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Life-history variation along environmental and harvest clines of a northern freshwater fish: Plasticity and adaptation

Kyle L. Wilson[1,2] | **Joe De Gisi**[3] | **Christopher L. Cahill**[1] | **Oliver E. Barker**[4] | **John R. Post**[1]

[1]Department of Biological Sciences, University of Calgary, Calgary, AB, Canada
[2]Earth to Ocean Research Group, Simon Fraser University, Burnaby, BC, Canada
[3]Fish and Wildlife Section, British Columbia Ministry of Forests, Lands, and Natural Resource Operations, Smithers, BC, Canada
[4]Yukon Department of Environment, Whitehorse, YT, Canada

Correspondence
Kyle L. Wilson
Email: kl_wilson@sfu.ca

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Abstract

1. Plasticity, local adaptation and evolutionary trade-offs drive clinal variation in traits associated with lifetime growth. Disentangling the processes and determinants that cause these traits to vary helps to understand species' responses to changing environments. This is particularly urgent for exploited populations, where size-selective harvest can induce life-history evolution.
2. Lake trout (*Salvelinus namaycush*) are an exploited fish with a life history adapted to low-productivity freshwaters of northern North America, which makes them highly vulnerable to ecosystem changes and overfishing. We characterized life-history variation across a broad and diverse landscape for this iconic northern freshwater fish and evaluated whether clinal variation was consistent with hypotheses for local adaptation or growth plasticity.
3. We estimated growth-associated traits for 90 populations exposed to a diversity of environments using a Bayesian multivariate hierarchical model. We tested for clinal variation in their somatic growth, size at maturity and reproductive allocation along environmental gradients of lake productivity, climate, prey and exploitation clines under competing hypotheses of plasticity and local adaptation.
4. Clinal life-history variation was consistent with growth plasticity and local adaptations but not harvest-induced evolution. Variation in somatic growth was explained by exploitation, climate and prey fish occurrence. Increased exploitation, from pristine to fully exploited conditions, led to increased somatic growth (from 32 to 45 mm/year) and adult life spans, and reduced age at maturity (from 11 to 8 years). Variation in size at maturity was explained by climate and, less certainly, prey fish occurrence, while reproductive allocation was explained by evolutionary trade-offs with mortality and other traits, but not environment. Lake trout life-history variation within this range was as wide as that observed across dozens of other freshwater species.
5. Lake trout life histories resulted from evolutionary trade-offs, growth plasticity and local adaptations along several environmental clines. Presuming a plastic response, we documented ~1.4-fold growth compensation to exploitation—lower growth compensation than observed in many freshwater fishes. These results suggest that harvested species exposed to spatially structured and diverse

environments may have substantial clinal variation on different traits, but due to different processes, and this has implications for their resilience and successful management.

KEYWORDS

Bayesian, biphasic growth, clinal variation, harvest-induced evolution, life-history trade-offs, plasticity, *Salvelinus namaycush*

1 | INTRODUCTION

Life-history theory predicts that resource constraints and energy allocation to biological functions lead to trade-offs among traits causing selection to operate on a multivariate suite of traits (Roff, 2002; Roff & Fairbairn, 2007). As environmental variation can alter selective gradients, the optimal suite of traits can be expected to vary across environments (i.e. clinal variation; Conover & Present, 1990; Bradford & Roff, 1995; Roff, 2002). Local adaptation and phenotypic plasticity are two of the most common mechanisms driving clinal variation (Bradford & Roff, 1995; Kawecki & Ebert, 2004; Stearns, 1989). Disentangling the mechanisms causing clinal variation is important because traits regulate populations, community interactions and species responses to changing environments (Moore, Yeakel, Peard, Lough, & Beere, 2014; Valladares et al., 2014; Zimmermann, Ricard, & Heino, 2018). Understanding the processes and determinants that shape life histories of exploited species is particularly critical because sustainable harvest theory rests on the assumption that populations respond to exploitation with plastic, compensatory life-history changes (Lester, Shuter, Venturelli, & Nadeau, 2014). Determining compensatory trait responses to exploitation and whether exploitation alters selective gradients helps to understand species resilience (Heino, Díaz Pauli, & Dieckmann, 2015; Kuparinen & Merilä, 2007; Law, 2000; Lester et al., 2014).

Both plasticity and local adaptation cause clinal variation in the suite of traits associated with somatic growth (Lorenzen, 2016; Roff, 2002). Growth-associated traits (e.g. growth rate, maturation, reproductive allocation) respond to density-independent and density-dependent environmental variation (Stearns, 1989), and variation in these traits regulates populations (De Roos, Persson, & McCauley, 2003; Hamel et al., 2010; Zimmermann et al., 2018). Density-dependent growth allows organisms to attain larger body sizes and mature earlier when per-capita competition is reduced (Post, Parkinson, & Johnston, 1999). The magnitude and duration of foraging seasons (e.g. degree-days) influence growth and development (Roff, 2002). Environmental gradients, like exploitation or climate, cause plastic responses in traits like size and age at maturity (i.e. maturation reaction norm) observed among many exploited taxa (Heino, Dieckmann, & Godø, 2002; Law, 2000). Growth rate and body size can also be under strong selection leading to fitness advantages for larger body sizes (Conover & Munch, 2002; Stearns, 1989) that may be counterbalanced by energetic costs (Blanckenhorn, 2000).

Size-selective harvest can cause compensatory changes in growth-associated traits (Conover & Munch, 2002; Edeline et al., 2007; Heino et al., 2015; Swain, Sinclair, & Hanson, 2007). Theory predicts that selective exploitation of large individuals increases per-capita resource availability leading to plastic, compensatory increases in juvenile somatic growth and reductions in age at maturity (Lester et al., 2014). Yet, theory also predicts that consistently high size-selective harvest can cause life-history evolution by favouring earlier maturation at smaller sizes and increased reproductive allocation (i.e. harvest-induced evolution; Law, 2000; Edeline et al., 2007; Lester et al., 2014). This evolved response is often maladaptive because natural selection and harvest selection act in different ways (Edeline et al., 2007), and the consequences of reduced body size are often undesirable for resource management (Jorgensen et al., 2007). In many cases, however, growth plasticity may buffer against selection on growth-associated traits and slow down harvest-induced evolution (Ernande, Dieckmann, & Heino, 2004; Lester et al., 2014).

Species inhabiting diverse environments across broad geographic ranges often display substantial life-history clines (Armbruster, Bradshaw, Ruegg, & Holzapfel, 2001; Jones, Augspurger, & Closs, 2017; Morrison & Hero, 2003). Many of these species have characteristics (e.g. long lives, poor artificial rearing) that make it difficult to design experiments or collect genotype–phenotype time-series to detect causal mechanisms explaining this variation (Sagarin & Pauchard, 2010; Frenne et al., 2013). These problems are often exacerbated for exploited species where experiments can be unpopular, and rigorous assessments of many broadly distributed populations are logistically challenging. Thus, monitoring agencies are often forced towards observational studies to assess patterns, which can make it difficult to learn about process (Sagarin & Pauchard, 2010). However, analysing life-history variation across a variety of environmental gradients as a natural experiment (Frenne et al., 2013) can complement manipulative experiments in non-natural settings. Observational studies can then test for alternative hypotheses that may explain clinal variation (Sagarin & Pauchard, 2010), which can help inform best practices for simultaneously managing numerous populations across a heterogenous landscape (Shuter, Jones, Korver, & Lester, 1998). Consequently, there is a need to develop an approach that simultaneously (a) describes species life histories (Lester, Shuter, & Abrams, 2004; Roff, Heibo, & Vøllestad, 2006); (b) accounts for correlations, trade-offs and uncertainty between traits (Helser & Lai, 2004); and (c) tests alternative hypotheses to explain clinal variation (Sagarin & Pauchard, 2010; Frenne et al., 2013).

TABLE 1 Predicted trait responses (positive +, negative − or null =) to exploitation, climate (growing degree-days > 5°C), prey fish occurrence and lake productivity (total dissolved solids, mg/L) gradients under growth plasticity and local adaptation hypotheses

Trait	Exploitation	Climate	Prey fish	Productivity
Growth plasticity				
Somatic growth rate (*h*)	+	+	+	+
Age at maturity (*T*)	−	−	−	−
Size at maturity (*L50*)	=	=	=	=
Reproductive allocation (*g*)	=	=	=	=
Local adaptation				
Somatic growth rate (*h*)	+	+ or (−)	=	+ or (−)
Age at maturity (*T*)	−	− or (+)	−	− or (+)
Size at maturity (*L50*)	−	− or (+)	+	− or (+)
Reproductive allocation (*g*)	+	−	−	−

Note. Alternative predictions for local adaptation to climate and productivity clines suggest selection may favour either (a) rapid juvenile growth with earlier maturation at smaller body sizes or (b) slower juvenile growth with later maturation at larger body sizes.

In this study, growth-associated traits were estimated for 90 lake trout (*Salvelinus namaycush*) populations across their native latitudinal range in western Canada. We tested for clinal variation along environmental gradients of lake productivity, climate, forage (i.e. prey fish occurrence) and exploitation because these clines are associated with forage resource quality, growing season duration and population density, respectively, and are known to shape life histories and selection regimes (Roff, 2002). We developed two hypotheses based on fish life-history theory to explain mechanisms underlying trait variation: growth plasticity and local adaptation (Table 1).

