

## PRE-SUBMISSION DRAFT OF ‘THE GOLT AND ITS CRITICS’<sup>2</sup>

Daniel Pauly

Institute for the Oceans and Fisheries, University of British Columbia,  
Vancouver, B.C, V6T 1Z4, Canada. Email: [d.pauly@oceans.ubc.ca](mailto:d.pauly@oceans.ubc.ca)

### Abstract

This contribution consists of the pre-submission version of a now-published article by the author, titled “The Gill-Oxygen Limitation Theory (GOLT) and its critics” (*Science Advances*, 2021:7: eabc6050), of two anonymous reviewers’ comments, and the author’s responses to these comments. The format of the citations -- ‘author(s), date’ -- was maintained, such as to allow the reader to quickly evaluate the references that were used. Also maintained were photos, which a reviewer wanted deleted, of pond aeration devices in Chinese fish farms. Overall, a comparison of the formally published version with that presented here allows one more case study of how peer-review improves submissions, or not.

### Table of Contents

<b>ABSTRACT .....</b>	<b>67</b>
<b>LIST OF FIGURES AND TABLES .....</b>	<b>68</b>
<b>LIST OF ACRONYMS AND SYMBOLS .....</b>	<b>68</b>
<b>INTRODUCTION .....</b>	<b>69</b>
<b>The need for a theory .....</b>	<b>69</b>
<b>How the GOLT defines growth .....</b>	<b>70</b>
<b>The scope of the GOLT .....</b>	Error! Bookmark not defined.
<b>COUNTERARGUMENTS TO THE GOLT.....</b>	<b>75</b>
<b>The terms of the debate.....</b>	<b>75</b>
<b>Gill lamellae <i>versus</i> book pages .....</b>	<b>75</b>
<b>The matter with exceptions, or exceptions matter .....</b>	<b>78</b>
<b>TWO MAJOR CHALLENGES TO THE GOLT .....</b>	<b>81</b>
<b>Fish growth vs reproduction .....</b>	<b>81</b>
<b>Temperature and maximum sizes .....</b>	<b>88</b>
<b>DISCUSSION .....</b>	<b>92</b>
<b>The nature of explanations .....</b>	<b>92</b>
<b>Some real issues with the GOLT .....</b>	<b>93</b>
<b>The GOLT and Evolution .....</b>	<b>94</b>

### ABSTRACT

The Gill-Oxygen Limitation Theory (GOLT) is presented to provide mechanisms for key aspects of the biology (food conversion efficiency, growth and its response to temperature, the timing of maturation, migrations, and others) in water-breathing ectotherms (WBE, i.e., fish and aquatic invertebrates). The

---

<sup>2</sup> Cite as: Pauly, D. 2021. Pre-submission draft of ‘The GOLT and its critics’, p. 67-115. In: D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III*. Fisheries Centre Research Reports 29(1).

GOLT's basic tenet is that the surface area of the gills or other respiratory surfaces of WBE cannot, as 2-dimensional structures, supply fish with sufficient oxygen to keep up with the growth of their 3-dimensional bodies. Notably, the reduced oxygen supply per body weight induces sexual maturation, and later a slowing and cessation of growth, all accompanied by an increase of physiological processes relying on glycolytic enzymes and a declining role of oxidative enzymes. Because the 'dimensional tension' underlying this argument is widely misunderstood, emphasis is given to a detailed, point-by-point presentation of the published objections to the GOLT and their refutation. Aside from having a wide theoretical scope, the GOLT has potential practical applications, e.g., in optimizing the way fish farmers aerate their ponds and in predicting how WBE populations will react to the warming and deoxygenation of the waters they inhabit<sup>3</sup>. The GOLT still needs to be refined and put on a solid quantitative basis, but this can only occur after the misconceptions surrounding it are put to rest.

