

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

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Abstract Insights from long-term subsistence fisheries data can improve our understanding of the population-specific responses of Arctic charr, *Salvelinus alpinus*, to environmental conditions. In this study, associations were found between temporal environmental variation and Arctic charr length- and weight-based growth using data from fish captured in the Hornaday River fishery. Overall, spring precipitation and summer air temperature appear to be the most important environmental influences on Arctic charr probably because of their respective impacts on the

opportunities for acquiring surplus energy for growth. A pattern of decreasing age-related importance of temperature and increasing age-related importance of precipitation suggested that the coupling between growth and environmental effects varied by life-period. The changing prominence of each variable seems to result from the shift in apportioning energy for increases in length to increases in weight, likely as a result of the onset of maturation. The linkage of population characteristics to environmental conditions provides a baseline reference against which future data may be compared to determine the significance of any observed changes in population characteristics as a result of continuing ecological change in the north.

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Introduction

Climate change has been identified as an important source of aquatic disturbance on a global scale (McCarthy, 2001; Woodward et al., 2010; Poesch et al., 2016), with Arctic ecosystems being among those seen as particularly vulnerable (Jimenez Cisneros et al., 2014). 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 altered by climate change (Kennedy et al. 2002; Linnansaari et al., 2012; Pachauri et al., 2014). Changes in these environmental conditions will have impacts, both direct and indirect, in aquatic ecosystems. Climate-driven cumulative effects resulting from changes to adjacent terrestrial ecosystems and cascading effects resulting from changes at lower trophic levels are also likely to significantly affect northern aquatic ecosystems and their biota (Finstad & Hein, 2012; Ulvan et al., 2012; Settele et al., 2015; Poesch et al., 2016).

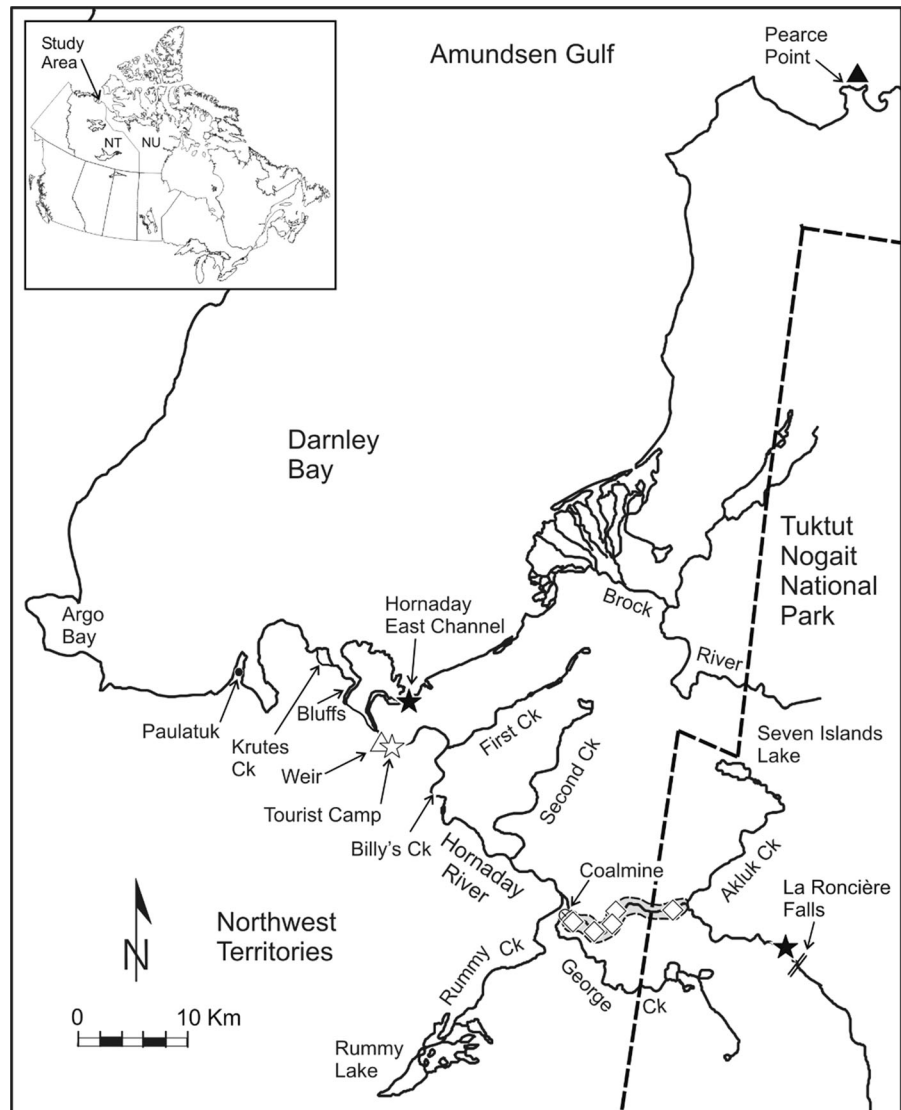
Salmonids are the most species-rich family present in the Arctic, with one species often noted for its distribution and abundance, ecologic diversity, and economic importance: Arctic charr, *Salvelinus alpinus* (L. 1758) (Reist et al., 2006, 2013). Arctic charr has a circumpolar distribution with a latitudinal range in North America extending from Ellesmere Island (83°N) in the north to northern New England (43°N) in the south. The species forms the basis of many community subsistence and/or commercial fisheries throughout the Arctic and subarctic regions, many of which are routinely monitored by government agencies in conjunction with local fishers. As a result, long-term datasets on the biological characteristics of the catch (e.g., age, length, and weight) have been compiled to assist managers in making informed decisions regarding conservation and use of these resources. In the face of increasing concerns about the impacts of northern development and/or climate change (Chu et al., 2005; Reist et al., 2006; Shuter et al., 2012; Reist et al., 2013), these databases now provide benchmarks against which the implications of large-scale anthropogenic impacts on Arctic charr may be gauged.

