

Dependence of feeding rates on body mass when food density is limiting to growth

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Abstract: Bioenergetics models are commonly used to predict effects of changes in metabolic rates and food availability on growth. However, food intake rate generally is assumed to vary as W^d , where $d = 2/3$, an assumption based on observations from feeding trials in laboratory studies. Further, the von Bertalanffy growth function (VBGF) is specifically integrated using this assumption. We argue that when considered from an ecological perspective, d is highly uncertain, dependent on how swimming speed, reactive distance, and prey biomass varies ontogenetically with the growth of a predator. Incorrectly specifying d leads to incorrect predictions of consumption and metabolism, especially at younger ages that are typically under-sampled. Three alternate means of detecting departures from $d = 2/3$ are provided, the most promising of which involves fixing initial length of the generalized VBGF to the length at endogenous feeding and directly calculating von Bertalanffy parameters (L_∞ , K , t_0). Using this approach, it may be possible to more accurately estimate consumption and metabolism and to characterize lifetime growth.

Résumé : Des modèles bioénergétiques sont communément utilisés pour prédire les effets de variations de la vitesse du métabolisme et de la disponibilité de nourriture sur la croissance. Cependant, il est généralement présumé que le taux d'ingestion de nourriture varie en fonction de W^d , où $d = 2/3$, une hypothèse qui repose sur des observations tirées d'essais d'alimentation dans des études en laboratoire. En outre, la fonction de croissance de von Bertalanffy (FCVB) est spécifiquement intégrée en utilisant cette hypothèse. Nous arguons que, pris dans une perspective écologique, d est très incertain et dépend des variations ontogéniques de la vitesse de nage, de la distance de réaction et de la biomasse de proies en fonction de la croissance d'un prédateur. L'établissement d'un d incorrect mène à des prédictions incorrectes de la consommation et du métabolisme, particulièrement pour les classes d'âge plus jeunes, typiquement sous-échantillonnées. Trois approches différentes sont présentées pour déceler les écarts par rapport à $d = 2/3$, dont la plus prometteuse consiste à définir la longueur initiale de la FCVB généralisée comme étant la longueur au stade d'alimentation endogène et à calculer directement les paramètres de von Bertalanffy (L_∞ , K , t_0). En utilisant cette approche, il pourrait être possible d'estimer la consommation et le métabolisme avec plus d'exactitude et de caractériser la croissance sur la durée de vie. [Traduit par la Rédaction]

Introduction

Bioenergetics models are commonly used to infer feeding rates from observed growth rates and to predict effects on growth of changes in metabolic and food availability conditions. In such models, maximum energy intake rates are typically assumed to vary approximately as the $2/3$ power of body mass (Hanson et al. 1997), based on arguments about variation in maximum digestion rate with gut surface area relative to body mass (Beverton and Holt 1959, though see Pauly 1981 for alternate interpretation). Then, achieved intake rates typically observed in field conditions are assumed to be some proportion (called “ p ” in the commonly used “Wisconsin model”; Hanson et al. 1997) of this maximum. When body mass is assumed to vary as the cube of length, and basal metabolic plus reproductive losses are assumed proportional to body mass, the $2/3$ power assumption for feeding rate then implies the widely used special von Bertalanffy model for length growth (von Bertalanffy 1938). However, direct estimates of the allometric rate of food consumption often vary from $2/3$ (Trudel et al. 2000; Sherwood et al. 2002b). The “generalized” von Bertalanffy model (Pauly 1981; Essington et al. 2001) is derived by allowing the food intake power parameter to differ from $2/3$. Good statistical

estimates of this power parameter cannot be obtained by fitting the generalized model to field growth data, and limited experience with trying to do so results in wide variation in the parameter estimate (Essington et al. 2001).

This paper argues that it is not in fact appropriate to assume that feeding rates vary as the $2/3$ power of body mass under field conditions where feeding rates are limited by food densities and prey sizes. We argue that in such situations, which are probably the most common in nature, feeding rate is limited by the volume of water searched per time for prey and by the density and size distribution of prey within this volume. These arguments are not new (Sherwood et al. 2002a, 2002b; Rennie et al. 2005), but their implications for bioenergetics models generally, and the von Bertalanffy growth function specifically, lead to several key findings and generalizations for how growth may be expected to vary over a lifetime. Scaling relationships for volume searched with body mass predict much lower powers than $2/3$, unless increasing mass also results in increasing mean size of prey captured, and a wide range of prey sizes is available in which case the power parameter may approach 1.0.

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Effect of size and prey density on food intake rate

Our aim in this section is to predict the “ d ” parameter in the general bioenergetics model

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

Here H is the energy intake rate per scaled mass W^d . The first term in eq. 1 is anabolism or energy intake rate, which represents food intake rate times the product of assimilation efficiency and proportion of assimilated food intake not lost to specific dynamic action and costs of tissue synthesis. Therefore, consumption rate = anabolism/ K_3 , where K_3 represents the proportion of ingested food available for growth (Temming and Herrmann 2009). The m parameter represents mass loss rate to metabolism and (for larger fish) reproductive products. The $d = 2/3$ assumption results from assuming that food intake is the product $p kW^d$, where kW^d represents maximum intake and p is the proportion of maximum consumption actually achieved. In bioenergetics modelling, observations of maximum consumption rate are based on laboratory feeding trials where animals are fed ad libitum. These trials typically result in d estimates close to $2/3$ (e.g., see references in Hanson et al. 1997). Equation 1 is an obvious oversimplification of the various processes leading to nutrients assimilation, transport, uptake, and eventual tissue growth. However, as it is the basis for the majority of bioenergetics models used to characterize fish growth, including the widely used von Bertalanffy growth model, it will form the foundation of the remainder of our discussion.

