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Separating Intrinsic and Environmental Contributions to Growth and Their Population Consequences

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ABSTRACT: Among-individual heterogeneity in growth is a commonly observed phenomenon that has clear consequences for population and community dynamics yet has proved difficult to quantify in practice. In particular, observed among-individual variation in growth can be difficult to link to any given mechanism. Here, we develop a Bayesian state-space framework for modeling growth that bridges the complexity of bioenergetic models and the statistical simplicity of phenomenological growth models. The model allows for intrinsic individual variation in traits, a shared environment, process stochasticity, and measurement error. We apply the model to two populations of steelhead trout (*Oncorhynchus mykiss*) grown under common but temporally varying food conditions. Models allowing for individual variation match available data better than models that assume a single shared trait for all individuals. Estimated individual variation translated into a roughly twofold range in realized growth rates within populations. Comparisons between populations showed strong differences in trait means, trait variability, and responses to a shared environment. Together, individual- and population-level variation have substantial implications for variation in size and growth rates among and within populations. State-dependent life-history models predict that this variation can lead to differences in individual life-history expression, lifetime reproductive output, and population life-history diversity.

Keywords: individual heterogeneity, von Bertalanffy, bioenergetics, Bayesian state space, *Oncorhynchus mykiss*.

Introduction

The expression of among-individual variation results from a complex interaction among genetic variation, phenotypic plasticity, population structure, and environmental conditions. An important goal of both ecology and evolutionary biology is documenting the presence of individual variation, the mechanisms underlying its maintenance, and its consequences for populations and communities. Both theory and empirical results suggest that the presence of persistent individual variation can have significant consequences for populations (Pfister and Stevens 2003; Vindenes et al. 2008; Zuidema et al. 2009; Kendall et al. 2011) as well as for communities (Bolnick et al. 2011). Furthermore, individual physiology and behavior mediate responses to environmental change (whether natural or anthropogenic). Thus, an understanding of individual heterogeneity is important for predicting the persistence of populations in the face of environmental change.

Somatic growth is an important but variable component of life histories. Persistent individual differences in growth are well documented for a range of taxa (plants: Harper 1977; Clark et al. 2007; mammals: Tinker et al. 2008; algae and invertebrates: Pfister and Stevens 2002). Because survival, maturity, reproductive success, and other vital rates are frequently related to an individual's size, variation in somatic growth has implications for both individual fitness and population dynamics (Kendall and Fox 2002). The link between size and vital rates has motivated the widespread use of structured population models (e.g., matrix models; Caswell 2001), but these models generally assume that individuals of a given size or state are equivalent (but see Parma and Deriso 1990; Pfister and Wang 2005; Coulson et al. 2006; Kendall et al. 2011; Jansen et al. 2012). Thus, the implications for incorporating individual variation in growth for population processes are largely unexplored (Pfister and Stevens 2003).

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Among-individual variation in somatic growth can arise from a variety of processes. For example, individuals within a population can vary in metabolic rates (von Bertalanffy 1938, 1957; Beverton and Holt 1959; Metcalfe et al. 1995) or behavioral traits (e.g., aggressiveness or territoriality; Magnuson 1962; Biro and Stamps 2010). Realized growth for an individual arises as a function of (1) an individual's phenotypic traits, (2) the environmental conditions shared by the entire population, and (3) stochasticity (Kruuk 2004). Stochasticity encompasses a range of unmeasured random processes affecting individual growth that could include (1) fluctuations in food captured by an individual, (2) variable responses to fluctuations in temperature, or (3) factors not directly linked to growth (e.g., predation avoidance). Methods that seek to document and understand individual variation must account for these distinct factors. This goal has proven elusive in practice (e.g., Knape et al. 2011).

There is a well-developed and sophisticated body of theory describing the physiology of growth (Kitchell 1977; Kooijman 2000), but often it is difficult to match this theory to available data and to estimate all the parameters from size trajectories alone (Fujiwara et al. 2005); there are usually too many free parameters and unobserved states to be estimable from available data. At the other extreme, there are growth models for which parameters are easy to estimate (e.g., von Bertalanffy growth) but that describe patterns in growth that may be difficult to link to underlying biological mechanisms. Thus, an unsolved question is how to represent individual variation efficiently in growth models. Recent analyses suggest that although individuals may vary across a wide suite of traits, genetic correlations among traits constrain the effective number of traits to a much smaller number (Kirkpatrick 2009). This observation motivates the development of low-dimensional summaries of among-individual variation that can be potentially connected to evolutionary models.

Here, we develop and apply a parametric Bayesian state-space framework for jointly estimating among-individual, environmental, and stochastic variation from observed time series. We strike a compromise between the simple but difficult-to-interpret growth models and the biologically sophisticated but statistically unidentifiable full bioenergetic models. We then describe a rearing experiment conducted with two California steelhead (*Oncorhyncus mykiss*) populations under common conditions and apply our statistical methods to estimate parameters for each population. We compare patterns of among-individual and between-population variation. We then use a state-dependent model of steelhead life history developed by Satterthwaite et al. (2009) to predict the optimal life-history strategies and expected lifetime output associated with projected growth trajectories. This allows us to quantify the predicted effect of individual

growth rate variability and stochasticity on the diversity of life-history pathways observed in populations. Furthermore, it provides a method for understanding the fitness consequences of individual variation under a range of environmental conditions.

Methods

Growth Model

We use as our starting point a general model of somatic growth, where the rate of growth of an individual of length x is

$$\frac{dx}{dt} = q - kx. \qquad (1)$$

Equation (1) is known as the specialized von Bertalanffy growth function (VBGF; von Bertalanffy 1957; Pauly 1981; Essington et al. 2001). Biologically, the parameter q contains processes contributing to energetic gains (anabolism; e.g., consumption rates linked to the quality of the environment), while the parameter k represents processes pertaining to energetic costs (catabolism; e.g., metabolic rates and associated behavioral traits). The VBGF arises from bioenergetic principles and is based on specific but reasonable assumptions about how growth rate scales with individual size (Essington et al. 2001; Mangel 2006). Descriptions of the derivation of the VBGF from bioenergetic principles and additional assumptions of the VBGF can be found elsewhere (e.g., von Bertalanffy 1938, 1957; Beverton and Holt 1959; Essington et al. 2001; Mangel 2006), and we refer readers to those references for a complete discussion.

Equation (1) describes the growth process of an individual. However, almost all applications of the VBGF involve fitting an integrated form of equation (1) to population-level data and interpreting estimated parameters as the values for an average individual in the population. As noted by many investigators (Sainsbury 1980; Wang 1998; Eveson et al. 2007), this interpretation is valid only if there is no heterogeneity among individuals; estimating parameters by ignoring individual variation will yield biased parameter estimates. Thus, two key questions are Is there biological evidence of among-individual variation, and How can we estimate its magnitude in the face of a variable environment and stochastic variation?

We develop a general model derived from equation (1) and apply it to steelhead trout. While we motivate and frame our analysis in the context of salmonid fish, our approach is applicable to a wide range of species. For salmonids, detailed studies of physiology show individual variation in physiological rates (Paszkowski and Olla 1985; Metcalfe et al. 1995; Gilmour et al. 2005; Burton et al. 2011) that can drive differences in activity, determine behavioral dominance hierarchies, and result in variation in

growth (Martin-Smith and Armstrong 2002; Morinville and Rasmussen 2003). However, the link between individual variation in traits and realized growth in a temporally variable environment is largely undescribed (Burton et al. 2011). We integrate equation (1) to obtain

$$x_i(t) = x_i(t-1)e^{-k_i} + \frac{q_i}{k_i}(1 - e^{-k_i}), \tag{2}$$

and we include the subscript i to make explicit that the parameters are tied to individuals.

