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Empirical evidence of plasticity in life history characteristics across climatic and fish density
gradients

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ABSTRACT

Understanding how environmental productivity and resource competition influence somatic growth rates and plasticity in life-history traits is a critical component of population ecology. However, evolutionary effects often confound the relationship between plasticity in life-history characteristics and environmental productivity. We used a unique set of experimentally stocked populations of rainbow trout (*Onchorynchus mykiss*) to empirically test predictions from life-history theory relating to patterns in immature growth rates, age- and size-at-maturity, and the energy allocated into reproduction across climatic and fish density gradients. Our results support theoretical predictions that plasticity in life-history characteristics is a function of environmental variables. In particular, we demonstrate that immature growth rates are best explained by climatic and density-dependent competition effects, and that age-at-maturity and the energy allocated to reproduction depends on juvenile growth conditions. Empirical evidence of these relationships helps to improve our understanding of optimal life-history strategies of fish populations.

INTRODUCTION

Density-dependent growth among fish populations is well documented and is hypothesized to be a function of competition for food resources (Post et al. 1999; Lorenzen and Enberg 2002; de Roos et al. 2003). Such processes are an example of a compensatory density-dependent response where the somatic growth rate is predicted to be inversely proportional to the population density. The negative feedback imposed by a compensatory density-dependent response acts to stabilize populations and this response is important for managing fisheries as it can counteract mortality of fish from either natural or anthropogenic factors (Hilborn and Walters 1992). For example, a decrease in population density has been shown to increase somatic growth rates, leading to an increase in survival and reproductive rates, and ultimately increased recruitment (Rose et al. 2001).

The relationship between key life-history characteristics that control compensatory density-dependent processes such as somatic growth rates, age- and size-at-maturation, and reproductive investment are summarized by the biphasic growth model (Lester et al. 2004; Quince et al. 2008). Recent studies in modeling fish growth have suggested that life-time growth patterns in fish are biphasic (made up of two phases): pre-maturation and post-maturation (Figure 1; Lester et al. 2004; Quince et al. 2008; Venturelli et al. 2010). The growth rate in the pre-maturation phase is constant (i.e. length is linearly related to age) and is related to the net rate of energy acquisition. In contrast, growth rate in the post-maturation phase declines with age as a proportion of surplus energy is invested into reproduction, following the traditional von Bertalanffy growth equation (Ricker 1975; Lester et al. 2004).

There are two well-documented theories related to life-history characteristics and the biphasic growth model that have important implications for understanding compensatory density-dependent growth. Firstly, a well-documented theory in life-history studies involves the

relationship between growth rates of immature fish and the optimal age- and size-at-maturation. It is hypothesized that the optimal age of maturity occurs when the fecundity benefits of reaching a large size are maximized, while the costs of delaying the onset of reproduction are minimized (Day and Rowe 2002; Johnston et al. 2007). Several theoretical studies have suggested that it is advantageous to postpone reproduction in order to produce larger egg mass (Stearns 1992; Hutchings 1993; Rochet 2000), but if juvenile mortality rates are high, delaying the onset of reproduction may not be beneficial (Hutchings 1996; Cichon and Kozłowski 2000). Secondly, life-history theory predicts that reproductive investment increases with growth rates as an adaptive response to changes in density resulting from high mortality (Lester et al. 2014). Overall, phenotypic plasticity should be expected so that individuals maximize their fitness by quickly responding to environmental variability (Stearns and Koella 1986; Lester et al. 2014). It is suggested that this plasticity in life-history characteristics may counteract evolutionary selective pressures and slow the rate of evolutionary changes (Stearns 1992).

Quantifying plasticity in life-history characteristics has important applications for fisheries management since populations with faster somatic growth rates are less vulnerable to over-exploitation, as faster rates are hypothesized to reduce the age-at-maturity, and increase reproductive investment (Leggett and Carscadden 1978; Conover and Munch 2002; Lester et al. 2014). However, evolutionary effects result in site-specific adaptation and hinder the ability to quantify how environmental productivity and density-dependent competition influence somatic growth rates and plasticity in life-history traits. As a result, an extensive amount of theoretical work has focused on predicting the response of life-history characteristics to environmental and evolutionary processes (Kuparienen and Merila 2007; Lester et al. 2014).

In this study, we used a unique set of data from annually stocked experimental populations of rainbow trout (*Onchorynchus mykiss*) to test predictions from life-history theory relating to plasticity in immature growth rates, age- and size-at-maturity, and reproductive investment across climatic and fish density gradients.

