

# Temporal instability of lake charr phenotypes: Synchronicity of growth rates and morphology linked to environmental variables?

Louise Chavarie<sup>1,2,3</sup>  | Steve Voelker<sup>4</sup> | Michael J. Hansen<sup>5\*</sup> | Charles R. Bronte<sup>6</sup> | Andrew M. Muir<sup>7</sup> | Mara S. Zimmerman<sup>8</sup> | Charles C. Krueger<sup>9</sup>

<sup>1</sup>Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

<sup>2</sup>Beaty Biodiversity Research Center, University of British Columbia, Vancouver, BC, Canada

<sup>3</sup>Scottish Centre for Ecology and the Natural Environment, IBAHCM, Rowardennan, Loch Lomond, Glasgow, UK

<sup>4</sup>SUNY College of Environmental Science and Forestry, Syracuse, NY, USA

<sup>5</sup>U.S. Geological Survey, Hammond Bay Biological Station, MI, USA

<sup>6</sup>U.S. Fish and Wildlife Service, Green Bay Fish and Wildlife Conservation Office, New Franken, WI, USA

<sup>7</sup>Great Lakes Fishery Commission, Ann Arbor, MI, USA

<sup>8</sup>Coast Salmon Partnership and foundation, Aberdeen, WA, USA

<sup>9</sup>Department of Fisheries and Wildlife, Center for Systems Integration and Sustainability, Michigan State University, East Lansing, MI, USA

## Correspondence

Louise Chavarie, Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway.  
Email: chavarie@ualberta.ca

## Funding information

Great Lakes Fishery Commission

## Abstract

Pathways through which phenotypic variation among individuals arise can be complex. One assumption often made in relation to intraspecific diversity is that the stability or predictability of the environment will interact with expression of the underlying phenotypic variation. To address biological complexity below the species level, we investigated variability across years in morphology and annual growth increments between and within two sympatric lake charr *Salvelinus namaycush* ecotypes in Rush Lake, USA. A rapid phenotypic shift in body and head shape was found within a decade. The magnitude and direction of the observed phenotypic change were consistent in both ecotypes, which suggests similar pathways caused the variation over time. Over the same time period, annual growth increments declined for both lake charr ecotypes and corresponded with a consistent phenotypic shift of each ecotype. Despite ecotype-specific annual growth changes in response to winter conditions, the observed annual growth shift for both ecotypes was linked, to some degree, with variation in the environment. Particularly, a declining trend in regional cloud cover was associated with an increase of early-stage (ages 1–3) annual growth for lake charr of Rush Lake. Underlying mechanisms causing changes in growth rates and constrained morphological modulation are not fully understood. An improved knowledge of the biology hidden within the expression of phenotypic variation promises to clarify our understanding of temporal morphological diversity and instability.

## KEYWORDS

allometry, dendrochronology, developmental stability, morphological modulation, otolith, plasticity, *Salvelinus namaycush*, temporal changes

\*Retired.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Evolutionary Applications* published by John Wiley & Sons Ltd

## 1 | INTRODUCTION

A rapidly changing climate can have wide-ranging effects on organisms across ecosystems, which fosters a need to understand how ecosystems will respond to this variation in terms of structure and function (Montoya José & Raffaelli, 2010; Pacifici et al., 2015). Contemporary climate change, including rapid increases in global temperatures, represents one of the most serious and current challenges to ecosystems, not only by threatening ecosystems directly (Norberg, Urban, Vellend, Klausmeier, & Loeuille, 2012), but also by contributing to cumulative and additive effects with other perturbations (e.g. industrial development, pollution, overharvest and nonnative species; CAFF, 2013; Poesch, Chavarie, Chu, Pandit, & Tonn, 2016). Ecosystems are mosaics of different habitats; climate change combined with abiotic and biotic variation across these habitats may lead to major eco-evolutionary responses (Grimm et al., 2013; Ware et al., 2019). Rapid biological responses to variation associated with environmental variation have already been detected at all levels, from individuals to species, communities and ecosystems (Heino, Virkkala, & Toivonen, 2009).

The importance of phenotypic variability has been emphasised in evolutionary and ecological population dynamics (Kinnison & Hairston, 2007; Schoener, 2011) because variation fuels evolutionary change (Stearns, 1989). Pathways through which phenotypic variation arises among individuals can be complex. Phenotypic variation can affect population dynamics such as through reproductive and mortality pathways (Bolnick et al., 2011). Furthermore, the magnitude of plasticity in the variation of trait expression differs among populations and ecotypes within a population (Skúlason et al., 2019). A conceptual framework to predict evolutionary and ecological consequences of climate change is currently limited by the scarcity of empirical data demonstrating phenotypic changes over time among individuals within ecosystems. The causes, patterns, and consequences of ecological and evolutionary responses to environmental variability need to be quantified across species, space and time.

Given rapid environmental changes are occurring within aquatic ecosystems, phenotypic differences among individuals must not be taken as negligible and ecologically inconsequential. Phenotypic variation is driven by switches along developmental pathways (West-Eberhard, 2003) that in some cases, can adjust immediately to variable environmental conditions (Japyassú & Malange, 2014). Environmental factors can induce a component of variation that introduces fine-grained variation around coarse-scale temporal trends, resulting in year-to-year variation in phenotypes but not in genotypes—because genetic changes are not expected to be so responsive (Merilä & Hendry, 2014). Thus, phenotypic variability, both in means and variance, can provide an evolutionary scope for a population in the face of changing selection regimes by affecting population dynamics and probabilities of extinction (Chevin, Lande, & Mace, 2010; Johnson, Grorud-Colvert, Sponaugle, & Semmens, 2014; Reed, Waples, Schindler, Hard, & Kinnison, 2010). Although models have often assumed stable ecological evolutionary

equilibrium (Maynard, Serván, Capitán, & Allesina, 2019; Skúlason et al., 2019; Svanbäck, Pineda-Krch, & Doebeli, 2009), temporal variation in phenotypes among cohorts within an ecotype may not be ecologically trivial in a rapidly changing world.

Lake charr are known to display intraspecific variation, mainly diversifying along a depth gradient, with shallow- versus deep-water ecotypes exploiting different prey resources within a lacustrine system (Chavarie et al., 2021). By selecting a case of co-existing shallow- and deep-water ecotypes of lake charr in Rush Lake, located at the southern edge of the species range (Figure A1; Chavarie et al., 2016), we examined the response of lake charr to environmental variation below the species level. Lake charr ecotypes in Rush Lake are likely to integrate diverse signals of climate variation across multiple trophic levels (Black, Matta, Helser, & Wilderbuer, 2013) because they exploit different prey items (Chavarie et al., 2016), invertebrates (deep-water ecotype) vs. foraging fish (shallow-water ecotype). Additionally, the effect of environmental variation, such as in temperature, on growth rates of aquatic organisms varies, especially across depths, in part because deep-water habitats are usually more environmentally stable (Jeppesen et al., 2014; Murdoch & Power, 2013; Thresher, Koslow, Morison, & Smith, 2007). Considering that growth chronologies provide robust data sets for assessment of temporal and spatial environmental variation and its ecological consequences, variation across cohorts, ecotypes, species, and communities can be assessed (Black, 2009).

In this study, we tested whether phenotypic expression of two Rush Lake lake charr ecotypes remained stable or changed over time. We predicted that if a rapid change in phenotypic expression occurred and this change was associated with environmental variation, the shallow-water ecotype would display a greater magnitude of variation than the deep-water ecotype due to the shallow-water habitat being more responsive and sensitive to contemporary climate change. We measured phenotypic expression in terms of morphology and growth chronology. The objectives of our study were to (1) quantify the morphological variation between and within lake charr ecotypes over a ten-year period, (2) determine whether patterns of growth chronologies expressed by ecotypes were temporally synchronous with each other and associated with the phenotypic variation displayed within each ecotype; and (3) examine whether annual growth rates of lake charr ecotypes were related to environmental variation by using tree-ring cross-dating techniques.

## 2 | MATERIAL AND METHODS

### 2.1 | Assignment of lake charr ecotypes

Rush Lake is a small lake (1.31 km<sup>2</sup>) that contains deep-water (>80 m) and is <2 km from Lake Superior (Chavarie et al., 2016). Rush Lake provided the first documented example of sympatric lake charr ecotypes in a small lake, diverging along a depth gradient. Two co-existing ecotypes of lake charr were found: a large stream-lined-bodied shallow-water lake charr (lean ecotype) and a small

plump-bodied deep-water ecotype (huronicus ecotype) (Figure A1; Chavarie et al., 2016; Hubbs, 1929).

Lake charr caught in 2007 were previously assigned to ecotype (Chavarie et al., 2016) and assignments for lake charr caught in 2018 used the same methodology (see Appendix B, Muir et al., 2014). Twenty sliding semi-landmarks and six homologous landmarks were digitized from each image to characterize head shape and 16 homologous and four sliding semi-landmarks were digitized from whole-body images to characterize body shape. Landmarks and semi-landmarks were digitized as *x* and *y* coordinates using TPSDig2 software (<http://life.bio.sunysb.edu/ecotype>). Digitized landmarks and semi-landmarks were processed in a series of Integrated Morphometrics Programs (IMP) version 8 (<http://www2.canisius.edu/~sheets/ecotypesoft>), using partial warp scores, which are thin-plate spline coefficients. Morphological methods and programs are described by Zelditch, Swiderski, and Sheets (2012) and specific procedures were described by Chavarie, Howland, and Tonn (2013). All morphological measurements were size standardized by using centroid sizes (Zelditch et al., 2012).

## 2.2 | Temporal morphological variation between ecotypes and years

All data from 2007 and 2018 were combined to align all samples in the same shape space and partial warps for temporal morphological analyses between ecotypes and years. Principal component analysis (PCA) of body- and head-shape data was used to visualize morphological variation between and within lake charr ecotypes and years using PCGen8 (IMP software). Canonical variate analyses (CVA) and validation procedures on body and head shape data were used to assess temporal differences within and between ecotypes using CVAGen (IMP software). Jackknife validation procedures included a test of assignment, with 1000 jackknife sets using 20% of our data as unknowns (Zelditch et al., 2012). Single-factor permutation multivariate analysis of variance (MANOVA) with 10,000 permutations of CVAGen was used to test whether body and head shape differed between and within (i.e. years) ecotypes. If MANOVA indicated differences among groups ( $\alpha < 0.05$ ), procrustes distance means were calculated for pairwise comparisons using TWOGROUP from the IMP software as post hoc tests (García-Rodríguez, García-Gasca, Cruz-Agüero, & Cota-Gómez, 2011). Procrustes distance for each pairwise comparison described the magnitude of difference between ecotypes and years. A bootstrapped Goodall's *F* statistic ( $N = 4900$  bootstraps; full Procrustes based) was used to determine whether pairwise comparison differed. Allometric trajectories in body and head shape were compared between ecotypes and years by regressing PC1 scores (size standardized data) against centroid size (i.e., measure of size) (e.g., variation in developmental pathways can result in allometric trajectory patterns that can be parallel, divergent, convergent, or common; Figure A2; Simonsen et al., 2017); an allometric relationship occurred if the slope differed from 0.

Relative body condition was compared between ecotypes and years in a 2-way analysis of variance (ANOVA), with main effects for ecotype and year and the interaction between ecotypes and years (Zar, 1999). To correct for size-related trends in body condition, relative body condition was defined as residuals from the power relationship between  $\log_{10}(W)$  and  $\log_{10}(TL)$  (Hansen et al., 2016). If the ecotype\*year interaction was significant, years were compared within ecotypes and ecotypes were compared within years in 1-way ANOVAs. To visualize the results, least-squares means ( $\pm$ SE) from the ANOVA were back-transformed from logarithms into original units of measure.

## 2.3 | Back-calculated length at age from otoliths: growth patterns displayed by ecotypes through time

Sagittal otoliths were used to estimate lake charr age and growth increments for fish sampled in 2007 and 2018. Otolith thin sections have been validated for age estimation of lake charr to an age of at least 50 years (for otolith preparation, see Appendix B; Campana, Casselman, & Jones, 2008). Otolith growth measurements can be used for several different purposes to gain ecological insight, but often need different analytical techniques to answer different questions. Towards this end, we used three analytical techniques and have provided a summary of the advantages and disadvantages of each (Table A1).

To determine whether patterns of growth chronologies expressed by ecotypes were temporally synchronous with each other, growth in length with age was modelled using a parameterization of the Von Bertalanffy length-age model (Gallucci & Quinn, 1979; Quinn & Deriso, 1999):

$$L_t = L_\infty \left( 1 - e^{-\left(\omega/L_\infty\right)(t-t_0)} \right) + \varepsilon$$

The length-age model describes back-calculated length  $L_t$  (mm) at age  $t$  (years) as a function of age at length = 0 ( $t_0$  = years; incubation time of embryos from fertilization to hatching), early annual growth rate ( $\omega = L_\infty \times K$  = mm/year; Gallucci & Quinn, 1979), theoretical maximum length ( $L_\infty$  = mm) and residual error ( $\varepsilon$ ). Parameters  $\omega$  and  $L_\infty$  were estimated using nonlinear mixed-effect models, package 'nlme' (R Core Team, 2016), with a fixed population effect (the average growth curve for the population from which individual fish were sampled), individual as random effect (growth curves for individual fish sampled from the population), and sex (male or female), ecotype (lean or huronicus) and sampled year (2007 or 2018) as fixed factors (to compare average growth curves between sexes, ecotypes and years; Vigliola & Meekan, 2009). Mixed-effects models are appropriate for modelling the within-group correlation of longitudinal, auto-correlated and unbalanced data, such as back-calculated growth histories (Pinheiro & Bates, 2000). Eight models of varying complexity were compared using AIC statistics (Burnham & Anderson, 2004): (1) ecotypes, sexes and sample years all included; (2) ecotypes and sample years both included; (3) ecotypes and sexes

both included; (4) sexes and sample years both included; (5) ecotypes only included; (6) years only included; (7) sexes only included; and (8) neither ecotypes, sexes nor years included.

