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Biphasic growth in fish II: Empirical assessment

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ABSTRACT

In [Quince, et al., 2008. Biphasic growth in fish I: Theoretical foundations. J. Theor. Biol., doi:10.1016/j.jtbi.2008.05.029], we developed a set of biphasic somatic growth models, where maturation is accompanied by a deceleration of growth due to allocation of energy to reproduction. Here, we use growth data from both hatchery-raised and wild populations of a large freshwater fish (lake trout, *Salvelinus namaycush*) to test these models. We show that a generic biphasic model provides a better fit to these data than the von Bertalanffy model. We show that the observed deceleration of somatic growth in females varies directly with gonad weight at spawning, with observed egg volumes roughly 50% of the egg volumes predicted under the unrealistic assumption of perfectly efficient energy transfer from somatic lipids to egg lipids. We develop a Bayesian procedure to jointly fit a biphasic model to observed growth and maturity data. We show that two variants of the generic biphasic model, both of which assume that annual allocation to reproduction is adjusted to maximise lifetime reproductive output, provide complementary fits to wild population data: maturation time and early adult growth are best described by a model with no constraints on annual reproductive investment, while the growth of older fish is best described by a model that is constrained so that the ratio of gonad size to somatic weight (g) is fixed. This behaviour is consistent with the additional observation that g increases with size and age among younger, smaller breeding females but reaches a plateau among older, larger females. We then fit both of these optimal models to growth and maturation data from nineteen wild populations to generate population-specific estimates of 'adapted mortality' rate: the adult mortality consistent with observed growth and maturation schedules, given that both schedules are adapted to maximise lifetime reproductive output. We show that these estimates are strongly correlated with independent estimates of the adult mortality experienced by these populations.

1. Introduction

The majority of fish species continue growing after maturation; they exhibit indeterminate growth, with size asymptotically approaching a maximum value. Size influences many significant characteristics of individual fish, such as vulnerability to predators, fecundity and choice of prey. In addition, the lifetime patterns of somatic growth exhibited by commercially exploited fish populations play a significant role in defining sustainable exploitation strategies for those populations. Thus much attention has been paid in the fisheries literature to developing and applying effective empirical and theoretical models of somatic growth in fish (Beverton and Holt, 1957).

Many of these growth models fall into one of two categories: (i) uniphasic models that assume a continuous rate of growth deceleration throughout life; (ii) biphasic models that assume that the growth pattern is significantly altered by the re-allocation of energy to reproductive tissue that occurs with maturity.

In a companion paper (Quince et al., 2008), we introduced a simple energetics framework for growth and reproduction in seasonally reproducing fish and we used this framework to develop a series of growth models that are explicitly biphasic. In this paper, we evaluate the ability of these biphasic models to describe various aspects of the growth and reproductive behaviour of a long-lived freshwater fish species (the lake trout, *Salvelinus namaycush*), as exemplified in data sets collected from 19 distinct wild populations, as well as data collected from three genetically distinct groups of individuals raised under controlled hatchery conditions.

2. Review of growth models

The growth models that we will use in this paper are summarised in Table 1, and discussed in detail in Quince et al.

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Table 1
Summary of growth models defined in Quince et al. (2008)

Model	Definition	Parameters
von Bertalanffy (vB)	$v_t = v_\infty - (v_\infty - v_0)\exp(-kt)$ $L_t = v_t^{1/3(1-\beta)}$	(v_0, h, k, β) $v_\infty = h/k$
Generic Biphasic (GB)	$v_t = v_0 + ht$: $t \leqslant T$ $v_t = v_\infty - (v_\infty - v_T)\exp(-k(t-T))$: $t > T$ $L_t = v_t^{1/3(1-\beta)}$	$(v_0, h, \beta, T^{a}, \alpha, \chi)$ $v_T = v_0 + hT$ & $e^{-k} = \chi$ $v_\infty = v_T + h\alpha/(1-\chi)$
GB gonad weights	$G_t = 0$: $t \leqslant T$ $G_t = \frac{\gamma h \Omega}{1-\beta}\left(\frac{v_t - v_C}{v_\infty - v_C}\right) v_t^{\beta/(1-\beta)}$:$t > T$	$v_C = v_T + h(\alpha - \chi)/(1-\chi)$ γ: ratio of energy densities Ω: $W = \Omega L^3$
Fixed g optimum (FGO)	GB with g fixed ($v_C = 0$) & (g', T) maximises R_0	(v_0, h, β, s)
Variable g optimum (VGO)	Maximises R_0 without constraint approx. GB with $v_C > v_T$	(v_0, h, β, s)

All growth is given as a function of a discrete age t (years). Fitted parameters are shown in brackets, derived parameters are not. Here L_t, W_t and G_t are length, somatic weight and gonad weight at age t; T is the last juvenile age, g is the ratio G_t/W_t; $g' = g^r$; R_0 is lifetime reproductive output; is the annual survival probability.

[a] The parameter T may be known.