MATERIALS AND METHODS

Fish population data

To examine plasticity in life-history traits, we used data on growth and maturity schedules from experimental stocked populations ($n=23$) in the southern interior of British Columbia, Canada (Table 1). Through the use of stocked populations, any observed differences in life-history characteristics among lakes are assumed to be a function of the environmental conditions, rather than genetic and or evolutionary differences among populations. The majority of lakes (18 of 23 lakes) had no known natural recruitment (due to a lack of spawning habitat) and were primarily monocultures of rainbow trout (Table 2). Lakes were stocked annually for several decades with rainbow trout and were monitored periodically to sample juvenile and/or adult fish (Table 2).

Fish from a common genetic origin were stocked as either Age-0 (fry) or Age-1 (yearlings) in the fall or spring, and the weight at release varied from 0.9 to 23.5 grams and stocking density varied from 35.7 to 694.4 yearlings $\cdot \text{ha}^{-1}$ among lakes (assuming a survival rate of 0.5 for fry to yearlings; Parkinson et al. 2004). Additionally, the study lakes varied in their physical characteristics, harvest regulations and angler effort. Fishery data was collected on a sub-set of study lakes and exploitation rates varied between 0 and 50% among lakes (Ward et al. 2013). Fish populations were periodically sampled between 1993 and 2012, and led to a total of 42 lake-years of data, although not all lake years were used to fit the necessary functions as a

result of data limitations (Table 2). Where multiple lake-years of data existed, data was pooled among years in the analysis of lifetime growth patterns.

Fish populations were sampled in each lake using a standard gillnet sampling protocol in the fall of the years documented in Table 2 (sampling details are described in detail in Ward et al. 2012). Two multi-mesh gangs of gillnets were set overnight in the littoral and pelagic habitat of each lake. This gillnet design is highly size-selective against small fish, and essentially non-size-selective for larger fish (Askey et al. 2007). The fork length of all captured fish was recorded and lapilli otoliths were collected from all non-clipped fish (certain year classes in some lakes had unique adipose or ventral clips). Otoliths were aged using transmitted light. The first year class of stocked fish (either Age-0 or Age-1) were fin clipped for at least one year during the study period to assess the presence or absence of natural recruitment. Lakes with natural recruitment were identified based on either the observed percentage of the first year class missing fin clips, and/or direct observations of fish spawning (Table 2). Lakes with natural recruitment were used only in the maturity analysis unless hatchery fish (which were from a common genetic origin) that had unique fin clips could be identified. Similarly, lakes with more diverse fish communities were only used to analyze maturity schedules since the estimate of rainbow trout fish density is likely to be highly biased in multi-species lakes. The gonads of all captured fish were examined to determine sex and maturity. Since rainbow trout spawn in the spring, and fish were captured in the fall, fish were considered immature if they showed no visible sign of gonad development and therefore, would be unable to spawn the following spring. For females, immature fish were identified as having small ribbon-like gonads, that were light pink in color and individual eggs were not visible to the naked eye. Similarly, for males, immature fish had thin transparent testes that lacked milt. Since maturity is a gradual, rather than

a binary (immature vs. mature) process, fish demonstrating visual evidence of gonad development were considered mature in the following analyses.

Model Development

In order to examine plasticity in life-history traits as a function of climatic conditions and fish density affects, we conducted a three stage analysis where we analyzed: (1) growth rates of immature fish, (2) maturity schedules and (3) lifetime growth patterns to estimate reproductive investment.

Immature Growth

The biphasic growth model (Lester et al. 2004) suggests that growth in length of immature fish is approximately linear due to a lack of energetic investment in reproduction (Figure 1). Since fish in these experimental lakes were stocked at a known age and size and had similar growth conditions in the hatchery prior to release, we modelled the length of fish (L_T) as a linear function of time in the lake (T ; when T is less than the age at maturity, described in detail below),

$$(1) \quad L_T = hT + L_S.$$

where L_S is the length of fish at $T = 0$ (stocking) and h is the growth rate of immature fish.

Estimates of h were obtained for each population by solving Equation (1) for h and using observed values of L_T , T and L_S (for fish that showed no signs of gonad development),

$$(2) \quad h = \frac{L_T - L_S}{T}.$$

Growth rates of immature fish (h) are expected to depend on climatic conditions and resource availability (Post et al. 1999; Venturelli et al. 2010; Askey et al. 2013). Annual growing