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 (Reist et al., 2006, 2013). By combining existing data with

environmental information (e.g., temperature, precipitation, etc.), it is possible to describe past relationships between climate and biological responses to climate-driven environmental variation (Power et al., 2000; Michaud et al., 2010; Godiksen et al., 2012). Responses (e.g., phenotypic plasticity and/or genetic adaptations) to overall environmental conditions have been seen as a strategy to perpetuate animal genomes (Venne & Magnan, 1989; Arnekleiv et al., 2006; Janhunen et al., 2009; Jonsson & Jonsson, 2014). Arctic charr are among the species known to be strongly influenced by climate variation (Chavarie et al., 2010; Finstad & Hein, 2012; Ulvan et al., 2012; Budy & Luecke, 2014) and have flexible life-history strategies adapted to local environmental conditions (Klemetsen et al., 2003; Klemetsen, 2010; Hammar, 2014). Thus, climate-driven increases in temperature and precipitation in Arctic areas may result in prevailing temperatures that are closer to thermal optimum for Arctic charr growth, longer growing seasons, increases in freshwater productivity (e.g., higher food ration access resulting in higher growth), and changes in the magnitude and timing of migration phenologies (Svenning & Gullestad, 2002; Finstad & Hein, 2012; Godiksen et al., 2012; Budy & Luecke, 2014; Gilbert et al., 2016). Thus, to mitigate for the possible impacts of climate change, fisheries management can use knowledge of past environmental–biological response relationships as a proxy for predicting possible climate-change effects on Arctic charr (Power et al., 2005; Kristensen et al., 2006).

One river for which it is possible to examine linkages between environmental variation and Arctic charr biological variation is the Hornaday River, Northwest Territories (69°21'N, 123°42'W; Fig. 1), where the subsistence catch has been monitored annually since 1990 (Harwood, 2009). Although limited life-history information exists for anadromous Arctic charr from the Hornaday River, studies suggest that fish from the Hornaday River go to sea and mature at earlier ages than in eastern Canada (Harwood, 2009), with smolts migrating to sea between the ages of 2 and 7 years (Harwood, 2009). Out migration coincides with the spring break up, which based on the freshet usually occurs between June 2 and 21 and the return upstream migrations commences in August (Harwood, 2009; Harwood & Babaluk, 2014; DFO, 2016). Age at first spawning, based on the youngest confirmed post-spawner caught to date, is 7 years, with few fish older than 10 years found in the Hornaday River (Harwood, 2009). Although fecundity and spawning

Fig. 1 Hornaday River (69°21'N, 123°42'W) and are with major landmarks of the area, adapted from Harwood & Babaluk (2014)



frequency are not known, it is assumed that most adults spawn every second year (Babaluk et al., 1998; Harwood, 2009; DFO, 2016).

In this study, available monitoring data for Arctic charr, caught near the mouth of the Hornaday River, were used to investigate possible linkages between measured population characteristics (e.g., age-specific length and weight) and climate-driven environmental variation. Specifically, we aimed to determine the influence of environmental variation (e.g., seasonal temperature and precipitation) on changes in length and weight characteristics using data on changes in length- and weight-based relative growths for 5–9-year-old Arctic charr gathered over a 13-year period (i.e., 1990–2003).

Establishing population biological characteristic linkages to past environmental conditions was also intended to provide a baseline reference against which future data might be compared to determine the significance of any observed changes occurring as a result of continuing ecological change at northern latitudes.

Materials and methods

Study area

The data for this study were collected from Arctic charr harvested from Hornaday River, a northward-

flowing river, which empties into Darnley Bay in the Amundsen Gulf region of the Western Arctic. The river varies in width (40–100 m) and depth (≤ 0.5 –3 m) along its 260-km length. Approximately 60 km upstream from the sea, a 20-m waterfall, La Roncière Falls, forms an impassable barrier to upstream fish migration (Harwood & Babaluk, 2014). The lower reaches of the river are the focus of an annual subsistence fishery for anadromous Arctic charr by residents from the nearby community of Paulatuk (69°21'N, 124°4'W).

Biological data

Fisheries and Oceans Canada, in conjunction with local fishers and the Fisheries Joint Management Committee (FJMC), monitored the anadromous catch (Reist et al., 1997) on the Hornaday in 1979, 1981, and 1990–2003, and collected biological data [fork length (mm), weight (g), sex, and age]. In 1979 and 1981, commercial harvesting was allowed, although catches did not exceed 6795 kg/year. In 1987, the fishery was closed to all but subsistence use, with annual catches in the 1990–2003 period varying between 1492 and 3850 kg (see Harwood (2009) for additional information). Aging was completed using sagittal otoliths read by the same reader at Fisheries and Oceans Canada following protocols described in Nordeng (1961) (Harwood, 2009; DFO, 2016).

Variations in net mesh 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 types and sizes, 11.4–16.6 cm (stretched measure, 3 panels) multimesh gillnets. Overall, 85% of the Arctic charr sampled during the monitoring program were caught using the 11.4 cm and 12.7 cm mesh nets, which included individuals ranging from 300 to 850 mm (Harwood, 2009). Data were further filtered to restrict analysis to specimens captured in a common period (mid-July to end of August) known to coincide with the known timing of late summer upstream migration of the stock and the annual subsistence fishery (Harwood, 2009; Harwood & Babaluk, 2014). To test for sexual dimorphism within an age-class, length and weight were compared between females and males across years using a two-way PerMANOVA in Past V.3 (Hammer et al., 2001).

Environmental data

Meteorological data for the years 1970–2003 were obtained from diverse sources for latitudinal and longitudinal co-ordinates as close to the Hornaday River mouth as possible (69°19'N, 123°4'). Monthly sea-surface temperatures (°C) were obtained from the Hadley Centre for Climate Prediction (U.K., Met Office, September 29, 2015). 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., 2003). The monthly air temperature (°C) and monthly precipitation (mm) from 1970 to 2003 were obtained from the Department of Geography of the Center for Climatic Research, University of Delaware (<http://climate.geog.udel.edu/~climate/index.shtml>, September 29, 2015). Data represent 0.5 degree latitude and longitude interpolations from a general circulation model simulation of historical meteorological station data. Meteorological data were processed to obtain seasonal averages (winter, spring, and summer) for each year. Winter was defined as the January–March period, spring was defined as the April–May period, and summer was defined as the June–August period.