1.1 | Hypotheses

In developing our plasticity hypothesis, we assumed reaction norms describing how traits would vary along environmental clines. We assumed that reproductive allocation and size at maturity would be fixed for a genotype and that age at maturity would decrease with increased growth rate (Dunlop, Heino, & Dieckmann, 2009; Lester et al., 2014). With a plastic response, we hypothesized that environmental clines would influence only juvenile growth rate and age at maturity, and not size at maturity or reproductive allocation, because growth compensation buffers against selective pressure on reproductive allocation and size at maturity (Dunlop et al., 2009; Lester et al., 2014). Specifically, we predicted that increased juvenile growth and reduced age at maturity would result from (a) climate and productivity increasing growing season duration and forage quality (Neuheimer & Taggart, 2007), (b) increased prey size spectrum from prey fish occurrence allowing for ontogenetic foraging shifts (Martin, 1966, 1970; Shuter, Giacomini, de Kerckhove, & Vascotto, 2015) and (c) exploitation reducing population density and competition for limited resources (Lester et al., 2014).

Under the local adaptation hypothesis, we predicted additional responses in reproductive allocation and size at maturity as these traits adjust to maximize fitness in variable environments. Specifically, we predicted that (a) increased net energy intake from climate and productivity would cause selection to favour either increased juvenile growth and earlier maturation at smaller body sizes or slower juvenile growth and later maturation at larger body sizes (McDermid, Shuter, & Lester, 2010), (b) prey fish occurrence would increase the prey size spectrum allowing juvenile lake trout to maintain their growth rates while delaying their size and age at maturity (Shuter et al., 2015), and (c) increased size-selective harvest would increase reproductive allocation and reduce size at maturity as smaller adult body sizes would now be advantageous to avoid size selectivity (Dunlop et al., 2009).

Our two hypotheses also predicted different responses in adult reproductive life spans caused by size-selective harvest (Depczynski & Bellwood, 2006; Lester et al., 2014). Under a local adaptation response, reduced size at maturity and increased reproductive allocation reduce adult body sizes and reproductive life spans. A plastic response to exploitation predicts that increased growth and reduced age at maturity can increase adult body sizes and life spans. We thus examined how lake trout adult life spans varied with exploitation. We then demonstrate how variation in life-history traits could be interlinked through evolutionary trade-offs. Last, we discuss how the processes underlying trait variation and trade-offs may influence the compensatory responses to environmental variation for this long-lived and variably exploited freshwater fish.

2 | MATERIALS AND METHODS

2.1 | Study species and landscape

Lake trout are endemic to North America and a valued game fish found in deep, cold waters throughout northern North America (Gunn, Steedman, & Ryder, 2004). Lake trout inhabit hundreds of freshwater lakes on the western edge of their native range, with 413 documented populations in British Columbia and Yukon Territory (Figure 1; McPhail, 2007). Lake trout are one of the only native game fishes accessible year-round to fishers of northern oligotrophic lakes,

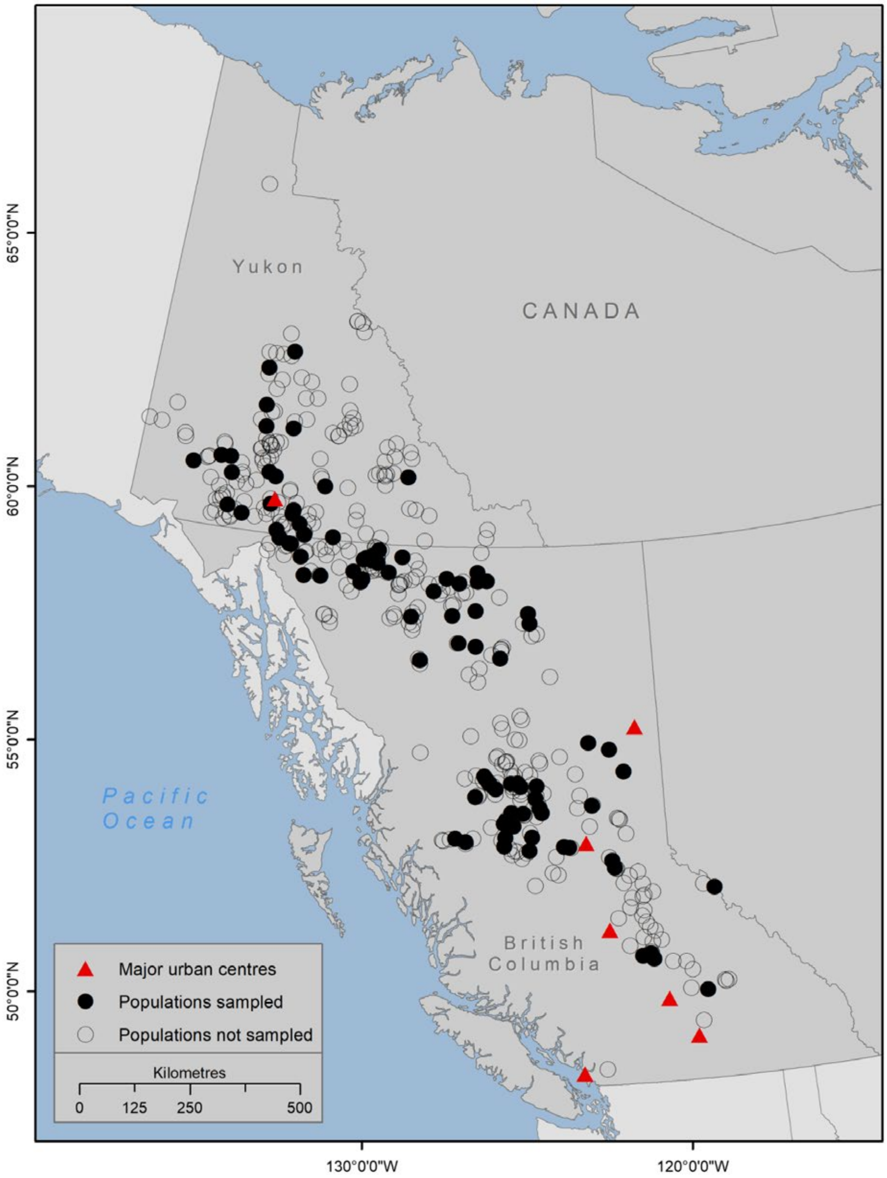

FIGURE 1 Distribution of known lake trout populations (including native and introduced populations, e.g. Alouette Lake) across western Canada and regional urban centres as major sources of exploitation

and their typical life history of slow growth and late maturation make them susceptible to overexploitation (Shuter et al., 1998). As a result, numerous lake trout population collapses have been documented throughout North America (Gunn et al., 2004). For these reasons, both British Columbia and Yukon list lake trout as a species requiring priority conservation actions (British Columbia Conservation Data Centre 2017; Environment Yukon 2010). British Columbia and Yukon's large gradients in latitude, longitude and elevation (range: 126–1,456 m) drive large environmental clines over short distances (e.g. range of −7.4 to +9.3°C mean annual air temperature), exposing lake trout populations to a diversity of environments.

2.2 | Statistical rationale

To explain lake trout life-history variation, we constructed a Bayesian model that estimated: (a) a logistic maturity model and a biphasic somatic growth model based on bioenergetics and life-history theory (Lester et al., 2004), and (b) a hierarchical multiple linear regression model that described trait–environment relationships (Helser & Lai, 2004). As part of step 2, we used a variable inclusion approach that separates the variable selection process from the estimation process of a covariate's effect size to determine whether environmental covariates were useful trait predictors (Royle & Dorazio, 2008).

We simultaneously estimated biphasic growth and maturity models following Wilson, Honsey, Moe, and Venturelli (2018). We explored relationships among juvenile growth rate, size at maturity and reproductive allocation and related these traits to environmental covariates such as climate, productivity, prey fish occurrence and exploitation gradients (Table 1). We estimated how the average trait value varied along environmental gradients using multiple regression assuming exchangeability among populations. This approach accounts for (a) correlations and trade-offs in life-history traits that result in differences in size and age structure between independent populations and (b) trait–environment relationships that influences life-history variation across their range.

2.3 | Lake trout data

Lake trout populations in British Columbia and Yukon have been opportunistically sampled since the 1950s with most sampling occurring since 1976. Fork length (±1 mm), age (years) and maturity were collected for 19,963 individuals in 144 lakes from several major watersheds including the Fraser, Skeena, Mackenzie and Yukon. Samples from any introduced populations were excluded from analyses (e.g. Alouette). Maturity was estimated from macroscopic inspection of gonad development. Individuals were classified as immature (no evidence of gonad development), maturing (initial gonad development, but unlikely to spawn by the next spawning season) or mature (e.g. gonads were fully developed, or there was evidence of past spawning activity). All individuals with unknown maturity were excluded from analysis. Only 90 lakes had sufficient data quality to reliably estimate growth and maturity (total of 8,946 length-at-age samples and 8,668 length-at-maturity samples). Lakes were included only if they had ≥20 size-at-age samples, ≥3 immature samples and ≥3 mature samples. Data were pooled across sexes because lake trout do not exhibit strong sexual dimorphism in traits (McDermid et al., 2010; McPhail, 2007). We pooled samples across years and sampling gears within lakes to create synthetic cohorts due to the lack of repeated measures within lakes over time (most lakes were sampled fewer than three times in total). Combining samples from different gears can reduce bias on trait estimates caused by size selectivity (Wilson et al., 2015). This synthetic cohort approach assumes that both environment and average life-history traits did not vary through time.

