Individual and Population Level Variation in Growth Parameters for Steelhead Trout *Oncorhynchus mykiss* in Central California

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Abstract

We fit a bioenergetics model based on a balance between mass and temperature-dependent anabolic and catabolic factors to growth data for juvenile steelhead trout (*Oncorhynchus mykiss*) from California. We grew fish from a small coastal stream (Scott Creek) conservation hatchery and a Central Valley (Coleman National Fish Hatchery on Battle Creek, Sacramento River) production hatchery in a common laboratory setting. Our growth model did not characterize the trajectories of all fish, likely as a consequence of enhanced growth via cannibalism or inhibited growth due to risk averse behavior such as avoidance of dominant individuals. For most individuals, however, it provides a close match and allows us to provide an excellent description of individual and stock-specific variation in specific rates of anabolism and catabolism. We use likelihood methods to conclude that there is a strong difference in the mean rates based on origin of the stock, with Central Valley fish having a higher maximal consumption ability but both strains having similar metabolic needs after standardizing for fish size and temperature. This suggests genetic differences between strains based on local adaptation and/or differing degrees of domestication). As a result, environmental change may affect the growth (and thus survival, life history, and demography) of the strains in different ways.

Introduction

Growth of juvenile salmonids has many important consequences for individual fitness and the resilience of populations to disturbance (Quinn 2005, Mangel 2006). In general, faster growth and larger size typically lead to higher survival in freshwater (but see Carlson *et al.* 2008) and larger size at smolting leads to higher marine survival (McGurk 1996). For adult females larger size leads to higher fecundity (Allen and Sanger 1960). In addition, for highly plastic species such as the steelhead trout, growth rates may affect the life history pathways followed by individual fish (Satterthwaite *et al.* 2010), with implications for life history
diversity and overall population dynamics. Thus, understanding and predicting juvenile growth rates is an important tool in preserving the life history diversity and population health of steelhead trout in the face of environmental change.

To date, most approaches to modeling the growth of fish have followed one of two strategies. First, many successful models use the von Bertalanffy growth equation (VBGE, von Bertalanffy 1938, Mangel 2006) or simple elaborations thereof (Fournier et al. 1998, Prajneshu and Venugopalan 1999). These models describe growth using relatively few parameters, which facilitates statistically rigorous means of fitting these models to data (Wang and Ellis 2005). However, there is little room to incorporate environmental effects into simple von Bertalanffy type models (except through seasonally dependent asymptotic size and growth rate), despite clear empirical evidence for the importance of environmental factors such as temperature (Wurtsbaugh and Davis 1977, Myrick and Cech 2000), food supply (Wurtsbaugh and Davis 1977), hydrodynamic and flow effects (Fausch 1984), and individual variation (McCarthy et al. 1992, Alvarez and Nicieza 2005). Furthermore, a statistically rigorous fit of a von Bertalanffy growth model to a given set of environmental conditions does not guarantee any degree of predictive power if environmental conditions change. Finally, the VBGE model is inherently individual-based but the parameters are difficult to interpret when applied to population means (Siegfried and Sanso 2006).

Second, parameter-rich bioenergetic models have been developed to allow the incorporation of a wealth of environmental effects and information (see Hanson et al. 1997 for a review). Such models have been used to predict responses to environmental changes on scales ranging from individuals to food webs and ecosystems (Ney 1993). Because these models are parameter rich, they are subject to bias when fitting and are difficult to present in a way that fully accounts for uncertainty across all parameters, and often require inadvisable cross-species borrowing of parameters (Hilborn and Mangel 1997, Trudel et al. 2004). In addition, despite their detail in accounting for various metabolic pathways, most bioenergetic models do a poor job coupling consumption and activity costs (Andersen and
Riis-Vestergaard 2004, Bajer 2004). Dynamic energy budget models (Kooijman 1986) may address this problem, but require additional hidden state variables that can never be compared against empirical observations, and thus require ad hoc choices of key parameters.

The goal of this paper is to use modeling to gain insights into the growth of age 0 *O. mykiss*. We use a modeling framework flexible enough to be extended to describe growth in the field while incorporating environmental effects on growth, mediated by changes in temperature and the difficulty of acquiring food. Our goal is to use a data-rich lab study to infer key parameters of an energy-balance model that strikes a compromise between the simplicity of VBGE models and the complexity of bioenergetic models. The model may be applied in the field for growth prediction, and therefore management.