#### LIST OF FIGURES AND TABLES<sup>4</sup>

- Figure 1** Different forms of the von Bertalanffy growth function (VBGF) and bluefin growth.  
**Figure 2.** Aerating systems that add dissolved oxygen to the water of ponds are common<sup>4</sup>.  
**Figure 3.** Two conceptions of the relationship between size at first maturity and maximum size.  
**Figure 4.** Schematic representation of the trajectory of water flows across the gills of a fish.  
**Figure 5.** Fish begin to mature when their growth starts to decline, not the converse.  
**Figure 6.** Fish, at higher temperatures, grow fast toward smaller maximum sizes.  
**Figure 7.** Simplicity vs. scope in explanations of growth/temperature relationship.  
**Table 1.** Physiological and related differences between young/small and older/larger WBE.  
**Table 2.** Arguments raised against the GOLT: claims by S. Lefevre and associates.  
**Table 3.** Arguments raised against the GOLT: issues regarding gill surface areas.  
**Table 4.** Arguments raised against the GOLT: mistaking cause and effect.  
**Table 5.** Arguments raised against the GOLT: different definitions of anabolism and catabolism.  
**Table 6.** Arguments raised against the GOLT: spawning vs. growth and vice-versa.  
**Table 7.** Theoretical vs empirical predictions of weight at first maturity.  
**Table 8.** Arguments raised against the GOLT: miscellaneous, mainly normative arguments.

#### LIST OF ACRONYMS AND SYMBOLS<sup>5</sup>

- °C:** degree Celsius (or centigrade); a measure of temperature;  
**A:** ratio of gill surface area (or metabolic rate) at  $W_{\infty}$  over the gill surface area (or metabolic rate) at  $W_{\infty}$ ;  
**ATP:** Adenosine triphosphate, the major supplier of 'energy' in living bodies;  
**b:** exponent of a length-weight relationship (LWR) of the form  $W = a \cdot L^b$ ;  $b \approx 3$  is very common;  
**C.I.:** confidence interval (here: 95%);  
**D:** a convenience parameter, i.e.,  $D = b \cdot (1-d)$ ;  
**d:** exponent of the relationship linking the rate of anabolism (H) and body weight (W);  
**d<sub>G</sub>:** exponent of the relationship linking the gill surface area of WBE and their body weight (W);  $d_G$  causes  $d_{O_2}$  and d;  
**d<sub>O<sub>2</sub></sub>:** exponent of the relationship linking the oxygen supply to the body ('metabolic rate') to its weight (W);  $d_{O_2}$  is caused by  $d_G$  and causes d;  
**dP:** difference between the oxygen partial pressure on either side of a membrane;  
**dw/dt:** rate of growth in weight;

<sup>3</sup> This highlighted section was removed from the published version to shorten its abstract.

<sup>4</sup> Not included in submitted and published versions.

<sup>5</sup> Not included in the submitted version.

- G:** gill surface area; respiratory surface area in WBE lacking gills;
- g:** gram, a measure of weight;
- GOLT:** Gill-Oxygen Limitation Theory;
- H:** coefficient of anabolism (as defined by the GOLT);
- k:** coefficient of catabolism (as defined by the GOLT);
- K:** growth coefficient (of dimension  $\text{time}^{-1}$ ) of the VBGF, expressing how fast the asymptotic length or weight is approached; note that  $K = k/3$ ;
- K<sub>I</sub>:** food conversion efficiency, i.e., individual growth during a time interval/food consumed during that interval;
- L<sub>∞</sub>:** asymptotic length, or mean length attained after an infinitely long time by a WBE of a given population whose growth is described by the VBGF;
- L<sub>m</sub>/L<sub>∞</sub>:** 'reproductive load';
- L<sub>m</sub>:** mean length at first maturity;
- L<sub>max</sub>:** the maximum observed length of a fish or other WBE in a given population;
- L<sub>t</sub>:** mean length at age *t* (e.g., as predicted by the VBGF);
- LWR:** length-weight relationship of the form  $W = a \cdot L^b$ ;
- O<sub>2</sub>:** Oxygen;
- OCLTT:** O<sub>2</sub> and capacity limitation of thermal tolerance; a hypothesis developed by the physiologist H.-O. Pörtner, and which shares some features with the GOLT.
- Q:** oxygen uptake by (or oxygen *supply* to) a WBE; this conceptually different from its *demand* (see text);
- t:** time, or age of a WBE;
- t<sub>0</sub>:** the (mostly negative) age WBE would have had at  $L = 0$  or  $W = 0$  if they had always grown according to the VBGF;
- U:** Krogh's diffusion constant (see Equation 2);
- VBGF:** von Bertalanffy Growth Function;
- W:** weight, here taken as equivalent to mass;
- W<sub>∞</sub>:** asymptotic weight, or mean weight attained after an infinitely long time by a WBE whose growth is describe by the VBGF;
- WBD:** Water-Blood Distance, i.e., the thickness of the tissue between the outside water and the blood;
- WBE:** Water-breathing Ectotherm, of water-breathing fish and invertebrates;
- W<sub>i</sub>:** weight at the inflexion point, i.e., where the growth rate ( $dw/dt$ ) is highest;
- W<sub>m</sub>:** mean weight at first maturity;
- W<sub>t</sub>:** mean weight at age *t* (e.g., as predicted by the VBGF).

