How can bioenergetics help us predict changes in fish growth patterns?

Brett T. van Poorten [a,*], Carl J. Walters [b]

[a] British Columbia Ministry of Environment, Vancouver, British Columbia, Canada
[b] Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada

A B S T R A C T

Individual growth rates are an important component of ecological processes and models. Understanding how and when growth rates may vary is necessary for predicting changes in size-specific rates like reproductive output, age at recruitment to fishing gear and even market prices. The von Bertalanffy growth function (VBGF) is the most common growth function used today. This model is integrated from a simple bioenergetics model; re-examining the link between von Bertalanffy growth and bioenergetics will help predict how environmental and demographic rates influence growth rates over time. In this paper, we discuss how a simple bioenergetics model can help predict density dependent growth and demonstrate how to incorporate environmental drivers into the VBGF based on the original bioenergetics model. Finally, we discuss difficulties and pitfalls in linking environmental and demographic variation to changes in growth.

1. Introduction

Growth is a necessary component of nearly all fisheries assessment models, whether it is explicitly incorporated in age- or length-structured models or indirectly inferred through calculations of biomass and yield in Schaefer production or delay-difference models (Beverton and Holt, 1957; Hilborn and Walters, 1992). From a fishery standpoint, size at age is often incorporated into calculations of size-based selection, economic value of the catch and egg deposition. From an ecological perspective, body size is also important in understanding predation, competition and consumption rates, which in turn can be used in ecosystem models (Walters et al., 2000). Similarly, changes in growth over time will impact all of these rates. Accurately estimating growth and how density dependent and independent factors drive changes in growth over time will impact our ability to evaluate various harvest and habitat management policies and their ability to achieve stated fisheries management objectives in a changing environment (Clark et al., 1999; Clark and Hare, 2002).

By far the most commonly used growth function in fisheries models is the von Bertalanffy growth function (Roff, 1980; Chen et al., 1992; Kimura, 2008), which predicts growth rate to smoothly decline as fish (or other species with asymptotic growth) age (von Bertalanffy, 1938). The von Bertalanffy growth function (VBGF) was formulated from a basic and very general bioenergetics model that helps explain the generally good ability of the von Bertalanffy model to fit to the growth of a wide variety of species. Variations in the model have been proposed for length-increment data, tag-recapture data and have included seasonality and environmental covariates (Hesler and Lai, 2004; Kimura 2008; Brunel and Dickey-Collas, 2010). However, the biological interpretation of the model is often criticized, especially since investment in reproductive tissues is not directly accounted for in the original model (Czamole'ski and Kozlowski, 1998). Many other growth models have been proposed, but they are often based on statistical fit or flexibility rather than their mechanistic relationship to consumption and metabolism (e.g. Schnute 1981). Despite often-strong opposition to the VBGF based on its simplifying assumptions and generalizations, its ubiquitous use facilitates comparisons across populations and species, making it difficult to justify the wide use of an alternative model at this time (Chen et al., 1992).

Variation in growth over time or year-classes is often linked to various demographic or environmental covariates. Growth may be driven by changes in the availability of prey for each competing individual (density-dependent growth) as well as other factors that may affect how often fish feed, their metabolic overhead or how efficiently they can assimilate captured prey. Understanding these interrelationships is important for accurately predicting

future changes in population egg deposition and fishery yield. Incorrectly interpreting how past growth patterns are driven by biotic and abiotic factors will lead to weak or misleading predictions of future growth potential. Examining how environmental and demographic factors affect the various components of a bioenergetics process (e.g. consumption, metabolism and reproductive investment) will provide insights into how we might expect growth to change in the future. These predictions are especially important when evaluating various fishery strategies or predictions of climate variation.

We provide a framework for examining and predicting variation in von Bertalanffy growth, that conforms with our current understanding of how various intrinsic and extrinsic factors affect the bioenergetic rates from which the model is derived. We show how to relate various bioenergetic processes to growth models by re-examining the derivation of the von Bertalanffy model. We show how to incorporate environmental and biological processes into growth models based on how we relate them to bioenergetic processes. We demonstrate how these calculations relate to data using a case study on Peruvian anchoveta (*Engraulis ringens*). Finally we discuss the implications of incorrectly accounting for the direct link between bioenergetics models and growth models and how this complicates and misinforms our ability to predict growth effects and broader ecosystem and fisheries effects.

