Change in Mean Body Size: Growth or Predation?

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In their freshwater and early ocean life stages salmonids experience rapid growth. Accurate measures of that growth can be important for comparison of habitats, bioenergetics models, and other applications. Growth can be measured as the difference of the mean of the size-frequency distribution at two times. Because smaller individuals tend to experience greater mortality than larger individuals, the apparent growth for the population is larger than the actual growth of individuals in the population. I describe a simple model of simultaneous growth and size-selective predation and use this model to explore the relationship between model parameters for size-selective predation and actual and apparent growth. I explore a method for estimating the mean actual growth of individuals in a population given the mean apparent growth of the population.

The model used is very similar to that of Munch et al. (2003). We assumed that growth and mortality were governed by two ordinary differential equations. The first is a size-dependent growth equation,

$$\frac{dx}{dt} = g(x) \tag{1}$$

where $x(t)$ is the size of an individual at time t and $g(x)$ is the instantaneous growth rate of an individual of size x.

The second is a size-dependent mortality equation,

$$\frac{dN(x,t)}{dt} = -m(x)N(x,t) \tag{2}$$

where $N(x,t)$ is the density of individuals of size x at time t and $m(x)$ is the instantaneous mortality rate for individuals of size x. The second equation is separable and can be solved for $m(x)$, or survival at time t.

$$S(t) = \exp\left(-\int_0^t m(x_t)\,dt\right) \tag{3}$$

Equation (1) can be solved explicitly for x_t, given x_0, as long as $g(x)$ is strictly positive. This allows us to change variables from time to size:

$$S(x_0) = \exp\left(-\int_{x_0}^{x_t} \frac{m(x)}{g(x)}\,dx\right) \tag{4}$$

Given an initial size-frequency distribution, f_0, the distribution at time t is

$$f_t(x_t) = f_0(x_0)\frac{S(x_0)}{\int_{-\infty}^{+\infty} S(x)\,dx}$$

I defined the mean apparent growth to be the difference in the means of the two distributions: f_0 and f_t. I defined the mean actual growth to be the mean growth rate computed with respect to the final distribution, f_t.

I used simple growth and mortality models in order to minimize the number of parameters requiring estimation: constant growth and linear mortality.

$$g(x) \equiv g_1 \tag{5}$$

$$m(x) \equiv \begin{cases} (m_1 - x)m_2 & x \le m_1 \\ 0 & x > m_1 \end{cases} \tag{6}$$

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The m_1 parameter can be thought of as the critical size beyond which size-selective mortality no longer applies. The m_2 parameter can be thought of as the strength of size-selection—the larger the m_2 parameter, the greater the difference in mortality rates across size.

I non-dimensionalized the system by focusing on the size-frequency initial distribution. I assumed the initial distribution was normal, with mean μ and standard deviation σ. All measures of size were then standardized against the mean and standard deviation of that distribution:

$$\widetilde{f_0}(x) = \frac{f_0(x+\mu)}{\sigma} = N(0,1)$$

$$\widetilde{g_1} = \frac{g_1}{\sigma}$$

$$\widetilde{m_1} = \frac{m_1 - \mu}{\sigma}$$

$$\widetilde{m_2} = \sigma m_2$$

$$\widetilde{f_t}(x_0 + \widetilde{g_1}) = \frac{\widetilde{f_0}(x_0)\left(\tilde{S}(x_0)\right)}{\int_{-\infty}^{+\infty} \tilde{S}(x)\,dx}$$

Mean actual growth was $\widetilde{g_1}$. Mean apparent growth was the mean of the $\widetilde{f_t}$ distribution.

I mapped the magnitude of the bias in apparent growth with respect to a fixed amount of actual growth, allowing $\widetilde{m_1}$ to vary between -1 and 12, $\widetilde{m_2}$ to vary between 0 and 5, and $\widetilde{g_1}$ to vary between 1 and 6. I also mapped the magnitude of the bias in apparent growth with respect to a fixed amount of apparent growth, allowing the mortality parameters to vary in the same way.

I performed model fitting on data from the Columbia Basin Fish and Wildlife Program (CBFWP) passive integrated transponder (PIT) tagging of wild-reared Chinook salmon from the Snake River Basin. The data for six years in particular were found to have a substantial number of recaptures at Lower Granite or Little Goose dams. Using the recapture data, I had a direct measure of actual growth against which I could compare the g_1 parameter from the fitted model. The model was first fitted with the g_1 parameter fixed at the value determined from the direct measure of growth in order to get best estimates for the mortality parameters. I then fitted the model using the lengths at tagging as the initial sample and the lengths at recapture as the final sample. I used a technique similar to that outlined by Munch et al. (2003)—with modifications to account for the differences in time between tagging and recapture among individuals. I repeated this process three further times, restricting the possible range of the m_1 and m_2 parameters to within 20%, 10%, and 1% of the best estimates determined using the direct measure of the growth. The apparent growth and the fitted values for g_1 were compared with the growth from the direct measure.