But suppose that food densities are low, such as most field conditions, so that the food intake component of HW^d is equal to the volume of water searched per time times prey mass per volume, i.e.:

$$(2) \quad \text{food intake rate} = (\text{volume searched per time}) \times (\text{prey mass per volume})$$

For visual feeding fish, volume searched per time can be expressed as the product of swimming speed (or water speed of a stationary fish, as in drift-feeding consumers in streams) times reactive area of the predator’s visual field:

$$(3) \quad \text{volume searched per time} = (\text{swimming speed}) \times (\text{reactive area}) \times (\text{search time})$$

There is little empirical evidence about how body size affects time spent searching, so we will treat it as independent of body size in the following derivations. We attempt to develop allometric relationships to predator mass W for the other components (Emerson et al. 1994).

Swimming speed (or mean water column velocity above waiting predators in flowing waters) likely varies as a power β_v of body length. Optimization arguments (Ware 1978) and limited field observations suggest that β_v should be less than about 0.4, implying that swimming speed as the $0.4/3 = 0.13$ power of body mass if mass varies as the cube of length, or more generally swimming speed should vary as

$$(4) \quad \text{swimming speed} \sim W^{\beta_v/3}$$

Thus, if reactive distance to prey is independent of predator size so that reactive area is constant (e.g., for filter-feeding fish or fish feeding on small prey such that visual acuity and prey detection range does not increase with predator size), we would expect food intake rate to vary as prey density times $W^{0.13}$ (i.e., very low $d = 0.13$).

But most commonly, larger fish target larger prey (reviewed in Werner and Gilliam 1984), so that mean prey length L_p increases with predator mass. Reactive distance to prey is likely to increase for larger prey and also depends on predator size; reactive area is proportional to the square of reactive distance. Assuming that reactive distance varies as powers of both prey length and predator length, combining the predator and prey lengths effects implies that reactive area should vary as

$$(5) \quad \text{reactive area} \sim (L_p^{\beta_p} W^{\beta_q/3})^2$$

The power parameters β_p and β_q show few consistent patterns in the literature. The prey length effect parameter β_p may range from as low as 0 for large piscivores to near 1.0 for planktivores. Many early studies on planktivores show reactive distances just proportional to prey length (reviewed in Gerking 1994; see also O’Brien 1979), while studies on other predators give lower powers (Hughes and Dill (1990) suggest a saturating function for Arctic grayling (*Thymallus arcticus*) feeding; data in Ware (1973) show reactive distances of trout (*Oncorhynchus mykiss*) to amphipods implying $\beta_p = 0.46$; data in Crowl (1989) show reactive distances of largemouth bass (*Micropterus salmoides*) to crayfish (*Procambarus acutus*) implying β_p ranging from near 0.0 in turbid conditions to 0.70 in clear water; Mazur and Beauchamp (2003) found no prey size effect, i.e., β_p near 0.0 in experiments on piscivorous freshwater salmonids). The predator length effect parameter β_q can also be much less than 1.0 (e.g., data on reactive distances of bluegill (*Lepomis macrochirus*) in Breck and Gitter (1983) imply β_q near 0.5; Mazur and Beauchamp (2003) provide regression equations indicating β_q of 0.05 and 0.25 for the two of their species for which a wide range of predator lengths was tested).

Combining predator swimming speed and reactive area relationships implies that volume searched per time should vary as $W^{\beta_v/3 + 2\beta_q/3} L_p^{2\beta_p}$. If mean prey length L_p is proportional to predator length, as is apparently common in fish (see e.g., Mittelbach and Persson 1998; Scharf et al. 2000), we then expect volume searched per time to vary as

$$(6) \quad \text{volume searched} \sim W^{\beta_v/3 + 2\beta_q/3} (W^{1/3})^{2\beta_p} = W^{\beta_v/3 + 2\beta_q/3 + 2\beta_p/3}$$

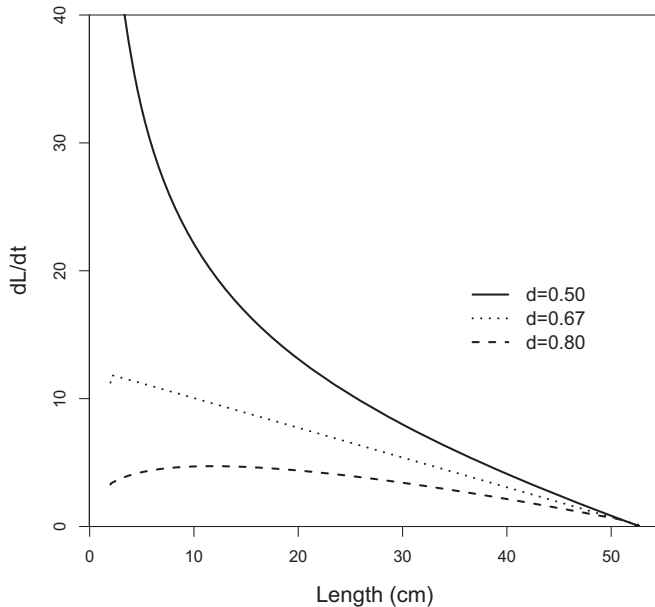
That is, we should expect d to be around

$$(7) \quad d = \beta_v/3 + 2\beta_q/3 + 2\beta_p/3 = (\beta_v + 2\beta_q + 2\beta_p)/3$$

This equation implies d should be larger than $2/3$ if β_p is near 1.0 as has been estimated for planktivores, even if $\beta_q = 0$ (i.e., even if reactive distance is independent of predator size).