## INTRODUCTION

### The need for a theory

While there is clear evidence that the generation of scientific data has been increasing exponentially since 1600, and that the rate of growth accelerated after WWII (Bornmann and Mutz 2015), it is not as clear that our knowledge about the natural world has also increased this fast. This may be because<sup>6</sup> to make sense of scientific data and their patterns, robust theories are required which can either provide an interpretative context for new findings or which cannot, in which case the new findings are either problematic or very interesting (Popper 2005).

However, a situation can emerge in which the practitioners of a given scientific discipline have forgotten how, “*odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service!*” (Darwin 1861). They not only publish articles that test nothing, but in the process appear to have become utterly theory-adverse and argue that the organisms or processes they study are so unique that only their *ad hoc* hypotheses can explain the data they generate.

This attitude is very problematic at a time when we, as a scientific community, are challenged to devise novel ways to protect marine and freshwater biodiversity threatened by overfishing, pollution, habitat modification (Boonstra et al. 2015; Reid et al. 2019), by global changes with its attendant ills, ocean, and freshwater warming (Pinsky 2013; Cheung et al. 2013a, 2013b; Liang et al. 2018; Schindler 1997), acidification, and deoxygenation (Bednaršek et al. 2016; Breitburg et al. 2018; Prince and Goodyear 2006).

This is why the Gill-Oxygen Limitation Theory (GOLT) is being introduced, and why the case is made for the GOLT to be seriously examined. Despite it being counterintuitive to the air-breathing mammals that we are, the GOLT is coherent in its content and the range of the phenomena that it claims to explain. A critical examination should replace dismissals based on untenable arguments, which have created the strange situation wherein the GOLT has become controversial, e.g., in internal deliberations of the Intergovernmental Panel for Climate Change (W.W.L. Cheung, IOF/UBC, pers. comm.)<sup>7</sup> even before it has become widely known.

To counter the tendency to **knock down**<sup>8</sup> proposed hypotheses (rather than *test* them), in this paper, after a brief presentation of the key tenets of the GOLT, a detailed presentation of the objections to the theory will be provided. Many of these objections do not pass simple tests of scholarship (e.g., they cite things that were not stated), strong evidence, or logic. Thus, the intention of the paper is primarily to clear the field of frivolous arguments, such that a serious debate can begin.

This contribution is also an attempt to change the minds of aquatic biologists about notions most think are obvious but which are incompatible with the fact that, for water-breathing ectotherms (WBE, i.e., most fish and aquatic invertebrates), life is shaped more by the distribution and concentration of dissolved oxygen and the temperature of the water surrounding them than by the availability of food, which is more important for endotherms (birds and mammals). The tendency to project our mammalian

<sup>6</sup> This highlighted section was removed from the published version (Pauly, D. 2021. The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Science Advances*, 7: eabc605) at the request of a reviewer (see the last section of this piece, i.e., RESPONSE TO REVIEWERS. In the following pages, highlighting refers mainly to formulations that were softened.

<sup>7</sup> Deleted from *Science Advances* version, as this journal does not allow for personal communications.

<sup>8</sup> Softened to ‘discredit.’

biases onto WBE has resulted in a misunderstanding of many features and life histories of fish and marine invertebrates.

These are strong claims, especially since the framework of an alternative vision of the lives of WBE, i.e., the GOLT (Pauly 1981, 2010) has, to date, not found many adherents. Recent extensive (Pauly 2019c) and shorter elaborations (Pauly and Cheung 2017a; Pauly 2019a) of the GOLT exist. Each explains parsimoniously a number of biological features, behaviors and experimental results on WBE that mostly have no other (simple) explanations (Table 1).

The Gill-Oxygen Limitation Theory (GOLT) presents a unifying theory-- based solely upon first principles and their corollaries-- that explains growth and related phenomena in both marine and freshwater fishes and aquatic invertebrates. It should replace several *ad hoc* hypotheses common in ichthyology, limnology and marine biology

### How the GOLT defines growth

The GOLT builds on concepts developed by von Bertalanffy (1934, 1938, 1949, 1951, 1960, 1964), who built on earlier work by Pütter (1920), and whose main feature is that organic growth ( $dw/dt$ ) can be seen as the difference between two processes, i.e.,

$$dw/dt = Hw^d - kw \quad \dots 1)$$

where the two terms on the right are usually called anabolism and catabolism, respectively, and where  $d < 1$ . That is, an increase of body mass ( $dw/dt$ ) is the difference between body mass that is newly ( $Hw^d$ ) synthesized and the body mass ( $kw$ ) that becomes unusable. As simple as Equation (1) seems to be, considerable confusion exists regarding the definition of the two terms on the right.