Thus, we assume that there is fixed individual variation in the gain and cost parameters. Because q_i is related to the amount of resources available to an individual, it is related to both the shared environment and the behavioral traits of that individual. The relationship between physiology, the environment, and growth reflects complicated trade-offs that vary as a result of differences in behavior and life history. We adopt a flexible form for relating q_i and k_i proposed by Snover et al. (2005, 2006). We let γ_t denote the shared environment at time t and ψ be a parameter that determines the degree to which q depends on environmental versus metabolic and behavioral factors; then

$$q_{i,t} = \gamma_t k_i^\psi, \tag{3}$$

and $q_{i,t}$ represents the growth conditions for an individual, given its traits and a shared environment at time t. Note that ψ is a population-level parameter; all individuals are assumed to have a shared link between behavior and the environment. Snover et al. (2005) explain why $0 \le \psi \le 1$. If $\psi = 0$, then k_i and q_i are independent, and individual activity has no effect on an individual's success at obtaining resources from the environment. Therefore, when $\psi = 0$, individuals with high k_i have slower growth. At the other extreme, $\psi = 1$, individuals with high k_i always have increased access to resources and therefore experience faster length-specific growth. For intermediate values of ψ, the relative growth rate for individuals with different k_i will change with an individual's length. For $0 < \psi < 1$, the value of k that has the highest growth rate at a given length depends on the shared environment, γ_t (fig. A1, available online). Thus, this model can qualitatively match the empirical observation that the relative success of individuals with different traits varies with the quality of the environment (Alvarez and Nicieza 2005; Burton et al. 2011).

Combining equations (2) and (3) gives

$$x_i(t+1) = x_i(t)e^{-k_i} + \gamma_t k_i^{\psi-1}(1 - e^{-k_i}), \tag{4}$$

and after n intervals (nominally days), the length of an individual is

$$x_i(t+n) = x_i(t)e^{-k_i n} + k_i^{\psi-1}(1 - e^{-k_i})\sum_{j=0}^{n-1}\gamma_{t+j}e^{-k_i j}. \tag{5}$$

Equation (5) is a deterministic model for individual

growth in a time-varying environment. We also expect stochastic processes to contribute to growth. To account for stochasticity, we assume that the environment the individual experiences is a random variable, $\tilde{\gamma}_t$, and can be approximated by a normal density, $\tilde{\gamma}_t \sim N(\gamma_t, \sigma^2)$. Note that γ_t can, in theory, take on negative values and produce negative growth (shrinking). In this stochastic framework, length is a random variable (denoted by capital letters; $X_i(t)$) and individuals are measured with error, so we let $Y_i(t)$ denote observed length. If the interval between observations is n_w (for $w = 1, 2, \ldots, W$ intervals) and the mean environment between measurement intervals can be approximated by a single constant, γ_w, then the full time-series model that incorporates process stochasticity and measurement error is

$$X_i(t) = x_i(t - n_w)e^{-k_i n_w}$$
$$+ k_i^{\psi-1}(1 - e^{-k_i})\gamma_w \sum_{j=0}^{n_w-1} e^{-k_i j} + z_t, \tag{6a}$$

where

$$z_t \sim N\left(0, \sigma^2[k_i^{\psi-1}(1 - e^{-k_i})]^2 \sum_{j=0}^{n_w-1} e^{-2k_i j}\right),$$

and

$$Y_i(t) = X_i(t) + z_{\text{obs}}, \tag{6b}$$

where $z_{\text{obs}} \sim N(0, \tau^2)$ (also see the appendix, available online). Equations (6a) and (6b) constitute an individual time-series model where fixed individual traits, a shared environment, and stochastic variation are all incorporated (Prado and West 2010). Note that both the expected value and the variance of an individual's length depend on an individual's trait, k_i. This model matches the structure of many data sets where uniquely marked individuals living in a shared but variable environment are observed repeatedly over time.

We note that this is far from the only possible model that could be derived and that a variety of alternative structures for modeling growth are reasonable. For example, various approaches with stochastic differential equations have been developed (e.g., Fujiwara et al. 2005; Gudmundsson 2005; Lv and Pitchford 2007). The model presented here has distinct advantages for parameter estimation (see below). In the sections that follow, we describe a rearing experiment on steelhead trout and then apply our model to estimate parameters from the steelhead data.

Study Species and Rearing Experiment

We apply the time-series model to a rearing experiment on California steelhead (*Oncorhynchus mykiss*; see Beakes

et al. 2010 and the appendix for the details of the experiment). Age-0 steelhead from two populations were raised in aquarium tanks at the National Marine Fisheries Service Laboratory in Santa Cruz, California. The first population derives from a conservation hatchery on a small coastal stream, Scott Creek (denoted CCC, for central California coast). The CCC population derives from a lineage of predominantly wild fish (Hayes et al. 2004). The second stock comes from a production hatchery, Coleman National Fish Hatchery, on Battle Creek, a tributary to the Sacramento River (denoted NCCV, for northern California Central Valley). Steelhead broodstock for Coleman hatchery derive predominantly from hatchery origin (Campton et al. 2004; USFWS 2011). Thus, while the populations derive from distinct rivers in different parts of California, the contrast between the CCC and NCCV populations also incorporates a comparison between fish of predominantly wild and predominantly hatchery backgrounds.

Fish were grown in cylindrical tanks (490 L), with 20 fish per tank and eight tanks of each stock (initial length ~40 mm), and raised on a diet supporting moderate but restricted growth, except for a period in which an ad lib. ration was available (hereafter "low" and "high" rations, respectively). Tanks were assigned to one of four feeding treatments, with two replicate tanks per treatment. In July, all tanks were placed on low rations distributed four days a week. The fish were kept on low rations, except during the treatment period, when one of the four treatment groups received eight continuous weeks of high rations daily (see fig. 1). Thus, all treatment groups received identical amounts of time at each ration level and experienced equivalent cumulative food per unit body mass over the course of the year, although the timing of food availability varied. The length of each individual was observed approximately every 4 weeks for a 10-month period. We included 100 CCC and 138 NCCV individuals in our analysis (see appendix).

Parameter Estimation

We were interested in estimating the joint posterior distribution of the parameters and unobserved, latent states for each individual (the length of individuals at each day of interest) by using Bayesian hierarchical methods (Cressie and Wikle 2011; appendix). We estimated parameters for each population independently, but within populations we estimated parameters for individuals in all treatments simultaneously. We estimated three shared environmental states for each population: γ_S, γ_L, and γ_H, corresponding to the first month of the experiment and the low- and high-ration treatments, respectively. We used a separate parameter for the first month because introducing fish into a novel environment should affect growth in addition to

the ration treatment. We estimated the length of each individual on each day it was measured and on the days when feeding treatments were changed (17 and 18 days for CCC and NCCV, respectively). We initially investigated the potential for tank-specific blocking effects, but there were no evident differences between tanks within a treatment, so we combined tanks into one analysis (fig. A4, available online). We did not attempt to estimate the measurement error but treated τ^2 as fixed (see below).

Preliminary analyses showed that ψ and the γ's were only weakly identifiable. To improve estimation, we performed all of our analyses conditioned on values of ψ. We estimated parameters for a range of values of ψ (from 0.1 to 1.0, in increments of 0.1) to investigate the effects of changing the relationship between individual traits and the environment. Models with $\psi = 0$ (the classic von Bertalanffy model) failed to converge in most cases; we do not discuss $\psi = 0$ further.

We considered two model structures for individual variation in k. In the first, we estimated a single, shared k for all individuals, so for this model we estimated $\{k, \gamma_S, \gamma_L, \gamma_H, \sigma^2\}$ (hereafter the single-k model). In the second, we estimated a k_i for each individual and assumed that the similarity among individuals in a population was hierarchical (hereafter the hierarchical-k model); we modeled each k_i as a random sample from a shared normal distribution, $k \sim N(\mu_k, \rho_k^2)$, where μ_k and ρ_k^2 are the mean and variance of k, respectively. Thus, for I individuals we estimated $\{k_1, k_2, ..., k_I, \mu_k, \rho_k^2, \gamma_S, \gamma_L, \gamma_H, \sigma^2\}$. For all parameters we used diffuse prior distributions (summarized in table A1, available online).

Incorporating measurement error is an important consideration in ecological models (Clark 2007). Steelhead measurements of length were relatively precise, but no empirical estimates of measurement error were made during the experiment (Beakes et al. 2010). Therefore, we fitted models assuming two values of measurement error ($\tau^2 = 1$ or 4 mm^2) to understand the consequences of including measurement error for other parameters.