degree-days (*GDD*, °C·days), an index of thermal energy, is known to influence growth rates in fish (Neuheimer and Taggart 2007; Venturelli et al. 2010). Annual growing degree-days represent the number of Celsius degrees that the mean air temperature is above a given base. We chose to use 5°C as a base temperature for calculating degree days. A base temperature of 5°C implies that growth is zero at less than 5°C and this temperature is a readily available thermal index (as it is used extensively in agriculture) and has recently been used to study climatic effects on fish growth (Venturelli et al. 2010; Lester et al. 2014). Annual growing degree-days (*GDD*) for the study lakes were obtained from ClimateBC4.71 (Wang et al. 2012) based on elevation and latitude and longitude (Table 1). Estimates of *GDD* ranged from 1036 to 1964 °C·days across the study lakes. *GDD* values were averaged across years and used to calculate a thermal age (T' ; i.e., calendar age in years times *GDD* accumulated per year),

$$(3) \quad T' = \frac{T \cdot GDD}{1000}.$$

The denominator of 1000 in Equation (3) is included for convenience because it implies that thermal age and calendar age are equivalent for populations living at $GDD = 1000$ °C·days.

After standardizing for *GDD*, a thermal immature growth rate (h') was calculated as

$$(4) \quad h' = \frac{L_T - L_S}{T'},$$

or in lake-age as,

$$(5) \quad h = \frac{h' \cdot GDD}{1000}.$$

In size-structured populations, consumption rates can vary greatly among individuals, and therefore, it has been suggested that an appropriate metric to measure the effects of competition must weight individuals within a population by their consumption rate. Bioenergetics and empirical studies suggest that consumption rates in fish should scale allometrically with mass (Walters and Post 1993; Post et al. 1999),

173 (6) Consumption $\propto$ (Mass)^{2/3}

174 and since

175 (7) Mass $\propto$ (Length)³

176 then, individual consumption rates can be scaled allometrically to length, where

177 (8) Consumption $\propto$ [(Length)³]^{2/3} $\propto$ (Length)².

178 Walters and Post (1993) used this allometric relationship to suggest that the appropriate metric
179 for expressing the density-dependence of exploitative competition should be

180 (9) Effective Density $\propto \frac{\sum_{i=1}^n (\text{Length})^2}{\text{Area}}$.

181 Therefore, we calculated the effective density of fish (D) at the time of gillnetting, based on the
182 number of fish caught in the gillnet N_G in 10mm length-bins l , the vulnerability of that length bin
183 to gillnets (v_l ; using parameter estimates from Askey et al. 2007 and Ward et al. 2012), the
184 midpoint of the length bin, L_l and the surface area of the lake, A .

185 (10) $D = \frac{1}{A} \sum_l^L \left(\frac{N_{G,l}}{v_l} \right) (L_l)^2$.

186 Walters and Post (1993) and Post et al. (1999) demonstrate theoretically and empirically that
187 growth declines as a function of effective density.

188 We use the following model to estimate the density-dependence of immature growth
189 rates, based on the theoretical work of Walters and Post (1993) and Post et al. (1999),

190 (11) $h = h_{max} e^{-\alpha D}$,

191 where h_{max} is the maximum growth rate when $D = 0$ and α is a shape parameter that determines
192 the rate of decline in growth with increasing density.

193 To determine if the thermal age concept is useful for analyzing growth patterns in
194 rainbow trout, we fit Equation (11) to the observed immature growth rate (Equation 2) as well as

the thermally-adjusted growth rate (h' ; Equation 4) across lakes. Equation (11) was log transformed and fit using non-informative priors given in Table 3.

Maturity Schedules

We used empirical data to determine the variability in age- and length-at-maturity in the experimental lakes. Since the date and age at stocking varied across lakes, age was calculated as a thermally adjusted lake-age, by calculating the proportion of the growing season ($^{\circ}\text{C}\cdot\text{days}$ / Annual GDD) accumulated for each year in the lake (herein 'lake age'). Estimates of length and lake age at 50% maturity (L_{50} and T_{50} respectively) were obtained for each lake year of data using binary data on maturity (1 = mature, 0 = immature). Maturity at length (M_L) was modeled as a logistic function (Quinn and Deriso 1999),

$$(12) \quad M_L = \frac{1}{1 + e^{-(aL+b)}}$$

and parameters were estimated using a logit transformation,

$$(13) \quad \ln\left(\frac{M_L}{1-M_L}\right) = aL + b,$$

where

$$(14) \quad L_{50} = \frac{-b}{a}.$$

Similarly, the lake age at 50% maturity (T_{50}) was estimated based on a logit transformation of the logistic function,

$$(15) \quad M_T = \frac{1}{1 + e^{-(a+bT)}}.$$

Since estimates of T_{50} reflect an observed age at which 50% of the population is mature based on fish captured in the fall (at the end of the growing season) and rainbow trout spawn in the spring, the age at which energy begins to be allocated to reproduction (T_M) occurs at the beginning of

the growing season before T_{50} . T_M was calculated by subtracting the time between capture and the beginning of the growing season from T_{50} (assumed to be June 1), which represents approximately 75% of the growing season.

