



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.

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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) uniphase 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)	$v_t = v_0 + ht: t \leq T$ $v_t = v_\infty - (v_\infty - v_T) \exp(-k(t - T)):$ $t > T$	$(v_0, h, \beta, T^3, \alpha, \chi)$ $v_T = v_0 + hT$ & $e^{-k} = \chi$
GB gonad weights	$L_t = v_t^{1/3(1-\beta)}$ $G_t = 0: t \leq T$ $G_t = \frac{\gamma h \Omega}{1 - \beta} \left(\frac{v_t - v_C}{v_\infty - v_C} \right) v_t^{\beta/(1-\beta)}: t > T$	$v_\infty = v_T + h\alpha/(1 - \chi)$ $v_C = v_T + h(\alpha - \chi)/(1 - \chi)$ γ : ratio of energy densities $\Omega: W = \Omega L^3$
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 ; $g' = g^T$; R_0 is lifetime reproductive output; s 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:

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

$$W = \Omega L^3 \quad (1)$$

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 (Kozłowski 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 uniphase 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 ≥ 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

Table 2

Summary of the five question addressed in the paper and the statistical methods and data used to answer them

Question	Approach	Data
1. Is growth biphasic?	Compare abilities of vB and GB models to represent lifetime growth patterns (see Sections 3.3 and 3.4)	Population level fits: <i>Sets 1 and 2</i> : length at age data derived from Lake Opeongo fish raised in the wild ($n = 2596$) and controlled hatchery ($n = 964$) conditions Hierarchical individual fits: <i>Sets 3 and 4</i> : individual length at age data from 18 Michipicoten and 17 Slate females raised under controlled conditions
2. Is adult deceleration in somatic growth linked to investment of energy in reproductive tissue?	Compare observed egg production with egg production predicted from GB fits to length at age data (see Section 3.5)	<i>Sets 1 and 2</i> : observed and predicted egg volumes from hatchery-raised Slate ($n = 53$) and Michipicoten ($n = 51$) females
3. Is the seasonal energy allocation pattern consistent with optimal reproductive investment?	Compare, over a typical growing season, the somatic growth rates of immature females with the somatic growth rates of adult females exhibiting gonadal development	<i>Set 1</i> : length by day over a growing season for 323 immature females and 281 developing adult females raised in the wild in Lake Opeongo
4. Which optimal investment model works best—the VGO or the FGO?	Compare abilities of the FGO and VGO models to provide an integrated description of somatic growth and maturity (see Section 3.6) Determine if the scaling of g is more consistent with the variable g or the fixed g assumption (see Section 4.4)	<i>Set 1</i> : mean length at age data and maturity status at length data from wild Lake Opeongo fish ($n = 2596$) <i>Set 2</i> : length and gonad weight data from wild Opeongo fish near spawning ($n = 201$) <i>Set 3</i> : length and egg volume data from hatchery-raised Opeongo fish at spawning ($n = 120$)
5. Do optimal investment models describe life history in the wild?	Compare observed adult survival with survival predicted from VGO and FGO model fits to length, age and maturity status data (see Sections 3.6 and 3.7)	<i>Sets 1-19</i> : mean length at age data and maturity status data from 19 wild populations from Ontario, Quebec and the Northwest Territories, Canada ($n = 126$ to 2596)

populations, a small minority of individuals exhibited individual growth patterns that deviated widely from the average pattern for the population – these outliers were eliminated from the data sets used in the growth curve fits (Blackie et al., 2003).

Sample size per population ranged from 126 to 2596 length at age values (median value = 316). Maturation status was also available for the majority of these data points.

3.1.2. Hatchery populations

Separate groups of fish from three wild populations were raised from fertilised eggs to maturity in experimental hatchery facilities. Fish from the Lake Opeongo population entered the hatchery as fertilised eggs in the fall of 1989 and were monitored through 1996. Fish from the Slate Island and Michipicoten populations entered the hatchery in the fall of 1992 and were monitored through 2002 (except 1997 when measurements were not taken). All fish were raised in controlled (natural light cycle, regulated feeding regime of production hatchery food provided at a rate of 1% body weight per day) hatchery environments throughout the period of data collection.

