

## Projecting the shrinking fish body size under ocean warming: tuna as an illustrative example

In Cheung *et al.* (2013)<sup>1</sup>, we developed and applied a mathematical model that projects decrease in body size under ocean warming and deoxygenation. Recently, in Pauly and Cheung (2017)<sup>2</sup>, we applied the model with more realistic parameterization of scaling coefficient between gill area and body weight of fish ( $d_G = 0.6$  to  $0.9$ ), and found that the projected decrease in maximum body size is substantially higher than the projections using a  $d_G$  value ( $d_G = 0.7$ ) for conventional fish growth model.

Particularly, the shrinking of fish with a higher  $d_G$ , such as yellowfin tuna which has a  $d_G$  value of  $0.9$  (Muir 1969)<sup>3</sup>, was found to be more sensitive to ocean warming; this contradicts the claim by Lefevre *et al.* (2017)<sup>4</sup>, which they made it based without having studied its theoretical or mathematical basis.

This note explains, using a generic tuna as an illustrative example, why fishes with high  $d_G$  value, such as tunas, are very sensitive to warming in terms of changes in maximum body size. Based on conventional fish growth theory established by von Bertalanffy (1951)<sup>5</sup>:

$$\frac{dW}{dt} = H \cdot W_t^d - k \cdot W_t^b \quad \text{Equation 1}$$

where  $W$  is body weight,  $t$  is time, and  $H$  and  $k$  are coefficients for anabolism and catabolism, respectively. Within the Gill-Oxygen Limitation Theory (GOLT), anabolism is oxygen-dependent while catabolism is not. Also, the rate of oxygen uptake is limited by gill area, and thus  $d = d_G$ . When the volume (mass) of fish grows, the gill area does not keep up, resulting in  $d_G < 1$ . Thus, fish stop growing and reach maximum body size when anabolism = catabolism. Assuming  $b = 1$  and solving equation 1 for  $dW/dt = 0$ , we have:

$$K = k \cdot (1 - d) \quad \text{Equation 2}$$

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{1-d}} \quad \text{Equation 3}$$

Assuming that  $H$  and  $k$  are temperature-dependent:

$$H = h \cdot e^{-j_1/T} \quad \text{Equation 4a}$$

$$k = g \cdot e^{-j_2/T} \quad \text{Equation 4b}$$

where  $h$  and  $g$  are constants in Arrhenius equation for anabolic and catabolic reactions, while  $j_1$  and  $j_2$  are the ratios of activation energy and Boltzmann constant for two types of reaction, respectively.

Using yellowfin tuna as an example, based on FishBase ([www.fishbase.org](http://www.fishbase.org)), under current condition,

$$L_{\infty} = 192.4 \text{ cm}$$

$$W_{\infty} = 0.0216 \cdot L_{\infty}^{2.981}$$

$$W_{\infty} = 139,209.6 \text{ g}$$

$$K = 0.37 \text{ year}^{-1}$$

Based on Cheung *et al.* (2011)

$$j_1 = 4500 \text{ K}$$

$$j_2 = 8000 \text{ K}$$

One can then estimate  $h$  and  $g$  by substituting  $H$  and  $k$  in Equations 2 and 3, with 4a and b, and rearranging them:

$$h = \frac{W_{\infty}^{(1-d)} \cdot k}{e^{-j_1/T}} \quad \text{equation 5a}$$

$$g = \frac{k}{e^{-j_2/T}} \quad \text{equation 5b}$$

Consider the conventional value of  $d = 2/3$  in the specific von Bertalanffy growth function  
 $k = K/(1-d) = 0.37/(1-2/3) = 1.11$

Comparing the distribution of yellowfin tuna with sea surface temperature fields for the 1971-2000 period (Cheung *et al.*, 2013), allowed the estimation of its average (or preferred) environmental water temperature:

$$T = 26 \text{ }^{\circ}\text{C} = 299.15 \text{ K}$$

Thus,

$$h = (1.11 \cdot 139209.6)^{(1-2/3)} / \exp(-4500/299.15) = 196248598$$

$$g = 1.11 / \exp(-8000/299.15) = 456473698554$$

If temperature increases by 1  $^{\circ}\text{C}$ ,

$$T' = 26 + 1 \text{ }^{\circ}\text{C} = 27 \text{ }^{\circ}\text{C} = 300.15 \text{ K}$$

The projected maximum body weight is

$$W'_{\infty} = \left(\frac{H}{k}\right)^{\frac{1}{(1-d)}} = \left(\frac{h \cdot e^{-j_1/T}}{g \cdot e^{-j_2/T}}\right)^{\frac{1}{(1-d)}}$$

$$= (196248598 \cdot \exp(-4500/300.15) / (456473698554 \cdot \exp(-8000/300.15)))^{1/(1-2/3)}$$

$$= 123846.3 \text{ g}$$

Thus, change in maximum body weight:

$$W'_\infty / W_\infty - 1 = (123846.3/139209.6 - 1) * 100\% = -11\%$$

Now, consider a more realistic  $d_G = 0.9$  for yellowfin tuna (Muir 1969):

$$k = K/(1-d) = 0.37/(1-0.9) = 3.7$$

$$h = (3.7 * 139209.6^{(1-0.9)}) / \exp(-4500/299.15) = 41256828$$

$$g = 3.7 / \exp(-8000/299.15) = 1.521579e+12$$

If temperature increases by 1 °C,

$$T' = 26 + 1 \text{ °C} = 24 \text{ °C} = 300.15 \text{ K}$$

The projected maximum body weight is

$$W'_\infty = \left( \frac{h \cdot e^{-j_1/T}}{g \cdot e^{-j_2/T}} \right)^{\frac{1}{(1-d)}}$$

$$= (41256828 * \exp(-4500/300.15) / (1.521579e+12 * \exp(-8000/300.15)))^{(1/(1-0.9))}$$

$$= 94271.77 \text{ g}$$

Thus, change in maximum body weight:

$$W'_\infty / W_\infty - 1 = (94271.77/139209.6 - 1) * 100\% = -32.3\%$$

Thus:

Temperature (K)	$d = d_G$	$W_\infty$ (g)	Change in $W_\infty$ (%)
296.15	2/3	139209.6	0
296.15	0.9	139209.6	0
297.15	2/3	123846.3	-11.2
297.15	0.9	94271.8	-32.8

Biologically, this means that fish with a higher  $d_G$  tends to have a lower ratio of the anabolic to catabolic rate constant, suggesting that the fish would spend relatively more energy for catabolic activities than anabolic activities. This corresponds to the life style of tuna-like species.

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## References

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