Annual growth increments were modelled using a linear mixed-effects model (Weisberg, Spangler, & Richmond, 2010), wherein annual growth increments were modelled as a function of a fixed age effect (age of the fish when the increment formed), a random year effect (year in which the increment formed), a random fish effect (unique identifier for individual fish) and residual variation. The fixed age effect accounts for the fact that growth increments decline with age approximating a negative exponential curve. The random year effect reflects average increment width associated with each year of growth, after accounting for age effects (i.e., growth increment declines with age). The random year effect accounts for year-to-year environmental effects as random draws from a normal distribution, with a different draw for each year. The random fish effect accounts for fish-to-fish variation in growth as random draws from a normally distributed population with a different draw for each fish. The last source of variation is unmodelled residual variation. Differences between sexes (male or female), ecotypes (lean or huronicus), and sample years (2007 or 2018) were tested by including sex, ecotype and sample year as fixed effects.

## 2.4 | Otolith increment cross-dating: growth of lake charr in relation to environmental variation

In recent decades, advancements in dendrochronological techniques have been increasingly applied to sagittal otoliths, leading to novel insights on how broad-scale climate variation can impact both freshwater and marine systems (Black, Boehlert, & Yoklavich, 2005; Black et al., 2013; Matta, Black, & Wilderbuer, 2010). The use of dendrochronological methods (i.e. cross-dating techniques) ensures that specific growth annuli are assigned to an exact year (Black, Biela, Zimmerman, & Brown, 2012; Black et al., 2005, 2013). In turn, this process enhances connection to common environmental signals across fish, which have synchronously limited growth in certain years. To assign otolith growth increments to exact calendar years, transverse sections of sagittal otoliths were aligned by calendar year and cross-dated visually using the list method (Yamaguchi, 1991) to confirm years when particularly large or small otolith increments would be expected. Thereafter, visual cross-dating was statistically confirmed using COFECHA software (Holmes, 1983). In using COFECHA, otolith time series with series intercorrelation values (i.e.,  $R_{bar}$ ) lower than 0.20 with the initial master chronology were removed and placed in a separate group that included more than one third of all fish sampled. In a previous study of lake charr otolith variation,  $R_{bar}$  values ranged from 0.42 to 0.97 (Black et al., 2013), supporting the assumption that otolith width series with  $R_{bar} < 0.20$  included anomalous inter-annual growth variation that did not match the initial master chronology. Otolith increment time series with  $R_{bar} < 0.2$  underwent a second round of cross-dating with COFECHA, separately from those that matched better with the initial master

chronology. Because otolith increment data grouped together by ecotype without *a priori* knowledge of ecotype, all subsequent chronologies and analyses were conducted separately based on ecotype assignment from the morphological analyses described above.

Dendrochronological detrending methods generally attempt to remove growth variation and emphasize inter-annual variation in growth controlled by climate (Fritts, 2012). The first approach to detrending used the ARSTAN program (Cook & Krusic, 2014) to fit cubic splines of various rigidity based on fish age. Thereafter, autoregressive modelling was used to enhance inter-annual growth variability and the resulting indexed time series averaged within calendar years using a bi-weight robust mean. Thereafter, we undertook a second regional chronology standardization (RCS) approach known to better enhance low-frequency signals compared to the cubic spline method (Table A1; Briffa & Melvin, 2011). This detrending method divided each raw growth increment value by that expected from the mean growth increment for each ecotype and age combined (Figure A3). These ratios were then multiplied by 100 and averaged within calendar years to yield a percentage change in growth for each year. In subsequent analyses of environmental influence on growth chronologies, data from each lake charr were truncated to feature only growth during young ages (age 1–3); which were excluded in earlier age-effect analyses but are a critical stage to phenotypic variation linked to environmental differences (Angilletta, Steury, & Sears, 2004; Georga & Koumoundouros, 2010; Ramler, Mitteroecker, Shama, Wegner, & Ahnelt, 2014). The approach employed for these comparisons corrected for age directly rather than using ARSTAN detrending (see Methods above and Table A1). We also limited the analysis to calendar years where each combination of ecotype and collection period included otolith data from at least seven fish. This constrained the calendar years investigated to 1986 to 2012 for huronicus ecotype and 1988 to 2010 for the lean ecotype.

Otolith increments, detrended with the ARSTAN program, were calculated as means within a year for both ecotypes and were initially compared against monthly resolution climate data for the corresponding year. Based on *a priori* knowledge of fish biology and lake-effect climate phenomena, temperature, precipitation and cloud cover were selected as environmental variables (Chavarie, Reist, Guzzo, Harwood, & Power, 2018; Voelker et al., 2019). Interpolated climate data (e.g. air temperature and precipitation) were obtained from ClimateNA version 5.6 software (Wang, Hamann, Spittlehouse, & Carroll, 2016). Cloud cover climate data from airports within 7 km of Lake Superior were obtained at daily resolution from the NOAA Great Lakes Environmental Research Laboratory (<https://www.glerl.noaa.gov/>) and summarized by month.

Pearson correlation values were calculated between each ecotype-specific growth chronology and monthly climate variables for the corresponding and previous two year (i.e., to detect lag effect). After initial inspection of correlations between annual growth increments and monthly climate variables, the number of potential explanatory variables was consolidated into seasonal means, whereas winter to spring was defined as December through the next April

for a corresponding year, summer was defined as June to August, and fall was defined as September to November. Autocorrelation was expected to be present in otolith increment time series and resulting chronologies due to year-to-year lags in growth owing to fat storage and subsequent metabolic withdrawals, skip spawning effects, and climate and climatic-effects on water temperature. Robust assessments and modelling of autocorrelation on short time series are statistically impossible. Thus, we quantified what proportional weighting of climate data among the corresponding and two previous years produced the largest gains in Pearson correlations between otolith growth increment and seasonal climate data from an individual year to provide a window into how climate signals are incorporated into fish growth.

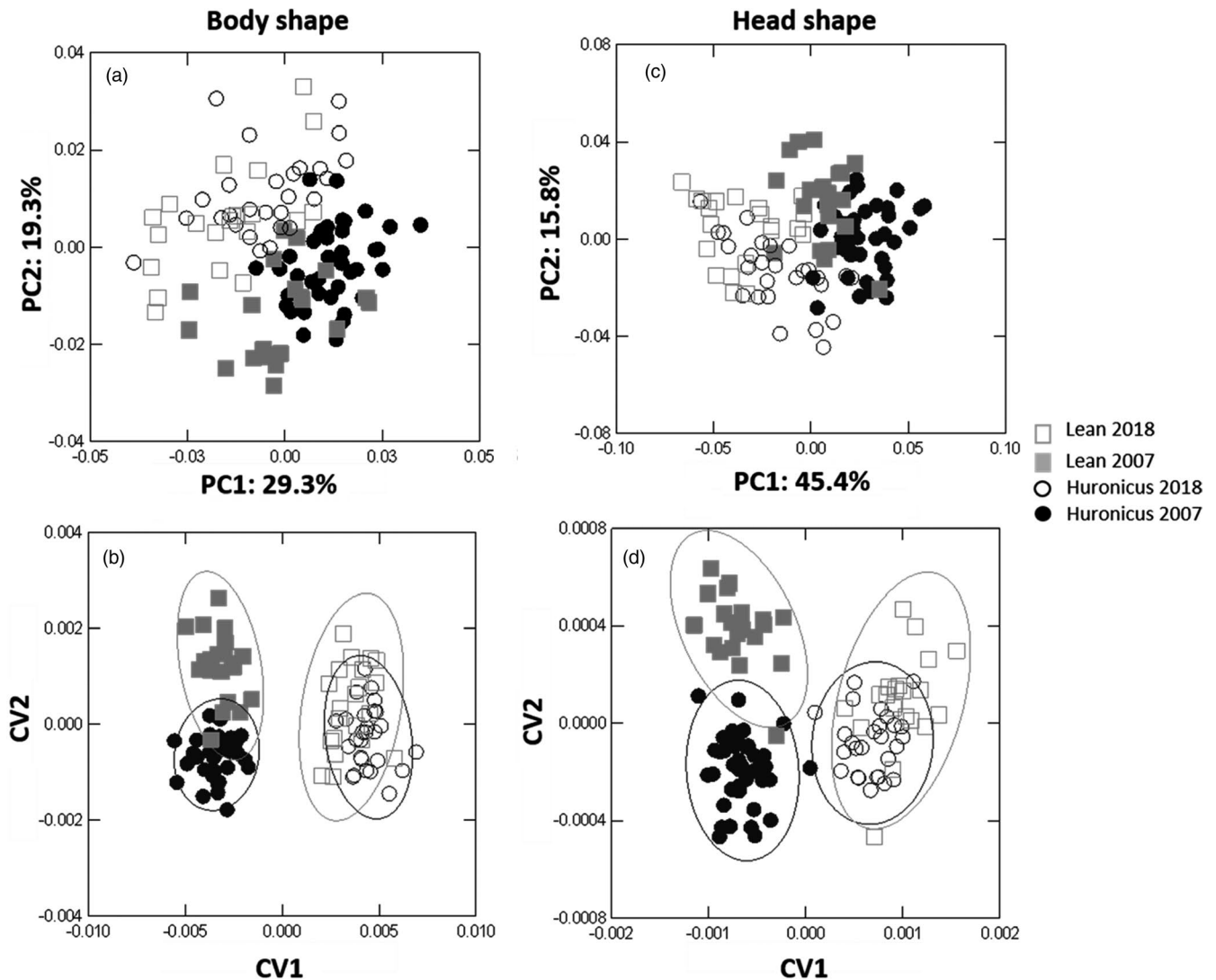
The influence of climate on otolith growth increment was assessed using forward selection multiple regression models, package 'lm' (R Core Team, 2016). More specifically: weighted temperature, precipitation, and cloud cover for each of four seasons as well as winter precipitation as snow (i.e., 13 total climate variables) were

introduced iteratively to identify, for each ecotype separately, the variables that explained the most variation in otolith growth, which variables were significant ( $\alpha < 0.05$ ), and which combination resulted in higher Akaike Information Criterion (AIC) values (Burnham & Anderson, 2004) and were retained in the models. No models with more than two variables increased AIC values.

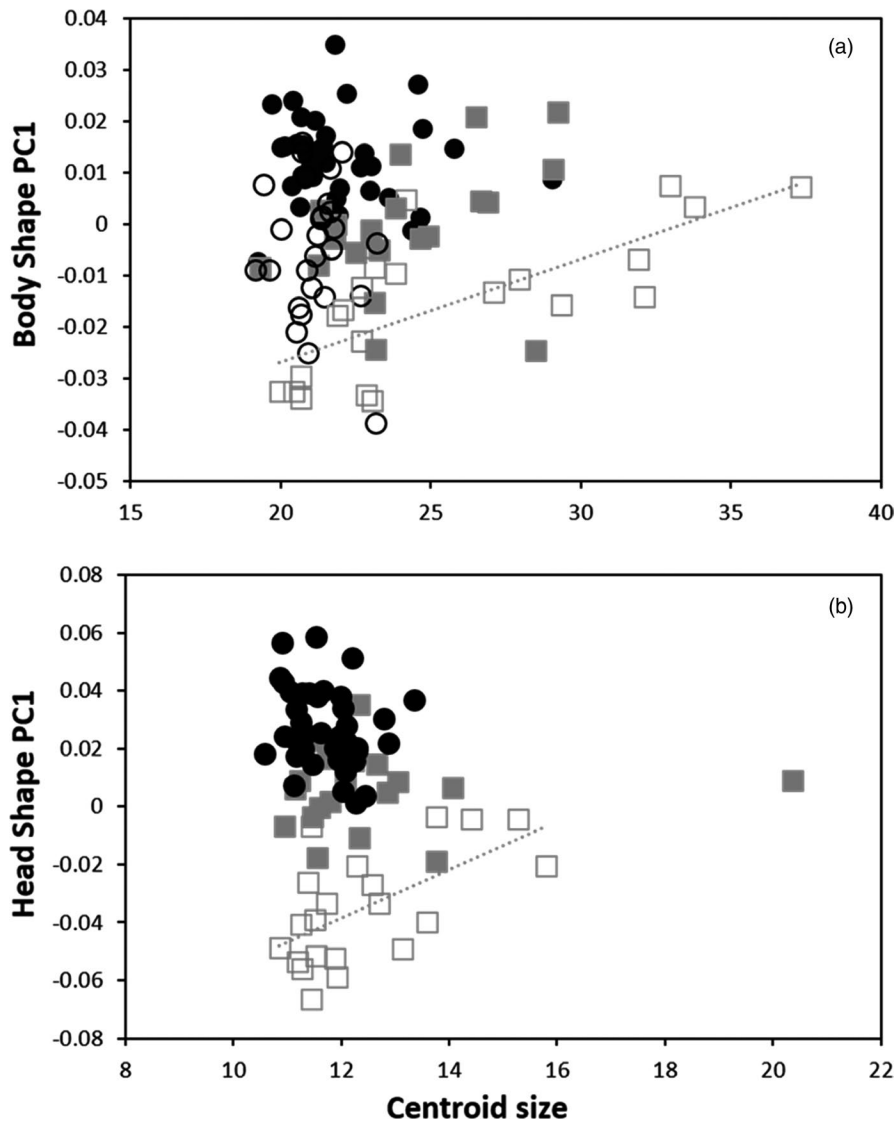
### 3 | RESULTS

#### 3.1 | Temporal morphological variation between ecotypes and years

In total, 107 lake charr were sampled, including 39 huronicus and 20 leans in 2007 and 27 huronicus and 21 leans in 2018. For both ecotypes, lake charr caught in 2007 had deeper bodies than lake charr caught in 2018 (Figure 1). The first two principal components explained 48.9% of the variation in lake charr body shape from Rush