2.4 | Life-history traits and trade-offs

Lake trout exhibit ontogenetic shifts in somatic growth schedules associated with reproduction (Minte-Vera, Maunder, Casselman, & Campana, 2016; Quince, Shuter, Abrams, & Lester, 2008). Length-at-age data were used to model biphasic growth assuming that: (a) the allometric exponents for net energy intake and losses were 2/3 (Quince et al., 2008 support an allometric exponent for lake trout of ≈0.69); (b) the timing of maturity was related to the onset of reproductive allocation and spawning events; (c) juveniles allocated all surplus energy to somatic growth; and (d) adults allocated surplus energy yearly to somatic growth and reproductive allocation at a proportion g that was constant with age. We then followed the discrete biphasic growth model (Lester et al., 2004), a recommended growth model for investigating life-history evolution in long-lived fishes (Dunlop et al., 2009; Wilson et al., 2018).

The Lester biphasic growth model (LM) describes immature growth as linear, and mature growth as a curvilinear von Bertalanffy model:

$$\widehat{L_a} = h(a - t_1) \text{ when } a \leq T, \tag{1}$$

$$\widehat{L_a} = L_\infty (1 - e^{-k(a-t_0)}) \text{ when } a > T, \tag{2}$$

$$t_1 = \frac{l_0}{-h}, \tag{3}$$

$$T = \frac{L50}{h} + t_1, \tag{4}$$

where $\widehat{L_a}$ is the predicted length at age a, h is juvenile growth rate (length per unit time), l_0 the hypothetical length (mm) at age 0 (i.e. the y-intercept), t_1 is the LM (immature) hypothetical age at length 0, $L50_l$ is the length (mm) where 50% of the population is mature, T is last immature age (LM parameter for age at maturity), L_∞ is asymptotic length, k is the von Bertalanffy (Brody) growth coefficient, and t_0 is the von Bertalanffy (adult) hypothetical age at length 0. Lester et al. (2004) showed that L_∞, k, and t_0 reflect bioenergetic trade-offs among growth, reproduction and mortality:

$$L_\infty = \frac{3h}{g}, \tag{5}$$

$$k = \ln\left(1 + \frac{g}{3}\right), \tag{6}$$

$$t_0 = T + \frac{\ln\left(1 - \frac{g(T - t_1)}{3}\right)}{\ln\left(1 + \frac{g}{3}\right)}, \tag{7}$$

where g is the reproductive cost to somatic growth (Kozlowski, 1996; Roff et al. 2006). Note that g captures the proportion of surplus energy allocated into direct (e.g. gonadal development) and indirect (e.g. behaviour and metabolism) reproductive costs. Lester et al. (2004) found that variation in late-stage juvenile and adult mortality M shapes optimal growth-associated traits such that:

$$g \approx 1.18(1 - e^{-M}), \tag{8}$$

$$T \approx \frac{1.95}{e^M - 1} + t_1, \tag{9}$$

Whether the above M depicts natural mortality M or total mortality Z depends on whether those traits respond to exploitation (see Table 1). For example, if reproductive allocation g were invariant to exploitation, then rearranging Equation 8 provides an empirical estimator of natural mortality for fish with a biphasic life history. Empirical natural mortality estimators derived from other life-history data are widely used in fish life-history analyses (Hoenig, 1983). As we lacked sample sizes to accurately estimate survivorship using age-based catch curves (~>200 sample sizes per population), we used the Lester et al. (2004) empirical estimators to approximate natural mortality (or total mortality, depending on the response of traits in Equations 8 or 9 to exploitation). We then evaluated the reliability of using reproductive allocation as an indicator of natural mortality by comparing natural mortality calculated from Equation 8 to catch curve estimates of natural mortality for nine unexploited lake trout populations.

The plasticity and local adaptation hypotheses predict different consequences of size-selective harvest on adult life spans (Depczynski & Bellwood, 2006; Lester et al., 2014). Under the local adaptation response, increased reproductive allocation and earlier age at maturity would result in shortened life spans whereas, under the plastic response, increased growth and earlier maturation would maintain or even increase adult life spans. We thus contrasted how lake trout adult life spans (estimated as the oldest individuals sampled in each population less their age at maturity; i.e. $T_{\max} - T$) varied along environmental and exploitation clines. As many of our populations had fewer sample sizes than recommended for longevity estimators ($N \sim 200$), we adjusted estimates of adult post-maturation life spans $E(T_{\max})$ for populations with fewer than 200 sample sizes (Hoenig, 1983; McDermid et al., 2010) such that:

$$E(T_{\mathrm{adult}(200),l}) = \left(\frac{\left[T_{\max} - t_{c_l}\right] \ln(2(200)+1)}{\ln(2N_l+1)} + t_{c_l} \right) - T, \tag{10}$$

where t_c is the age of the youngest fish and N_l is the number of ages samples, and T is the age at maturity for the lth population. We used linear regression to test the influence of exploitation on adult life span.

Life-history trade-offs between traits were predicted by jointly solving Equations 8 and 9 across a range of natural mortalities (e.g. M = 0.01–1.0 year^{-1}) and other traits, with the mortality range taken from a life-history compendium of North American freshwater fishes (Randall & Minns, 2000). From these equations, we predicted the: (a) expected trade-off between age at maturity and mortality, (b) ratio between size at first reproduction and maximum body size, (c) relationship between reproductive allocation and somatic growth, and (d) relationship between reproductive allocation and size at maturity. We used this approach to show how relationships and trade-offs between traits could result from a given mortality condition acting as a selective pressure on growth-associated traits. We compared posterior mean trait values for each population to observed trait values from a variety of fish species in Randall and Minns (2000).

We characterized life-history traits across lake trout populations using a Bayesian hierarchical model where the vector θ_l represents the lth population's traits with a multivariate normal distribution (Helser & Lai, 2004). We assumed populations were panmictic and had a unimodal optimal life-history strategy. The multivariate normal distribution had a mean vector μ composed of five traits ($L50, \delta, h, \ln g, l_0$; where δ is steepness in size at maturity) describing the average trait for the average population (i.e. hyperpriors), and a variance–covariance matrix Σ, which had a vague inverse-Wishart prior. Reproductive allocation g_l was assumed to be log-normally distributed to improve numerical performance, similar to previous studies on the VBGF growth coefficient κ (Pilling, Kirkwood, & Walker, 2002). That is,

$$\theta_l = \begin{pmatrix} L50_l \\ \delta_l \\ h_l \\ \ln g_l \\ l_{0_l} \end{pmatrix} \sim \mathrm{MVN}(\mu, \Sigma), \quad \text{for } l = 1, 2, \ldots, N_{\mathrm{lakes}}, \tag{11}$$

where the main diagonal of Σ (a 5 × 5 matrix) represents trait-specific variance (e.g. σ^2_{L50}) and the off-diagonals represent covariance between different traits (e.g. $\sigma^2_{L50,h}$). The distributions for the parameters h were truncated positive, and g had a maximum upper bound of $3/(T_l - t_{1_l})$ resulting from energetic limits on reproductive allocation at the time of maturity (Lester et al., 2004). We used a normally distributed likelihood (truncated positive) with a multiplicative error structure to model size at age for each fish i across each population:

$$L_{i,l} \sim \mathrm{Normal}(\widehat{L_{i,l}}, \widehat{L_{i,l}} cv_L), \tag{12}$$

with a constant coefficient of variation in length at age cv_L, and a corresponding standard deviation of $\widehat{L_{i,l}} cv_L$. The maturation schedule P_{MT} was a function of length and was described using the following logistic function:

$$P_{MT_{i,l}} = \frac{1}{1 + e^{\left(-\ln(19) \frac{(L_{i,l} - L50_l)}{\delta_l} \right)}}, \tag{13}$$

where $L50$ was the size at 50% maturity, and δ was the length increment after $L50$ to reach 95% maturity. The likelihood that a captured fish was mature was as follows:

$$MT_{i,l} \sim \mathrm{Bernoulli}(P_{MT_{i,l}}). \tag{14}$$

2.5 | Environmental clines

We tested our hypotheses (Table 1) that variation in life-history traits was related to environmental clines by reparameterizing Equation 11 into a hierarchical regression following Helser and Lai (2004). Hence, each trait's central tendency could vary along environmental gradients such that,

$$\theta_l = \begin{pmatrix} L50_l \\ \delta_l \\ h_l \\ \ln g_l \\ l_{0_l} \end{pmatrix} = \begin{pmatrix} L50 + \omega_{L50} \beta_{L50} x_l \\ \delta_l \\ h + \omega_h \beta_h x_l \\ \ln g + \omega_g \beta_g x_l \\ l_{0_l} \end{pmatrix} \sim \mathrm{MVN}(\omega \beta X_l + \mu, \Sigma), \quad \text{for } l = 1, 2, \ldots, N_{\mathrm{lakes}}, \tag{15}$$

where X_l is a vector of different environmental covariates, β is a vector of coefficients for those covariates, and ω is a vector of inclusion parameters for that covariate and trait (Royle & Dorazio, 2008). Each β coefficient had independent normal priors, for example, $\beta_{\mathrm{h,Exploitation}} \sim N(0, 1/\sqrt{0.001})$, and each ω inclusion parameter had independent Bernoulli priors with probability of 0.5 (i.e. a fair coin flip).