Opeongo individuals reached sexual maturity after 4, 5 or 6 years in the hatchery. Michipicoten and Slate individuals matured at ages 6, 7 or 8. For the Opeongo fish, growth prior to maturity was monitored at the group level by periodically taking random samples of fish from the holding tanks, measuring their lengths and weights and then returning them to the tanks. After 4 years in the hatchery, monitoring of growth at the individual level was initiated by taking annual measurements of the length and weight of marked individuals. Individual level monitoring of Slate and Michipicoten growth was begun several years prior to maturity—after fish had spent just 3 years in the hatchery. At maturity, data on growth and reproductive investment were collected from individual fish as follows: in late September (2–3 weeks prior to the natural spawning time) individual females were weighed, measured and examined for external signs of egg development (e.g. colour changes, distended abdomen); eggs were stripped

from each mature female at these weekly inspections by gentle pressure applied to the abdomen and the volume of stripped eggs was measured; stripping inspections ended when no further eggs could be obtained (typically by late October); annual reproductive investment for an individual was defined as the sum of all weekly egg volume samples; somatic weight was estimated as total weight less total egg weight, estimated from egg volume assuming a specific gravity of 1.05 (Kamler, 1992; Shuter et al., 2005).

3.2. Bayesian fitting methods

We used Bayesian methods where appropriate because they permit models of arbitrary complexity to be fit to multiple data sets through the use of an explicit likelihood function. Errors trade-off naturally between the different model components, and the final product is a complete distribution of plausible parameter values for the fitted model, rather than a single best-fit value. These methods have been successfully used to describe organismal growth patterns in a number of recent studies (e.g. Essington et al., 2001; Helser and Lai, 2004; Siegfried and Sanso, 2006). All our Bayesian fits were obtained using Markov Chain Monte Carlo (MCMC) methods (Gilks et al., 1996) as implemented in the JAGS software (Plummer, 2005) for Gibbs sampling (Gilks et al., 1996). Non-informative or weakly informative prior distributions were used to ensure that the estimated posterior distributions were determined by the data alone. See the online supplementary material for details. We used the deviance information criterion (DIC, Spiegelhalter et al., 2002) to compare model fits: the smaller the DIC value the better the fit, with a difference greater than seven considered significant.

3.3. Population level fits of vB and GB curves to length at age data

To compare the relative effectiveness of the vB and GB models as descriptors of Opeongo lifetime growth patterns (Table 2,

question 1), we used a population level Bayesian procedure to fit the vB and GB models to the lifetime growth data from the Opeongo hatchery fish (details in online supplement). The fitted parameters were v_0 , h and k for the vB model and v_0 , h , α and γ for the GB model. In order to compare the GB model with the commonly used three parameter version of the von Bertalanffy growth model, we fixed β at $\frac{2}{3}$ for both models, in which case $v \equiv L$. The last age before reproduction, T , was fixed at its modal value of 4. We repeated this procedure using the lifetime growth data from the wild Opeongo fish. Here, we set T equal to the largest integer smaller than T_{50} , the age at which 50% of female fish were mature. We estimated T_{50} from a logistic regression of maturation status versus age for wild Opeongo females.

3.4. Hierarchical fits to individual size at age data

To compare the relative effectiveness of the vB and GB models as descriptors of Slate and Michipicoten lifetime growth patterns (Table 2, question 1), we used a Bayesian hierarchical procedure (Helser and Lai, 2004; Spiegelhalter et al., 1996) to fit both models to the data from each population, with beta fixed at $\frac{2}{3}$ as explained above. The hierarchical procedure was chosen because it could incorporate the extensive information on individual juvenile growth trajectories that were available for Slate/Michipicoten fish and unavailable for the Opeongo fish. For all Slate/Michipicoten individuals, at least two and frequently three years of juvenile growth were recorded. For the Opeongo fish the three years of juvenile length measurements were not resolved to individuals (see online supplement).

