



Growth functions that incorporate the cost of reproduction



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ARTICLE INFO

Article history:

Received 12 September 2015

Received in revised form 19 October 2015

Accepted 20 October 2015

Available online 12 November 2015

Keywords:

Biphasic growth

Integrated modelling

Reproduction

Maturity

Arctic lake trout

Salvelinus namaycush

ABSTRACT

As the commonly-used von Bertalanffy growth function (VB) does not explicitly incorporate changes in growth due to allocation of energy to reproduction, a more flexible function could be used when attempting to model juvenile and adult growth simultaneously. Here we review biphasic growth models, with emphasis on those that explicitly incorporate the cost of reproduction, and propose two new models: the von Bertalanffy logistic- L_{∞} (VB log- L_{∞}) and the Cost of Reproduction (CoR) models. We fitted the models to eight data sets from males and females of four unfished or lightly-fished Arctic lake trout (*Salvelinus namaycush*) populations, and compared their fits to those of the commonly-used growth functions. In all cases, a biphasic growth model fitted the data better than simpler models such as the VB and the Richards models. Of the biphasic models, those that explicitly represent the reproductive process fitted the data best, particularly the Quince–Boukal model with the allometric exponent on the growth rate–weight relationship $\beta = 0.8$. The proposed models and the Quince–Boukal model provide a smooth transition between juvenile and adult growth by incorporating a logistic function with parameters dependent on the proportion of mature fish (or probability of being mature) at age. In addition to fitting growth models to the size-at-age data, we also attempted an integrated estimation for the three models that predict the age at maturity (the models are simultaneously fit to two data components, size at age and maturity at age.) The integrated estimation was the best compromise between modeling the two biological processes (growth and reproduction), but the separated estimation provided similar results in most cases, and may be easier to implement. We believe that taking the cost of reproduction into consideration is central for growth curves used in stock assessment models, as changes in growth trajectories may impact the perception of stock status. Future research should focus on the sensitivity of management advice to these growth curves for commercially-important fish stocks. For data-poor stocks, the models based on first principles, such as the Quince–Boukal model, can be used to produce management advice based on life history invariants, taking into account information on metabolic rates that can be obtained from other studies.

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1. Introduction

The von Bertalanffy growth function (VB curve, von Bertalanffy, 1938), the most widely used equation to model fish growth, is based on the assumption that the change in body weight over time results from the difference between the somatic process of building up (anabolism) and breaking down (catabolism). The VB model states

that anabolic processes scale with $\beta = 2/3$ of the body mass, while catabolic processes scale linearly with body mass (i.e., exponent η of the relationship between body mass and the energy used in catabolic process is 1). As von Bertalanffy (1957) states, “there will be growth so long as building up prevails over breaking down; the organism reaches a steady state if and when both processes are equal.” In terms of length, the growth rates decrease linearly with the increase in size (LVB model in Quinn and Deriso, 1999: pg. 132). von Bertalanffy (1957) also proposed that different metabolic types should be considered for different species (e.g. $\beta \neq 2/3$), but β is rarely changed in growth models. Metabolic studies, however, indicate that β for fishes shows a normal distribution centered on 0.79

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Table 1
Discontinuous biphasic growth: separate models for juveniles and adult growth. VB curve—von Bertalanffy growth function.

Reference	Juvenile growth	Adult growth	Application
Brody (1945)	Exponential	VB curve	
Day and Taylor (1997)	Power function of body mass	VB curve	
Roff (1983)	Constant growth rate	Growth rate is inversely proportional to the gonadosomatic index	American plaice
Lester et al. (2004, 2014)	Linear	VB curve	Walleye
Soriano et al. (1992)	VB curve	VB curve	Nile perch

(s.e. = 0.011) and ranges from 0.40 to 1.29 (Clarke and Johnston, 1999).

The cost of reproduction is not considered explicitly in the classic VB curve. However, Essington et al. (2001) considered η to be the allometric slope of all energy expenditure, i.e. also includes other energetic costs apart from catabolism, such as swimming and reproduction. The assumption of $\eta = 1$ is supported by empirical data: η was 1.02 on average (median 0.97, range 0.9–1.1) for the 17 species-locations combinations compiled by Essington et al. (2001).

Because fish are indeterminate growers, i.e., surplus energy is partially allocated to reproduction and partially to growth after the onset of maturity, there have been suggestions that the cost of reproduction should be explicitly taken into account when modelling fish growth (e.g., Brody, 1945; Roff, 1983). Several authors (e.g., Day and Taylor, 1997; Soriano et al., 1992) have proposed that two separate equations should be used: one for immature individuals (i.e., juveniles), where all surplus energy is devoted to somatic growth, and one for mature individuals, where a proportion of surplus energy is allocated to reproduction. Other authors (e.g., Laslett et al., 2002; Quince et al., 2008a) have proposed continuous functions that model a smooth transition between growth phases that may or may not be related to the cost of reproduction.

In this paper we review the continuous biphasic growth models and propose two new models (the Cost of Reproduction model, CoR, and the von Bertalanffy with L_∞ as a logistic function of age, VB log- L_∞) that explicitly incorporate the cost of reproduction and integrate maturity information as an extra likelihood component. We fit all models to data sets from males and females of four populations of Arctic lake trout *Salvelinus namaycush* (Walbaum 1792), and compare the fits to those of commonly-used growth functions.

2. Biphasic growth models

In this section we review the literature on biphasic growth models and propose two new models. Although not all biphasic growth models have been proposed to explicitly model the cost of reproduction, they may be able to mimic the changes due to the allocation of energy into reproduction. We found three types of modelling approaches in the literature: (i) discontinuous models, in which a separate model is used for each growth phase, and the age of transition is externally determined; (ii) continuous models with closed-form solutions, which are in essence a modification of the basic VB model with a smooth transition between growth phases and (iii) continuous models with no closed-form solution, which are based on first principles, do not have an analytical solution, and must be integrated numerically.

2.1. Discontinuous models

In this modelling approach, one function is chosen to model growth up to the age t_x and another to model growth for older animals. The age t_x is set externally and may be the age at maturity (Table 1). Brody (1945) (see also Quinn and Deriso, 1999: p. 134) proposed that length will increase exponentially to the age t_x and thereafter will follow a VB curve. Roff (1983) proposed that

the juvenile growth rate is constant, while the adult growth rate is inversely proportional to the gonadosomatic index. Day and Taylor (1997) suggested that the juvenile growth rate is a power function of body mass, while the adult growth trajectory follows a VB curve. Lester et al. (2004, 2014) argue that fish grow linearly until they mature (at t_x), then they grow following a VB curve. Soriano et al. (1992) proposed that two VB curves joined at age t_x . The disadvantage of those models is that t_x must be specified in advance. For these biphasic curves to be continuous the predictions for $L(t_x)$ and the derivatives at t_x for the two functions must match (Quinn and Deriso 1999: p.134). An option for using this approach would be to do a grid search for the best t_x .

2.2. Continuous models

Biphasic growth can also be modelled using a function to model the transition between phases. These models can be thought of as an individual changing smoothly between growth phases through its lifetime or as an aggregate summary of the somatic growth of a population of individuals that have discontinuous changes of phases at a range of ages. We found two groups of models in the literature: those with closed-form solutions for the expected length at age and those with recursive equations, for which the expected length at age is obtained by numerical integration, as no closed-form solution exist.

Six continuous biphasic growth models with closed-form solutions are listed in Table 2. All are based on modifications to the VB curve. Soriano et al. (1992) proposed models that include a hyperbolic function to create either L_∞ or k at age as a proportion of the overall L_∞ or k . The growth increment decreases to a minimum and is suddenly followed by the largest growth increment, which then steadily declines. Soriano et al.'s (1992) models were motivated by changes in diet that lead to the largest growth increment occurring when fish are thought to have fully switched to a new diet (e.g., from planktivore to piscivore). Porch et al. (2002) proposed a model in which the VB curve K coefficient declines exponentially with age. Ohnishi et al. (2012) proposed a VB model that considered that the proportion of energy allocated to reproduction changes smoothly with age following a logistic curve ("S-type" curve), with its inflection point at the age of sexual maturation. Laslett et al. (2002) proposed a VB curve with two growth parameters k and a logistic function that determines how K changes from one phase to the next. The curve makes a smooth transition between two growth parameters (k_1 and k_2). We propose the VB logistic- L_∞ model, by assuming a logistic transition between two asymptotic lengths $L_{\infty 1}$ and $L_{\infty 2} = L_{\infty 1} + \delta_{L_\infty}$. We choose L_∞ rather than k because changes in L_∞ performed better in other applications (e.g., time-varying growth, unpublished results). Also, near-linear growth for juveniles seen in many species is well modelled with a large L_∞ that is not compatible with the size of old individuals, indicating that modelling changes in L_∞ with age could provide a reasonable approach to modelling growth. In the VB log- L_∞ model, the asymptotic length at age is given by

$$L_{\infty, a} = L_{\infty 1} + (\delta_{L_\infty} \times p(a)) \quad (1)$$

Table 2

Continuous biphasic growth: closed-form models.

Model	Parameters	Equation	Reference
VB-hyper L_{∞}	5 $\phi = \{L_{\infty}, t_0, k, h, t_h\}$	$L(a) = L_{\infty} \left[1 - h \left((a - t_h)^2 + 1 \right)^{-1} \right] \left\{ 1 - \exp[-k(a - t_0)] \right\}$	Soriano et al. (1992)
VB-hyperK	5 $\phi = \{L_{\infty}, t_0, k, h, t_h\}$	$L(a) = L_{\infty} \left\{ 1 - \exp \left[-k \left[1 - h \left((a - t_h)^2 + 1 \right)^{-1} \right] (a - t_0) \right] \right\}$	Soriano et al. (1992)
VB-damped	5 $\phi = \{L_{\infty}, t_0, k_1, k_2, \lambda\}$	$L(a) = L_{\infty} \left\{ 1 - \exp \left[(k_2/\lambda) (\exp(-\lambda a) - \exp(-\lambda t_0)) - k_1(a - t_0) \right] \right\}$	Porch et al. (2002)
VB-S	6 $\phi = \{L_{\infty}, t_0, k, v, \lambda, t_m\}$	$L(a) = L_{\infty} \left\{ 1 - \exp \left[-k \left((1 - v)(a - t_0) - (v/\lambda) \left\{ \ln(1 + \exp(-\lambda(a - t_m))) - \ln(1 + \exp(-\lambda(t_0 - t_m))) \right\} \right) \right] \right\}$	Ohnishi et al. (2012)
VB-logK	6 $\phi = \{L_{\infty}, t_0, k_1, k_2, \alpha, \beta\}$	$L(a) = L_{\infty} \left\{ 1 - \exp(-k_2(a - t_0)) \left[1 + \exp(-\beta(a - t_0 - \alpha)) / (1 + \exp(\beta\alpha)) \right]^{-k_2 - k_1/\beta} \right\}$	Laslett et al. (2004)
VB log- L_{∞}	6 $\phi = \{L_{1,\infty}, L_{2,\infty}, t_0, k, t_{50}, t_{95}\}$	$L(a) = \left\{ L_{1,\infty} + (L_{2,\infty} - L_{1,\infty}) \left[1 + \exp \left((-\ln(19)(a - t_{50})) / (t_{95} - t_{50}) \right) \right]^{-1} \right\} \left\{ 1 - \exp[-k(a - t_0)] \right\}$	This study

Once $L_{\infty,a}$ is obtained, the VB curve is used to compute the expected size at age. The transition $p(a)$ can be assumed to be a consequence of maturity, and can be modelled using a logistic maturity-at-age function.

