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## Growth, mortality, and life-history scaling across species

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### ABSTRACT

**Hypothesis:** Allometric scaling of mortality versus adult body size across species is predicted by evolutionary life-history theory to be present (and precise) only if all the species in the data set share the same value for the ‘height’ parameter in their body-size growth curves.

**Results:** This basic prediction is tested and supported in a large fish data set, with the various species spanning the entire range of marine environments, and having about a  $12 \times$  range in growth curve height.

*Keywords:* allometry, body size, fish, maturity, optimal life history.

In this paper, we explore a central question in the comparative study of life histories: When should we expect to find good allometries for adult mortality rates ( $Z_a$ ) versus adult body mass ( $M_a$ ) across species? When should  $Z_a = C \cdot M_a^{-p}$ , where  $C$  and  $p$  are the *same* for all species in the data set? Evolutionary life-history theory tells us when species in a collection are expected to share the same constant  $C$  and exponent  $p$  (Charnov, 1993, 2011). To see how to predict the constant, let us first review an ESS (evolutionarily stable strategy)  $M_a$  argument for a simple determinate growing organism in a non-growing population. [For more general cases and arguments, see references in Charnov (2011).]

$R_0$ , the net reproductive rate, is a Darwinian fitness measure appropriate for a non-growing population, and can be written as  $R_0 = S_a \cdot V_a$  (Charnov, 1993, p. 8), where  $S_a$  is the chance of living to age  $a$  (first reproduction) and  $V_a$  is the average number of offspring produced over an individual’s adult life if she is alive at age  $a$ . The optimal (or ESS)  $a$  is where  $\frac{dR_0}{da} = 0$  or  $\frac{d \ln V_a}{da} = -\frac{d \ln S_a}{da}$ .

Since  $S_a$  can be written as  $e^{-\int_0^a Z(x)dx}$ , the optimum is where  $\frac{d \ln V_a}{da} = Z_a$  (equation 1).

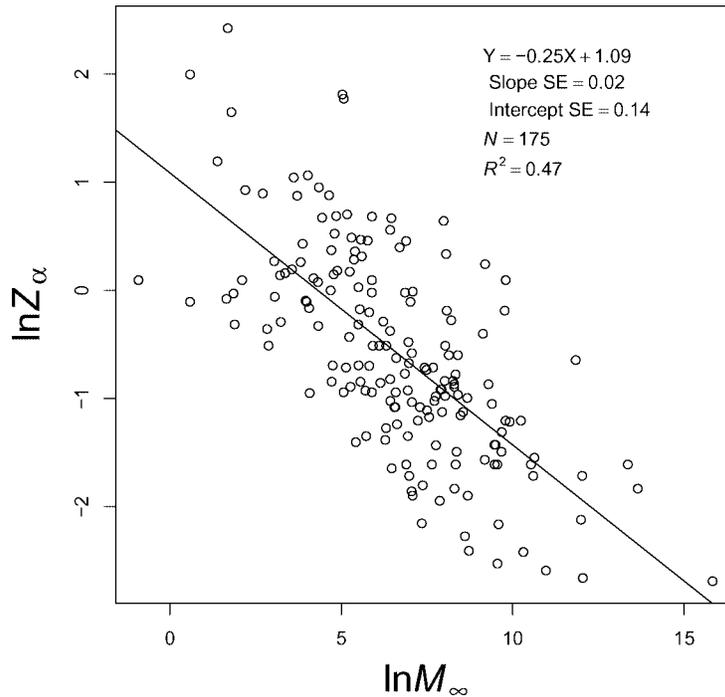
Suppose we have determinate growth, where production of offspring is just diverted self-growth, and assume that the  $Z(x)$  curve is flat near possible ages of first reproduction;

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**Fig. 1.** Mortality near adulthood ( $Z_a$ ) vs. asymptotic size ( $M_\infty$ ) in fish, uncorrected for differences in the height of the body-size growth curve. Data for all three figures kindly provided by David Griffiths and Chris Harrod, from their 2007 paper; units are in years and grams, respectively.

then (Charnov, 1991, 1993, p. 78),  $V_a \propto \frac{dM_a}{d\alpha}$  and  $\ln V_a = \ln \frac{dM_a}{d\alpha} + C'$ , where  $C'$  is a constant. Many pre-reproductive growth curves, particularly for fish, can be approximated by the simple growth model  $dM/dT = A \cdot M^{0.67}$ , which leads through equation (1) to  $Z_a = 0.67A \cdot M_a^{-0.33}$  (equation 2), where  $A$  is the 'height' of the growth curve.