Statistical analysis

Meteorological data were examined for temporal trends against an index of time. 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 conditions (Power et al., 2000). Multicollinearity among environmental variables was assessed using the Variance Inflation Factor (VIF). Environmental data were normalized (since they have different units), and a principal component analysis (PCA) was performed to characterize the overall variation in environmental conditions among years (1970–2003).

Length- and weight-at-age data for all years (1979, 1981, and 1990–2003) and individuals were pooled, which included Arctic charr ranging from 2 to 10 years. Data were then fit with the von Bertalanffy growth models (Ricker, 1975):

$$FL(t) = FL_{\infty} \left(1 - e^{K(t-t_0)} \right) \text{ and}$$

$$W(t) = W_{\infty} \left(1 - e^{K(t-t_0)} \right),$$

where $L(t)$ and $W(t)$ are, respectively, the fork length (mm) and weight (g) at age t (years); L_{∞} and W_{∞} are, respectively, the asymptotic length and weight; K is the growth coefficient, and t_0 is the theoretical age when the fish would have had a fork length or weight of zero. Resulting von Bertalanffy models were used to represent the average growth of Arctic charr during the study period.

To determine the effects of environmental variables on growth, a subset of the data were used. The subset included fish aged (5–9) as these were commonly captured each year with sufficient samples to calculate a mean (Online appendix, Table S1 and S2) and included only data from the longest available continuous period (1990–2003), to ensure no data gaps existed in the dataset used for the estimation of relative growth. The differences between age-specific mean annual size estimates were then calculated within the same cohort over the entire 1990–2003 period. Because annual growth decreases with age, annual age-specific growth estimates were centered on the mean age-interval growth estimate predicted by the von Bertalanffy equation to obtain an estimate of relative growth that accounted for the influence of age on growth (Ricker, 1975). For example, to estimate how much a fish aged 6 in 1991 grew over the previous year, the mean size of age 6 in 1991 was subtracted from the mean size of age 5 from the same cohort in 1990, and the resulting value was centered on the mean increase in size during the age 5–6 interval based on the von Bertalanffy equation as estimated above. Linear regressions were then used with year as the predictor variable to determine if there were changes in relative growth over time for each age-class.

Relative growth estimates (length and weight) were used as response variables in multiple regressions with environmental predictor variables that included summer sea-surface temperature (SSST), summer air temperature (Tsummer), and precipitation during spring (Pspring), summer (Psummer), and winter (Pwinter). Model selection was performed using AICc with all combinations of predictor variables and a null model included as potential candidate models. A total of 32 additive models were assessed, with no

interaction terms being considered. Finally, post hoc linear regressions were used to visualize the direction and the magnitude of the age-specific effects of each environmental variable on relative growth. Analyses were conducted in R version 3.4.2 (R Core Team, 2017).

Results

No significant temporal trends (all regression $P > 0.05$) were found for any of the examined environmental variable datasets (Fig. 2) and VIF values were lower than 3 indicating no significant collinearity among variables. The interaction of sex with year representing the sexual dimorphism within a year was not significant in length or weight for all ages (all $P \geq 0.05$), except for age 8 ($P < 0.05$). As differences between female and male at age 8 were not consistent among years (6 of 9 years showing significant differences between sexes) and sample sizes were generally small, female and male data were pooled for all age-classes (Online Appendix, Table S1 and S2).

PCA completed on the normalized environmental variables data yielded two combinations of climate variables that explained 63.7% of the observed variation (Fig. 3). The first PCA axis (PC1 = 34.1%) contrasted winter, spring, and summer precipitations, capturing the difference between wet and dry years. The second PCA axis (PC2 = 29.6%) represented both summer air and sea-surface temperatures, capturing differences between cold and warm years.

Von Bertalanffy growth models, based on Arctic charr fork length and weight data for all fish aged 2–10 years, were estimated as follows (Fig. 4):

Length

$$FL(t) = 705.0(1 - e^{0.23(t-t_0)});$$

Weight

$$W(t) = 4068.5(1 - e^{0.26(t-t_0)})^3$$

The relative growth in length (a) and weight (b) were variable among ages and years (Fig. 5). Linear regressions found no significant trends in length- or weight-based relative growth for any of