Three additional continuous models are included in our review, those that have no closed-form solution, but are rather modeled using recursive equations (Table 3). The first is the Gompertz function (Gompertz, 1825) with delayed development (Thornley and France, 2007). The Gompertz growth function has three parameters, the initial weight W_0 , the initial specific growth rate μ_0 and the proportional rate at which growth rates declines D_m . In the Gompertz function, the growth rate starts to decline at age $a=0$. Thornley and France (2007) proposed a model for which the proportional rate at which the growth rate declines is also variable, delaying the onset of the maximum proportional rate, supposedly to a later age, perhaps related to reproduction. This is achieved by replacing D with $D(a)$, a two-parameter equation as a function of age a : $D(a) = D_m(1 - \exp(-ka))$. The parameter k determines how quickly D moves to D_m , which is the maximum proportional rate of decline of the growth rate. The differential equation of changes in weight over age cannot be integrated analytically; thus numerical integration methods must be applied. Also, the length-weight parameters are necessary to transform weight at age to length at age. The second recursive model was proposed by Quince et al. (2008a,b) based on previous work by Lester et al. (2004) and generalized by Boukal et al. (2014). The Quince–Boukal model is based on first principles and bioenergetics considerations. Unlike the commonly-used VB curve, which assumes that the metabolic cost increases linearly with weight ($\eta = 1$), while the energy intake scales with $\beta = 2/3$ of body weight, the Quince–Boukal releases those two assumptions, and replaces them by the assumption that the instantaneous growth rate (dW/dt) scales with β of body weight (i.e., $\beta = \eta$) and β can be a range of values. The cost of reproduction is implicitly included in the Quince–Boukal model. Quince et al. (2008a) proposed the model in a transformed unit, proportional to length. Boukal et al. (2014) presented alternative formulations of the model in units of length or weight, and also generalized it to allow for non-isometric growth (Eq. (T3.6)). The model depends on seven parameters (Eqs. (T3.4, T3.5, and T3.7): L_0 the length at age 0, β the allometric exponent in the growth rate-weight relationship, c the coefficient in the allometric growth rate-weight relationship, q the conversion factor between somatic and gonadic investment, r the relative reproductive investment, and the two parameters of the maturity-at-age curve. The number of parameters can be reduced by assuming that the energy allocation to reproduction maximizes fitness.

We propose a third recursive model, the Cost of Reproduction (CoR) Model. We start with the von Bertalanffy growth model for

length and include a term for the cost of reproduction after maturity that scales with the cube of the length (or linearly with body mass, if the exponent of the length-weight relationship is equal to 3). The VB curve assumes the growth rate decreases linearly with length:

$$\frac{dL}{da} = \alpha - \theta L \quad (2)$$

where L is length, α and θ are parameters. The solution for this differential equation (reparametrized in the standard way) is:

$$L_a = L_{\infty} (1 - e^{-k(a-t_0)}) \quad (3)$$

where $L_{\infty} = \frac{\alpha}{\theta}$ is the asymptotic maximum length, $k = \theta$ (in time units⁻¹), and t_0 is the theoretical age at which the length is 0. We suggest the inclusion of a term that explicitly takes into account the cost of reproduction:

$$\frac{dL}{da} = \alpha - \theta L - p(a)rL^3 \quad (4)$$

where $p(a)$ is the proportion of fish mature at each age a (Eq. (T3.9)) and r is a parameter. The cost of energy used in reproduction is assumed to be proportional to the body mass when the exponent of the length-weight relationship is equal to 3.

We approximated the differential equation by a difference equation with small time steps (Euler integration method), so that the growth increment is:

$$G_a = \alpha - \theta L_{a-1} - p(a)rL_{a-1}^3 \quad (5)$$

The length at age a is:

$$L_a = L_{a-1} + G_a \quad (6)$$

The model is initiated at L_{a_0} , the length at age a_0 , which is also a parameter. Age a_0 can be chosen to be an age close to the minimum age in the data set, well before the onset of maturity. In this case $p(a)rL_{a-1}^3 = 0$, because $p(a) = 0$. The first growth increment is, therefore:

$$G_{a_0+1} = \alpha - \theta L_{a_0} \quad (7)$$

G_{a_0+1} can be used as a parameter instead of α , so that:

$$\alpha = G_{a_0+1} + \theta L_{a_0} \quad (8)$$

The maturity-at-age proportion, $p(a)$, is modelled using a two-parameter logistic function (Eq. (T3.10)). Therefore, the CoR model has six parameters: L_{a_0} , G_{a_0+1} , θ , r , t_{50} and t_{95} . We assumed in this application that $a_0 = 0$ days and $L_{a_0} = 1$ mm because we want to model growth starting at a very early age. In initial fits of the model, the L_{a_0} was estimated, but did not change from the assumed value, so for the results presented here this parameter was fixed at 1 mm.

Table 3
Continuous biphasic growth: recursive biphasic growth models. a is age, $L(a)$ denotes the length at age a , $W(a)$ is the weight at age a and $p(a)$ is the proportion mature at age a . The age when 50% of the individuals are mature is t_{50} , the age when 95% of the individuals are mature is $t_{95} = t_{50} + \delta_{95}$.

Model	Parameters	Recurrence equations	References
GDD: Gompertz with delayed Development	4 $\phi = \{W_0, \mu_0, k, D_m\}$	$W(0) = W_0$ (T3.1) $W(a+1) = W(a) * \left\{ 1 + \mu_0 \exp \left[-D_m \left(a - \left(1 - \exp(-ka)/k \right) \right) \right] \right\}$ (T3.2) $L(a) = (W(a)b^{-1})^{1/d}$ (T3.3) $L(0) = L_0$ (T3.4)	Thornley and France (2007) pp. 190–192
Quince–Boukal	7 $\phi = \{L_0, \beta, c, q, r, t_{50}, t_{95}\}$	$p(a) = \left\{ 1 + \exp \left[-\ln(19) * (a - t_{50}) / (t_{95} - t_{50}) \right] \right\}^{-1}$ (T3.5) $L(a) = (W(a)b^{-1})^{1/d}$ (T3.6)	Boukal et al. (2014) Quince et al. (2008a, b), Lester et al. (2004)
	6 $\phi = \{L_{a_0}, G_{a_0+1}, \theta, r, t_{50}, t_{95}\}$	$L(a+1) = \left\{ \left[L(a)^{(1-\beta)^d} + (1-\beta)cb^{-(1-\beta)} \right] \left[1 + q^{-1}(1-\beta)rp(a+1) \right]^{-1} \right\}^{[(1-\beta)^d]^{-1}}$ (T3.7) $L(a_0) = L_{a_0}$ (T3.8)	This study
CoR: cost of reproduction		$p(a) = \left\{ 1 + \exp \left[-\ln(19)(a - t_{50}) / (t_{95} - t_{50}) \right] \right\}^{-1}$ (T3.9) $L(a+1) = L(a) + G_{a_0+1} + \theta L_{a_0} - \theta L(a) - rp(a)L(a)^3$ (T3.10)	

Our CoR is similar to the VB-logK model, but is more plausible because as the VB-logK implicitly modifies both anabolism and catabolism at maturity, using the same parameter. The transition depends on the allocation of energy to reproduction.

2.3. Simple growth functions

The models we have reviewed are compared to the VB (von Bertalanffy, 1938) and the Richards (Richards, 1959; Schnute, 1981) models reparametrized in terms of L_1 (the average length of the youngest age well represented in the sample, a_1) and L_2 (the average length of the oldest age well represented in the sample, a_2) (Schnute and Fournier, 1980; Methot and Wetzel, 2013):

$$L_a = \left[L_1 + (L_2 - L_1) \times \left(\frac{1 - \exp(-k(a - a_1))}{1 - \exp(-k(a_2 - a_1))} \right) \right]^{1/\nu} \quad (9)$$

This is “expected-value” parametrization, i.e., two of the parameters are equal to the values predicted by the model for ages a_1 and a_2 (Ross, 1970). The model reduces to the VB growth curve when $\nu = 1$. For the VB curve, this parameterization was found to be best in the sense that it exhibits “close-to-linear” behavior when using least-square estimation, i.e., the estimators follow more closely the asymptotic assumptions of being unbiased, normally distributed, and with minimum variance, similar to a linear model (Ratkowsky, 1986). This behavior helps improve convergence regardless of initial values (Ratkowsky, 1986). In addition, the parameters have straightforward biological interpretation, as none is an extrapolation beyond the data (if a_1 and a_2 are chosen to be within the data range; Schnute and Fournier, 1980).

3. Methods

3.1. Model fits

The models were fit using maximum likelihood. The objective function was composed of the length-at-age likelihood or a combination of the length-at-age likelihood and the maturity-at-age likelihood.

Length-at-age likelihood: The observed length of fish i at age a was assumed to be:

$$L_{a,i} = \hat{L}_a + e_i \quad (10)$$

where \hat{L}_a is the predicted average length at age a and e_i is a normally-distributed random variable $e_i \sim N(0, \sigma_a^2)$. The error,

which is assumed to be process error (i.e., variation in length at age in the population, and not in the observations, e.g. measurement error), was modeled with the standard deviation as a linear function of the average length at age:

$$\sigma_a = \alpha_\sigma + \beta_\sigma L_a \quad (11)$$

The length-at-age likelihood component was the product of normal distributions for each observation, each centered at the average length predicted by the growth model and with variance equal to σ_a^2 . For ease of implementation, the likelihoods were transformed into negative log-likelihoods and summed over all observations (NLL_{age}).

Maturity-at-age likelihood: The maturity-at-age likelihood was assumed to be a Bernoulli distribution with parameter p modeled following a logistic function of age $p(a)$, which depends on two parameters: t_{50} , the age at 50% maturity, and t_{95} the age at 95% maturity (Eqs. (T3.5) and (T3.9)):

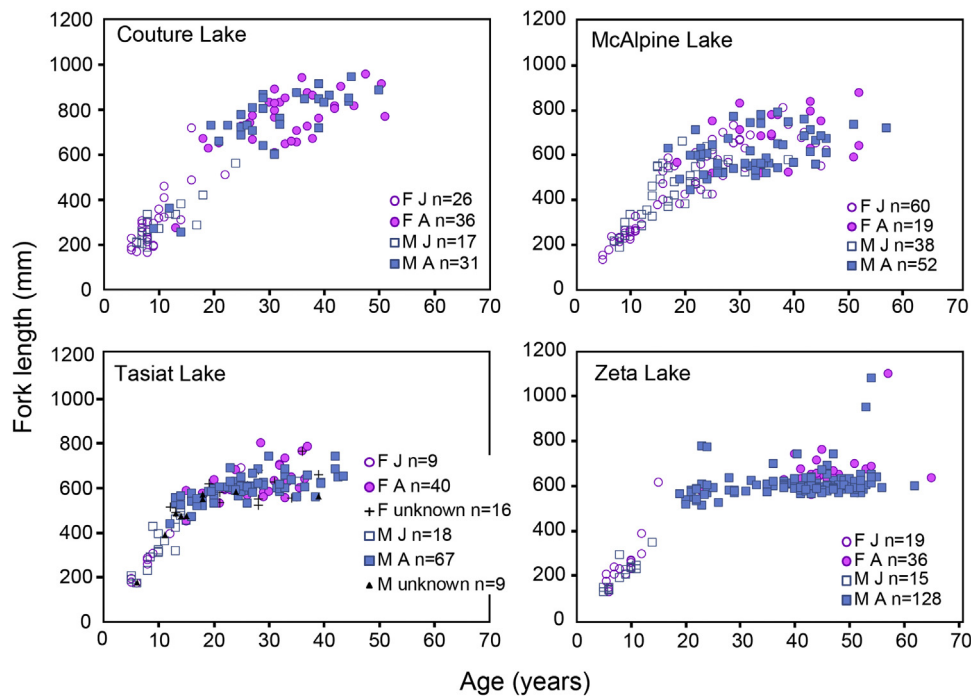
$$\pi(x) = p(a)^x (1 - p(a))^{1-x} \quad (12)$$

where $p(a)$ is the probability of being mature at age a , x is a random variable such that $x = 0$ for immature individuals, and $x = 1$ for mature individuals. To reduce the correlation among parameter estimates, we replaced the parameter t_{95} by $t_{95} = t_{50} + \delta_{95}$. The maturity-at-age likelihood was obtained by the product of Eq. (12) over each observation. For ease of implementation, the likelihoods were transformed into negative log-likelihoods and summed over all observations (NLL_{mat}).