3.5. Estimating egg volumes from individual fits

We pooled the weight-length data from the two stocks and used a zero-intercept regression of W against L^3 (R Development Core Team, 2006) to obtain an estimate of $\Omega = 1.177 \times 10^{-5} \text{ g mm}^{-3}$. We obtained an estimate of 1.0 for γ using unpublished bomb calorimetric data for both somatic and gonad tissue from the study of lipids in hatchery-raised lake trout by Henderson and Wong (1998). This value of γ reflects the high somatic fat level typical of hatchery-raised lake trout and hence should apply to the Slate and Michipicoten fish used in our study. This gave us sufficient information to determine the model predicted gonad weights. To convert these into egg volumes for comparison with our observations, we also used data on spawning gonad weight and spawning egg volume from the Henderson and Wong study, to estimate the ratio of egg volume to ovary wet weight, finding a value of 0.75 for this ratio.

3.6. Concurrent population level fits to individual data on size, maturity status and age

To fit an optimal investment model (VGO or FGO see Table 1) to data from a wild population (Table 2, questions 4 and 5), we used a population level Bayesian procedure that makes explicit use of both length at age data and maturity status at age and length. The four parameters of either optimum growth model (v_0 , s , h , β see Table 1) predict both length at age and maturation age ($T + 1$) and length (L_{T+1}). We exploited this property of the models to carry out a simultaneous fit to both the length at age data and the maturation data available from our 19 wild populations. We used population level fits, assuming each population was characterised by a single somatic growth curve and maturation schedule. Details of the fitting procedure are provided in the online supplementary material.

In preliminary studies we found it difficult to simultaneously fit s and β for the optimal growth models. This reflected both the complimentary nature of these variables, and the fact that most populations lacked a large number of unbiased juvenile data points, consequently the Bayesian fits showed signs of slow convergence (Gelman, 1996). To address this we fixed β at a predetermined value. As discussed in Quince et al. (2008), juvenile growth in length in the biphasic models is a linear function of age raised to the power $\frac{1}{3}(1 - \beta)$. We therefore fit this function to the wild Opeongo population, for which high quality juvenile growth from scales was available (Section 3.1.1), and determined that β lies with 95% confidence between 0.67 and 0.71, with a median prediction of 0.69. In the absence of β estimates for the other populations, we decided to fix β at this median prediction of 0.69 for all 19 populations. Thus the fits themselves provide estimates for the parameters v_0 , s and h , where s is the survival probability to which the population members are adapted.

3.7. Estimating survival probabilities from cohort abundances

To compare observed survival rates with those predicted from our optimal investment model fits (Table 2, question 5), we estimate survival probabilities from the yearly age distributions of the wild populations using a Bayesian procedure that assumes: (i) the survival probability s after maturity at age $T + 1$ is constant; (ii) the abundance of each cohort at maturity is log-normally distributed. Details are provided in the online supplementary material. We preferred this Bayesian procedure over the more commonly used Robson-Chapman (RC) estimator, which is based on similar assumptions, because it generates a complete range of plausible survival probabilities rather than a single value (Chapman, 1960). We compared our survival predictions with RC estimates and found broad agreement between the two, with the majority of the RC estimates lying within the Bayesian confidence intervals.

4. Results

4.1. Is growth biphasic?

For all data sets, GB fits were demonstrably superior to vB fits (Fig. 1). For the Opeongo stock, the GB model generated DIC values that were much lower than the vB model for both the wild (26493 vs. 26777, $\Delta\text{DIC} = 284$) and the hatchery (7573 vs. 7768, $\Delta\text{DIC} = 195$) data. Similarly, for both the Michipicoten (717 vs. 924, $\Delta\text{DIC} = 207$) and Slate (782 vs. 853, $\Delta\text{DIC} = 71$) stocks, the GB model generated significantly lower DIC values. In addition, residual plots for all four sets of fits (Fig. 2) demonstrate systematic, age-specific biases in the vB fits that are absent from the GB fits: consistent under-prediction is followed by progressively increasing over-prediction as age increases from pre-maturity to post-maturity.

