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The Bertalanffy growth equation: Theory of Paulys auximetric plots

Eric L. Charnov

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by

Eric L. Charnov

Department of Biology

The University of New Mexico

Albuquerque, NM 87131-0001

(rlc@unm.edu)

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Abstract: I review properties of the BGE, with reference to plots of loge K versus loge L_∞ (or W_∞).

The Bertalanffy growth (BG) equation is the most widely used descriptor of body size growth for fish (and other indeterminate growers). Its usual integral form (two parameters) is $L = L_\infty\left(1 - e^{-k \cdot X}\right)$, where L = length, L_∞ = asymptotic length, X is age, and k is the growth coefficient. In weight (W), the equation is $W = W_\infty\left(1 - e^{-k \cdot X}\right)^3$. In this paper, we review and point out some of the properties of the BG equation, beginning with the differential equation form for weight (W). We begin with to dW/dt, since it is the key to answering theoretically a question originally posed by Pauly (19??): If one has a collection of populations/species with various W_∞, L_∞ and k values, what information is present in a plot of log k versus log L_∞ (or log W_∞)? Pauly called this the "auximetric" (growth measuring) plot; it is widely used in fisheries.

The differential equation form of the BG equation is:

$$\frac{dW}{dt} = A \cdot W^{2/3} - B \cdot W \qquad \textbf{(1)}$$

Length (L) is related to weight by the rule:

$$W = a \cdot L^3 \qquad \textbf{(2)}$$

The asymptotic weight W_∞ is where $\frac{dW}{dt} = 0$, thus $W_\infty^{1/3} = \frac{A}{B}$ **(Eqn. 3)**,

$\left(\text{or } L_\infty = \left(\frac{W_\infty}{a}\right)^{1/3}\right)$.

Notice that Eqn. 2 allows us to write $\frac{dW}{dt} = a \cdot 3L^2 \cdot \frac{dL}{dt}$ or $\frac{dL}{dt} = \frac{dW}{dt}\left(\frac{1}{a \cdot 3L^2}\right)$.

Now, combining this with Eqns. 1, 2 and 3, we can show that

$\frac{dL}{dt} = \frac{B}{3}\left[L_\infty - L\right] = k\left[L_\infty - L\right]$, so that $k = \frac{B}{3}$. This is the differential equation for length.

Since $k = \frac{B}{3}$ and $W_\infty^{1/3} = \frac{A}{B}$, $k = \left(\frac{A}{3}\right) W_\infty^{-1/3}$ so that

$\log k = \log\left(\frac{A}{3}\right) - \frac{1}{3}\log W_\infty$ **(Eqn. 4)**. We can use Eqn. 2 to transform W_∞ to L_∞:

$$k = \left(\frac{A}{3}\right)\left(\frac{1}{a^{1/3}}\right) \cdot L_\infty^{-1}$$

$$\log k = \left[\log\left(\frac{A}{3}\right) - \frac{1}{3}\log a\right] - \log L_\infty \qquad \textbf{(Eqn. 5)}$$

Consider the following thought experiment, with reference to Eqns. 4 and 5, illustrated in Figure 1. We have two (many) populations/species plotted as log *k* versus log W_∞ (or log L_∞). If the line connecting 1 to 2 has a slope of −⅓, the two species *have the same A* (Fig. 1a). If the slope is steeper than −⅓, the larger-bodied has a smaller *A*; a slope less steep than $-⅓$ means that A is larger for the larger species. In terms of log k versus log L_∞ (Fig. 1b), A is the same if the connecting line has a slope of -1, assuming no shape change (a is the same; Eqn. 2) between the two data points. The same rules hold for comparisons with lots of data points, both within and among species. Fig. 1 is what Pauly (19??) called the auximetric plot. *It contains information about* A. If the plot of log k versus log W_∞ has a slope of $-⅓$, log $A/3$ is the *intercept* of the line. A for each data point is estimated as $A = 3 \cdot k \cdot W_\infty^{1/3}$. We can estimate A from the k, L_∞ data if we know the shape coefficient of Eqn. 2.

What Is A in the BG Equation?

Since A of dW/dt is a key parameter in the auximetric plot, it seems worthwhile to ask what it means. In Bertalanffy's original derivation [ref.?], the $A \cdot W^{2/3}$ term was anabolism, the building of *new* tissue. It is probably reasonably interpreted as the intake of nutrition (food), which is assumed to scale with $W^{2/3}$. The $B \cdot W$ term is catabolism, the breakdown of tissue (*but* $B \cdot W$ also must include reproductive allocation). While fisheries scientists no longer accept this simple physiological interpretation, it may well be useful to treat the $A \cdot W^{2/3}$ term as the scaling of new tissue production.

