



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



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## ABSTRACT

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.

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## 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 Kozłowski, 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

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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)

$$\frac{dW}{dt} = HW^d - mW^n \quad (1)$$

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:

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

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 ( $W = aL^b$ ), which implies that

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

where  $b = 3$  and

$$K = m(1 - d) \quad (4a)$$

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

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:

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

or

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

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

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

Two important implications become apparent as the special VBGF is re-examined in terms of the original bioenergetics parameters rather than just  $K$  and  $L_\infty$ . 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  $L_\infty$  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  $L_\infty$  (Pitcher and Macdonald, 1973; Cloern and Nichols, 1978; Fontoura and Agostinho, 1996). The bioenergetics parameter basis of  $L_\infty$  also helps illustrate how covariates that act on only consumption or metabolism will affect asymptotic length. Having  $H$  and  $m$  both contained in  $L_\infty$  also helps explain the strong correlation between  $L_\infty$  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

used (Mangel 2006) and assumes allometries of consumption and metabolism continue throughout the lifetime of a species (Lester et al., 2004). The  $t_0$  parameter of Eq. (4), defined as the theoretical age at which length is zero, is meant to reflect the length at hatch, but in fitting the model to aged fish, especially older fish vulnerable to the sampling gear, this parameter ends up accounting for ontogenetic shifts in diet, activity and energy allocation (especially increased allocation to reproductive tissue and behavior). As fish grow, so too does cruising speed (Bainbridge, 1958; Ware, 1978), attack rate (Bystrom and Garcia-Berthou, 1999), gape size (Persson et al., 1996) and visual acuity (Hairston et al., 1982). The effects of these ontogenetic changes have important implications for consumption, metabolism and growth (van Poorten and Walters, 2016; Giacomini et al., 2013). For example, studies on two similar lake trout (*Salvelinus namaycush*) lakes that differed only in the availability of forage fish revealed differences in growth and also metabolism (Pazzia et al., 2002). Obviously lake trout feeding solely on invertebrates will have a lower rate of energy intake because of the lower energy density and higher specific dynamic action associated with digesting chitinous species. However activity costs were also higher because larger lake trout were maladapted to fine-scale movements associated with finding and consuming smaller prey (Pazzia et al., 2002; Sherwood et al., 2002). Similarly, Tetzlaff et al. (2010) found that a largemouth bass (*Micropterus salmoides*) population with insufficient abundance of large prey exhibited a much lower allometric anabolic scaling factor ( $d$ ) than a nearby population with abundant large prey, presumably because energy densities of prey are insufficient to promote growth and due to increased foraging costs associated with attacking many small prey items. Understanding and appropriately accounting for ontogenetic diet or habitat shifts will be necessary in resolving these issues (e.g. Coggins and Pine, 2010). Alternately, directly estimating allometric scaling parameters, especially  $d$ , will help resolve these issues. Ontogenetic changes account for imperfect fits that have led to a search for more flexible growth curves which, although rarely mechanistically linked to the biology of growth, are more likely to account for a variety of growth patterns (e.g. Schnute 1981).

The second criticism of the VBGF is the simplicity of the bioenergetics assumptions. The allometric scalar to catabolism ( $n$ ) was set to 1.0 in the VBGF for mathematical convenience so Eqs. (2) and (4) could be integrated to give a closed form solution (Essington et al., 2001). Walters and Essington (2010) have shown that  $d$  and  $n$  are not separately estimable using numerical integration and deviations from the allometric assumptions ( $d = 2/3$ ;  $n = 1$ ) are difficult to detect due to observation error. Direct laboratory estimates of metabolism across body sizes for many species show metabolism consistently varies approximately with weight to the 0.8 power (Hanson et al., 1997; Clarke and Johnston, 1999). A meta-analysis by Essington et al. (2001) shows that  $n = 1$  only applies if reproductive investment is considered. Similarly, several authors have argued against the constraint that  $d = 2/3$ . Pauly (1981, 2010) Pauly (1981, 2010) argues that the first component of Eq. (1) relates to oxidative metabolism of consumed resources, so  $d$  relates to the relative growth of gill tissue surface area. Alternatively, scaling up constraints in transporting nutrients within fractal distribution networks (e.g. blood vessel networks) suggest the  $d$  parameters should be set closer to  $3/4$  (West et al., 1997, 2001). Later work confirmed this, but also suggested considerable variation across species (Moses et al., 2008). Finally, van Poorten and Walters (2016) argue that  $d$  is in fact widely variable across populations and set by prey size availability and size spectra.