**FIGURE 1** PCA of lake charr body and head shape with percentage representing the variation explained by that component in (a) and (c), respectively, and CVA of lake charr body and head shape with 95% confidence ellipses delineating groups in (b) and (c)



**FIGURE 2** Allometric trajectories in body and head shape of lean and huronicus lake charr ecotypes from 2007 and 2018. PC1 scores of body shape (a) and head shape (b) are plotted against centroid size. Lean are represented by squares and huronicus by circles, whereas filled symbols are individual sampled in 2007 and empty symbols are lake charr caught in 2018. Only lean 2018 regressions were significantly different from 0, for both body and head shape (body shape:  $R^2 = 0.56$ ,  $p \leq 0.01$ ; head shape:  $R^2 = 0.36$ ,  $p \leq 0.01$ )

Lake (Figure 1a). Body shape differed between years within each lake charr ecotype (CVA, Axis 1  $\lambda = 0.015$ ,  $p < 0.01$  and Axis 2  $\lambda = 0.29$ ,  $p < 0.01$ ; Figure 1b). Jackknife classification of body shape had a 54.3% rate of correct year and ecotype assignment (i.e., ecotypes and years as different factors). Body shape means differed between ecotypes and years (Permutation MANOVA,  $F = 11.7$ ,  $df = 3$ ,  $p \leq 0.01$ ), and the magnitude of these differences was slightly larger between ecotypes than between years. Pairwise body shape comparisons differed between ecotypes for both 2007 and 2018 ( $F$  tests;  $p \leq 0.05$ ; Figure A4). For lean and huronicus lake charr sampled in 2007, the Goodall's  $F$  was 21.1 and distance between means was  $0.030 \pm 0.0028$  (SE), whereas for the lean and huronicus sampled in 2018, the Goodall's  $F$  was 18.2 and distance between means was  $0.032 \pm 0.0031$  (SE). Pairwise body shape comparisons also differed between years for both ecotypes ( $F$  tests;  $p \leq 0.05$ ). For huronicus 2007 vs. 2018, the Goodall's  $F$  was 10.8 and distance between means was  $0.020 \pm 0.0012$  (SE), whereas for the lean 2007 vs. 2018, the Goodall's  $F$  was 10.4 and distance between means was  $0.025 \pm 0.0024$  (SE). Allometric trajectories in body shape did not

differ between 2007 and 2018, except for leans sampled in 2018 ( $R^2 = 0.56$ ,  $p \leq 0.01$ ).

For both ecotypes, lake charr from 2007 had deeper heads than lake charr from 2018 (Figures 1 and A4). The first two principal components explained 61.2% of the variation in lake charr head shape (Figure 1c). Head shape differed between years within each lake charr ecotype (CVA, Axis 1  $\lambda = 0.012$ ,  $p < 0.01$  and Axis 2  $\lambda = 0.13$ ,  $p < 0.01$ ; Figure 1d). Jackknife classification on head shape had a 49.5% rate of correct year and ecotype assignment (i.e. ecotypes and years as factors). Head shape differed between ecotypes and years (Permutation MANOVA,  $F = 21.75$   $df = 3$ ,  $p \leq 0.01$ ), and the magnitude of these differences was slightly larger between years than between ecotypes. Pairwise comparisons of head shape differed between ecotypes for both 2007 and 2018 ( $F$  tests;  $p \leq 0.05$ , Figure A4). For lean and huronicus sampled in 2007, Goodall's  $F$  was 21.7 and distance between means was  $0.040 \pm 0.0035$  (SE), whereas for the lean and huronicus sampled 2018, Goodall's  $F$  was 21.0 and distance between means was  $0.048 \pm 0.0044$  (SE). Pairwise head shape comparison also differed between years for

both ecotypes (F tests;  $p \leq 0.05$ ). For the huronicus, Goodall's  $F$  was 54.9 and distance between means was  $0.063 \pm 0.0036$  (SE), whereas for the lean, Goodall's  $F$  was 38.6 and distance between means was  $0.063 \pm 0.0041$  (SE). Allometric trajectories in head shape did not differ except for lean lake charr in 2018 ( $R^2 = 0.36$ ,  $p < 0.01$ ; Figure 2).

Relative body condition differed between ecotypes and years (ecotype\*year:  $F_{1,134} = 15.0$ ;  $p < 0.01$ ; Figure 3). Within years, relative body condition of the huronicus ecotype was higher than the lean ecotype in 2007 ( $F_{1,66} = 25.4$ ;  $p < 0.01$ ) but similar to the lean ecotype in 2018 ( $F_{1,68} = 0.2$ ;  $p = 0.7$ ). Within ecotypes, relative body condition of the huronicus was higher in 2007 than in 2018 ( $F_{1,80} = 55.1$ ;  $p < 0.01$ ) but the lean ecotype did not differ between years ( $F_{1,54} = 0.4$ ;  $p = 0.5$ ).

### 3.2 | Otoliths back-calculated growth: growth patterns displayed by ecotypes through time

Length at age of lake charr was best described by a single model that included both ecotypes and sample years (Table 1). Lean lake charr grew faster to a longer asymptotic length than huronicus lake charr in 2007 and 2018 (Figure 4). Lean and huronicus lake charr sampled in 2018 grew faster at early age than those sampled in 2007, whereas both ecotypes sampled in 2007 grew to longer asymptotic length than those sampled in 2018. The early growth rate of lean lake charr sampled in 2007 was a similar rate to huronicus lake charr sampled in 2018. In contrast, the asymptotic length of lean lake charr sampled in 2018 was similar to the asymptotic length of huronicus lake charr sampled in 2007.

Average otolith growth increments (corrected for age) differed between lean and huronicus ecotypes ( $F_{1,1927} = 16.9$ ;  $p < 0.01$ ), but not between males and females ( $F_{1,1927} = 0.4$ ;  $p = 0.52$ ; Table 2) or between sampling years ( $F_{1,1927} = 0.08$ ;  $p = 0.77$ ; Table 2). Average annual growth increments of huronicus and lean lake charr fluctuated

without a specific trend prior to calendar year 2009 and then declined steadily between 2009 and 2018 (Figure 5). For huronicus lake charr, average annual growth increments varied without temporal trend from 1977 until 1988, increased slowly and erratically between 1989 until 2009, and then declined steadily between 2009 and 2018. Average annual growth increments of huronicus lake charr were smallest in 2015–2018. For lean lake charr, average annual growth increments varied erratically from 1984 through 1990, declined from 1991 through 1995, increased from 1996 through 2009 and then declined between 2009 and 2018. Average annual growth increments of lean lake charr were nearly as small in 2015–2018 as in 1991–1995. Over the entire period, mean annual growth increments were 44% more variable for lean than for huronicus ecotypes (i.e., growth varied more among years for leans than huronicus overall; Table A2). From 2009 to 2018, mean increment width declined 20% faster for leans than huronicus (i.e., growth of leans declined faster after 2009 than growth of huronicus). Prior to 2009, mean increment width was 76% higher for leans than huronicus (i.e., leans grew faster before 2009 than huronicus).

### 3.3 | Otolith increment cross-dating: growth of lake charr in relation to environmental variation

Inter-annual climate variation, particularly when including lagged effects, was correlated with fish growth for both ecotypes, as demonstrated by Pearson correlations regularly exceeding 0.2 (Figure 6). For both lake charr ecotypes and year-corresponding and lagged effects, annual otolith growth increments were positively correlated with summer air temperatures (except for the lean ecotype with corresponding year, slightly negative) and fall precipitation (i.e., more growth with warmer temperatures and more precipitation) and negatively correlated with summer and fall cloud cover (i.e., more growth with less cloud cover). In comparison, the direction of the relationship with winter to spring temperatures and precipitation as snow differed between the two ecotypes (Figures 6 and A5). For each set of seasonal variables, inclusion of weighted climate data from previous years, to accommodate lagging effects, tended to strengthen correlations. Overall, based on the forward selection multiple regression models, the total amount of variation in otolith annual growth increments explained by climatic variables was greater for the lean ecotype than huronicus ecotype ( $R^2 = 0.56$  vs 0.35; Table A3). These regression models confirmed that growth increments of huronicus ecotypes were most strongly associated with winter to spring temperatures and precipitation as snow and secondarily with summer temperature, whereas the lean ecotype was most strongly associated with winter to spring temperatures and previous fall precipitation (Table A3). Between ecotype differences in the relationship of annual growth increment with winter and spring temperatures and with precipitation as snow were then examined more closely, where regression analyses confirmed these differences (Figures 6 and A5). Specifically, differences in annual growth increments between ecotypes for any given year indicated

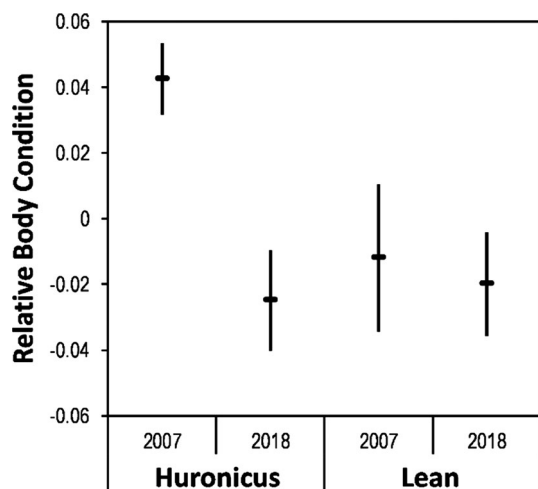
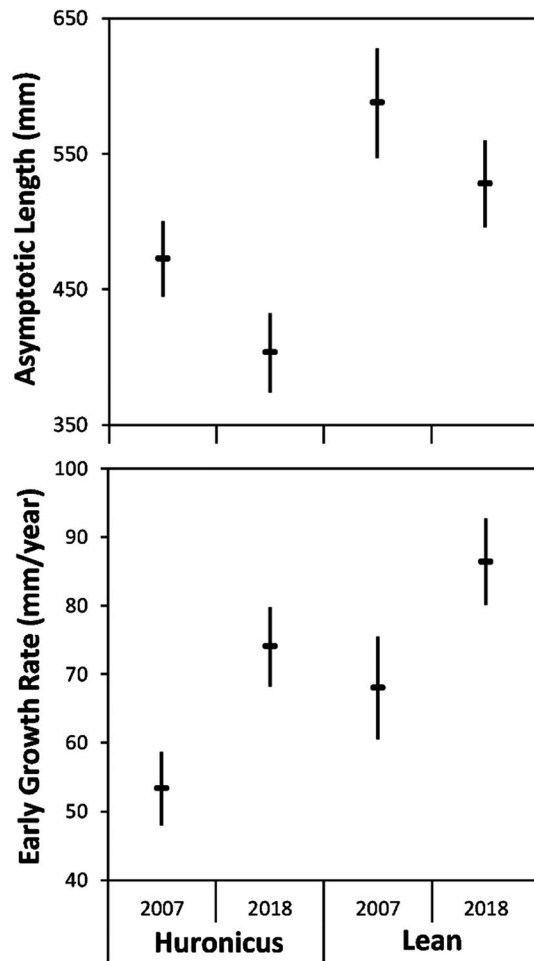


FIGURE 3 Relative body condition of huronicus and lean lake charr sampled from Rush Lake, in 2007 and 2018

Model	df	logLik	AIC	$\Delta_i$	$e^{(-0.5\Delta_i)}$	$w_i$
Years + Morphs	19	-7672.0	15382.0	0	1.00	0.93
Morphs + Years + Sexes	31	-7662.6	15387.2	5.2	0.08	0.07
Years + Sexes	19	-7687.4	15412.7	30.7	0.00	0.00
Morphs	13	-7702.4	15430.8	48.8	0.00	0.00
Morphs + Sexes	19	-7697.7	15433.5	51.5	0.00	0.00
Years	13	-7705.7	15437.4	55.4	0.00	0.00
Sexes	13	-7729.0	15484.0	102.0	0.00	0.00
Null	10	-7732.9	15485.8	103.8	0.00	0.00

**TABLE 1** Tests of fixed effects for differences between lake charr ecotypes (lean, huronicus), sample years (2007, 2018) and sexes (male, female) from a nonlinear mixed-effects model of back-calculated length at sagittal otolith age, with random fish effects (fish-to-fish variation in growth) sampled in Rush Lake



**FIGURE 4** Asymptotic length (mm) and early growth rate (mm/year; first year) calculated from sections sagittal otoliths of huronicus and lean lake charr sampled from Rush Lake, in 2007 and 2018

that cold and snowy winters tended to favour growth for the huronicus ecotype whereas warmer winters with less snow favoured growth for the lean ecotype (Figures 6 and A5).

