



**Opinion** is intended to facilitate communication between reader and author and reader and reader. Comments, viewpoints or suggestions arising from published papers are welcome. Discussion and debate about important issues in ecology, e.g. theory or terminology, may also be included. Contributions should be as precise as possible and references should be kept to a minimum. A summary is not required.

## *Theoretical analysis of the relationship between production per unit biomass and animal body size: a comment*

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Banse and Mosher (1980) showed that across a wide spectrum of animal species, annual production to biomass (P/B) ratio of a population is related to body mass at maturity of the constituent individuals by an allometric equation with an exponent of about  $-1/3$ . This relationship has been widely used as a short-cut to estimate secondary production, but little attention has been paid to the theoretical background of the relationship.

Recently Roa and Quiñones (1998), hereafter called R&Q, argued that the relation can be understood from growth following the Von Bertalanffy growth equation. This is a surprising result: why does not mortality rate play a role? However, it can be shown that the analysis provided by R&Q is flawed. First, the result is based on a rather unreliable assumption. Second, the mathematical analysis, i.e. the linkage between assumptions and conclusions, is erroneous.

R&Q assume that the empirical regularity found by Banse and Mosher reflects an underlying relationship at the level of mass specific growth rates. They then proceed by considering the mass specific growth rate for individual animals at the age of maturity (the mass specific growth rate might be labelled the P/B ratio of an individual) as representative for the annual P/B ratio of the population.

A simple example will show that this approach (assuming a direct relationship between the mass specific growth rate for an individual and the annual P/B ratio of the population) is not generally valid. Consider a stationary population, that is, a population that has a constant birth rate and a stable age distribution. Suppose further that each individual follows the same linear growth trajectory  $y = cx$ , where  $y$  is individual

mass,  $x$  is age in years and  $c$  is a constant growth rate, and that each individual dies at a fixed age  $a$ . The per capita production equals the growth rate  $c$ , and the per capita biomass equals  $\frac{1}{2}ca$ . Hence, the P/B ratio of the population equals  $2/a$  (note that the mass specific growth rate at age  $x$  is  $1/x$ ). The P/B ratio in this example is solely determined by the fixed life span (i.e. the mortality function) of the animals, and the (linear) growth rate  $c$  does not play any role. Thus, a population of fast-growing, but long-living animals, will have a lower P/B ratio than a population of short-living slow growers.

Contrary to R&Q, I have simply ignored the difference between the instantaneous P/B ratio and the annual P/B ratio. For stationary populations this difference is irrelevant, as the instantaneous P/B ratio (here expressed in  $\text{year}^{-1}$ ) multiplied by one (year) reveals the annual P/B ratio.

In fact, the simple example presented above provides nothing new, since it has been shown that for stationary populations the P/B ratio is equal to the inverse of the mean life span multiplied by the ratio of mean mass at death to mean mass of live individuals (Van Straalen 1985). The latter ratio may depend on both the growth equation and the mortality function. In the example presented above (linear growth and a fixed life span) the ratio was equal to two. Another well-known example refers to a population with a constant instantaneous mortality rate. In that case, the mean mass at death equals the mean mass of live individuals, and the P/B ratio is inversely related to the mean life span (i.e. similar to the instantaneous mortality rate), whatever the growth function is. More examples, including vari-

ous cases where growth is of the Von Bertalanffy type, were provided by Allen (1971). So, R&Q's assumption that the P/B ratio of a population only depends on growth-related characteristics and that the mortality function can be ignored, lacks theoretical support.

My second concern is about the mathematical analysis. Proceeding with the mass specific growth rate for individuals at the age of maturity (which R&Q labeled P/B) and assuming that growth is of the Von Bertalanffy type, R&Q arrive at the following result:

$$\frac{dW/dt|_{\alpha}}{W_{\alpha}} = \beta k \frac{1 - (W_{\alpha}/W_{\infty})^{1/\beta}}{(W_{\alpha}/W_{\infty})^{1/\beta}},$$

where  $dW/dt|_{\alpha}$  is the individual growth rate at the age of maturity;  $W_{\alpha}$  the mass at maturity;  $W_{\infty}$  the asymptotic mass;  $k$  the Von Bertalanffy growth coefficient; and  $\beta$  the exponent of the mass-length relationship, which is usually set equal to 3. R&Q continue by assuming that for all species mass at maturity is a constant fraction  $1/b$  of asymptotic mass, i.e.  $W_{\alpha}/W_{\infty} = 1/b$ . This assumption gives

$$\frac{dW/dt|_{\alpha}}{W_{\alpha}} = \beta k \frac{1 - b^{-1/\beta}}{b^{-1/\beta}},$$

which means that the mass specific growth rate at the age of maturity is not directly related to the mass at maturity, but only to the Von Bertalanffy growth coefficient  $k$  and the two coefficients  $\beta$  and  $b$ , both of which were assumed to be constant across species. This result is somewhat trivial, as scaling the (two-parameter) Von Bertalanffy growth function to asymptotic size (that is what in fact happened), implies that the growth coefficient  $k$  is the only parameter left. Yet, R&Q obtained another result. They only replaced  $W_{\alpha}/W_{\infty}$  by  $1/b$  in the numerator and arrived at

$$\frac{dW/dt|_{\alpha}}{W_{\alpha}} = \beta k \frac{1 - b^{-1/\beta}}{(W_{\alpha}/W_{\infty})^{1/\beta}},$$

or

$$\log \frac{dW/dt|_{\alpha}}{W_{\alpha}} = \log \beta + \log k + \log(1 - b^{-1/\beta}) + \frac{1}{\beta} \log W_{\infty} - \frac{1}{\beta} \log W_{\alpha}.$$

Ignoring the parameters  $k$  and  $W_{\infty}$  (and thus implicitly using the additional assumption that  $k$  and  $W_{\infty}$  are constant across species), R&Q concluded that a between-species allometric relationship exists between the mass specific growth rate at maturity and the mass at maturity with a coefficient of  $-1/\beta$ , i.e.

$$\frac{dW/dt|_{\alpha}}{W_{\alpha}} \propto W_{\alpha}^{-1/\beta}.$$

However, combining the assumptions that  $W_{\infty}$  is constant and that the ratio  $W_{\alpha}/W_{\infty}$  is constant must imply that  $W_{\alpha}$  is a constant and therefore the allometric relationship provided makes no sense. This plethora of assumptions only allows the conclusion that everything is constant.

Now that the claim of R&Q appears to be unsubstantiated, we are still left with the problem what explains the empirical relationship between the P/B ratio and the size at maturity. A detailed analysis is beyond the scope of this comment, but it might be interesting to note that under certain conditions the problem boils down to the three so-called Beverton-Holt invariants (Charnov 1993). If the instantaneous mortality rate  $M$  is constant, then for a stationary population  $P/B = M$ . Application of the three Beverton-Holt invariants,  $M/k$ ,  $W_{\alpha}/W_{\infty}$ , and  $W_{\infty}^{1/3} = k^{-h}$ , yields

$$P/B \propto W_{\alpha}^{-1/3h}$$

If  $h = 1$  the result is similar to the empirical relationship obtained by Banse and Mosher (1980). Both empirical and theoretical support for the value  $h = 1$  exists (Galluci and Quinn 1979, Kooijman 1986, 1988, 1993). Charnov (1993) proposed a life-history theory for the Beverton-Holt invariants.

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