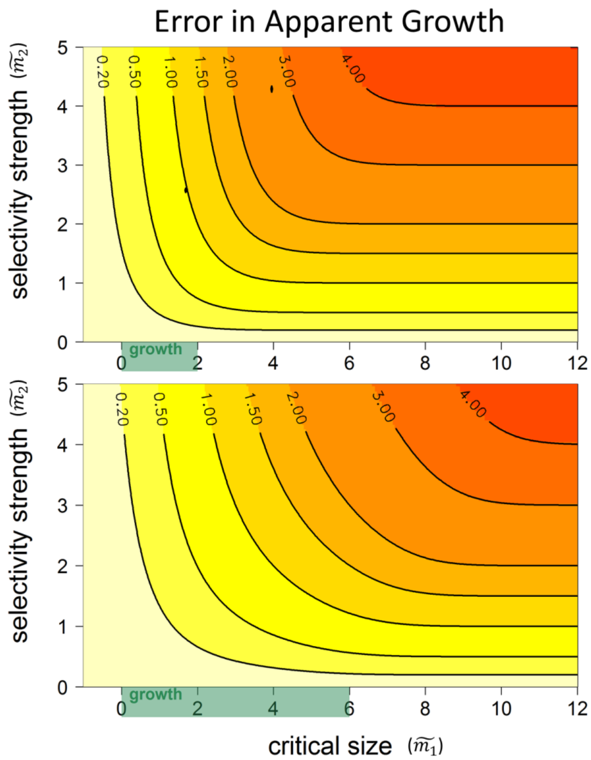

Fig. 1. Map of error in apparent growth. The x-axis shows the $\widetilde{m}_1$ parameter (critical size) and displays the amount of actual growth used in the figure ($\widetilde{g}_1$, in green). The y-axis shows the $\widetilde{m}_2$ parameter (strength of selectivity). The contours (and shading) indicate the absolute magnitude of the error for an actual growth of 2 (a) and 6 (b) in non-dimensionalized units.

The model exploration revealed behavior in keeping with the simple nature of the model. For large values of m_1 (critical size), only a tiny fraction of the population escapes predation and the magnitude of the apparent growth bias is determined solely by m_2 (strength of selectivity). As the critical size decreases, it can mitigate the effects of selectivity as a greater portion of the population escapes size-selective predation—the greater the strength of selectivity, the more a small change in the fraction of survivors can matter (Fig. 1). The nature of the error in apparent growth is similar when considered from the point-of-view of a fixed amount of apparent growth (Fig. 2).

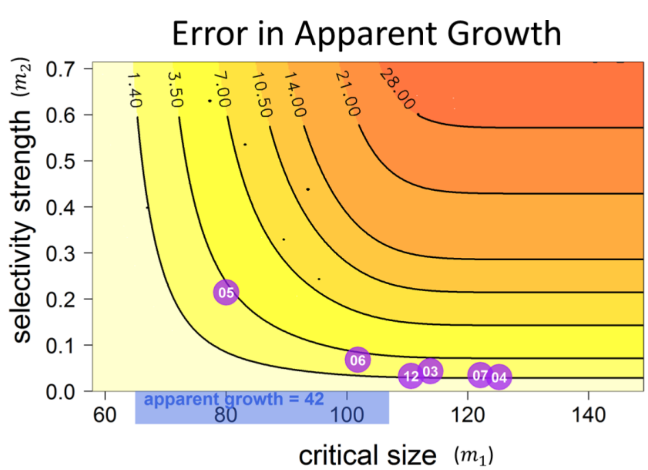

Fig. 2. Map of error in apparent growth for a fixed value of apparent growth. This map is shown in actual units in order to best display the fitted values for the data used (years 2003-2007 and 2012). Mean initial size (65mm) and mean apparent growth (42mm) were computed as averages across years.

Table 1. For each year of PIT tag data with substantial recaptures, the distribution of initial size and directly measured growth are characterized by mean and standard deviation. The absolute error with respect to the actual (directly measured) mean growth is listed in subsequent columns. "Apparent growth" refers to the difference in mean for the two populations. "Unrestricted Model" refers to the fitted model with no restrictions on the growth or mortality parameters. "Restricted (X%)" refers to a fitted model in which the growth parameter was unrestricted, but the mortality parameters were constrained to fall within X% of the "best fit" mortality parameters. The "best fit" mortality parameters were computed by fitting the model while constraining the growth parameter to the directly measured value.