We estimated the posterior distribution of parameters and latent states by using a mix of Gibbs and Metropolis Markov chain Monte Carlo (MCMC) algorithms to sample parameters (Gelman et al. 2004) and used standard techniques to assess model convergence and diagnostics (see the appendix). All results represent 4,500 samples from the posterior distribution. We performed all analyses in R (ver. 2.13.1; R Development Core Team 2011).

To compare the single-k and hierarchical-k models, we used posterior predictive loss (Gelfand and Ghosh 1998; Clark and Bjørnstad 2004). Predictive loss identifies the model, m, that provides a balance between a goodness-of-fit term, G_m, and model complexity term, P_m. The preferred
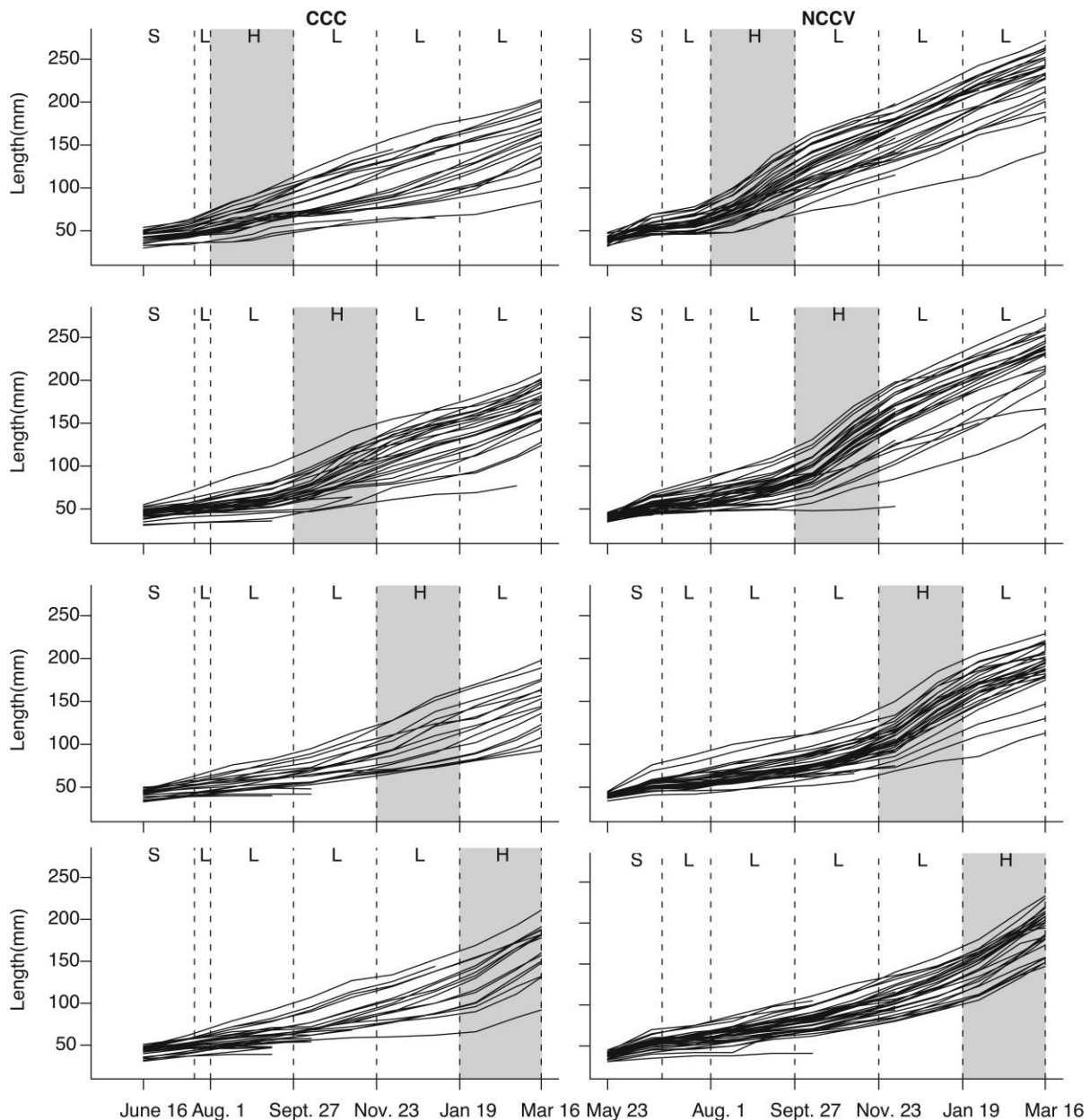
Figure 1: Observed growth trajectories for steelhead from two populations (CCC, *left*; NCCV, *right*) in the four feeding treatments (rows) in 2006–2007. Lines indicate length trajectories for individual steelhead. "S" indicates the first month of the experiment, "L" indicates the low-ration treatment, and "H" and shading indicate the high-ration experiment. From top to bottom, the rows correspond to treatments 1–4.

model is the one that minimizes the sum $D_m = G_m + P_m$ (see the appendix).

Connecting Individual Variation to Populations and Fitness

We performed two simulation exercises to examine the consequences of individual variation for populations. First, we

used the estimated parameters to simulate steelhead growth and to examine the consequences of individual heterogeneity and process stochasticity for the distribution of lengths in the population. We performed independent simulations of more than 50,000 steelhead individuals, using the posterior parameter estimates for both the single-k and hierarchical-k models and both with and without process stochasticity (four scenarios in total). We compared the

simulated lengths to the observed distribution of lengths at the end of the growth experiment (see appendix).

Next, we connected projected individual growth trajectories with a state-dependent life-history model to understand the consequences of individual variability in growth on life-history expression and reproductive output of female steelhead. Steelhead are facultatively anadromous, able to complete their entire life cycle in freshwater or emigrating to the ocean at various ages before returning to spawn. Both fecundity (DuBois et al. 1989) and marine survival (Bond et al. 2008) are size dependent. Given this biology, life-history theory predicts that optimal life histories will depend on size-dependent trade-offs between increased growth opportunities (and thus, ultimately, higher fecundity) and higher mortality risks in different habitats. Mangel (1994) and Thorpe et al. (1998) formalized these trade-offs and showed how dynamic state-variable models (Mangel and Clark 1988; Clark and Mangel 2000) could be used to predict life histories and fitness of Atlantic salmon (*Salmo salar*). Satterthwaite et al. (2009) adapted this model to Scott Creek steelhead (corresponding to the CCC population), using length as a state variable and using local measurements of growth, survival, and fecundity to quantify these trade-offs. The parameterized model identifies optimal life-history decisions as a function of individual fish sizes and growth rates. Then, given a specified growth trajectory, forward iteration (Mangel and Clark 1988) along each individual growth trajectory yields a predicted life history (resident vs. anadromous and, if anadromous, age at ocean entry).

We adapted the Satterthwaite et al. (2009) model to explore how variation in growth trajectories due to both variation in k and environmental quality affects the distribution of reproductive output among individuals, life-history diversity, and, for the hierarchical-k model, the relative fitness of individuals with different traits. We simulated individuals under six scenarios: two methods for modeling k (single k or hierarchical k) under three growth environments (high, low, and very low growth: γ_H, γ_L, and γ_{VL}, respectively). The first two environments correspond to the feeding treatments in the tank experiment, and the third, γ_{VL}, was chosen to approximate the growth curves of wild CCC fish documented by Hayes et al. (2008; parameter values and details of the simulations are presented in the appendix). We produced 50,000 individual growth trajectories in each scenario, all of which included process stochasticity. We used such a large number of simulated growth trajectories because large amounts of stochasticity in growth required many replicates to provide relatively smooth plots of fitness as a function of k. We then used the Satterthwaite et al. (2009) model to predict the life history for each simulated individual, as described in the appendix. We characterized life-history diversity by using

the Shannon diversity index ($-\sum_i p_i \log(p_i)$, where p_i is the proportion of the population adopting life history i, summed over all nonzero p_i). Given a life-history prediction for each growth trajectory, we calculated expected lifetime egg production for each individual. Lifetime egg production is discounted by survival until reproduction, but when tracking life-history diversity we tracked potential pathways rather than accounting for fish dying before expressing a life history. We analyzed the CCC population only, because we lacked site-specific survival and fecundity estimates for the NCCV population.