The models that explicitly include the cost of reproduction can be fit in three ways: (i) simultaneously to both the proportion mature-at-age and size-at-age data, with all parameters free (integrated estimation), (ii) only to size-at-age data with all the parameters free (full estimation), and (iii) only to size-at-age data with the reproductive parameters fixed to external values obtained by fitting the proportion mature-at-age model to the mature-at-age data only (external estimation). These three options are compared. When using integrated estimation, the data components may be given different emphasis by multiplying the corresponding negative log-likelihood (NLL_{age} or NLL_{mat}) by a coefficient (λ). In fisheries stock assessment models, for example, the conclusions drawn can depend heavily on the relative weight assigned to different data components (Francis, 2011). We explored this issue briefly using the CoR model, by comparing the parameter estimates obtained for the Tasiat Lake females data using different values of λ for the maturity-at-age data, while keeping $\lambda = 1$ for the size at age. In the

Table 4Sample sizes (*n*), age (*a*, years) and fork-length (FL, mm) ranges of fish sampled by lake, sex and maturity stage.

Lake	Latitude	Longitude	Females	Adult	Unknown	Males	Adult	Unknown	Total
Couture	60°07' N	75°25' W	n	26	36	17	31		110
			a	5–22	13–51	6–24	9–50		5–51
			FL	166–718	276–956	187–562	256–945		166–956
McAlpine	66°35' N	102°46' W	n	60	19	38	52		169
			a	5–46	18.5–52	7–39	17–57		5–57
			FL	134–810	520–878	190–660	444–790		134–878
Tasiat	59°11' N	75°17' W	n	9	40	18	67	9	159
			a	5–25	14–52	5–35.5	12–43.5	6–39	5–43.5
			FL	173–690	450–800	173–630	437–743	174–583	173–800
Zeta	71°06' N	106°33' W	n	19	36	15	128		198
			a	5.5–47	23–65	5–39	19–62		5–65
			FL	127–630	560–1100	126–347	512–1080		126–1100
		Total	n	114	131	88	278	9	636

**Fig. 1.** Scatterplot of fork length vs. age for males (M), females (F), juveniles (J), adults (A) and animals with unknown maturity of Arctic lake trout *Salvelinus namaycush* the four lakes studied. *n* is the sample size.

case of using the full estimation, the values of \hat{t}_{50} and $\hat{\delta}_{95}$ were used to compute an “implied” likelihood, which we define as the NLL of those values, given the maturity-at-age data. The implied likelihood was used to compare the plausibility of those values with the ones obtained using the integrated or the external estimation.

The recursive models were integrated using the Euler method, using daily time steps for the CoR and annual time steps for the Quince–Boukal and GDD models. The models were implemented using ADMB (Fournier et al., 2012).

When fitting the Quince–Boukal model, we found that for some combination of parameters that included high values of β led to unrealistic predictions for greater ages (the fish were predicted to “shrink”). We thus implemented a version of the models that would include a high penalty for “shrinking.” This was done by adding a value to the objective function when $L(a) < L(a-1)$. The value is computed using the `posfun()` procedure in ADMB (Fournier, 2015).

3.2. Model comparison

We compared different models fit to the same data sets, using Akaike Information Criterion for small sample sizes (AIC_c , Hurvich

and Tsai, 1989; Burnham and Anderson, 2002), which is based on a modification of the AIC (Akaike, 1973). The most parsimonious model is that with the lowest AIC_c , which is defined as:

$$AIC_c = -2\ln l + 2m + \left[\frac{2m(m+1)}{n-m-1} \right] \quad (13)$$

where $\ln l$ is the log-likelihood, m is the number of parameters, and n is the sample size. We also compared the separate likelihood components (for size-at-age and maturity-at-age data) of models, when appropriate.

3.3. Data sets

We fitted the models to eight data sets of males and females from four unfished or lightly-fished populations of Arctic lake trout *S. namaycush* (Table 4, Fig. 1). Fish were collected in 2002 and 2003 from Zeta Lake, Couture Lake, McAlpine Lake, and Tasiat Lake. All of the lakes are mesoscale lakes (areas between 50 and 400 km²) found in isolated regions of the Canadian Arctic and sub-Arctic. Lake trout were sampled in July or August with gillnets, using multi-mesh panels ranging, by 1/2” intervals, from 1 to 6”, plus 7 and

8" ones. This sampling approach was used to best sample all size classes in the lake. The fish were measured to the nearest millimeter (fork length) weighed to the nearest 0.1 g, and the sex and maturity stage (juvenile or adult) were determined through internal examination. The maturity stage was unavailable for some specimens from the Tasiat Lake. Only the size-at-age data were used for those fish. The sagittal otoliths were removed from the fish and embedded and sectioned through the core prior to image enhancement and age determination. The accuracy of the age interpretations was confirmed using the bomb-radiocarbon method (Campana et al., 2008).

4. Results

4.1. Model fits of proposed models: CoR and VB log- L_{∞}

We examined the fits to data for Tasiat Lake females (Table 5) in detail to gain insights about the two proposed models. Initially, the values for the maturity parameters were estimated externally from the growth model by fitting the logistic model (Eq. (T3.10)) to the maturity-at-age data only (Run 0, $\hat{t}_{50} = 12.868$ years, $\hat{\delta}_{95} = 7.330$ years, $NLL_{ma} = 8.628$) and used to fit the CoR and the VB log- L_{∞} models.

To first explore the variability-at-age assumptions, we initially fit the CoR model only to size-at-age data with the maturity parameters fixed based on the fit of the logistic model (T3.9) to the maturity-at-age data (external estimation), with three variability options. The lowest AIC_c was obtained for the model with constant CV over ages ($AIC_c = 712.677$, Run 1, Fig. 2a, Table 5). A two-parameter variability-at-age function led to a worse fit ($AIC_c = 715.021$, not in Table 5), but better than the model with constant standard deviation ($AIC_c = 720.299$, not in Table 5). Based on these results, we chose to conduct the remaining the model fits using the constant CV assumption ($\alpha_{\sigma} = 0$; $\sigma_a = \beta_{\sigma} L_a$).

For the CoR model, the size-at-age data had enough information to estimate the 50% maturity parameter t_{50} (Run 2, $AIC_c = 715.167$, Table 5) conditioned on a fixed $\hat{\delta}_{95} = 7.330$. However the estimated t_{50} was slightly smaller ($\hat{t}_{50} = 12.470$ years) than that estimated using maturity-at-age data only ($\hat{t}_{50} = 12.868$ years). The negative log-likelihood for the maturity-at-age data (NLL_{mat}) implied for Run 2 was 8.559, almost the same as NLL_{mat} when fitting only to the maturity-at-age data (Run 0; $NLL_{mat} = 8.528$). The model converged to a greater age at 50% maturity and a knife-edge transition between the two growth phases ($\hat{t}_{50} = 13.999$, $\hat{\delta}_{95} = 0.0004$) when δ_{95} was also estimated (Run 3). This run had a better fit to the size-at-age data (lower NLL_{age}), but higher AIC_c (714.016), and implied an infinite NLL_{mat} , which indicates the incompatibility of those parameters estimates with the maturity-at-age data. When the CoR model was fit to both data components simultaneously (Run 4), the model fitted the size-at-age data about the same as Run 1, which had the maturity parameters estimated externally ($NLL_{age} = 351.767$ vs. 352.005), and the maturity-at-age data about the same as Run 0 ($NLL_{mat} = 8.679$ vs. 8.528). The inclusion of the maturity-at-age data in Run 4 led to a lower estimate of $\hat{\delta}_{95}$ (6.129) than the model that fit only to maturity-at-age data ($\hat{\delta}_{95} = 7.330$), but not as low as in Run 3 ($\hat{\delta}_{95} = 0.0004$), when only size-at-age data were used. The estimates from Run 4 represent the best compromise between the two data components based on the implied data weighting of the likelihood functions and sample sizes (Fig. 2c).

When the importance of the maturity-at-age data is increased 10 times ($\lambda = 10$), the CoR model fits the size-at-age data almost as well as when no maturity data are used (Run 5, $NLL_{age} = 352.052$, Table 5), and only slightly improves the fit to the maturity data ($NLL_{mat} = 8.530$), in comparison with Run 4 ($\lambda = 1$). When the weight is increased to $\lambda = 100$ times (Run 6, Table 5), at least for this data

Table 5
Fit of the logistic model (proportion mature at age), the Cost of Reproduction model (CoR) and the VB log- L_{∞} models to the size-at-age and/or the maturity-at-age data for female Arctic lake trout of Lake Tasiat. λ is a coefficient that is multiplied to the likelihood to change the weight given to this data component in the model fit. m is the number of estimated parameters. For the VB log- L_{∞} $L_{2,\infty} = L_{1,\infty} + \delta_{L,\infty}$.