For the early life stages of both ecotypes, defined here as ages 1–3, annual growth increments were correlated with cloud cover only. A negative relationship between early life-stage growth and summer cloud cover (i.e., more growth with less cloud cover)

occurred for both the huronicus ( $R^2 = 0.19$ ,  $p = 0.01$ ) and lean ( $R^2 = 0.43$ ,  $p < 0.01$ ; Figure 7) ecotypes. Annual growth of early life-stage lake charr appeared to be correlated with the temporal trend of summer cloud cover. For example, cloud cover in July has decreased by up to 33% over the past three decades, resulting in higher annual growth in early life-stage lake charr from 2007 to 2018 (Figure 7).

#### 4 | DISCUSSION

In this study, we demonstrated a rapid phenotypic shift that occurred for two lake charr ecotypes in a small lake. Within the last decade, a major decline in annual growth increments has occurred with a corresponding morphological shift in body and head shape for both lean and huronicus ecotypes. Even though the lean (shallow-water) ecotype displayed a greater annual growth variation over the years than the huronicus (deep-water) ecotype, both ecotypes displayed similar magnitude and direction of morphological changes in the most recent decade yielding an analogous 'sensitivity' in phenotypic change, meaning similar 'responsiveness' independent of habitats. We interpret these results to mean that the response threshold that determines individual sensitivity to a particular cue (i.e., environmental variables) caused similar phenotypic changes by individuals of both ecotypes (Baerwald et al., 2016; Moczek, 2010), in spite of differences in sensitivity between growth responses of the two ecotypes.

Declining body size has been suggested to be an universal response to climate warming across taxa (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Sheridan & Bickford, 2011). Accordingly, synchronous change in growth rates of fishes has been observed at global scales, with major declines in growth linked to climate change (Baudron, Needle, Rijnsdorp, & Tara Marshall, 2014; Jeffrey, Côté, Irvine, & Reynolds, 2017; Thresher et al., 2007). Despite growing evidence of ecotypic patterns emerging in the context of variation in global climate (Millien et al., 2006), little is known of how growth trajectories and their associated phenotypic reaction norms will integrate environmental variables and cause differences within (e.g., cohorts) and among ecotypes, especially in freshwater ecosystems (Heino, Dieckmann, & Godø, 2002; Johnson et al., 2014). To our knowledge, few other field studies have demonstrated a temporal

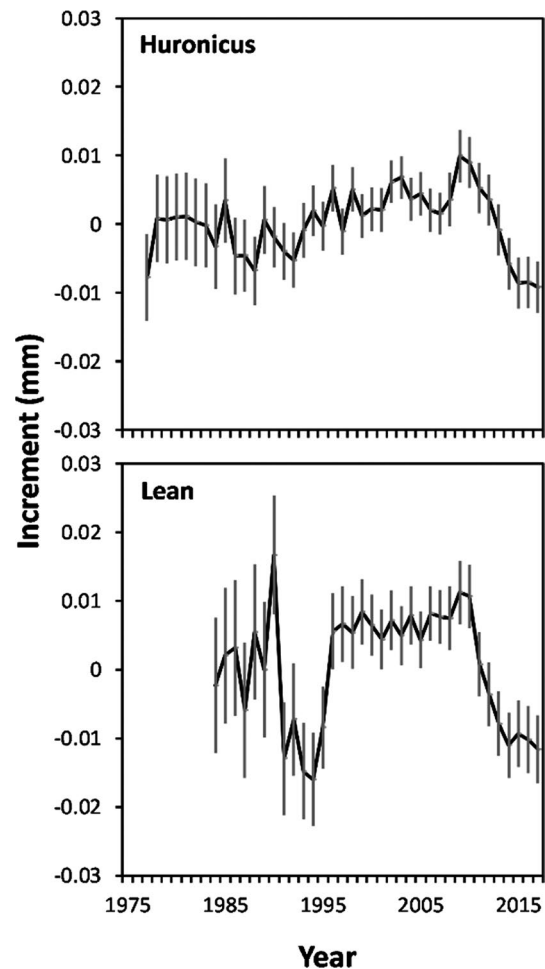


**TABLE 2** Tests of fixed effects for differences between lake charr morphs (huronicus or lean), sample years (2007 or 2018), and sexes (males or females) from a linear mixed-effects model of annual sagittal otolith growth increments as a function of a fixed age effect (age of increment formation), random year effects (year of increment formation) and random fish effects (fish-to-fish variation in growth) sampled in Rush Lake

Morph	Effect	df Numerator	df Denominator	F-Ratio	p-Value
Both	Age	34	1927	718.5	≤0.01
	Ecotype	1	1927	16.9	≤0.01
	Sex	1	1927	0.4	0.5
	Year	1	1927	0.08	0.8
Huronicus	Age	30	1182	515.4	≤0.01
	Sex	1	1182	0.05	0.8
	Year	1	1182	0.9	0.3
Lean	Age	34	682	255.9	≤0.01
	Sex	1	682	1.4	0.2
	Year	1	682	0.6	0.4

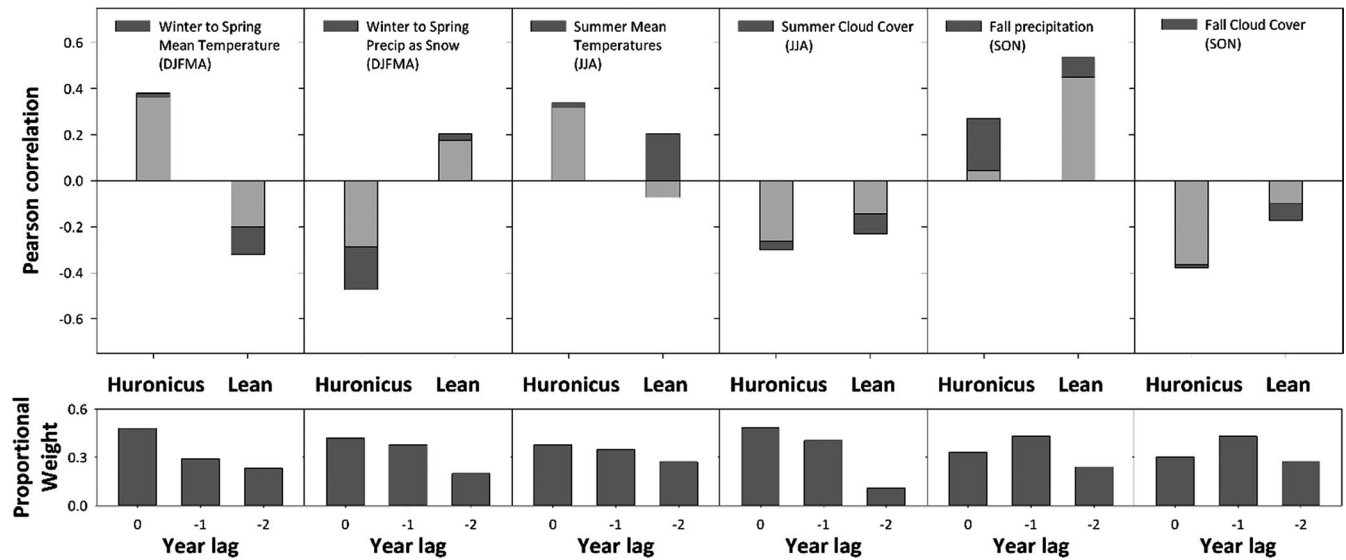
change in morphology and growth rate, within an ecotype much less, temporal changes that were consistent between ecotypes (but see Svanbäck et al., 2009 for an example of consistent phenotypic variation, in magnitude and direction between ecotypes (PC1: 2003 to 2004)). In our study, a decline in annual growth increment for lean and huronicus ecotypes occurred at the same time as a consistent phenotypic shift in morphology and these changes occurred within the time frame of a decade. Growth rate in fishes has been shown to drive intraspecific morphological differentiation (Chivers, Zhao, Brown, Marchant, & Ferrari, 2008; Olsson, Svanbäck, & Eklöv, 2007; Tonn, Holopainen, & Paszkowski, 1994) and to regulate morphological expression (Franklin, Skúlason, Morrissey, & Ferguson, 2018; Olsson, Svanbäck, & Eklöv, 2006; Svanbäck, Zha, Brönmark, & Johansson, 2017). A possible explanation is that at higher growth rates, energy is allocated to somatic growth and morphology modulation in addition to metabolic maintenance, but that at lower growth rates, energy is used almost exclusively for metabolic maintenance and/or reproduction (Olsson et al., 2006; Svanbäck et al., 2017). Our results concur with this latter mechanism because lake charr sampled in 2007 had higher annual growth rates and less morphological overlap between ecotypes than lake charr sampled in 2018, although underlying mechanisms remain uncertain. Variation in developmental rate associated with juvenile growth rates has been demonstrated to have an effect on the origin of some ecotypes (Alexander & Adams, 2004; Helland, Vøllestad, Freyhof, & Mehner, 2009; McPhee, Noakes, & Allendorf, 2015). Yet how variation in early development and juvenile growth rate influence later morphology remains ambiguous, with almost no attention focused on among-individual variation within an ecotype.

The effect of growth rate heterogeneity on morphological modulation (e.g., heterochony, allometry; Klingenberg, 2014) has been observed to constrain or enhance morphological differences in several fish species (Heino, 2014; Jacobson, Grant, & Peres-Neto, 2015; Olsson et al., 2006). Exposure to different environmental conditions is known to have asymmetrical impacts on the stability of developmental pathways during early life stages (Lazić, Kaliontzopoulou, Carretero, & Crnobrnja-Isailović, 2013; Robinson & Wardrop, 2002). Organisms can be affected by a single perturbation of the timing or



**FIGURE 5** Annual growth increments (mm; random year effects from a linear mixed-effects model that also included fixed age effects and random fish effects; Weisberg et al., 2010) by calendar year for huronicus and lean lake charr ecotypes sampled from Rush Lake, in 2007 and 2018

rate in development, which has been perceived to be a means to produce trait novelty (e.g. heterochony; Lazić, Carretero, Crnobrnja-Isailović, & Kaliontzopoulou, 2015; Parsons, Sheets, Skúlason, & Ferguson, 2011; Westneat, Wright, & Dingemanse, 2015).

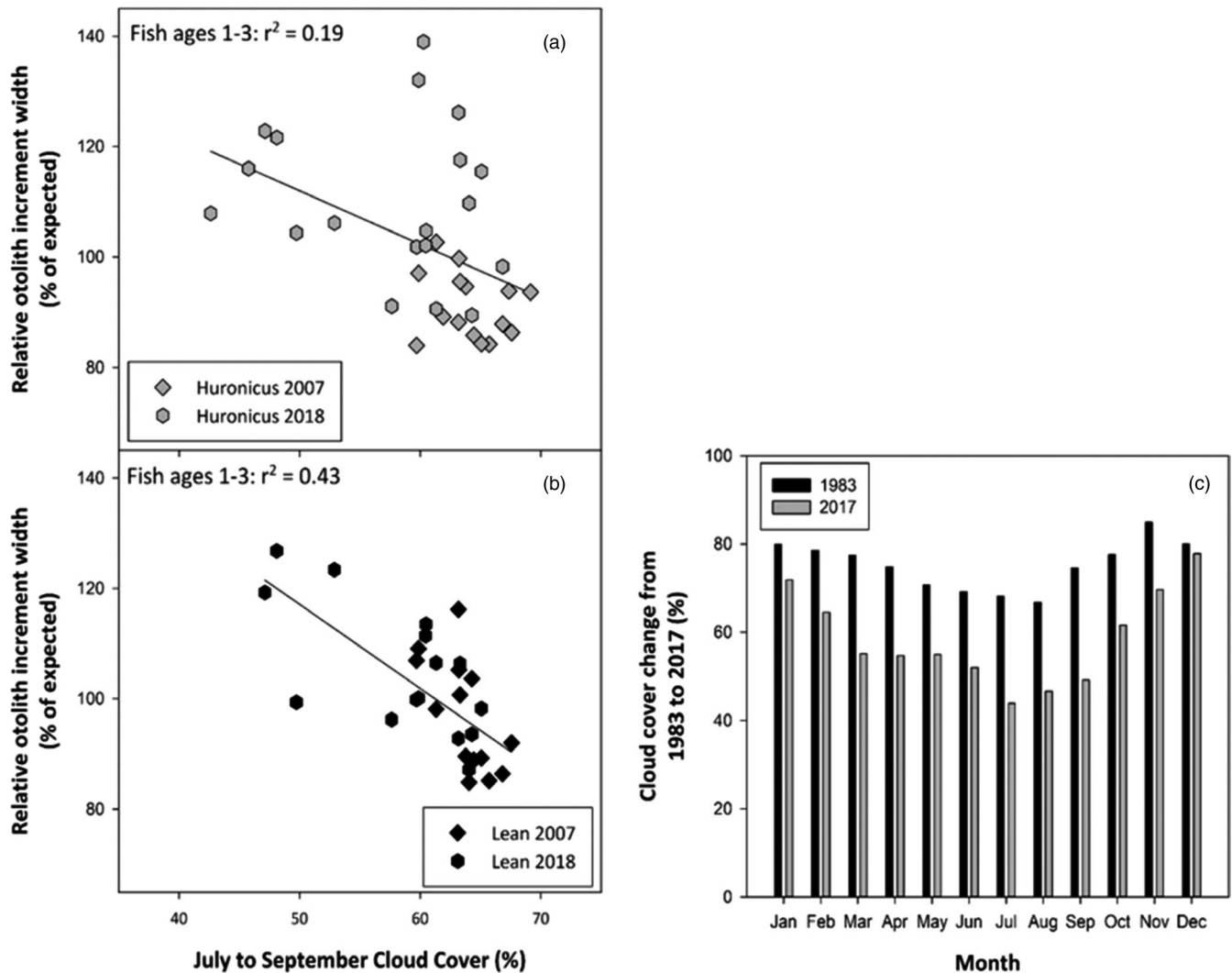


**FIGURE 6** Pearson correlation coefficients between ARSTAN-detrended otolith growth increments and selected seasonal climate variables for each ecotype. Results include data combined across fish sampled in 2007 and 2018. Correlation values for each ecotype that used a proportional weighting scheme for seasonal variables across the current and two previous years are represented by dark bars, whereas light bars indicate correlation values with no weighting. Panels including proportional weight values (i.e. sum of weights equal to one) whereby the combination of weights was optimized to maximize correlation values shown in dark bars within the panel immediately above. Year lags correspond to the current year = 0, one previous year = -1 and two previous years = -2

Allometry, the shape variation associated with size variation (Zelditch et al., 2012) is also seen as a canalized process and an interacting agent that can limit morphological variation (Klingenberg, 2010). At the very least, some of our results represent a case of plastic allometry for the lean ecotype in 2018. Considering that the lean body condition did not markedly differ between sampling years and was within the species range values (Hansen, Guy, Bronte, & Nate, 2021), we are confident that morphological differences were not due to starvation of individuals.