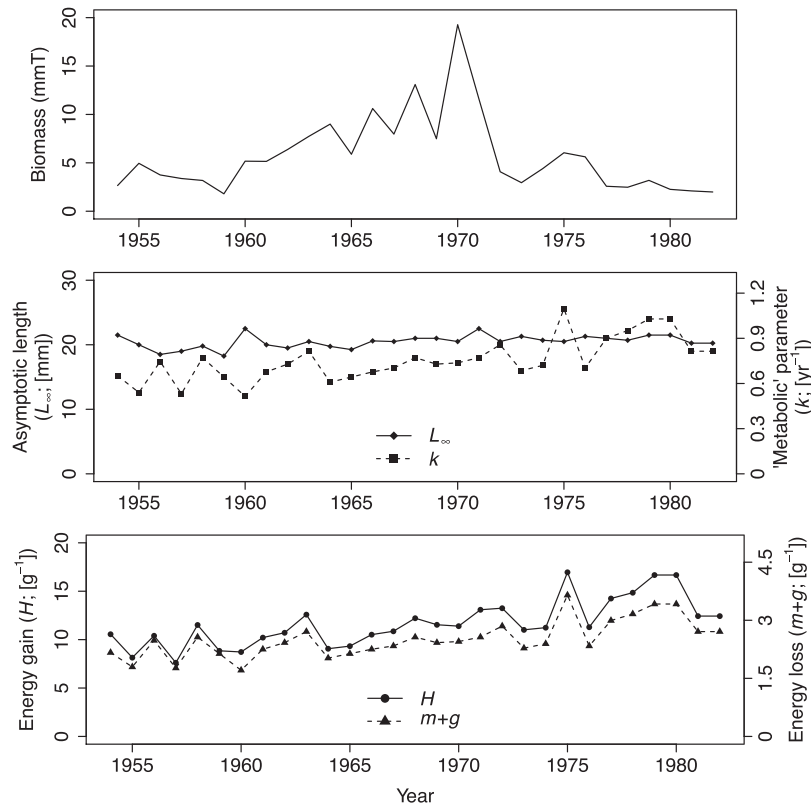
In fact, explicitly accounting for reproductive investment may be the most important and consistent means of improving the fit of growth models, and this point was not directly accounted for in deriving the original VBGF. Recent models (e.g. Lester et al., 2004; Quince et al., 2008a) suggest separately modelling somatic growth

and reproductive investment. They assume  $n$  is equal to  $d$  for juvenile fish (technically incorrect, but the error imposed on growth estimates is minimal; Lester et al., 2004), which then results in the prediction that juvenile length growth rate should be constant with age. The extra catabolic cost of producing and maintaining reproductive tissues is then imposed on fish once they pass the age at maturity, resulting in a 'biphasic growth' curve with linear growth for juveniles and von Bertalanffy growth post-maturity (Lester et al., 2004; Quince et al., 2008a). The result is a better fit to some empirical length-at-age data (Quince et al., 2008b). Alternately,  $n$  and  $d$  could differ, resulting in decreasing juvenile growth rate, but additional slowing of growth past the age at maturity (Stamps et al., 1998; Charnov et al., 2001). However, accounting for biphasic growth is often not an issue as size at age data are often derived from samples of older fish, where reproductive investments are already occurring. In this case, simply allowing  $t_0$  to represent the joint effects of ontogenetic diet shifts and the additional investment in reproduction will often sufficiently alleviate the fitting problem.

Accounting for reproductive investment more directly may help us understand variation in the von Bertalanffy 'metabolic' parameter ( $K$ ) over time. While the special von Bertalanffy model would predict that all environmental variability would affect energy intake resulting in changes in somatic (length) growth, variation in allocation of energy to reproductive tissues may also vary, thereby affecting energy loss. While many researchers have assumed that  $K$  is invariant, variation in the timing of maturity onset would directly cause variation in apparent  $K$ . For example, throughout the development of the Peruvian anchoveta (*Engraulis ringens*) fishery, Palomares et al. (1987) found  $L_\infty$  was relatively constant, but  $K$  steadily increased over time (Fig. 1, center panel) suggesting either an increased allocation to reproductive tissues or an earlier age at maturity as per capita consumption increased (Fig. 1, bottom panel).