Results

Inspection of empirical growth trajectories suggests both individual and population differences in growth as well as strong growth responses to experimental feeding treatments (fig. 1). For both populations, predictive-loss criteria showed that growth models incorporating individual variation were preferred to models without individual variation (fig. 2). This was true for all values of ψ considered and for both measurement error scenarios (figs. 2 and, available online, A2). In both populations, $\psi = 0.2$ provided the lowest value of D_m among the models considered and therefore best matched observed growth. For the remainder of the article, we focus on $\psi = 0.2$ and $\tau^2 = 1$. Results using other values of ψ and $\tau^2 = 4$ produce very similar results (see appendix).

Both the estimated posterior median k among individuals in the population and the individual variability in k
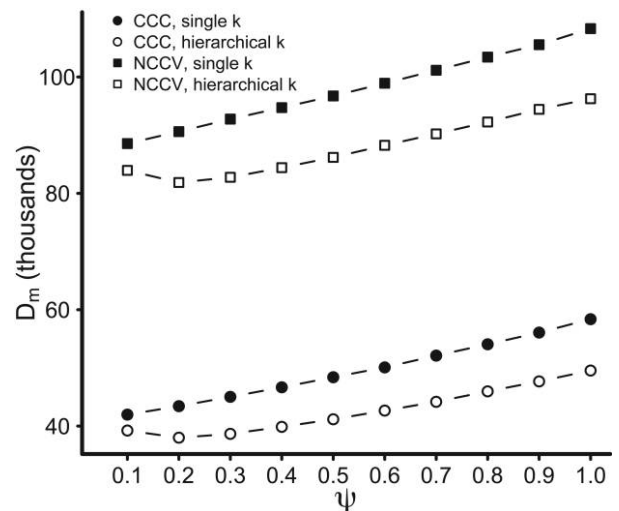

Figure 2: Model comparison using a posterior predictive loss criterion for $\tau^2 = 1$. Lower values of D_m indicate a better match between model and data. Both populations had minimum D_m at $\psi = 0.2$. Comparisons of model fit are valid only within populations (see appendix for details).

differed substantially between the populations. We esti-mate a nearly twofold difference in median k (0.00031 and 0.00017 for CCC and NCCV, respectively; fig. 3). Higher k's indicate higher estimated average activity costs within the CCC population, although there is substantial overlap in estimates of k between populations. Posterior estimates of k_i show strongly left-skewed distributions for both populations (fig. 3). The left-skewed distribution in k is evident in all four treatments of both populations. As measured by the coefficient of variation (CV), individual variation is higher in the CCC population (posterior median CV [95% credible intervals] = 0.57 [0.49–0.65] and 0.48 [0.41–0.56] for CCC and NCCV, respectively; fig. A5, available online).

Among-individual variation in k resulted in strong among-individual and between-population differences in growth in response to ration treatments. At the low ration, the populations had similar mean estimated growth rates, but variation in individual k translated into a roughly two-fold range in individual growth rates (fig. 4). However, the majority of individuals were estimated to have growth rates near 0.4 mm day^{-1} at the low ration. While both populations exhibited a strong growth response to the high-ration treatment (figs. 1, 4), the magnitude of the growth response to the high-ration treatment differed sub-stantially between populations. The CCC population at the high ration grew at a rate ≈1.6 times that of the fish at low ration ($\gamma_L = 2.08 \pm 0.06$, $\gamma_H = 3.38 \pm 0.12$; pos-terior median ± SD), while under the high ration the NCCV population grew at a rate ≈2.4 times that under

the low ration ($\gamma_L = 2.60 \pm 0.20$, $\gamma_H = 6.27 \pm 0.08$). When the treatment groups were compared at a standard length of 50 mm, the difference in growth rates was par-ticularly striking (fig. 5). Under the high ration, there was virtually no overlap in growth rates between CCC and NCCV individuals. Furthermore, the CCC individual with the lowest k under high rations had growth similar to the population median growth in the low-ration treatment (figs. 4, 5, and, available online, A6). In contrast, even the individual with the smallest estimated k in the NCCV pop-ulation had higher expected growth under the high ration than any individual under low-ration conditions.

We compared growth and variability on a monthly time step to match the time between measurements in the ex-periment. The NCCV population had significantly higher estimated variation than the CCC, but in both populations the standard deviation of process stochasticity was much less than the expected growth rate (fig. 5). Generally, ex-pected growth was more than twice as large as the sto-chasticity in monthly growth.

We found evidence of an effect of feeding treatment on the estimates of k (fig. A4). Lower estimates of k were associated with treatments 3 and 4, which correspond to the treatments that received high rations at the end of the experiment (fig. 1). While this pattern is arguably present in the CCC population, it is striking in the NCCV (fig. A4). This result indicates an interaction between the early environment experienced by individuals and their sub-sequent growth.
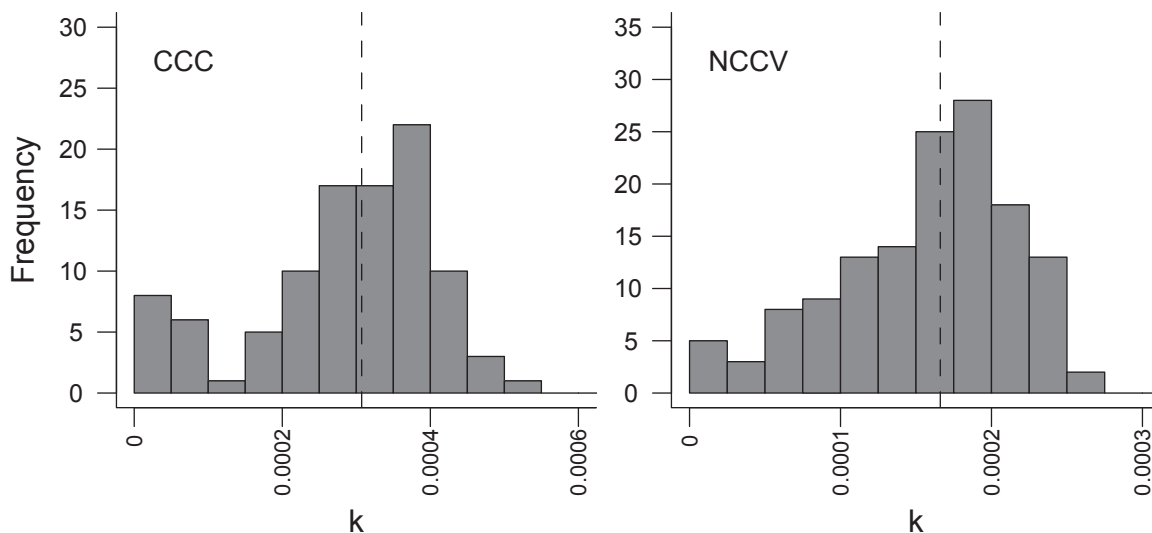