(2008). All are expressed in terms of changes in size v $(= L^{3(1-\beta)})$, where L is length, based on the following simple energetics framework:

$$\frac{dW}{d\tau} = \alpha W^{\beta} - \gamma W^{\delta} - R(W)$$

$$W = \Omega L^3 \tag{1}$$

where W is somatic weight, τ age in days, α, β, γ, δ, and Ω are constants, and $R(W)$ represents diversion of energy to reproduction. Eq. (1) defines the net energy available to an individual for new somatic growth as the balance of the gross rate at which the individual is able to extract energy from its environment (αW^{β}) and the costs the individual must incur to maintain itself in that environment (γW^{δ}). In the generalised von Bertalanffy model (the vB model), the set of parameters $(\alpha, \beta, \gamma, \delta, \Omega)$ are assumed fixed throughout life, with $\delta = 1$. The costs of reproduction, incurred when the individual matures, are seen as either negligible or as compensated for by concurrent reductions in other costs, i.e. $R(W) \equiv 0$. This allows us to associate somatic weight W with total weight in this model. The result is a smooth, asymptotic growth pattern for length whose form is constant throughout life.

In all our biphasic models, β and δ are taken to be approximately equal so that the energy available for somatic growth prior to sexual maturity varies as $(\alpha - \gamma)W^{\beta}$; after maturity the additional cost of reproduction $R(W)$ is incurred. This is assumed to vary within each season. Initially $R(W) = 0$. At some point during the growing season, $R(W)$ is re-set to equal $R(W) = (\alpha - \gamma)W^{\beta}$ so that somatic growth ceases. For females this energy is channelled into gonadal growth thus $dG/d\tau = \gamma R(W)$, and, at spawning, $g = G/W$, where G is gonad weight, γ is the ratio of somatic to gonadal wet weight energy densities and g is the ratio of annual investment in reproduction to somatic weight at spawning. This discrete switch from somatic to gonadal growth is the optimal allocation strategy within a season (Kozlowski and Teriokhin, 1999), and ensures that Eq. (1) is never negative.

Our different biphasic models are distinguished by differences in the assumptions used to determine when this switch from somatic to gonadal growth occurs. In the generic biphasic (GB) model, we impose a vB growth curve post-maturation by assuming that the proportion of the season devoted to reproduction will decay exponentially as a function of the number of years of reproductive experience. For both the fixed g and variable g optimum (FGO and VGO, respectively) models, we impose the assumption that reproductive investment is adjusted to maximise lifetime reproductive output given a constant mortality rate, in the presence (FGO) and absence (VGO) of the constraint that g be a fixed proportion of somatic weight at spawning. All three models are characterised by a distinct break in the growth pattern at maturity; length does not asymptotically approach a maximum value until after maturity.

3. Methods

Organisms that exhibit long pre- and post- maturation growth periods provide the best opportunity for assessing whether biphasic models are more effective than uniphasic models at describing fish growth patterns—only such organisms provide sufficient information to permit these two potentially different phases of growth to be accurately characterised. Therefore, we chose the lake trout, a late maturing, long lived freshwater salmonid species as the test organism in our evaluation of biphasic growth models.

We used both Bayesian and frequentist statistics to address five questions that bear directly on the ability of biphasic growth models to describe the behaviour of fish in the wild, and to improve our understanding of the forces shaping that behaviour (Table 2).

3.1. *The data*

3.1.1. *Wild populations*

Samples of individual fish were taken from 19 native populations in Ontario, Quebec and the Northwest Territories, Canada. Samples from Lake Opeongo, Ontario were collected over the period 1994 from 2005 by sampling annually from the angler harvest on the lake (Shuter et al., 1987). The data from the remaining 18 populations were obtained from intensive gill net surveys carried out over a 10 day period, annually over 1 to 3 years—data ideally collected from each individual: day of capture, fork length, weight, sex, maturity status, gonad weight, age (from otoliths). Since the sampling for a lake was often done at different points within consecutive growing seasons, otolith age estimates were increased by 1 for fish caught after the mid growing season date (June 21st) so that individual age estimates used in the growth curve fits would more accurately reflect the number of growing seasons contributing to the observed length values.

For all populations, the capture gear provided representative samples of both the age and size distributions of the adult segment of each population and of the older juveniles. For all lakes, sampling of the younger age groups was biased toward larger fish. For Lake Opeongo, unbiased estimates of mean length at age for all younger age groups (ages <7) were available from a separate study (Matuszek and Shuter, 1990) that derived individual length at age (end of growing season) estimates from measurements to annular marks on fish scales taken from a large ($n = 261$) unbiased sample of adults, using a method validated for the Lake Opeongo population. For the other lakes the bias was reduced by defining an appropriate minimum capture length, and truncating the distributions modelling the lengths at age at this value (see supplement on Bayesian model fitting).

For the Lake Opeongo population, the length at age values from scales were supplemented by a sample of 1030 female fish with ages $\geqslant 5$. For the remaining 18 populations, length at age data was pooled across sexes since there was no evidence of significant sexual dimorphism in those populations where sample size for both sexes was large enough to effectively test for it. In a few