Growth functions that incorporate the cost of reproduction

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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 modeling 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

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