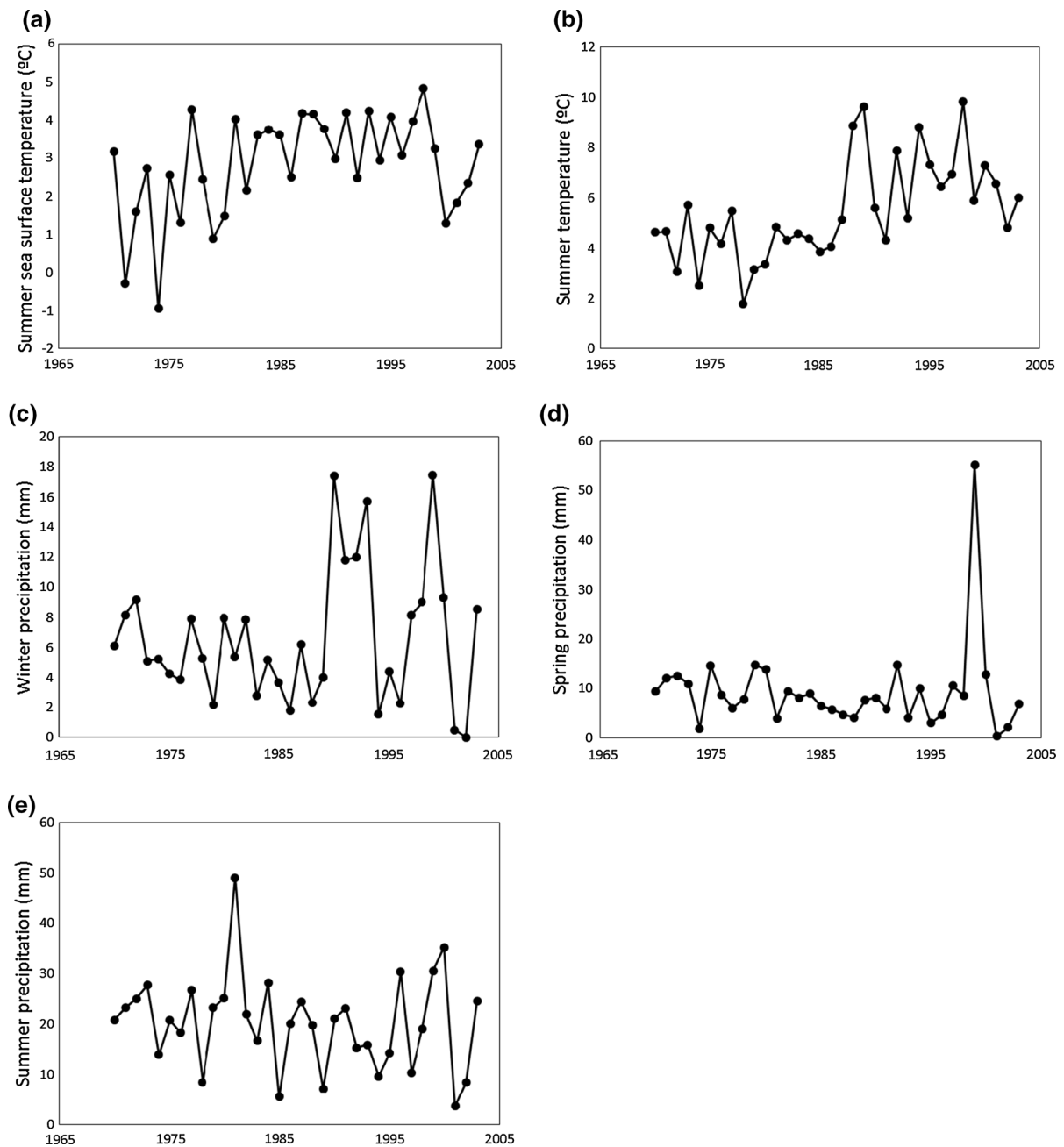


Fig. 2 Meteorological data for the Hornaday River area from 1970 to 2003 used as predictor variables in regression models explaining the variation in the mean length and weight characteristics of Hornaday River Arctic char. Plots of summer sea surface temperature ($^{\circ}\text{C}$; June–August) in (a), summer

temperature ($^{\circ}\text{C}$ June–August) in (b), total winter precipitation (mm; January–March) in (c), total spring precipitation (mm; April–May) in (d), and total summer precipitation (mm; June–August) in (e)

the considered age-classes over time (1990–2003) (all regression $P > 0.05$) (Fig. 6).

For relative growth in fork length, six multiple regression models with environmental variables had

ΔAICc values < 2 and were considered equally supported, with AICc values ranging from 492.5 to 494.3 (Table 1). For relative growth in weight, seven multiple regression models with environmental

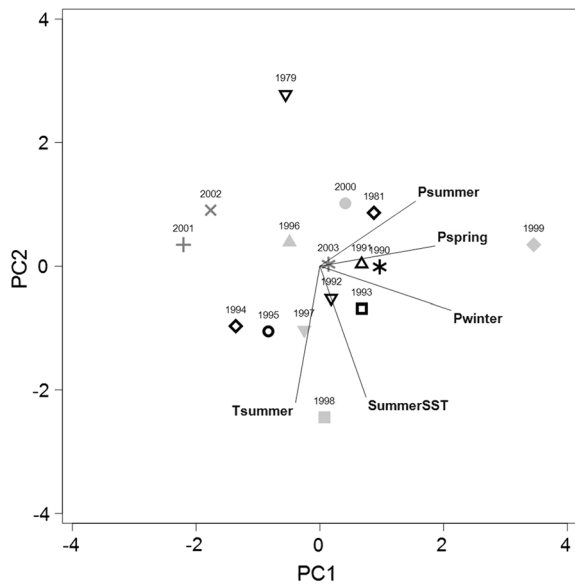


Fig. 3 Biplot of the two principal component axes for environmental variables used in regression models (see Tables 1 and 2), illustrating climate differences among years (1979, 1981, and 1990–2003). PC1 and PC2 explain 34.5% and 27.4%, respectively

variables had ΔAICc values < 2 and were considered equally supported, with AICc values ranging from 761.2 to 762.7 (Table 1). In all the length- and weight-supported models, precipitation was an important environmental variable, especially spring precipitation, which was included in all models (Fig. 7).

Post hoc linear regression evidence was found for age-specific relative length and weight growth effects. Age-6 was the only significant trend found with respect to temperature, with a decrease of growth (length) occurring with an increase in summer air temperature ($R^2 = 0.86$, $P \leq 0.01$). Temperature had no influence on weight growth, resulting in non-significant correlations for all age-classes and generally low correlative values.

Spring precipitation had no influence on length growth at younger age-classes (Age-5 and Age-6), but Age-7–Age-9 growth were positively influenced ($R^2_{\text{Age7}} = 0.31$, $P = 0.04$; $R^2_{\text{Age8}} = 0.10$, $P = 0.3$; and $R^2_{\text{Age9}} = 0.30$, $P = 0.05$). In contrast, summer and winter precipitations had no influence on length growth at all age-classes. For weight, a similar pattern of results was obtained, with spring precipitation having no influence at younger age-classes (Age-5 and Age-6), but significant positive influence on older age-