There is another way to interpret the A coefficient. Rewrite Eqn. 1 as

$\frac{dW}{dt} = A \cdot W^{2/3}\left[1 - \frac{B}{A} \cdot W^{1/3}\right]$; but by Eqn. 3, $\frac{dW}{dt} = A \cdot W^{2/3}\left[1 - \left(\frac{W}{W_\infty}\right)^{1/3}\right]$ **(Eqn. 6)**.

Thus, dW/dt is proportional to $W^{2/3}$ at any fixed W/W_∞ value with A (and the W/W_∞ term) determining the "height" of the ⅔ power function. For example, at very small body size, $W/W_\infty \approx 0$ and Eqn. 6 becomes $dW/dt \approx A \cdot W^{2/3}$; A is the height of the power function ($W^{2/3}$) growth curve at small W.

A interpreted this way is also true for the size at fastest growth. The max of $\frac{dW}{dt}$ is

where $\frac{\partial\left(dW/dt\right)}{\partial W} = 0$, which implies from Eqn. 1 that $\frac{2}{3}W^{-1/3} \cdot A - B = 0$. We combine

this with Eqn. 3 for W_∞ to show that $W/W_\infty = 0.296$ at the max of dW/dt. Putting this into Eqn. 6 shows that $\frac{dW}{dt} = \frac{A}{3} \cdot W^{2/3}$ **(Eqn. 7)** at the size of fastest growth; thus, $A/3$ is the

height of *this* ⅔ power function for dW/dt at fastest growth. Table 1 shows a simple way to estimate dW/dt at fastest growth ($W = 0.296 \cdot W_\infty$).

Table 1. Max dW/dt

Since $\frac{dW}{dt} = A/_3 \cdot W^{2/3}$ (Eqn. 7), we have $dW/_{dt} = A/_3 \left(0.296 \cdot W_\infty\right)^{2/3}$ at fastest growth. But $k = \frac{A}{3} \cdot W_\infty^{-1/3}$ (Eqn. 4), so that

$\max \frac{dW}{dt} = (0.296)^{2/3} \cdot k \cdot W_\infty = 0.44 \cdot k \cdot W_\infty$; the maximum growth rate is estimated by 0.44 of the product of k times W_∞.

Discussion: Auximetric Plots

Several general patterns are know for auximetric plots; here we will interpret them in terms of A values.

First, plots of log k verus log L_∞ for different populations within a single species *always* show slopes steeper than -1 [Pauly?]. This means that lower A's are always associated with larger-bodied populations. Second, taxonomically diverse plots, such as species/populations grouped into families, typically show k, L_∞ plots with slopes near -1. These plots mean that, within families, the various species occur in a range of habitats that yield the same average log A at any body size. This is quite different from the within-species case, where bigger always occurs in lower A habitats.

Third, plots with very diverse taxa likewise suggest A does not change with body size, as on average; here the slope $\approx -1/3$ for k vs. W_∞.

Our fourth pattern is that A increases with higher environmental temperature and is higher in the tropics (temperature vs. tropic graph: L_∞, k). Finally, A is not related to trophic level.

Figure 1a.

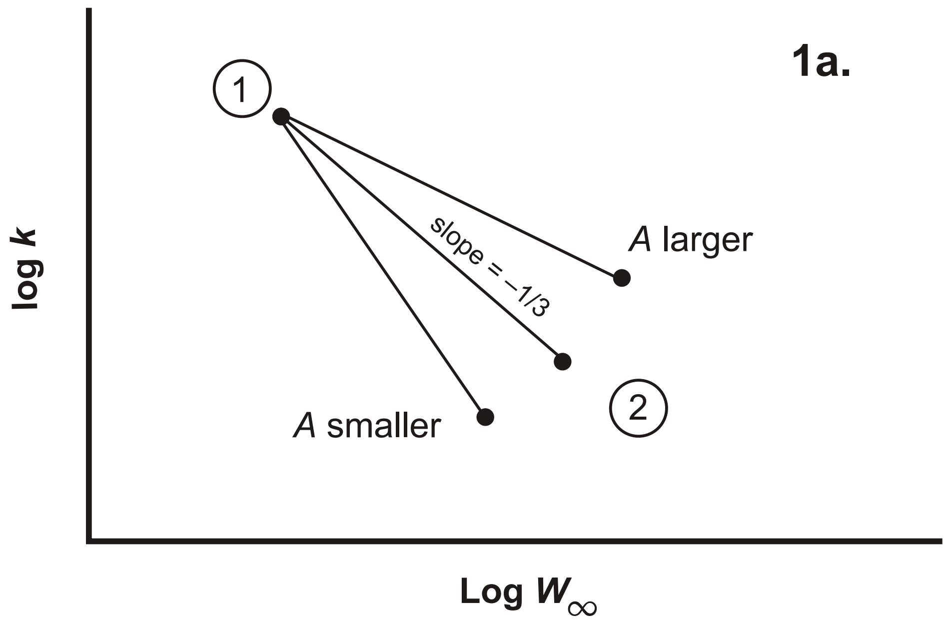

Figure 1b.