Run	Model	Variation	Data used		Likelihood or implied likelihood		Parameter estimates or fixed values						Correlation matrix		
			Maturity-at-age	Size-at-age	m	NLL_{mat}	NLL_{age}	AIC_c	t_{50} years	δ_{95} years	θ days $^{-1}$	r	G_1	β_{σ}	Min cor
0	Logistic		Yes	No	2	8.528		712.677	12.868	7.3					
1	CoR	t_{50} , δ_{95} fixed	No	Yes	4	8.528	352.005	712.677	12.868	7.3	1.03E-10	3.57E-10	0.10	0.100	-0.30
2	CoR	t_{50} estimated, δ_{95} fixed	No	Yes	5	8.559	352.075	715.167	12.470	7.3	2.71E-13	3.57E-10	0.10	0.101	0.65
3	CoR	t_{50} , δ_{95} estimated	No	Yes	6	infinity	350.284	714.016	13.999	4E-4	2.71E-13	3.49E-10	0.10	0.098	0
4	CoR	t_{50} , δ_{95} estimated	Yes	Yes	6	8.679	351.767		13.043	6.1	1.03E-10	3.55E-10	0.10	0.100	0
5	CoR	t_{50} , δ_{95} estimated	Yes, $\lambda = 10$	Yes	6	8.530	352.052		12.88	7.2	9.40E-12	3.57E-10	0.10	0.101	0.64
6	CoR	t_{50} , δ_{95} estimated	Yes, $\lambda = 100$	Yes	6	8.528	352.088		12.869	7.3	1.03E-10	3.57E-10	0.10	0.100	0.65
7	VB log- L_{∞}	t_{50} , δ_{95} fixed	No	Yes	5	8.528	353.007	717.135	12.868	7.3	0.0003436	757.195	548.95	0.102	-0.99
8	VB log- L_{∞}	t_{50} , δ_{95} estimated	No	Yes	7	13.255	345.187	706.339	9.42	4.9	6.082E-16	-28305.605	8.491E+12	0.091	0.008
9	VB log- L_{∞}	t_{50} , δ_{95} estimated	Yes	Yes	7	10.807	346.352		9.755	6.5	1.9E-12	-40251.02	8.491E+12	0.092	No matrix
10	VB		No	Yes	4		362.376	733.419			K (days $^{-1}$)	L_1 (mm)	746.93	0.118	-0.93
11	Richards		No	Yes	5		351.373	713.763			0.0001827	6.906E-09	652.92	0.099	-0.92
											0.0004648	27.28			0.0006

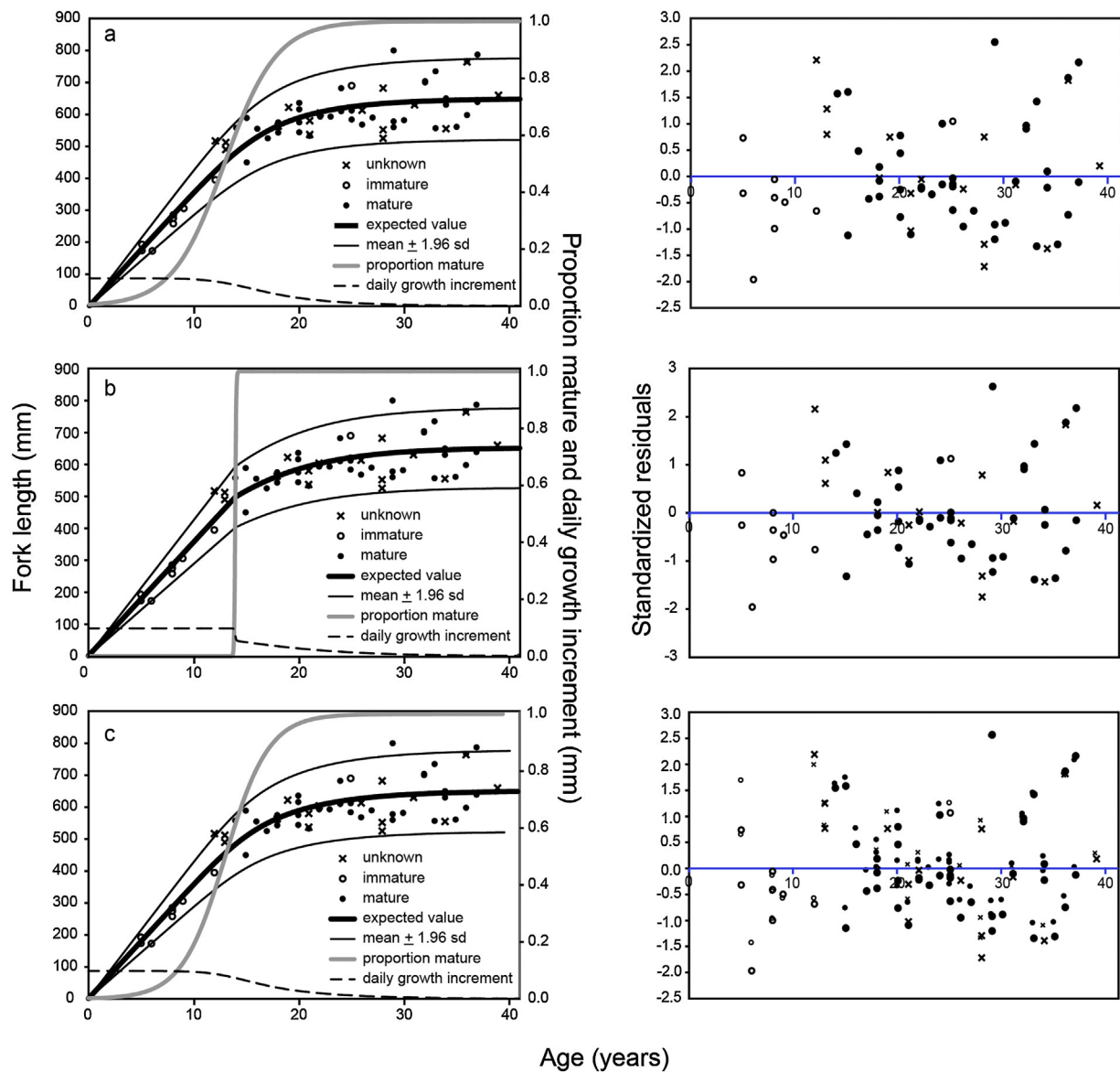


Fig. 2. Fits (left panels) and residuals (right panels) of the CoR model to the Tasiat Lake female data. (a) Run 1, maturity parameters estimated externally ($\hat{t}_{50} = 12.868$, $\hat{\delta}_{95} = 7.3$), model fit to size-at-age data only with maturity parameters fixed to the external estimates. (b) Run 3, maturity parameters estimated internally within the CoR model fit to size-at-age data only ($\hat{t}_{50} = 13.998$, $\hat{\delta}_{95} = 0.0004$). (c) Run 5, maturity parameters estimated internally within the CoR model fit to both size-at-age and maturity-at-age data ($\hat{t}_{50} = 13.043$, $\hat{\delta}_{95} = 7.2$).

set, the estimates of the maturity parameters were almost identical to those obtained in Run 0, indicating that the external estimation of the maturity parameters is equivalent to increase the weight of the maturity-at-age data to about 100 times in the model.

The VB log- L_{∞} model fit to size-at-age data alone with fixed maturity parameters (Run 7, $AIC_c = 717.135$, Table 5) had a worse fit than the equivalent CoR model (Run 1 $AIC_c = 712.677$, Table 5). However, unlike the CoR model, the VB log- L_{∞} model was able to estimate both maturity parameters using only size-at-age data (Run 8, $AIC_c = 706.339$, $\hat{t}_{50} = 9.420$, $\hat{\delta}_{95} = 4.874$), without considerably degrading the implied fit to the maturity-at-age data ($NLL_{mat} = 13.255$). This fit, though, was obtained at very unrealistic values for the growth parameters (Table 5) that allowed for the peculiar shape of the curve (Fig. 3b). Convergence was problematic, but was attained. The inclusion of the maturity-at-age data in the VB log- L_{∞} model (Run 9) resulted in similar estimates for both the maturity and growth parameters as Run 8 (Fig. 3b and c), indicating that the size-at-age data provided information about the growth transition (and therefore about the age at maturity if

the model assumptions are correct). However, there is no guarantee that this fit had indeed arrived to the global minimum because the Hessian matrix for this run was not positive definite.

The CoR model fitted only to the size-at-age data had a lower AIC_c (Run 1 $AIC_c = 712.677$, Run 3 $AIC_c = 714.016$, Table 5, Fig. 2) than the von Bertalanffy (Run 10, $AIC_c = 733.419$, Fig. 4, Table 5). However the Richards model fitted the data very similarly to the CoR model (Run 11, $AIC_c = 713.763$, Table 5, Fig. 4). The VB log- L_{∞} model with maturity parameters estimated internally by fitting only to size-at-age data had the lowest AIC_c (Run 8, $AIC_c = 706.339$, Table 5, Fig. 3b). The fits to the size-at-age data were worse for both the von Bertalanffy (Run 10, $NLL_{age} = 362.376$) and the Richards (Run 11, $NLL_{age} = 352.22$) models when compared to any of the CoR model fits or the two fits of the VB log- L_{∞} model when maturity parameters are estimated (Table 5). All fits of the CoR model showed no patterns in the residuals (Fig. 2). The VB log- L_{∞} model had almost the same residual pattern as the CoR model (Fig. 3). The VB curve, on the other hand, had the poorest residual pattern of all fitted models (Fig. 4).

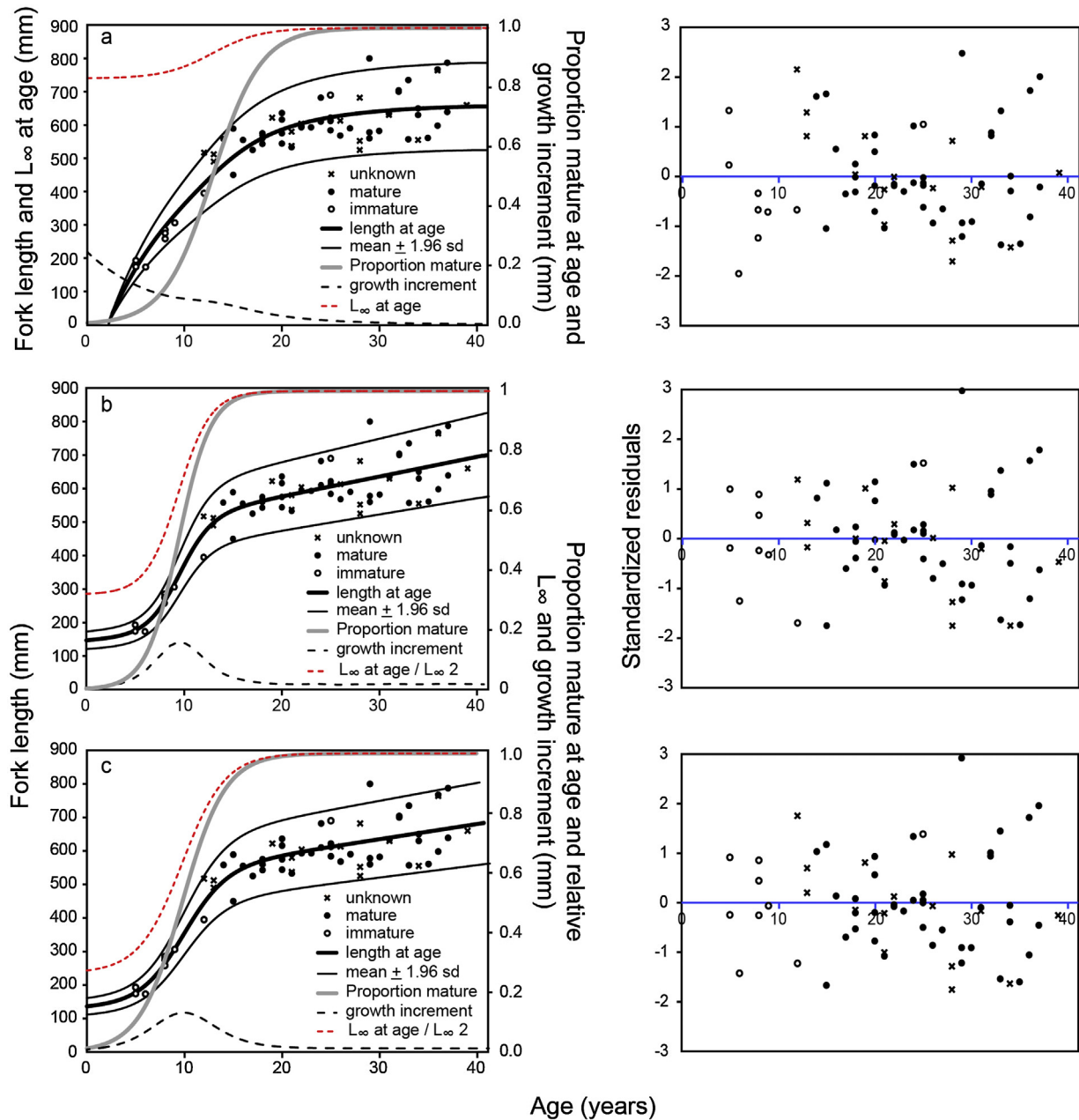


Fig. 3. Fits (left panels) and residuals (right panels) of the VB log- L_{∞} model to the Tasiat Lake females data. The left panels include the expected value of the size at age (black thick line), the variability of size-at-age (mean \pm 1.96 standard deviation, sd, black thin line), the estimated proportion mature (gray thick line), the daily growth increment (dashed line) and the L_{∞} at age (dashed red line). In the panels (a) and (b) the L_{∞} at age is shown as proportion of the $L_{\infty,2}$. (a) External estimation (Run 7): maturity parameters estimated externally ($\hat{t}_{50} = 12.868$, $\hat{\delta}_{95} = 7.3$), and VB log- L_{∞} model fit to size-at-age data only with maturity parameters fixed to the external estimates. (b) Full estimation (Run 8): maturity parameters estimated internally within the VB log- L_{∞} model fit to size-at-age data only ($\hat{t}_{50} = 9.420$, $\hat{\delta}_{95} = 4.9$). (c) Integrated estimation (Run 9): maturity parameters estimated internally within the VB log- L_{∞} model fit to both size-at-age and maturity-at-age data simultaneously ($\hat{t}_{50} = 9.755$, $\hat{\delta}_{95} = 6.5$).