4.2. Is adult deceleration of somatic growth linked to re-allocation of production to reproductive products?

Observed egg volumes exhibited a highly significant positive correlation with the predicted egg volumes (Fig. 3: $r = 0.74$, $p = 2.2 \times 10^{-16}$, $df = 102$). Regressing the two quantities against each other, using a geometric mean regression to account for the fact that both variables have errors, we found that the intercept was not significantly different from zero (Ricker, 1973; Draper and Smith, 1998; Analytical Software Inc., 2003). Performing a simple linear regression forced through the origin we obtained a

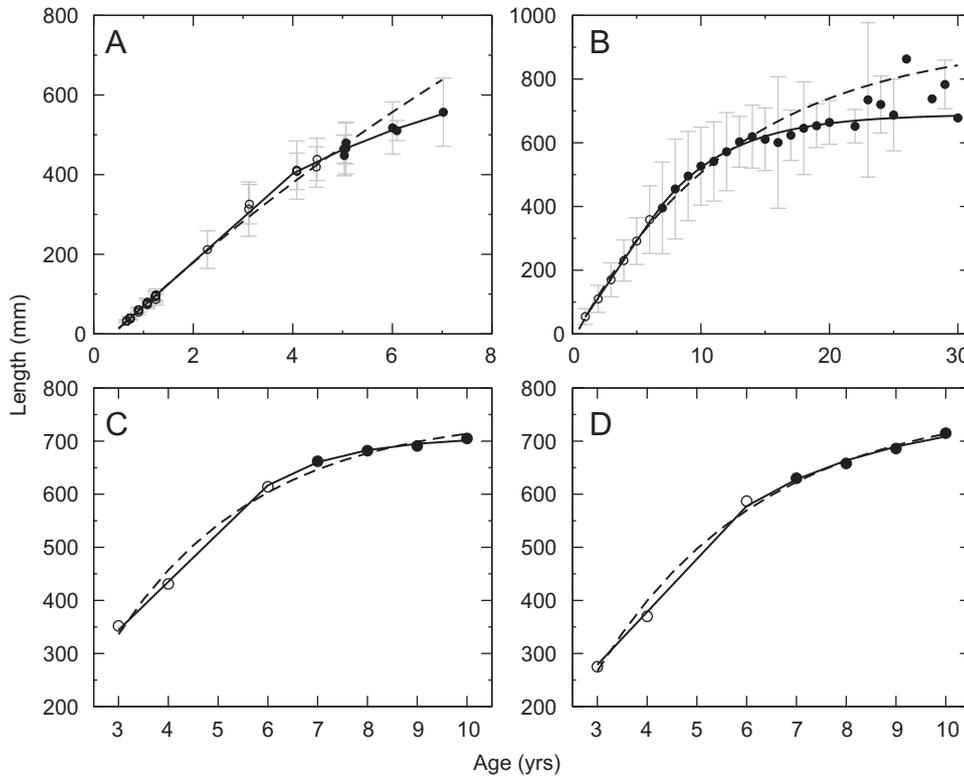


Fig. 1. Fits to age-length data for: (A) the Opeongo hatchery population; (B) the wild Opeongo population; (C) a single Michipicoten individual; (D) a single Slate individual. Juvenile growth is shown as open circles and adult growth as filled circles with errors bars giving the range (2 std. devs.) in the populations. The solid line shows posterior mean predictions for length using the GB model, the dashed line the vB model predictions.