Reproductive Investment and Lifetime Growth Patterns

Based on the theory of biphasic growth (Lester et al. 2004), length of immature fish ($T < T_M$) is described by Equation (1), but the growth of mature fish ($T > T_M$), length is described by bi-phasic parameterization of the von Bertalanffy growth model,

$$(16) \quad L_T = L_\infty (1 - e^{[-K(T-t_o)]}),$$

Where L_T is the length at age T , L_∞ is the asymptotic length, K determines how fast fish approach L_∞ and t_o is the theoretical age when $L = 0$ (Hilborn and Walters 1992). Lester et al. (2004) reparameterized Equation (16) in terms of the immature growth rate (h), reproductive investment (g) and the age at which energy begins to be allocated to reproduction (T_M), so that

$$(17) \quad L_\infty = \frac{3h}{g},$$

$$(18) \quad K = \ln \left(1 + \frac{g}{3} \right).$$

The t_o parameter must be adjusted from Lester et al. (2004) derivation when modeling fish based on time in the lake, where the length at T_M is

$$(19) \quad L_{T_M} = hT_M + L_S$$

And substituting into equation (15),

$$(20) \quad hT_M + L_S = L_\infty (1 - e^{[-K(T_M-t_o)]}),$$

and replacing L_∞ and K with equation (17) and (18),

$$(21) \quad t_o = T_M + \frac{\ln[1 - g(hT_M + L_S)/3h]}{\ln[1 + g/3]}.$$

Male and female fish may exhibit variation in lifetime growth patterns as a result of differential T_M and g values (in addition to gender-specific differences in growth efficiency and metabolism; Rennie et al. 2008). The energetic basis of the biphasic growth model is well-developed for females (since egg production is a large portion of g), but the male cost of reproduction is harder to justify. Therefore, we fit Equation (16) to observed data on mean length at age for females, pooled across all lake-years. Mean length at age was used to ensure that each age class had equal weighting in the analysis. Estimates of g were constrained on the interval $\left[0, \frac{3h}{hT_M + L_S}\right]$ as a result of the logarithmic bounds in Equation (21), and assumed to come from a hierarchical distribution with vague priors (Table 3). Mean estimates of h across lake-years were assigned based on the observed immature growth rates and we fit the Lester parameterization of the von Bertalanffy growth model to length at lake-age.

Data Analysis

All analyses were conducted using Bayesian techniques as we were interested in exploring the uncertainty of the estimated parameters. The analysis was run using openBUGS (Bayesian Inference Using Gibbs Sampling) software, version 3.2.1 (available at <http://www.openbugs.info/w/>). Vague priors were used for each model (Table 3). For each model, we ran the MCMC for 200,000 iterations, and discarded the first 50,000 to remove any "burn-in" effects. Chains were initialized from two different starting points. Convergence of the chains was visually assessed by monitoring trace plots of the Markov chains as well as examining the Gelman-Rubin convergence diagnostics (provided in the BRugs package for the R programming environment).

We used hierarchical models to estimate parameters for immature growth and the amount of reproductive investment. Hierarchical models allow for information from other sampling units (other lakes) to be incorporated and are known to improve estimates on lakes (Askey et al. 2007). Vague prior distributions were used for all estimated parameters (Table 3). Where stated, we compared candidate models in a Bayesian framework using the DIC statistic (Spiegelhalter et al. 2002). The DIC statistic combines goodness-of-fit measure, $\overline{D(\theta)}$ (the posterior mean of the deviance) with a measure of model complexity (p_D). We calculated a Δ DIC, and models with Δ DIC values between 0 and 5 are considered to have a substantial level of empirical support, and those with Δ DIC values greater than 10 are thought to have essentially no support.

RESULTS

Immature Growth

Immature growth rate (h) varied two-fold among lakes ($h = 76.1$ to 159.2 mm·year⁻¹). The thermally adjusted growth rate (h') was a better predictor of growth as a function of effective density than the immature growth (h) (Δ DIC=70.82). Since immature growth was best predicted by fish density and climate (Figure 2) we applied the thermal age concept in our analysis to account for differences in growth rates as a function of climatic differences among lakes.

The growth model shown in Figure 2 was generated using the posterior estimates for the parameters in Equation (11): $h'_{max} = 113.9$ mm·°C⁻¹·days⁻¹·10⁻³ (σ =4.79), $\alpha = 0.010$ (σ =1.63·10⁻³). Across a range of effective density and growing degree days, immature growth rates (h) are negatively related to effective density and positively related to the annual growing degree days (Figure 2b).