An additional contribution of this work is to help define an ecologically significant difference between *O. mykiss* from different Distinct Population Segments (DPSs) or Evolutionarily Significant Units (ESUs), terms which have both been applied to distinct lineages worthy of separate consideration and protection under endangered species legislation.

According to Waples (1991), for purposes of the Endangered Species Act (ESA), a “species” is defined to include “any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature.” Federal agencies charged with carrying out the provisions of the ESA have struggled for over a decade to develop a consistent approach for interpreting the term “distinct population segment.” Of the 15 evolutionarily significant units (ESUs) of steelhead listed by NOAA Fisheries, 7 occur throughout California and are currently listed or candidates for listing under the Endangered Species Act (Busby *et al.* 1996). These include: Klamath Mountain Province; Northern California; Central California Coast (where our CCC fish were sourced); South-Central California Coast, Southern California; and Central Valley (where our NCCV fish were sourced).

The genetic distinctiveness of CCC fish has already been demonstrated (Pearse *et al.* 2009), but an important consideration in how and to what extent the different DPSs should be managed as distinct units is whether they differ in ecologically relevant traits.
As mentioned above, size and growth rate have numerous impacts on survival, demography, and life history, thus an understanding of differential growth in fish from different DPSs provides management insights. Common garden experiments (Beakes et al. in review) can show differential growth in a common environment, suggesting genetic differences in the capacity for growth, but a more mechanistic understanding of how growth responds to the environment is necessary for managing these DPSs in the face of expected environmental change (Lindley et al. 2007).

Lindley et al. (2007) state that regional-scale climate models for California are in broad agreement that temperatures in the future will warm significantly, total precipitation may decline, and snowfall will decline significantly. Melack et al. (1997) (as cited in Lindley et al. 2007) states that predicting the response of salmon to climate warming requires examination of the responses of all life history stages to the cumulative effects of likely environmental changes in the lakes, rivers and oceans inhabited by the fish. These fish may face a radically altered environment in the future, for example by 2100, mean summer temperatures in the Central Valley region may increase by 2-8°C, precipitation will likely shift to more rain and less snow, with significant declines in total precipitation possible, and hydrographs will likely change, especially in the southern Sierra Nevada mountains (Lindely et al. 2007). Warming may increase the activity and metabolic demand of predators, reducing the survival of juvenile salmonids (Vigg and Burley, 1991). For example, Peterson and Kitchell (2001) showed that on the Columbia River, pikeminnow predation on juvenile salmon during the warmest year was 96% higher than during the coldest. Marine and Cech (2004) demonstrate that as juvenile salmonids are put under temperature stress, they are more susceptible to predation. Reese and Harvey (2002) demonstrate that temperature can reduce competitive advantage of salmonids with invasive species. Jensen (1990) found that variable temperature seems to increase feeding and growth in brown trout over stable temperatures. However temperature may not be the only important consideration. For example, Sogard et al. (2009) hypothesized that summer growth of
O. mykiss in Central Coast streams is constrained more by consumption rates than by temperature, highlighting the importance of a modeling framework that can incorporate multiple factors simultaneously.

Because our model is a compromise among curve-fitting methods and detailed mass balance approaches; we call it a Compromise BioEnergetics Model (CBEM). We briefly describe the laboratory experiments and show how the CBEM, which is developed for field work, applies in the laboratory. We explain the numerical method that we use to predict mass from the CBEM and how we estimate the parameters in the model. We treat the parameters as data, characterized by stock of origin, and explain the likelihood methods we use to analyze the data. By treating the parameters of the CBEM as data, we conclude that the growth experiments provide overwhelming evidence for different rates of consumption according to stock of origin, although there is also considerable within-stock variation.

Methods

We combine features of VBGE models, bioenergetic models, and dynamic energy budgets. By modeling the effects of body size and temperature on anabolism using well established results from the literature, we incorporate some detailed insights from bioenergetic models into a modeling framework that, like VBGE models, has only a few parameters that must be fitted. Similar to dynamic energy budget models, but without resorting to hidden state variables, we incorporate an interaction between activity levels and consumption using fundamental insights from behavioral ecology (Clark and Mangel 2000, Mangel and Munch 2005).