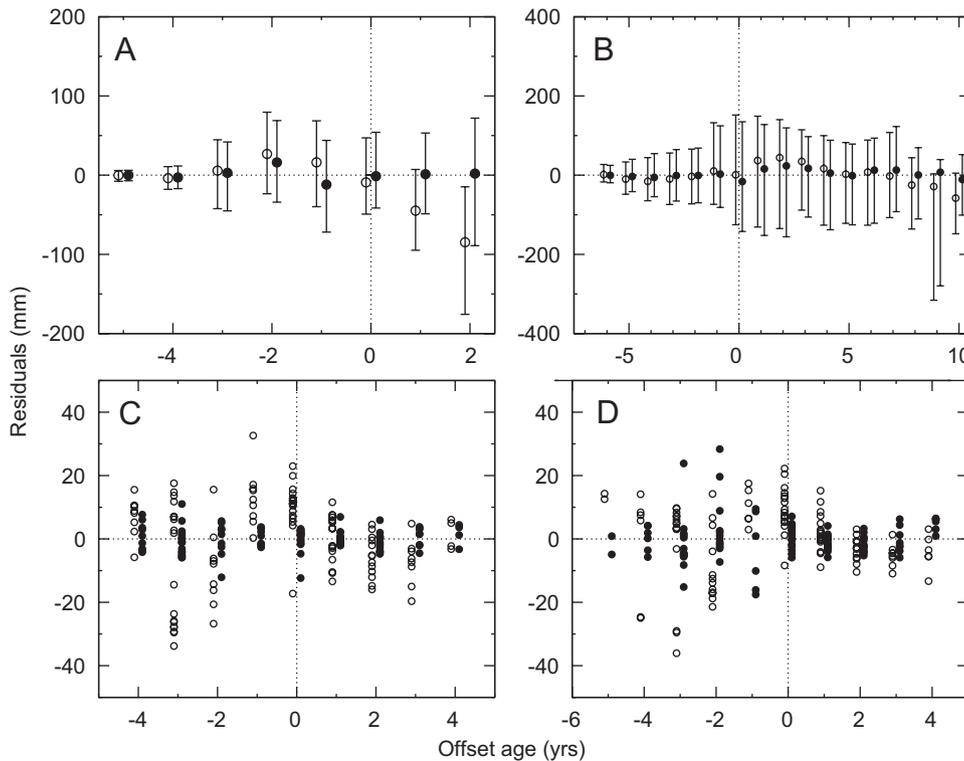


Fig. 2. Residuals for the GB model (filled circles) and vB model (open circles), defined as observed length minus the posterior mean of the model prediction, for fits to age-length data for: (A) the Opeongo hatchery population; (B) the wild Opeongo population; (C) all Michipicoten individuals; (D) all Slate individuals. The x-axis is age but offset so that zero corresponds to the first mature year. For the population data medians are shown with error bars giving 95% confidence intervals.

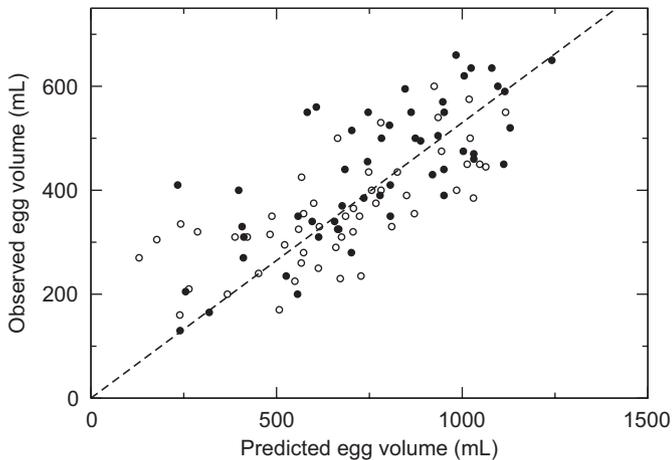


Fig. 3. Observed egg volumes (*y*-axis) plotted against predictions from hierarchical fits of the GB model (*x*-axis) for hatchery-raised fish of Michipicoten (solid circles) and Slate (open circles) stocks. The dashed line shows the prediction that observed volumes are 53% of predicted obtained by a simple linear regression forced through the origin (R Development Core Team, 2006).

proportionality constant of 0.53 (R Development Core Team, 2006). The observed egg volumes are 53% of what should be expected given the assumptions of the generic biphasic model.

4.3. Is the seasonal energy allocation pattern consistent with selection for optimal reproductive investment?

The optimal energy allocation pattern within a growing season specifies that breeding females should allocate available energy exclusively to somatic tissue at the beginning of the growing season and then, part-way through the season, switch to allocating exclusively to reproductive tissue (Kozłowski, 1996). If fish are following this strategy, we would not expect to see somatic growth in females within an age group once they had begun ovarian development. We used analysis of covariance on the length at capture data (categorical variables = age, year; covariate = julian date of capture) from the Lake Opeongo harvest data set to test for this behaviour. Well sampled age groups of females captured with developing ovaries over the period May through September (ages 7–11, $n_{age} > 48$, $n_{total} = 281$) did not exhibit detectable somatic growth (rate = -0.09 mm/day, $p > 0.05$). In contrast, well-sampled age groups of females captured with undeveloped ovaries over the same time period (ages 5–8, $n_{age} > 30$, $n_{total} = 323$) did exhibit significant somatic growth (rate = 0.31 mm/day, $p < 0.0001$). In both analyses, fish in each age group were observed evenly distributed over the 5 month sampling interval, providing a similar opportunity to detect somatic growth. These findings are consistent with the fundamental assumption of our biphasic models that adults switch their allocation of energy from soma to gonads part way through each growing season.