Figure 3: Estimated among-individual variation in k for $\psi = 0.2$ and $\tau^2 = 1$. Histograms of median estimates of k in each population. Dashed lines show the estimated median k among individuals in each population. Note different X-axis scales between the populations.
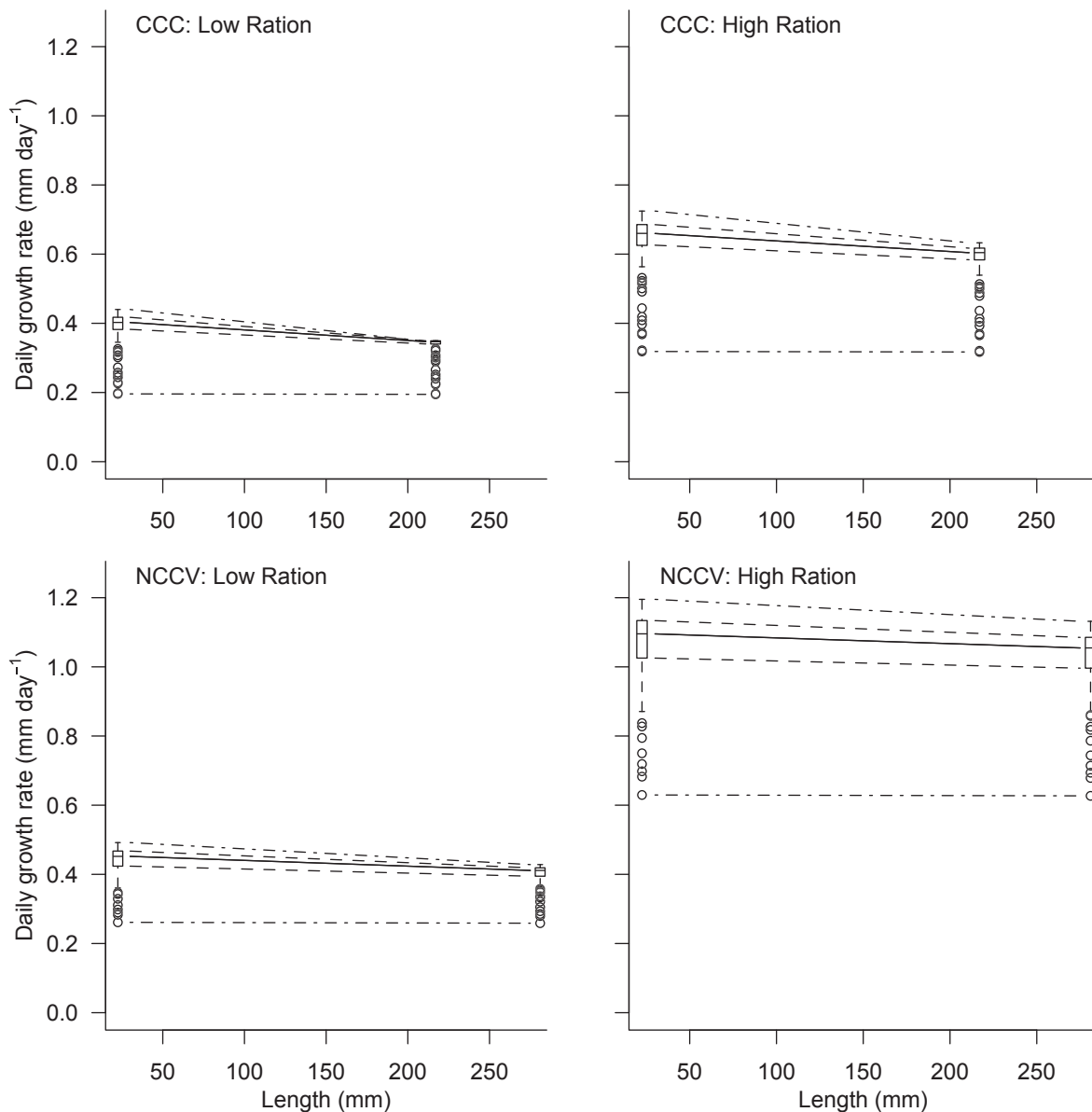
Figure 4: Estimated among-individual variation in growth for CCC and NCCV steelhead populations under the two feeding treatments for $\psi = 0.2$ and $\tau^2 = 1$. Solid lines indicate among-individual median growth, dashed lines show the interquartile range, and dash-dotted lines show individuals with maximum and minimum estimated k_i. Median posterior estimated k_i were used for each individual. Points show extreme estimates of growth for individuals. Expected daily growth rates are plotted across the range of lengths observed in each population (30–211 mm for CCC and 30–275 mm for NCCV).

For all individuals in both ration treatments, individuals with higher k had higher growth rates. While models with $0 < \psi < 1$ allow for individuals with high k to have lower growth than low-k individuals (see fig. A1), we found no evidence that individuals with high estimated k experienced reduced growth across the range of lengths observed in the population under the conditions of this experiment.

Population processes. Simulations showed the consequences of including individual variation for the distribution of lengths (fig. 6). The distribution of lengths resulting from individual variation without process stochasticity was peaked and strongly left-skewed, reflecting the estimated distribution of k in both populations. Simulations using both a single k for all individuals and process
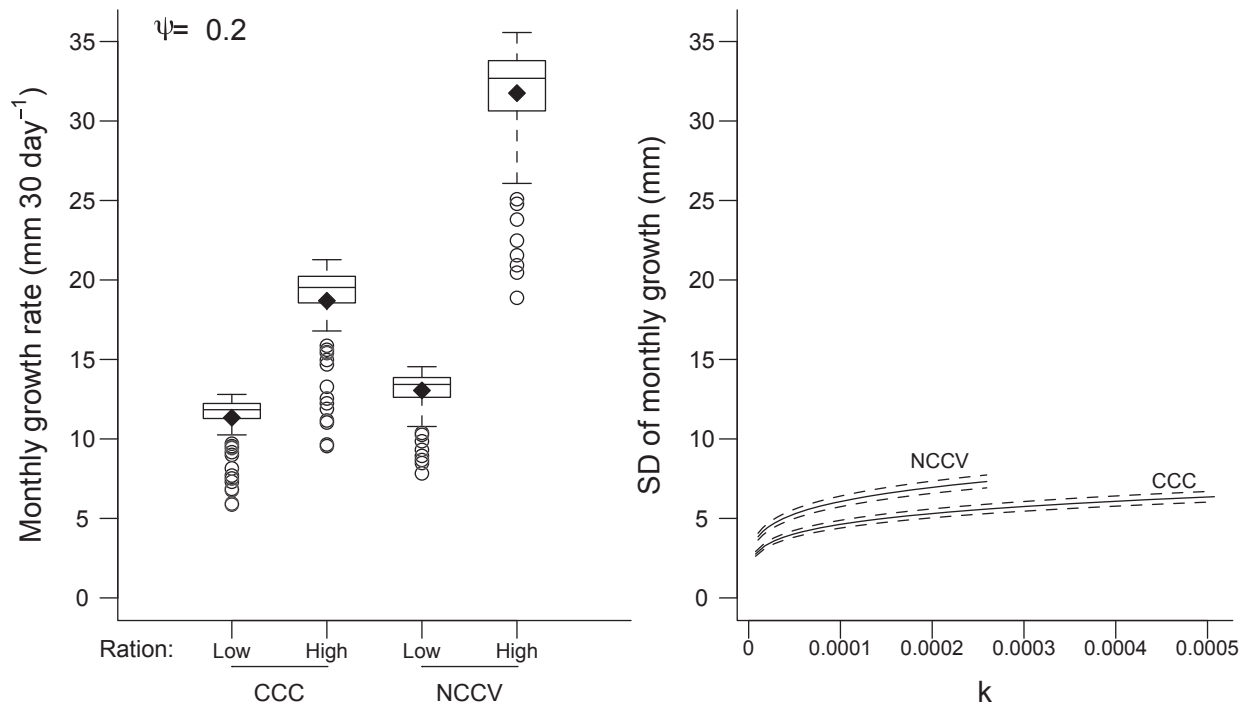
Figure 5: Growth responses to feeding treatments in the CCC and NCCV populations with $\psi = 0.2$ and $\tau^2 = 1$. *Left*, distribution of expected monthly growth rate for 50-mm individuals under two ration treatments. Growth rates were calculated from the posterior median estimate of k_i for each individual. Boxplots show median, interquartile range, and whiskers 1.5 times the length of the interquartile range. Individuals beyond the whiskers are shown with circles. Diamonds indicate within-group mean. *Right*, posterior estimates of process stochasticity in growth for the two populations. Median (solid line) and 95% credible intervals (dashed lines) are shown. Results are plotted across the range of k_i estimated for each population.

stochasticity generated an approximately normal distribution of lengths. Incorporating both individual variation and process stochasticity generated distributions of lengths with a mean length similar to the shared k distribution but with a higher variance and a negatively skewed distribution. Such heavy-tailed distributions provided the closest match to the empirical distribution of lengths observed in the CCC and NCCV populations (fig. 2).

