

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

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## 17 **Abstract**

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

## 34 **Introduction**

35 Growth of juvenile salmonids has many important consequences for individual fitness and  
36 the resilience of populations to disturbance (Quinn 2005, Mangel 2006). In general, faster  
37 growth and larger size typically lead to higher survival in freshwater (but see Carlson *et al.*  
38 2008) and larger size at smolting leads to higher marine survival (McGurk 1996). For adult  
39 females larger size leads to higher fecundity (Allen and Sanger 1960). In addition, for highly  
40 plastic species such as the steelhead trout, growth rates may affect the life history pathways  
41 followed by individual fish (Satterthwaite *et al.* 2010), with implications for life history

42 diversity and overall population dynamics. Thus, understanding and predicting juvenile  
43 growth rates is an important tool in preserving the life history diversity and population  
44 health of steelhead trout in the face of environmental change.

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

60 Second, parameter-rich bioenergetic models have been developed to allow the incorpor-  
61 ation of a wealth of environmental effects and information (see Hanson *et al.* 1997 for a  
62 review). Such models have been used to predict responses to environmental changes on  
63 scales ranging from individuals to food webs and ecosystems (Ney 1993). Because these  
64 models are parameter rich, they are subject to bias when fitting and are difficult to present  
65 in a way that fully accounts for uncertainty across all parameters, and often require in-  
66 advisable cross-species borrowing of parameters (Hilborn and Mangel 1997, Trudel *et al.*  
67 2004). In addition, despite their detail in accounting for various metabolic pathways, most  
68 bioenergetic models do a poor job coupling consumption and activity costs (Andersen and

69 Riis-Vestergaard 2004, Bajer 2004). Dynamic energy budget models (Kooijman 1986) may  
70 address this problem, but require additional hidden state variables that can never be com-  
71 pared against empirical observations, and thus require *ad hoc* choices of key parameters.

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

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

83 According to Waples (1991), for purposes of the Endangered Species Act (ESA), a  
84 “species” is defined to include “any distinct population segment of any species of vertebrate  
85 fish or wildlife which interbreeds when mature.” Federal agencies charged with carrying out  
86 the provisions of the ESA have struggled for over a decade to develop a consistent approach  
87 for interpreting the term “distinct population segment.” Of the 15 evolutionarily significant  
88 units (ESUs) of steelhead listed by NOAA Fisheries, 7 occur throughout California and are  
89 currently listed or candidates for listing under the Endangered Species Act (Busby *et al.*  
90 1996). These include: Klamath Mountain Province; Northern California; Central Califor-  
91 nia Coast (where our CCC fish were sourced); South-Central California Coast, Southern  
92 California; and Central Valley (where our NCCV fish were sourced).

93 The genetic distinctiveness of CCC fish has already been demonstrated (Pearse *et al.*  
94 2009), but an important consideration in how and to what extent the different DPSs  
95 should be managed as distinct units is whether they differ in ecologically relevant traits.

96 As mentioned above, size and growth rate have numerous impacts on survival, demography,  
97 and life history, thus an understanding of differential growth in fish from different DPSs  
98 provides management insights. Common garden experiments (Beakes *et al.* in review) can  
99 show differential growth in a common environment, suggesting genetic differences in the  
100 capacity for growth, but a more mechanistic understanding of how growth responds to the  
101 environment is necessary for managing these DPSs in the face of expected environmental  
102 change (Lindley *et al.* 2007).

103 Lindley *et al.* (2007) state that regional-scale climate models for California are in broad  
104 agreement that temperatures in the future will warm significantly, total precipitation may  
105 decline, and snowfall will decline significantly. Melack *et al.* (1997) (as cited in Lindley  
106 *et al.* 2007) states that predicting the response of salmon to climate warming requires  
107 examination of the responses of all life history stages to the cumulative effects of likely  
108 environmental changes in the lakes, rivers and oceans inhabited by the fish. These fish  
109 may face a radically altered environment in the future, for example by 2100, mean summer  
110 temperatures in the Central Valley region may increase by 2-8°C, precipitation will likely  
111 shift to more rain and less snow, with significant declines in total precipitation possible,  
112 and hydrographs will likely change, especially in the southern Sierra Nevada mountains  
113 (Lindley *et al.* 2007). Warming may increase the activity and metabolic demand of preda-  
114 tors, reducing the survival of juvenile salmonids (Vigg and Burley, 1991). For example,  
115 Peterson and Kitchell (2001) showed that on the Columbia River, pikeminnow predation  
116 on juvenile salmon during the warmest year was 96% higher than during the coldest. Ma-  
117 rine and Cech (2004) demonstrate that as juvenile salmonids are put under temperature  
118 stress, they are more susceptible to predation. Reese and Harvey (2002) demonstrate that  
119 temperature can reduce competitive advantage of salmonids with invasive species. Jensen  
120 (1990) found that variable temperature seems to increase feeding and growth in brown  
121 trout over stable temperatures. However temperature may not be the only important  
122 consideration. For example, Sogard *et al.* (2009) hypothesized that summer growth of

123 *O. mykiss* in Central Coast streams is constrained more by consumption rates than by  
124 temperature, highlighting the importance of a modeling framework that can incorporate  
125 multiple factors simultaneously.

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

## 135 **Methods**

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

144 To apply one modeling framework to both field and lab systems, we make a key as-  
145 sumption about the different contexts of modeling growth in the laboratory versus in the  
146 field. In the lab, food availability is finite, depletable, and a known variable. By contrast,  
147 in the field, measuring the amount of food available even in a single location is a Herculean  
148 task given tremendous short and long term variability (e.g., Rand *et al.* 1993). Further-

149 more, from the perspective of an individual fish, even if it is territorial, the amount of food  
 150 available in a given watershed is essentially infinite, with the real limit on consumption  
 151 being set by the costs of acquiring food, which include energy spent traveling and search-  
 152 ing, swimming costs of maintaining station in flow (Fausch 1984), conflict with inter- and  
 153 intraspecific competitors (Li and Brocksen 1977), and predation risk (Johnsson *et al.* 2004).

