

## Letter

## Female Fish Grow Bigger – Let's Deal with It

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The recent contribution of Marshall and White [1], which is based on the correct observation that reproductive output tends to scale hyperallometrically with fish size, suggests that existing growth models, including the Gill-Oxygen Limitation Theory (GOLT) [2–4], are flawed because they do not explicitly account for this allometry.

The GOLT is structured around the fact that gills, because they have to function as a (2D) surface perpendicular to an oxygen-rich water flow, cannot keep up with the growing (3D) bodies they have to supply with oxygen. Thus, any factor, such as elevated temperature, that causes oxygen demand by the body to increase will result in respiratory stress in large adult fish, which have a low gill area: body weight ratio.

There is a good reason why growth is not thought of as being influenced by reproduction in the context of the GOLT. This theory implies that growth determines the timing and intensity of reproduction, not the other way around [2,3], or put differently, fish do not stop growing because they reproduce; rather, when their growth starts to decline, they reproduce [5,6]. This is the only way that the reduction of size at first maturity occurring in stressful environments (e.g., increased temperature, which increases oxygen demand while reducing supply), which is always accompanied by a simultaneous reduction of maximum size (e.g., see [7]), can be causally explained.

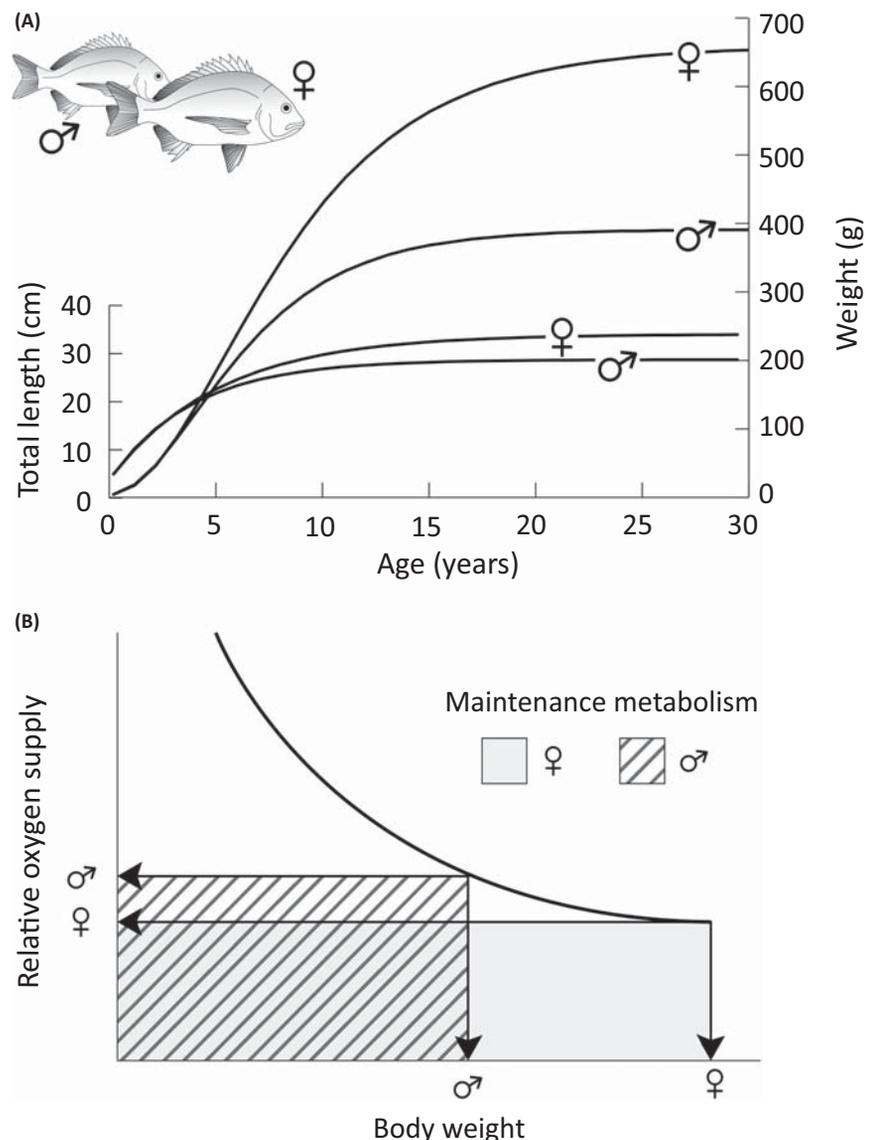
Also, reproduction cannot be the reason why growth rate declines with fish size, as evidenced by every goldfish that lives a lonely, sexless life in an aquarium and

which nevertheless will cease to grow at some point.

More importantly, in 664 of 825 fish species (i.e., >80%) whose growth parameters were reported for both sexes in the same study in FishBase (<http://www.fishbase.org>, accessed 8 November 8,

2018), it was the females that grew faster and reached a larger size than the males, despite having the higher reproductive output (see the example in Figure 1).

Fish spend an overwhelming amount of the 'energy' they have acquired (i.e., ATP, synthesized using food + oxygen) on



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**Figure 1. Female Fish Grow Bigger.** In fishes, it is mostly the females that grow to be big and strong, despite their higher reproductive output. The typical growth curve shown here refers to females and males of black bream (*Acanthopagrus butcheri*) from an estuary in Western Australia [7] (A) and as reflected in a plot (not to scale) of their gill area per body weight (and hence relative O<sub>2</sub> supply) versus their body weight (B). The better growth of the females is explained by their lower maintenance metabolism, due to a lower rate of activity (see text).

various activities (i.e., not on protein synthesis). Thus, for a given food intake, they only need to reduce their activity level by a small extent to mobilize, prior to spawning, the ATP required for the synthesis of gonadal products [8]. This applies especially to females, which, for example, do not engage to the same extent in fights with conspecifics or expend as much energy on courtship. This is why females can grow bigger than males.

Finally, we should cease to view the egg production by individual ‘big old fecund females’ (BOFFs [9]) in the same manner that we view pregnancies in mammals. BOFFs, like all other fish, have gills that cannot keep up with the increasing weight of their body, and thus they will suffer from a low oxygen supply per unit weight. However, spawning, and the resultant body weight loss due to released eggs, reduces the post-spawning mass of their metabolically active tissues thus increasing their gill area (in relation to body weight), and thus makes it possible for them to grow again until the next season.

There is obviously more to growth and growth models than this. However, the ultimate goal of a comprehensive theory of growth, which would apply to all types of growth in all kinds of organisms, ranging from bacteria to fish to hibernating bears and tomatoes [10], does not make it superfluous to identify and test domain-specific theories and models applying to a specific set of constraints. Thus, the GOLT applies only to water-breathing animals because they must extract the oxygen that they require from a dense and viscous medium that contains little of it (in comparison with air [3]). The effort this implies, particularly in large/old individuals (e.g., in BOFFs), does not need to be considered in theories of growth that apply to air-breathing homeotherms, to which acquiring the food needed to fuel their metabolic furnace is a constant preoccupation.

Thus, reproductive output, even when hyperallometric, does not inhibit the growth of female fish, and even less that of male fish, even if this is counterintuitive.

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<https://doi.org/10.1016/j.tree.2018.12.007>

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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