We modelled relationships between traits and lake productivity, climate, prey fish occurrence and exploitation pressure. Environmental variables for each lake were characterized by annual averages as these clines did not exhibit significant temporal trends (Supporting Information Appendix S1). We approximated lake productivity by total dissolved solids (TDS in mg/L). Prey fish occurrence was taken from historical fishery-independent and fishery-dependent observations of suitable prey fish species—occurrence related positively to lake trout biomass (Supporting Information Figure S1.3). Despite a wide variety of freshwater fishes found in our study range, only round whitefish *Prosopium cylindraceum*, pygmy whitefish *Prosopium coulterii*, lake whitefish *Coregonus clupeaformis*, least cisco *Coregonus sardinella* and kokanee salmon *Oncorhynchus nerka* were considered suitable prey fish because they overlap with lake trout habitats, were observed in lake trout guts and influence their prey size spectrum (Shuter et al., 2015). Lake productivity and the occurrence of any of the prey fish species above (binary response) were directly measured on all 90 lakes. However, we developed proxies of climate and exploitation as these were not explicitly measured. We approximated the climate gradient with growing degree-days > 5°C (GDD) derived from mean annual air temperature (°C). The GDD metric integrates the magnitude and duration of the foraging season (Neuheimer & Taggart, 2007). Long-term average GDD was estimated at the latitude–longitude–elevation of each lake's centroid coordinates via ClimateWNA (Wang, Hamann, Spittlehouse, & Murdock, 2012) and accurately measured climate differences between lakes (Supporting Information Figure S1.4).

We approximated exploitation on the 90 lakes using a multivariate analysis of travel distance, fishery infrastructure and access-related features, as these characteristics were believed to influence fishing activity (see Supporting Information Appendix S2 for details; Kaufman, Snucins, Gunn, & Selinger, 2009). Lakes were classified 1–5 based on clustering analyses. Class 1 lakes corresponded to pristine populations with no infrastructure (e.g. no roads, marinas, lodges or campgrounds) and no reported angling guiding. Class 2 lakes were remote backcountry and wilderness lakes that lacked road access but experienced some use by anglers or outfitters. Class 3 lakes were backcountry lakes farther from highways that lacked paved road access or private residences but had some public facilities (e.g. recreational site). Class 4 lakes were lakes with paved or gravelled road access within 0.5–1.0 hours from the closest urban centre, but with low density of private residences and infrastructure. Class 5 lakes were lakes with high infrastructure (e.g. combinations of marinas, lodges, campgrounds, close to urban areas) and fishing activity suggesting high exploitation. These exploitation classes were positively related to both angler effort density and total catch from angler surveys of 30 lakes in Yukon (Supporting Information Figure S2.6,S2.7) and did not trend through time (Supporting Information Figure S1.5) suggesting a reasonable approximation of harvest pressure.

Our environmental clines were statistically independent of one another. All covariates had variance inflation factors ≤ 1.4 suggesting multicollinearity among biogeographic predictors was not problematic (Zuur, Ieno, & Elphick, 2010). The productivity gradient (TDS) was log-transformed to normalize across-lake variation. We centred all covariates on their mean from sampled and unsampled populations (see Figure 1) and standardized the climate (GDD) and productivity (TDS) gradients by 2σ prior to analysis. We thus interpreted the intercepts μ (from Equation 15) as the expected life histories for lake trout populations experiencing an average environment in our landscape.

All combinations of all lake trout trait–environment hypotheses were evaluated with the inclusion variables (ω) for a total number of models tested of 2^{12} (i.e. inclusion is a Bernoulli trial, and each of 3 traits has 4 environment covariates for 12 total trials). Inference on the “top model” was then based on trait–environment associations that have the highest inclusion probability in the posterior. The effect size and 95% credible intervals (CI) for a given trait–environment relationship were based on posterior draws that included the latent variable, as the MCMC algorithm only samples the prior distribution when the covariate is excluded. Uncertain covariates had posterior probability close to 0.5, that is, the trait–environment association was as likely as a fair coin flip. Closeness of a given inclusion probability to zero or one indicated higher certainty that the trait–environment association should be excluded or included, respectively.

We assessed the biological significance of each trait–environment association based on effect sizes and inclusion probability. We first determined whether the 95% CI of a given environmental covariate included 0. We then inferred empirical support for a covariate if the posterior inclusion probability > 0.5 (Barbieri & Berger, 2004). We tested our hypotheses that exploitation influenced the three traits of interest based on their estimated effect size 95% CI (Table 1). For example, we assumed that if 95% of the posterior mass for $\beta_{h,\text{Exploitation}}$ was positive, and either $\beta_{g,\text{Exploitation}}$ was positive or $\beta_{L50,\text{Exploitation}}$ was negative, then this would provide evidence for selection and local adaptation to size-selective exploitation. Similarly, we assumed that if $\beta_{h,\text{Exploitation}}$was positive and exploitation had no effect on *g* or *L*50, then this would provide evidence for growth plasticity because growth plasticity buffers against selection on reproductive allocation and size at maturity (Ernande et al., 2004; Lester et al., 2014). If the plasticity hypothesis was supported, we attempted to quantify the scope of that plasticity (i.e. growth compensation). We defined growth compensation as the ratio between marginal effect of exploitation (independent of other environmental effects) on somatic growth rates in the fully exploited (h_F) and unexploited state (h_M) based on results from our hierarchical regression such that:

$$\frac{h_F}{h_M} = \frac{\bar{h} + \omega_{h,\text{Exploitation}}\beta_{h,\text{Exploitation}}\max(x_{\text{Exploitation}})}{\bar{h} + \omega_{h,\text{Exploitation}}\beta_{h,\text{Exploitation}}\min(x_{\text{Exploitation}})}. \tag{16}$$

We compared posterior mean growth rates along the exploitation gradient to provide further evidence for the degree of compensation.

2.6 | Statistical validation

We implemented our model in JAGS run through R in *rjags* and *run.jags* (Denwood, 2016; Plummer, 2003; R Core Team 2017) using 12 MCMC chains. The JAGS code for this model can be found in Supporting Information Appendix S3, and summary data on population locations, environmental variables, sample sizes and life-history traits can be found in Supporting Information Appendix S4. Each chain took 5,000 samples of the posterior, with a burn-in period of 50%, and thinning rate of 50 for a total chain length of 550,000 iterations. Starting parameter values were jittered for each chain. Model suitability and MCMC chain convergence to a common posterior mode were validated in several complementary ways. Convergence of the MCMC chains was inspected visually on traceplots. In addition, we ensured that parameters had an effective sample size $\geq 1{,}000$ and low per cent error for the Markov chain relative to the parameter's standard deviation (Gelman et al., 2013). We used the Gelman–Rubin diagnostic test on each parameter to determine whether independent chains converged to a common posterior distribution, with potential scale reduction factors (PSRF) < 1.1 suggesting convergence. We then used graphical posterior predictive checks to test for model misspecification and assessed bias using standardized residuals comparing predicted to observed lengths at age.

3 | RESULTS

Life-history traits were highly variable and correlated among western Canada's lake trout populations (Table 2 and Supporting Information Table S6.1, Appendix S5). The range of posterior mean traits across populations revealed ninefold variation in juvenile growth rate (range: 10–85 mm/year), threefold variation in size at maturity (range: 282–767 mm), eightfold variation in age at maturity (range: 4.0–32.0 years) and 11-fold variation in reproductive allocation (range: 0.04–0.46 year^{-1}). Post-maturation adult life spans ranged from 3 to 55 years with a mean of ~28 years (Table 2). We estimated both positive and negative correlations between traits suggesting substantial statistical and biological trade-offs between traits (Supporting Information Table S6.1). For example, h was strongly and positively correlated with ln g, strongly and negatively correlated with l_0 and weakly negatively correlated with $L50$.

Estimates of growth and maturity parameters passed most diagnostic and MCMC convergence checks. All global and population-specific traits passed the Gelman–Rubin diagnostic with PSRFs < 1.1 indicating convergence to a common posterior distribution (with the exception of traits from one lake, Moberly). Life-history traits of all populations had an effective sample size > 2,000. Although 99.6% of all standardized residuals fell within $\pm 2\sigma$ across lakes, there was a tendency to underpredict length at age for fish ≥ 600 mm (Supporting Information Figure S6.1). With this exception, posterior predictive checks suggested no systematic biases associated with the biphasic growth model on a per lake basis as most size-at-age samples were contained within the posterior predictive distribution 95% CI (Supporting Information Appendix S7 and Figure S6.2). Most lake-specific traits had unimodal posterior distributions except for McBride and Moberly, which had bimodal distributions, and some lake-specific traits had wide tails on one side of their posterior distribution (Supporting Information Appendix S5).