## 154 Overview of the Model

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

$$\frac{dW(t)}{dt} = fc\phi(T(t))W(t)^{0.86} \frac{a(t)}{a(t) + \kappa(t)} - (1 + a(t))\alpha e^{0.071T(t)}W(t) \quad (1)$$

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

171 We assume that each day the fish maximizes its net rate of mass gain by optimizing  
 172 the right hand side of equation 1 with respect to  $a$ . This is possible since increases in  $a$

173 increase both consumption and total catabolic costs but at different rates (Mangel and  
174 Munch 2005).

175 The term  $a/(a + \kappa)$  is similar to the parameter  $P$  (fraction of maximum consumption  
176 achieved) in bioenergetic models (e.g. Railsback and Rose 1999), but  $a$  affects catabolic  
177 costs as well. The anabolic term describes the relative energy density of food versus fish  
178 tissue ( $f$ , discounted for conversion efficiency), the daily maximum consumption (weight of  
179 food)  $c$  of a one gram fish under optimal temperature conditions, the allometric scaling of  
180 consumption with fish weight  $W(t)^{0.86}$ , and a function  $\phi(T(t))$  describing how maximum  
181 consumption scales with temperature. The basal catabolic term depends on a measure of  
182 weight-specific catabolic costs  $\alpha$  and the effect of temperature ( $e^{0.071T(t)}$ , Brett and Groves  
183 1979). Both  $c$  and  $\alpha$  are allowed to vary across individuals.

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

$$\frac{dW(t)}{dt} = f \min\{q(t), c\phi(T(t))W(t)^{0.86}\} - \alpha e^{0.071T(t)}W(t) \quad (2)$$

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

## 193 **Overview of the Laboratory Growth experiments**

194 We measured growth in juveniles from two stocks of California steelhead (Beakes *et al.* in  
195 review). The first stock comes from a conservation hatchery (<http://www.mbstp.org/index.html>)  
196 on a small coastal stream, Scott Creek; we denote this stock as Central California Coast



197 (CCC). The second stock comes from a production hatchery, Coleman National Fish Hatch-  
198 ery on Battle Creek, on the Sacramento River (<http://www.fws.gov/NCCV/>); we denote  
199 this stock as Northern California Central Valley (NCCV). Our goal is to obtain estimates  
200 of the mean and variance in  $c$  and  $\alpha$  for fish from these two stocks by modeling growth  
201 under common, controlled conditions. This will allow further use of our model to describe  
202 growth in the field, with only  $\kappa(t)$  needing to be fitted from field data (Satterthwaite *et*  
203 *al* 2010). Consequently, we can develop models explicitly linking  $\kappa(t)$  to environmental  
204 factors such as flow and drift density, while also allowing projections of future fish growth  
205 under changing temperature or food availability. In the process of fitting this model to our  
206 lab data, we can also investigate evidence for local adaptation or effects of domestication  
207 when comparing fish from two stocks of origin.

208 Results of our experiments are fully described in Beakes *et al.* (2009) and summarized  
209 here. In 2006, we transferred NCCV steelhead from the hatchery to the laboratory during  
210 the second week of June (mean FL 4.31cm  $\pm$  .17cm, where  $\pm$  represent plus or minus 1  
211 standard deviation), and CCC steelhead in the third week of May (mean FL 3.95cm  $\pm$   
212 .05cm). In 2007, we received both NCCV (mean FL 3.62cm  $\pm$  0.14cm) and CCC (mean  
213 FL 4.36cm  $\pm$  0.15cm) steelhead in the second week of May. We randomly assigned fish to  
214 cylindrical tanks (490 L) with 20 fish per tank with eight tanks of each stock. A continual  
215 flow of oxygenated fresh water supplied comparable water quality between tanks. Pieces  
216 of PVC pipe within each tank provided hiding habitat. Fish received *ad libitum* rations  
217 May and June to facilitate acclimation to the aquarium system.

218 Our objective was to provide fish with a diet supporting moderate but restricted growth  
219 except for an eight week period in which *ad libitum* ration was available. In July, all tanks  
220 were placed on moderate rations. The sixteen tanks were assigned to four treatment groups  
221 with two replicate tanks per treatment. During the treatment period, fish received eight  
222 continuous weeks of *ad libitum* rations. The treatment periods were August 1 - September  
223 26, September 27 - November 22, November 23 - January 18, and January 19 - March

224 16. Outside of treatment periods we maintained fish on moderate rations distributed four  
 225 days a week and supplemented with *Spirulina* algae three days a week (See - Beakes *et*  
 226 *al* in review for more detailed description of how ration levels were defined and the ration  
 227 schedule). *Spirulina* did not add growth potential to low ration periods but was readily  
 228 consumed by fish and was used to maintain relative gut fullness and limit hunger based  
 229 aggression.

