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Fish growth: Bertalanffy *k* is proportional to reproductive effort

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Abstract By comparing the Bertalanffy *descriptive* growth equation (BG) with a reproductive-allocation growth (RAG) equation, I show that the BG k parameter is approximately equal to about 0.55 times the proportion of an adult body mass given to reproduction per unit of time, the reproductive effort; thus, k may be useful in predicting average fecundity. This also means that the Beverton–Holt k/M dimensionless number is really a lifetime reproductive allocation since the average adult life span is about $1/M$ years.

Keywords Dimensionless · Reproduction · Life history · Auximetric plot

The differential equation form of the Bertalanffy growth (BG) equation is

$$\frac{\mathrm{d}W}{\mathrm{d}t} = A \times W^{2/3} - B \times W \quad (1)$$

where W is weight (mass). If length (L)is $\propto \mathrm{W}^{1/3}$, as is usually assumed, an equivalent equation is $\frac{\mathrm{d}L}{\mathrm{d}t} = k[L_\infty - L]$, where k and asymptotic length (L_∞) are the more usual parameters fit to fish data. Setting Eq. 1 equal to zero yields the asymptotic weight $W_\infty^{1/3} = {}^{A}\!/_{B}$, from which we can get L_∞; it is straightforward to show that $k = {}^{B}\!/_{3}$. Notice that $k = \frac{4}{3} \times W_\infty^{-1/3}\left(\text{or } k \propto {}^{1}\!/_{L_\infty}\right)$, a $-1/3$ power function across species with the same A.

If we solve Eq. 1 for weight (length) at age t, beginning at $W{\sim}0$ at $t{\sim}0$, we get the familiar growth equations that fit well so much fish data:

$$L(t) = L_\infty\left(1 - e^{-k \times t}\right) \quad (2)$$

$$W(t) = W_\infty\left(1 - e^{-k \times t}\right)^3 \quad (3)$$

Finally, we can look at $\frac{\partial\left(\frac{\mathrm{d}W}{\mathrm{d}t}\right)}{\partial W} = 0$ to find the size ($W_{\max}$) at fastest growth:

$$\left(\frac{W_{\max}}{W_\infty}\right)^{1/3} = \frac{L_{\max}}{L_\infty} = \frac{2}{3} \quad (4)$$

$$\frac{W_{\max}}{W_\infty} \approx 0.30 \quad (5)$$

One of the greatest questions in fish growth is whether the BG equation is merely a very good descriptor of size versus age, or whether the parameters have real biological meaning. Von Bertalanffy (1938) derived the equation from a physiological argument that assigned meaning to the terms, but the equation is now mostly used as a descriptor.

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There is an additional puzzle here. Beverton and Holt (1959) showed that when the k parameter in the BG equation is divided into the "adult instantaneous mortality rate" (M), the dimensionless M/k ratio is approximately invariant; M and k are proportional, with their ratio $\left(\frac{M}{k}\right) \approx 1.5 - 2.0$. Charnov (1993) showed that indeterminate growth for reptiles has the *same* numeric rule $\frac{M}{k} \approx 1.5$, while Pauly (1980) confirmed the rule in a large data set for fish. Of course, fishery scientists have long used the invariance in M/k to estimate the hard-to-measure M from the easy-to-measure k. It is puzzling, however, that k is so strongly related to M if k has no deeper biological meaning.

In what follows, I will suggest that the BG equation is an approximation to a growth process that really has two parts: pre- and post-maturation. I will further suggest that its fitted parameters, particularly k, are (is) closely related to meaningful biological parameters in the *real* underlying production/reproductive-allocation process.

The real difficulty with the BG equation is that lifetime growth must reflect food input minus (non-growth) output, *but* much of the output *must be reproductive allocation*, which is zero before the age of first breeding (α) and some fraction of body mass afterward (Roff 1983, Charnov 1993, Day and Taylor 1997, Lester et al. 2004). The simplest two-part growth model that is BG-like (and includes reproductive allocation) is due to Charnov (1993, p. 142): growth follows

$$\frac{dW}{dt} = A \times W^{2/3} \tag{6a}$$

prior to initiation of reproduction at size W_α (age α), and follows

$$\frac{dW}{dt} = A \times W^{2/3} - C \times W \tag{6b}$$

after α. $C \times W$ is the per-unit-time allocation to reproduction, and C is the proportion of a body mass (W) given to reproduction per unit of time; C is often called "reproductive effort." Growth in length prior to reproduction will be linear, and the asymptotic size (where $\frac{dW}{dt} = 0$) will be

$$W_\infty^{1/3} = A/C. \tag{7}$$

Call this scheme the "reproductive allocation growth (RAG) equation." Of course, there are other possible RAG equations, but I consider only the simplest here (e.g., Charnov et al. 2001); Shuter et al. (2005) offer strong empirical support for *this* RAG growth scheme.