4.2. Fits to the Quince–Boukal model

In initial explorations, we found that special attention was needed to fit the Quince–Boukal model because of the high correlation among the parameters. We used the Tasiat Lake females' data sets to explore the best way to fit the model. The two parameters of the length (in mm) and weight (in kg) relationship were estimated externally from the available data for all lakes ($\hat{b} = 0.00551$ and $\hat{d} = 3.107$, s.e. (\hat{d}) = 0.0156). The maturity-at-age parameters were fixed to the external estimates (Table 5). We fixed the parameter q (relative cost of producing somatic tissue compared to reproductive tissue) to 1.0, as a reasonable assumption that the energetic cost of producing the two tissues is the same. Similarly to Boukal et al.

(2014), we initially fixed the parameter β (the allometric exponent in the growth rate–weight relationship). The values we used were to $\beta = 2/3$ (as assumed in the VB model, the CoR model and in the model of Lester et al., 2004), $\beta = 3/4$ (as predicted by the Metabolic Theory of Ecology, Brown et al., 2004; and estimated for *Salvelinus alpinus*, Killen et al., 2010), $\beta = 0.80$ and $\beta = 0.88$ (average empirical estimates for teleost fish, e.g., Clarke and Johnson, 1999; Killen et al., 2010) and $\beta = 1.036$ estimated for *Salvelinus fontinalis* (Killen et al., 2010). We also attempted to estimate q and β , but there was no information in the data on q to indicate a change from the assumed value of 1.0. The parameters had to be estimated in phases, the estimates from one phase were used as starting points for the next estimation phase. The order of estimation that worked the best was: L_0 in

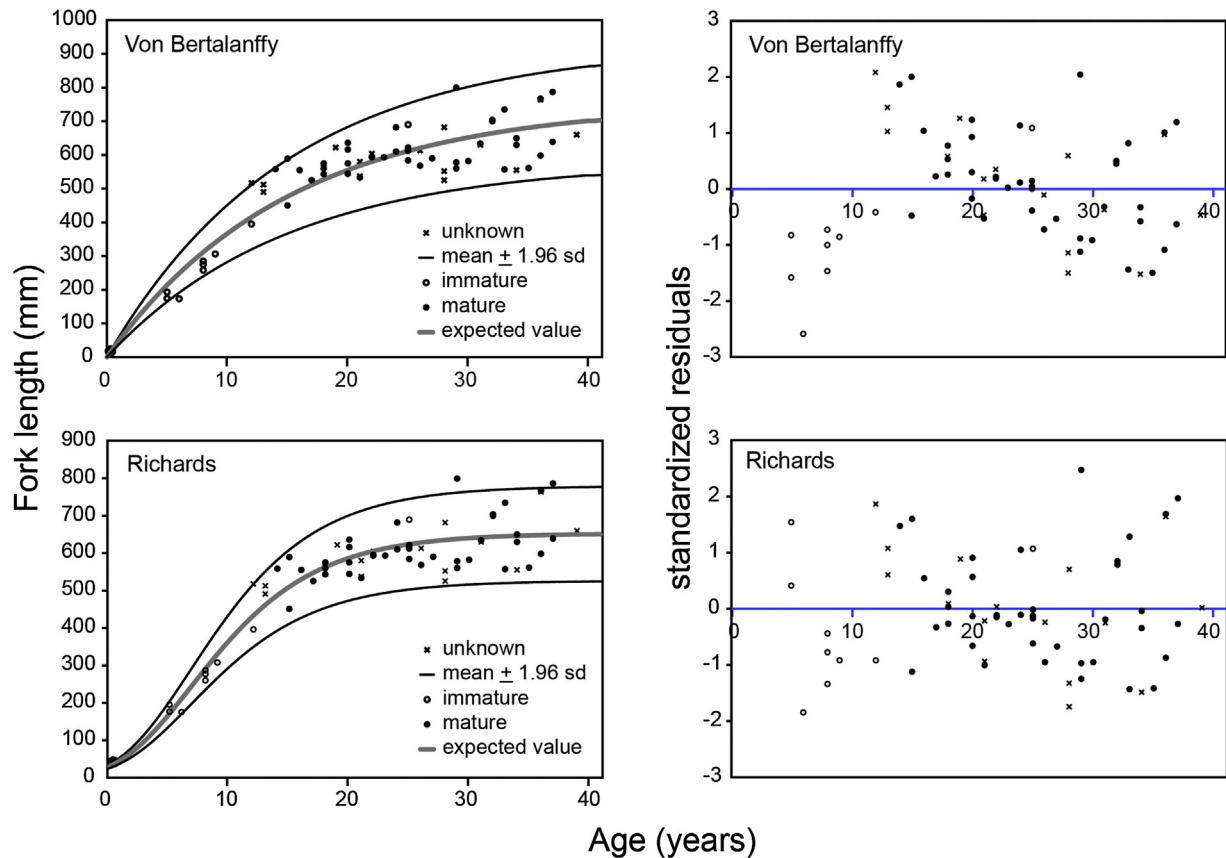


Fig. 4. Fits (left panels) and residuals (right panels) of the Von Bertalanffy (Run 10) and Richards (Run 11) growth models to the Tasiat Lake females size-at-age data.

Table 6

Parameter estimates and AIC_c of the Quince–Boukal model fit to the Lake Tasiat females data set for different assumption of β , the allometric exponent of the growth rate–weight relationship. The fixed parameters were: the conversion factor between somatic and gonadic investment ($q = 1$), the intercept ($b = 0.00551$) and exponent ($d = 3.107$) of the fork length (in mm)–weight (in kg) relationship, the age (in years) at 50% maturity $t_{50} = 12.868$ and the difference (in years) of the age at 95% maturity and t_{50} , $\delta = 7.330$.

Parameter estimates	$\beta = 2/3$	$\beta = 3/4$	$\beta = 0.8$	$\beta = 0.88$	$\beta = 1.04$	β estimated
β Allometric exponent in the growth rate–weight relationship						1.06 (0.21)
c Coefficient in the allometric growth rate–weight relationship	25.02 (0.68)	10.41 (0.23)	5.63 (0.29)	2.11 (0.11)	0.31 (0.02)	0.23 (0.58)
r Relative reproductive investment	0.15 (0.01)	0.23 (0.02)	0.27 (0.02)	0.34 (0.02)	0.52 (0.03)	0.56 (0.34)
Correlation between estimates of c and r	0.87	0.96	0.97	0.98	0.99	–0.99
L_0 length at age 0	0.00 (0.03)	10.79 (9.41)	31.56 (8.86)	56.19 (7.89)	88.49 (6.83)	92.57 (32.36)
β_σ Slope of the variability (Eq. (11))	0.10 (0.01)	0.10 (0.01)	0.10 (0.01)	0.10 (0.01)	0.09 (0.01)	0.09 (0.01)
AIC_c	717.2	707.6	706.7	705.8	705.2	707.5

phase 1, c in phase 2, r in phase 3, β in phase 4, and the variability parameter in the last phase. The model with the lowest AIC_c was the one with $\beta = 1.036$ (Table 6). The worst AIC_c was for the VB-like assumption of $\beta = 2/3$. The parameter estimates were highly correlated. Curves with similar shapes along the range of the data were found with different combination of parameters. Nevertheless, the curves had different implications for extrapolation beyond the data range (Fig. 5).

4.3. Comparisons of fits of size-at-age data of all reviewed models

AIC_c was computed for the models fit to size-at-age data only. All models within 0–2 units from the best fitting model (lowest AIC_c) are considered to have support from the data (Table 7). The performance of the simple models was very poor; the VB model, for example, was within 9–35 AIC_c units of the best-fitting model. A biphasic growth model was the best for all data sets. Of the models that are modifications of the basic VB model, VB log- L_∞ with t_{50} and δ_{95} estimated (7-parameter model) and the VB-S (6-parameter model) were selected the most (three times each).

Of the recursive biphasic growth models, the Gompertz Delayed Development model was within two units of the best-fitting models for three data sets. The Quince–Boukal model was fit with five options for β . The model with $\beta = 2/3$ was never selected and the model with $\beta = 3/4$ was selected only once. The models with β larger than 0.8 were selected for two or more data sets. The models with large values of β that were implemented with a penalty (PEN) for shrinking were still selected for two data sets each. The model with β estimated was selected for three of the data sets. We also attempted to estimate t_{50} and δ_{95} for $\beta = 0.8$. This model was selected as the best by four data sets. Because of high correlation among parameters, several starting points must be used until arriving at model convergence. The CoR model was not selected for any of the data sets to be within 2 AIC_c units of the best-fitting model.

The estimates of β , the allometric exponent in growth rate–weight relationship in the Quince–Boukal model ranged from 0.63 to 1.14 (Table 8). For lakes for which this model was selected among the best-fitting ones, the estimates were $\hat{\beta} = 1.04$ (Couture Lake females and Tasiat Lake females) and $\hat{\beta} = 1.14$ (Zeta Lake males).

Table 7
Delta AIC_c (difference between AIC_c of the best fitting model and the model in each line) for the models fit only to size-at age data. The list of models and acronyms are in Tables 2 and 3. PEN=penalties. The parameter estimates for the proportion mature curve are plotted in Fig. 7.