To apply one modeling framework to both field and lab systems, we make a key assumption about the different contexts of modeling growth in the laboratory versus in the field. In the lab, food availability is finite, depletable, and a known variable. By contrast, in the field, measuring the amount of food available even in a single location is a Herculean task given tremendous short and long term variability (e.g., Rand et al. 1993). Further-
more, from the perspective of an individual fish, even if it is territorial, the amount of food
available in a given watershed is essentially infinite, with the real limit on consumption
being set by the costs of acquiring food, which include energy spent traveling and search-
ing, swimming costs of maintaining station in flow (Fausch 1984), conflict with inter- and
intraspecific competitors (Li and Brocksen 1977), and predation risk (Johnsson et al. 2004).

Overview of the Model

We model the rate of change in mass \((W(t))\) at time \(t\) in days as a balance of anabolic
factors (first term on the right hand side below) and catabolic factors (second term on the
right hand side)

\[
\frac{dW(t)}{dt} = fcφ(T(t))W(t)^{0.86} \frac{a(t)}{a(t) + κ(t)} - (1 + a(t))αe^{0.071T(t)}W(t)
\]

The terms in Equation 1 can be interpreted as follows: there is some maximum amount
of energy, \(fcφ(T(t))W(t)^{0.86}\), a fish can potentially take in during a day, depending on its
size and temperature on that day, \(T(t)\). How close the fish comes to the maximal intake
depends on its activity \(a\) compared to how difficult it is to acquire food \(κ(t)\). The basic
catabolic costs of the fish \(αe^{0.071T(t)}W(t)\) also depend on its size and temperature. When
the anabolic term exceeds the catabolic term, net growth occurs and in the reverse situation
the fish loses mass. The combination of either high or low values of \(c\) and \(α\) have different
implications. When \(α\) is high and \(c\) is low, we expect the fish to have very slow growth,
and to have very little response to changes in food availability. If \(α\) and \(c\) are both high,
growth is poor when food scarce, but responds well to an abundant supply of food. For a
low \(α\) with a low \(c\) growth is slow, but not as slow as for high \(α\), and fish respond poorly
to increased food. For low \(α\) and high \(c\) growth is fast and responds well to increased food
availability.

We assume that each day the fish maximizes its net rate of mass gain by optimizing
the right hand side of equation 1 with respect to \(a\). This is possible since increases in \(a\)
increase both consumption and total catabolic costs but at different rates (Mangel and Munch 2005).

The term \( a/(a + \kappa) \) is similar to the parameter \( P \) (fraction of maximum consumption achieved) in bioenergetic models (e.g. Railsback and Rose 1999), but \( a \) affects catabolic costs as well. The anabolic term describes the relative energy density of food versus fish tissue \( (f, \text{ discounted for conversion efficiency}) \), the daily maximum consumption \( (\text{weight of food}) \ c \) of a one gram fish under optimal temperature conditions, the allometric scaling of consumption with fish weight \( W(t)^{0.86} \), and a function \( \phi(T(t)) \) describing how maximum consumption scales with temperature. The basal catabolic term depends on a measure of weight-specific catabolic costs \( \alpha \) and the effect of temperature \( (e^{0.071T(t)}, \text{Brett and Groves 1979}) \). Both \( c \) and \( \alpha \) are allowed to vary across individuals.

We can apply this same modeling framework to the lab if we add a variable \( q(t) \) to denote the total amount of food available on day \( t \), and assume the cost of food acquisition in the laboratory is small. In this case, \( \kappa \) approaches 0, \( a \) will be small, and \( a/(a + \kappa) \) approximately 1. Growth in the laboratory can then be modeled as

\[
\frac{dW(t)}{dt} = f \min\{q(t), c\phi(T(t))W(t)^{0.86}\} - \alpha e^{0.071T(t)}W(t)
\]  

(2)

The first term on the right hand side indicates that a fish will eat the lesser of either all the food available to it, or the maximal amount it can consume based on its size and temperature. This model can readily be applied to the growth of fish in a lab environment where temperature and food supply are known, once we estimate the share of the total food is available to each individual fish.