It remains to ask how changes in mean prey size L_p are likely to affect the prey biomass per volume in eq. 2. From observations on size spectra (relationships between biomass and body mass), we would expect biomass density to decrease slowly with increases in L_p . Typically, numerical densities of organisms vary as roughly the -1.0 power of potential prey mass, which means that biomass (numbers \times mass) is nearly constant over a wide range of prey sizes and is likely to be a dome-shaped function of size within any major prey type, like zooplankton or forage fish (see reviews and theoretical arguments in Boudreau and Dickie 1992; Thiebaut and Dickie 1993; Duplisea et al. 1997; Havlicek and Carpenter 2001; Sprules 2008; Hartvig et al. 2011; Trebilco et al. 2013). This means that prey biomass density should not change much if L_p is proportional to predator length $W^{1/3}$; but if predators increase the range of prey lengths taken as they grow, total selected prey biomass per volume can actually increase as predators grow (i.e., the prey mass per volume component of eq. 2 can be a weakly increasing function of predator length). Assuming that this increase with predator length can be described as a power function with power

Fig. 1. Variation in length growth rate dL/dt with length L predicted by the general bioenergetics model, for alternative d parameter values. The value $d = 2/3$ predicts a linear (von Bertalanffy) relationship.



parameter β_s , selected prey biomass should vary with predator mass as $W^{\beta_s/3}$. Combining this assumption about higher biomass density of total prey selected with the prediction from eq. 6 about volume searched, we conclude that food intake should typically vary as

$$(8) \quad \text{Food intake rate} \sim W^{\beta_v/3 + 2\beta_q/3 + 2\beta_p/3} W^{\beta_s/3}$$

That is, d should vary as $d = (\beta_v + 2\beta_q + 2\beta_p + \beta_s)/3$, an even higher power of body mass than predicted just from predator search parameters. But note again that the $2/3$ “base” value for d in eqs. 7–8 comes from assuming mean prey size and hence reactive distance proportional to predator length, which is certainly not a universal pattern; if this proportionality is violated (i.e., if the length distribution of prey is severely truncated for some reason (e.g., Pazzia et al. 2002; Sherwood et al. 2002a) or if the predator selects the same size of prey no matter how large it is), the $2/3$ base vanishes and d can be as low as $(\beta_v + 2\beta_q)/3$.

The basic result from these volume-searched and prey abundance calculations is that d cannot be reliably predicted from known body size relationships since all of the β parameters are highly uncertain. About all that can be safely predicted is that d is likely to be in the wide range

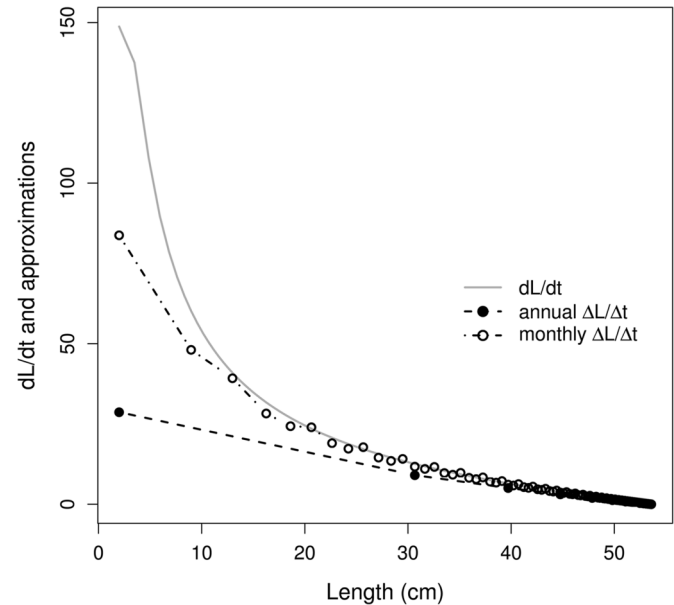
$$(9) \quad (\beta_v + 2\beta_q)/3 < d \leq (\beta_v + 2\beta_q + 2\beta_p + \beta_s)/3$$

In fact, d may vary widely among species and even within a population over time because of variation in the size distribution of prey and the effect of predator size on what part of this prey distribution is actually taken when encountered (e.g., Fox 1989; Galarowicz et al. 2006), even if effects of predator body size on swimming speed and reactive distance (β_v and β_q) are well known and stable.

Testing for departure from the von Bertalanffy assumption

To examine possible ways of detecting departure from the von Bertalanffy assumption $d = 2/3$, we generated simulated length growth curves by integrating the general bioenergetics model for a range of d values while assuming W proportional to L^3 .

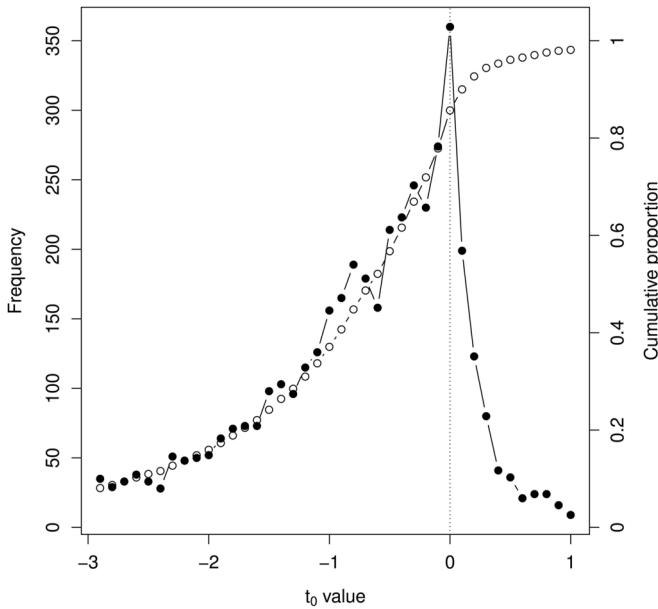
Fig. 2. Comparison of dL/dt with discrete time $\Delta L/\Delta t$ estimates from annual versus monthly length increment sampling, for a case where $d = 0.3$.



We found as in previous studies that attempts to estimate d from the simulated length-at-age data result in extremely unstable estimates when there is any realistic random variation in the “observed” mean lengths-at-age. More, we found that fitting the “special” von Bertalanffy model $L(a) = L_\infty[1 - e^{-K(a-t_0)}]$ results in very tight fits to the “data” for age- $a \geq 1$, even when random sampling effects are absent (i.e., it is not possible to detect departures of d from $2/3$ just by looking at deviation patterns from the standard model).