		Lake Sex	Couture M	Couture F	McAlpine M	McAlpine F	Tasiat M	Tasiat F	Zeta M	Zeta F
Model	Type	n	48	62	90	79	94	65	143	55
		Min AIC _c	549.5	731.6	1040.5	898.7	1000.9	705.2	1584.9	625.6
		NLL model with lowest AIC _c	266.3	361.5	513.8	442.8	494.0	348.3	787.2	305.9
		Number of parameters								
VB		4	18	9	11	19	35	28	17	12
Richards		5	16	10	3	5	8	9	19	6
VB-hyperL _∞		5	21	11	3	13	16	13	40	7
VB-hyperK		5	21	11	3	13	16	13	40	7
VB-damped		5	21	11	3	13	16	13	40	7
VB-S		6	5	6	1	0	9	4	0	12
VB-logK		6	5	8	3	4	0	4	0	9
VB log-L _∞	t_{50} and δ_{95} fixed	5	9	7	3	13	12	12	0	7
VB log-L _∞	t_{50} and δ_{95} estimated	7	0	3	7	18	11	1	2	12
GompertzDD		4	11	2	4	2	5	8	5	1
Quince–Boukal	$\beta = 2/3$, t_{50} and δ_{95} fixed	4	18*	5*	9*	12	11	12	46	7
Quince–Boukal	$\beta = 3/4$, t_{50} and δ_{95} fixed	4	30*	3	38*	17	4	2	17	19
Quince–Boukal	$\beta = 0.8$, t_{50} and δ_{95} fixed	4	16	2	13	22	3	2	13	12
Quince–Boukal	$\beta = 0.8$ PEN, t_{50} and δ_{95} fixed	4	16	2	393	558	3	2	13	134
Quince–Boukal	$\beta = 0.8$, PEN t_{50} and δ_{95} est	6	14	6	0	5	7	1	0	0
Quince–Boukal	$\beta = 0.88$, t_{50} and δ_{95} fixed	4	16	1	15	31	2	1	8	17
Quince–Boukal	$\beta = 1.04$	4	15	0	21	50	4	0	1	28
Quince–Boukal	$\beta = 1.04$ PEN	4	100	359*	1668*	2650*	4	0	1	1542
Quince–Boukal	β estimated	5	18	2	9	12	4	2	0	9
CoR	t_{50} and δ_{95} fixed	4	17	6	9	6	5	8	24	5
CoR	t_{50} and δ_{95} estimated	6	22	10	8	5	7	9	5*	8*

* Indicates models for which the Hessian matrix does not appear to be positive definite.

Table 8
Estimates of β , the allometric exponent of the growth rate-weight relationship, for the Quince–Boukal model with the maturity parameters fixed to the values estimated externally by fitting a logistic model to the maturity-at-age data.

Lake	Sex	$\hat{\beta}$	$se(\hat{\beta})$	Correlations of the estimates of β with the following parameter estimates			
				L_0	c	r	β_σ
Couture	M	0.99	0.16	0.89	−1.00	0.99	0.00
Couture	F	1.04	0.15	0.94	−1.00	0.98	0.00
McAlpine	M	0.63	0.03	0.00	−1.00	0.89	0.00
McAlpine	F	0.64	0.02	0.00	−0.99	0.74	0.00
Tasiat	M	0.88	0.11	0.97	−1.00	0.98	0.00
Tasiat	F	1.04	0.26	0.99	−1.00	1.00	−0.02
Zeta	M	1.14	0.05	0.86	−1.00	0.94	0.00
Zeta	F	0.67	0.03	0.00	−0.99	0.95	0.00

On those runs, the correlation among parameter estimates was extremely high.

4.4. Integrated fits

We compared the fits of each data component to three models that are suitable for either integrated or external estimation (CoR, VB log-L_∞ and Quince–Boukal $\beta = 0.8$, Table 9) to assess whether we were better off with the integrated estimation, rather than the external estimation. Examples of the fits of those three models are shown in Fig. 6. The NLL_{age} in the integrated estimation was smaller in most cases for any of the three models than the external estimation. The difference in NLL units, however, was larger than one for one (CoR), three (VB log-L_∞), and four data sets (Quince–Boukal $\beta = 0.8$). These improvements in the fit to the size-at-age data came at a minimal cost to the fits to the maturity-at-age data: the NLL_{mat} of the integrated fit was different by less than one unit for seven of the eight data sets, for any of the models. Performing the integrated estimation improved the size-at-age fits without compromising the maturity-at-age fits. However the estimation of growth, with the maturity parameters fixed at values estimated externally provides about the same results, with a few exceptions. For example, the fit of the CoR for Couture Lake males and the Quince–Boukal $\beta = 0.8$ for the McAlpine Lake males and females, the integrated estima-

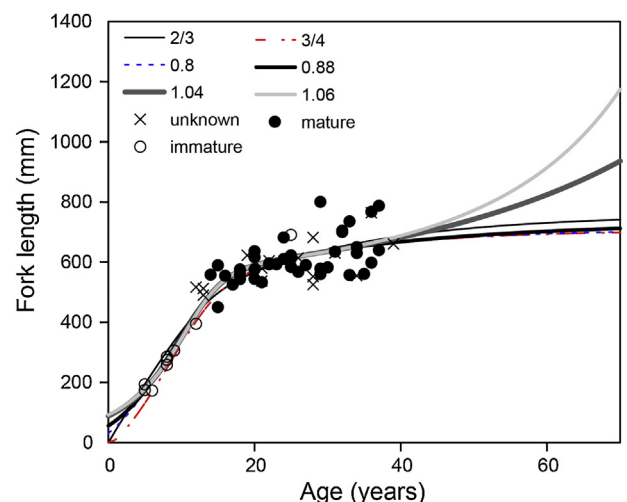


Fig. 5. Fits of the Quince–Boukal model with different assumptions about the parameter β , the allometric exponent of the growth rate-weight relationship, to the Tasiat Lake females size-at-age data.

Table 9

Negative log-likelihood (NLL) for the maturity-at-age and size-at-age data (NLL_{mat} and NLL_{age}) and delta AIC_c for the integrated models fit simultaneously to size-at-age and maturity-at-age data. For comparison, the NLL_{mat} proportion mature model (Run 0 in Table 5) is also included. CoR is the Cost of Reproduction model, VB log-L_∞ is the Von Bertalanffy Logistic-L_∞ model. *m* is the number of parameters, *n* is the sample size.

			Lake	Couture	Couture	McAlpine	McAlpine	Tasiat	Tasiat	Zeta	Zeta
Model	<i>m</i>	Estimation	Sex	M	F	M	F	M	F	M	F
CoR	6	Integrated	<i>n</i>	48	62	90	79	94	65	143	55
			Delta AIC _c	8.2*	Infinity*	6.5*	0	2.4	6.7*	13.8	0
			NLL _{mat}	12.0	Infinity	34.0	30.4	21.9	8.7	0.6	7.6
	6	Full	NLL _{age}	278.8	364.2	520.6	448.0	498.7	351.8	794.0	311.0
			NLL _{mat}	270.9	360.6	516.5	445.2	497.3	346.7	786.4	309.8
			NLL _{mat} implied	23.4	Infinity	62.4	Infinity	Infinity	Infinity	Infinity	Infinity
VB log-L _∞	4	External	NLL _{age}	278.8	364.5	520.7	448.1	498.9	352.1	800.1	310.7
			Delta AIC _c	0	3.8	0	7.3	8	2.3*	0	2.6
			NLL _{mat}	12.3	7.7	33.9	30.4	22.4	10.8	0.3	7.6
	7	Full	NLL _{age}	273.0	362.4	516.2	450.5	499.8	346.2	786.0	311.0
			NLL _{mat}	266.3	359.3	516.3	446.4	497.4	345.2	786.1	310.0
			NLL _{mat} implied	161.9	56.8	33.9	30.4	56.3	13.3	0.3	8.2
Quince-Boukal $\beta = 0.8$	5	External	NLL _{age}	273.7	364.0	516.2	450.5	501.1	353.0	787.3	310.6
			Delta AIC _c	6.6	0	8.7	73.2*	0	0	3.2	0.5
			NLL _{mat}	12.4	7.1	34.7	44.5	21.8	8.9	0.7	9.4
	6	Full	NLL _{age}	277.6	362.4	521.0	470.5	497.6	348.2	789.0	309.0
			NLL _{mat}	274.5	361.9	513.8	445.4	497.5	346.6	786.3	305.9
			NLL _{mat} implied	176.7	29.8	Infinity	292.7	22.6	33.1	19.7	Infinity
VB	4	External	NLL _{age}	278.4	362.5	712.6	724.1	497.6	349.0	794.6	375.4
Richards	4		NLL _{age}	279.5	365.8	521.8	454.5	513.9	362.4	796.9	314.6
Proportion mature	5		NLL _{age}	277.3	365.2	516.3	446.5	498.9	351.4	796.9	310.2
	2		NLL _{mat}	12.0	7.0	33.9	30.4	21.8	8.5	0.0	7.6
			Min AIC _c	587.5	752.4	1115.7	970.0	1052.0	727.7	1588.0	650.0

* Indicates models for which the Hessian matrix does not appear to be positive definite.

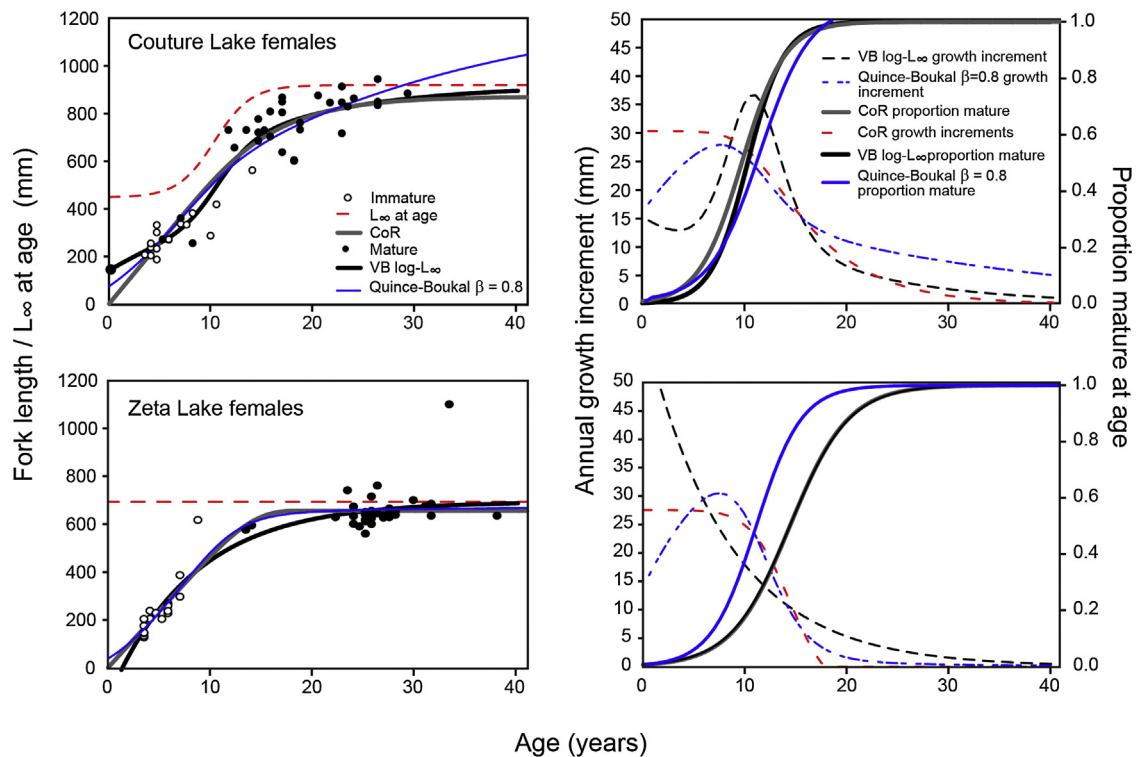


Fig. 6. Fits of the CoR, VB log-L_∞ and Quince-Boukal with $\beta = 0.8$ models using integrated estimation to two data sets. (a) Fits to the Couture Lake Males data, the model with the lowest AIC_c was the VB log-L_∞. (b) Fits for the Zeta Lake Females data, the model with the lowest AIC_c was CoR, but the Quince-Boukal with $\beta = 0.8$ was within 0.5 AIC_c units.

tion allowed for a much better fits to the size-at-age data than the external estimation. The integrated estimation may be the best compromise between the modeling of the two biological processes, but the separated estimation may provide similar results and may be easier to implement.