**Overview of the Laboratory Growth experiments**

We measured growth in juveniles from two stocks of California steelhead (Beakes et al. in review). The first stock comes from a conservation hatchery (http://www.mbstp.org/index.html) on a small coastal stream, Scott Creek; we denote this stock as Central California Coast
(CCC). The second stock comes from a production hatchery, Coleman National Fish Hatchery on Battle Creek, on the Sacramento River (http://www.fws.gov/NCCV/); we denote this stock as Northern California Central Valley (NCCV). Our goal is to obtain estimates of the mean and variance in $c$ and $\alpha$ for fish from these two stocks by modeling growth under common, controlled conditions. This will allow further use of our model to describe growth in the field, with only $\kappa(t)$ needing to be fitted from field data (Satterthwaite et al 2010). Consequently, we can develop models explicitly linking $\kappa(t)$ to environmental factors such as flow and drift density, while also allowing projections of future fish growth under changing temperature or food availability. In the process of fitting this model to our lab data, we can also investigate evidence for local adaptation or effects of domestication when comparing fish from two stocks of origin.

Results of our experiments are fully described in Beakes et al. (2009) and summarized here. In 2006, we transferred NCCV steelhead from the hatchery to the laboratory during the second week of June (mean FL 4.31cm ± .17cm, where ± represent plus or minus 1 standard deviation), and CCC steelhead in the third week of May (mean FL 3.95cm ± .05cm). In 2007, we received both NCCV (mean FL 3.62cm ± 0.14cm) and CCC (mean FL 4.36cm ± 0.15cm) steelhead in the second week of May. We randomly assigned fish to cylindrical tanks (490 L) with 20 fish per tank with eight tanks of each stock. A continual flow of oxygenated fresh water supplied comparable water quality between tanks. Pieces of PVC pipe within each tank provided hiding habitat. Fish received ad libitum rations May and June to facilitate acclimation to the aquarium system.

Our objective was to provide fish with a diet supporting moderate but restricted growth except for an eight week period in which ad libitum ration was available. In July, all tanks were placed on moderate rations. The sixteen tanks were assigned to four treatment groups with two replicate tanks per treatment. During the treatment period, fish received eight continuous weeks of ad libitum rations. The treatment periods were August 1 - September 26, September 27 - November 22, November 23 - January 18, and January 19 - March 9
16. Outside of treatment periods we maintained fish on moderate rations distributed four
days a week and supplemented with *Spirulina* algae three days a week (See - Beakes *et
al* in review for more detailed description of how ration levels were defined and the ration
schedule). *Spirulina* did not add growth potential to low ration periods but was readily
consumed by fish and was used to maintain relative gut fullness and limit hunger based
aggression.

In 2006, we used relatively warm temperatures; in 2007 we chilled the water temper-
atures. The temperature changed over the course of the experiment to match natural
seasonal cycles. Photoperiod matched that at Santa Cruz, CA, USA. Gradual transitions
in light level mimicked dawn and dusk patterns. We initially marked all fish with elas-
tomer tags; at 6.5 cm all fish were injected with Passive Integrate Transponder (PIT) tags
to distinguish individuals. We checked tanks daily for mortalities and siphoned to remove
feces and other waste material. We measured weights approximately every 4 weeks for a
ten month period. In December the maximum number of fish/tank was reduced to fifteen
in order to maintain higher water quality. Final size measurements used for our growth
modeling included the period from June to March of each year. Excess fish were selected
at random and euthanized.

**Energy Balance in the Lab Experiments**

We characterize the growth experiment in the laboratory by modeling the mass $W_i(t)$ of
the $i^{th}$ fish in a tank as

$$\frac{dW_i(t)}{dt} = f \min\{q_i(t), c_i(T(t))W_i(t)^{0.86}\} - \alpha_i e^{0.071T(t)}W_i(t)$$

(3)
where $\alpha_i$ and $c_i$ are the catabolic and anabolic growth parameters for the $i^{th}$ fish, and

$$ q_i(t) = \frac{Q(t)}{\sum_{j=1}^{N_I} W_j(t)} W_i(t) $$

is the amount of food available to the $i^{th}$ fish. Behavioral interactions in salmonids, particularly in lab settings, typically result in dominance hierarchies that have large influences in individual feeding success (e.g., Metcalfe 1986, Harwood et al. 2003), but we do not model these factors here.

Equation (4) is similar to equation (??) but subscripted with $i$, for the $i$th fish in a tank and coupled with equation (??) to take into account the apportioning schemes. $Q(t)$ is the total food put into the tank at time $t$, and $N_I$ is the number of fish in the tank. We assume that $\alpha_i$, the catabolic cost parameter for fish $i$ and, $c_i$, the consumption parameter for fish $i$, are constant throughout the fish’s life in the tank and independent of behavior (e.g. aggression) and temperature (since the effects of temperature on both consumption and catabolism are modeled explicitly). Variation among fish in these parameters leads to variability in fish growth and it is the variation in these parameters that we wish to capture.