Maturity Schedules

We detected differences in the size- and age-at-maturity among males and females (Figure 3a). Females matured at larger sizes than males (female L₅₀ range: 272 – 307 mm; male L₅₀ range: 148 – 258 mm) and matured at older ages than males (female T₅₀ range: 1.4 – 2.8 Years; male T₅₀ range: 0.4 – 2.0 Years). Immature growth rate varied 3-fold among lakes used in the maturity analysis (range: 84.4 – 264.9 mm·year⁻¹). Variation in the age at maturity (T₅₀) for both males and females was explained by immature growth rates (Figure 3b)

$$(22) \quad T_{50} = \xi h^{-\lambda}.$$

Parameter estimates for females were: $\xi = 18.84$ mm and $\lambda = 0.4524$ and for males: $\xi = 1.63 \cdot 10^3$ mm and $\lambda = 1.4695$. This suggests that immature growth rates can be used to predict sex-specific age at maturity (T₅₀) in the analysis of lifetime growth patterns. The observed relationship between h and T₅₀, and h and density and growing degree days (Equation 11) suggests that the age at maturity (T₅₀) varies between 1.5 and 3.5 years for females across a density and climatic gradient (Figure 3c).

Reproductive Investment and Life-Time Growth Patterns

The biphasic growth model fit the observed data on mean length at time in the lake well (Figure 4). Estimates of g varied substantially among lakes for females (range: 0.29 – 0.63), and none of the probability intervals from the posterior distribution overlapped with 0, suggesting that all lakes demonstrate evidence of asymptotic growth. Across lakes, estimates of female g increased as a linear function of the immature growth rate ($R^2 = 0.5614$; Figure 5), and parameter estimates for the slope and intercept were $4.037 \cdot 10^{-3}$ and 0.0295 respectively. Using

these estimated parameters, lifetime growth trajectories can be predicted knowing information about effective density and size of fish stocked (Figure 6).

DISCUSSION

We analyzed data from experimental stocked populations of rainbow trout to determine how climatic-driven variation in productivity and density-dependent competition affect plasticity in life-history characteristics relating to growth processes in fish by controlling for genetic differences among populations. Our results provide substantial evidence that the observed plasticity in life-history characteristics is a function of environmental variables. In particular, we examined trends in three life-history characteristics that determine somatic growth: immature growth rates, age-at-maturity and the energy allocated into reproduction.

Variation in growing conditions has been theoretically demonstrated to influence plasticity in life-history characteristics, but empirical verification of this relationship across both fish density and environmental gradients is relatively unknown (Stearns and Koella 1986; Roff 1992; Stearns 1992; Day and Rowe 2002). Through the use of stocked experimental populations, we were able to isolate the environmental effects on growth from the genetic differences among populations and we found that immature growth rates were best explained by climatic and density-dependent competition effects, and that age-at-maturity and the energy allocated into reproduction was a function of immature growth rates. Using this information, we developed predictive relationship for lifetime patterns of growth for rainbow trout as a function of population density and environmental characteristics.

Populations in our experimental lakes varied substantially in both fish density and growing degree days. We found that both growing degree days and fish density had large impacts on the growth rates of immature fish. At a constant fish density, immature growth rates

varied two-fold across the observed range of growing degree days. Similarly, at a constant growing degree days, immature growth rates varied two-fold across the observed range of fish densities. In our study, we chose to use 5°C as a given base temperature based on recommendations from Chezik et al. 2014 and data availability for temperature across a wide landscape. It is important to recognize that part of the observed variation in h' may be a statistical artifact (Chezik et al. 2014). Regardless, our results suggest that environmental conditions (growing degree days) and fish density are key predictors of relative growth rates of immature fish among our experimental lakes. Our results complement other studies that suggest that growing degree days provide a useful method for understanding and interpreting growth patterns at a landscape scale in the absence of more detailed information (Venturelli et al. 2010; Chezik et al. 2014; Lester et al. 2014).

Fish growth patterns are known to be a function of food availability and temperature (Walters and Post 1993; Post et al. 1999; Askey et al. 2013). Therefore, we examined variation in immature growth rates over a large gradient in fish density and growing degree days. In our study lakes, we were able to analytically account for fish densities in order to decouple the relationships between climatic influences on productivity and on fish density. Highly productive, unfished systems are often correlated with high fish densities. Since fishing reduces fish density, it is important to understand how growth patterns vary across a gradient in both fish density and productivity (growing degree days). Our ability to control fish densities through stocking led to an 8-fold variation in effective density estimates (range: 6.85 to 56.75 mm²·10⁻⁶) and we suggest that this approximates the broad range of density possible for native populations of rainbow trout in lakes (unpublished data). Since all of the lakes in this study were fished, it is likely that anglers have removed the bolder and/or faster growing individuals in the population (Nuhfer and

Alexander 1994; Biro and Post 2008). This may result in an underestimation of growth rates, where the magnitude of the bias is suspected to vary with the exploitation rate.