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

## 241 Energy Balance in the Lab Experiments

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

$$\frac{dW_i(t)}{dt} = \underbrace{f \min\{q_i(t), c_i \phi(T(t)) W_i(t)^{0.86}\}}_{\text{Energy Intake}} - \underbrace{\alpha_i e^{0.071T(t)} W_i(t)}_{\text{Catabolic Cost}} \quad (3)$$

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

$$q_i(t) = \underbrace{Q(t)}_{\text{food available}} \underbrace{\frac{W_i(t)}{\sum_{j=1}^{N_I} W_j(t)}}_{\text{portion for } i\text{th fish}} \quad (4)$$

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

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

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

264 Over the course of our experiments, the observed mass of a single fish may vary between  
 265 2 to 3 orders of magnitude. Thus we choose the distance function to be a sum of squares

266 of relative errors (with the subscript indexing fish suppressed)

$$d = \sum_t \frac{((\textit{experimental mass})_t - (\textit{predicted mass})_t)^2}{(\textit{experimental mass})_t^2}. \quad (5)$$

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

## 270 **Fitting Data**

271 To minimize the number of parameters to be estimated, we took several parameters from  
272 the literature. We modeled  $\phi(T(t))$ , the temperature-dependence of maximal daily con-  
273 sumption, using the algorithm first described by Thornton and Lessem (1978), and param-  
274 eterized for California steelhead by Railsback and Rose (1999). This parameterization is  
275 more suitable than those used by Rand *et al.* (1993) or Sullivan *et al.* (2000) because it  
276 allows for the most consumption at higher temperatures, consistent with observed rapid  
277 growth in warm coastal lagoons (Hayes *et al.* 2008) and Central Valley rivers (Satterth-  
278 waite *et al.* 2009b). We assume that maximal consumption scales as  $W^{0.86}$  (Moses *et al.*  
279 2008, Jobling 1994, p. 100). We assume that catabolism scales linearly with weight (Es-  
280 sington *et al.* 2001) and with  $e^{0.071T(t)}$  based on Brett and Groves (1979). We calculated  
281  $f$ , the relative density of food versus fish tissue, as 2.148 based on nutritional information  
282 provided on the Silver Cup feed used in lab experiments and energy densities of fish tissues  
283 reported by Hartman and Brandt (1995), assuming that about 30% of ingested energy is  
284 unavailable for growth or respiration (Brett and Groves 1979).

285 To solve equations (??, ??) we use a 4th order Runge-Kutta scheme (Press *et al* 2007)  
286 with a daily time step, and interpolate  $W(t)$  with a cubic spline for days on which it  
287 was not measured. We solve equation (??) over a grid of parameter values  $\alpha_{grid} =$   
288  $[\alpha_1, \dots, \alpha_m, \dots, \alpha_{M_\alpha}]$  and  $c_{grid} = [c_1, \dots, c_n, \dots, c_{N_c}]$  and obtain the values  $(\alpha_m^*, c_n^*)$  that

289 minimize the distance from equation (5).

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

$$d(\alpha_m, c_n, i) = \sum_{\tau=\text{observed days}} \frac{(W_i^{(\alpha_m, c_n)}(\tau) - W_i^e(\tau))^2}{(W_i^e(\tau))^2} \quad (6)$$

293 Once we have solved equations (??,??) with  $(\alpha_m, c_n)$  for all  $(m, n)$ ,  $1 \leq m \leq M_\alpha$ ,  $1 \leq n \leq$   
 294  $N_c$  for the  $i$ th fish, we then find the pair  $(\alpha_{m_i}^*, c_{n_i}^*)$  such that,

$$d(i) = d(\alpha_{m_i}^*, c_{n_i}^*, i) = \min_{\alpha_m, c_n} \{d(\alpha_m, c_n, i)\} \quad (7)$$

295 We reserve  $i$  to indicate fish, while  $m$  and  $n$  indicate parameter values in the grid. For  
 296 each fish, set a minimizing pair of parameter values  $\alpha_i = \alpha_{m_i}^*$  and  $c_i = c_{n_i}^*$ .

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

$$RE(i) = \left\{ \left| \frac{(W_i^{(\alpha_{m_i}^*, c_{n_i}^*)}(\tau) - W_i^e(\tau))}{(W_i^e(\tau))} \right| \middle| \tau = \text{observed days} \right\} \quad (8)$$

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

- 302 1. We interpolate the mass data for all time intervals to estimate  $q_i(t)$ .
- 303 2. We compute the mass trajectory for every fish based on its starting size and these  
 304 estimates of  $q_i(t)$ .
- 305 3. We compute the relative distance for every day for every fish.
- 306 4. We compute the maximum relative distance for every fish.

307 5. We consider that a trajectory is acceptable for further analysis if it has positive  $\alpha_{m_i}^*$   
 308 and  $c_{n_i}^*$ , more than 3 measured time points and a MRE(i) less than 1/3.

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

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

$$f(\alpha_i, c_i | \mu_\alpha, \mu_c, \sigma_\alpha, \sigma_c, \rho) = \frac{1}{2\pi\sigma_\alpha\sigma_c\sqrt{1-\rho^2}} \exp\left(-\frac{1}{2(1-\rho^2)}\left(\frac{(\alpha_i - \mu_\alpha)^2}{\sigma_\alpha^2} - \frac{2(\alpha_i - \mu_\alpha)(c_i - \mu_c)}{\sigma_\alpha\sigma_c} + \frac{(c_i - \mu_c)^2}{\sigma_c^2}\right)\right). \quad (9)$$

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

$$L(\vec{\alpha}, \vec{c} | \mu_\alpha, \mu_c, \sigma_\alpha, \sigma_c, \rho) = \prod_{i=1}^{N_f} f(\alpha_i, c_i | \mu_\alpha, \mu_c, \sigma_\alpha, \sigma_c, \rho) \quad (10)$$

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

$$\vec{\theta} = (\mu_{\alpha C}, \mu_{cC}, \sigma_{\alpha C}, \sigma_{cC}, \rho_C, \mu_{\alpha S}, \mu_{cS}, \sigma_{\alpha S}, \sigma_{cS}, \rho_S) \quad (11)$$