It is not possible to measure $\alpha_i$ and $c_i$ directly; we infer them from measuring fish masses $W_i(t)$ over time. With the directly measured growth histories of each individual, we can calculate the growth parameters $\alpha_i$ and $c_i$ for all fish in a tank. In particular, we find the $\alpha_i$ and $c_i$ that minimize a distance measure (defined below) between the observed mass of the fish and the solution of equations (??, ??). Our approach is essentially a non-linear least squares method for parameter estimation (Mangel 2006).

Over the course of our experiments, the observed mass of a single fish may vary between 2 to 3 orders of magnitude. Thus we choose the distance function to be a sum of squares
of relative errors (with the subscript indexing fish suppressed)

\[ d = \sum_t \frac{(\text{experimental mass}_t - \text{predicted mass}_t)^2}{(\text{experimental mass}_t)^2}. \]  

(5)

We use relative error to reduce the bias at large fish weights, and the summation is over all measured times. Although occasionally an individual trajectory has missing mass data, \( Q(t) \) and \( T(t) \) are known for all days

**Fitting Data**

To minimize the number of parameters to be estimated, we took several parameters from the literature. We modeled \( \phi(T(t)) \), the temperature-dependence of maximal daily consumption, using the algorithm first described by Thornton and Lessem (1978), and parameterized for California steelhead by Railsback and Rose (1999). This parameterization is more suitable than those used by Rand et al. (1993) or Sullivan et al. (2000) because it allows for the most consumption at higher temperatures, consistent with observed rapid growth in warm coastal lagoons (Hayes et al. 2008) and Central Valley rivers (Satterthwaite et al. 2009b). We assume that maximal consumption scales as \( W^{0.86} \) (Moses et al. 2008, Jobling 1994, p. 100). We assume that catabolism scales linearly with weight (Elsington et al. 2001) and with \( e^{0.071T(t)} \) based on Brett and Groves (1979). We calculated \( f \), the relative density of food versus fish tissue, as 2.148 based on nutritional information provided on the Silver Cup feed used in lab experiments and energy densities of fish tissues reported by Hartman and Brandt (1995), assuming that about 30% of ingested energy is unavailable for growth or respiration (Brett and Groves 1979).

To solve equations (??, ??) we use a 4th order Runge-Kutta scheme (Press et al 2007) with a daily time step, and interpolate \( W(t) \) with a cubic spline for days on which it was not measured. We solve equation (??) over a grid of parameter values \( \alpha_{\text{grid}} = [\alpha_1, \ldots, \alpha_m, \ldots, \alpha_M] \) and \( c_{\text{grid}} = [c_1, \ldots, c_n, \ldots, c_N] \) and obtain the values \( (\alpha_m^*, c_n^*) \) that
minimize the distance from equation (5).

We denote a solution of equation (5) with \((\alpha_m, c_n)\) by \(W_i^{(\alpha_m, c_n)}(t)\) and the measured values of fish masses be \(W_\varepsilon^i(t)\). The distance between \(W_\varepsilon^i(t)\) and \(W_i^{(\alpha_m, c_n)}(t)\) is the sum of relative deviations between the observed and predicted growth at the observation times

\[
d(\alpha_m, c_n, i) = \sum_{\tau = \text{observed days}} \frac{(W_i^{(\alpha_m, c_n)}(\tau) - W_\varepsilon^i(\tau))^2}{(W_\varepsilon^i(\tau))^2}
\]  

(6)

Once we have solved equations (5, 6) with \((\alpha_m, c_n)\) for all \((m, n)\), \(1 \leq m \leq M_\alpha, 1 \leq n \leq N_c\) for the \(i\)th fish, we then find the pair \((\alpha^*_m, c^*_n)\) such that,

\[
d(i) = d(\alpha^*_m, c^*_n, i) = \min_{\alpha_m, c_n} \{d(\alpha_m, c_n, i)\}
\]  

(7)

We reserve \(i\) to indicate fish, while \(m\) and \(n\) indicate parameter values in the grid. For each fish, set a minimizing pair of parameter values \(\alpha_i = \alpha^*_m, c_i = c^*_n\).