It is important to note that the biphasic theory described by Lester et al. (2004) does not assume that the entire immature growth phase is linear, only that growth is linear in the time period before maturity. Since initial body size and prey size spectrum varied across the study lakes, the true growth trajectory is likely composed of several linear phases. But, for simplicity, the linear growth trajectory estimated in our study represents the combination of these ecological processes and denotes the best empirical fit to the data.

We examined sex-specific maturity schedules in our study lakes. As expected, males matured at smaller sizes and earlier ages than females. The optimal time to reach maturity is suggested to occur when the fecundity benefits of reaching a large size are balanced by the costs of delaying the onset of reproduction (Stearns and Koella 1986; Day and Rowe 2002). Sexual dimorphism is common in fish populations and is hypothesized to be a function of variation in optimal life history strategies among sexes (Rennie et al. 2008). The presence of precocious males (where certain males in the population mature much earlier than others) in salmonid populations is well-documented and precocious males are often associated with higher mortality rates (Myers 1984). The majority of theoretical and empirical studies on maturation processes in fish involve only females due to their more predictable maturation schedules (Lester et al. 2004). However, understanding and quantifying the impacts of variation in life-history strategies between the sexes is useful in fisheries management.

We found that variation in the time to reach maturity was best explained by variation in immature growth rates among populations. This relationship clearly demonstrates the evolutionary trade-off between the optimal size and age to reach maturity. Our results suggest

that neither of these life-history parameters is fixed for this hatchery population of rainbow trout and that the time to reach maturity declines as immature growth rates increase. In other words, this suggests that if populations experience poor growth rates, it is advantageous for individuals to delay the onset of maturation and continue growing until the fecundity benefits of reaching a larger size are balanced with the costs to delaying maturation. This relationship was demonstrated for both males and females, but the presence of precocious males lead to males maturing at lower ages than females for a given immature growth rate.

Since males and females matured at different ages, we examined life-time growth patterns separately for the sexes. Several bioenergetic studies involving sexual dimorphism suggest that the energetic costs of reproduction are less in males as the energy required to produce sperm is less than the energy required to produce eggs (Rennie et al. 2008). However, it has been argued that in order to fully understand the true energetic costs associated with reproduction in males, one must study the full suite of energetic costs of reproduction (including those such as courtship activities and brood defenses) (Lester et al. 2004). Estimates of g for both males and females ranged from approximately 0.11 to 0.45 in our study. Lester et al. (2004) provides an empirical relationship between g and annual mortality, using this relationship, our estimates of g result in annual mortality estimates of 0.09 to 0.48. These results compliment other studies that have investigated natural mortality for rainbow trout populations in British Columbia (Parkinson et al. 2004). Similarly, other studies that have estimated gonad somatic index (GSI, wet weight of gonads / total weight) for rainbow trout suggest values between 0.014 and 0.136 for males (Lamot 1990) and 0.15 to 0.20 for females (Estay et al. 2012). Lester et al. (2014) demonstrated that g should be greater than GSI (1.73 times GSI) based on the assumption that gonads have a higher energy density than somatic tissues and length-based estimates of g

also reflect the energy associated with reproductive behaviour. Our estimated values of g are within the suggested range by Lester et al. (2014). We found no difference in estimates of reproductive investment, g , between males and females in the same lake. Since these populations reached maturity (but never actually spawned due to the absence of spawning habitat in the study lakes), this suggests that the total energetic costs associated with maturation are higher than previously reported for male rainbow trout and that GSI is not an accurate measure of the energy allocated in reproduction, i.e. there are likely other energetic costs to maturation, in addition to producing gonads, that impact g . For example, Quinn (2011) demonstrated that male salmonids undergo the development of secondary sex characteristics, such as the development of hump and longer jaw, and developing these characteristics likely has an energetic cost. Therefore, through an analysis of life-time growth patterns, our results suggest that the observed sexual dimorphism in our study lakes is a function of variation in the age-at-maturity among males and females, rather than the amount of reproductive investment.