Clinal variation was consistent with our hypotheses of plasticity in juvenile growth rate and local adaptations on size at maturity (Tables 3 and 4). Juvenile somatic growth rate h was positively related to climate, exploitation and prey fish occurrence consistent with our predictions for growth plasticity (Figure 2; Tables 3 and 4). However, size at maturity $L50$ was related to climate and prey occurrence in the direction consistent with local adaptations of delayed maturation at larger body sizes (Figure 3). Reproductive allocation was unrelated to any environmental gradients (Tables 3 and 4). Age at maturity T was influenced by the same covariates as h and $L50$ because T must vary positively with $L50$ and inversely with h, consequent of Equation 6. The "top model" (representing 21% of MCMC draws) was a useful predictor of h and $L50$ ($R^2 = 0.22$ and 0.17, respectively) and included $h \sim f$(climate, exploitation, prey) and $L50 \sim f$(climate, prey) while excluding all other covariates. Climate effects on h and $L50$ increased when we removed Shuswap, the warmest population in the dataset (Figures 2c and 3c).

TABLE 2 Mean and 95% credible intervals (CI) for average lake trout life-history traits: juvenile somatic growth (h), reproductive allocation (g), size at age-0 ($l0$), size at 50% maturity ($L50$), age at maturity (T), steepness in size at maturity (δ), coefficient of variability in size at age (cv_L), Brody growth coefficient (κ), maximum body size (L_∞) and adult life span (T_{adult})

Trait	Value
h (mm/year)	37 (33–42)
g (year^{-1})	0.15 (0.12–0.17)
$l0$ (mm)	123 (100–146)
$L50$ (mm)	486 (455–521)
T (years)	9.8 (8.6–11.2)
δ (mm)	238 (209–2,678)
cv_L	0.14 (0.14–0.14)
κ (year^{-1})	0.05 (0.04–0.06)
L_∞ (mm)	796 (686–844)
T_{adult} (years)	29 (3–55)

TABLE 3 Mean and 95% credible intervals (CI) for estimated relationships between juvenile somatic growth rate (h), size at maturity ($L50$), and reproductive allocation (g) and gradients of exploitation, climate (degree-days > 5°C, GDD), prey fish species diversity and productivity (TDS)

Trait|environment	Mean (95% CI)	Inclusion probability
h|Climate	8.93 (4.60–13.19)	1.00
h|Exploitation	3.16 (1.62–4.68)	0.99
$L50$|Climate	58.76 (21.70–94.71)	0.99
h|Prey fish	6.53 (2.44–10.75)	0.88
$L50$|Prey fish	23.56 (−14.37 to 60.72)	0.56
$L50$|Productivity	−11.70 (−36.13 to 11.90)	0.38
$L50$|Exploitation	6.30 (−9.03 to 22.27)	0.26
h|Productivity	1.58 (−0.93 to 3.86)	0.08
ln g|Prey fish	−0.06 (−0.17 to 0.00)	0.01
ln g|Climate	0.03 (0.00–0.04)	0.00
ln g|Productivity	0.01 (−0.01 to 0.04)	0.00
ln g|Exploitation	0.01 (−0.00 to 0.02)	0.00

Note. Relationships ranked by descending inclusion probability; empirical support for inclusion ≥0.5 (Barbieri & Berger, 2004).

TABLE 4 Mean lake productivity (total dissolved solids, TDS), climate (growing degree-days, GDD), prey fish occurrence and life-history traits (juvenile somatic growth rate *h*, age at maturity *T*, size at maturity *L*50, reproductive allocation *g* and adult life span T_{adult}) for lake trout populations across exploitation classes (range in parentheses)

Class	TDS (mg/L)	GDD (>5°C)	Prey fish	*h* (mm/year)	*T* (years)	*L*50 (mm)	*g* (year^{-1})	T_{adult} (years)
1	133 (18–324)	616 (328–973)	0.44 (0–1)	27 (13–37)	13 (8–32)	428 (340–583)	0.17 (0.07–0.32)	20 (3–39)
2	96 (14–306)	733 (413–1,055)	0.68 (0–1)	35 (10–66)	13 (5–31)	497 (321–685)	0.14 (0.04–0.29)	28 (7–52)
3	101 (26–279)	877 (559–1,087)	0.82 (0–1)	42 (23–68)	9 (4–17)	480 (282–708)	0.18 (0.09–0.42)	30 (11–48)
4	113 (37–386)	883 (513–1,147)	0.85 (0–1)	49 (22–85)	9 (4–16)	483 (333–752)	0.21 (0.07–0.46)	30 (13–45)
5	89 (46–148)	933 (649–1,919)	0.92 (0–1)	45 (19–69)	9 (4–20)	514 (365–768)	0.17 (0.06–0.33)	32 (11–47)

Variation in juvenile somatic growth rates and age at maturity was strongly associated with exploitation, consistent with our plasticity hypothesis (Figure 4). Specifically, the predicted positive association between exploitation and juvenile somatic growth rates and the negative association between exploitation and age at maturity were supported (Tables 3 and 4; Figure 4a,d). Neither size at maturity nor reproductive allocation were associated with exploitation suggesting weak support for harvest-induced evolution (Figure 4b,c). Somatic growth compensation ratio increased with exploitation with a maximum compensatory response of ~1.4-fold (Figure 4a). This compensatory response was independent of other environmental covariate and predicted a reduced age at maturity by 3 years from unexploited to fully exploited conditions (Table 5; Figure 4d). Consistent with our plasticity hypothesis, size-selective harvest appeared to increase adult life spans by ~10 years ($F = 5.34$; $df = 1, 88$; $p = 0.0232$; Figure 5; Table 4).

Life-history relationships and trade-offs between traits were present across populations, and some traits varied as much in western Canada's lake trout as was observed across 79 fish species throughout North America (Figure 6; see movie in Supporting Information Appendix S8). Empirical estimates of natural mortality based on reproductive allocation in Equation 8 were consistent with catch curve estimates of natural mortality on nine unexploited populations ($R^2 = 0.54$) suggesting Equation 8 provided a reasonable descriptor of lake trout natural mortality (Supporting Information Figure S9). Relationships among lake trout life-history traits were consistent with predictions from Equations 8 and 9, which assumed that late-stage juvenile and adult mortality alters selective pressures on growth-associated traits. For example, the predicted trade-off between mortality and time to maturity ($T - t_1$) was evident across lake trout populations (Figure 6a). There was a positive linear relationship between size at first reproduction (i.e. one year after maturity) and maximum body size, and unexploited populations tended towards the lower end of this relationship (Figure 6b). Variation in reproductive allocation had a positive curvilinear relationship with juvenile somatic growth rates (Figure 6c) and negative curvilinear relationship with size at maturity (Figure 6d). Proportional increases in mortality when mortality was already low led to changes in both allocation and growth rates, while the same increase when mortality was already high led to disproportionate changes in growth (Figure 6c).

4 | DISCUSSION

Clinal variation in lake trout life histories suggested three processes influenced growth-associated traits: plasticity in juvenile growth, local adaptations in size at maturity and evolutionary trade-offs with reproductive allocation. We observed strong evidence for three reaction norms in juvenile growth (Figure 7): (a) plasticity along a climate gradient, (b) density-dependent growth compensation due to exploitation and (c) plasticity driven by prey fish occurrence. Figure 7 illustrates how variation in lifetime growth and maximum body size depended on how traits responded to these three clines using empirical relationships found in our study. As predicted from harvest-induced evolution theory, variation in lifetime growth depended on whether size-selective harvest selects for increased reproductive allocation (Figure 7b—red line; Heino et al., 2015), or growth plasticity buffers against selection (Figure 7b—grey line; Ernande et al., 2004). We found strong support for our growth plasticity hypothesis, as our empirical results were consistent with the prediction that increased per-capita food availability via exploitation, increased degree-days facilitating longer growing seasons and available prey fish (higher quality foraging) would increase growth, reduce age at maturity and increase adult reproductive life span (Lester et al., 2014). Adult life spans observed in our study (~29 years) were higher than observed in other southern (~17 years) and northern (~24 years) lake trout populations (McDermid et al., 2010). We also documented that lake trout do not appear to be undergoing harvest-induced evolution, especially considering our hypothesis was conservative, although size at maturity appears to be adapting to climate and prey fish occurrence (Figure 7). Harvest-induced evolution often selects for slower growth (Conover & Munch, 2002; Heino et al., 2015) suggesting a negative association between growth and exploitation might have been expected, yet this response was clearly positive. We considered the predicted growth response to exploitation as positive in our local adaptation hypothesis because size-selective harvest does not always favour slow growth but depends on the interaction between size selectivity and the buffer provided by growth compensation (Dunlop et al., 2009; Lester et al., 2014). Although the growth plasticity hypothesis was supported, our study design lacked strong inference because we did not have genotypic data or common garden experiments used to test for genotype–phenotype associations in estimating reaction norms. Ideally, combinations of these methodologies could be used to more clearly disentangle these processes

