



TECHNICAL COMMENT

EVOLUTIONARY ECOLOGY

Comment on “Metabolic scaling is the product of life-history optimization”

Rainer Froese¹ and Daniel Pauly^{2*}

White *et al.* (Science 377, p. 834–839, 2022) propose that reproduction reduces the somatic growth of animals. This contradicts the common observations that non-reproducing adults are not larger than those that reproduced as well as the very example the authors provide of a fish that reproduces while its growth continues to accelerate, which is common in larger fish.

In animal species, growth rates of body weight accelerate toward a maximum after which it slows until growth ceases altogether. White *et al.* (1) present a metabolic model based on the assumption that “[...] resource allocation to survival, growth and reproduction is limited [...]” with “[...] growth ceasing when all of production is allocated to reproduction.”

The problem with this widespread assumption is lack of support in the real world: (i) in most animal species, reproductive effort is not constant, but varies seasonally. (ii) resource availability is not constant and limited but also varies seasonally, typically with a “time of plenty” during which any previous, reproduction-related loss in body weight is easily compensated for (2); in other words, other than assumed by White *et al.* (1), reproduction and growth need not occur simultaneously. (iii) many pets and livestock are prevented from reproduction but exhibit the same growth trajectories as their parents. (iv) males usually have much lower investment in reproduction than females, yet they do not differ much in body size (e.g., dogs, cats, horses) or end up being smaller than females, as is the case in about 80% of fish species with known maximum size by sex (3). (v) dominant males in harem-building species, which indeed spend a lot of energy in the context of reproduction, do not cease growing but rather tend to be larger than bachelors. Clearly, in all these common-knowledge cases, somatic growth is not governed or limited by reproduction.

To illustrate their predictions, the authors selected growth data of animals whose growth patterns are “reasonably well approximated by the von Bertalanffy growth equation” (VBGE) (4). However, the authors did not realize that the growth patterns of the species they give as an example directly contradict their main

assumption that somatic growth slows with the onset of reproduction. We illustrate this by examining their Fig. 1B, meant to describe the growth of the “North Sea” stock of female Atlantic horse mackerel *Trachurus trachurus* based on previously published VBGE growth parameters (5), i.e., $L_{\infty} = 34.3$ cm, $K = 0.16/\text{year}^{-1}$ and $t_0 = -4.73/\text{year}$, and a length-weight relationship of the form $W = a \cdot L^b$, with $a = 0.0032$ and $b = 3.29$. The high absolute value of t_0 implies that horse mackerel have a length of 16 cm at age 0, which is not possible, and suggests that the original age determinations overlooked the first 2 annual rings. However, this should not affect their estimation of L_{∞} , from which asymptotic weight can be estimated as $W_{\infty} = 360$ g. As (5) included no data on age or mean size at first maturity, estimates of these two parameters for the North Sea were taken from (6), i.e., 2 years and 18.5 cm total length, corresponding to a weight at first maturity $W_m = 47$ g.

White *et al.* (1) did not realize that the growth patterns of the species they give as example contradict their main assumption that somatic growth slows with the onset of reproduction.

The inflexion point (W_i) of the VBGE, corresponding to its maximum growth rate (dW/dt) is related to its asymptotic weight through $W_i = 0.296 \cdot W_{\infty}$. Since $W_i = 106$ g \gg $W_m = 47$ g, this example shows that growth in North Sea horse mackerel accelerates after first maturation and spawning (Fig. 1), and thus refutes the contention that reproduction reduces growth. This case is not unique: thousands of them in hundreds of species could be generated using the growth parameters and age or size at maturity in FishBase (7). Indeed, rules can be derived from analyses of these data which show that W_m becomes a small fraction of W_i in iteroparous species that reach large sizes (3, 8).

Fish do not have to “choose” between somatic growth or reproduction, because in the real world, these do not occur simultaneously, but rather sequentially. Also, fish use only a small fraction of their “energy”, about 10%, for

each of these two activities (8), the rest being mainly devoted to other activities, such as darting about. Thus, reducing movement rate, given the same food and oxygen consumption can easily produce the savings required for growth or reproduction. This is the reason, incidentally, why aquaculturists raise fish which have been selected to be calmer than their wild congeners.

While there is no doubt that the resources available to an organism have an upper limit, this limit varies strongly with season and environment and is usually mitigated by migration, the buildup of fat or other reserves, hibernation or other adaptations. Most species have evolved phenologies characterized by phases of reproduction or growth relative to the time of plenty, when resource availability is above the annual average, thus minimizing or avoiding any overall trade-off between resources used for somatic growth or reproduction (9).

It seems to us that the argument for an evolution of optimal combination of growth and reproduction unconstrained by physics or geometry cannot be made by a model based on unrealistic assumptions and by applying a growth model whose derivation was explicitly based on surfaces limiting the growth of organisms (3, 4, 8). Also, in their conclusions, the authors first correctly restate the common knowledge that metabolism, growth, and reproduction have coevolved to maximize fitness within physical constraints. However, in the subsequent sentence they claim that their approach has expanded the “phenotypic space in which evolutionary optimization operates.” Given the conflicts of their reasoning with common knowledge of the interplay of growth and reproduction in a wide range of animals, we cannot agree with this assertion.

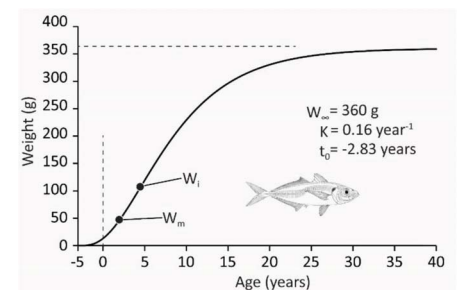


Figure 1. Von Bertalanffy growth curve of Atlantic horse mackerel *Trachurus trachurus* (L.)

Adjusted for erroneous age reading from Fig. 1B in White *et al.* (1), with an L-W exponent $b = 3.29$; this shows that the weight of *T. trachurus* at first maturity and spawning (W_m) is much smaller than the weight at which their growth is fastest (at W_i). This finding, which is easily generalizable to hundred of other species, refutes the claim that reproduction reduces growth.

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REFERENCES AND NOTES

1. C. R. White, L. A. Alton, C. L. Bywater, E. J. Lombardi, D. J. Marshall, *Science* **377**, 834–839 (2022).
2. E. A. Trippel *et al.*, *J. Exp. Mar. Biol. Ecol.* **451**, 35–43 (2014).
3. D. Pauly, *Sci. Adv.* **7**, eabc6050 (2021).
4. L. Von Bertalanffy, *Q. Rev. Biol.* **32**, 217–231 (1957).
5. T. van der Hammen, J. J. Poos, "Data evaluation of data limited stocks: Dab, Flounder, Witch, Lemon Sole, Brill, Turbot and Horse mackerel" (Report C110/12, IMARES Wageningen University, 2012).
6. D. Sarhage, *Ber. dt. Wiss. Komm. Meeres. N.F.* **21**, 122–169 (1970).
7. R. Froese, D. Pauly, FishBase (2022); www.fishbase.org
8. R. Froese, C. Binohlan, *J. Fish Biol.* **56**, 758–773 (2000).
9. F. Koch, W. Wieser, *J. Exp. Biol.* **107**, 141–146 (1983).

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