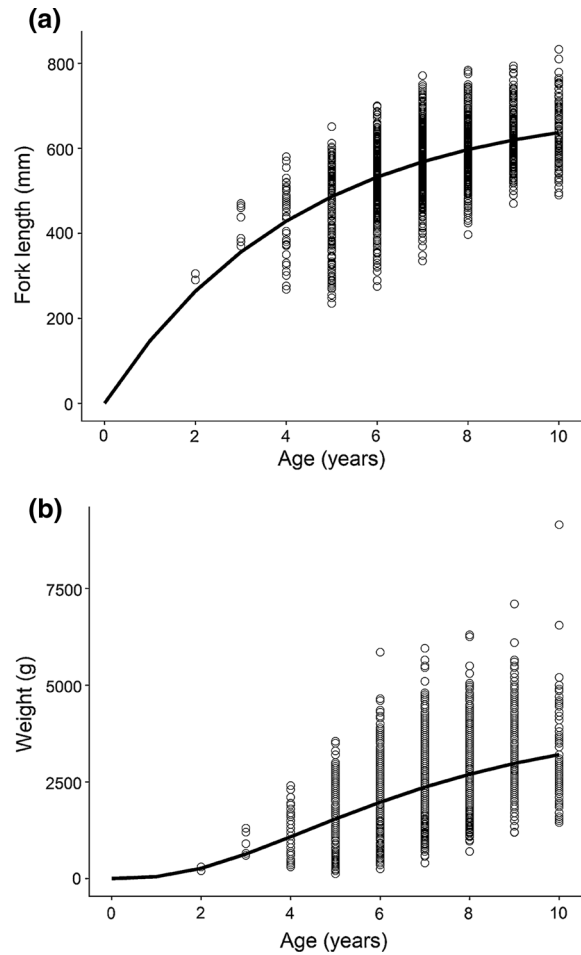


Fig. 4 Von Bertalanffy growth curve fitted for individual lengths and weights at age-of-capture resulting in mean growth curves based on fork length (a) and weight (b). All years (1979–2003) and individuals were pooled, which included all Arctic charr aged 2–10

classes ($R^2_{\text{Age7}} = 0.34$, $P = 0.03$ and $R^2_{\text{Age9}} = 0.48$, $P \leq 0.01$). Summer and winter precipitation also had no influence in weight growth ($P > 0.05$).

Discussion

General associations between temporal environmental variations and Hornaday Arctic charr relative growth in length and weight were found at the population level, with age-specific differences suggesting that the coupling between growth and environmental fluctuations varies by life-period. The strength of relationships in this study were generally low, highlighting the

complexity of interactions between climate variability and population responses (Rogers & Schindler, 2011; Griffiths et al., 2014). Changes in population biological characteristics may be correlated with other environmental variables for which long-term data in the Canadian Arctic are scarce, e.g., extent of sea-ice coverage, date of ice out, or prey availability, for which other studies have demonstrated significant

Fig. 6 Linear regression with 95% CI of estimates of annual relative growth based on fork length (mm) of Hornaday Arctic charr, aged 5–9 years captured from 1990 to 2003, with sea-surface and air temperatures, and precipitation variables used as regression explanatory variables

correlations (Gudbergsson, 2004; MacKenzie & Köster, 2004; Dempson et al., 2008; Harwood et al.,