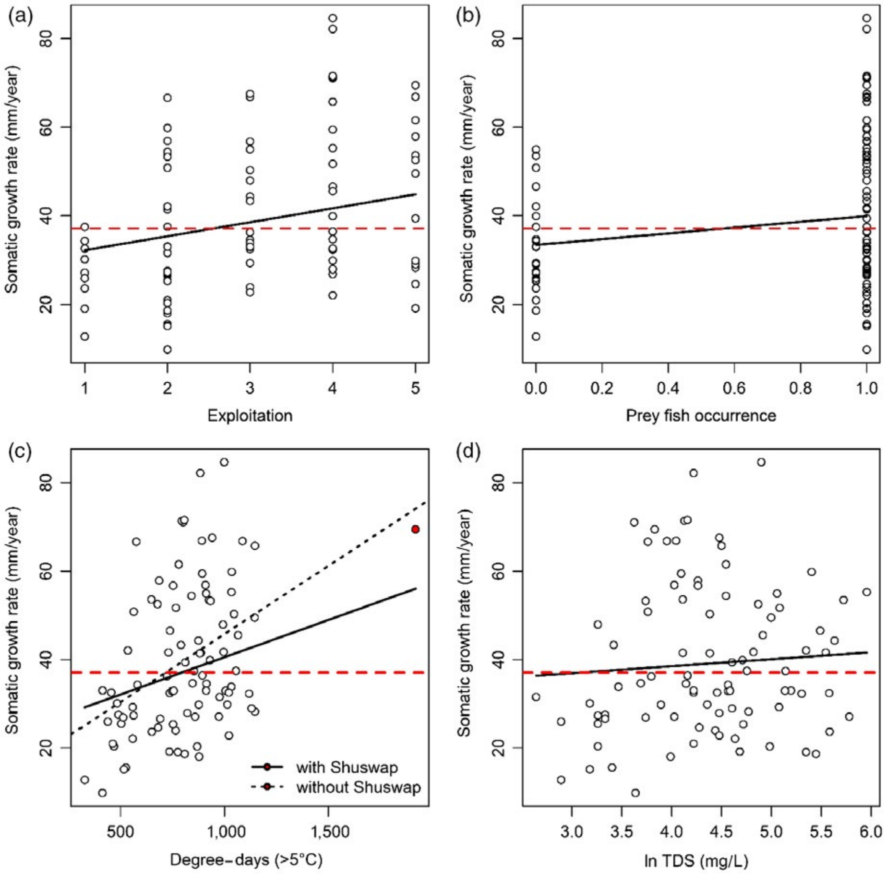

FIGURE 2 Observed (open circles) and posterior mean predicted (black line) lake trout juvenile somatic growth rate along environmental clines. Red dashed lines show average somatic growth rate across all populations. Relationship with growing degree-days > 5°C fitted with (solid line—panel c) and without (dashed line—panel c) warmest lake, Shuswap

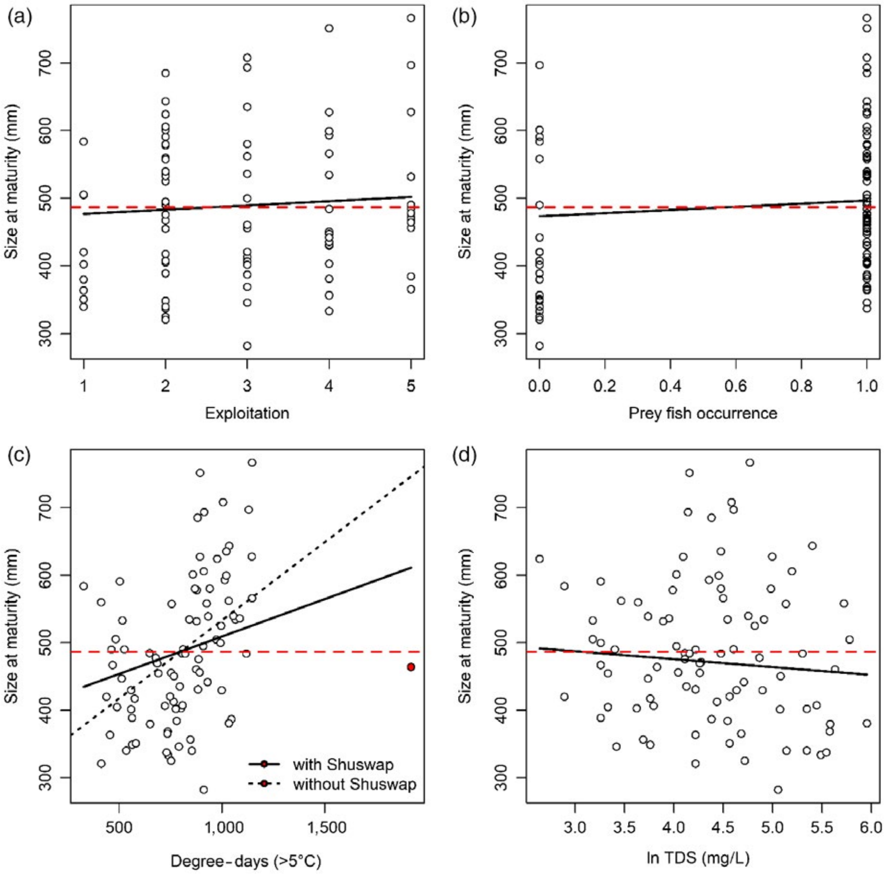

FIGURE 3 Observed (open circles) and posterior mean predicted (black line) lake trout size at maturity along environmental clines. Red dashed lines show average size at maturity across all populations. Relationship with growing degree-days > 5°C fitted with (solid line—panel c) and without (dashed line—panel c) warmest lake, Shuswap

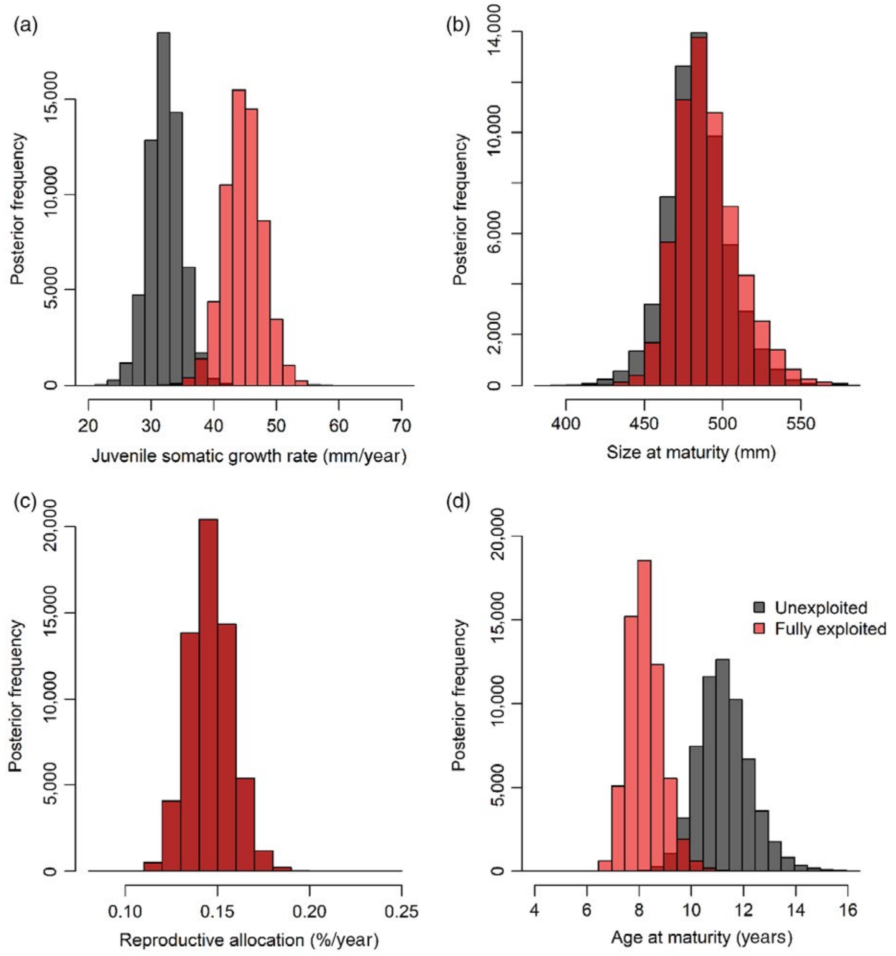

FIGURE 4 Variation in average lake trout life-history traits as a function of exploitation. Overlap between unexploited and exploited trait distributions shown in darker red

(Bradford & Roff, 1995; Dunlop et al., 2009; Kawecki & Ebert, 2004; Swain et al., 2007).