Year	Initial Size		Actual Growth		Apparent Growth Error	Unrestricted Model Error	Restricted (20%) Error	Restricted (10%) Error	Restricted (1%) Error
	Mean	SD	Mean	SD					
2003	63.2	7.0	42.5	10.3	+1.8	-8.5	-3.0	-3.0	-0.4
2004	63.2	6.4	41.3	8.9	+2.1	-7.0	0.3	0.3	0.3
2005	62.9	7.0	44.5	9.4	+2.6	-5.0	-5.0	-3.0	-0.1
2006	66.2	7.1	35.1	9.1	+3.1	-3.6	-3.6	-3.6	-0.4
2007	65.6	6.4	43.7	8.6	+0.9	-8.2	-4.0	-3.2	-0.4
2012	63.4	6.4	36.0	8.8	+1.5	-6.5	-1.5	-1.5	-0.4

The first phase of the model fitting exercise produced best fit mortality parameters consistent with weak selectivity, except in the case of 2005 which suggested much greater selectivity focused on smaller individuals (Fig. 2). The error in the apparent growth measures were less than 10% of the actual growth in all cases and were about one quarter of the standard deviation in the directly measured growth (Table 1). The fitting methodology applied without restrictions to the mortality model parameters produced estimates that were more negatively biased than the apparent growth measures were positively biased. This improved substantially when restricting the fitting algorithm to mortality parameters within 20% of the "best fit" parameters. Further restricting mortality parameters to within 10% of the best fit parameters did not result in corresponding improvement in the estimate of actual growth. Only the restriction within 1% of the best fit mortality parameters produced estimates of growth that were better than the apparent growth estimate. Full details are shown in Fig. 3 and Table 1.

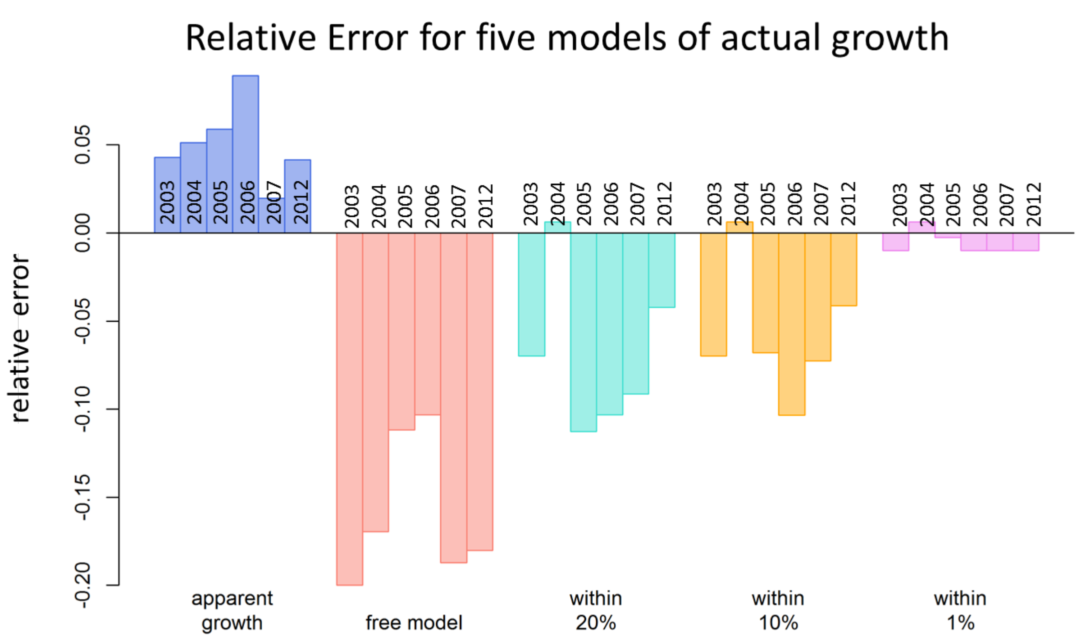

Fig. 3. Relative error in growth measure with respect to directly measured mean growth. For "apparent growth" this is the computed difference in the mean size for samples 1 and 2. For the other models, it is the fitted value for g_1. For the "free model", m_1 and m_2 were unconstrained. For the "within X%" models, m_1 and m_2 were constrained to be within X% of the "best fit" model (parameterized using g_1 equal to the directly measured mean growth).

The model characterizes the behavior of a system involving size-selective predation well. Based on the behavior of the fitting algorithms with the overall model and PIT tag data, some changes are needed if this process is to be useful for characterizing the magnitude of the bias when apparent growth is used in place of directly measured growth. Accurately characterizing the predator field to within 1% of the effective mortality model parameters is at least as difficult a goal as directly measuring the growth of the population of interest. There is, however, some hope that further investigation will reveal models that will allow this process to function more accurately.

Future work includes investigation of different mortality models. A simple modification to the existing model—adding a baseline of size-independent mortality—may yield a much better fit to the data. Additionally, a more complex model which is mechanistically linked to the distribution of the size of predators may be able to provide a better fit to the data. A more realistic growth model may also be useful, but simple linear models have not worked well (results not shown). Once the best performing mortality and/or growth models are found, I will explore the kind of priors on the mortality model parameters that best facilitate accurate reconstruction of the mean actual growth.

REFERENCES

Munch, S. B., M. Mangel, and D.O. Conover. 2003. Quantifying natural selection on body size from field data: winter mortality in *Menidia menidia*. Ecology 84: 2168-2177.