7-21-2007

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The Bertalanffy growth equation: Theory of Pauly's auximetric plots

by

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Keywords: growth—fish; growth—temperature; macroecology; latitude

Abstract: I review properties of the BGE, with reference to plots of loge K versus loge $L_\infty$ (or $W_\infty$).
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, \( L_\infty = \) asymptotic length, \( X = \) age, and \( k = \) 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 \( W_\infty, L_\infty \) and \( k \) values, what information is present in a plot of \( \log k \) versus \( \log L_\infty \) (or \( \log W_\infty \))? Pauly called this the “auximetric” (growth measuring) plot; it is widely used in fisheries.

The differential equation form of the BG equation is:

\[
\frac{dW}{dt} = A \cdot W^{2/3} - B \cdot W
\]  

(1)

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

\[
W = a \cdot L^3
\]

(2)

The asymptotic weight \( W_\infty \) is where \( \frac{dW}{dt} = 0 \), thus \( W_\infty^{2/3} = \frac{A}{B} \) (Eqn. 3),

\[
\left( \text{or } L_\infty = \left(\frac{W_\infty}{a}\right)^{\frac{3}{2}} \right).
\]
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 \( \overline{W}^{\frac{1}{3}} = \frac{A}{B} \), \( k = \left( \frac{A}{3} \right) \overline{W}^{\frac{1}{3}} \) so that

\[ \log k = \log \left( \frac{A}{3} \right) - \frac{1}{3} \log \overline{W}_\infty \] (Eqn. 4). We can use Eqn. 2 to transform \( W_\infty \) to \( L_\infty \):

\[ k = \left( \frac{A}{3} \right) \left( \frac{1}{a^{\frac{1}{3}}} \right) \cdot L_\infty \]

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 \( \log W_\infty \) (or \( \log L_\infty \)). If the line connecting 1 to 2 has a slope of \( -\frac{1}{3} \), the two species have the same \( A \) (Fig. 1a). If the slope is steeper than \( -\frac{1}{3} \), the larger-bodied has a smaller \( A \); a slope less steep
than $-\frac{1}{3}$ means that $A$ is larger for the larger species. In terms of $\log k$ versus $\log L_\infty$ (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 $\log W_\infty$ has a slope of $-\frac{1}{3}$, $\log A/3$ 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 $k, L_\infty$ 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

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

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

$$\frac{\partial (dW/\partial t)}{\partial W} = 0,$$

where $\frac{\partial (dW/\partial t)}{\partial W} = 0$, which implies from Eqn. 1 that $\frac{2}{3} W^{-1/3} \cdot A - B = 0$. We combine this with Eqn. 3 for $W_\infty$ 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 $2/3$ power function for $dW/dt$ at fastest growth. Table 1 shows a simple way to estimate $dW/dt$ at fastest growth ($W = 0.296 \cdot W_\infty$).
Discussion: Auximetric Plots

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

First, plots of log $k$ versus log $L_\infty$ 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 $k$, $L_\infty$ 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 $\approx -\frac{1}{3}$ for $k$ vs. $W_\infty$.
Our fourth pattern is that $A$ increases with higher environmental temperature and is higher in the tropics (temperature vs. tropic graph: $L_{\infty}, k$). Finally, $A$ is not related to trophic level.
Figure 1a.

![Graph showing log k vs. log W_\infty with points 1 and 2, and a line with slope = -1/3.]

A larger

A smaller

Figure 1b.

![Graph showing log k vs. log L_\infty with points 1 and 2, and a line with slope = -1.]

A larger

A smaller