The relative allocation of energy to standard metabolic rate ( $m$ ) versus reproductive tissues ( $g$ ) is not generally estimable from field data (Walters and Essington, 2010). However, assigning informative priors on metabolic rate based on existing laboratory studies (Hanson et al., 1997) or through meta-analysis (Essington et al., 2001) would help resolve the relative allocation of energy to reproductive versus somatic tissue. Clearly, changes in reproductive investment will have strong implications for estimates of spawning stock biomass and egg deposition, even if maximum sizes are relatively invariant.

Environmental variables can affect three aspects of the energy allocation process and therefore growth. The first is energy intake, which can vary because of changes in intra- or interspecific densities, competition, foraging time, productivity of prey resources, or spatial range collapse/expansion that alters both intraspecific densities and access to food resources. The second is metabolic rate, which may change due to rapid and sustained changes in growth rates and consumption (Rosenfeld et al., 2014) as well as environmental factors, particularly temperature and oxygen concentration. Finally, reproductive investment and timing may vary in some species (e.g. Johnston and Post, 2009), which would be perceived as an increased energy loss. Changes in environmental drivers may affect multiple physiological mechanisms and so do not affect the four basic bioenergetics parameters from Eq. (1) ( $H$ ,  $m$ ,  $d$ , and  $n$ ) independently. Careful consideration of the derivation of the VBGF will help to evaluate different hypotheses of which environmental variables affect which bioenergetics processes. Further, placing changes in growth and metabolism within the ecological context in which these changes occur will further help understand the mechanisms driving growth variation.



**Fig. 1.** Trend in total stock biomass (top panel), von Bertalanffy (middle panel) and bioenergetics parameters (bottom panel) estimated for Peruvian anchoveta from 1954 to 1982. Data from Palomares et al. (1987).

### 3. Predictions of von Bertalanffy parameters with changes in intraspecific competition

Prey density should have a strong influence on fish growth, since available prey directly influences consumption, unless fish can compensate at low prey densities by considerably varying their daily foraging time. However, measured prey density is rarely proportional to the number of prey particles in front of an individual's nose. Many researchers have shown that fine-scale predator avoidance behavior will strongly dampen predator-prey dynamics (Turner and Mittelbach, 1990; Lima and Dill, 1990; Lundvall et al., 1999). Small prey species spend most of their time in refuges to minimize predation risk, as do small predators. Prey densities in these refuges can be quickly exhausted due to localized competition, so foraging bouts into adjacent "foraging arenas" (Walters and Juanes, 1993) are necessary. However these forays into the foraging arena also expose fish to predation, so time spent foraging is related to prey density, predation risk and physiological constraints (e.g. temperate fish must accumulate a certain lipid reserve to survive winter). These dynamics can be captured by recognizing the influence of vulnerability exchange rates between total prey volumes (which we measure) and vulnerable biomass in the foraging arenas, which are subject to consumption by prey species (Ahrens et al., 2012).

Walters and Post (1993) argued that foraging arena dynamics will influence von Bertalanffy growth by including measured prey density and 'effective competitor density' which the von Bertalanffy model implies should vary as the sum over competitor ages of

squared body lengths times numbers or density at age  $[\sum_{i=1}^A (N_i L_i^2)]$ .

The squared length effect is proportional to consumption rate under the von Bertalanffy (1938) assumptions. As with the special VBGF,

the Walters and Post (1993) density dependent growth model assumes a shared prey resource among size-classes, although they demonstrate how asymmetric competition can be modeled. This model shows that asymptotic size should vary with competitor density, which can easily be visualized as parallel Ford-Walford plots (Ricker 1975) with intercepts (and therefore  $L_\infty$ ) inversely proportional to density.

An alternate means of predicting density dependent growth is to incorporate prey density and intraspecific competitive strength directly into the derivation of asymptotic length. This can be achieved by estimating consumption from two directions: one based on observed growth, the other based on prey densities. If we assume von Bertalanffy growth, then individual consumption ( $q$ ) should be equal to (Essington et al., 2001)

$$q = \frac{HW^{2/3}}{K_3} \quad (7)$$

where  $K_3$  is the product of assimilation efficiency times the proportion of assimilated food energy not lost to specific dynamic action and other energy costs proportional to food intake (Temming and Herrmann, 2009). Using the derivation of  $L_\infty$  and  $K$  above, Eq. (7) can be re-cast as a function of body length (sensu Beverton and Holt 1957: p 112)