However, this exercise did suggest two possible approaches for detecting at least cases where $d \ll 2/3$. The first is by direct examination of estimates of length growth rate dL/dt as a function of length L . The $d = 2/3$ assumption implies that this relationship should be linear, decreasing from KL_∞ at $L = 0$ to 0 at $L = L_\infty$. Values of $d < 2/3$ cause the relationship to be concave (decreasing more rapidly at low values of L), while $d > 2/3$ causes the relationship to be flat or domed for low L (Fig. 1). Such curvature patterns are nearly invisible when dL/dt is approximated by annual changes in L (i.e., by $L(a+1) - L(a)$), but they are quite visible for young fish when monthly data (e.g., from tagging or length frequency progression) are used to calculate approximate dL/dt as $\Delta L/\Delta t$ with $\Delta t = 1/12$ year (Fig. 2) or less. An important point about dL/dt from Figs. 1–2 is that effects of $d < > 2/3$ are mainly “visible” for fish less than 1 year of age. Note, however, it is obviously not wise to use short-term (monthly) $\Delta L/\Delta t$ estimates for young fish while expecting the pattern in Fig. 1 for fish that experience strong seasonal changes in H and m (eq. 1) due to changes in temperature and food availability. Regardless, such young fish are most often not included in growth model fitting; higher or lower first year growth rates than predicted by von Bertalanffy fits to data for older fish are usually attributed to ontogenetic changes in foraging behavior or prey availability for small juveniles. However, this is exactly the point made in the previous section; prey size typically increases with predator size (Mittelbach and Persson 1998), and the $d = 2/3$ assumption may not capture this change. A more realistic representation for some species may be an ontogenetic shift in the value of d used, but such an abrupt shift is unlikely to be estimable and will be largely unnecessary in most species if allometry of consumption is assumed to vary from $d = 2/3$. Unfortunately, because of the difficulty in interpreting short-term growth

Fig. 3. Frequency distribution of estimates of the von Bertalanffy t_0 parameter in FishBase, as of 2014.



in young fish either because of temperature effects or their absence due to selective sampling, it will be difficult to detect a divergence from $d = 2/3$ using this approach.

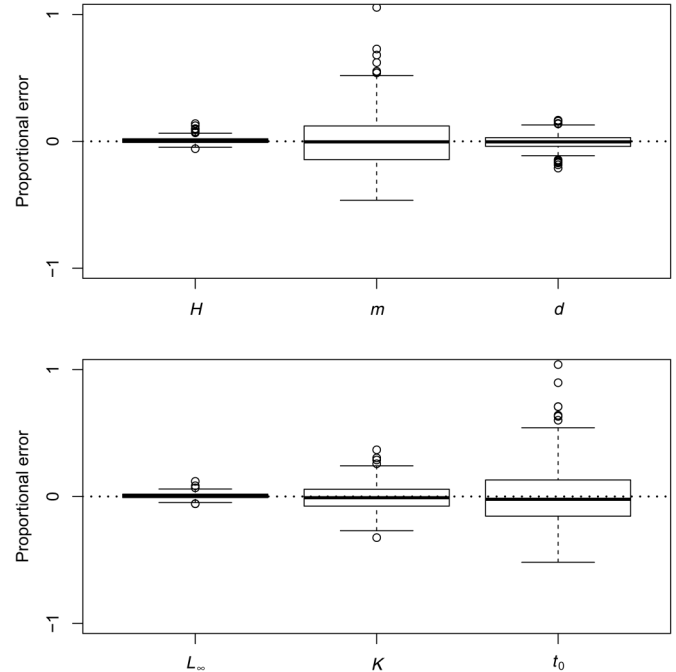
The second approach is to fit the special von Bertalanffy model, then examine the t_0 parameter representing apparent age at $L = 0$ (or apparent body size at age-0). For $d < 2/3$, the estimated t_0 parameter can be a quite large negative, indicating large apparent size at age-0; in contrast, $d > 2/3$ results in weakly positive t_0 estimates. Larger negative t_0 estimates than expected from size at hatching are extremely common in growth curve fitting; for the 4608 growth parameter sets now in FishBase (<http://www.fishbase.org/>; D. Palomares, personal communication), fully half are less than -0.5 (Fig. 3). Probably the most common cause of large negative t_0 estimates is size-selective sampling, where younger fish (ages 1-3) are underrepresented. This size-selective sampling will also disproportionately sample faster-growing fish (“Lee’s phenomenon”; Ricker 1975), causing an upward bias in growth and downward bias in t_0 . This is especially common when size data are collected from commercial fisheries. Large negative t_0 values in FishBase occur widely across fish families and even within species for which many growth curves are reported (i.e., there is no clear tendency for more negative t_0 values to be reported for small planktivores that might face restricted prey size distributions that would lead to lower d as indicated in the previous section). But in cases where careful sampling procedures are used to avoid selection of larger individuals at younger ages, it is certainly possible to detect at least occurrence of $d \ll 2/3$.

Estimating generalized von Bertalanffy parameters from sampled data

A final means of detecting departures from the $d = 2/3$ assumption is to estimate d directly using length-at-age data. If we assume a relatively smooth increase in prey size with predator size, then we can anchor the generalized von Bertalanffy growth curve at a t_0 predicted from known age at hatch (or larval settlement). Integrating eq. 1 shows how d relates to the special von Bertalanffy parameters (L_∞, K, t_0 ; Pauly 1981; Essington et al. 2001; van Poorten and Walters, in press):

$$(10) \quad L(a) = L_\infty [1 - e^{-K(a-t_0)}]^{1/3(1-d)}$$

Fig. 4. (Top panel) Boxplots of proportional error in bioenergetics parameters estimated using 200 randomly sampled fish between ages 2 and 10. Growth was simulated using 200 datasets generated with mean parameter values of $H = 8, m = 0.8,$ and $d = 0.67$ and CV of 0.1. (Bottom panel) Boxplots of proportional error in von Bertalanffy parameters calculated from simulated and estimated bioenergetics parameters.