4.4. Which optimal investment model best describes growth and investment patterns? VGO or FGO?

In Fig. 4, we show fits of the VGO and FGO growth models to the wild Opeongo population: age-length predictions and maturation estimates for both models are provided, as well as an independent maturation estimate derived from a 2D logistic regression of maturation against age and length (R Development Core Team, 2006). The VGO model fits the maturation and growth data for younger fish well, but progressively diverges from growth data for older ages. In contrast, the FGO model does better at

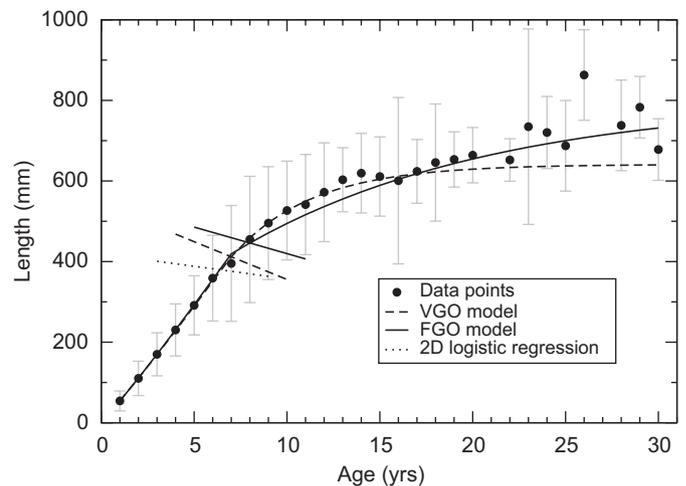


Fig. 4. The Bayesian fits of the fixed *g* (FGO) and variable *g* (VGO) optimum growth models to 2596 length at age data points and 1030 observations of maturation status. The empirical length data is shown as mean lengths-at-age (filled circles) with grey error bars giving range (two std. devs.). The solid line shows the mean lengths at age for the FGO model fit and the dashed that of the VGO model. Also shown, bisecting the growth curves, are the P50 maturation lines where the model predicted probability of observing a mature fish is 50% (solid black—FGO, dashed black—VGO, dotted—2D logistic regression). Mature fish will lie above and to the right of these lines.

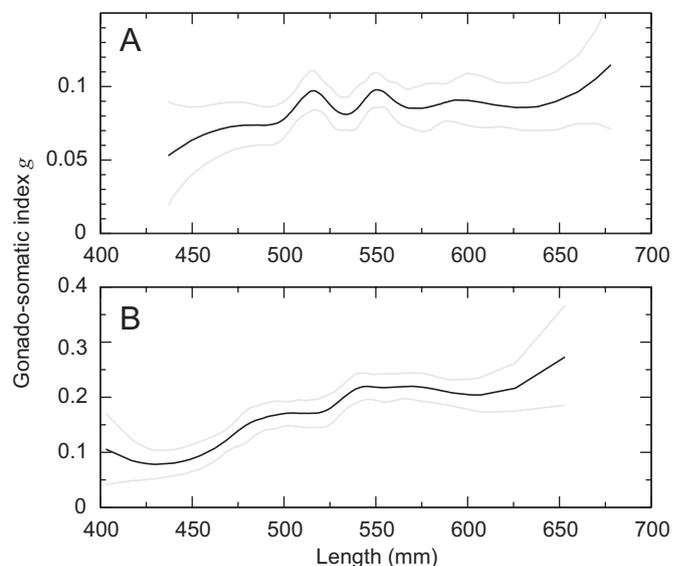


Fig. 5. Scaling of gonado-somatic index with length (*mm*) for wild (A) and hatchery-raised (B) female lake trout from Lake Opeongo. The results show medians (black line) and 95% confidence intervals (grey lines) from a Bayesian non-parametric regression.

predicting the sizes of older fish but is not good at predicting maturation and size data for younger fish.