$$q = \frac{3aKL_\infty L^2}{K_3} \quad (8).$$

To estimate consumption from prey density, it is necessary to estimate density of prey in the foraging arena. Foraging arena theory (Walters and Juanes, 1993) states that the dynamics of prey density ( $V$ ) vulnerable to consumption by the fish will be equal to input from an invulnerable pool that is outside the foraging arenas ( $B-V$ ; which we measure when sampling large areas rather than

just within foraging arenas) less output back to the invulnerable pool and consumption by the fish in the foraging arenas:

$$\frac{dV}{dt} = v_1(B - V) - v_2V - aV \sum_i^A (N_i L_i^2) \quad (9)$$

where  $B$  is total prey biomass,  $a$  is the effective rate of search,  $N_i L_i^2$  is the product of squared body lengths and predator abundances for age- $i$  (effective density; Walters and Post, 1993; Post et al., 1999) and  $v_1$  and  $v_2$  are the vulnerability exchange rates of prey resources into and out of the foraging arena. At equilibrium, prey density in the foraging arena is equal to

$$V = \frac{v_1 B}{v_1 + v_2 + a \sum_{i=1}^A (N_i L_i^2)}. \quad (10)$$

Consumption of prey in the foraging arena will be equal to  $q = aV p_f \sum_{i=1}^A (N_i L_i^2)$ , where  $i$  represents age-classes and  $p_f$  is the proportion of time an individual predator actively searches for prey. Therefore, predicted individual consumption is  $\alpha L^2 p_f V$  and substituting in Eq. (10), this becomes

$$q = \frac{aL^2 p_f v_1 B}{v_1 + v_2 + a \sum_{i=1}^A (N_i L_i^2)}. \quad (11)$$

Equating Eqs. (8) and (11) and solving for  $L_\infty$  gives a density dependent estimate of  $L_\infty$  in a particular year  $t$ :

$$L_{\infty,t} = \frac{\beta_1 B_t}{1 + \beta_2 \sum_{i=1}^A (N_{i,t} L_{i,t}^2)} \quad (12)$$

where

$$\beta_1 = \frac{p_f v_1 K_3}{(v_1 + v_2)}$$

and

$$\beta_2 = \frac{a}{v_1 + v_2}.$$

Eq. (12) assumes that there is no dynamic adjustment to foraging time unless  $p_f$  is treated as variable, which implies that predation risk does not change over time. This assumption can be relaxed if predator densities are known (Walters and Korman 1999). Either the Walters and Post (1993) or Eq. (12) can be used to mechanistically estimate density dependence in growth assuming von Bertalanffy growth.

Alternately, one might ask how changes in consumption must have impacted total mortality on lower trophic levels. These investigations do not require assumptions of fine-scale predator-prey dynamics but do make assumptions regarding diet composition, energy conversion efficiencies and energy densities of prey and predators. He et al. (2015) used a coupled bioenergetics-stock assessment model to show how variation in growth and abundance of predators in Lake Huron affected relative mortality rates of prey. This novel modelling approach first predicts how von Bertalanffy parameters  $L_\infty$  and  $K$  and length-weight parameters for each predator changed over time (He and Bence, 2007; He et al., 2008), which informed a bioenergetics model. Coupled with extensive data and simple models explaining maturity, diet composition, thermal habitat and energy densities of predators and prey, they were able to estimate individual consumption patterns. When linked with a statistical catch-at-age model, it was possible to make inferences about the relative impact predation had on total mortality rates of prey. The He et al. (2015) model is somewhat similar to some ecosystem models (Walters et al., 2000) and again points to the importance of including growth variation in predictions of

predation rates. This approach is obviously data intensive and cannot be used as a predictive tool without understanding dynamics of prey species, but represents a new direction for stock assessment.

#### 4. Predictions of von Bertalanffy parameters with changes in environment

Temperature is the most obvious environmental variable to influence growth in ectothermic species. Several authors have described how to incorporate intra-annual temperature variation into the  $K$  parameter. For example, Pitcher and Macdonald (1973) showed how growth may oscillate throughout the growing season and suggested that the sine-wave function they apply to  $K$  could be fit to temperature data. Cloern and Nichols (1978) showed how a similar model could be integrated over time to predict how annual growth would vary with seasonal changes in the environment (although temperature was not explicitly mentioned). Fontoura and Agostinho (1996) expanded this notion by considering variation in metabolism at an enzymatic level and incorporated metabolic and growth declines at extreme temperatures. Walters and Essington (2010) took this notion a step further by formulating a new 'general' bioenergetics model based on Eq. (1) and explicitly including temperature as a Q10 multiplier on anabolism and catabolism. A Q10 temperature coefficient is a common physiological measure of the rate of change of a biological function as temperature increases by 10 °C. This model could be fitted to tag-recapture and size-at-age data and the effect size of temperature on each of these two processes could be estimated.