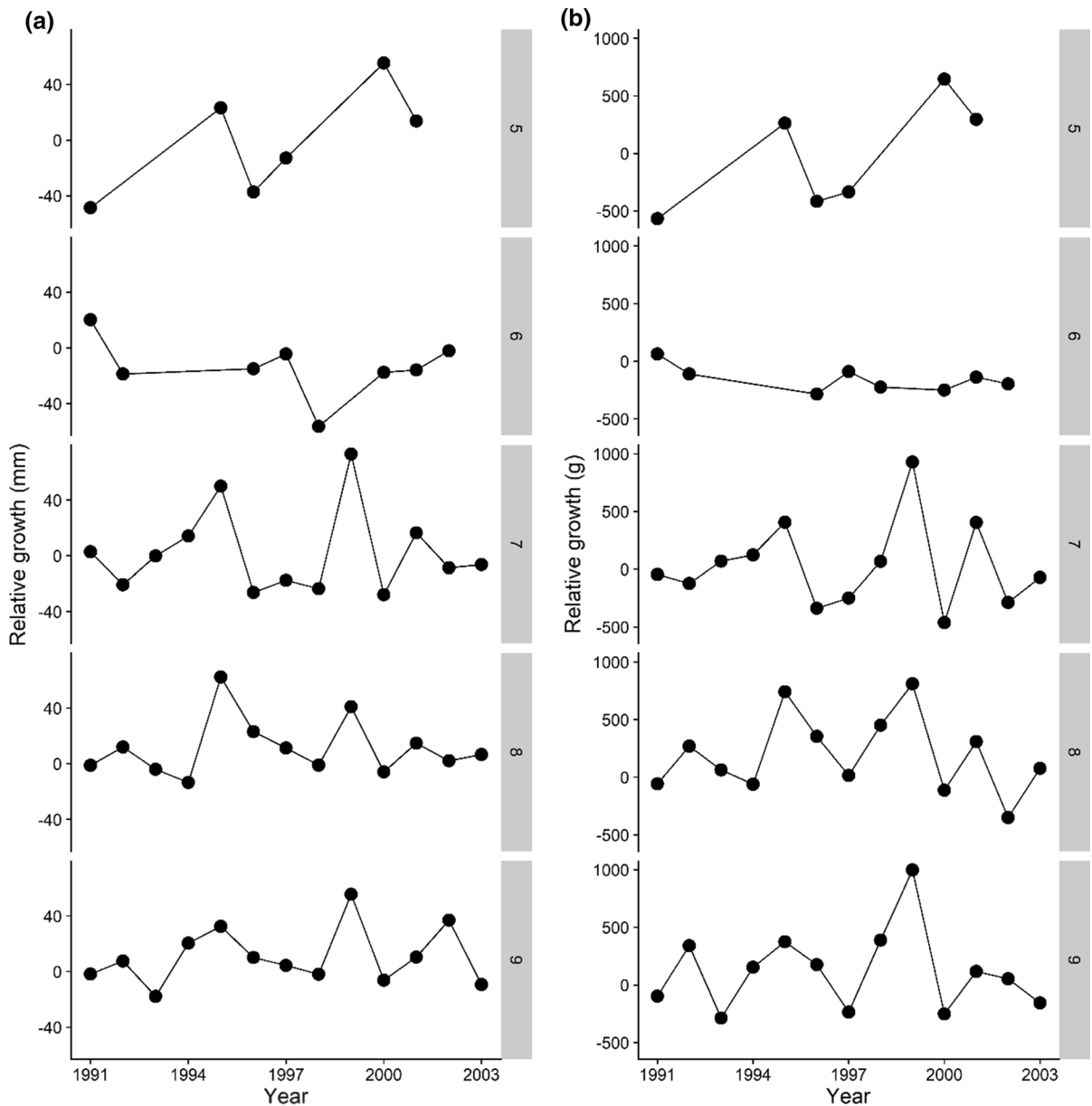
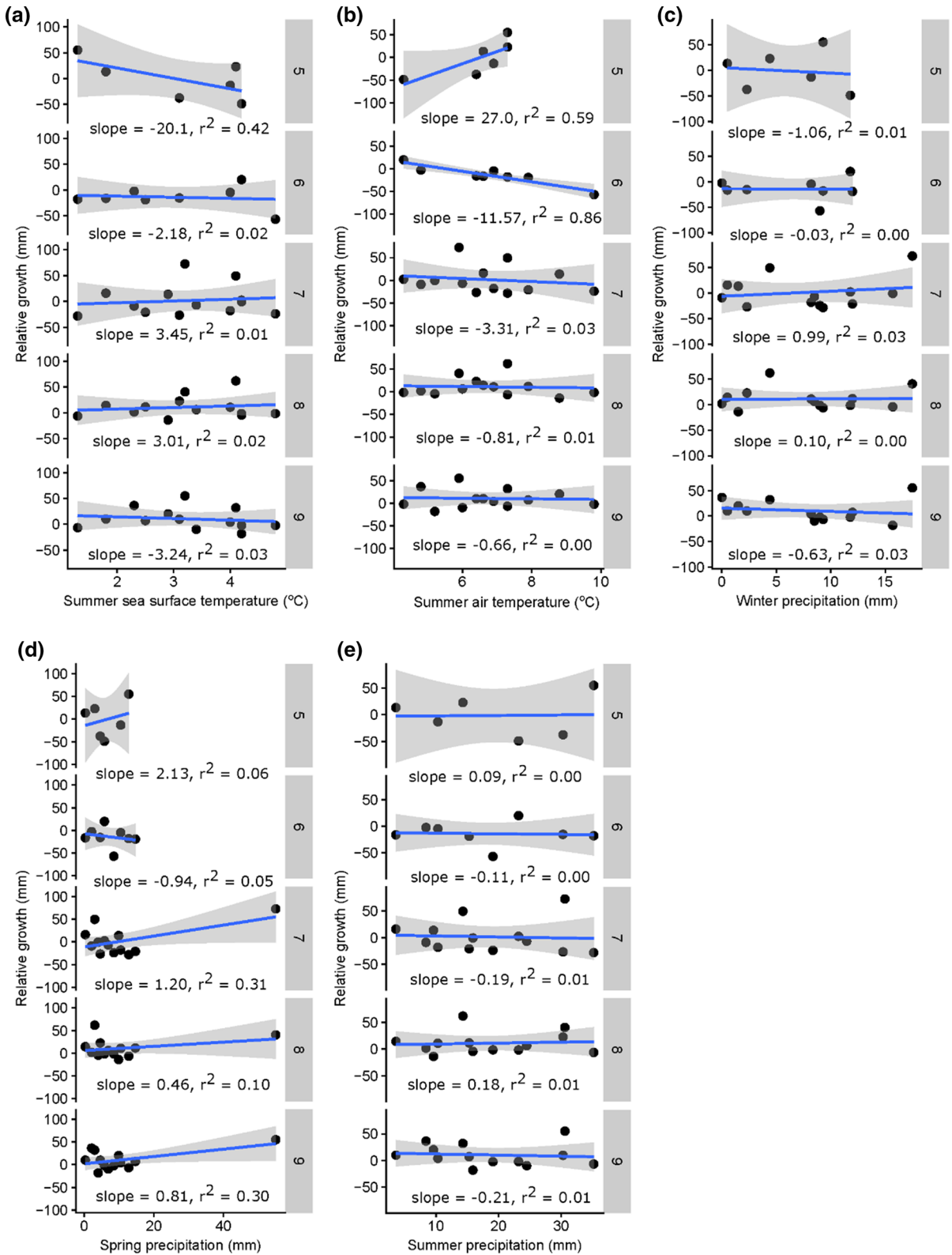


Fig. 5 Estimates of annual relative growth based on fork length (mm) (a) and weight (g) (b) from 1990 to 2003 capture data. No significant trends were found for any age-class (all $P > 0.05$)



2013; Budy & Luecke, 2014). While population responses to variation in environmental conditions can be seen on shorter time scales (i.e., extreme climatic events, 1–5 years), by examining long-term data, this study provides a broader timescale perspective with a more consistent climatic change impact perspective (Poesch et al., 2016).

The scope at which life-history characteristics are examined, from general (population) to specific (individual) perspectives, can influence the outcome of an investigative framework, since biological responses are not necessarily uniform over lifetimes (Clutton-Brock & Sheldon, 2010). At the population

Fig. 7 Linear regression with 95% CI of estimates of annual relative growth based on weight (g) of Hornaday Arctic charr, aged 5–9 years captured from 1990 to 2003, with air and sea-surface temperatures, and precipitation variables used as regression explanatory variables

level, length and weight growth models were mostly influenced by precipitation, spring precipitation particularly, and summer temperature. The significant correlation was with air temperature, rather than with SST, despite the coastal nature of anadromous Arctic charr in Arctic Canada. Their repeated movement between coastal and estuarine waters, and the their

Table 1 Relative fork length (mm) growth estimates from multiple regression models with environmental predictor variables: summer sea-surface temperature (SSST), summer

air temperature (Tsummer), and precipitation during spring (Pspring), summer (Psummer), and winter (Pwinter)