More complex models (see Charnov *et al.*, 2001; Charnov and Gillooly, 2004; Charnov, 2011) give a constant different from the 0.67 in equation (2), but generally growth curve height ( $A$ ) enters the power function in exactly this multiplicative way; thus  $Z_a$  will only show an across-species allometry ( $Z_a \propto M_a^{-0.33}$  across species) if all of the species have the same (similar)  $A$  values. Differences in  $A$  among species will contribute scatter to the plot, and any correlations between  $A$  and  $M_a$  will distort the slope from the expected  $-0.33$ .  $A$ , the growth curve 'height', is known to vary greatly with many environmental and other factors (endotherms vs. ectotherms, environmental temperature within ectotherms, primates vs. typical mammals, etc.); we expect  $Z_a \propto M_a^{-0.33}$  only if we control for  $A$  among the species. We can do this by plotting only species having approximately the same  $A$  [e.g. primates vs. typical mammals (Charnov and Berrigan, 1993)], or by plotting  $Z_a/A$  vs.  $M_a$ .

Griffiths and Harrod (2007) compiled a database comprising natural mortality near maturation sizes ( $Z_a$ ), body-size growth curves, and estimated asymptotic size [ $M_\infty$ , proportional to  $M_a$  (Charnov, 1993)] for 175 species of fish. The various fish species occupied virtually all marine environments (demersal, benthopelagic, pelagic, reef associated) except

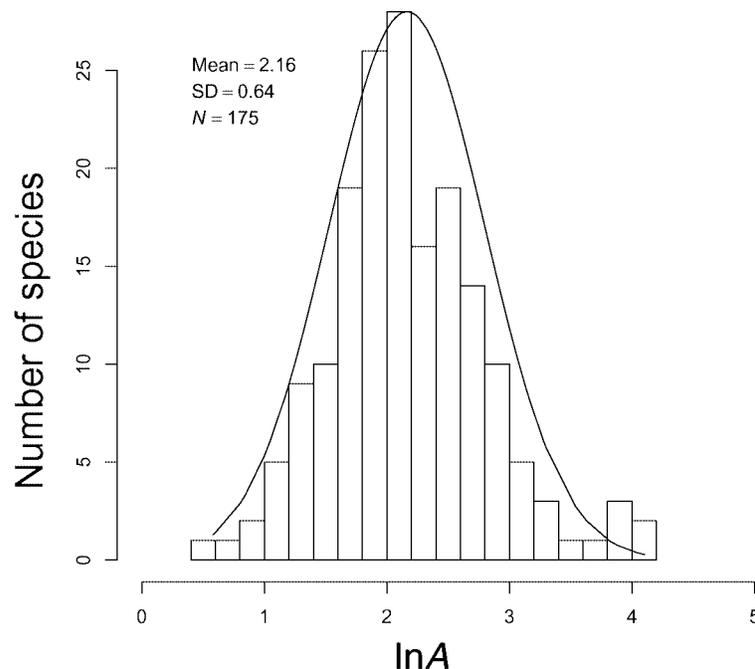
deep water, and included all major phylogenetic groups (48 fish families are represented). They included some freshwater and estuarine species.

If we plot  $\ln Z_a$  vs.  $\ln M_\infty$  for the 175 species, we obtain Fig. 1, a roughly linear relation with a slope of  $-0.25$  and  $R^2 = 0.47$ . This level of precision (or less) is common for across-species  $Z_a$  vs.  $M$  plots for fish (e.g. Cury and Pauly, 2000).