where

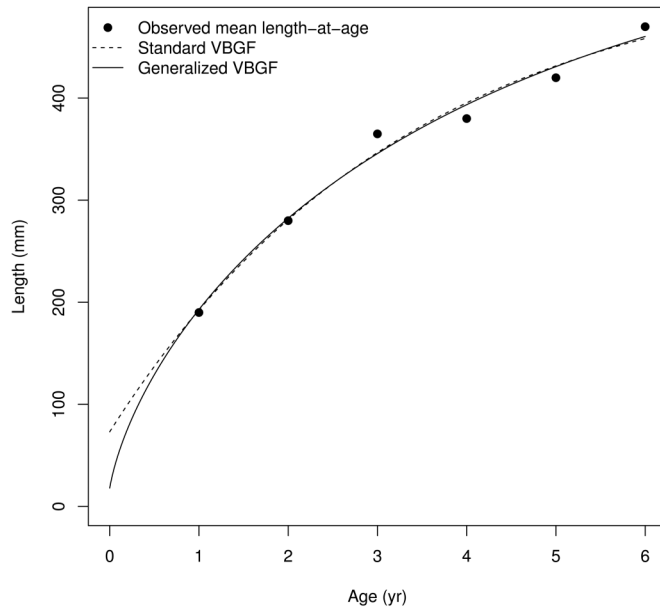
$$L_\infty = \left(\frac{Ha^{d-1}}{m} \right)^{\frac{1}{3(1-d)}}, \quad K = m(1-d), \quad t_0 = \frac{\log_e \left[1 - \left(\frac{L_H}{L_\infty} \right)^{3(1-d)} \right]}{K}$$

and L_H is the length at hatch, yolk absorption, or settlement. This means we can calculate $L_\infty, K,$ and t_0 by estimating $H, m,$ and d assuming normally distributed errors. Simulation-evaluation over a wide range of $H, m,$ and d shows this method to be remarkably reliable in predicting the underlying growth pattern from populations with a range of actual d values, even when younger ages are excluded from the sample (Fig. 4).

Unfortunately, selective sampling of larger individuals at young ages can obviously cause downward bias in the d parameter estimate. But if we are willing to assume some knowledge about the size vulnerability or size selectivity function $V(L)$ used in the growth sampling and about the coefficient of variation (CV) of length for young ages, the predicted mean lengths-at-age can be corrected for effects of $V(L)$ on the mean observed length. If $\bar{L}(a)$ is the mean length-at-age predicted by the growth model, and length is assumed to be normally distributed around this mean with standard deviation $\sigma_l = \bar{L}(a)CV$, then the observed mean length $L_{obs}(a)$ should be

$$(11) \quad L_{obs}(a) = \frac{\int_L V(L)N[\bar{L}(a), \sigma_l]LdL}{\int_L V(L)N[\bar{L}(a), \sigma_l]dL}$$

Fig. 5. Observed mean length-at-age (mm) for sterile (triploid) kokanee with fitted special and generalized von Bertalanffy growth functions. The generalized VBGF was constrained to a 25 mm length at hatch.

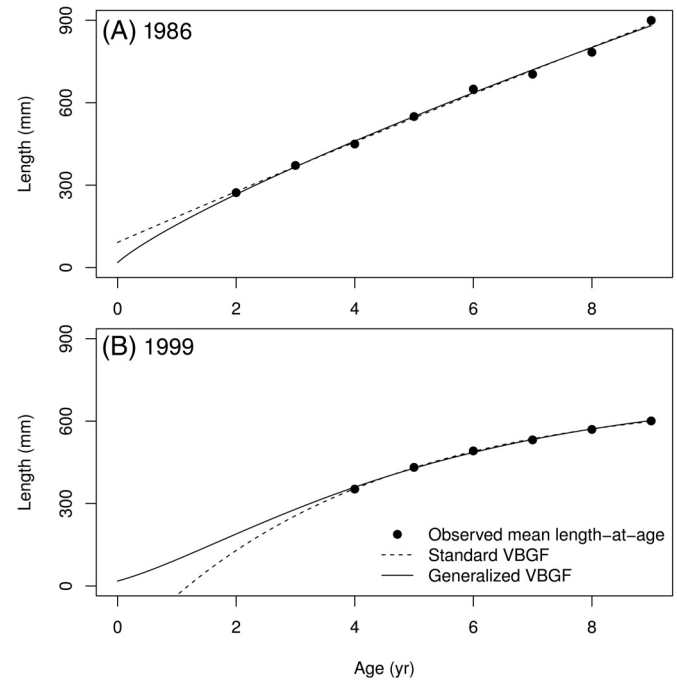


where $N[\bar{L}(a), \sigma_L]$ is the normal probability density function. Various numerical schemes can be used to evaluate the integrals in eq. 11; the simplest is to just sum the numerator and denominator over a large number of fine L steps. This equation follows from the statistical definition of the mean of a random variable (L in this case), with relative probability of observing a length L fish given by $V(L)N$ and scaled to sum to 1.0 over all L by the denominator term in the equation. Equation 11 can either be used to directly predict mean observed length as a function of the growth model parameters and $V(L)$ or applied as a correction factor to the observed mean lengths at age. Using eq. 11, it is possible to determine how d estimates vary with assumed selectivity by fitting the model for a range of assumptions about $V(L)$, from flat ($V(L) = 1$) representing nonselective sampling to strongly selective as is at least possible and hence provide a range of possible d values.