When compared to lake charr ecotypes from other lakes, the genetic diversity and divergence of lake charr in Rush Lake is low for both ecotypes (Chavarie et al., 2016). This low genetic diversity and divergence favour the hypothesis that phenotypic variation is the result of phenotypic plasticity rather than genetic adaptations (although rapid genetic change cannot be excluded). Epigenetically mediated biological complexity is known to be an important process to tailor phenotypic reaction norms (e.g., linear and nonlinear) to selective environmental pressures (Crozier & Hutchings, 2014; Duclos, Hendrikse, & Jamniczky, 2019; Ramler et al., 2014). An organism's response to change (abiotic and biotic) can include variation in the mean phenotype itself, but it can also include differences in the phenotypic variance (O'Dea, Lagisz, Hendry, & Nakagawa, 2019). A rapid change in the environment can induce changes in the phenotypic variance within an ecotype by exposing previously hidden cryptic genetic variation or by inducing new epigenetic changes (O'Dea, Noble, Johnson, Hesselton, & Nakagawa, 2016). It has been hypothesized that heritable epigenetic mechanisms can lead to phenotypic variation generated by bet hedging strategies, whereas phenotypic variability buffers varying environments (O'Dea et al., 2016).

Spatial and temporal fluctuations of trophic resources in Rush Lake could have influenced how individuals used these resources and the resulting annual growth rate patterns (influenced by density-dependent fluctuations and intraspecific competition; Jacobson et al., 2015; Svanbäck et al., 2009). Such spatial and temporal periodicity can occur at different scales (e.g., for temporal periodicity: seasonal, inter-annual, decadal) and be driven by fluctuations in abiotic (e.g., temperature, precipitation, light and nutrients) and biotic processes (e.g. growth, reproduction and trophic interactions), thereby shaping species behaviour and 'rewiring' food webs (Bartley et al., 2019; McMeans, McCann, Humphries, Rooney, & Fisk, 2015). In this study, some aspects of body and head shape shifts may have been mediated by changes in growth rates and body condition, which likely, were induced by variation in food availability and abiotic conditions. Body condition can affect body shape in fish, and often reflects bulkiness of individuals, and consequently body depth (Borcherding & Magnhagen, 2008; Jacobson et al., 2015; Olsson et al., 2006; Svanbäck et al., 2017). Although both ecotypes were subjected to annual growth rate declines, the huronicus ecotype was more affected by body condition changes than the lean ecotype, which might suggest physiological differences between ecotypes in the dynamics of energy processing (e.g., metabolism and reproduction) and storage (Goetz et al., 2013). For example, in 2018, 30.8% of the huronicus females were in a resting reproductive stage compared to only 8.3% of lean females. In contrast to females, all males in 2018 of both ecotypes were reproductively mature (*Unpublished data*). Although no sexual dimorphism occur in lake charr (Esteve, McLennan, & Gunn, 2008), differences in energetic requirements associated with reproductive output appear related to the apparent skipped spawning patterns observed by ecotype and sex.



**FIGURE 7** Otolith increment growth variation among ecotypes and collection periods for ages 1–3 plotted versus regional cloud cover from July to September for the same year without weighting or lag-effects included in (a) and (b). Data were detrended using regional chronology standardization (see Methods and Table A1). Within a given year, ecotype and collection period, otolith growth data for early-stage growth were averaged across ages 1–3. In (c), reductions in regional cloud cover by month from 1983 to 2017. Shown here are the predicted values for 1983 and 2017 using linear regressions fitted to inter-annual cloud cover data by month across the same time period. These two years represent endpoints for which otolith data were replicated enough to allow chronology construction. Cloud cover data were from airports within 7 km of Lake Superior since the lake itself strongly controls nearby weather (see Voelker et al., 2019)

Many examples exist of taxa where population growth fluctuated over time as a result of variation in resource levels, often were influenced by environmental changes (Ohlberger, 2013; Persson & De Roos, 2003). Given that fish otoliths offers a unique broad comparative tool to link abiotic factors as driving size changes (Gardner et al., 2011), we were able to detect similarities and differences of annual growth rates of lake charr ecotypes correlated to environmental variation. In our study, cloud cover was the main environmental variable that had steadily decreased over the same time period that lake charr growth declined (except for early stage) and morphology shifted in Rush Lake (Figure 7). Environmental heterogeneity is thought to have stronger effects on morphology at early life stages (Johnson et al., 2014; Morris, 2014; Ramler et al., 2014), suggesting that the effects of the cloud cover on lake charr might have been more significant at age 1–3 years than during later stages of life. The

effect of cloud cover on growth at age 1–3 was stronger in the lean than the huronicus ecotype, which might explain why allometry was detected only for the lean ecotype in 2018. The relationship between lake charr annual otolith growth and cloud cover could be related to how solar irradiance can co-vary with other climate variables that may affect fish growth (Poesch et al., 2016; Reist et al., 2006). Additionally, when higher temperatures are accompanied by suitable net addition of food ration (e.g. from direct and indirect effects of temperature and precipitation factors), increases in growth could be expected up to the point of the optimum metabolic temperature of the species (Elliott & Elliott, 2010; Elliott & Hurley, 2003).

Response to winter climate appeared to vary between ecotypes but it is unclear why the deep-water ecotype would show higher annual growth increments in years with warm winter temperatures and low snow cover (via direct or lagging effects) and the shallow-water

ecotype would have higher annual growth increments in years with cold winter temperature and high snow level. These results could be explained in part by reduced habitat partitioning between ecotypes during winter, along with an increase of intraspecific competition, affecting energy storage (Amundsen, Knudsen, & Klemetsen, 2008). Another explanation, which is not exclusive of the previous one, could be that each ecotype's prey types, density, and quality (e.g., time response to environmental variable) are modified differently by lagging effects from winter environmental conditions (e.g., ice cover duration, ice and snow thickness). The lean ecotype is known to feed on forage fish whereas the huronicus ecotype mainly feeds on the invertebrate *Mysis* (Chavarie et al., 2016). Invertebrates can differ in response time and magnitude to environmental changes compared to forage fishes (Heino et al., 2009; Wrona et al., 2016; Wrona et al., 2006). This hypothesis of a differential response of prey items to environmental conditions seems to be strengthened by correlations when weighted climate data from previous years were included with lake charr growth. This result might be expected for an organism in which growth rates may draw on a mixture of recently acquired and stored resources or where climate variables in one year may affect the abundance and composition of prey in subsequent years. For the most part, winter environmental conditions can play an essential role in ecological and evolutionary processes that define life-history characteristics (e.g., somatic growth, size and age at maturity, reproduction investment and longevity) of lacustrine species (Shuter, Finstad, Helland, Zweimüller, & Hölker, 2012).

## 5 | CONCLUSION

One assumption often made in relation to intraspecific diversity, mostly tested experimentally or modelled, is that a stable or predictable environment interacts with underlying variation in expression of phenotypes (Skúlason et al., 2019; Wagner & Schwenk, 2000). In our study, the magnitude and direction of the observed phenotypic shift in both annual growth and morphology over a single decade were consistent for each ecotype and suggested similar pathways to which phenotypic variation was expressed. The degree of phenotypic variation that occurs within an ecotype theoretically depends on the relative strength and timing of mechanisms that drive phenotypic change (Wood et al., 2020). In our case, the observed phenotypic shift was relatively small, but nonetheless, detectable (i.e., cryptic eco-evolutionary dynamics; Kinnison, Hairston, & Hendry, 2015). Several questions arise from our results, but one of interest is the organism's capacity for phenotype acclimation to a changing environment (via phenotypic plasticity and adaptation; Gorsuch, Pandey, & Atkin, 2010; Huey & Berrigan, 1996). Was this phenotypic shift an isolated event or does this type of change occur frequently in this lake and elsewhere? Answers to the question of phenotypic acclimation and the frequency of its occurrence within and among systems would require long data sets collected over multiple decades and would help to fill an important knowledge gap about nonequilibrium population dynamics affecting evolutionary dynamics.

Mechanisms that connect annual growth increments with morphological modulation are not fully understood (Olsson et al., 2006, 2007; Svanbäck et al., 2009); however, the biology underlying phenotypic variation can have major implications for populations responding to climate change. Multidimensional phenotypic variability and its influence on patterns of population dynamics is a relatively poorly studied phenomena (Westneat et al., 2015), but individual and population resistance and resilience to climatic changes may depend on this variability (Johnson et al., 2014). The similarity in phenotypic response expressed by both ecotypes raises the question whether organisms in small lakes are more vulnerable to climate change than those in large lakes. Small lakes generally sustain a higher degree of habitat coupling (e.g., littoral-pelagic; Dolson, McCann, Rooney, & Ridgway, 2009; Schindler & Scheuerell, 2002), which is critical to food-web dynamics. Thus, the degree of habitat coupling found in each freshwater ecosystem might translate to its degree of vulnerability to climate change. Field studies, such as ours, that focus on temporal phenotypic instability within an aquatic ecosystem promise to clarify our understanding of how the interplay among phenotypes, trophic dynamics, and environmental context influences both ecosystem and evolutionary processes (Ware et al., 2019).

## ACKNOWLEDGEMENTS

We thank the Huron Mountain Club for access to their lands, housing, and lakes and for sharing their knowledge of the lake charr of Rush Lake. Special thanks to Kerry Woods, Director of Research, Huron Mountain Club Wildlife Foundation for coordinating and supporting the project. Financial support was provided by the Great Lakes Fishery Commission. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

## CONFLICT OF INTEREST

The authors declare that they have no competing interests.

## DATA AVAILABILITY STATEMENT

The data sets supporting the conclusions of this article are included within the article. Raw data will be available on Dryad (<https://doi.org/10.5061/dryad.xd2547dg1>).

## ORCID

Louise Chavarie  <https://orcid.org/0000-0002-1327-7872>

## REFERENCES

- Alexander, G. D., & Adams, C. E. (2004). Exposure to a common environment erodes inherited between-population trophic morphology differences in Arctic charr. *Journal of Fish Biology*, 64(1), 253–257. <https://doi.org/10.1111/j.1095-8649.2004.00276.x>
- Amundsen, P.-A., Knudsen, R., & Klemetsen, A. (2008). Seasonal and ontogenetic variations in resource use by two sympatric Arctic charr morphs. *Environmental Biology of Fishes*, 83(1), 45–55. <https://doi.org/10.1007/s10641-007-9262-1>