We found strong evidence that the estimated energy allocated in reproduction is a function of immature growth rate. Conversely, in an analysis across species, Lester et al. (2004) and Shuter et al. (2005) found that the energy allocated in reproduction was a function of mortality rates, where populations with higher mortality rates exhibited a greater reproductive effort, and female reproductive investment (g) is largely density-independent. In our study, g is not directly measured, but rather estimated based on the lifetime growth trajectory. It is possible that other factors may influence this parameter such as parameter correlation with L_{∞} or biology (if fish outgrow their food source, then the lifetime growth trajectory may reach an asymptote regardless of the energetic contribution to reproduction).

Our empirical evidence, combined with information from Lester et al. (2004) and Venturelli et al. (2010) suggest that immature growth rates are positively correlated with both growing degree days and mortality. Life-history and evolutionary theory predict that the evolutionary response of an increase in mortality rates is a decrease in the age-at-maturity and an increase in reproductive investment (Stearns and Koella 1986; Kuparienen and Merila 2007). Therefore, by using experimental stocked populations, we demonstrate that reproductive effort is positively correlated with immature growth rates and this relationship represents this optimal life-history strategy.

Identifying and quantifying the strength of the compensatory response of somatic growth rates has important implications for fisheries management (Hilborn and Walters 1992; Askey et al. 2013). Understanding the mechanisms that lead to the compensatory nature of density-dependent somatic growth is a critical aspect of managing for sustainable fisheries and has been a key facet of fisheries research for decades (Beverton and Holt 1957; Walters and Post 1993; Grant and Imre 2005). Several authors have begun to examine the relationship between life-history characteristics and density-dependent processes (Walters et al. 2000; de Roos and Persson 2002; Lester et al. 2014) in order to understand how plasticity in life-history characteristics is related to growth processes, but these relationships are often confounded by environmental and genetic effects. By using a unique set of data where it was possible to control for evolutionary and genetic differences among populations, we were able to examine the plasticity in life-history characteristics as a function of environmental effects.

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577 Table 1. Physical characteristics of the study lakes. Growing degree days is calculated using a
 578 base temperature of 5°C and represents the five-year average between 2007 and 2012.

Lake	Elevation	Growing Degree Days		UTM Zone	Easting	Northing
	(masl)	(°C·Days)				
Amphitheatre	1070	1429	11	299438	5631379	
Billy	1450	1111	10	648800	5585572	
Buchanan	1020	1062	10	581523	5785339	
Butterfly	756	1078	10	488236	5991765	
Dennis	1193	1343	11	303180	5634464	
Emerald	727	1243	10	525055	6031073	
Flyfish	1354	1076	11	346908	5551011	
Garcia	1052	1316	10	666542	5547897	
Grizzly East	962	1071	10	555849	5951809	
Gypsum	1458	1100	10	651687	5579781	
Jackpine	1300	1198	11	298681	5533393	
McConnell	1258	1250	10	680409	5600241	
Moss 1	615	1964	10	596714	5466870	
Moss	540	1702	10	595788	5466776	
Otipemisewak	803	1089	10	546765	5954442	
Pratt	1302	1227	10	710238	5589562	
Stake	1320	1212	10	669955	5583457	
Ten Mile	707	1388	10	536234	5880377	
Tom Campbell	1077	1492	10	699816	5711229	
Tory	730	1273	10	592540	5631592	
Turquoise	808	1488	10	647437	5572714	
Tyner	1332	1219	10	684270	5519611	
Yellow	750	1274	11	299024	5468334	

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580 Table 2. Fish community data of the study lakes used to explore relationships among rainbow
581 trout life history parameters. Species codes are EB: eastern brook trout (*Salvelinus fontinalis*);
582 KO: kokanee salmon (*Oncorhynchus nerka*); LKC: lake chub (*Couesius plumbeus*); LSU:
583 longnose sucker (*Catostomus catostomus*); NSC: northern pikeminnow (*Ptychocheilus*
584 *oregonensis*); PMC: peamouth chub (*Mylocheilus caurinus*); RSC: redbside shiner (*Richardsonius*
585 *balteatus*); YP: yellow perch (*Perca flavescens*).

Lake	Sampling Year	Natural Recruitment (% of Age-1 catch)	Rainbow trout Monoculture	Immature Growth	Maturity	Female Growth
Amphitheatre	2010	Yes – 11	Yes	X		
	2011			X		
	2012			X		
Billy	2009	No – 9	Yes	X		X
	2010			X		X
	2011			X		
Buchanan	2000	No – 0	No – NSC, PMC		X	
	2001	No – 0			X	
Butterfly	2008	Yes - Unknown	No – EB		X	
Dennis	2010	No – 1	Yes	X		X
	2011			X		
	2012			X		
Emerald	2009	Unknown	No - LKC	X	X	X
Flyfish	2011	No - 0	Yes	X		
Garcia	1993	No – 3	No - RSC		X	
Grizzly East	2009	No – 9	No – LSU		X	
	2010				X	