Output from the state-dependent life-history model showed how predicted patterns of life-history variation are strongly tied to both the environment and an individual's k. For both single- and hierarchical-k simulations, high-growth environments (γ_H) were dominated by individuals that emigrated to the ocean at age 1, with a small number of fish maturing as freshwater residents (table 1). Low-growth environments (γ_L) saw a mix of residents and age-1 and age-2 emigrants, while the very-low-growth environments (γ_{VL}) showed the greatest diversity of life histories, and individuals were split nearly evenly among residents and age-2 and age-3 emigrants. Overall, the single-k models produced less life-history variation than did hierarchical-k models, but the predicted life-history proportions were usually within 5% (table 1).

Our analysis showed strong effects of the environmental quality on the range and distribution of expected lifetime reproductive output in the CCC population. The distribution of reproductive output was approximately symmetric, right-skewed, and extremely right-skewed in the high-, low-, and very-low-growth environments, respectively (fig. 7). In very-low-growth environments, more than 30% of individuals (newly emerged fry) had expected reproductive output of fewer than 2 eggs, while that of a few individuals was more than 50. Note that the variation in the single-k simulations arose exclusively from stochastic processes, because all individuals had identical values of k, while that in the hierarchical-k simulations resulted from a mix of individual differences and stochastic forces. While there were some mild differences between the single- and hierarchical-k models—most notably in high-growth environments, where the hierarchical model clearly had larger variance than the single-k model—the qualitative patterns of individual variation in reproductive output were similar between the scenarios.

With the hierarchical-k model, life-history strategies and fitness are predicted to vary across individuals with different
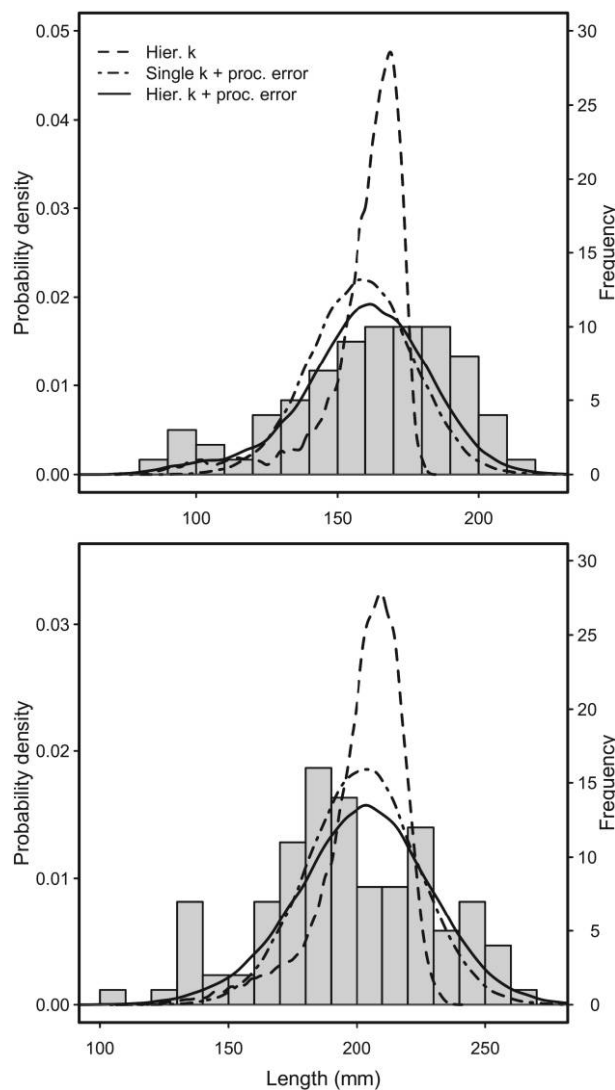
Figure 6: Simulated and observed distributions of length at the end of the steelhead growth experiment for the CCC (*top*) and NCCV (*bottom*) populations. Lines show the smoothed densities of 50,000 simulated individuals for three scenarios: (1) individual variation in *k* (hierarchical) without process stochasticity (dashed line), (2) a single, shared *k* with process stochasticity (dash-dotted line), and (3) individual variation in *k* with process stochasticity (solid line). Histograms show observed distribution of lengths at the end of the experiment ($n = 75$ for CCC and $n = 106$ for NCCV). See text for simulation details. Note that *X*-axis scales differ between panels.

k's (fig. 8). Importantly, the range of life-history strategies employed and fitness differed across values of *k* (fig. 8). For example, in the low-growth environment, individuals with low *k* (e.g., $k = 0.0001$) were predominantly age-2 emigrants, while individuals with high *k* (e.g., $k = 0.0006$) were predominantly age-1 emigrants. In all three environments, there was a strong pattern of variation in fitness with *k*.

Under high-growth conditions, fitness increased dramatically with *k* before leveling off. Similar patterns were observed under low-growth conditions, with expected fitness increasing quickly before flattening out at high *k*. In contrast, under very-low-growth conditions, mean fitness was virtually flat across all values of *k*. In all three scenarios, the range of fitnesses predicted increased with *k*. An increase in skew with *k* was very evident in the very-low-growth environment, where individuals with high *k* predominantly had very low (near 0) fitness while a small number of individuals had very high fitness (fig. 8).

Discussion

Our analysis provides strong evidence for fixed individual heterogeneity within populations, strong differences between populations, and between-population differences in response to a variable environment. The high levels of individual variation motivate three main questions: (1) Are the estimated amounts of individual variation attributable to fixed differences reasonable? (2) What might drive between-population differences? and (3) How do these methods and laboratory experiments inform our understanding of natural populations? We address each question in turn.

Individual heterogeneity estimated in both populations was greater than the reported range in metabolic rate variation in salmonids (Burton et al. 2011). Studies of salmonids have documented at least threefold variation among individuals in resting metabolic rate (Metcalfe et al. 1995; Burton et al. 2011), which is much less than the range between the lowest and highest *k*'s in our study ($\approx$25-fold in NCCV and $\approx$60-fold in CCC; fig. 3). However, variation in *k* should be much larger than the observed variation in resting metabolic rates. For example, the maximum metabolic rate may be up to 7 times resting metabolism (Mangel and Munch 2005), and increasing consumption likely implies higher activity and a larger multiplier of baseline metabolic rate (Mangel and Munch 2005; Satterthwaite et al. 2010). Thus, while variation in metabolic rates should contribute to variation in *k*, this parameter represents the net cost effects of metabolism and behavior and also interacts with the food environment to determine the gains from foraging success and food conversion. Estimated variation in *k* translates into a roughly twofold range in growth rates in both populations (fig. 5), which is consistent with the wide variation in size-at-age documented in the field (e.g., Sogard et al. 2009). Thus, *k* likely conflates variation in basal metabolic rates with other mechanisms, such as behavioral choices and activity costs, affirming the complexity of the relationship among metabolic rates, behavior, and realized growth (Biro and Stamps 2010; Burton et al. 2011).

Table 1: Life-history pathways taken by simulated steelhead assuming a single, shared k (single k) or with each individual having a unique k (hierarchical k)

Model, environment	Resident	Emigrants			Uncommitted	Shannon diversity
		Age 1	Age 2	Age 3		
Single k:						
γ_H	9.3	90.7	0	0	0	.13
γ_L	9.2	63.4	27.4	0	0	.37
γ_{VL}	23.6	0	33.7	39.1	3.6	.52
Hierarchical k:						
γ_H	8.6	87.4	4.0	<.1	<.1	.20
γ_L	8.1	59.1	32.4	.4	<.1	.39
γ_{VL}	27.3	<.1	26.7	38.7	7.3	.55

Note: Values are percentages of 50,000 simulated individuals predicted to take on a resident, stream-dwelling life history or emigrate to the ocean at one of three ages, assuming survival. "Uncommitted" indicates fish that had not committed to a life-history pathway after 3 years. We show the variation in life history expected under three environmental conditions (γ_H, γ_L, and γ_{VL}) that correspond to high, low, and very low food availability, respectively (see appendix). "Shannon diversity" is a measure of the population-level variation in life history, with higher values indicating greater population variability in life history.