In the GOLT, anabolism refers to the synthesis of body tissues (including gonad material); the process requires an amino acid pool to provide building blocks for proteins and ATP to provide the 'energy' required for synthesis. Here, ingested food is not 'energy'; rather, food is oxidized (i.e., 'burnt') to generate ATP, which may be considered to be 'energy' (Cox and Nelson 2008).

Thus, the process of anabolism requires oxygen, which must enter the body through some permeable surface. Therefore, in fish, the parameter  $d$  in Equation (1) is equivalent to the exponent ( $d_G$ ) of a relationship linking gill surface area ( $G$ ) to body weight of the form  $G = a \cdot W^{d_G}$ , and which determines how much anabolism can occur. For this reason, the oxygen consumption of fish scales with body weight with a factor ( $d_{O_2}$ ) should be and is near  $d_G$  (De Jager and Dekker 1975). As we shall see below,  $d_G$  – and hence  $d_{O_2}$  as well – drops below 1 once fish have grown past a certain body mass (and past metamorphosis in teleosts).

In contrast, catabolism, as defined in the GOLT, is directly proportional to body weight because it consists of the spontaneous denaturation of the proteins and other molecules contributing to that weight. Protein molecules can fulfill their function (e.g., as enzymes) only if they maintain their native quaternary structure. In the long term, they cannot maintain that structure because, notably, they are constantly subjected to Brownian motion (Brandts 1967; Goldberg and St. John 1976; Hawkins 1991). Thus, all such molecules have half-lives, which become shorter when temperature increases (Somero 1995). Spontaneous loss of quaternary structure by molecules occurs throughout the body and requires no 'energy' (beyond the kinetic energy of Brownian motion). Thus, catabolism as defined in the GOLT

requires no oxygen either. It is therefore weight-proportional even if the process of denaturation proceeds at different rates in different molecule types because the ratios between molecule types would not change much in the course of ontogeny (at least past the larval stage).

Integrating the differential equation in (1) is straightforward, and when  $d$  in that equation is set equal to  $2/3$ , this yields the von Bertalanffy Growth Function (VBGF), which for length has the form:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad \dots 2)$$

where  $L_t$  is the mean length (however measured) at age  $t$  of the WBE in question,  $L_\infty$  their asymptotic length, i.e., the mean length they would attain after an infinitely long time,  $K$  a growth coefficient (of dimension  $\text{time}^{-1}$ ) and  $t_0$  is the (usually negative) age they would have had at a length of zero if they had always grown in the manner predicted by the equation (which they usually have not; see e.g., Pauly 1998). Combining this equation with a length-weight relationship (LWR) of the form  $W = a \cdot L^b$  leads to a version of the VBGF that can express growth in weight, i.e.

$$W_t = W_\infty(1 - e^{-K(t-t_0)})^b \quad \dots 3)$$

where  $W_\infty$  is the mean weight attained after an infinitely long time, and all other parameters are as defined previously.

When  $d \neq 2/3$  but is still  $<1$ , the integration of Equation (1) yields what may be called the generalized VBGF; for length, this is