587 Table 2. Continued

Lake	Year	Natural Recruitment (% of Age-1 catch)	Rainbow trout Monoculture	Immature Growth	Maturity	Female Growth
Gypsum	2009		Yes	X		X
	2010	No – 4		X		X
	2011			X		
	2012			X		
Jackpine	2011	No – 0	Yes			X
McConnell	2009	No – 3	Yes	X		
	2010	No – 7	Yes	X		
Moss	2001	Yes – 48	Yes		X	
Otipemisewak	2008	Yes – 51	No – LSU, RSC		X	
Pratt	2010	Yes – 18	Yes			X
Stake	2009	No – 3	Yes	X		X
	2010	No – 0		X		X
	2011			X		X
	2012			X		
Tom Campbell	2003	No – 0	Yes		X	
	2004	No – 0			X	
Tory	2009	No – 3	Yes	X	X	
	2010			X		X
Turquoise	2009	No – 7	Yes	X		
	2011			X		
Tyner	2009	No – 1	Yes			X
Yellow	2011	Unknown	No – EB, YP		X	

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Table 3. Prior distributions used in the analysis. N indicates a normal distribution (mean, precision); G: gamma distribution (shape 1, shape 2); LN: normal distribution (log mean, precision). I indicates a bounded prior [lower, upper].

Equation	Parameter	Description	Prior and distribution
(11)	$\ln(h_{max})$	Maximum immature growth rate	$N(0.78,0.01)$
(11)	α	Decline in immature growth rate with fish density	$N(0,0.01)$
(13)	b	Logistic regression intercept	$N(\bar{b}, \tau_b)I[-\infty, 0]$
(13)	$\bar{b}$	Hyperprior for b	$N(-7,0.1)$
(13)	τ_b	Precision of b	$G(0.01,0.01)$
(13)	L_{50}	Length at 50% maturity	$N(\overline{L_{50}}, \tau_{L_{50}})I[0, \infty]$
(13)	$\overline{L_{50}}$	Hyperprior for L_{50}	$N(350,0.001)$
(13)	$\tau_{L_{50}}$	Precision of L_{50}	$G(0.1,0.1)$
(15)	T_{50}	Age at 50% maturity	$N(\overline{T_{50}}, \tau_{T_{50}})I[0, \infty]$
(15)	$\overline{T_{50}}$	Hyperprior for T_{50}	$N(3,1)$
(15)	$\tau_{T_{50}}$	Precision of T_{50}	$G(0.1,0.1)$
(16)	g	Reproductive investment	$LN(\bar{g}, \tau_g)I\left[0, \frac{3h}{hT + L_S}\right]$
(16)	$\bar{g}$	Hyperprior for g	$N(\ln(0.5), 1)$
(16)	τ_g	Hyperprior for precision of g	$G(0.1,0.1)$

List of Figures

Figure 1. Graphical representation of the biphasic growth model. Growth prior to the age at maturation (T_M) is a linear process, whereas growth after T_M follows a von Bertalanffy trajectory. The depression of fish growth trajectories from the linear growth patterns of immature fish represents the energy that is allocated into reproduction (g).

Figure 2. (a) Variation in observed immature growth rate (h) as a function of effective density. Error bars represent 95% confidence intervals. The model predicted relationship from Equation (11) is shown for 1000 °C·Days (solid line), and 1500 °C·Days (dashed line). (b) Variation in the immature growth increment (h) as a function of growing degree days and effective density.

Figure 3. (a) Variation in age at 50% maturity (T_{50}) and length at 50% maturity (L_{50}) for females (solid circles) and males (open circles). (b) Variation in age at 50% maturity as a function of immature growth rate and model predicted relationship for females (solid line) and males (dashed line). (c) Age at 50% maturity for females as a function of effective density and growing degree days.

Figure 4. Fit of the biphasic growth model to mean length at age data for immature (open circles) and mature (solid circles) for females. The dashed and solid line represent the immature and mature phases respectively.

Figure 5. Variation in reproductive investment (g) as a function of the immature growth rate (h) and model predicted relationship.

Figure 6. Model predicted lifetime growth patterns for fish stocked at length = 100 mm and 800 °C·Days (thin line) and 1600 °C·Days (thick line), at fish densities of $5 \text{ mm}^2 \cdot \text{ha}^{-1} \cdot 10^{-6}$ (solid line) and $50 \text{ mm}^2 \cdot \text{ha}^{-1} \cdot 10^{-6}$ (dashed line) respectively.

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624 **Figure 1**

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641 **Figure 6**

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