The NCCV population showed both reduced individual variation and a stronger growth response to feeding treatment relative to the CCC population. This indicates that identical food environments were experienced very differently by the two fish populations; individual heterogeneity and population-level traits mediate the interaction between the food environment and growth. The populations differ in their origin (California's Central Valley vs. coastal California) and in the history of the populations: NCCV fish derive mainly from a long-term hatchery population, whereas CCC individuals come from a conservation hatchery that uses parents of wild origin each generation. Thus, our analysis is not ideally situated to explicitly separate the effects of hatchery rearing from local adaptation to river conditions. However, the observation of lower base activity costs and strong responses to high-ration conditions in the NCCV population are consistent with the effects of hatchery domestication observed in experimental studies (van Leeuwen et al. 2011; Lorenzen et al. 2012). Furthermore, since growth rates have been documented to trade off with swimming performance and mortality risk (Munch and Connover 2003), we speculate that the NCCV population may have gained growth potential but lost aspects of predator avoidance behavior (Johnsson and Abrahams 1991). Indeed, our behavioral observations while feeding these fish indicated that NCCV fish would rapidly surface and consume added food while CCC fish remained in their PVC shelters, sometimes allowing uneaten food to accumulate even during low-ration periods (Beakes et al. 2010).

The preferred model occurred with $0 < \psi < 1$ for the hierarchical-k model (figs. 2, A2). With ψ in this range, at large sizes individuals with low k experience faster growth than fish with high k; this crossover occurred at progressively

smaller sizes as the quality of the environment declined (fig. A1). We do not have data from fish growing under low-ration or starvation conditions to directly assess this pattern of growth, but the behavior of the model matches experimental evidence of context-dependent growth (Burton et al. 2011) and suggests a mechanism by which variation in k may be maintained. In times of abundant resources, individuals with high k achieve faster growth than low-k individuals, but in times of limited resources the converse occurs. An additional possibility is that fish with different intrinsic k's correspond to alternative life histories (fig. 8; Morinville and Rasmussen 2003).

Our simulations show strong environmental dependence for the diversity of life histories and relative fitness of individuals with different k's in the CCC population. The importance of individual heterogeneity in k relative to stochasticity for population dynamics also varied across environments. Individual variation in k generated some increased variation in life history under all environmental scenarios (table 1), and values of k were associated with distinct sets of life-history strategies (fig. 8), but the effects of variation in k were most apparent in the γ_H environment (fig. 7). Similarly, patterns in variation of fitness as a function of k suggest different selective regimes under different environments. In an environment with high food availability, we predict strong selection for increasing k across the range of k modeled and thus that variability in k has the strongest effects on fitnesses in this environment. As food availability decreases, the expected reproductive output becomes nearly flat across values of k, suggesting a weak selective surface. This reduced variation in reproductive output across values of k results in the convergence of the distribution of reproductive output expected for single-k versus hierarchical-k models in low-growth en-
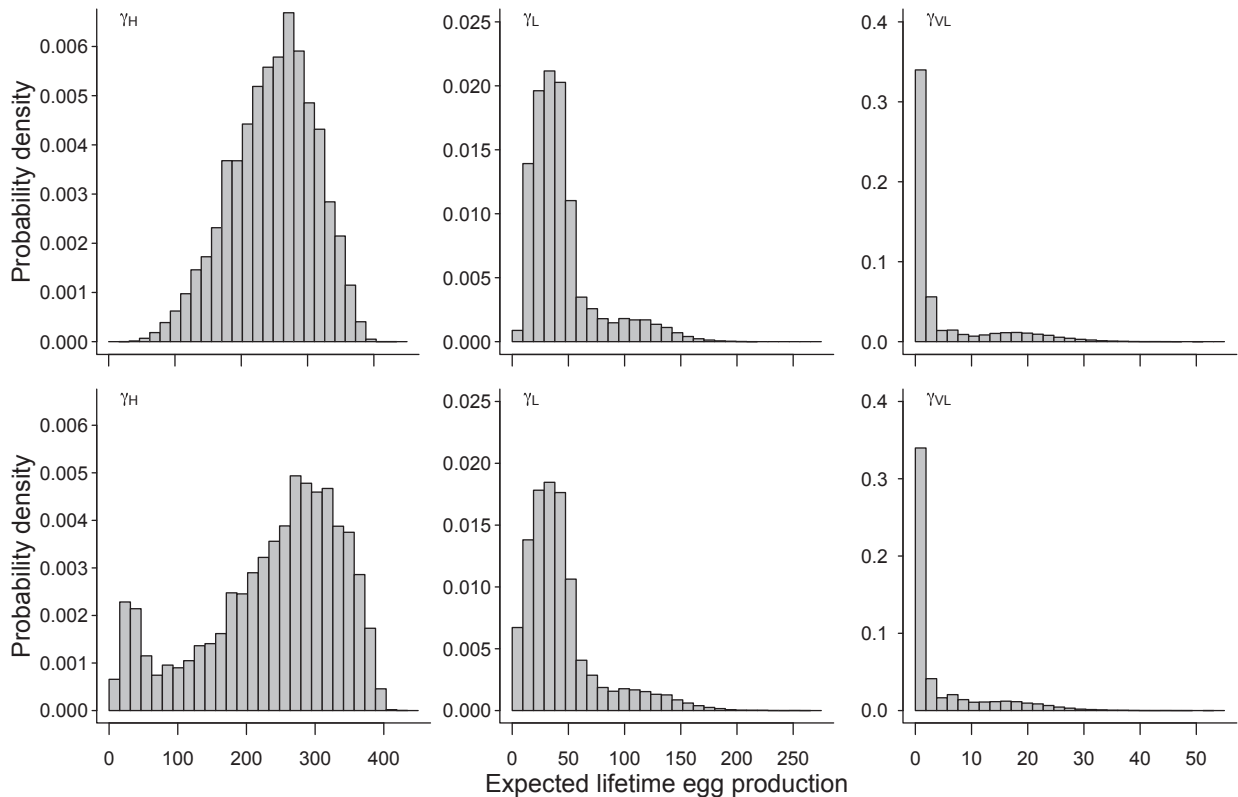
Figure 7: Distribution of individual fitnesses under three environmental conditions (high growth [γ_H], low growth [γ_L], or very low growth [γ_{VL}]) for the single-k (*top*) and hierarchical-k (*bottom*) models. Histograms represent 50,000 simulated female steelhead.

vironments (fig. 7). The equivalent fitness of different values of k might be expected in the γ_{VL} scenario, since γ_{VL} most closely approximates natural conditions. In a population subject to selection, values of k that are not strongly selected against will persist (Mangel and Stamps 2001). Thus, the CCC population appears to maintain a range of k that results in roughly equivalent expected fitness in a low-growth environment but includes some values that would have low fitness in a higher-growth environment. Our results therefore suggest that variability in k can have important consequences for population dynamics, particularly in populations that experience shifting or variable environmental conditions. Thus, modeling and understanding individual variability are important, even if the realized variability in fitness between models that ignore individual variation and those that include it is relatively small in a particular environment.

In this analysis, we find no case in which an individual with an intermediate or low k is explicitly favored over individuals with a high k. However, recall that we assumed

no relation between k and freshwater survival because there are no data available on this relationship. As higher k should be associated with bolder or more aggressive behavior (Snover et al. 2005), in nature we expect increased mortality or predation risk for high-k individuals. With this additional mechanism, our results suggest that selection more strongly favors cautious fish in lower-productivity environments, since the advantages of high k, as expressed through growth alone, would be reduced. However, this mechanism must remain speculative for now.