- Angilletta, M. J. Jr, Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in Ectotherms: Fitting pieces of a life-history puzzle1. *Integrative and Comparative Biology*, 44(6), 498–509. <https://doi.org/10.1093/icb/44.6.498>
- Baerwald, M. R., Meek, M. H., Stephens, M. R., Nagarajan, R. P., Goodbla, A. M., Tomalty, K. M. H., Thorgaard, G. H., May, B., & Nichols, K. M. (2016). Migration-related phenotypic divergence is associated with epigenetic modifications in rainbow trout. *Molecular Ecology*, 25(8), 1785–1800. <https://doi.org/10.1111/mec.13231>
- Bartley, T. J., McCann, K. S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M. M., MacDougall, A. S., Tunney, T. D., & McMeans, B. C. (2019). Food web rewiring in a changing world. *Nature Ecology & Evolution*, 3(3), 345–354. <https://doi.org/10.1038/s41559-018-0772-3>
- Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20(4), 1023–1031. <https://doi.org/10.1111/gcb.12514>
- Black, B. A. (2009). Climate-driven synchrony across tree, bivalve, and rockfish growth-increment chronologies of the northeast Pacific. *Marine Ecology Progress Series*, 378, 37–46.
- Black, B. A., Biela, V. R., Zimmerman, C. E., & Brown, R. J. (2012). Lake trout otolith chronologies as multidecadal indicators of high-latitude freshwater ecosystems. *Polar Biology*, 36(1), 147–153. <https://doi.org/10.1007/s00300-012-1245-9>
- Black, B. A., Boehlert, G. W., & Yoklavich, M. M. (2005). Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(10), 2277–2284. <https://doi.org/10.1139/f05-142>
- Black, B. A., Matta, M. E., Helsler, T. E., & Wilderbuer, T. K. (2013). Otolith biochronologies as multidecadal indicators of body size anomalies in yellowfin sole (*Limanda aspera*). *Fisheries Oceanography*, 22(6), 523–532. <https://doi.org/10.1111/fog.12036>
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192. <https://doi.org/10.1016/j.tree.2011.01.009>
- Borcherding, J., & Magnhagen, C. (2008). Food abundance affects both morphology and behaviour of juvenile perch. *Ecology of Freshwater Fish*, 17(2), 207–218. <https://doi.org/10.1111/j.1600-0633.2007.00272.x>
- Briffa, K. R., & Melvin, T. M. (2011). A Closer Look at Regional Curve Standardization of Tree-Ring Records: Justification of the Need, a Warning of Some Pitfalls, and Suggested Improvements in Its Application. In M. K. Hughes, T. W. Swetnam, & H. F. Diaz (Eds.), *Dendroclimatology: Progress and Prospects* (pp. 113–145). Springer.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33(2), 261–304. <https://doi.org/10.1177/0049124104268644>
- CAFF (2013). *Arctic Biodiversity Assessment. Status and Trends in Arctic Biodiversity*. Akureyri: Conservation of Arctic Flora and Fauna.
- Campana, S. E., Casselman, J. M., & Jones, C. M. (2008). Bomb radiocarbon chronologies in the Arctic, with implications for the age validation of lake trout (*Salvelinus namaycush*) and other Arctic species. *Canadian Journal of Fisheries and Aquatic Science*, 65, 733–743.
- Chavarie, L., Adams, C. E., Swanson, H. K., Ridgway, M. S., Tonn, W. M., & Wilson, C. C. (2021). Ecological Diversity. In: A. Muir, C. C. Krueger, M. J. Hansen, & S. Riley (Eds.), *The lake charr Salvelinus namaycush: Biology, ecology, distribution, and management*. Fish & fisheries series 39. Springer Nature Switzerland AG.
- Chavarie, L., Howland, K. L., & Tonn, W. M. (2013). Sympatric polymorphism in lake trout: the coexistence of multiple shallow-water morphotypes in Great Bear Lake. *Transactions of the American Fisheries Society*, 142(3), 814–823. <https://doi.org/10.1080/00028487.2013.763855>
- Chavarie, L., Muir, A. M., Zimmerman, M. S., Baillie, S. M., Hansen, M. J., Nate, N. A., Yule, D. L., Middel, T., Bentzen, P., & Krueger, C. C. (2016). Challenge to the model of lake charr evolution: shallow- and deep-water morphs exist within a small postglacial lake. *Biological Journal of the Linnean Society*, 120.3(2017), 578–603. <https://doi.org/10.1111/bij.12913>
- Chavarie, L., Reist, J. D., Guzzo, M. M., Harwood, L., & Power, M. (2018). Influences of environmental variation on anadromous Arctic charr from the Hornaday River, NWT. *Hydrobiologia*, 840(1), 157–172. <https://doi.org/10.1007/s10750-018-3828-0>
- Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology*, 8(4), e1000357. <https://doi.org/10.1371/journal.pbio.1000357>
- Chivers, D. P., Zhao, X., Brown, G. E., Marchant, T. A., & Ferrari, M. C. O. (2008). Predator-induced changes in morphology of a prey fish: the effects of food level and temporal frequency of predation risk. *Evolutionary Ecology*, 22(4), 561–574. <https://doi.org/10.1007/s10662-007-9182-8>
- Cook, E., & Krusic, P. (2014). *ARSTAN version 44h3: A tree-ring standardization program based on detrending and autoregressive time series modeling, with interactive graphics*. Palisades, New York, USA: Tree-Ring Laboratory, Lamont-Doherty Earth Observatory of Columbia University.
- Crozier, L. G., & Hutchings, J. A. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications*, 7(1), 68–87. <https://doi.org/10.1111/eva.12135>
- Dolson, R., McCann, K., Rooney, N., & Ridgway, M. (2009). Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos*, 118(8), 1230–1238. <https://doi.org/10.1111/j.1600-0706.2009.17351.x>
- Duclos, K. K., Hendrikse, J. L., & Jamniczky, H. A. (2019). Investigating the evolution and development of biological complexity under the framework of epigenetics. *Evolution & Development*, 21(5), 276–293. <https://doi.org/10.1111/ede.12301>
- Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology*, 77(8), 1793–1817. <https://doi.org/10.1111/j.1095-8649.2010.02762.x>
- Elliott, J. M., & Hurley, M. A. (2003). Variation in the temperature preference and growth rate of individual fish reconciles differences between two growth models. *Freshwater Biology*, 48(10), 1793–1798. <https://doi.org/10.1046/j.1365-2427.2003.01129.x>
- Esteve, M., McLennan, D. A., & Gunn, J. M. (2008). Lake trout (*Salvelinus namaycush*) spawning behaviour: the evolution of a new female strategy. *Environmental Biology of Fishes*, 83(1), 69–76.
- Franklin, O. D., Skúlason, S., Morrissey, M. B., & Ferguson, M. M. (2018). Natural selection for body shape in resource polymorphic Icelandic Arctic charr. *Journal of Evolutionary Biology*, 31(10), 1498–1512. <https://doi.org/10.1111/jeb.13346>
- Fritts, H. (2012). *Tree rings and climate*. Elsevier.
- Gallucci, V. F., & Quinn, T. J. (1979). Reparameterizing, fitting, and testing a simple growth model. *Transactions of the American Fisheries Society*, 108(1), 14–25.
- García-Rodríguez, F. J., García-Gasca, S. A., Cruz-Agüero, J. D. L., & Cota-Gómez, V. M. (2011). A study of the population structure of the Pacific sardine *Sardinops sagax* (Jenyns, 1842) in Mexico based on morphometric and genetic analyses. *Fisheries Research*, 107(1), 169–176. <https://doi.org/10.1016/j.fishres.2010.11.002>
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*, 26(6), 285–291. <https://doi.org/10.1016/j.tree.2011.03.005>
- Georga, I., & Koumoundouros, G. (2010). Thermally induced plasticity of body shape in adult zebrafish *Danio rerio* (Hamilton, 1822).

- Journal of Morphology*, 271(11), 1319–1327. <https://doi.org/10.1002/jmor.10874>
- Goetz, F., Jasonowicz, A., Johnson, R., Biga, P., Fischer, G., & Sitar, S. (2013). Physiological differences between lean and siscowet lake trout morphotypes: Are these metabolotypes? *Canadian Journal of Fisheries and Aquatic Sciences*, 71(3), 427–435. <https://doi.org/10.1139/cjfas-2013-0463>
- Gorsuch, P. A., Pandey, S., & Atkin, O. K. (2010). Temporal heterogeneity of cold acclimation phenotypes in Arabidopsis leaves. *Plant, Cell & Environment*, 33(2), 244–258.
- Grimm, N. B., Chapin, F. S., Bierwagen, B., Gonzalez, P., Groffman, P. M., Luo, Y., Melton, F., Nadelhoffer, K., Pairis, A., Raymond, P. A., Schimel, J., & Williamson, C. E. (2013). The impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment*, 11(9), 474–482. <https://doi.org/10.1890/120282>
- Hansen, M. J., Guy, C. S., Bronte, C. R., & Nate, N. A. (2021). Life History and Population Dynamics. In A. Muir, C. C. Krueger, M. J. Hansen, S. Riley (Eds.), *The lake charr Salvelinus namaycush: Biology, ecology, distribution, and management. Fish & fisheries series 39*. Springer Nature Switzerland AG.
- Hansen, M. J., Nate, N. A., Chavarie, L., Muir, A. M., Zimmerman, M. S., & Krueger, C. C. (2016). Life history differences between fat and lean morphs of lake charr (*Salvelinus namaycush*) in Great Slave Lake, Northwest Territories, Canada. *Hydrobiologia*, 783(1), 21–35. <https://doi.org/10.1007/s10750-015-2633-2>
- Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, 84(1), 39–54. <https://doi.org/10.1111/j.1469-185X.2008.00060.x>
- Heino, M. (2014). Quantitative traits. In S. X. Cadrin, L. A. Kerr, & S. Mariani (Eds.), *Stock identification methods*, Second Edition (pp. 59–76). London: Academic Press/Elsevier.
- Heino, M., Dieckmann, U., & Godø, O. R. (2002). Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, 56(4), 669–678.
- Helland, I. P., Vøllestad, L. A., Freyhof, J., & Mehner, T. (2009). Morphological differences between two ecologically similar sympatric fishes. *Journal of Fish Biology*, 75(10), 2756–2767. <https://doi.org/10.1111/j.1095-8649.2009.02476.x>
- Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement.
- Hubbs, C. L. (1929). The fishes. In B. H. Christy (Ed.), *The book of Huron Mountain: a collection of papers concerning the history of the Huron Mountain Club and the antiquities and the natural history of the region* (pp. 153–164). Marquette, MI: Huron Mountain Club.
- Huey, R., & Berrigan, D. (1996). Testing evolutionary hypotheses of acclimation. *Animals and Temperature: Phenotypic and Evolutionary Adaptation*, 59, 205–237.
- Jacobson, B., Grant, J. W. A., & Peres-Neto, P. R. (2015). The interaction between the spatial distribution of resource patches and population density: consequences for intraspecific growth and morphology. *Journal of Animal Ecology*, 84(4), 934–942. <https://doi.org/10.1111/1365-2656.12365>
- Japyassú, H. F., & Malange, J. (2014). Plasticity, stereotypy, intra-individual variability and personality: Handle with care. *Behavioural Processes*, 109, 40–47. <https://doi.org/10.1016/j.beproc.2014.09.016>
- Jeffrey, K. M., Côté, I. M., Irvine, J. R., & Reynolds, J. D. (2017). Changes in body size of Canadian Pacific salmon over six decades. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(2), 191–201.
- Jeppesen, E., Meerhoff, M., Davidson, T. A., Trolle, D., Sondergaard, M., Lauridsen, T. L., Beklioglu, M., Brucet Balmaña, S., Volta, P., González-Bergonzoni, I., & Nielsen, A. (2014). Climate change impacts on lakes: an integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes. *Journal of Limnology*, 73(s1), 88–111. <https://doi.org/10.4081/jlimnol.2014.844>
- Johnson, D. W., Grorud-Colvert, K., Sponaugle, S., & Semmens, B. X. (2014). Phenotypic variation and selective mortality as major drivers of recruitment variability in fishes. *Ecology Letters*, 17(6), 743–755. <https://doi.org/10.1111/ele.12273>
- Kinnison, M. T., & Hairston, N. G. Jr (2007). Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Functional Ecology*, 21(3), 444–454. <https://doi.org/10.1111/j.1365-2435.2007.01278.x>
- Kinnison, M. T., Hairston, N. G. Jr, & Hendry, A. P. (2015). Cryptic eco-evolutionary dynamics. *Annals of the New York Academy of Sciences*, 1360(1), 120–144.
- Klingenberg, C. P. (2010). Evolution and development of shape: integrating quantitative approaches. *Nature Reviews Genetics*, 11, 623–635. <https://doi.org/10.1038/nrg2829>
- Klingenberg, C. P. (2014). Studying morphological integration and modularity at multiple levels: concepts and analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1649), 20130249. <https://doi.org/10.1098/rstb.2013.0249>
- Lazić, M. M., Carretero, M. A., Crnobrnja-Isailović, J., & Kaliontzopoulou, A. (2015). Effects of environmental disturbance on phenotypic variation: An integrated assessment of canalization, developmental stability, modularity, and allometry in lizard head shape. *The American Naturalist*, 185(1), 44–58. <https://doi.org/10.1086/679011>
- Lazić, M. M., Kaliontzopoulou, A., Carretero, M. A., & Crnobrnja-Isailović, J. (2013). Lizards from urban areas are more asymmetric: using fluctuating asymmetry to evaluate environmental disturbance. *PLoS One*, 8(12), e84190. <https://doi.org/10.1371/journal.pone.0084190>
- Matta, E. M., Black, B. A., & Wilderbuer, T. K. (2010). Climate-driven synchrony in otolith growth-increment chronologies for three Bering Sea flatfish species. *Marine Ecology Progress Series*, 413, 137–145.
- Maynard, D. S., Serván, C. A., Capitán, J. A., & Allesina, S. (2019). Phenotypic variability promotes diversity and stability in competitive communities. *Ecology Letters*, 22(11), 1776–1786. <https://doi.org/10.1111/ele.13356>
- McMeans, B. C., McCann, K. S., Humphries, M., Rooney, N., & Fisk, A. T. (2015). Food web structure in temporally-forced ecosystems. *Trends in Ecology & Evolution*, 30(11), 662–672. <https://doi.org/10.1016/j.tree.2015.09.001>
- McPhee, M. V., Noakes, D. L. G., & Allendorf, F. W. (2015). Developmental rate: A unifying mechanism for sympatric divergence in postglacial fishes? *Current Zoology*, 58(1), 21–34. <https://doi.org/10.1093/czoolo/58.1.21>
- Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications*, 7(1), 1–14. <https://doi.org/10.1111/eva.12137>
- Millien, V., Kathleen Lyons, S., Olson, L., Smith, F. A., Wilson, A. B., & Yom-Tov, Y. (2006). Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, 9(7), 853–869. <https://doi.org/10.1111/j.1461-0248.2006.00928.x>
- Moczek, A. P. (2010). Phenotypic plasticity and diversity in insects. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1540), 593–603. <https://doi.org/10.1098/rstb.2009.0263>
- Montoya José, M., & Raffaelli, D. (2010). Climate change, biotic interactions and ecosystem services. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549), 2013–2018. <https://doi.org/10.1098/rstb.2010.0114>
- Morris, M. R. (2014). Plasticity-mediated persistence in new and changing environments. *International Journal of Evolutionary Biology*, 2014, 1–18. <https://doi.org/10.1155/2014/416497>
- Muir, A. M., Bronte, C. R., Zimmerman, M. S., Quinlan, H. R., Glase, J. D., & Krueger, C. C. (2014). Ecomorphological diversity of Lake Charr *Salvelinus namaycush* at Isle Royale, Lake Superior. *Transactions of the American Fisheries Society*, 143(4), 972–987.

