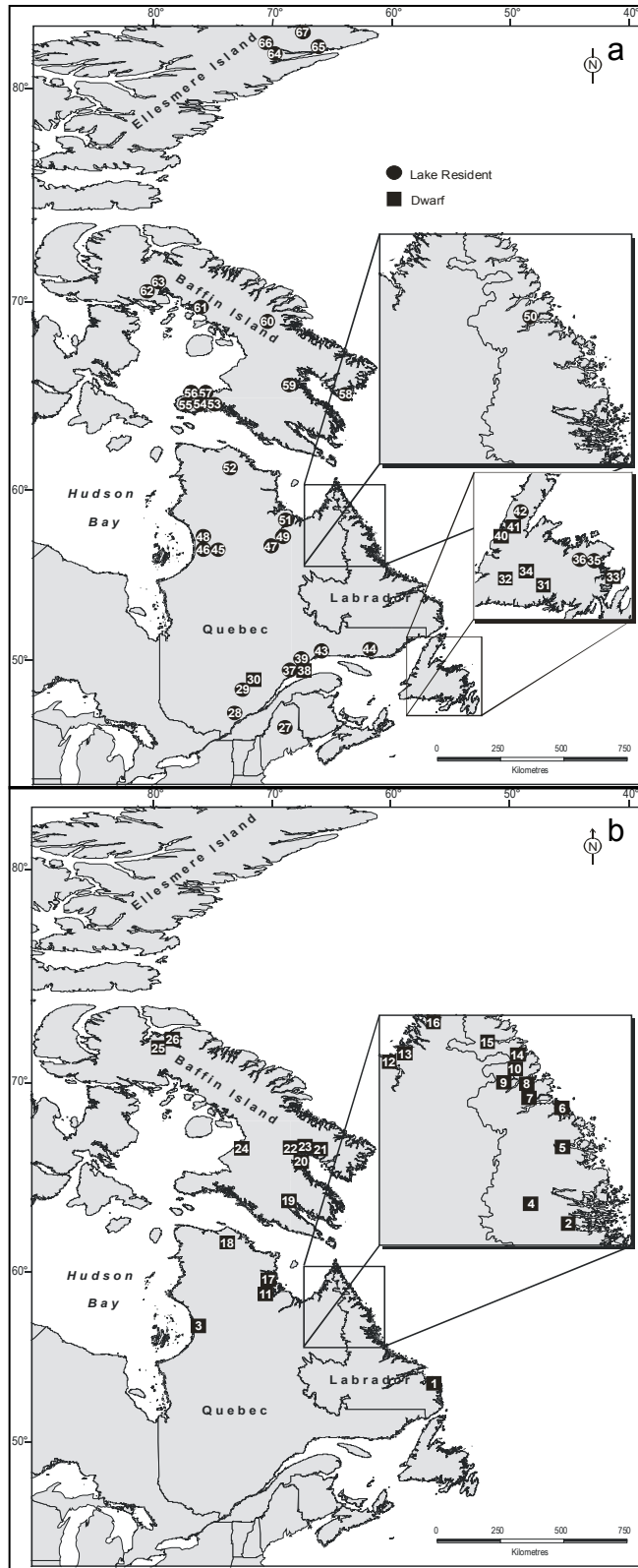
Fig. 3.1. Map of lacustrine (a) and anadromous (b) Arctic charr populations sampled in this study.