Our worked example predicts life histories based on a growth-survival trade-off parameterized in the field and then applied to three growth environments. However, the conclusion that variation in size-at-age leads to variation in life histories is likely general, and it is certainly the case that variation in size-at-age would be expected to affect fitness even without life-history plasticity. The amount of variation in size-at-age that we predict to be due to variation in k and/or stochasticity is likely to have substantial impacts on both fitness and life-history diversity. For ex-
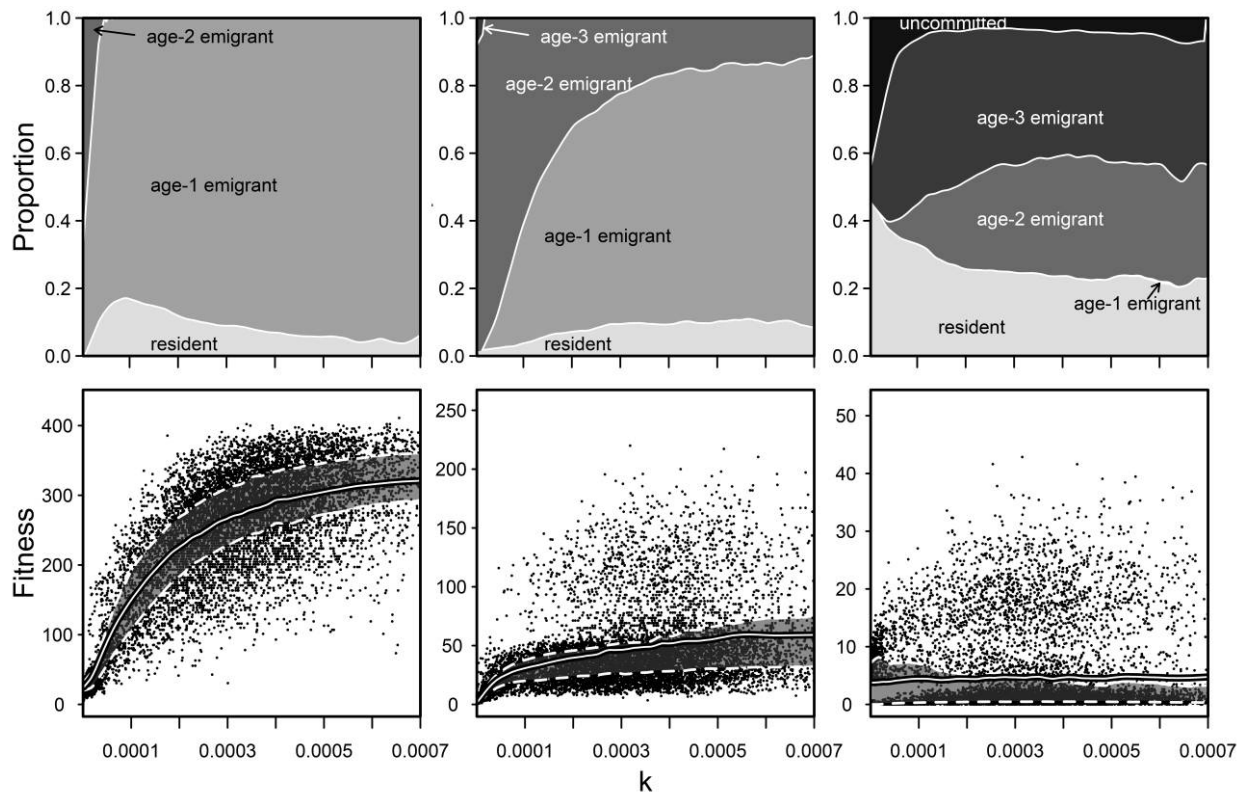
Figure 8: Life-history variation and fitness consequences of variation in k for the CCC population under three environmental conditions: high growth (γ_H; *left*), low growth (γ_L; *middle*), and very low growth (γ_{VL}; *right*) *Top*, proportions of 50,000 simulated female steelhead employing different life-history strategies as a function of k. Proportions as a function of k were LOWESS smoothed for clarity. *Bottom*, simulated fitness of female steelhead under three environmental conditions (for figure clarity, only 10,000 individuals are plotted). Points show individual fish, the shaded region with dashed borders shows the smoothed interquartile range of fitness, and the white line with black borders shows mean fitness. Note that the *Y*-axis differs among panels.

ample, larger fish are more fecund and more likely to survive emigration, so the amount of variation in size-at-age that we predict to be due to variation in k is likely to have a substantial impact on fitness regardless of life-history expression.

An additional point of interest is the effect of feeding treatment on estimated k. In particular, NCCV fish that experienced high rations late in the year (treatments 3 and 4) had estimates of k noticeably lower than those of individuals that experienced high rations early (treatments 1 and 2; fig. A4). While extreme conditions, such as starvation, greatly affect the potential for future growth (compensatory growth; Morgan and Metcalfe 2001; Metcalfe et al. 2002; Sogard and Olla 2002; Mangel and Munch 2005), we observed strong evidence of treatment effects on growth under moderate-ration conditions. One potential explanation for observed patterns may be changes in allocation to growth in length versus growth in weight, as individuals who experience low-quality environments early in life may

shift to a strategy of adding weight over one of increasing in length (Metcalfe et al. 2002). More generally, this result suggests that the environment experienced early in life strongly affects performance later in life (Mangel 2008). Thus, the inclusion of context-dependent, individual-level traits in the growth model may be warranted and highlights the necessary simplifications made in our model of growth. We collapsed all individual variation to a single parameter, k_i, and assumed that this parameter was fixed regardless of an individual's experiences. Reducing individual heterogeneity to a single parameter has statistical benefits as well as biological motivation (Kirkpatrick 2009), but this result motivates future models that can incorporate such context-dependent individual effects.

We recognize that the VBGF has limitations and that by necessity our model is a simplification of a complicated growth process; there are many factors that affect growth that are not explicitly incorporated into our model (see Kooijman 2000; Fujiwara et al. 2004). The estimated pro-

cess stochasticity, σ^2, absorbs both truly random processes that affect growth and uncertainty that arises from model misspecification. Examples of potential misspecification include the assumption that the range of temperatures experienced during the experiment does not affect growth and that the quality of the environment can be described by constant parameters linked to feeding treatments (γ_H and γ_L). In light of the extensive literature on temperature effects on growth and size-dependent consumption rates (e.g., Railsback and Rose 1999), neither of these assumptions is strictly true. However, our estimates of process stochasticity are reasonably low (fig. 5), suggesting that our model matches the available data well and that the consequences of misspecification are relatively minor. Furthermore, such assumptions are necessary to ensure that the statistical model can be estimated.

A reasonable question is how state-space methods like the one outlined here to might be applied to studying somatic growth in natural populations. Generally, using time-series models for the growth of individuals has inherent appeal. Most notably, it avoids the many biases that arise from ignoring the time-series structure of growth data (see Fujiwara et al. 2005; Clark et al. 2007; Eveson et al. 2007). In practical terms, this type of analysis provides several avenues for integrating data from captive and natural populations. First, the estimates of individual variation in terms of CV(k) from captive populations can be used as reasonable prior information for individual variation in natural populations. Second, the Bayesian framework provides the potential for the direct incorporation of auxiliary prior information. In our example, we knew the timing and abundance of food because it was experimentally controlled. In natural populations, information about food availability is sparse. However, surveys of the abundance of food resources (e.g., insect abundance, in the case of riverine salmonids) are available in some instances and could be incorporated as a covariate to inform estimation of γ. More generally, expressing and estimating γ as a function of measurable proxy environmental variables instead of as free parameters could enable this type of model to be fitted to natural population data.

Finally, the estimated distribution of k is of interest for modeling individual variation in k in natural populations. In the absence of information, other authors have used gamma (e.g., Snover et al. 2005, 2006), normal (e.g., Pilling et al. 2002; Eveson et al. 2007), or lognormal density to describe individual variation in k. Our results show a strongly left-skewed distribution for k (fig. 3), which none of those distributions can accommodate. The empirical distribution of k generates left-skewed distributions of length-at-age (fig. 6). While there are certainly other process that can generate skewed distributions in length-at-age (e.g., size-dependent mortality; Carlson et al. 2010), the observation of skewed distributions in length-at-age in many fish species may be at least partially attributable to individual variation (e.g., Pfister and Stevens 2002; Fujiwara et al. 2004). Clearly, additional research is needed to understand the interaction between individual variation in growth and observed patterns of size in natural populations.

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