The VGO model predicts that *g* should increase with length. This contrasts with the empirical observation that *g* often appears invariant in fish populations (Lester et al., 2004). In this section we examine the scaling of gonado-somatic index with length. From the angler harvest survey we selected all females caught after the 12th of August. This arbitrary date was deemed close enough to spawning, which occurs in early October, for gonad weights, or at least their dependence on length, to reflect their values at spawning. We then calculated *g* for these fish and removed those with $g < 0.02$ as being unlikely to spawn that year. This gave 201 data points. For the hatchery-raised fish, gonad weight was

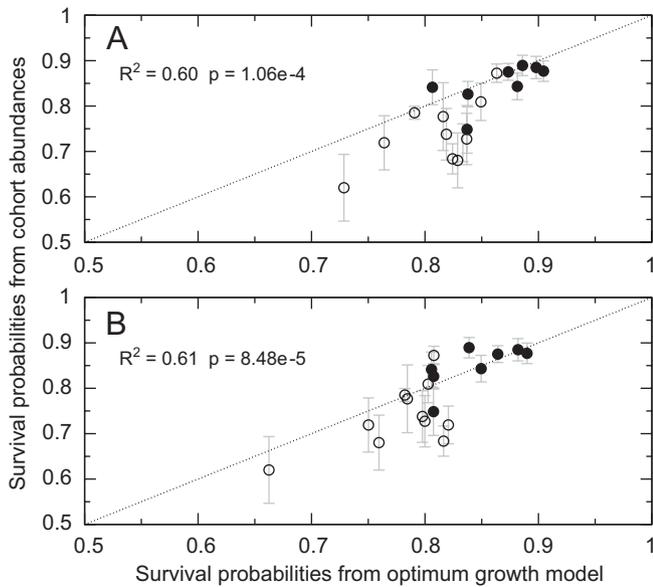


Fig. 6. Survival probabilities s determined from cohort abundances compared to those estimated from fitting the optimal growth models. The values are means over posterior distributions. The error bars give ranges (two std. devs.) in the estimates from the cohort abundances. The results from Pearson's correlations between means are also shown. The filled circles show the eight lakes from the Northwest Territories, the open circles the eleven lakes from Quebec and Ontario. (A) VGO model and (B) FGO model.

estimated by dividing egg volume by 0.75, which is the ratio of egg volume to gonad weight calculated in Section 3.5. This provided 120 g samples. We estimated the relationship between g and L for the two populations using a Bayesian procedure based on thin plate splines—see Crainiceanu et al. (2005) for implementation details (priors, sample lengths, number of knots, etc.). We found a strong positive association between g and L in the hatchery population and weak suggestions of a positive relationship (particularly for smaller fish) in the wild population (Fig. 5).

4.5. Do optimal fitness models describe life history in the wild?

Comparing survival probabilities from fitting the optimum growth models with those estimated from cohort abundances (Fig. 6), we found highly significant positive correlations for both data sets. When zero intercept regressions are performed on both data sets, the gradients are close to one (0.94 ± 0.02 and 0.97 ± 0.01 for the VGO and FGO models, respectively). The optimal growth model predictions are better for the lightly exploited lakes from the Northwest territories than for the more heavily exploited lakes from Ontario and Quebec.

5. Discussion

In Quince et al. (2008) we introduced a general framework for seasonal biphasic growth models based on simple energetics arguments. In this paper, we showed that (i) biphasic growth models provide a better description of the life time somatic growth pattern of lake trout females than the uniphasic vB model; (ii) the magnitude and timing of the shift in somatic growth pattern associated with the growth phase is consistent with a reallocation of energy at sexual maturity from somatic growth to reproductive tissue; (iii) associations between growth, reproductive investment and survival observed in wild populations are consistent with growth models that assume that annual repro-

ductive investment has been adjusted by selection to maximise lifetime reproductive output.

Although observed and predicted egg volumes were strongly correlated, the observed value was found to be substantially less ($\approx 53\%$) than the predicted value. The discrepancy has two mutually compatible explanations: (i) if the energy for gonad production is first stored as lipid and then converted to gonadal tissue (as is likely, see Blanchard et al., 2005), then this extra conversion step would incur energetic costs, causing observed egg volumes to be proportionately less than predicted; (ii) the framework assumes that there are no metabolic costs associated with maintaining gonadal mass—inclusion of these costs would cause observed egg volumes to be proportionately less than predicted.