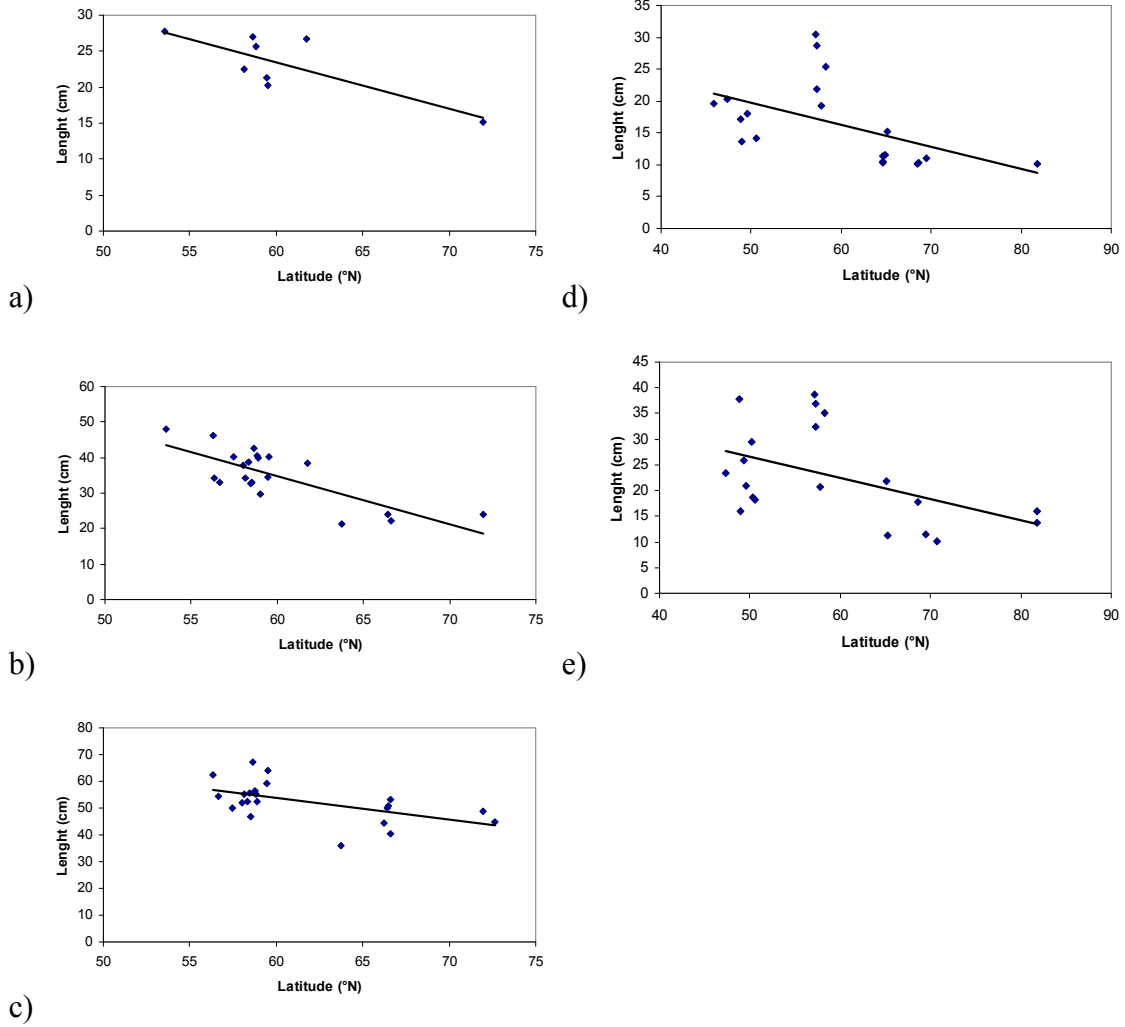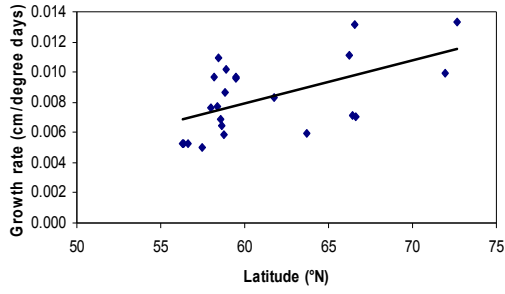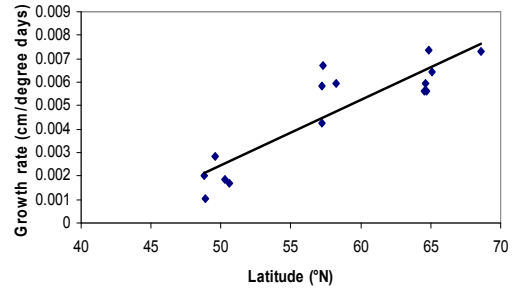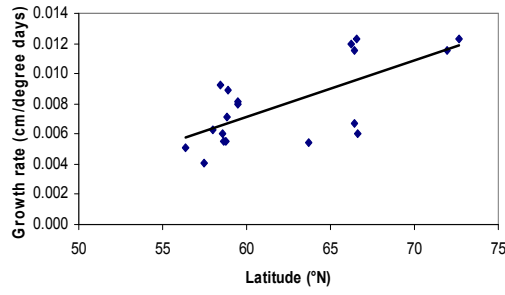
a)