Of the three models fit using integrated estimation, the Quince-Boukal $\beta = 0.8$ was the one that fitted best (less than 0.5 AIC_c units of difference to the best fitting model) for most data sets (4), followed by the VB log-L_∞ (3) and the CoR (2) models. Growth parameters estimates for the VB log-L_∞ model were frequently unrealistic to have the required shape (e.g., very low value

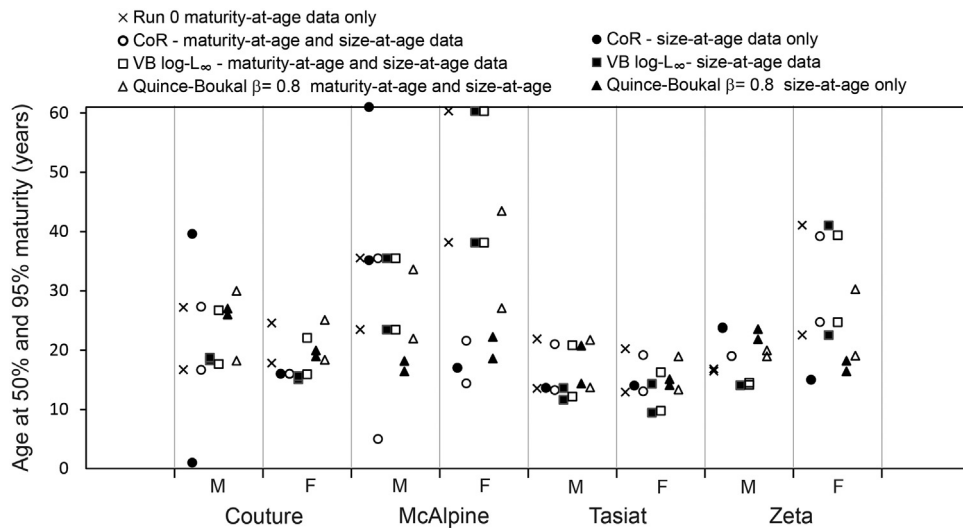


Fig. 7. Estimates of t_{50} (bottom symbols) and t_{95} (top symbols) obtained from the logistic model fit maturity-at-age, the CoR, VB log- L_{∞} and Quince–Boukal with $\beta=0.8$ models fit to size-at-age data (full estimation) or size-at-age and maturity-at-age data (integrated estimation) for all lakes, for males (M) and females (F). When a knife-edge transition was estimated, only one symbol was drawn as $t_{50} = t_{95}$.

for t_0 and very high values for $L_{\infty 2}$; in Fig. 3b and c, the L_{∞} at age is graphed relative to $L_{\infty 2}$).

The results from the full estimation (all parameters estimated from model fits to only size-at-age data) were compared to the external estimation of the maturity-at-age parameters. For most data sets and for the three models, the NLL_{age} was smaller for the full estimation, as expected (Table 9). However, only for Quince–Boukal $\beta=0.8$ model, the full estimation runs had the lowest AIC_c more frequently than the external estimation runs (Table 7), suggesting that there is little information indicating that the change in growth rates is caused by something other than maturation. The implied fit to the maturity-at-age data with those estimates of maturity parameters degraded considerably, as shown by larger NLL_{mat} , which may even be infinite in some cases. Using the external estimation, the CoR models tends to estimate knife-edge transitions (t_{95} equal to t_{50}) for most cases (Fig. 7), and both the VB log- L_{∞} and the Quince–Boukal $\beta=0.8$ models tend to estimate abrupt transitions in several cases. This indicates that the size-at-age data alone do not have enough information to estimate the δ_{95} (and thus the age at 95% maturity).

The estimates of the maturity parameters from the integrated models in general corresponded to slightly narrower maturity-at-age curves than the estimates coming from maturity-at-age data alone, indicating that while the maturity-at-age data inform growth estimation, given that the model is correct, the size-at-age data also have some information about the maturity process. For example, it is noteworthy that for the Zeta Lake males data, which does not have enough information in the transition age between immature and mature (Fig. 1), the estimate of t_{50} from Run 3 (CoR) and from Quince–Boukal models get closer to that estimated for the females of the same lake, that have a more balanced sampled size between mature and immature fish (Fig. 7). Also, the estimates of the maturity parameters from the Quince–Boukal models fit using the integrated estimation tend to be more similar among lakes than those obtained from the other models, including the stand-alone maturity at age model (Run 0).

5. Discussion

To the best of our knowledge, we have reviewed all published biphasic growth models and proposed two new models, the von Bertalanffy logistic- L_{∞} (VB log- L_{∞}) and the Cost of Reproduction (CoR) models. Furthermore we implemented all continuous models and fitted them to Arctic lake trout data sets for which size-

at-age and maturity-at-age data were available, using maximum likelihood. In general, we found that a biphasic model that simultaneously represented the growth of adult and juvenile animals was better than a simple growth model such as the VB or the Richards, which were between 3 and 35 AIC_c units from the best models fit to size-at-age data only. The biphasic models that explicitly incorporate the reproduction process fitted the data best. Integrated estimation using both size-at-age and maturity-at-age data was the best compromise between modelling the two processes. Nevertheless, external estimation produced similar results in most cases, and it may be easier to implement, especially when no maturity-at-age data were collected in addition to size-at-age data. Biphasic growth has been shown to exist for Arctic lake trout by other authors. Quince et al. (2008b) showed that a biphasic growth model provided better fits to Arctic lake trout female growth. We chose in this review to fit all models using a normal likelihood. However there are indications that the Arctic lake trout shows resource polymorphism, with some individuals achieving much larger sizes, because of a cannibalistic diet (Blackie et al., 2003). For example, in the unfished Zeta Lake, a few animals with extreme sizes were found. Further studies should investigate either use of robust likelihood functions when fitting growth models (e.g., Chen and Fournier, 1999) or the explicit inclusion of growth polymorphism in the model.

We were able to fit all models. However, it was more difficult to achieve convergence for some models (e.g., the Quince–Boukal model) because of high correlation among parameters, and other models converged to estimates that were not biologically interpretable, such as the VB log- L_{∞} model.

The Quince–Boukal model was the one that produced the best fits in general. This model is based on first principles of allocation of energy to growth and reproduction and takes into account that both the allometric exponents in growth rate–weight (β) and length–weight (d) may differ among species (as opposed to the common assumptions of $\beta=2/3$ and isometric growth $d=3$). Although one can attempt to estimate β as we have done here, there is little information on the size-at-age data to estimate this parameter, and size-at-age curves with different values for β may look indistinguishable, given different combinations of the other parameters (see Fig. 2 in Boukal et al., 2014). Both β and d can be fixed to external values derived from metabolic studies and length–weight studies, respectively. Uncertainty on those parameters may be incorporated as prior distributions (in Bayesian estimation) or as penalty func-

tions (in likelihood estimation). In the data we used to illustrate the model fits, the value for β was key to the model fits, the model was best supported by the data for rather higher values of β . As shown by Boukal et al. (2014), the implication of different values for β on the species fitness as measured by the lifetime reproductive investment is dramatic. By knowing β and the optimal evolutionary age at maturation (that can be assumed to be t_{50}), one also knows a corresponding natural mortality coefficient.

The MLE value of β from the fit to the Quince–Boukal model ranged toward larger values (average $\beta = 0.879$) similar to what was estimated for other species of the same genus using metabolic studies ($\beta = 0.748$ for *Salvelinus alpinus* and $\beta = 1.036$ for *Salvelinus fontinalis*, Killen et al., 2010). However, the uncertainty of the estimates is high for some data sets. The β parameter of Lake Tasiat females, for example, has a 95% confidence interval of 0.648–1.476, which includes about the whole range for teleost fish (69 species in Fig. 1b of Clarke and Johnson, 1999). Nevertheless, the greater β estimates are compatible with lower natural mortality and greater longevity (Quince et al., 2008b; Boukal et al., 2014), as shown by the Arctic lake trout. This agreement is another indication of the consistency of the best growth model with the general life history of the species.

The recursive models were implemented using a difference approximation to the differential equation. While the Quince–Boukal model was implemented with an annual time step, the CoR model was implemented in a daily step, which makes it a computationally intensive procedure. It would be preferable to have an algebraic solution to the differential equation, but we are not aware of its existence. The computational demands are not a concern for traditional growth modelling using current computational resources, but more sophisticated analysis such as the high multi-dimensional integrals needed to integrate age-length data with growth increment data obtained from tagging may be problematic (Laslett et al., 2002; Aires-da-Silva et al., 2015). Convergence was also problematic for some data sets, and further reparameterization may be required to improved convergence.

5.1. The proposed models

In addition to the models from the literature, we have proposed two growth models that take the cost of reproduction into account. One model is based on first principles and the other model is based on prior performance, but both are based on a modification of the VB model. Both include a logistic maturity function to model the transition from a juvenile growth phase to an adult growth phase. These growth models usually perform better than the von Bertalanffy and Richards growth models for the eight data sets that we evaluated, based on AIC_c. We expect similar performance for other species that show changes in growth rates when individuals become mature and expend energy on reproduction.

The VB log- L_{∞} model most often performed better than the CoR model. However, the parameters of the VB log- L_{∞} model were often unrealistic. Unrealistic parameters are not necessarily a concern if the growth model is simply used to describe mean length at age, and no biological meaning is inferred from the parameter estimates. Realistic parameter values may also be desirable if extrapolating outside the range of the data. Given the similarity of the two models' performances, we recommend the CoR model because it is based on first principles and the parameter estimates are more realistic.

We assumed that the length at age 0 days is 1 mm in the CoR model. Estimating this parameter is similar to t_0 in that it occurs at an age lower than there are data and can be thought of as a convenient way to add flexibility into the model without adding meaning. We found that estimating this parameter for one data set did not improve the likelihood. Future research should investigate estimating this parameter. Alternative parameterizations may improve the

estimability, for example, by starting the model at a greater older age close to the youngest observed age (similarly to Schnute and Fournier (1980) parameterization of the von Bertalanffy growth function).

5.2. Reproductive biology information

The growth curves that include the cost of reproduction require information on aspects of reproductive biology. In this paper, we used the maturity at age and approximate weight (length cubed) as a proxy for the cost of reproduction in the CoR model and the maturity at age multiplied by a constant in the Quince–Boukal model. When all parameters were estimated based only on the size-at-age data, the estimates of the growth transition parameters (proportion mature at age) were frequently more abrupt and sometimes incompatible with the maturity-at-age data (as shown by the implied likelihood NLL_{mat} of those values). This incompatibility may indicate that maturity-at-age data do not appropriately account for all the cost of reproduction, which may also include energetic cost with behavior or larger gonads. The model fit might be improved if other aspects, such as the frequency of spawning and fecundity, are also taken into consideration. We suggest that sampling programs for growth information should always include sampling for information on reproductive biology so that these growth curves can be applied. For most cases, there was not much difference between models that estimated the maturity curve externally from the growth model or internally in the growth model, when using integrated estimation. We expect that this will be the case in most applications since maturity sampling should usually be adequate to precisely estimate the maturity-at-age curve. Frequently, however, the growth and reproduction studies are not done simultaneously, and a maturity-at-length, rather than maturity-at-age, curve is obtained. The transformation of length into ages will need to be incorporated in the likelihood to fit a biphasic model, such as those proposed here. In this case, an integrated estimation approach might be more efficient. Further research should include application of these models to a wider range of data sets to determine if their superior performance is general or case specific.