320 and equation (10) is replaced by

$$L(\vec{\alpha}, \vec{c} | \vec{\theta}) = \prod_{i=1}^{N_{fC}} f(\alpha_i, c_i | \mu_{\alpha C}, \mu_{cC}, \sigma_{\alpha C}, \sigma_{cC}, \rho_C) \cdot \prod_{i=1}^{N_{fS}} f(\alpha_i, c_i | \mu_{\alpha S}, \mu_{cS}, \sigma_{\alpha S}, \sigma_{cS}, \rho_S) \quad (12)$$

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

## 325 Results

326 We used a grid for which  $0 \leq \alpha \leq .011$  and  $c$  and  $0 \leq c \leq .12$ . We screened 550 trajectories  
 327 and 318 met our criteria for acceptance. There is considerable variation in the growth of  
 328 individual fish in the tanks (Figure 1) and there are cases in which the CBEM model fits  
 329 poorly (an example is shown in (Figure 2)).

330 Our main results are shown in Figures (3A and 3B). Taking both strains together,  
 331 our estimates of  $c$  for individual fish ranged from  $[7 \times 10^{-3}$  to  $0.105]$  and  $\alpha$  ranged from  
 332  $2 \times 10^{-4}$  to  $1 \times 10^{-2}$ . There was a tendency for fish with higher estimates for  $\alpha$  to have  
 333 higher estimates for  $c$  as well, suggesting a correlation between metabolic rate and maximal  
 334 consumption capacity. Parameter estimates tended to separate out by strain, particularly  
 335 due to higher values of  $c$  for NCCV fish (Figure 3B). In the left hand panel we show  
 336 the data points and the 95 % contour associated with the likelihood in equation 10. In  
 337 panel (B) we show the data, separated by origin of stock for the likelihood associated with  
 338 equation (12) (i.e., allowing the mean of  $c$  and  $\alpha$  to vary between strains). The values of  
 339 AIC and BIC for equation (10) (i.e., ignoring possible strain effects) are -5005 and -4985  
 340 respectively and for equation (12) they are -5068 and -5031 respectively. These very large  
 341 differences in AIC and BIC provide clear support for the model in which the stock origins  
 342 are separated.

343 For all fish taken together, the mean value of  $c$  is  $0.0418 \pm 0.149$  and the mean value of  
344  $\alpha$  is  $0.0042 \pm 0.0018$ , with a correlation of 0.54. For just NCCV fish,  $c = 0.044 \pm 0.015$   
345 and  $\alpha = 0.004 \pm 0.0015$  with a correlation of 0.58. For just CCC fish,  $c = 0.037 \pm 0.014$   
346 and  $\alpha = 0.0044 \pm 0.0021$  with a correlation of 0.64. Thus the two strains appear similar  
347 in metabolic costs ( $\alpha$ ) once the effects of size and temperature are accounted for, but it  
348 appears that NCCV fish have a higher maximum food consumption ability.

## 349 Discussion

350 Our quantitative estimates of  $c$  and  $\alpha$  can be compared to other, independently derived  
351 estimates of similar parameters in other bioenergetic models. The oxygen consumption  
352 reported by Rand *et al.* (1993) can be converted (Satterthwaite *et al* 2010) into an estimate  
353 of 0.00607 for  $\alpha$  in the units used by our model, compared to the global mean of 0.00418  
354 estimated here. The consumption coefficient  $c$  is sensitive to the type of food provided and  
355 the allometry of consumption assumed (Rand *et al* 1993), but if we assume consumption  
356 of energy (as opposed to wet weight of food) is what is constrained, the product of  $f \cdot c =$   
357  $2.148 \cdot 0.418 = 0.898$  for the grand mean is comparable to the estimate for  $f \cdot c = 0.297 \cdot$   
358  $0.628 = 0.187$  as described in Satterthwaite *et al.* (2010). Thus our estimates for  $c$  and  $\alpha$   
359 from this model are within an order of magnitude of independently derived estimates.

360 There are at least four reasons for a fish being excluded from our analysis. First,  
361 we did not include fish for which we had three or fewer data points (this excluded 90  
362 of the original 640 fish in our experiments). Second, we did not allow for cannibalism  
363 (which we observed – see Beakes *et al.* 2009) in the growth model. Cannibalism will  
364 cause one trajectory to suddenly disappear and may cause an abrupt increase in the other  
365 trajectory; neither outcome can be captured by equation (3) and such trajectories was  
366 excluded. Third, we assume that the individuals could get food without an expenditure  
367 of energy (compare equations (1) and (2)). This enormously simplifies the estimation  
368 problem because otherwise we would have to estimate  $\kappa(t)$  in equation (1) for each fish.



369 However even in a tank fish must expend some energy to obtain food and the model may  
370 have underestimated that energy for some fish. Fourth, these fish have surely evolved to  
371 deal with a starvation risk/predation risk trade-off (*sensu* Mangel and Clark 1988, Clark  
372 and Mangel 2000). It is well known that individual animals express variation (‘personality  
373 traits’) in dealing with such trade-offs and growth of some subordinate individuals may  
374 have been suppressed by interactions with dominant individuals (Bell and Sih, 2007, Frost  
375 *et al* 2007, Stamps 2007, Dyer *et al* 2008). Our modeling framework does not account for  
376 individual variation in risk avoidance; doing so requires a much more detailed behavioral  
377 model.