Predicting how temperature changes will influence growth (especially when considering climate change) is complicated. This is primarily because temperature does not simply affect basal metabolic rate of the population being considered, but includes effects on burst and sustained swimming speeds due to the influence of temperature various enzymes involved in active metabolic processes (Fontoura and Agostinho, 1996). Moreover, temperature also strongly drives patterns of prey availability in all aspects of the ecosystem implying that temperature affects both metabolism and consumption (Kitchell et al., 1977; DeStasio et al., 1996; Ficke et al., 2007; van Poorten and Walters, 2010). Assuming consumption and metabolism scale similarly with temperature implies that temperature only affects  $K$  in the VBGF, as assumed by most authors (e.g. Pitcher and Macdonald, 1973; Cloern and Nichols, 1978; Fontoura and Agostinho, 1996). However, if temperature does not scale similarly for energy intake ( $H$ ) and loss ( $m$ ), such as at temperatures approaching the upper incipient lethal temperature, these two processes will need to be incorporated into von Bertalanffy growth, although they will not be individually estimable (Walters and Essington, 2010).

Other environmental variables will also influence growth rates, but often to a lesser extent than temperature. Obviously more extreme fluctuations in other environmental drivers can have pronounced effect on growth. For example, salinity variations common in estuarine areas may impact metabolic rate due to the increased effort exerted to osmoregulate (reviewed in Boeff and Payan, 2001). Dissolved oxygen also varies dramatically in many aquatic systems, such as temperate lakes and high productivity marine habitats like seagrass beds. These extreme variations may influence both consumption and metabolic rates as organisms shift energy away from feeding metabolism and towards basal metabolism (Niklitschek and Secor, 2010). Indeed, in some systems, oxygen limitation may be a greater constraint on growth than consumption, so that Pauly (1981, 2010) contend that growth of species in some environments may be limited by gill surface area.

Care is needed when predicting environmental effects on the various components of growth. For example, high turbidity may

lead to decreased foraging efficiency of predators (De Robertis et al., 2003) or may lead to increased metabolic cost and decreased respiratory efficiency due to tissue repair of gills, excessive mucus secretion and interference with gill excretory function (reviewed in Bunt et al., 2004). Alternately, growth may be affected due to the need to switch foraging activities to more energetically costly modes of search (Sweka and Hartman, 2001). Environmental variables often interact with one another, making their impacts difficult to separate or interpret. For example, various authors have found an interactive effect between dissolved oxygen and salinity on metabolism (Buentello et al., 2000; Niklitschek and Secor, 2009; Hanks and Secor, 2011). The decision of whether to consider multiple interacting variables may largely depend on whether they contribute to the management question being posed.

The effects of environmental variables on the bioenergetics processes that contribute to growth are complex and somewhat species- and context-specific. Great care should be taken when considering which variables to include in models for predicting changes in growth. An important consideration is the intended use of the growth model being developed. Even if the effects of specific environmental variables on growth can be estimated, can future patterns in these variables be predicted with enough certainty to answer the management questions being posed? In the long-term, are extremes in particular environmental variables likely to drive growth variation, or just result in occasional aberrations in the overall pattern? Moreover, is there any ability to alter these environmental variables (e.g. turbidity, discharge), or are they just 'noise'? If specific environmental variables are unpredictable or unmanageable, there may be no need to include them in growth models.

## 5. Applications and implications

Actually predicting what drives variation in growth is obviously complicated. As discussed above, many extrinsic factors will affect various aspects of growth (consumption, metabolism, reproduction) and different environmental drivers will interact to some extent. For example, temperature, dissolved oxygen and salinities can all vary within estuarine environments. Controlled experiments have demonstrated that each of these variables and several of their interactions affect consumption and metabolism in different ways, yet many models only consider temperature (Niklitschek and Secor, 2009, 2010). Disentangling important effects is difficult unless data are particularly informative.