- Murdoch, A., & Power, M. (2013). The effect of lake morphometry on thermal habitat use and growth in Arctic charr populations: implications for understanding climate-change impacts. *Ecology of Freshwater Fish*, 22(3), 453–466. <https://doi.org/10.1111/eff.12039>
- Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A., & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change*, 2, 747. <https://doi.org/10.1038/nclimate1588>
- O'Dea, R. E., Noble, D. W., Johnson, S. L., Hesselson, D., & Nakagawa, S. (2016). The role of non-genetic inheritance in evolutionary rescue: epigenetic buffering, heritable bet hedging and epigenetic traps. *Environmental Epigenetics*, 2(1), dvv014.
- O'Dea, R. E., Lagisz, M., Hendry, A. P., & Nakagawa, S. (2019). Developmental temperature affects phenotypic means and variability: A meta-analysis of fish data. *Fish and Fisheries*, 20(5), 1005–1022. <https://doi.org/10.1111/faf.12394>
- Ohlberger, J. (2013). Climate warming and ectotherm body size – from individual physiology to community ecology. *Functional Ecology*, 27(4), 991–1001. <https://doi.org/10.1111/1365-2435.12098>
- Olsson, J., Svanbäck, R., & Eklöv, P. (2006). Growth rate constrain morphological divergence when driven by competition. *Oikos*, 115(1), 15–22.
- Olsson, J., Svanbäck, R., & Eklöv, P. (2007). Effects of resource level and habitat type on behavioral and morphological plasticity in Eurasian perch. *Oecologia*, 152(1), 48–56. <https://doi.org/10.1007/s00442-006-0588-8>
- Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., Corlett, R. T., Huntley, B., Bickford, D., Carr, J. A., Hoffmann, A. A., Midgley, G. F., Pearce-Kelly, P., Pearson, R. G., Williams, S. E., ... Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5, 215. <https://doi.org/10.1038/nclimate2448>
- Parsons, K. J., Sheets, H. D., Skúlason, S., & Ferguson, M. M. (2011). Phenotypic plasticity, heterochrony and ontogenetic repatterning during juvenile development of divergent Arctic charr (*Salvelinus alpinus*). *Journal of Evolutionary Biology*, 24(8), 1640–1652. <https://doi.org/10.1111/j.1420-9101.2011.02301.x>
- Persson, L., & De Roos, A. M. (2003). Adaptive habitat use in size-structured populations: linking individual behavior to population processes. *Ecology*, 84(5), 1129–1139.
- Pinheiro, J. C., & Bates, D. M. (2000). Linear mixed-effects models: basic concepts and examples. In *Mixed-effects Models in S and S-Plus. Statistics and Computing* (pp. 3–56). New York, NY: Springer. [https://doi.org/10.1007/0-387-22747-4\\_1](https://doi.org/10.1007/0-387-22747-4_1)
- Poesch, M. S., Chavarie, L., Chu, C., Pandit, S. N., & Tonn, W. (2016). Climate change impacts on freshwater fishes: A Canadian Perspective. *Fisheries*, 41(7), 385–391. <https://doi.org/10.1080/03632415.2016.1180285>
- Quinn, T. J. II, & Deriso, R. B. (1999). *Quantitative fish dynamics*. Oxford University Press.
- R Core Team (2016). *R: A language and environment for statistical computing*. <http://www.R-project.org/>
- Ramler, D., Mitteroecker, P., Shama, L. N. S., Wegner, K. M., & Ahnelt, H. (2014). Nonlinear effects of temperature on body form and developmental canalization in the threespine stickleback. *Journal of Evolutionary Biology*, 27(3), 497–507. <https://doi.org/10.1111/jeb.12311>
- Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J., & Kinnison, M. T. (2010). Phenotypic plasticity and population viability: the importance of environmental predictability. *Proceedings of the Royal Society B: Biological Sciences*, 277(1699), 3391–3400. <https://doi.org/10.1098/rspb.2010.0771>
- Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., King, J. R., & Beamish, R. J. (2006). An overview of effects of climate change on selected arctic freshwater and anadromous fishes. *AMBIO: A Journal of the Human Environment*, 35(7), 381–387.
- Robinson, B. W., & Wardrop, S. L. (2002). Experimentally manipulated growth rate in threespine sticklebacks: Assessing trade offs with developmental stability. *Environmental Biology of Fishes*, 63(1), 67–78. <https://doi.org/10.1023/A:1013820101348>
- Schindler, D. E., & Scheuerell, M. D. (2002). Habitat coupling in lake ecosystems. *Oikos*, 98(2), 177–189. <https://doi.org/10.1034/j.1600-0706.2002.980201.x>
- Schoener, T. W. (2011). The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics. *Science*, 331(6016), 426. <https://doi.org/10.1126/science.1193954>
- Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1(8), 401–406. <https://doi.org/10.1038/nclimate1259>
- Shuter, B. J., Finstad, A. G., Helland, I. P., Zweimüller, I., & Hölker, F. (2012). The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences*, 74(4), 637–657. <https://doi.org/10.1007/s00027-012-0274-3>
- Simonsen, M. K., Siwertsson, A., Adams, C. E., Amundsen, P.-A., Præbel, K., & Knudsen, R. (2017). Allometric trajectories of body and head morphology in three sympatric Arctic charr (*Salvelinus alpinus* (L.)) morphs. *Ecology and Evolution*, 7(18), 7277–7289. <https://doi.org/10.1002/ece3.3224>
- Skúlason, S., Parsons, K. J., Svanbäck, R., Räsänen, K., Ferguson, M. M., Adams, C. E., Amundsen, P.-A., Bartels, P., Bean, C. W., Boughman, J. W., Englund, G., Guðbrandsson, J., Hooker, O. E., Hudson, A. G., Kahilainen, K. K., Knudsen, R., Kristjánsson, B. K., Leblanc, C.-L., Jónsson, Z., ... Snorrason, S. S. (2019). A way forward with eco evo devo: an extended theory of resource polymorphism with postglacial fishes as model systems. *Biological Reviews*, 94(5), 1786–1808.
- Stearns, S. C. (1989). The evolutionary significance of phenotypic plasticity. *BioScience*, 39(7), 436–445. <https://doi.org/10.2307/1311135>
- Svanbäck, R., Pineda-Krch, M., & Doebeli, M. (2009). Fluctuating population dynamics promotes the evolution of phenotypic plasticity. *The American Naturalist*, 174(2), 176–189. <https://doi.org/10.1086/600112>
- Svanbäck, R., Zha, Y., Brönmark, C., & Johansson, F. (2017). The interaction between predation risk and food ration on behavior and morphology of Eurasian perch. *Ecology and Evolution*, 7(20), 8567–8577. <https://doi.org/10.1002/ece3.3330>
- Thresher, R. E., Koslow, J. A., Morison, A. K., & Smith, D. C. (2007). Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proceedings of the National Academy of Sciences*, 104(18), 7461. <https://doi.org/10.1073/pnas.0610546104>
- Tonn, W. M., Holopainen, I. J., & Paszkowski, C. A. (1994). Density-dependent effects and the regulation of Crucian carp populations in single-species ponds. *Ecology*, 75(3), 824–834. <https://doi.org/10.2307/1941738>
- Vigliola, L., & Meekan, M. G. (2009). The back-calculation of fish growth from otoliths. In B. S. Green, B. D. Mapstone, G. Carlos, & G. A. Begg (Eds.), *Tropical Fish Otoliths: Information for Assessment, Management and Ecology. Reviews: Methods and Technologies in Fish Biology and Fisheries* (Vol. 11, pp. 174–211). Dordrecht: Springer. [https://doi.org/10.1007/978-1-4020-5775-5\\_6](https://doi.org/10.1007/978-1-4020-5775-5_6)
- Voelker, S. L., Wang, S. Y. S., Dawson, T. E., Roden, J. S., Still, C. J., Longstaffe, F. J., & Ayalon, A. (2019). Tree-ring isotopes adjacent to Lake Superior reveal cold winter anomalies for the Great Lakes region of North America. *Scientific Reports*, 9(1), 4412. <https://doi.org/10.1038/s41598-019-40907-w>
- Wagner, G. P., & Schwenk, K. (2000). Evolutionarily stable configurations: functional integration and the evolution of phenotypic stability. In M. K. Hecht, R. J. Macintyre, & M. T. Clegg (Eds.), *Evolutionary*

- biology (Vol. 31, pp. 155–217). Boston, MA: Springer. [https://doi.org/10.1007/978-1-4615-4185-1\\_4](https://doi.org/10.1007/978-1-4615-4185-1_4)
- Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One*, 11(6), e0156720. <https://doi.org/10.1371/journal.pone.0156720>
- Ware, I. M., Fitzpatrick, C. R., Senthilnathan, A., Bayliss, S. L. J., Beals, K. K., Mueller, L. O., Summers, J. L., Wooliver, R. C., Van Nuland, M. E., Kinnison, M. T., Palkovacs, E. P., Schweitzer, J. A., & Bailey, J. K. (2019). Feedbacks link ecosystem ecology and evolution across spatial and temporal scales: Empirical evidence and future directions. *Functional Ecology*, 33(1), 31–42. <https://doi.org/10.1111/1365-2435.13267>
- Weisberg, S., Spangler, G., & Richmond, L. S. (2010). Mixed effects models for fish growth. *Canadian Journal of Fisheries and Aquatic Sciences*, 67(2), 269–277. <https://doi.org/10.1139/F09-181>
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.
- Westneat, D. F., Wright, J., & Dingemans, N. J. (2015). The biology hidden inside residual within-individual phenotypic variation. *Biological Reviews*, 90(3), 729–743. <https://doi.org/10.1111/brv.12131>
- Wood, Z. T., Fryxell, D. C., Moffett, E. R., Kinnison, M. T., Simon, K. S., & Palkovacs, E. P. (2020). Prey adaptation along a competition-defense tradeoff cryptically shifts trophic cascades from density- to trait-mediated. *Oecologia*, <https://doi.org/10.1007/s00442-020-04610-2>
- Wrona, F. J., Johansson, M., Culp, J. M., Jenkins, A., Mård, J., Myers-Smith, I. H., Prowse, T. D., Vincent, W. F., & Wookey, P. A. (2016). Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime. *Journal of Geophysical Research: Biogeosciences*, 121, 650–674.
- Wrona, F. J., Prowse, T. D., Reist, J. D., Hobbie, J. E., Lévesque, L. M. J., & Vincent, W. F. (2006). Climate impacts on Arctic freshwater ecosystems and fisheries: Background, rationale and approach of the Arctic Climate Impact Assessment (ACIA). *AMBIO: A Journal of the Human Environment*, 35, 326–329.
- Yamaguchi, K. (1991). *Event history analysis*. Sage.
- Zar, J. H. (1999). *Biostatistical analysis* (pp. 663). Prentice-Hall.
- Zelditch, M. L., Swiderski, D. L., & Sheets, H. D. (2012). *Geometric morphometrics for biologists: a primer*. Academic Press.

**How to cite this article:** Chavarie L, Voelker S, Hansen MJ, et al. Temporal instability of lake charr phenotypes: Synchronicity of growth rates and morphology linked to environmental variables?. *Evol Appl*. 2021;14:1159–1177. <https://doi.org/10.1111/eva.13188>

## APPENDIX A

**TABLE A1** Listing and comparison of analytical methods used to analyse otolith growth data for different purposes and occurrence in our study

Analytical method for otolith growth	Advantages	Disadvantages	Our study
Nonlinear mixed-effects modelling	Uses all data, so it can be used with all fish morphology measurements to back-calculate fish growth and asymptotic length	Cross-dating not confirmed, more environmental noise not related to climate drivers	Table 1, Table 2, Figure 5, Figure 6, Table A2
Cross-dated and ARSTAN-detrended	Conventional approach for identifying climate drivers of inter-annual variation in long-lived organisms such as trees	Short age span of fish excludes identification of decadal or greater environmental drivers (i.e. 'segment length curse'). Some loss of data when otolith time series do not cross-date	Figure 7, Table A3, Figure A5.
Cross-dated and RCS-detrended	Alternative approach for identifying climate drivers that preserves decadal and longer signals	Not as efficient at accurately extracting inter-annual variation compared to ARSTAN-detrending	Figure 8, Figure A3

**TABLE A2** Difference in annual growth increments (mm; random year effects from a linear mixed-effects model that also included fixed age effects and random fish effects; Weisberg et al., 2010) by calendar year for huronicus and lean lake charr ecotypes sampled from Rush Lake, in 2007 and 2018 (see Figure 6)

Metric	Huronicus	Lean	%
SD	0.0049	0.0088	44
Slope	-0.002	-0.0026	20
Decline	0.018	0.024	24
Mean	0.0004	0.0018	76

