

On confusing cause and effect in the oxygen limitation of fish

This letter deals with the critique by Lefevre et al. (2017, 2018) of the use of Gill-Oxygen Limitation Theory (GOLT) to explain observed and predict further decreases of the maximum body size of fish under warming.

Given ocean warming, the GOLT predicts a reduction in the size of fish due to their inability to compensate, via their gill surface, for the increased metabolic rate that results from higher temperatures (Cheung et al., 2013). Lefevre et al. (2017, 2018) objected to this because they believe that fish can grow gills as needed, such that the oxygen supply cannot be limiting their metabolism. Pauly and Cheung (2018) responded to this claim, refuted its various elements, and reiterated the basic dimensional argument that is at the basis of the GOLT.

First, Lefevre et al. (2018) stated that GOLT was based on the assumption: “when the gill surface area grows, it will eventually deplete the water of oxygen and more surface area would be useless...” and “...that large gills and large fishes are less effective at oxygenating blood”. Pauly and Cheung (2018) do not make such assumptions.

What we stated, rather, is that gill surface area—because it must function as surface (otherwise, it could not take in oxygen and release carbon dioxide)—can grow in only two dimensions (width and height), although growing in depth would not contribute to increase the rate of gaseous exchange (see Figure 1). Given the high efficiency of gill lamellae blood countercurrent systems, the rate of oxygen absorption through the gill would be negligible for gill lamellae placed *behind* a first set of lamellae because “second row” lamellae would be bathed in a flow of deoxygenated water, not to mention those in the “third row,” etc. This also applies to increases in the depth of individual lamellae and is, in fact, analogous to all other flow exchange systems such as car radiators, as illustrated in Figure 1.

Second, Lefevre et al. (2018) wrongly assume that the catabolic term in the general von Bertalanffy growth function (VBGF) requires oxygen and that “[...] all evidence indicates that maintenance oxygen demand decreases with mass”. However, the catabolic (second) term of the general VBGF, $dW/dt = H \cdot W^d - k \cdot W^b$, is oxygen-independent as the spontaneous, temperature-dependant denaturation (i.e., loss of the quaternary structure) of the body's protein molecules does not require oxygen (Cox & Nelson, 2008). Therefore, it is reasonable to expect that catabolism is directly proportional to biomass (weight) and $b = 1$. Thus, it is incorrect for Lefevre et al. (2018) to claim that the mathematical model of Pauly and Cheung (2018) generates biologically unreasonable outcome because oxygen demand decreases with mass and $b < 1$. Instead, our analysis with exponents d ranging

from 0.6 to 0.9 (as prompted by a criticism in Lefevre et al., 2017) found that the shrinking effect reported in Cheung et al. (2013) was amplified rather than reduced (Pauly & Cheung, 2018).

In conclusion, we suspect that Lefevre et al. (2018) confuse cause and effect when they mention that “the activity of oxidative enzymes falls with body mass in fishes (Davies & Moyes, 2007)” as an argument against our interpretation that big/old fish stop growing because their gills deliver less oxygen per unit body mass than in young/small fish.

In fact, this quote begs questions about the reason(s) for what is indeed the well-documented, but widely misunderstood transition from a preponderance of oxidative enzymes in the muscle tissues of

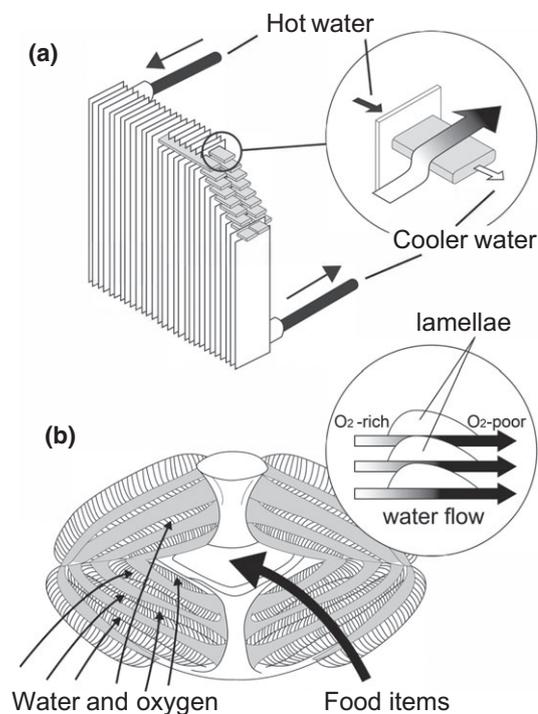


FIGURE 1 Illustrating the similarity between systems for cooling car engines and for extracting oxygen from water. (a) Schematic representation of a car's radiator, which can grow in width and height, but not in depth, as air, once it has passed by a first row of lamellae (insert), cannot pick up more heat. (b) Frontal view of the interior of a manta's mouth (*Mobula japonica*; adapted from Figure 3.20A of Wegner (2015)), illustrating the two dimensionality of breathing, that is, the fact that once water has passed through the gills (insert), it has become depleted of oxygen, and it would be useless for it to pass through more gill structure

young/small fish to a preponderance of glycolytic enzymes in the same tissues of old/large fish (Burness, Leary, Hochachka, & Moyes, 1999; Davies & Moyes, 2007; Norton, Eppley, & Sidell, 2000; Somero & Childress, 1980). To us, it seems obvious that the reason why fish increasingly shift to glycolytic metabolism is due to the decline of gill surface area per unit body mass (and hence the reduction in relative oxygen supply) that invariably occurs as fish grow.

It is important to clarify these claims so that progress can be effectively made to understand how climate change is affecting the body size of marine fishes.

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