Model	Intercept	Slope	R^2	df	AICc	Delta	Weight
Pspring + Pwinter	2.71	Pspring: 1.29; Pwinter: - 1.59	0.22	4	492.5	0.00	0.180
Pspring + Pwinter + Tsummer	23.84	Pspring: 1.35; Pwinter: - 1.78; Tsummer: - 3.05	0.24	5	493.0	0.49	0.140
Pspring + Psummer + Pwinter	7.86	Pspring: 1.36; Psummer: - 0.41; Pwinter: - 1.34	0.23	5	493.8	1.22	0.099
Pspring + Psummer + Pwinter + Tsummer	30.25	Pspring: 1.44; Psummer: - 0.44; Pwinter: - 1.53; Tsummer: - 3.18	0.26	6	494.1	1.60	0.082
Pspring + Psummer	4.10	Pspring: 1.06; Psummer: - 0.59	0.19	4	494.2	1.61	0.081
Pspring	- 4.93	Pspring: 0.86	0.15	3	494.3	1.79	0.075

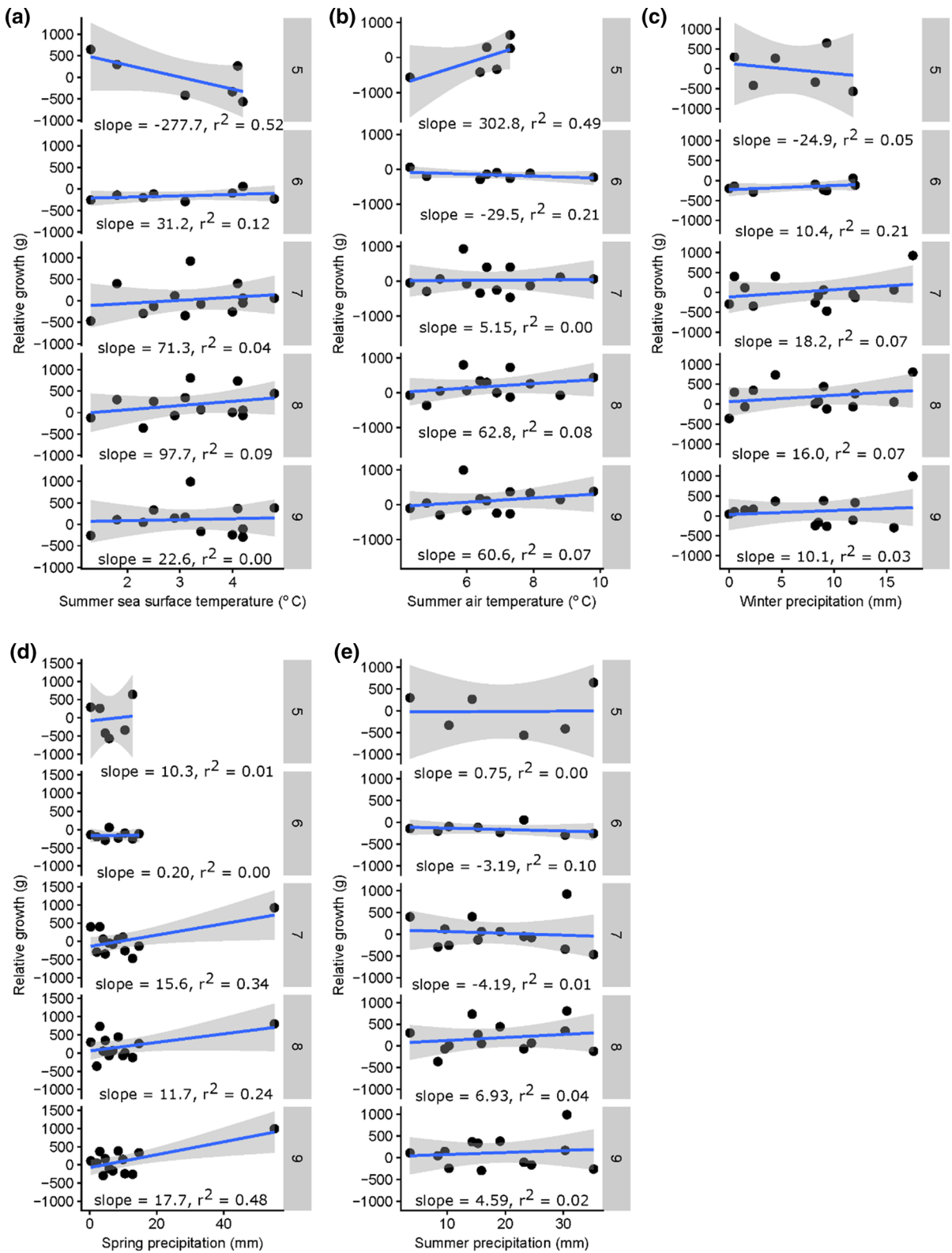
Model selection was performed using AICc with all combinations of predictor variables and a null model included as potential candidate models (32 possibilities, no interactions). Models within $< 2 \Delta AICc$ values of the top ranked model were considered equally supported and are presented

Table 2 Relative weight (g) growth estimates from multiple regression models with environmental predictor variables: summer sea-surface temperature (SSST), summer air

temperature (Tsummer), and precipitation during spring (Pspring), summer (Psummer), and winter (Pwinter)

Model	Intercept	Slope	R^2	df	AICc	Delta	Weight
Pspring + Psummer	25.97	Pspring: 17.88; Psummer: - 7.82	0.31	4	761.2	0.00	0.16
Pspring	- 93.80	Pspring: 15.25	0.27	3	761.5	0.53	0.12
Pspring + Psummer + Tsummer	- 208.70	Pspring: 17.49; Psummer: - 7.27; Tsummer: 34.12	0.33	5	761.9	0.87	0.10
Pspring + Tsummer	- 348.10	Pspring: 15.03; Tsummer: 38.36	0.29	4	762.0	0.97	0.096
Pspring + Pwinter	- 33.92	Pspring: 18.58; Pwinter: - 12.44	0.29	4	762.3	1.27	0.083
Pspring + Psummer + Pwinter	49.80	Pspring: 19.78; Psummer: - 6.71; Pwinter: - 8.50	0.32	5	762.7	1.72	0.066

Model selection was performed using AICc with all combinations of predictor variables and a null model included as potential candidate models (32 possibilities, no interactions). Models within $< 2 \Delta AICc$ values of the top-ranked model were considered equally supported and are presented



general occupancy of shallow depths (Spares et al., 2012; Moore et al., 2016) imply that measures of SST that average temperatures over broad spatial scales, including deeper oceanic areas and areas of marginal ice zones, do not adequately represent the thermal conditions experienced by shore-dwelling Arctic charr as well as ambient air temperatures.