Applying this generalized von Bertalanffy model to data from sampled populations shows promise in recovering some information about d directly. For example, sterile kokanee (*Oncorhynchus nerka*) stocked in British Columbia lakes (T. Godin, Freshwater Fisheries Society of BC, personal communication) provide an interesting test, as these fish devote almost no energy towards reproduction (although some secondary sexual characteristics do sometimes occur). Figure 5 shows the generalized model predicts a similar length-at-age for older age classes, but accurately reflects a decelerating growth rate in the first year. The generalized VBGF predicts a lower metabolic parameter ($K = 0.19$) relative to the special VBGF ($K = 0.30$), reflecting a lower loss in energy due to reproductive investment. The generalized VBGF estimates d as 0.48 for this population.

Another extreme growth pattern is found in rainbow trout (*Oncorhynchus mykiss*) in Quesnel Lake, British Columbia (Sebastian et al. 2003). These fish grow rapidly throughout their life often without approaching an asymptotic length, a phenomenon typical of populations with high or complete (as in semelparous species) spawning mortality, so that contribution of ingested energy to reproduction is limited to the last year or two. Using samples taken in 1999 (Fig. 6B), the generalized VBGF shows increasing growth rate in the first year, with accompanying d estimated at 0.8. The special VBGF fit to the same data estimates an unrealisti-

Fig. 6. Observed mean length-at-age (mm) for Quesnel Lake rainbow trout in 1986 (A) and 1999 (B) with fitted special and generalized von Bertalanffy growth functions. The generalized VBGF was constrained to a 25 mm length at hatch.



cally high t_0 (1.2 years). However, when each model was fit to data from the same population in 1986, a different problem occurs (Fig. 6A). The data from 1986 shows near-linear growth, and thus it is not possible to estimate all three parameters (H , m , and d or L_{∞} , K , and t_0). In this case, numerical optimizers set m and K to unrealistically low values, and the other two parameters are estimated. One could constrain m to be at least the product of mass lost to reproduction and the frequency of spawning, but this still leaves unrealistically high L_{∞} estimates. Clearly, there is no “asymptotic size” for this population, which is the problem commonly cited when the von Bertalanffy growth model is fitted to similar data (Knight 1968; Roff 1980). The available sizes of prey for this and similar large-bodied rainbow trout (and other populations with similar growth trajectories) is perfectly matched to this predator; juveniles grow large enough to overcome gape limitations and swimming speed constraints that lead to piscivory (Mittelbach and Persson 1998), and then optimal prey sizes (various age classes of kokanee in this case) are always available. It appears that linear growth is simply not well described by either the generalized or the special von Bertalanffy model; however, a departure from $d = 2/3$ due to patterns of prey availability provides a plausible explanation.

Discussion

As shown in Essington et al. (2001), food intake estimates based on back-calculation using observed growth rates and bioenergetics models that assume $d = 2/3$ can be grossly biased upward (by as much as 300%) for young fish, if d is in fact much lower. Likewise, food intake estimates can be biased downward by close to 100% if d is in fact near or above 0.8. Our proposal to avoid assumptions of $d = 2/3$ provides a more biologically realistic mechanism linking bioenergetics theory to observed growth patterns. Further, by constraining the growth pattern to begin at a hypothesized starting length, it is at least possible to estimate d using the generalized VBGF.

It should be noted that there is nothing wrong with using the special von Bertalanffy model as a purely descriptive representation of mean length-at-age for age-1+ fish no matter what d actually generated the growth pattern, for example in stock assessment models for populations that have stable growth patterns or for which changes in growth have been closely monitored (e.g., He and Bence 2007). In this case, the exact parameter values may not be as important as the growth pattern exhibited by older fish. Even in our case studies (Figs. 5–6), the special VBGF captured mean growth of older fish at least as well as the generalized VBGF. However, in cases where biological interpretations of the parameters estimated from patterns in growth are an important aspect of an analysis, we recommend using the generalized VBGF as demonstrated here.

The rate at which ontogenetic transitions through preferred prey types and sizes may vary across populations and species. There are several well-known accounts of species that quickly transition through various invertebrate types to fish (Graeb et al. 2006), but these abrupt changes in growth are more likely to be the exception than the norm (Werner and Gilliam 1984). The VBGF and arguments made here all assume constant relationships between mass and various ecological processes (e.g., smooth transition among prey sizes). There are models that explicitly attempt to incorporate a change in growth rate due to ontogenetic niche shift, and they may be more appropriate in certain situations (e.g., He and Stewart 2002). However, an abrupt transition from one prey type to the next will usually only result in a slight departure from the growth pattern predicted by the generalized VBGF.

Ontogenetic changes in diet are associated with various other bioenergetics changes not captured in the present discussion. Perhaps most important is the improved net growth efficiency and reduced foraging costs associated with larger prey items (Pazzia et al. 2002). Populations of lake trout (*Salvelinus namaycush*) constrained to zooplankton were shown to have higher foraging costs (Sherwood et al. 2002b), lower assimilation efficiency, and a lower proportion of consumed mass digested (chiton versus bone; Pazzia et al. 2002). We have necessarily ignored these factors, as they will be quite variable across foraging environments and are not predictably variable with predator or prey body size. Further, as we only focused on the ecological drivers inherent in d , it was unnecessary to discuss these extraneous factors. However, for more detailed bioenergetics models, these factors should be considered as they may play an important role in accurately predicting fine-scale growth patterns and their implications on consumption within a particular system.

It is important to note here that while growth is commonly believed to be limited by food availability in the wild, this notion is not universally held. Pauly (1981, 2010) argues that energy intake is in fact limited by oxidative metabolism of consumed food. Hence, gill surface area, which increases at a rate greater than $2/3$ of body mass, is the limiting factor on anabolism. This will be especially true for tropical fishes, where oxygen saturation levels are driven by water temperatures and salinity levels. However, many species rarely experience oxygen levels low enough to limit normal metabolic processes throughout the life of a fish, so oxygen intake and gill surface area are unlikely to limit growth for these species (Pedersen 1987). Likewise, West et al. (1997, 2001) argues that anabolism scales with weight raised to the $3/4$ power based on transportation limits imposed by fractal networks (e.g., circulatory and respiratory systems) carrying resources to cells. These limitations do well to represent evolutionary patterns to body design and growth but generally will not affect daily variation in growth and consumption because of the constraints proposed here, namely adequate food supply.