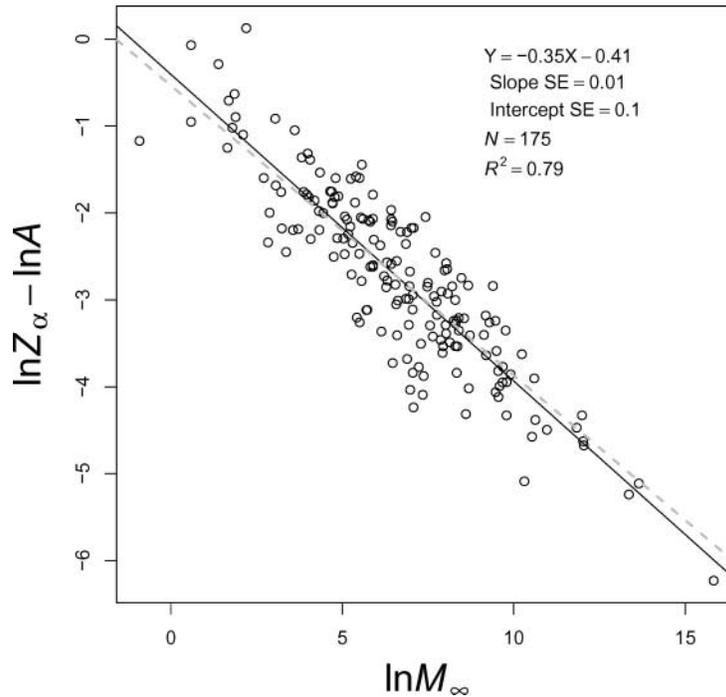
All of the species in Griffiths and Harrod's data set had fitted Bertalanffy body-size growth curves ( $dM/dT = AM^{0.67} - BM$ ). The Bertalanffy equation merely describes body size growth while the underlying reproductive allocation that produces the growth curve is adjusted by natural selection in a similar way to the determinate growth case described earlier; Charnov and Gillooly (2004) show that ' $A$ ' in the first term here plays the same 'height role' as ' $A$ ' in the simple growth model of equation (2); it becomes the 'height' parameter of the  $Z_a$ ,  $M$  scaling. [See Charnov (2008) for the argument that  $B$  is simply (proportional to) reproductive effort.]

We estimated  $A$ , the growth curve 'height' for the various species, the distribution of which is shown in Fig. 2. ' $A$ ' follows a lognormal distribution and 95% of the  $\ln A$  values are contained within  $\sim 2.5$  logarithm units; that is,  $A$  varies by a factor of  $12 \times (e^{2.5} \sim 12)$ . If we correct each  $Z_a$  by dividing by the  $A$  from the associated body-size growth curve, Fig. 3 results. The slope is now  $-0.35$ , and the  $R^2 = 0.79$ , a very tight scaling relation.

Many environmental variables (e.g. water temperature, foraging habits, food type) differ greatly among the habitats and some correlate with phylogeny, thus driving the variation in  $A$  seen in Fig. 2 (Griffiths and Harrod, 2007). However, when simply corrected for the heights of



**Fig. 2.** The distribution of  $A$ , the height of the Bertalanffy body-size growth curves, among the 175 species. 95% of the  $A$  values fall within about 2.5 natural logarithm units, or a multiplier of about  $12 \times$  for  $A$ . This spread is about the separation in growth curve height observed between endothermic eutherian mammals and typical ectotherms.



**Fig. 3.**  $Z_a/A$  vs.  $M_\infty$ . As predicted, the scaling is much more precise, and the slope near the expected  $-1/3$ . Dashed line is best-fit  $-1/3$  slope line for comparison.

their body-size growth curves, the species all fall on the same scaling line for  $Z_a$  vs. body mass, just as evolutionary life-history theory leads us to expect. Although not all life-history allocation models predict power functions for  $Z_a$  vs.  $M_a$ , it is a very common result, and *always* requires we correct by the height of the body-size growth curve to produce good across-species allometries.

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