

Geometrical constraints on body size

In a recent *TREE* Perspective, Atkinson and Sibly¹ wondered why 'organisms are usually bigger in colder environments', and briefly reviewed life-history, genetic and physiological hypotheses they considered relevant. However, size limitations occur in all organisms, whether influenced by temperature or not, and a satisfying explanation should therefore consider factors affecting all organisms. Such a general factor is geometry, and especially the different exponents relating surfaces and volumes, which provide powerful and inescapable constraints for growth.

In endotherms, these exponents manifest themselves as the exponent of body mass, wherein heat is generated in approximate proportion to length cubed, and that of body surface (length squared), through which body heat is lost. Hence the explanatory power of Bergmann's rule. This rule is modified in some very large mammals, for which dumping excess body heat can become a problem, solved in whales and elephants by flukes equipped with countercurrent heat exchangers, and by very large ears, respectively. In insects, the limiting surface is that of the fine network of trachea that brings oxygen to individual body cells, but which can not keep up with increasing body mass, simply because of its reduced dimensionality – hence the size limitation inherent in the bauplan of insects.

Another size-limiting implication of the different dimensions of surface and mass is the need for large terrestrial animals to increase the relative cross section of their legs – a surface – as their volume increases. This is what requires the column-like legs of moas, rhinos or large dinosaurs. A similar argument applies to plants (cf. trees trunks versus grasses).

In animals that breathe water through gills, the surfaces that are limiting though the effect of gravity or heat production are of little importance, and the limiting surface for body size is that of the gills^{2,3}. It is difficult for air breathers such as us humans to realize this, but breathing water is hard work: fish spend about 10–30% of their energy on breathing itself, that is, on extracting oxygen from a medium in which it is far less abundant, and in which its diffusion rate is 300 000 times slower than in air. When comparing different species, or different sizes within the same species, the oxygen uptake of fish turns out to be related mainly to gill area^{2,3}. Gills grow, in fish, in proportion to powers of body weight ranging from 0.5 (in guppies) to 0.9 (in tunas). Thus, large representatives of a given species will always have smaller relative gill area (gill area/body weight) than smaller ones. As oxygen in excess of routine requirements is required for growth, the latter will cease when a size (L_m) is reached at which relative gill area is just sufficient to cover routine metabolism. Hence any factor which reduces routine metabolism – such as lower temperature or abundant food – will have the effect of increasing L_m .

I have elaborated on these basic principles in a number of publications²⁻⁶, and have shown that they and/or their corollaries explain a large number of phenomena previously thought to be unrelated. Examples are the distribution of fish in

thermal gradients; their migrations; the predictability of their size at first maturity (L_m) relative to their L_∞ values; the generation of daily rings on the otoliths of fishes, the statoliths of squids and the shells of bivalves; the sexual dimorphism of many fish species in which the females (which have lower metabolism) reach larger size than the males.

Also, based on a very large number of applications of the von Bertalanffy equation, I have established that among similar fishes (populations of the same, or closely allied species), L_m is proportional to $k^{0.5}$ (as in Fig. 2 of Atkinson and Sibly, which is based on some of the data I assembled)⁷. This relationship, which has been extensively used in fisheries biology in the past decade, combined with one relating k with the natural mortality of fishes⁸, can easily be shown to meet the criteria in Box 3 of Atkinson and Sibly, thus validating what they chose to call the 'Bertalanffy/Perrin model'.

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Reply from D. Atkinson and R.M. Sibly

Pauly has provided examples of limitations on body size which support the idea that a decrease in ratio of surface areas to body volume or mass during growth may help to explain size limitations in all organisms. We agree with this idea, and have mentioned that this well-known geometrical principle is usually used to explain Bergmann's rule in endotherms¹, and was used by von Bertalanffy in his theory of growth to explain limitations on body size². We also agree that Pauly's elaboration on the idea that gill surface area limits oxygen supply to tissues hence growth rate and final size (L_m) provides plausible hypotheses to account for a variety of phenomena previously thought to be unrelated.

For readers who have not seen the relevant papers^{3,4}, it is the gill surfaces (not mass, for instance) that 'grow, in fish, in proportion to powers of body weight ranging from 0.5 (in guppies) to 0.9 (in tunas)'. However, we wish to make two further

points about this. First, these examples showing exponents differing from 2/3 – the value that would be expected if growth were isometric – reveal that the allometry is not solely a product of constraints imposed by isometric growth. Adaptive analyses, similar to the one we presented are valuable here, because they can help explain why allometric exponents differ from those predicted solely on the basis of a proposed constraint^{5,6}. Second, we consider that critical experiments still need to be done to test some of the ideas. For instance, we have proposed tests^{1,2} that would identify the precise role of oxygen supply, including the extent to which it acts as: (1) a selective (ultimate) factor altering the slope of the reaction norm of temperature against size-at-maturity, and (2) a proximate mechanism controlling the timing of maturation under different thermal regimes.

When trying to understand effects of temperature on growth and body size, it is important also to stress the other, thermal, limitation on physiology proposed by von Bertalanffy⁷. A modern description of this limitation is that the rate at which resources are acquired by an organism is less sensitive to temperature (for example, due to temperature-insensitive diffusion affecting oxygen uptake) than are the speed of processes that limit the rate of metabolism required for body maintenance. Pauly states that 'any factor which reduces routine metabolism – such as lower temperature ... – will have the effect of increasing L_m '. However, this implies that lower temperature reduces routine metabolism more than the rate of uptake of oxygen that would otherwise have limited growth rate at a smaller size. Thus, Pauly did not make explicit that the relative temperature-insensitivity of resource uptake is also required, along with the geometrical principle, to make his (and von Bertalanffy's) explanation logically complete.

We are encouraged that empirical relationships derived from fisheries data correspond with the predictions made by life-history theory that are illustrated in our Box 3. We are also pleased to acknowledge that the optimality model and its associated physiological mechanisms and applications that we described owe a lot not only to Ludwig von Bertalanffy and Nicolas Perrin, but also to others including David Berrigan, Ric Charnov and Daniel Pauly.

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