6. Conclusions

The biphasic growth models, in particular those that explicitly include the reproductive process in the growth dynamics, fitted the data better than the simple growth models. This improvement can translate into higher-quality scientific advice when these results are used in stock assessments. In the context of fisheries stock assessment, the models reviewed in this paper can be used in two ways: (i) in highly-structured stock assessments, the models can be used to have a more precise estimate of growth and therefore improve the interpretation of length-composition data, which are more frequently available than age-frequency data; (ii) in assessing data-poor stocks, by using the methods related to the “life-history invariants” (e.g., Prince et al., 2015). The improved performance of the growth models that include cost of reproduction might be understated when they are used in stock assessment models that fit to length-composition data. In these stock assessment models, the fit of the expected length-composition data to the observed length-composition data, particularly for greater lengths, influences the estimates of absolute abundance and fishing mortality (Maunder and Piner, 2015). Therefore, it is important to get the growth curve correct for the greater ages. Unfortunately, there is often a lack of information at greater ages. Consequently, a slight improvement in the fit to the age-length data at greater ages due to the inclusion of the cost of reproduction may be influential for stock assessment results. For this reason, we believe that taking the cost of reproduc-

tion into consideration is valuable for growth curves used in stock assessment models. Future research should investigate the sensitivity of management quantities, derived from integrated stock assessment models, to these growth curves compared standard growth curves for commercial fish stocks. Recent attempts to assess data-poor stocks have included the use of life history ratios (or life-history invariants) to take the most information from length-frequency data (Prince et al., 2015; Hordyk et al., 2015a,b), which are typically the most inexpensive data to obtain when sampling small-scale fisheries, for example. Those life-history invariants are based on the parameters of the von Bertalanffy growth curve, which we have shown to be the poorest fitting model, based on AIC_c, in our study. Some of the reviewed models explicitly include the cost of reproduction and can be used to derive life-history invariants, and potentially improve the predictability of the methods based on such information. When assuming that a population has evolved to produce the maximum life-span reproductive output, the Quince–Boukal model explicitly connects metabolic rates, exponent of the length-weight relationship, optimal age at reproduction, and natural mortality (and thus longevity). As such, the life-history invariant methods can be improved to include auxiliary information such as estimates of β derived from metabolic studies.

Acknowledgements

This research was stimulated by discussion at the Growth Workshop of the Center for the Advancement of Population Assessment Methodology (CAPAM). This manuscript was greatly improved by comments from André Punt, William Bayliff, and one anonymous reviewer. We are grateful to Christine Patnode for assistance with the artwork.

References

- Aires-da-Silva, A.M., Maunder, M.N., Schaefer, K.M., Fuller, D.W., 2015. Improved growth estimates from integrated analysis of direct aging and tag-recapture data: an illustration with bigeye tuna (*Thunnus obesus*) of the eastern Pacific Ocean with implications for management. *Fish. Res.* 163, 126–199, <http://dx.doi.org/10.1016/j.fishres.2014.04.001>.
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), *Second International Symposium on Information Theory*. Akademiai Kiado, Budapest, pp. 267–281.
- Blackie, C.T., Weese, D.J., Noakes, D.L.G., 2003. Evidence for resource polymorphism in the lake charr (*Salvelinus namaycush*) population of Great Bear Lake, Northwest Territories, Canada. *Écoscience* 10, 509–514, <http://www.jstor.org/stable/42901561>.
- Boukal, D.S., Dieckmann, U., Enberg, K., Heino, M., Jørgensen, C., 2014. Life-history implications of the allometric scaling of growth. *J. Theor. Biol.* 359, 199–207, <http://dx.doi.org/10.1016/j.jtbi.2014.05.022>.
- Brody, S., 1945. *Bioenergetics and Growth*. Reinhold Publishing Corporation, New York.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, van, M., West, G.B., 2004. Towards a metabolic theory of ecology. *Ecology* 85, 1771–1789, <http://dx.doi.org/10.1890/03-9000>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, Second ed. Springer-Verlag, New York, <http://www.springer.com/us/book/9780387953649>.
- Campana, S.E., Casselman, J.M., Jones, C.M., 2008. Bomb radiocarbon chronologies in the Arctic, with implication for the age validation of lake trout (*Salvelinus namaycush*) and other Arctic species. *Can. J. Fish. Aquat. Sci.* 65, 733–743, <http://dx.doi.org/10.1139/f08-012>.
- Chen, Y., Fournier, D., 1999. Impacts of atypical data on Bayesian inference and robust Bayesian approach in fisheries. *Can. J. Fish. Aquat. Sci.* 56, 1525–1533, <http://dx.doi.org/10.1139/f99-076>.
- Clarke, A., Johnson, N.M., 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. *J. Anim. Ecol.* 68, 893–905, <http://dx.doi.org/10.1046/j.1365-2656.1999.00337.x>.
- Day, T., Taylor, P.D., 1997. von Bertalanffy's growth equation should not be used to model age and size at maturity. *Am. Nat.* 149, 381–393, <http://www.jstor.org/stable/2463400>.
- Essington, T.E., Kitchell, J.F., Walters, C.J., 2001. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. *Can. J. Fish. Sci.* 58, 2129–2138, <http://dx.doi.org/10.1139/f01-151>.
- Fournier, D.A., (2015). An Introduction to AD Model Builder for use in nonlinear modeling and statistics. Version 11.4. <http://admb-project.org/documentation/manuals>.
- Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., Sibert, J., 2012. AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Software* 27, 233–249, <http://dx.doi.org/10.1080/10556788.2011.597854>.
- Francis, R.I.C.C., 2011. Data weighting in statistical fisheries stock assessment models. *Can. J. Fish. Sci.* 68, 1124–1138, <http://dx.doi.org/10.1139/f2011-025>.
- Gompertz, B., 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philos. Trans. R. Soc. London* 123, 513–583 <http://www.jstor.org/stable/107756>.
- Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N., Prince, J., 2015a. Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. *ICES J. Mar. Sci.* 72, 204–216, <http://dx.doi.org/10.1093/icesjms/fst235>.
- Hordyk, A., Ono, K., Valencia, S., Loneragan, N., Prince, J., 2015b. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *Ices J. Mar. Sci.* 72, 217–231 <http://dx.doi.org/10.1093/icesjms>.
- Hurvich, C.M., Tsai, C.-L., 1989. Regression and time series model selection in small samples. *Biometrika* 76, 297–307, <http://www.jstor.org/stable/2336663>.
- Killen, S.S., Atkinson, D., Glazier, D.S., 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecol. Lett.* 13, 184–193, <http://dx.doi.org/10.1111/j.1461-0248.2009.01415.x>.
- Laslett, G.M., Everson, J.P., Polacheck, T., 2002. A flexible maximum likelihood approach for fitting growth curves to tag-recapture data. *Can. J. Aquat. Sci.* 59, 976–986, <http://dx.doi.org/10.1139/f02-069>.
- Lester, N.P., Shuter, B.J., Abrams, P.A., 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proc. R. Soc. London* 271, 1625–1631, <http://dx.doi.org/10.1098/rspb.2004.2778>.
- Lester, P.N., Shuter, B.J., Venturelli, P., Nadeau, D., 2014. Life-history plasticity and sustainable exploitation: a theory of growth compensation applied to walleye management. *Ecol. Appl.* 24, 38–54, <http://dx.doi.org/10.1890/12-2020.1>.
- Maunder, M.N., Piner, K.R., 2015. Contemporary fisheries stock assessment: many issues still remain. *ICES J. Mar. Sci.* 72, 7–18, <http://dx.doi.org/10.1093/icesjms/fsu015>.
- Methot, R.D., Wetzel, C.R., 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fish. Res.* 142, 86–99, <http://dx.doi.org/10.1016/j.fishres.2012.10.012>.
- Ohnishi, S., Yamakawa, T., Okamura, H., Akamine, T., 2012. A note on the von Bertalanffy growth function concerning the allocation of surplus energy to reproduction. *Fish. Bull.* 110, 223–229, <http://fishbull.noaa.gov/1102/ohnishi.pdf>.
- Porch, C.E., Wilson, C.A., Nieland, D.L., 2002. A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenic changes in growth rates. *Fish. Bull.* 100, 149–152, <http://fishbull.noaa.gov/1001/por.pdf>.
- Prince, J., Hordyk, A., Valencia, S.R., Loneragan, N., Sainsbury, K., 2015. Revisiting the concept of Beverton–Holt life-history invariants with the aim of informing data-poor fisheries assessment. *ICES J. Mar. Sci.* 72, 194–203, <http://dx.doi.org/10.1093/icesjms/fsu011>.
- Quince, C., Shuter, B.J., Abrams, P.A., Lester, N.P., 2008a. Biphasic growth in fish I: theoretical foundations. *J. Theor. Biol.* 254, 197–206, <http://dx.doi.org/10.1016/j.jtbi.2008.05.029>.
- Quince, C., Shuter, B.J., Abrams, P.A., Lester, N.P., 2008b. Biphasic growth in fish II: empirical assessment. *J. Theor. Biol.* 254, 207–214, <http://dx.doi.org/10.1016/j.jtbi.2008.05.030>.
- Quinn, T.J., Deriso, R.B., 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York.
- Ratkowsky, D.A., 1986. Statistical properties of alternative parameterizations of the von Bertalanffy growth curve. *Can. J. Fish. Aquat. Sci.* 43, 742–747, <http://dx.doi.org/10.1139/f86-091>.
- Richards, F.J., 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10, 290–301, <http://dx.doi.org/10.1093/jxb/10.2.290>.
- Roff, D.A., 1983. An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.* 40, 1395–1404, <http://dx.doi.org/10.1139/f83-16>.
- Ross, G.J.S., 1970. The efficient use of function minimization in non-linear maximum-likelihood estimation. *J. R. Stat. Soc. Ser. C* 19, 205–221, <http://dx.doi.org/10.2307/2346325>.
- Schnute, J., 1981. A versatile growth-model with statistically stable parameters. *Can. J. Fish. Aquat. Sci.* 38, 1128–1140, <http://www.nrcresearchpress.com/doi/abs/10.1139/f81-153#.ViUrrCu0csQ>.
- Schnute, J., Fournier, D., 1980. A new approach to length-frequency analysis: growth structure. *Can. J. Aquat. Sci.* 37, 1337–1351, <http://dx.doi.org/10.1139/f80-172>.
- Soriano, M., Moreau, J., Hoenig, J.M., Pauly, D., 1992. New functions for the analysis of two-phase growth of juvenile and adult fishes, with application to Nile Perch. *Trans. Am. Fish. Soc.* 121, 486–493.
- Thornley, J.H., France, J., 2007. *Mathematical Models in Agriculture: Quantitative Methods for the Plant, Animal and Ecological Sciences*, Second ed. CABI, Wallingford.
- von Bertalanffy, L., 1938. A quantitative theory of organic growth. *Hum. Biol.* 10, 181–213, <http://www.jstor.org/stable/41447359>.
- von Bertalanffy, L., 1957. Quantitative laws in metabolism and growth. *Q. Rev. Biol.* 32, 217–231, <http://dx.doi.org/10.1086/401873>.