Three related processes likely influenced the climate-mediated reaction norm on juvenile growth. First, increased growing degree-days increases growing season duration leading to higher growth rates and reduced development time in many indeterminately growing species (Neuheimer & Taggart, 2007). Second, while most lake trout populations in our study appear isolated from metapopulation effects, there is evidence for some functional connectivity and intermittent gene flow between a subset of neighbouring populations in this region (Northrup, Connor, & Taylor, 2010), which can favour plasticity over local adaptation (Sultan & Spencer, 2002). Third, summer thermocline depths appear unconstrained by basin depth in 89 of 90 lakes in our region (excluding Dezadeash but see Mackenzie-Grieve & Post, 2006) suggesting lake trout can thermoregulate year-round in these lakes. This result may be spurious if lakes with constrained depths yielded insufficient samples because of low abundance or capture probabilities. Nonetheless, our results are qualitatively consistent with findings in McDermid et al. (2010) that climate, but not post-glacial origin, was positively associated with lake trout juvenile growth. McDermid et al. (2010) argued that lake trout's limited optimal thermal range of 8–12°C near lake thermoclines may have buffered growth and size-dependent traits from adaptive differentiation while isolated in glacial refugia, and these thermal ranges appear available year-round in many northern freshwater lakes. Our findings suggest that, within a region, traits like maximum body size or size at maturity may also be tracking climate. However, we posit that climate effects are likely dome-shaped and not linear—this notion is supported by the increased effect of climate after removing Shuswap Lake (Figure 2c). If this relationship is dome-shaped, then the body size–climate relationship may not be broadly applicable across larger climate ranges (i.e. McDermid et al. (2010) spanned the entirety of lake trout biogeographic range). Warming tends to

TABLE 5 Posterior mean and 95% credible intervals (CI) for growth compensation ratio across exploitation classes (EC) measured as the ratio between population-specific posterior mean juvenile somatic growth rates *h* and the average growth for unexploited populations

Exploitation class	$h_{EC}/\bar{h}_{EC=1}$
1	1.0 (0.52–1.36)
2	1.28 (0.51–2.27)
3	1.55 (0.86–2.49)
4	1.83 (0.90–3.09)
5	1.66 (0.77–2.54)

Note. Comparison is irrespective of climate, prey community and productivity effects.

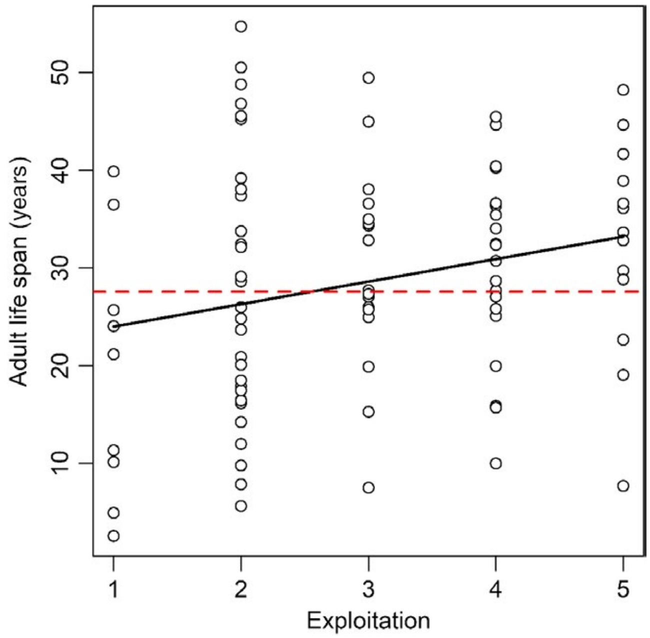

FIGURE 5 Variation in lake trout adult life span (i.e. years after maturation) as a function of exploitation (black line). Average adult life span shown in red

reduce thermally suitable lake trout habitat, which can reduce their growth as they shift from foraging near productive surface habitats to seeking thermal refugia (Mackenzie-Grieve & Post, 2006; Tunney, McCann, Lester, & Shuter, 2014). We caution against using our apparent reaction norm as a forecast for how lake trout may respond to climate change (Valladares et al., 2014), and suggest that future work focuses on a mechanistic understanding of lake trout life-history variation across the entirety of their climate range.

Density-dependent growth plasticity is a common type of compensation observed in exploited fishes (Heino et al., 2015; Law, 2000; Lorenzen, 2016). The magnitude of this compensation varies among fishes and constrains the growth buffer against size-selective harvest (Lester et al., 2014). Exploitation increased somatic growth rates approximately twofold and reduced the age at maturity of walleye *Sander vitreus* (Lester et al. 2014), rainbow trout *Oncorhynchus mykiss* (Post et al., 1999; Ward, Post, Lester, Askey, & Godin, 2017) and yellow perch *Perca flavescens* (Headley & Lauer, 2008). Lake trout populations nearer their southern range limit also display twofold growth variability that corresponds to reduced age at maturity, but exploitation alone does not explain this variation (Shuter & Lester, 2004). Heavily exploited lake whitefish and lake trout populations with a similar climate as our northern populations show lower growth compensation of ~1.2-fold and ~1.5-fold, respectively (Healey, 1978, 1980). These values support our estimate of ~1.4-fold growth compensation and suggest that lake trout growth compensation in western Canada may be intermediate compared to other freshwater fishes. Interestingly, growth compensation was lower in heavily exploited populations (1.65-fold) compared to intermediately exploited populations (1.83-fold;

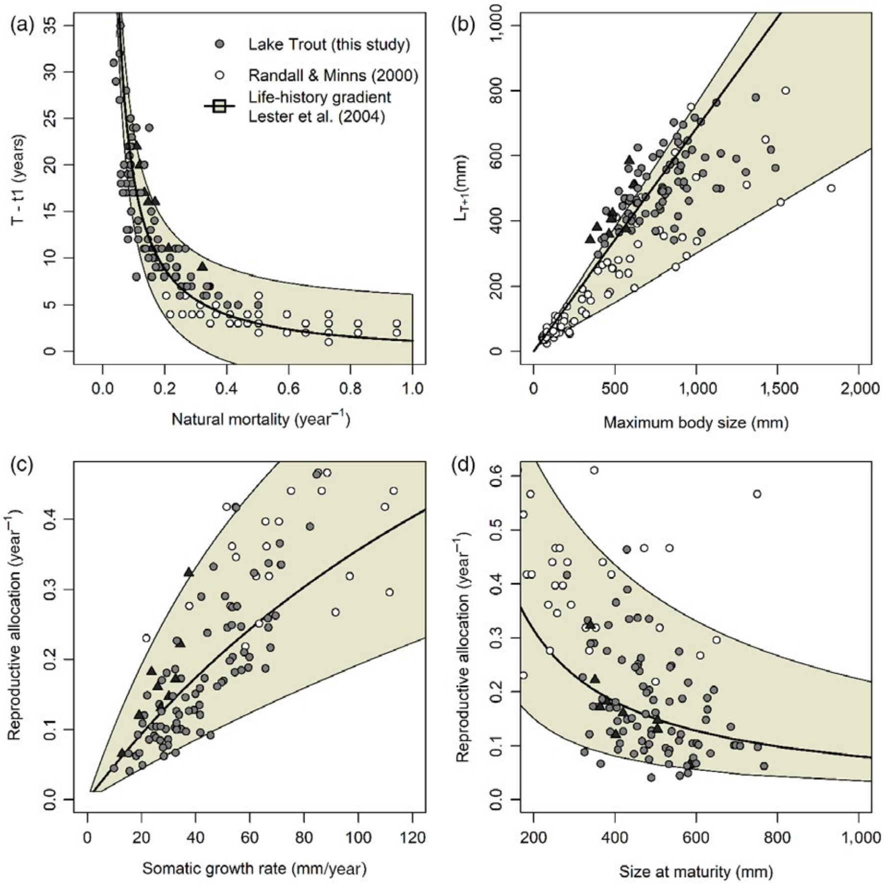

FIGURE 6 Life-history gradients for lake trout in western Canada (exploited populations in grey points; unexploited in black triangles) compared to North American freshwater fishes (white points). Empirical and predicted life-history gradients between: (a) natural mortality (calculated from reproductive allocation) and time to maturity ($T - t_1$); (b) maximum body size and size at first reproduction (L_{T+1}); (c) reproductive allocation and growth; and (d) reproductive allocation and size at maturity. Shaded region highlights predicted range of life-history relationship. Black lines show relationship between average trait values in this study