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

382 Because a model that allowed mean values of  $c$  and  $\alpha$  to vary between strains fit much  
383 better than a model assuming no differences between strains, we can conclude that stock  
384 origin has a significant effect on growth capacity in these fish, suggesting genetic differences.  
385 These differences may reflect local adaptation to very different growing conditions in the two  
386 systems (Beakes *et al* in review), although it is important to note that hatchery practices  
387 (NCCV focused on production, CCC focused on conservation) differ along with the riparian  
388 habitats (warm and food rich for NCCV, less warm and lower food availability for CCC)  
389 so it is unclear whether this reflects local adaptation to different river environments or to  
390 different hatcheries. In addition, we cannot rule out genetic drift rather than divergent  
391 selection as the cause of this difference (Adkison 1995). While estimates of  $\alpha$  were similar  
392 between strains, consumption ability was higher for NCCV fish, and among individuals  
393 as  $\alpha$  increased there was a greater increase in  $c$  for NCCV fish as compared to CCC fish.  
394 This difference in consumption capacity is likely to have significant implications for the  
395 response of these ecologically distinct population segments to a changing environment. For

396 example, if flow alterations lead to food availability changing to become more flashy with  
397 large pulses separated by periods with little if any food [**Joe may be able to provide**  
398 **cites suggesting this possibility**], NCCV fish will likely be better equipped to take  
399 maximal advantage of high food pulses and thus better able to ride out the lulls between  
400 pulses. NCCV fish may also be better equipped to deal with the increases in metabolic  
401 rates expected if temperatures increase (e.g. the Catabolic Cost component of equation  
402 (3)), provided that there is enough food available for NCCV fish to utilize their greater  
403 feeding capacity. At the same time, the low consumption of CCC fish may reflect behavioral  
404 patterns where the fish are choosing to shelter, minimizing predation risk, and as a result  
405 feed less. Although this difference may be a result of increased domestication in the NCCV  
406 fish due to differing hatchery practices and not a difference displayed by wild fish as well, if  
407 these DPSs do differ in their predation avoidance behavior the CCC fish may be better able  
408 to deal with increased predation risk due to introduced predators or increased temperatures  
409 that boost activity and metabolic needs of piscivorous fish [**again Joe may have some**  
410 **cites**] (Vigg and Burley 1991). Because  $f$  and  $c$  are multiplied together and we assumed  
411 constant  $f$ , it may be that the apparent higher food consumption ability we inferred for  
412 NCCV fish actually reflects more efficient conversion of the same amount of food into fish  
413 tissue. However, behavioral observations (NCCV fish were aggressive feeders striking at  
414 the surface as soon as food was added, CCC fish tended to remain in their PVC shelters)  
415 and the amount of uneaten food observed on the bottom of the tanks (higher for CCC  
416 fish) suggest that consumption rather than conversion efficiency is the main driver of this  
417 difference.

418 The growth model we use here is a key component of our state dependent life history  
419 theory (Satterthwaite *et al.* 2009, 2010), which relates water policy to growth, survival  
420 and smolting of steelhead. The results of our common laboratory study show the potential  
421 for substantial differences both between stocks and among individuals within a stock in  
422 the capacity for growth. Tyler and Bolduc (2008) found similar individual variation in

423 young-of-year rainbow trout. These intrinsic differences in growth capacity interact with  
424 responses to environmental differences experienced by each local population. Thus, an  
425 understanding of local differences in the genetics, physiology, and foraging behavior of  
426 fish is important in site - or population-specific predictions of how growth will respond to  
427 changes in the environment. The capacity to predict growth responses is itself an essential  
428 component in successfully managing the environment to encourage the recovery of steelhead  
429 populations and the maintenance of anadromy, see Satterthwaite *et al*(2009, 2010). Thus  
430 our model, appropriately parameterized from data for the DPS under consideration, can  
431 be used to predict the context-specific effects of management on growth rates in different  
432 DPSs. This will allow predicting other size-related traits of management interest, such as  
433 survival (Carlson *et al* 2008), and life history (Satterthwaite *et al* 2010), which may feed  
434 into demographic models and projections of DPS viability.

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441 Vincenzi for comments on a previous version of the manuscript.

## 442 **Literature Cited**

443 Adkison, M. D. 1995. Population differentiation in Pacific salmon: local adaptation, genetic  
444 drift, or the environment. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2762-2777  
445 Allen, G. H. and G. A. Sanger. 1960. Fecundity of rainbow trout from actual count of  
446 eggs. *Copeia* 1960:260-261

447 Alvarez, D. and A. G. Nicieza. 2005. Is metabolic rate a reliable predictor of growth  
448 and survival of brown trout (*Salmo trutta*) in the wild? Canadian Journal of Fisheries and  
449 Aquatic Sciences 62:643-649.

450 Andersen, N. G. and J. Riis-Vestergaard. 2004. Alternative model structures for bioen-  
451 ergetics budgets of a cruising predatory gadoid: incorporating estimates of food conversion  
452 and costs of locomotion. Canadian Journal of Fisheries and Aquatic Sciences 61:2413-2424.

453 Bajer, P. G., G. W. Whitley, and R. S. Hayward. 2004. Widespread consumption-  
454 dependent systematic error in fish bioenergetics models and its implications. Canadian  
455 Journal of Fisheries and Aquatic Sciences 61:2158-2167.

456 Beakes, M. P., W. H. Satterthwaite, E. Collins, D. Swank, J. E. Merz, R. Titus, S.  
457 Sogard, and M. Mangel. in press. Smolt transformation in two california populations of  
458 steelhead: effects of temporal variability in growth. Transactions of the American Fisheries  
459 Society.

460 Bell, A. M. and A. Sih. 2007. Exposure to predation generates personality in three-  
461 spined sticklebacks (*Gasterosteus aculeatus*). Ecology Letters 10:828-834.

462 Bertalanffy, L. von 1938. A quantitative theory of organic growth (Inquiries on growth  
463 laws. 2). Human Biology 10: 181-213.

464 Brett, J. R. and T. D. D. Groves 1979. Physiological energetics. Pages 279-352 in W.  
465 S. Hoar, D. J. Randall and J. R. Brett, editors. Fish Physiology. Vol. 8 Academic Press,  
466 New York.