Consider the Peruvian anchoveta example (Palomares et al., 1987) from above. Direct estimation of time-varying von Bertalanffy parameters indicated the metabolic parameter ( $K$ ) varied widely while the asymptotic length ( $L_\infty$ ) was relatively stable over time, even though densities (Fig. 1, top panel) and presumably various environmental factors like temperature changed dramatically over the 30-year time-series. As both  $H$  and  $m$  determine  $L_\infty$ , both must have varied similarly to result in changes in  $K$  but not  $L_\infty$  (Fig. 1 bottom panel). Various ecological scenarios must be considered to form hypotheses. One scenario is that overall range contraction may have occurred as abundance declined (Rodríguez-Sánchez et al., 2002). This would result in densities remaining relatively constant as abundance declined so that available food per individual and consumption ( $H$ ) would be invariant. Another scenario may have seen individuals reduce their feeding rate as abundance declined to reduce predation mortality (Anholt and Werner, 1998). Reduced feeding rate would result in consumption rate again remaining constant (Eq. (9)), resulting in  $H$  and  $m$  remaining constant, meaning both  $L_\infty$  and  $K$  would also remain relatively constant over the time series. It is more likely a phenotypic response to high fishing mortality (Law, 2000) resulted in

increased reproductive investment, meaning earlier maturity or higher reproductive investment (Trippel, 1995). In this scenario, both consumption and reproductive investment would increase (e.g. both  $H$  and  $m$  increase), leading to an increase in  $K$  but not  $L_\infty$ . Evaluating each possible scenario can be difficult and rationalizing and confirming hypotheses will be onerous, however the cost of incorrect assumptions with respect to predictions of consumption and growth rates may lead to bad management recommendations.

Strong predicted changes in environmental variables to levels far from biological optima will often be strongly mediated by behavioral adaptation. Behavioral thermoregulation is a commonly observed phenomenon used by animals to minimize stress and optimize performance in otherwise harsh environments. For example, as temperatures increase in many coldwater systems, fish adjust their distribution to take advantage of colder habitats to balance the need for food against the cost of high metabolism (Mackenzie-Grieve and Post, 2006). While adjustments in habitat use to limit exposure to high body temperatures may mediate the direct effects of increasing temperature, these adjustments are also likely to cause restriction in spatial habitat use, hence increase intraspecific density and competition that result in indirect effects on consumption rate or prey selection. Cheung et al. (2013) predicted size and distributional changes in global demersal fish based on predictions of benthic temperature and oxygen under climate change scenarios. Their results predict a general decline in body size across a wide variety of species because of increases in metabolism relative to consumption. However, this study does not account for fine-scale behavioral adaptation, which would help mediate subtle changes in temperature and oxygen. Conversely, moving to darker, colder habitats will likely effect foraging efficiency, meaning growth will decline even if metabolism ( $K$ ) stays constant. Large-scale predictions such as those in Cheung et al. (2013) are difficult to validate and it may not be possible to estimate behavioral responses across a large number of species. However, as demonstrated in Mackenzie-Grieve and Post (2006), some fish can easily persist and thrive in habitats for which their optimal environmental conditions no longer exist.

Misunderstanding the cause of growth variation may lead to poor management decisions. When examining factors influencing growth variation in Pacific halibut (*Hippoglossus stenolepis*), Clark et al. (1999) concluded that decadal-scale variation in productivity has been a primary driver in growth. As more data emerged and new models were developed, it became clear that productivity changes were directly affecting recruitment strength and growth was actually entirely density-dependent (Clark and Hare, 2002). This difference obviously has strong implications for short-term recruitment predictions and overall predictions of optimal harvest rates within different Pacific decadal oscillation (PDO) regimes.

## 6. Conclusions

Growth in fish can be incredibly plastic owing to the various ways in which external factors influence activity, prey availability and the ability of an organism to efficiently integrate consumed energy into body tissue. Although we have outlined various ways that growth may change across populations, it is not at all clear for any particular stock what will happen as changes occur in one or more ecological or environmental variables. We have reiterated how the VBGF is formulated from a general bioenergetics model (von Bertalanffy, 1938), which can help in formulating and predicting how various changes in extrinsic factors will be included in the VBGF. For example, using basic bioenergetic and ecological arguments, we see how changes in density translate into changes in consumption and therefore  $L_\infty$ . Likewise, predicting how various environmental variables and their interactions will impact

consumption and metabolism separately allows for the appropriate inclusion of these variables into  $L_{\infty}$  and  $K$  of the VBGF. Finally, changes in reproductive rates and timing will directly influence both these variables as well.

Careful consideration of alternate ecological and bioenergetic pathways can lead to testable hypotheses that will help determine what the primary driver(s) of growth may be in any particular situation. It is important to accurately identify these primary drivers as they will help determine when growth may be directly manipulated or controlled and what changes we may expect in the future.

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