b)

c)

d)

e)

Fig 3.2. Plots of weighted average length-at-age latitudinal gradients for anadromous populations at age 4 (a), age 6 (b) and age 11 (c) and normal lacustrine populations at age 4 (d) and age 6 (f).
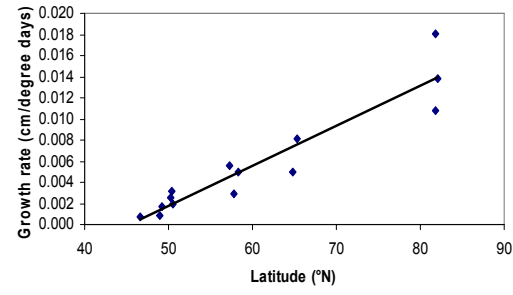
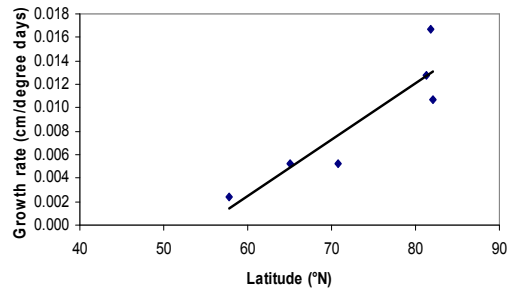Fig 3.3. Plots of weighted average growth rate latitudinal gradients for anadromous populations at age 10 (a) and age 13 (b) and normal lacustrine populations at age 3 (c), at age 10 (d) and at age 16 (e).
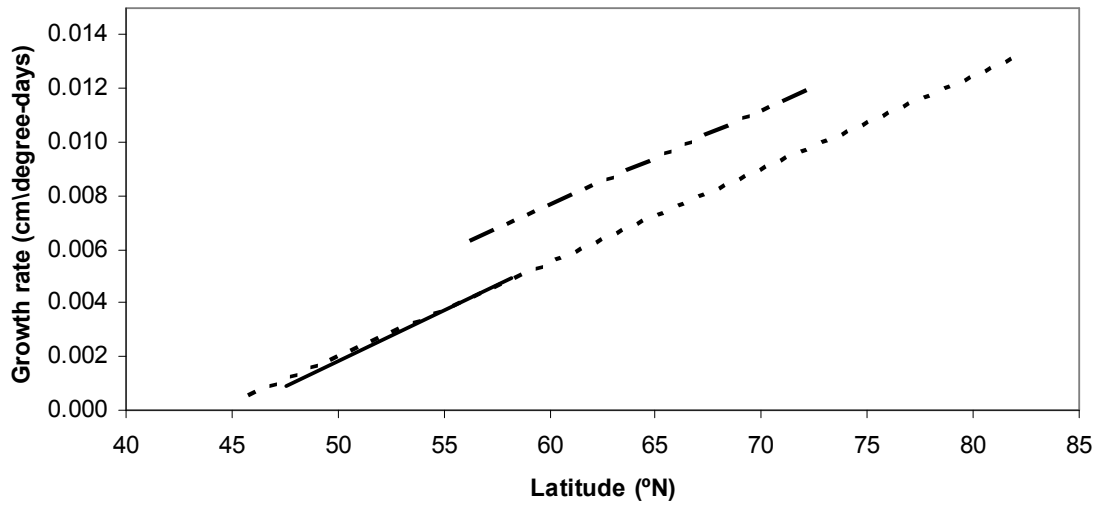
Fig. 3.4. Latitudinal average regression trend of growth rate (cm/cumulative degree-days<0°C) for anadromous Arctic charr (—— - - ——, $y = 0.0004x - 0.0138$, $p = <0.01$), normal lacustrine Arctic charr (---, $y = 3.49*10^{-4} x - 0.015$, $p = <0.01$) and dwarf lacustrine Arctic charr (—, $y = 3.75*10^{-4} x - 0.017$, $p = <0.01$) where X denotes latitude (°N).
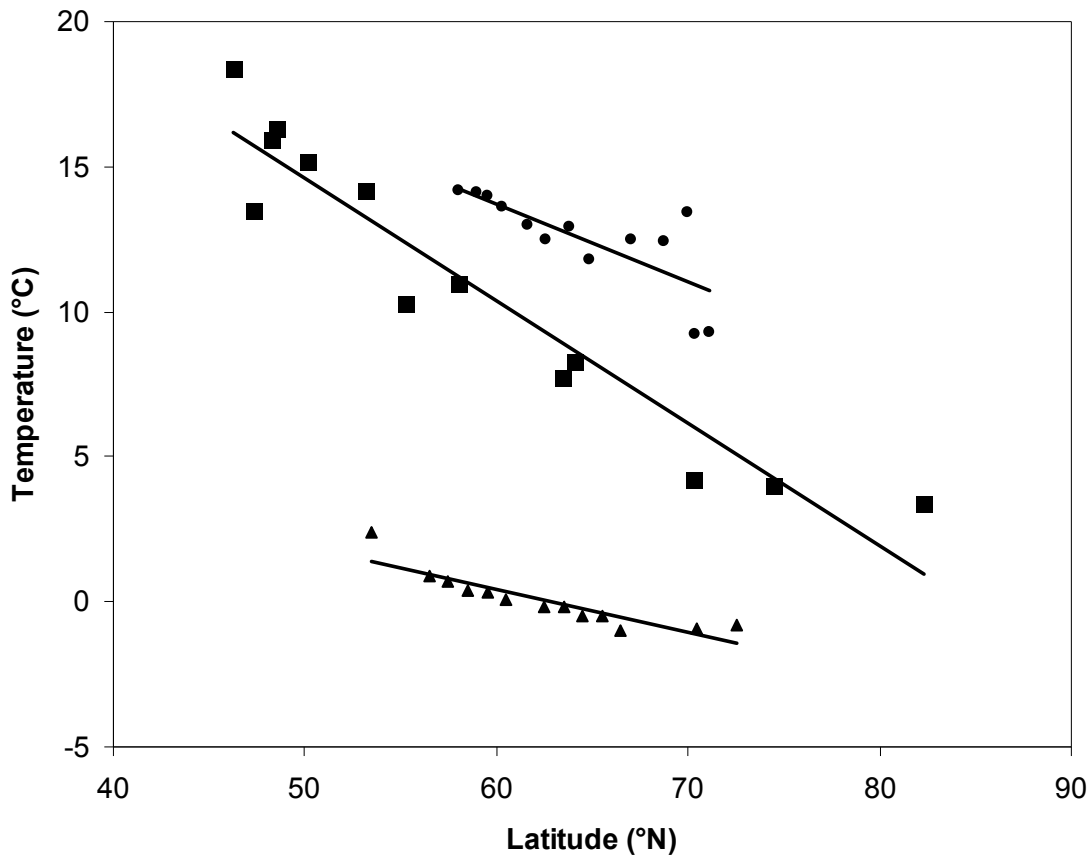
Fig 3.5. Latitudinal regression plots of July mean air temperature (°C) climate normals (1961-1990) for eastern Canada (■) and Norway (●) and the annual climate normal (1961-1990) for the Labrador Current (▲).Climates normals were obtained from Environment Canada (http://www.ec.gc.ca/), the Norway Meteorological Institute (http://met.no/english/index.html) and from the Hadley Center for Climate Prediction and Research (http://www.metoffice.gov.uk/research/ hadleycentre/). The Canadian and Norwegian data are from stations located at sea-level within the latitudinal range of the Arctic charr populations. For Canada, Norway and the Labrador coast, respectively, the equation of the regression is y = -0.421x + 35.64, y = -0.269x + 29.82 and y = -0.15x + 9.36. Regression models explain 91(Canada), 59 (Norway) and 80 (Labrador) percent of the variation in the data and have significantly different slopes (ANCOVA p<0.05).