467 Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference. A Practical  
468 Information-Theoretic Approach. Springer Verlag, New York.

469 Burnham, K. P. and D. R. Anderson 2004. Multimodel Inference: Understanding AIC  
470 and BIC in model selection. Sociological Methods Research 33: 261-304.

471 Busby P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, *et al.* 1996.  
472 Status review of west coast steelhead from Washington, Idaho, Oregon, and California.  
473 NOAA Tech. Memo. NMFS-NWFSC-27. Northwest Fish. Sci. Cent., Seattle, WA.

474 Carlson, S. M., E. M. Olsen, and L. A. Vollestad, 2008. Seasonal mortality and the  
475 effect of body size: a review and an empirical test using data on individual brown trout.  
476 *Functional Ecology* 22: 663-673.

477 Clark, C. W. and M. Mangel. 2000. *Dynamic state variable models in ecology: methods*  
478 *and applications*. Oxford University Press, New York.

479 Dyer, J. R. G., D. P. Croft, L. J. Morrell, and J. Krause. 2008. Shoal composition  
480 determines foraging success in the guppy. *Behavioral Ecology* 20:165-171.

481 Essington, T. E., J. F. Kitchell, and C. J. Walters. 2001. The von Bertalanffy growth  
482 function, bioenergetics and the consumption rates of fish. *Canadian Journal of Fisheries*  
483 *and Aquatic Sciences* 58:2129-2138.

484 Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth  
485 rate to net energy gain. *Canadian Journal of Zoology* 62:441-451.

486 Frost, A. J. and A. Winrow-Giffen, P. J. Ashley, and L. U. Sneddon. 2007. Plasticity in  
487 animal personality traits: does prior experience alter the degree of boldness? *Proceedings*  
488 *of the Royal Society B* 274:333-339.

489 Fournier, D. A., J. Hampton, and J. R. Sibert. 1998. MULTIFAN-CL: a length-  
490 based, age-structured model for fisheries stock assessment, with application to South Pacific  
491 albacore, *Thunnus alalunga*. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2105-  
492 2116.

493 Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioen-  
494 ergetics 3.0. Sea Grant Technical Report, University of Wisconsin Sea Grant Institute,  
495 Madison, WI.

496 Hartman, K. J. and S. B. Brandt. 1995. Estimating energy density of fish. *Transactions*  
497 *of the American Fisheries Society* 124:347-355.

498 Hayes, S. A., M. H. Bond, C. V. Hanson, E. V. Freund, J. J. Smith, E. C. Anderson,  
499 A. J. Ammann, and R. B. MacFarlane. 2008. Steelhead growth in a small central Cali-  
500 fornia watershed: upstream and estuarine rearing patterns. *Transactions of the American*

501 Fisheries Society 137:114-128.

502 Hilborn, R. and M. Mangel. 1997. The ecological detective: confronting models with  
503 data. Princeton University Press, Princeton, NJ.

504 Jensen, A. J. 1990. Growth of Young Migratory Brown Trout *Salmo trutta* Correlated  
505 with Water Temperature in Norwegian Rivers. Journal of Animal Ecology, Vol. 59, No. 2  
506 (Jun., 1990), pp. 603-614

507 Jobling, M. 1994. Fish bioenergetics. Chapman and Hall, London.

508 Johnsson, J. I., A. Rydeborg, and F. Sundstrom. 2004. Predation risk and the territory  
509 value of cover: an experimental study. Behavioral Ecology and Sociobiology 56:388-392.

510 Kooijman, S. A. L. M. 1986. Population dynamics on the basis of budgets. Pages  
511 266-297 in J. A. J. Metz and O. Diekmann, editors. The dynamics of physiologically struc-  
512 tured populations. Springer Lecture Notes in Biomathematics. Springer-Verlag, Berlin,  
513 Germany.

514 Li, H. W. and R. W. Brocksen. 1977. Approaches to the analysis of energetic costs  
515 of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). Journal of Fish  
516 Biology 11:329-341.

517 Lindley, S. T., R. S. Schick, E. Mora, P. B. Adams, J. J. Anderson, S. Greene, C. Han-  
518 son, *et al.* 2007. Framework for assessing viability of threatened and endangered Chinook  
519 salmon and steelhead in the Sacramento-San Joaquin basin. San Francisco Estuary and  
520 Watershed Science Volume 5, Issue 1, Article 4, pp. 1-26.

521 Mangel, M. 2006. The Theoretical Biologist's Toolbox. Cambridge University Press,  
522 Cambridge, UK.

523 Mangel, M. and C. W. Clark. 1988. Dynamic state variable modeling in ecology:  
524 methods and applications. Princeton University Press, Princeton, NJ.

525 Mangel, M. and S. B. Munch. 2005. A life-history perspective on short and long-term  
526 consequences of compensatory growth. American Naturalist 166:E 155-176.

527 Mangel, M. and W. H. Satterthwaite. 2008. Combining proximate and ultimate ap-

528 proaches to understand life history variation in salmonids with application to fisheries,  
529 conservation, and aquaculture. *Bulletin of Marine Science* 83:107-130

530 Marine, K.R. and J.J. Cech Jr. 2004. Effects of High Water Temperature on Growth  
531 Smoltification, and Predator Avoidance in Juvenile Sacramento River Chinook Salmon.  
532 *North American Journal of Fisheries Management* 24: 198-210

533 McCarthy, I. D., C. G. Carter, and D. F. Houlihan. 1992. The effect of feeding  
534 hierarchy on individual variability in daily feeding of rainbow trout, *Oncorhynchus mykiss*  
535 (Walbaum). *Journal of Fish Biology* 41:257-263.