At the conclusion of this process, we have estimates \(\alpha_i, c_i\) for each fish. To estimate the quality of the fit for fish \(i\) we compute the set of relative errors,

\[
RE(i) = \left\{ \frac{(W_i^{(\alpha^*_m, c^*_n)}(\tau) - W_\varepsilon^i(\tau))}{(W_\varepsilon^i(\tau))} \right\} \bigg|_{\tau = \text{observed days}}
\]  

(8)

and choose the maximum of these, which we denote by MRE\((i)\). The maximum relative error is used to compute the acceptability of a trajectory for further analysis. To summarize, we use the following procedure:

1. We interpolate the mass data for all time intervals to estimate \(q_i(t)\).
2. We compute the mass trajectory for every fish based on its starting size and these estimates of \(q_i(t)\).
3. We compute the relative distance for every day for every fish.
4. We compute the maximum relative distance for every fish.
5. We consider that a trajectory is acceptable for further analysis if it has positive $\alpha^*_m$ and $c^*_n$, more than 3 measured time points and a MRE(i) less than 1/3.

A Gaussian Likelihood for $\alpha_i, c_i$ and Model Selection

Our next step is to treat $\alpha^*_m$ and $c^*_n$ as data, for which we suppress the indices $m$ and $n$ and thus refer to $\alpha_i$ and $c_i$. We assume that these are independent random variables, for $i = 1, 2, ... N_f$, the total number of fish that met the criterion described in point 5 above, and are each drawn from a bivariate normal distribution. With the hypothesis that there is no difference between the CCC and NCCV fish, this density is

$$f(\alpha_i, c_i | \mu_\alpha, \mu_c, \sigma_\alpha, \sigma_c, \rho) = \frac{1}{2\pi\sigma_\alpha\sigma_c\sqrt{1-\rho^2}} \exp\left( -\frac{1}{2(1-\rho^2)} \left( \frac{(\alpha_i - \mu_\alpha)^2}{\sigma_\alpha^2} + \frac{(c_i - \mu_c)^2}{\sigma_c^2} - 2\frac{(\alpha_i - \mu_\alpha)(c_i - \mu_c)}{\sigma_\alpha\sigma_c} \right) \right).$$

(9)

The likelihood of the data (denoted by $\overrightarrow{\alpha} = (\alpha_1, \alpha_2, ..., \alpha_{N_f})$ and $\overrightarrow{c} = (c_1, c_2, ..., c_{N_f})$) under this assumption is

$$L(\overrightarrow{\alpha}, \overrightarrow{c} | \mu_\alpha, \mu_c, \sigma_\alpha, \sigma_c, \rho) = \prod_{i=1}^{N_f} f(\alpha_i, c_i | \mu_\alpha, \mu_c, \sigma_\alpha, \sigma_c, \rho)$$

(10)

We also consider an alternative model in which the NCCV and CCC fish each have their own means and correlations. We thus let $N_{fC}$ denote the number of NCCV fish and $N_{fS}$ the number of CCC fish. Our model now involves a parameter vector

$$\overrightarrow{\theta} = (\mu_{\alphaC}, \mu_{cC}, \sigma_{\alphaC}, \sigma_{cC}, \rhoC, \mu_{\alphaS}, \mu_{cS}, \sigma_{\alphaS}, \sigma_{cS}, \rhoS)$$

(11)

and equation (10) is replaced by
\[ L(\mathbf{\alpha}, \mathbf{c} | \mathbf{\theta}) = \prod_{i=1}^{N_{1C}} f(\alpha_i, c_i | \mu_{\alpha C}, \mu_{c C}, \sigma_{\alpha C}, \sigma_{c C}, \rho C) \cdot \prod_{i=1}^{N_{1S}} f(\alpha_i, c_i | \mu_{\alpha S}, \mu_{c S}, \sigma_{\alpha S}, \sigma_{c S}, \rho S) \quad (12) \]

We then choose the values of the parameters that maximize the likelihood. To select the better model using the maximum likelihood values, we use the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) (Hilborn and Mangel 1997, Burnham and Anderson 1998, Hurvich and Tsai 1989).

Results

We used a grid for which \(0 \leq \alpha \leq 0.11\) and \(c\) and \(0 \leq c \leq 0.12\). We screened 550 trajectories and 318 met our criteria for acceptance. There is considerable variation in the growth of individual fish in the tanks (Figure 1) and there are cases in which the CBEM model fits poorly (an example is shown in Figure 2).