Temperature appears to dominate more at younger ages and is replaced by precipitation at older ages when individuals approach expected asymptotic size, with the change likely reflecting age-specific shifts in importance between increases in length and reproduction (Klemetsen et al., 2003). Physiological demands can induce diverse age-specific reactions to common environmental stimuli, with gonad development holding significant implications for responses to environmental variation as a result of the implications for fitness of diverting surplus energy to gonad formation (Wootton, 2012; Jonsson et al., 2013; Murdoch et al., 2015). The general pattern of age-related changes in the importance of environmental variables with the onset of maturation would agree with the observed marked change in the Hornaday Arctic charr.

Temperature is an important, if not the most important, factor affecting fish physiology and behavior (Parra et al., 2009; Elliott & Elliott, 2010). For Hornaday Arctic charr below the age of maturation, temperature affected relative growth in length. Growth, however, is a complex phenomenon dependent on both temperature and food supply, which reflects the interaction of several axes in a multidimensional niche (Elliott, 1994; Magnuson et al., 1979; Larsson et al., 2005; Elliott & Elliott, 2010). Without suitable net addition of ration, a rise in temperature will reduce increases in length, i.e., scope for growth, as a result of increased metabolic costs (Russell et al., 1996; Kristensen et al., 2006; Sogard et al., 2012). In this study, the low correlation between summer precipitation and temperature might suggest that increased metabolic demands associated with the increasing temperature were not associated with sufficient precipitation-driven increases in productivity (as described below) to meet growth. Negative field-based relationships between growth and temperature, for Arctic charr and other salmonids, have been reported elsewhere (Kristensen et al., 2006; Rikardsen et al., 2007; Elliott & Elliott, 2010; Michaud et al., 2010; Almodóvar et al., 2012; Griffiths et al., 2014). Under natural conditions, where feeding is restricted,

the best growth rates have been observed at temperatures lower than those typically reported from laboratory experiments (Elliott, 1994; Jobling, 1994; Morita et al., 2010; Jonsson & Jonsson, 2014). Hesthagen et al. (2004) have also demonstrated that the strength of temperature–growth relationships can vary as a function of age in salmonids, suggesting that age-specific effects in salmonids might be more common than originally thought.

The lifetime fitness of several anadromous Arctic charr populations have been found to be contingent on productivity differences between freshwater and marine habitats and their connectivity (Gross et al., 1988; Finstad & Hein, 2012; Gilbert et al., 2016). Changes in the flow regime (e.g., timing and intensity) of rivers into estuaries via run-offs positively influence nutrient concentrations (Beamish, 1993; Linnansaari et al., 2012) and redistributions, with beneficial consequences for the availability, quality, size, and spatial distribution of prey items for fish (Kennedy et al., 2002; Torres et al., 2003; Finstad et al., 2011; Finstad & Hein, 2012). Potential variations in prey resources would ultimately be reflected in coastal fisheries (Dempson et al., 2002; Salen-Picard et al., 2002; Darnaude et al., 2004). In the context of the Hornaday River system, permafrost might have minimized groundwater flows such that rain events have the potential to cause pulses of high water flows in the river and its tributaries, thereby increasing freshwater discharge in Darnley Bay (i.e., estuary habitat) (Babaluk et al., 1998; Harwood, 2009). Variations in seasonal phenologies (e.g., ice break-up and out migration) related to variations in precipitation and flow have been linked to changes in the quality and quantity of prey in Darnley Bay (Walsh, 2008) and implicated in recent changes in Arctic charr growth rates (Harwood, 2009). Indeed, high growth rates linked with extreme precipitation events were observed in this study. Variations in seasonal phenologies related to river flow and precipitation can also affect Arctic charr downstream and/or upstream migration by influencing timing and/or facilitating access to specific habitats (Berg, 1995; Finstad & Hein, 2012; Harwood & Babaluk, 2014; Gilbert et al., 2016). Thus, precipitation may play an important role in this system through indirect bottom-up effects by enhancing productivity and by increasing connectivity (Harwood & Babaluk, 2014).

Conclusion

Findings from this study indicated some environmental effects on Hornaday River Arctic charr growth. Overall, spring precipitation and summer air temperature seem to be the most important environmental influences on Arctic charr probably because of their respective impacts on opportunities for acquiring surplus energy for growth. The pattern of decreasing age-related importance of temperature and increasing age-related importance of precipitation-driven nutrient availability suggested that the coupling between growth and environmental effects varied by life-period. Environmental variables alone, however, did not account for all the temporal variations in changes of length and weight growth throughout years, implying that other factors are important for determining Hornaday River population biological characteristics (e.g., density, Parra et al. (2011); prey base, Dempson et al. (2008); or ocean water mass movements, Pálsson & Thorsteinsson (2003)). Furthermore, as has been noted by Michaud et al. (2010), cumulative environmental conditions may have a more important impact on biological characteristics than single season variation.

Arctic charr, as a species, have been known to be sensitive to minor changes in inhabited biotic and abiotic environments (Langeland, 1995; Reist et al., 2013). As cold-water specialists, Arctic charr are especially vulnerable to climate change because it will significantly alter the evolved physiological strategies for dealing with the thermal environments of the Arctic, e.g., cool summers and long winters (Shuter et al., 2012). A great deal remains unknown about the mechanism(s) likely to govern Arctic charr survival and resilience responses to climate change (Power et al., 2008). As highlighted in this study, insights from long-term fisheries and environmental data can improve understanding of the population-specific responses of Arctic charr at local scales to climate change. Furthermore, the development and implementation of integrated monitoring techniques that include collaborations with local communities and other disciplines (e.g., meteorology, oceanography, limnology, etc.) would greatly improve our abilities to detect and manage climate change impacts on fish populations.

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