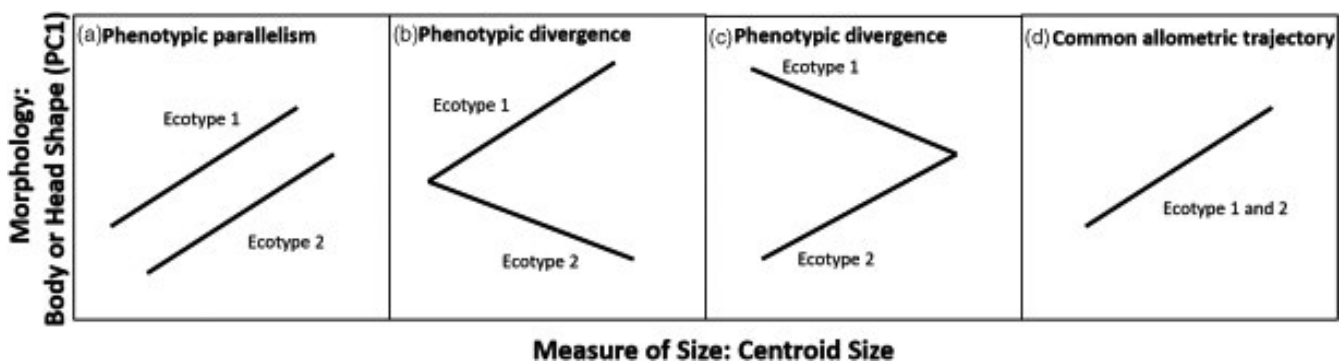


**TABLE A3** Forward selection multiple regression modelling of detrended otolith increment growth chronologies for lake charr ecotypes (huronicus or lean) sampled in Rush Lake in 2007 and 2018, as predicted by weighted seasonal climate variables

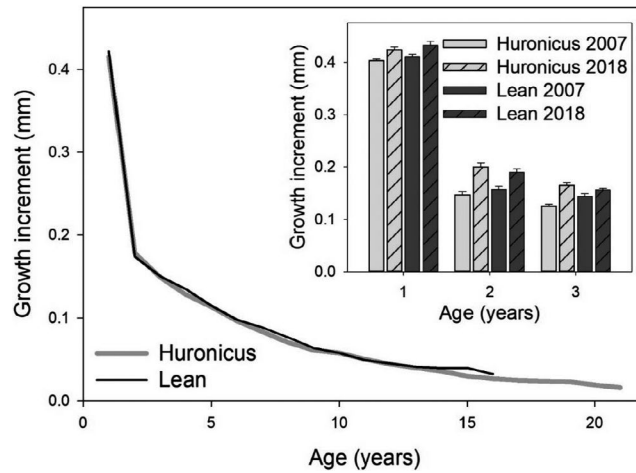
	Models	R <sup>2</sup>	p-value	AIC
Huronicus	Twin	0.23	0.01	-90.3
	SNwin	0.26	<0.01	-91.5
	SNwin + Tsum	0.35	<0.01	-93.1
Lean	Twin	0.31	<0.01	-59.6
	Pfal	0.37	<0.01	-61.5
	Twin + Pfal	0.56	<0.01	-67.7

Note: Environmental variables are represented as follow: Twin, winter temperature, SNOWin, winter snow; Tsum, summer temperature, and Pfal, fall precipitation.

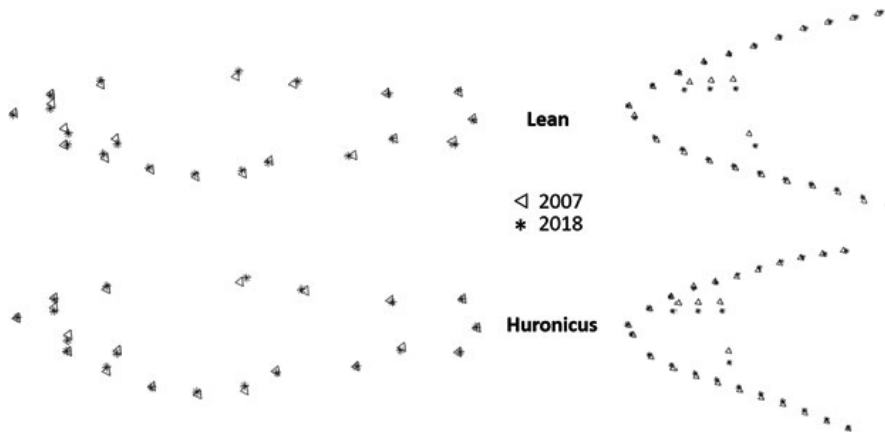
**FIGURE A1** Lean-like (a) and huronicus (b) lake charr *Salvelinus namaycush* ecotypes of Rush Lake. Illustration by P. Vecsei, after Chavarie et al. (2016). The lean ecotype has a long head, long maxillae and a posterior eye position, which are all characteristics for piscivorous feeding (Janhunen, Peuhkuri, & Piironen, 2009; Keeley, Parkinson, & Taylor, 2007; Proulx & Magnan, 2004). The huronicus ecotype, with smaller gape and higher eye position than the lean ecotype, appears adapted for low-light vision and as a vertical migrating predator feeding on the invertebrate opossum shrimp (*Mysis* spp.) as its main prey (Hrabik, Jensen, Martell, Walters, & Kitchell, 2006; Muir et al., 2014)



**FIGURE A2** Possible pattern of allometric trajectories between two putative ecotypes, figure is modified from Simonsen et al. (2017). Allometric trajectory patterns can be (a) parallel, (b) divergent, (c) convergent or (d) common



**FIGURE A3** Otolith growth increments plotted by age between lake charr ecotypes (lines) and detailed across the first three years of life (inset) for lake charr morphs (huronicus or lean) sampled in 2007 and 2018



**FIGURE A4** Configuration of Procrustes mean for the lean and huronicus ecotypes, for 2007 and 2018. Landmarks and semi-landmarks are represented in triangle for 2007 and a star for 2018

## APPENDIX B

### METHODS

#### Sampling

Lake charr ecotypes were caught with bottom-set gillnets in June 2007 and September 2018. Gillnets were deployed at depths from 10 to 83 m. Sets were made using 183 m long by 1.8 m high multifilament nylon gillnets consisting of stretch-mesh sizes from 50.8 to 114.3 mm, in 12.7 mm increments. Date, time, GPS location, and minimum and maximum water depth were recorded for each net set. All fish caught were photographed in lateral view (Muir et al., 2014), and sagittal otoliths were removed for analysis of age and growth.

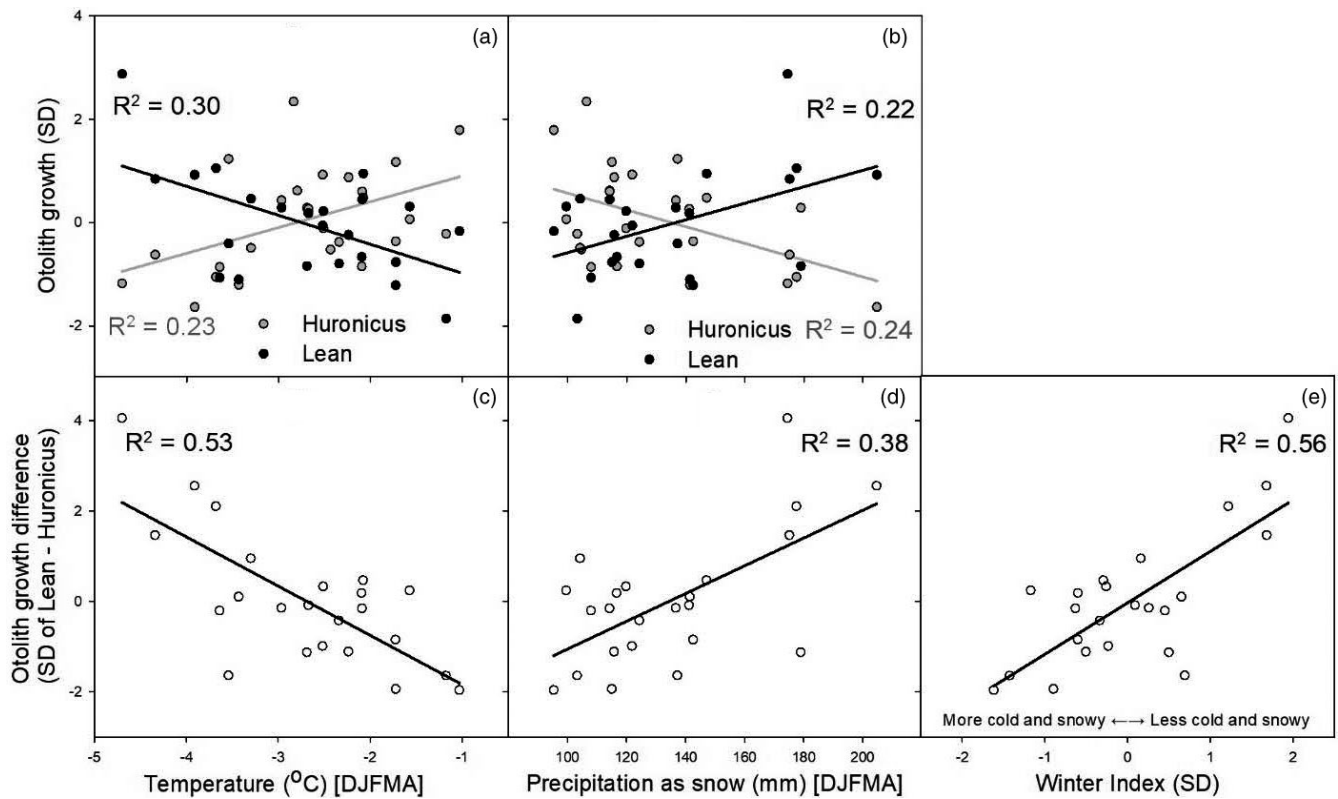
#### Assignment of lake charr ecotypes

Ecotypes were assigned to each individual using a combination of Bayesian cluster analyses using head and body shape information (MCLUST; Fraley & Raftery, 2009) and a visual identification by experienced lake charr biologists (M.J. Hansen & C. C. Krueger).

Disagreements between model and visual assignments were settled using decision rules described by Muir et al. (2014).

#### Age assignment and growth increments from otoliths

One otolith from each fish was embedded in epoxy. A Buehler Isomet 1000 Precision Saw was used to remove a thin transverse section (400  $\mu\text{m}$ ) containing the nucleus perpendicular to the sulcus. Sections were mounted on glass slides and polished. Digital images of otolith sections were captured for age and growth assessment. Criteria for annulus demarcation followed those of Casselman and Gunn (1992). Age estimates were used to inform demarcation of growth increments, measured from the nucleus to the maximum ventral radius of the otolith, and radial measurements at each annulus were used to back-calculate length at age using the biological intercept back-calculation model (Campana, 1990). The biological intercept (sagittal otolith radius = 0.137 mm; age-0 lake trout length = 21.7 mm; Hansen et al., 2012) was based on equations describing



**FIGURE A5** Standard deviations (SD) of ARSTAN-detrended growth increment versus previous winter temperatures and precipitation as snow. Growth SD between lake charr ecotypes sampled in Rush Lake in 2007 and 2018, plotted versus weighted winter climate variables (a, b), SD of the difference between ecotype growth versus weighted winter variables (c, d) and SD of the difference between ecotype growth plotted versus a 'winter index' that averaged the SD of sign-reversed temperature and precipitation as snow

relationships between length, age in days and sagittal otolith width of age-0 lake charr (Bronte, Selgeby, Saylor, Miller, & Forester, 1995).

- Bronte, C. R., Selgeby, J. H., Saylor, J. H., Miller, G. S., & Forester, N. R. (1995). Hatching, dispersal, and bathymetric distribution of age-0 wild lake trout at the Gull Island Shoal complex, Lake Superior. *Journal of Great Lakes Research*, 21(Supplement 1), 233–245.
- Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences*, 117, 59–71.
- Casselman, J. M., & Gunn, J. M. (1992). Dynamics in year-class strength, growth, and calcified-structure size of native lake trout (*Salvelinus namaycush*) exposed to moderate acidification and whole-lake neutralization. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(Suppl. 1), 102–113.
- Chavarie, L., Muir, A. M., Zimmerman, M. S., Baillie, S. M., Hansen, M. J., Nate, N. A., Yule, D. L., Middel, T., Bentzen, B., & Krueger, C. C. (2016). Challenge to the model of lake charr evolution: Shallow- and deep-water morphs exist within a small postglacial lake. *Biological Journal of the Linnean Society*. <https://doi.org/10.1111/bij.12913>
- Fraley, C., & Raftery, A. E. (2009). *MCLUST version 3 for R: Normal mixture modeling and model-based clustering* (pp. 56). Department of Statistics, University of Washington.

- Hansen, M. J., Nate, N. A., Krueger, C. C., Zimmerman, M. S., Kruckman, H. G., & Taylor, W. W. (2012). Age, growth, survival, and maturity of lake trout morphotypes in Lake Mistassini, Quebec. *Transactions of the American Entomological Society (Philadelphia)*, 141, 1492–1503.
- Hrabik, T. R., Jensen, O. P., Martell, S. J., Walters, C. J., & Kitchell, J. F. (2006). Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 2286–2295.
- Janhunen, M., Peuhkuri, N., & Piironen, J. (2009). Morphological variability among three geographically distinct Arctic charr (*Salvelinus alpinus* L.) populations reared in a common hatchery environment. *Ecology of Freshwater Fish*, 18, 106–116.
- Keeley, E., Parkinson, E., & Taylor, E. (2007). The origins of ecotypic variation of rainbow trout: a test of environmental vs. genetically based differences in morphology. *Journal of Evolutionary Biology*, 20, 725–736.
- Proulx, R., & Magnan, P. (2004). Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis* M.). *Evolutionary Ecology Research*, 6, 503–522.
- Simonsen, M. K., Siwertsson, A., Adams, C. E., Amundsen, P.-A., Præbel, K., & Knudsen, R. (2017). Allometric trajectories of body and head morphology in three sympatric Arctic charr (*Salvelinus alpinus* (L.)) morphs. *Ecology and Evolution*, 7(18), 7277–7289. <https://doi.org/10.1002/ece3.3224>