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Letter

Aquatic Life History Trajectories Are Shaped by Selection, Not Oxygen Limitation

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Pauly [1] argues that, as espoused in the gill-oxygen limitation theory (GOLT), growth slows as size increases because oxygen supply via the gills is unable to keep up with the oxygen demands of an increasingly large body. Thus, according to GOLT, growth determines the timing of reproduction, and fish reproduce when they become oxygen limited and growth starts to decline. GOLT has been critiqued on physiological grounds [2,3], and we agree with those critiques. Large fish are no more oxygen limited than small fish, primarily because their respiratory surface area matches their metabolic demand for oxygen over a large size range (see Table 1 in [4]).

The main point of Pauly's critique of Marshall and White [5] is that female fish often grow larger than male fish and that this is a challenge to the idea that reproduction limits growth. Pauly's conclusion is based on the assumption that female fish have 'higher reproductive outputs' than male fish, and the implicit argument that were reproduction to strictly limit size, the sex with the higher reproductive output should be smaller. Pauly's assumption that female fish have higher reproductive outputs than male fish is unsupported by data. There is no pattern of females investing relatively more in reproduction than males in fish (or other water-breathing ectotherms [6]). Indeed for the species given by Pauly [1], females invest relatively less in reproduction than males as a proportion of body mass (see figure 5.5 in G.A. Sarre, PhD thesis, Murdoch University, 1999). Importantly, the costs of reproduction alone do not drive size or growth, so when females invest more in reproduction than males, this alone would not drive sexual dimorphism [7]. Instead, it is our view that selection optimises body size. Accordingly, we suspect (and theory predicts [7]) females are sometimes larger because selection favours greater size and the increased fecundity this affords.

Pauly [1] points to lone goldfish as evidence for reproduction not limiting growth. For this argument to hold, one would have to assume that body size is solely a product of a single constraint, rather than optimisation by evolutionary forces. It is our view that any one trait is not driven solely by a constraint (be that oxygen supply limitations, or energy demands of reproduction, or anything else). Instead, a trait will be the product of selection, where multivariate constraints and trade-offs will be balanced so as to maximise fitness. Thus, removing the energy costs of reproduction by artificially preventing it, as in the goldfish example, will not then result in unlimited growth. Instead, the various endocrine pathways have evolved to set body size so as to prepare organisms to pay the evolutionarily anticipated costs of reproduction, even if they are not actually paid under unnatural conditions of complete isolation.

Pauly [1] states that fish spend most of their energy on activity and that only a small reduction in activity yields the resources necessary for reproduction. These assertions have no support; indeed, they are contradicted by data (Table 1). The average expenditure on respiration is 35%; respiration occurs not only for activity but also tissue maintenance and synthesis, so energy spent purely on activity will be some fraction of 35%. The average expenditure on reproduction is 17% (and can be as high as 29% in older, larger fish), so individuals would have to reduce their activity by more than half to offset the energy devoted to reproduction. Such a reduction seems unlikely given the massive fitness consequences of doing so, especially for species that undergo arduous migrations during the reproductive phase. Instead, all formal theory and the existing data strongly support the idea that reproduction is costly.

Pauly [1] argues that energy expenditure on courtship and fighting drives sexual size dimorphism; males spend more energy on activities than females so they cannot attain the same size. Theory and data suggest the opposite. Parker [7] provides empirical support for the theoretical prediction that in fishes where males fight each other, males are actually larger than females because intrasexual selection favours greater size.

Crucially, Pauly [1] makes the argument that larger female fish, upon reproducing and losing metabolically active mass, are relieved from oxygen limitation and can then resume growth. Based on this argument, fish should increase in size after each reproductive bout, thus bringing them to extreme oxygen limitation. Consequently, as fish get larger and more oxygen limited, according to Pauly's argument, each reproductive bout should be smaller and smaller. Instead, we see the opposite in 95% of fish species [5].

Pauly [1] argues that even though air breathers and water breathers often show very similar growth trajectories, different processes produce these trajectories and their similarity is merely coincidental. This seems very unlikely. Our position is that growth trajectories are shaped by increasing allocation to costly reproduction in all animals. Ultimately, our difference of opinion comes down to causality. Pauly's GOLT argues that body size in fish is limited by gill area; instead, we believe that organs evolve to provide capacity to meet an organism's requirements.

Table 1. Compilation of Estimated Energy Budgets in Fish for How Ingested Energy Is Devoted to Respiration, Growth, and Reproduction[a]

Species	Energy for respiration (%)	Energy for growth (%)	Energy for reproduction (%)
Micropterus salmoides	39.5	27.4	12.5
Anguilla anguilla	7		20
Engraulis mordax		13	11
Gasterosteus aculeatus	36.5	7	6.5
Esox lucius	16	8	16
Gadus morhua (3 year old)	36.6	50.9	12.5
G. morhua (9 year old)	49.1	21.7	29.2
Coregonus albula	41		23
Coregonus pollan	57		27
Average	35	21	17

[a]Summarised from Dabroski [8].

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