Suppose growth follows this RAG model, but we fit the data with the BG equation. What will k be equal to? One approach to this would be to use the RAG equations to generate simulated growth data that we then fit with the BG equation. A simpler approach is as follows. The BG (Eq. 2) allows us to solve for the relative size at first reproduction (R):

$$R = \frac{L_\alpha}{L_\infty} = 1 - e^{-k \times \alpha} \tag{8}$$

Equation 6a and 6b also may be integrated to give the size at first reproduction ($L \sim 0$ at $t \sim 0$, L_α at age α), and combined with Eq. 7 to show that the RAG model yields (Charnov 1993, p. 142):

$$R = \frac{L_\alpha}{L_\infty} = \frac{1}{3} \times \alpha \times C \tag{9}$$

If BG and RAG models are to give approximately the same R value at the same α, Eqs. 8 and 9 may be combined to show that:

$$k \approx \frac{-\ln(1-R)}{3 \times R} \times C \tag{10}$$

k is proportional to C for species with the same R value. The proportionality constant is only weakly dependent upon R; it's 0.45 if R=0.47 and rises to 0.66 if R=0.79, values that bracket most fish data (Beverton 1992). If $R = 2/3$, k=0.55×C. As noted by Jensen (1996), $R \approx 2/3$ because RAG models put the fastest growth ($W_{\max}$) at the size of first reproduction (W_α) since growth slows only *because* of the reproductive allocation; if data are well fit by the BG equation, $W_{\max} \approx 0.3 \times W_\infty$ or $L_{\max} = 2/3 \times L_\infty$ (Eqs. 4 and 5 here): thus, $L_{\max} = L_\alpha = 2/3 \times L_\infty$.

As noted in Charnov (1993, p. 66), M/k values typically average. 1.5–2.0; if we take a mid-value of 1.75, its inverse yields k/M=0.57. If k=0.55×C and k/M=0.57, the dimensionless ratio $C/M \approx 1$; fish are predicted to allocate one average adult body mass to reproduction over the average lifetime (=1/M). (Note that the average adult is of weight [mass], $\overline{W}$, and allocates $C \times \overline{W}$ mass to reproduction per unit of time; thus, C is the proportion of $\overline{W}$ given to reproduction per unit of time.) Lester et al. (2004) turned the RAG model into a life-history evolution model and showed that the optimal life-history set $C/M \approx 1$. Using the yearly "Gonadosomatic Index" (GSI) to estimate C, Gunderson (1997) showed that GSI $\approx 55 \times \mathrm{M}$ for about 30 fish stocks; clearly, 0.55 is not unity. Lester et al. (2004) suggested that GSI underestimates C because gonad tissue contains greater energy per unit weight than body tissue.

A number of life-history evolution models make the C/M number an approximate invariant (Charnov 1993, 2002, 2005, Lester et al. 2004). C/M is a surprising and important number in the study of life histories (see Charnov 2002, 2005, Charnov et al. 2007 for discussion of the many places it turns up); thus, it seems fitting that the Beverton and Holt (1959) k/M number, the most venerable of life-history's dimensionless numbers, is really C/M in disguise.

It is straightforward to show that the growth rate ($\mathrm{d}W/\mathrm{d}t$) at $W_{\max}$ (Eq. 5) is $0.444 \times k \times W_{\infty}$; thus, $k \times W_{\infty}$ measures the maximum body size growth rate for an individual. Provided $\overline{W} \propto W_{\infty}$ across species, $k \times W_{\infty}$ *also* measures the average reproductive rate for an individual. When combined with the mass per egg (W_0), $\left(\frac{k}{0.55}\right) \times \left(\frac{\overline{W}}{W_0}\right)$ measures the per-unit-of-time egg production of the average adult. This may be useful in stock/recruit theory to predict population egg production. We have many thousands of estimates of k; perhaps we should re-label k the reproduction coefficient, rather than calling it the growth coefficient?

If we fit the two-part RAG scheme (Eqs. 6a and 6b) to size-at-age data, post-maturation (age α) growth is a BG equation; thus, the growth coefficient associated with this post-α BG equation is $\frac{C}{3}$, directly estimating reproductive effort (see first paragraph of this paper, Charnov 1993). This direct estimate could be used to test the BG k versus C relation of Eq. 10. Equations 6a and 6b are the simplest RAG schemes; it may prove too simple. Alternatives include (see also Charnov et al. 2001) (1) pre-α growth follows $\frac{\mathrm{d}W}{\mathrm{d}t} = A \times W^{\delta}$, with $\delta < 2/3$ giving growth in length less than linear, (2) reproductive allocation follows $c \times W^{\delta_1}$, where $\delta_1 > 1$ allows increasing reproductive effort with weight, or (3) larval growth follows a different growth scheme and the simple RAG only applies after some age (Lester et al. 2004). These added complexities are beyond the scope of this paper; I urge other scholars to explore these, and other, possibilities.

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