Our two optimal growth models varied in their ability to describe observed behaviour: (i) the VGO model performed better at predicting maturation while the FGO model performed better at predicting length at older ages; (ii) increases in gonado-somatic index with length were observed among smaller individuals from both the hatchery-raised and wild Opeongo populations; (iii) estimates of adult survival probabilities for the two models were equally consistent with independent estimates of adult survival derived from cohort analysis. Several plausible explanations for this pattern of observations can be suggested:

1. g has an inherent maximum, set by such factors as the metabolic costs associated with gonadal maintenance or the need to maintain the streamlined body form required for efficient foraging;
2. in the wild, different individuals may adopt different reproductive allocation strategies, with those individuals that mature earlier and favour reproductive allocation over somatic growth experiencing somewhat lower survival rates; in this situation, individuals with lower reproductive allocation strategies would come to dominate the older larger age groups so that, at the population level, individual variation in VGO-type strategies would appear like a fixed g strategy;
3. γ , the ratio of the wet weight energy density of somatic tissue to gonad tissue, may decrease with size; larger fish may produce eggs with higher lipid concentrations that aid offspring survival (Berkeley et al., 2004; Kamler, 2005); this implies that $g' (= g/\gamma)$, may be increasing even if g is relatively fixed and therefore the VGO strategy can only be accurately detected by measuring tissue energy content rather than tissue weight.

Our fits of the FGO and VGO models to the growth and maturity patterns of wild populations generated estimates of two ecologically interesting parameters s and β . The s estimate for a particular population is the annual survival probability expected for the population given its observed life history, under the assumption that the observed life history has been adapted to maximise lifetime reproductive output. The fact that these s estimates were strongly correlated with independent estimates of s derived from cohort analysis implies that these populations have responded to the selective pressures imposed by the mortality rates they experience, and have adapted their reproductive strategies accordingly (Roff, 1984). In fisheries, it is more common to speak in terms of instantaneous mortalities (M , where $s = e^{-MY}$ and Y is the length of a year) than of survival probabilities. The fitted value of s provides an estimate of what we call the 'adapted mortality' of a population, the mortality that would generate the observed growth and maturation data if the population were at an adaptive evolutionary equilibrium. The estimate of adapted mortality generated by fitting our optimal growth models to life history data provides a simple way to evaluate the intensity of artificial selection that a recently implemented exploitation regime may

impose on the life history of an exploited population (Conover and Munch, 2002). If the current mortality rate greatly exceeds the estimate of adapted mortality rate, intense selection is likely occurring. For example in Fig. 6, we see that the lake trout populations from heavily exploited lakes in Ontario and Quebec appeared to be adapted to mortalities lower than those they are currently experiencing, suggesting that some evolution to earlier maturation times and greater investment in reproduction may be expected in these populations. In contrast, the lightly exploited populations from the Northwest Territories showed a close correspondence between adapted and current mortality estimates.

Our results with lake trout differ somewhat from those of Roff et al. (2006), who found it necessary to introduce an additional mortality term associated with reproduction in order to get their fixed- g optimal growth model to match observed growth and maturation data from perch and arctic charr. It is difficult to definitively determine the origin of this discrepancy, but it may be due to their assumption of a 100% conversion efficiency from somatic mass to gonadal mass. Reducing this efficiency term toward the value of 50% that we observed in our study could play the same role as their introduced mortality term in improving the fit between observed and predicted behaviour.

While we were only able to obtain separate estimates of s and β from one population (the Opeongo population), the resulting value for β (0.69) is well within the range (0.6–0.9) expected given the framework. The value of β realised in the wild will be a combination of physiological constraint and ecological opportunity. Under ad libitum feeding conditions in the hatchery, physiological constraints would appear to impose a value for β near 0.7 (Hanson et al., 1997). In the wild, the value for β could be significantly smaller in environments where the relative availability of forage suitable for large fish is low. In general, we believe that, if good quality juvenile growth data are available, then estimates of both β and s will contain useful information about the environment a population has recently been experiencing. For instance, with better data, it should be possible to determine if β is smaller for planktivorous lake trout populations than for piscivorous ones. In general we expect values of β and s realised in the wild will be strongly affected by the abundance and diversity of prey, and the abundance and diversity of predators, respectively.

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Appendix A

Supplementary data associated with this article can be found in the online version of [10.1016/j.jtbi.2008.05.030](https://doi.org/10.1016/j.jtbi.2008.05.030).

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