Our main results are shown in Figures (3A and 3B). Taking both strains together, our estimates of \(c\) for individual fish ranged from \([7 \times 10^{-3} \text{ to } 0.105]\) and \(\alpha\) ranged from \(2 \times 10^{-4} \text{ to } 1 \times 10^{-2}\). There was a tendency for fish with higher estimates for \(\alpha\) to have higher estimates for \(c\) as well, suggesting a correlation between metabolic rate and maximal consumption capacity. Parameter estimates tended to separate out by strain, particularly due to higher values of \(c\) for NCCV fish (Figure 3B). In the left hand panel we show the data points and the 95 % contour associated with the likelihood in equation 10. In panel (B) we show the data, separated by origin of stock for the likelihood associated with equation (12) (i.e., allowing the mean of \(c\) and \(\alpha\) to vary between strains). The values of AIC and BIC for equation (10) (i.e., ignoring possible strain effects) are -5005 and -4985 respectively and for equation (12) they are -5068 and -5031 respectively. These very large differences in AIC and BIC provide clear support for the model in which the stock origins are separated.
For all fish taken together, the mean value of \( c \) is 0.0418±0.149 and the mean value of \( \alpha \) is 0.0042 ± 0.0018, with a correlation of 0.54. For just NCCV fish, \( c = 0.044 \pm 0.015 \) and \( \alpha = 0.004 \pm 0.0015 \) with a correlation of 0.58. For just CCC fish, \( c = 0.037 \pm 0.014 \) and \( \alpha = 0.0044 \pm 0.0021 \) with a correlation of 0.64. Thus the two strains appear similar in metabolic costs (\( \alpha \)) once the effects of size and temperature are accounted for, but it appears that NCCV fish have a higher maximum food consumption ability.

**Discussion**

Our quantitative estimates of \( c \) and \( \alpha \) can be compared to other, independently derived estimates of similar parameters in other bioenergetic models. The oxygen consumption reported by Rand *et al.* (1993) can be converted (Satterthwaite *et al.* 2010) into an estimate of 0.00607 for \( \alpha \) in the units used by our model, compared to the global mean of 0.00418 estimated here. The consumption coefficient \( c \) is sensitive to the type of food provided and the allometry of consumption assumed (Rand *et al.* 1993), but if we assume consumption of energy (as opposed to wet weight of food) is what is constrained, the product of \( f \cdot c = 2.148 \cdot 0.418 = 0.898 \) for the grand mean is comparable to the estimate for \( f \cdot c = 0.297 \cdot 0.628 = 0.187 \) as described in Satterthwate *et al.* (2010). Thus our estimates for \( c \) and \( \alpha \) from this model are within an order of magnitude of independently derived estimates.

There are at least four reasons for a fish being excluded from our analysis. First, we did not include fish for which we had three or fewer data points (this excluded 90 of the original 640 fish in our experiments). Second, we did not allow for cannibalism (which we observed – see Beakes *et al.* 2009) in the growth model. Cannibalism will cause one trajectory to suddenly disappear and may cause an abrupt increase in the other trajectory; neither outcome can be captured by equation (3) and such trajectories was excluded. Third, we assume that the individuals could get food without an expenditure of energy (compare equations (1) and (2)). This enormously simplifies the estimation problem because otherwise we would have to estimate \( \kappa(t) \) in equation (1) for each fish.
However even in a tank fish must expend some energy to obtain food and the model may have underestimated that energy for some fish. Fourth, these fish have surely evolved to deal with a starvation risk/predation risk trade-off (*sensu* Mangel and Clark 1988, Clark and Mangel 2000). It is well known that individual animals express variation (‘personality traits’) in dealing with such trade-offs and growth of some subordinate individuals may have been suppressed by interactions with dominant individuals (Bell and Sih, 2007, Frost *et al* 2007, Stamps 2007, Dyer *et al* 2008). Our modeling framework does not account for individual variation in risk avoidance; doing so requires a much more detailed behavioral model.

Nevertheless, we have shown that a compromise between purely descriptive (von Bertalanffy) models and parameter rich models of growth can adequately describe a large subset of our data and can lead to new and novel insights into the life histories and growth patterns of these fish.