Chapter 4 General conclusion

In this thesis, variations in the biological characteristics of Arctic charr related to environmental factors were investigated. Environmental variables influenced length-at-age and weight-at-age variations of western Arctic charr from the Hornaday River, although with varying degrees of importance as fish aged (Chapter 2). Environmental factors as represented by latitude also influenced the length-at-age and growth rate (cm/degree day > 0^0C) characteristics of anadromous and lacustrine (both normal and dwarf) populations of Arctic charr along a latitudinal gradient in the eastern Arctic (Chapter 3), although differences in the significance of the effect were found among and between life-history types. Existing spatial and temporal patterns of biological characteristic of North America Arctic charr in relation to climate found in this thesis are summarized below.

The temporal case study of the Hornaday River (Chapter 2) demonstrated that seasonal climate variability had critical effects on biological characteristics of Arctic charr, with temperature and precipitation having significant influence on variations in mean length-at-age and mean weight-at-age of six to nine year-old Arctic charr. The effect of August precipitation on Arctic charr weight was consistent over the studied period of the life-cycle and positively correlated. Precipitation appears to act through its influence on nutrient exports to the nearshore marine area, extending the period of high marine productivity that in turn yields higher quality and quantity of food, thereby increasing foraging opportunities and promoting improvements in fish condition reflected in weight gain. Temperature had its greatest effect on younger fish and decreased in importance as fish aged. Age-specific differences in the influence of environmental factors suggests climate-induced variation in local environments will unevenly effect

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resident fish. The age-related changes also implicate the onset of maturation as being a key determinant of individual responses to environmental variation. Temperature drives age-related changes in growth that slow earlier under warmer conditions, provided precipitation driven nutrient availability is sufficient to facilitate maturation. Such understanding of climate variability and associated biological effects contributes to the understanding of the year-to-year variability in stock characteristics. By identifying the key climate-driven biological parameters associated with a fish population, long-term environmental and biological studies become a valuable asset for monitoring and predicting climate change impacts on that population as this thesis has demonstrated.

The latitudinal analysis of eastern North America Arctic charr populations showed that geographic variation in length-at-age and growth rate varied among life-history types, with evidence of latitudinal compensation in growth rate offsetting shorter-growing seasons along the gradient in normal and dwarf lacustrine Arctic charr populations. Anadromous Arctic charr populations, however, exhibited less evidence of latitudinal compensation in biological characteristics. In particular, a consistent positive correlation between age-specific growth rate and latitude for both normal and dwarf lacustrine Arctic charr indicated faster growth for northern lacustrine Arctic charr. In contrast, for anadromous populations, only four age-classes with higher growth rates were observed with increased latitude. A more stable thermal environment associated with anadromous Arctic charr summer marine occupancy seems to lessen the need for latitude compensation. Morphotype-specific latitudinal responses related to habitat, suggested the importance of pronounced temperature gradients resulting in favourable geographic variation for this type of charr. Such patterns possibly explain discrepancies between countergradient studies and are relevant for understanding the potential effects

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of climate change in different regions. Climate change will not be uniform throughout and the degree of temperature shifts will vary locally. Latitudinal variation in temperature and associated patterns of morphotype-related growth rate changes, therefore, may reflect future scenarios of temperature-driven shifts in Arctic charr biological characteristics over time. Such information is important in the creation of predictive models and will be of specific use in the design of adaptive management scenarios aimed at mitigating climate-driven impacts on valuable Arctic charr stocks.

Finally, the understanding of potential impacts developed here is based only on a limited number of studies of Arctic charr responses to environmental variability. Additional studies such as this one will be needed to increase our general knowledge of Arctic charr and their relation with climate. For example, this study addresses only mean population responses to climate variation. Understanding of individual variation within populations is required to better manage stocks in the face of the rapid changes in climate predicted to occur in the near future. Furthermore, detailed studies of latitudinal differences in other key life-history parameters (e.g., age-at-maturity) are needed to better predict individual and population-level responses to climate change. To document issues related to Arctic charr and climate change, understanding the role played by environmental variables on life-history, the timing of their effects and the implications of regional climate change for Arctic charr must also be examined. More accurate models based on such information could then be developed to predict the impacts of climate change at local levels. Therefore, this study encourages additional research in the Arctic to acquire the data on Arctic charr necessary to better understand the future of the species in the Arctic.