536 McGurk, M. D. 1996. Allometry of marine mortality of Pacific salmon. *Fishery Bulletin*  
537 94:77-88.

538 Melack J. M., J. Dozier, C. R. Goldman, D. Greenland, A. M. Milner, and R. J.  
539 Naiman. 1997. Effects of climate change on inland waters of the Pacific coastal mountains  
540 and western Great Basin of North America. *Hydrological Processes* 11:971-992.

541 Moses, M. E., C. Hou, W. H. Woodruff, G. B. West, J. C. Nekola, W. Zuo, and J.  
542 H. Brown. Revisiting a model of ontogenetic growth: estimating model parameters from  
543 theory and data. *American Naturalist* 171:632-645.

544 Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge.  
545 *Transactions of the American Fisheries Society* 122:736-748.

546 Prajneshu, and Venugopalan, R. 1999. von Bertalanffy growth model in a random  
547 environment. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1026-1030.

548 Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 2007. *Numerical*  
549 *Recipes: The Art of Scientific Computing* . Third Edition. Cambridge University Press,  
550 Cambridge and New York.

551 Price, E. O. 2002. *Animal Domestication and Behavior*, CABI Publishing, Wallingford,  
552 Oxon, UK.

553 Pearse, D.E., S. A. Hayes, M. H. Bond, C. V. Hanson, E. C. Anderson, R. B. MacFar-  
554 lane, and J. C. Garza. 2009. Over the falls? Rapid evolution of ecotypic differentiation in

555 steelhead/rainbow trout (*Oncorhynchus mykiss*). *Journal of Heredity* 100:515-525.

556 Peterson J.H. and J. F. Kitchell. 2001. Climate regimes and water temperature changes  
557 in the Columbia River: bioenergetic implications for predators of juvenile salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1831-1841.

558

559 Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon*. University of Wash-  
560 ington Press, Seattle, WA.

561 Railsback, S. F. and K. A. Rose. 1999. Bioenergetics modeling of stream trout growth:  
562 temperature and food consumption effects. *Transactions of the American Fisheries Society*  
563 128:241-256.

564 Rand, P. S., D. J. Stewart, P. W. Seelbach, M. L. Jones, and L. R. Wedge. 1993.  
565 Modeling steelhead population energetics in Lakes Michigan and Ontario. *Transactions of*  
566 *the American Fisheries Society* 122:977-1001.

567 Reese, C. D. and B. C. Harvey. 2002. Temperature-Dependent Interactions between  
568 Juvenile Steelhead and Sacramento Pikeminnow in Laboratory Streams. *Transactions of*  
569 *the American Fisheries Society* 2002; 131: 599-606

570 Satterthwaite, W.H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G.  
571 Titus, S. M. Sogard, and M. Mangel. 2009. Steelhead Life History on California's Central  
572 Coast: Insights from A State Dependent Model. *Transactions of the American Fisheries*  
573 *Society* 132:532-548.

574 Satterthwaite, W.H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus,  
575 S. M. Sogard, and M. Mangel. 2010. State-dependent life history models in a changing  
576 (and regulated) environment: steelhead in the California Central Valley. *Evolutionary*  
577 *Applications* in press, DOI: 10.1111/j.1752-4571.2009.00103.x

578 Siegfried, K. I. and B. Sansó. 2006. Two Bayesian methods for estimating parameters  
579 of the von Bertalanffy growth equation. *Environmental biology of fishes* 77:301-308.

580 Sogard, S.M., T. H. Williams, and H. Fish. 2009. Seasonal Patterns of Abundance,  
581 Growth, and Site Fidelity of Juvenile Steelhead in a Small Coastal California Stream.



582 Transactions of the American Fisheries Society 138:549-563.

583 Stamps, J. A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals.  
584 Ecology Letters, 10:355-363.

585 Sullivan, K., D. J. Martin, R. D. Cardwell, J. E. Toll, and S. Duke 2000. An analysis  
586 of the effects of temperature on salmonids of the Pacific Northwest with implications for  
587 selecting temperature criteria. Sustainable Ecosystems Institute, Portland, OR, USA.

588 Thornton, K. W. and A. S. Lessem. 1978. A temperature algorithm for modifying  
589 biological rates. Transactions of the American Fisheries Society 107:284-287.

590 Trudel, M., D. R. Geist, and D. W. Welch. 2004. Modeling the oxygen consumption  
591 rates of Pacific salmon and steelhead: an assessment of current models and practices.  
592 Transactions of the American Fisheries Society 133:326-348.

593 Tyler, J. A. and M. B. Bolduc. 2008. Individual variation in bioenergetic rates of  
594 young-of-year rainbow trout. Transactions of the American Fisheries Society 137:314-323.

595 Vigg, S. and C. C. Burley. 1991. Temperature-dependent maximum daily consumption  
596 of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia  
597 River. Canadian Journal of Fisheries and Aquatic Sciences 48:2491-2498.

598 Wang, Y. and N. Ellis. 2005. Maximum likelihood estimation of mortality and growth  
599 with individual variability from multiple length-frequency data. Fish Bulletin 103:380-391.

600 Waples, R. S. 1991. Definition of "species under the Endangered Species Act: appli-  
601 cation to Pacific salmon. U.S. Department of Commerce, NOAA Technical Memorandum  
602 NMFS-NWFSC-194.

603 Wurtsbaugh, W. A. and Davis, G. E. 1977. Effects of temperature and ration level on  
604 the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. Journal of Fish  
605 Biology 11: 87-98.