Because a model that allowed mean values of c and $\alpha$ to vary between strains fit much better than a model assuming no differences between strains, we can conclude that stock origin has a significant effect on growth capacity in these fish, suggesting genetic differences. These differences may reflect local adaptation to very different growing conditions in the two systems (Beakes *et al* in review), although it is important to note that hatchery practices (NCCV focused on production, CCC focused on conservation) differ along with the riparian habitats (warm and food rich for NCCV, less warm and lower food availability for CCC) so it is unclear whether this reflects local adaptation to different river environments or to different hatcheries. In addition, we cannot rule out genetic drift rather than divergent selection as the cause of this difference (Adkison 1995). While estimates of $\alpha$ were similar between strains, consumption ability was higher for NCCV fish, and among individuals as $\alpha$ increased there was a greater increase in c for NCCV fish as compared to CCC fish. This difference in consumption capacity is likely to have significant implications for the response of these ecologically distinct population segments to a changing environment. For
example, if flow alterations lead to food availability changing to become more flashy with
large pulses separated by periods with little if any food. Joe may be able to provide
cites suggesting this possibility], NCCV fish will likely be better equipped to take
maximal advantage of high food pulses and thus better able to ride out the lulls between
pulses. NCCV fish may also be better equipped to deal with the increases in metabolic
rates expected if temperatures increase (e.g. the Catabolic Cost component of equation
(3)), provided that there is enough food available for NCCV fish to utilize their greater
feeding capacity. At the same time, the low consumption of CCC fish may reflect behavioral
patterns where the fish are choosing to shelter, minimizing predation risk, and as a result
feed less. Although this difference may be a result of increased domestication in the NCCV
fish due to differing hatchery practices and not a difference displayed by wild fish as well, if
these DPSs do differ in their predation avoidance behavior the CCC fish may be better able
to deal with increased predation risk due to introduced predators or increased temperatures
that boost activity and metabolic needs of piscivorous fish. Joe may have some
cites] (Vigg and Burley 1991). Because $f$ and $c$ are multiplied together and we assumed
constant $f$, it may be that the apparent higher food consumption ability we inferred for
NCCV fish actually reflects more efficient conversion of the same amount of food into fish
tissue. However, behavioral observations (NCCV fish were aggressive feeders striking at
the surface a soon as food was added, CCC fish tended to remain in their PVC shelters)
and the amount of uneaten food observed on the bottom of the tanks (higher for CCC
fish) suggest that consumption rather than conversion efficiency is the main driver of this
difference.

The growth model we use here is a key component of our state dependent life history
theory (Satterthwaite et al. 2009, 2010), which relates water policy to growth, survival
and smolting of steelhead. The results of our common laboratory study show the potential
for substantial differences both between stocks and among individuals within a stock in
the capacity for growth. Tyler and Bolduc (2008) found similar individual variation in
young-of-year rainbow trout. These intrinsic differences in growth capacity interact with responses to environmental differences experienced by each local population. Thus, an understanding of local differences in the genetics, physiology, and foraging behavior of fish is important in site- or population-specific predictions of how growth will respond to changes in the environment. The capacity to predict growth responses is itself an essential component in successfully managing the environment to encourage the recovery of steelhead populations and the maintenance of anadromy, see Satterthwaite et al (2009, 2010). Thus our model, appropriately parameterized from data for the DPS under consideration, can be used to predict the context-specific effects of management on growth rates in different DPSs. This will allow predicting other size-related traits of management interest, such as survival (Carlson et al 2008), and life history (Satterthwaite et al 2010), which may feed into demographic models and projections of DPS viability.

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Captions for Figures

Figure 1. Mass trajectories from fish measured approximately every four weeks in tank 10 (CCC fish) in the 2006 lab experiment, illustrating the large variation in growth among individuals in a single tank.

Figure 2. Examples of good (panel A) and poor (panel B) fits of the CBEM for individual growth trajectories. Panel (A) has a $d = 0.009$ and was included for further analysis. Panel (B) has $d = 0.39$ and was rejected.

Figure 3. Comparison of the distribution of $\alpha$ and $c$ assuming that all of the lab data come from a single stock or from two different stocks. In panel (A) we show the data points and the 95% contour (ellipse) associated with the likelihood based on a single growth model for both stocks combined. In panel (B) shows the data and contours separated by stock (circles = Scott Creek, crosses = Coleman Hatchery). As explained in the text, the statistical evidence greatly supports the notion of separate stocks.
Simon et al, Figure 2

**A**

*fish 10, Tank 3, year 2007, d=0.009*

**B**

*fish 2, Tank 3, year 2006, d=0.39*