While beyond the specific discussion here about the scaling of consumption with body size, it should be noted that consumption estimates will also be affected by the second term in eq. 1: that of energy loss. This second term (mW) is much more complicated

than depicted in eq. 1, especially since significant changes in energy loss rates occur owing to variation in activity (Pazzia et al. 2002; Sherwood et al. 2002b; Rennie et al. 2005; reviewed in Giacomini et al. 2013) and to devotion to reproductive tissue after maturity (e.g., during spawning; Charnov et al. 2001). If the allometry of energy loss changes dramatically over the lifetime of a fish, eq. 1 will certainly lead to imprecise predictions of consumption (Sherwood et al. 2002a). We emphasize that eq. 1 is a gross simplification of the manifold processes contributing to fish growth and will only lead to a general estimate of consumption. We do not discount the potential effects of energy loss variation within and across species (Giacomini et al. 2013), but emphasize that a closer look at the scaling of energy allocation should be considered as an important area for future research and discussion.

This discussion highlights the importance of considering ecological constraints in growth models. While bioenergetics models include many detailed processes, parameters used to define growth patterns are often based on laboratory studies (Ney 1993), which can lead to errors in predictions of growth or consumption (van Poorten and Walters 2010; reviewed in Chipps and Wahl 2008). The assumption that $d = 2/3$ appears to be a gross simplification when considering all the uncertainties outlined here. Our suggestion to consider the generalized VBGF in place of the special VBGF seems sensible, especially in light of its effects on calculation of von Bertalanffy parameters and predictions that come from them.

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References

- Beverton, R.J.H., and Holt, S.J. 1959. A review of the lifespans and mortality rates of fish in nature and their relationship to growth and other physiological characteristics. Ciba Found. Colloq. Ageing, 5: 142–180. doi:10.1002/9780470715253.ch10.
- Boudreau, P.R., and Dickie, L.M. 1992. Biomass spectra of aquatic ecosystems in relation to fisheries yield. Can. J. Fish. Aquat. Sci. 49(8): 1528–1538. doi:10.1139/f92-169.
- Breck, J.E., and Gitter, M.J. 1983. Effect of fish size on the reactive distance of bluegill (*Lepomis macrochirus*) sunfish. Can. J. Fish. Aquat. Sci. 40(2): 162–167. doi:10.1139/f83-026.
- Charnov, E.L., Turner, T.F., and Winemiller, K.O. 2001. Reproductive constraints and the evolution of life histories with indeterminate growth. Proc. Natl. Acad. Sci. 98: 9460–9464. doi:10.1073/pnas.161294498. PMID:11481502.
- Chipps, S.R., and Wahl, D.H. 2008. Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. Trans. Am. Fish. Soc. 137: 298–313. doi:10.1577/T05-236.1.
- Crowl, T.A. 1989. Effects of crayfish size, orientation, and movement on the reactive distance of largemouth bass foraging in clear and turbid water. Hydrobiologia, 183: 133–140. doi:10.1007/BF00018718.
- Duplisa, D.E., Kerr, S.R., and Dickie, L.M. 1997. Demersal fish biomass size spectra on the Scotian Shelf, Canada: species replacement at the shelfwide scale. Can. J. Fish. Aquat. Sci. 54(8): 1725–1735. doi:10.1139/f97-077.
- Emerson, S.B., Greene, H.W., and Charnov, E.L. 1994. Allometric aspects of predator-prey interactions. In Ecological morphology. Edited by P.C. Wainwright and S.M. Reilly. University of Chicago Press, Chicago, Ill. pp. 123–139.
- Essington, T.E., Kitchell, J.F., and Walters, C.J. 2001. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. Can. J. Fish. Aquat. Sci. 58(11): 2129–2138. doi:10.1139/f01-151.
- Fox, M.G. 1989. Effect of prey density and prey size on growth and survival of juvenile walleye (*Stizostedion vitreum vitreum*). Can. J. Fish. Aquat. Sci. 46(8): 1323–1328. doi:10.1139/f89-170.
- Galarowicz, T.L., Adams, J.A., and Wahl, D.H. 2006. The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. Can. J. Fish. Aquat. Sci. 63(8): 1722–1733. doi:10.1139/f06-073.
- Gerking, S.D. 1994. Feeding ecology of fish. Academic Press, San Diego, Calif.
- Giacomini, H.C., Shuter, B.J., and Lester, N.P. 2013. Predator bioenergetics and the prey size spectrum: Do foraging costs determine fish production? J. Theor. Biol. 332: 249–260. doi:10.1016/j.jtbi.2013.05.004. PMID:23685066.
- Graeb, B.D.S., Mangan, M.T., Jolley, J.C., Wahl, D.H., and Dettmers, J.M. 2006. Ontogenetic changes in prey preference and foraging ability of yellow perch: insights based on relative energetic return of prey. Trans. Am. Fish. Soc. 135: 1493–1498. doi:10.1577/T05-063.1.

- Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.E. 1997. Fish bioenergetics 3.0. Madison, Wisc.
- Hartvig, M., Andersen, K.H., and Beyer, J.E. 2011. Food web framework for size-structured populations. *J. Theor. Biol.* **272**: 113–122. doi:10.1016/j.jtbi.2010.12.006. PMID:21146543.
- Havlicek, T.D., and Carpenter, S.R. 2001. Pelagic species size distributions in lakes: are they discontinuous? *Limnol. Oceanogr.* **46**: 1021–1033. doi:10.4319/lo.2001.46.5.1021.
- He, J.X., and Bence, J.R. 2007. Modeling annual growth variation using a hierarchical Bayesian approach and the von Bertalanffy growth function, with application to lake trout in southern Lake Huron. *Trans. Am. Fish. Soc.* **136**: 318–330. doi:10.1577/T06-108.1.
- He, J.X., and Stewart, D.J. 2002. A stage-explicit expression of the von Bertalanffy growth model for understanding age at first reproduction of Great Lakes fishes. *Can. J. Fish. Aquat. Sci.* **59**(2): 250–261. doi:10.1139/f02-008.
- Hughes, N.F., and Dill, L.M. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Can. J. Fish. Aquat. Sci.* **47**(10): 2039–2048. doi:10.1139/f90-228.
- Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. *J. Fish. Res. Board Can.* **25**(6): 1303–1307. doi:10.1139/f68-114.
- Mazur, M.D., and Beauchamp, D.A. 2003. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. *Environ. Biol. Fishes.* **67**: 397–405.
- Mittelbach, G.G., and Persson, L. 1998. The ontogeny of piscivory and its ecological consequences. *Can. J. Fish. Aquat. Sci.* **55**(6): 1454–1465. doi:10.1139/f98-041.
- Ney, J.J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. *Trans. Am. Fish. Soc.* **122**: 736–748. doi:10.1577/1548-8659(1993)122<0736:BMTGPO>2.3.CO;2.
- O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton: recent research with planktivorous fish and their zooplankton prey shows the evolutionary thrust and parry of the predator-prey relationship. *Am. Sci.* **5**: 572–581.
- Pauly, D. 1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforschung.* **28**: 251–282.
- Pauly, D. 2010. Gaspung fish and panting squids: oxygen, temperature and the growth of water-breathing animals. Edited by O. Kinne. International Ecology Institute, Oldendorf/Luhe.
- Pazzia, I., Trudel, M., Ridgway, M., and Rasmussen, J.B. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). *Can. J. Fish. Aquat. Sci.* **59**(10): 1593–1605. doi:10.1139/f02-128.
- Pedersen, C.L. 1987. Energy budgets for juvenile rainbow trout at various oxygen concentrations. *Aquaculture.* **62**: 289–298. doi:10.1016/0044-8486(87)90171-2.
- Rennie, M.D., Collins, N.C., Shuter, B.J., Rajotte, J.W., and Couture, P. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. *Can. J. Fish. Aquat. Sci.* **62**(4): 767–780. doi:10.1139/f05-052.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* **191**.
- Roff, D.A. 1980. A motion for the retirement of the von Bertalanffy function. *Can. J. Fish. Aquat. Sci.* **37**(1): 127–129. doi:10.1139/f80-016.
- Scharf, F.S., Juanes, F., and Rountree, R.A. 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.* **208**: 229–248. doi:10.3354/meps208229.
- Sebastian, D., Dolighan, R., Andrusak, H., Hume, J., Woodruff, P., and Scholten, G. 2003. Summary of Quesnel Lake kokanee and rainbow trout biology with reference to sockeye salmon. Stock Management Report No. 17, Province of British Columbia, Victoria, B.C.
- Sherwood, G.D., Kovacs, J., Hontela, A., and Rasmussen, J.B. 2002a. Simplified food webs lead to energetic bottlenecks in polluted lakes. *Can. J. Fish. Aquat. Sci.* **59**(1): 1–5. doi:10.1139/f01-213.
- Sherwood, G.D., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J.B. 2002b. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. *Can. J. Fish. Aquat. Sci.* **59**(2): 229–241. doi:10.1139/f02-001.
- Sprules, W.G. 2008. Ecological change in Great Lakes communities — a matter of perspective. *Can. J. Fish. Aquat. Sci.* **65**(1): 1–9. doi:10.1139/f07-136.
- Temming, A., and Herrmann, J.P. 2009. A generic model to estimate food consumption: linking von Bertalanffy's growth model with Beverton and Holt's and Ivlev's concepts of net conversion efficiency. *Can. J. Fish. Aquat. Sci.* **66**(4): 683–700. doi:10.1139/F09-028.
- Thiebaut, M.L., and Dickie, L.M. 1993. Structure of the body-size spectrum of the biomass in aquatic ecosystems: a consequence of allometry in predator-prey interactions. *Can. J. Fish. Aquat. Sci.* **50**(6): 1308–1317. doi:10.1139/f93-148.
- Trebilco, R., Baum, J.K., Salomon, A., and Dulvy, N.K. 2013. Ecosystem ecology: size-based constraints on the pyramids of life. *Trends Ecol. Evol.* **28**: 423–431. doi:10.1016/j.tree.2013.03.008. PMID:23623003.
- Trudel, M., Tremblay, A., Schetagne, R., and Rasmussen, J.B. 2000. Estimating food consumption rates of fish using a mercury mass balance model. *Can. J. Fish. Aquat. Sci.* **57**(2): 414–428. doi:10.1139/f99-262.
- van Poorten, B.T., and Walters, C.J. How can bioenergetics help us predict changes in fish growth patterns? *Fish. Res.* [In press]. doi:10.1016/j.fishres.2015.07.031.
- van Poorten, B.T., and Walters, C.J. 2010. Estimation of bioenergetics parameters for rainbow trout (*Oncorhynchus mykiss*) using capture-recapture data with comparison to estimates from a laboratory-based model. *Open Fish Sci. J.* **3**: 69–79. doi:10.2174/1874401X01003010069.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Hum. Biol.* **10**: 181–213.
- Ware, D.M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Board Can.* **30**(6): 787–797. doi:10.1139/f73-134.
- Ware, D.M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *J. Fish. Res. Board Can.* **35**(2): 220–228. doi:10.1139/f78-036.
- Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**: 393–425. doi:10.1146/annurev.es.15.110184.002141.
- West, G.B., Brown, J.H., and Enquist, B.J. 1997. A general model for the origin of allometric scaling laws in biology. *Science.* **276**: 122–126. doi:10.1126/science.276.5309.122.
- West, G.B., Brown, J.H., and Enquist, B.J. 2001. A general model for ontogenetic growth. *Nature.* **413**: 628–631. doi:10.1038/35098076. PMID:11675785.