606 **Captions for Figures**

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

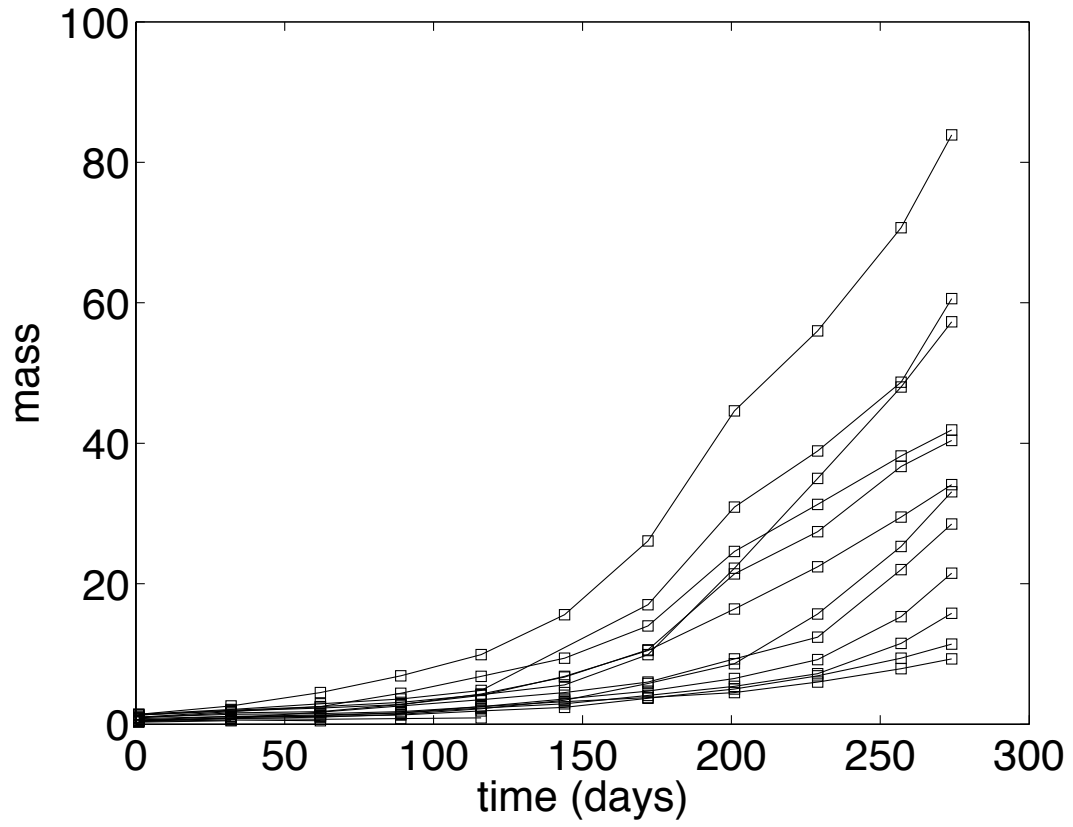
610

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

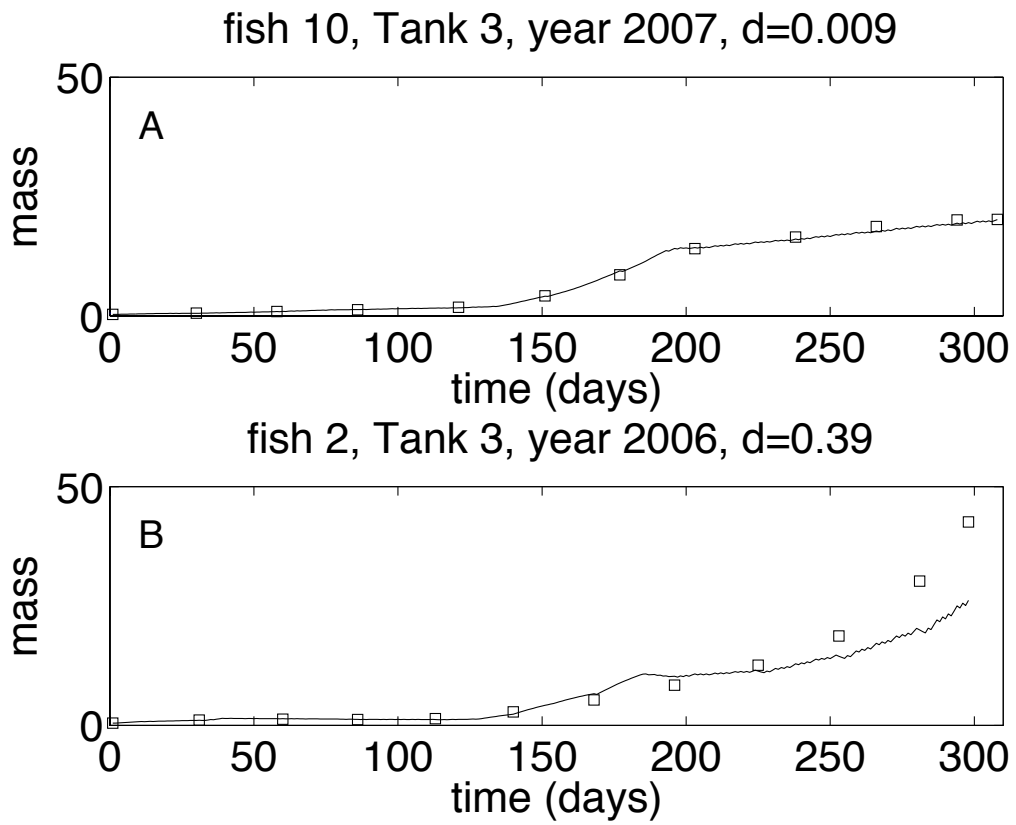
614

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

Simon et al, Figure 1



Simon et al, Figure 2



Simon et al, Figure 3A 3B