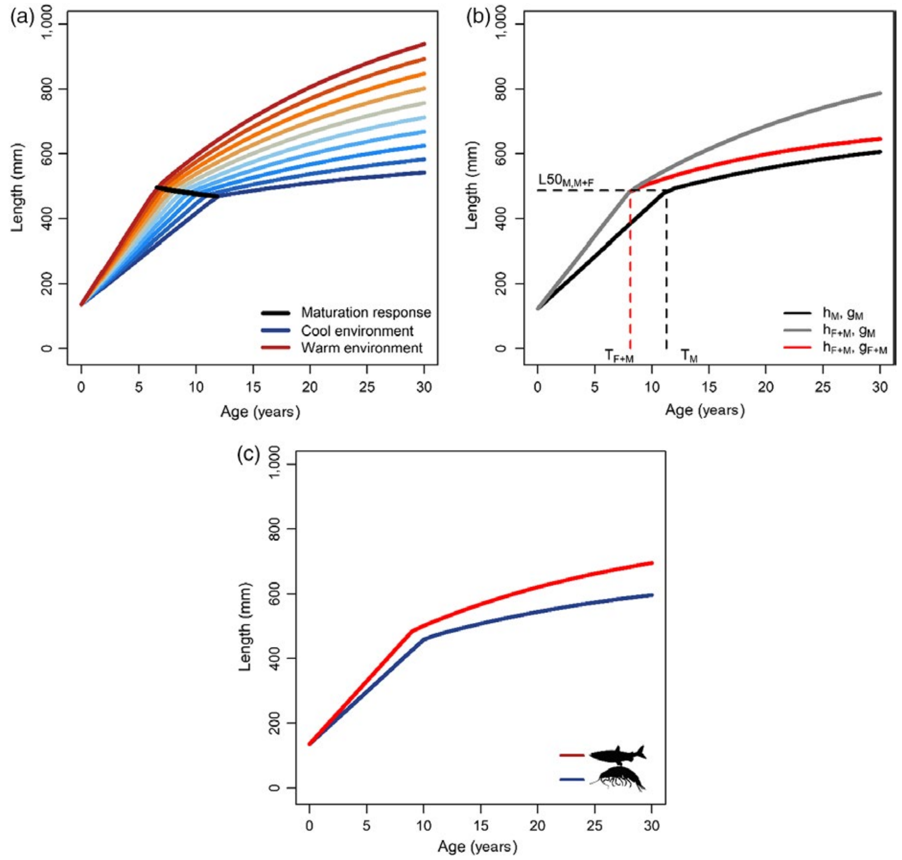

FIGURE 7 Lake trout lifetime growth schedules explained by three sources of clinal variation on growth rate and size at maturity: (a) climate gradient, (b) size-selective exploitation gradient and (c) prey fish occurrence (i.e. fish or zooplankton diet). Lifetime growth schedules in panel b resulted from interplay between *h*, age at maturity *T* and reproductive allocation *g* under three mortality scenarios (assuming constant size at maturity *L*50): (a) unexploited population with *h* and *g* adapted to natural mortality *M* (black line), (b) exploited population with *g* adapted to *M* and *h* adapted to total mortality *F* + *M* (plasticity; grey line) and (c) exploited population with both *g* and *h* adapted to total mortality (local adaptation; red line). Scenario 3 was explored by assuming correlation between *g* and *h* (ρ = 0.83; Supporting Information Table S6.1) instead explained a hypothetical relationship between *g* and exploitation (fitted using post hoc linear model regressing posterior mean *g* to exploitation cline)

Table 5) indicating some potential that high exploitation may reduce growth (Heino et al., 2015; Dunlop, Eikeset, & Stenseth, 2015). The growth compensation ratio of 1.4-fold should serve as a conservative baseline for lake trout populations subjected to shorter and/or cooler growing seasons. However, interactions between habitat, climate and prey size spectrum may afford a wider range of growth compensation (Shuter & Lester, 2004).

Growth plasticity and local adaptations to forage quality and prey size structure may act in concert to shape lake trout life histories. Plasticity has been argued to have allowed lake trout to take advantage of the abundant, heterogenous lakes of post-glacial northern North America (Chavarie, Howland, Harris, & Tonn, 2015; Muir, Hansen, Bronte, & Krueger, 2016). Common garden experiments on two Ontario lake trout genotypes found variable forage quality led to plasticity in juvenile growth and age at maturity (McDermid, Ihssen, Sloan, & Shuter, 2007). Similarly, we found that prey fish occurrence led to increased juvenile growth consistent with plasticity. However, contemporary life-history variation of lake trout is explained not only by life-history plasticity, but also by genetic differentiation and local adaptation on traits like size at maturity (McDermid et al., 2007). Lake trout life histories shift with changes in both forage quality and ontogenetic shifts in a piscivorous or zooplanktivorous diet (i.e. prey size structure, Martin, 1966, 1970; Shuter et al., 2015). Overall, we found similar associations between prey fish occurrence as observed in Martin (1966, 1970)—that a piscivorous diet increases growth and delays maturity at larger body sizes compared to a zooplanktivorous diet. However, we observed uncertainty in the effect on size at maturity with a mean increase of ~24 mm, lower than the ~38–63 mm increase observed for Opeongo lake trout following *Coregonus* spp. introductions (Martin, 1970). Our observations are consistent with Martin (1966, 1970) that increased prey size spectrum may allow for an initial plastic increase in growth that may fix as larger size at maturity. Most lake trout populations have been sufficiently isolated to have allowed for local adaptation, although much of the evidence supports sympatric, rather than allopatric, divergence (Harris et al., 2015). Interestingly, this sympatric divergence is associated with lake trout morphs that specialize on different prey and/or habitats (Harris et al., 2015). If the plasticity associated with prey fish that we observed is adaptive, it may serve as the basis for local adaptations we observed in size at maturity and, perhaps, polymorphisms (Chavarie et al., 2015). Identifying genotype–phenotype associations across these populations would help to disentangle these intertwined mechanisms.

Life-history variation in traits like reproductive allocation was as high within lake trout as observed among dozens of other freshwater fish species (Randall & Minns, 2000). Most of the variation in reproductive allocation was explained by life-history trade-offs presuming that natural mortality shaped the optimal suite of traits associated with lifetime growth (Lester et al., 2004)—these trade-offs can emerge as bivariate trait correlations (Roff & Fairbairn, 2007). We found the correlation between size at first reproduction and maximum body size (a ratio commonly studied in life-history evolution) decreased with adult mortality (Figure 6b) consistent with patterns observed across global fishes (Thorson, Munch, Cope, & Gao, 2017). These trade-offs have consequences for life-history evolution particularly when size-selective harvest increases late-stage juvenile and adult mortality, which may favour increased reproductive allocation (Dunlop et al., 2009; Lester et al., 2004; Roff et al., 2006). We showed that reproductive allocation was positively correlated with juvenile growth but negatively correlated with size at maturity. Note that, as adult mortality increases, the gradient between growth and reproductive allocation (Figure 6c) gets wider suggesting that: (a) when adult mortality is high, increased adult mortality favours increased growth over increased reproductive allocation (upper range in Figure 6c), and (b) when adult mortality is low, increased mortality favours increased reproductive allocation over increased growth (lower range in Figure 6c). This latter pattern is likely the case for our nine unexploited populations (Figure 6c—black triangles). Our results suggest low adult natural mortality constrains the buffering capacity provided by growth compensation, and even moderate rates of size-selective harvest on such populations may induce undesirable evolutionary responses (Heino et al., 2015; Jorgensen et al., 2007; Shuter et al., 2005). This highlights an opportunity for understanding how this buffering capacity varies with environment to inform spatially oriented management to protect populations at high exploitation (e.g. Moberly) or subjected to colder climates or lack of suitable prey fish (e.g. *Coregonus* spp.) where growth and adult body sizes may be low.

There are basic and applied implications if we consider trait variation as a plastic response to changing environments (Valladares et al., 2014). Plasticity models typically result in less conservative management recommendations than local adaptation by presuming a common response across populations. Although trait divergence can drive lake trout life-history variation (McDermid et al., 2007; Muir et al., 2016), results from our study were consistent with predictions under the growth plasticity hypothesis and local adaptations in size at maturity. We documented a 1.5-fold maximum compensatory growth response to exploitation, thus quantifying a baseline slope for the density-dependent growth reaction norm (assuming our functional form). Furthermore, we observed the probabilistic maturation reaction norm in age at maturity (but not size at maturity) commonly observed in exploited animal populations (Heino et al., 2002). Lastly, we observed life-history gradients in reproductive allocation and size at maturity that influenced maximum body size, and this variation may be driven by trade-offs with mortality and other traits. We observed large gradients between (a) growth and reproductive allocation, (b) age at maturity and mortality, and (c) size at maturity and maximum body size and associated the determinants of these gradients to life-history trade-offs and environmental variation. The range of mortality observed here is near the lower limit recorded for North American freshwater fishes, suggesting western Canada's lake trout population production may be constrained by environment or biology (Randall & Minns, 2000; Shuter et al., 2005). The revealed mortality–maturity trade-off may limit lake trout's ability to withstand increased mortality due to exploitation through growth compensation alone. For example, the curvilinear maturation reaction norm shows that a doubling in mortality from 0.135 to 0.27 year^{-1} reduces age at maturity from 14 to 6 years. If growth rate is plastic and size at maturity fixed at 480 mm, for example, then growth would have to increase from 35 mm/year (when $T = 14$ years) to ≥76 mm/year to mature by age 6. In our study, only two lake trout population exhibited growth in this range (Bridge and Laberge) suggesting low growth compensation in western Canada's lake trout, presumably driven by low thermal energy and ecosystem production. We suggest future work addresses how growth compensation may interact with other compensatory mechanisms (e.g. survival compensation) to influence the resilience and evolution of exploited populations (Heino et al., 2015; Lester et al., 2014; Zimmermann et al., 2018).

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AUTHORS' CONTRIBUTIONS

K.W. and J.P. conceived the ideas for the manuscript; K.W. led the project and designed methodology; K.W., J.D.G., C.C., O.B. and J.P. wrote the manuscript; and J.D.G. and O.B. provided data.

DATA ACCESSIBILITY

All supplemental materials, environmental and biological data, and the JAGS model used for this manuscript are available at https://doi.org/10.5281/zenodo.1181830 (Wilson, 2019).

ORCID

Kyle L. Wilson https://orcid.org/0000-0002-0870-0509

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SUPPORTING INFORMATION

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