2. Expressing growth curve parameters in terms of bioenergetics parameters

Bioenergetics models provide a useful framework for understanding how growth may change as conditions like temperature and food availability change. One of the simplest bioenergetics models (Paloheimo and Dickie, 1965) predicts growth rate as the difference between net energy intake (consumption less associated energetic costs, such as activity and specific dynamic action) and losses (metabolism and reproductive investment)

$$\frac{dW}{dt} = HW^d - mW^n \tag{1}$$

where W is weight, H and m are the mass-specific energy gain and loss rates and d and n are allometric scalars relating anabolism and catabolism to mass, respectively. In the original derivation, von Bertalanffy (1938) integrated this model to formulate a simple growth equation. He specified losses as catabolism, but the term should really encompass all losses including shedding of reproductive products (Essington et al., 2001). Three key assumptions were used in deriving the von Bertalanffy model for length growth from Eq. (1). The first two were used to specify a growth equation in units of weight, namely that metabolism varies directly with mass ($n = 1$) and consumption varies as the 2/3 power of mass ($d = 2/3$). Setting $dW/dt = 0$ and $n = 1$, Eq. (1) can be rearranged to solve for the asymptotic weight as $W_\infty = \left(\frac{H}{m}\right)^{\frac{1}{1-d}}$. Integrating Eq. (1) leads to the generalized VBGF for weight:

$$W_t = W_\infty(1 - e^{-K(t-t_0)})^{\frac{1}{1-d}}, \tag{2}$$

where $K = m(1 - d)$. As pointed out in Essington et al. (2001), setting $n = 1$ is not biologically meaningful, but mathematically necessary in order to find a closed-form solution (Eq. (2)). The VBGF can be used to estimate growth in length by implementing the third assumption imposed by von Bertalanffy (1938), that weight is proportional to length cubed $\left(W = aL^b\right)$, which implies that

$$L_t = L_\infty(1 - e^{-K(t-t_0)})^{\frac{1}{b(1-d)}} \tag{3}$$

where $b = 3$ and

$$K = m(1 - d) \tag{4a}$$

$$L_\infty = \left(\frac{Ha^{d-1}}{m}\right)^{\frac{1}{b(1-d)}}. \tag{4b}$$

When applying the von Bertalanffy assumptions ($d = 2/3$, $n = 1$ and $b = 3$), the model simplifies from the generalized VBGF (Eq. (3); Pauly, 1981) to either of the standard formulations of the special VBGF:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \tag{5a}$$

or

$$L_t = L_0 e^{-Kt} + L_\infty\left(1 - e^{-Kt}\right). \tag{5b}$$

To integrate Eq. (1), it is necessary to specify a constant of integration for a unique solution (Mangel 2006), which is either t_0 (a theoretical age at zero-length; Eq. (5a)) or L_0 (an initial length, often set to the length at hatch or yolk resorption; Eq. (5b)). Obviously, both Eqs. (5a) and (5b) are equivalent. Note that under the von Bertalanffy assumptions the asymptotic length simplifies to

$$L_\infty = \frac{H}{m} a^{-1/3}. \tag{6}$$

Two important implications become apparent as the special VBGF is re-examined in terms of the original bioenergetics parameters rather than just K and L_∞. The first is that the Brody 'growth' coefficient, K, (Ricker, 1975) is actually proportional to the metabolic parameter, (i.e. $K = m/3$; Eq. (4a)). Within the formulation of Eq. (1), high m or K implies the asymptotic size will be approached more quickly because of greater metabolic costs (Ricker 1975). It is true that organisms with high metabolic rates (specifically standard metabolic rate, SMR) often also exhibit high growth rates, largely due to the high metabolic cost of growth and consumption (Rosenfeld et al., 2014). Consuming large quantities of food requires maintenance of the digestive tract, a cost not captured within standard calculations of specific dynamic action. Growth also incurs high metabolic costs associated with construction and reorganization of tissues and higher repair costs (reviewed in Rosenfeld et al., 2014). While this interpretation is somewhat semantic, it may have important implications when attempting to explain variation in von Bertalanffy parameters.

The second implication that comes from Eqs. (1)–(5) is that L_∞ is a scaled ratio of mass-specific consumption and metabolic costs (H and m, respectively) (Eq. (6)). This suggests that external factors that similarly influence both consumption and metabolism will cancel out of the asymptotic length parameter. An example is temperature, which exponentially increases both metabolism and maximum feeding rate within a wide range of temperatures, until enzymatic breakdown begins to occur at high temperatures. It has been noted by several authors that seasonal variation in growth rates will be driven by changes in K, rather than L_∞ (Pitcher and Macdonald, 1973; Cloern and Nichols, 1978; , Fontoura and Agostinho, 1996). The bioenergetics parameter basis of L_∞ also helps illustrate how covariates that act on only consumption or metabolism will affect asymptotic length. Having H and m both contained in L_∞ also helps explain the strong correlation between L_∞ and K, which has been statistically-derived but still biologically relevant (Gallucci and Quinn, 1979; Pilling et al., 2002; Hesler and Lai, 2004).

There are two main criticisms of the VBGF. The first is the inflexibility in the model, which often leads to an implausible prediction of asymptotic size, or unrealistic extrapolation to young or old ages (Knight 1968; Schnute and Fournier 1980). The root cause of these concerns is the assumption that the allometries of consumption and metabolism are invariant over the ages being considered. These ages can be limited using Eq. (5b), where L_0 becomes the length of the initial age being considered and t becomes time (age) since the initial age. However, the formulation in Eq. (5a) is more commonly