$$L_t = L_\infty(1 - e^{-KD(t-t_0)})^{1/D} \quad 4)$$

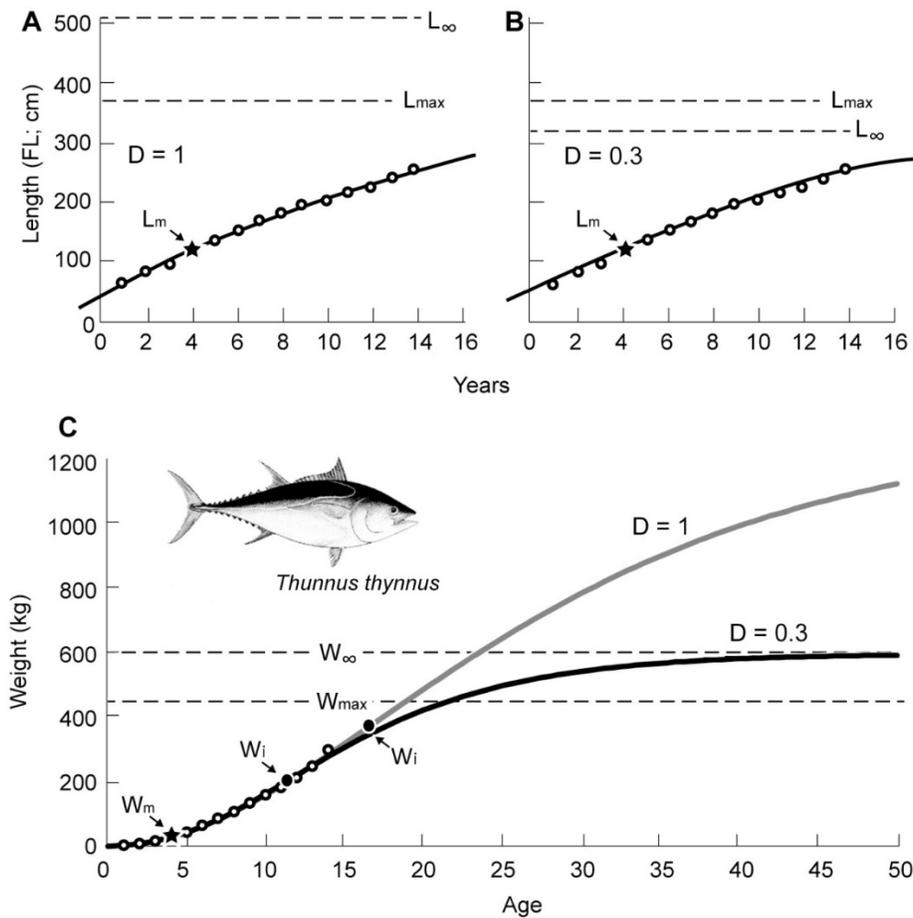
where  $D = 3(1-d)$ . Note that here, the exponent of the LWR is equal to 3, as is (nearly) the case in the overwhelming majority of fish (Froese 2006; see also [www.fishbase.org](http://www.fishbase.org)) and invertebrate species (see [www.sealifebase.org](http://www.sealifebase.org)).

For weight, the generalized VBGF is

$$W_t = W_\infty(1 - e^{-KD(t-t_0)})^{b/D} \quad 5)$$

where  $D = b(1-d)$ , which makes Equation (5) more versatile than Equation (3).

When  $d = 0.75$  (and thus  $D = 0.75$ ), Equation (4) is equivalent to the “general model” of West *et al.* (1997) which, however, is not general because the value of  $d$  does vary between taxa (Pauly 1981, 2019). Note that whether one uses the standard VBGF or its generalized versions (including versions which account for ubiquitous seasonal growth oscillations; Pauly 2019c), a reasonably good fit to length/age data pairs is obtained, including estimates of asymptotic lengths ( $L_\infty$ ) that are close to observed maximum lengths ( $L_{max}$ ). Important exceptions are tuna and other large WBE with relatively high values of  $d$  (i.e.,  $0.90 \leq d \leq 0.95$ , and hence  $0.3 \geq D \geq 0.15$ ). In such cases, the estimates of  $L_\infty$  that are obtained are much higher than  $L_{max}$  (Figure 1).



**Figure 1 Different forms of the von Bertalanffy growth function.** The VBGF fitted to bluefin tuna (*Thunnus thynnus*) length-age data pairs of Sella (1929). **A:** The standard VBGF (Equation 2), which assumes  $d = 2/3$ , and hence  $D = 1$  (which thus can be omitted). **B:** The same length-at-age data, fitted by Equation 4, with  $b = 3$  and  $D = 0.3$ , corresponding to  $d = 0.9$  (Muir and Hughes 1969). **C:** Two versions of the generalized VBGF for weight (Equation 5), with  $D = 1$  and  $D = 0.3$ , with weights converted from lengths using  $W = 0.0182 \cdot L^3$  (from FishBase), where  $W$  is in g, and (fork) length is in cm. Note the position of  $L_m$  (from Corriero *et al.* 2005) relative to  $L_{max}$  and  $L_{\infty}$  and  $W_m$  relative to  $W_{max}$  and  $W_{\infty}$ , and that the weights at inflection points of the growth curves ( $W_i$ ) are much higher than  $W_m$ , i.e., that bluefin tuna growth is still accelerating when they reach maturity.

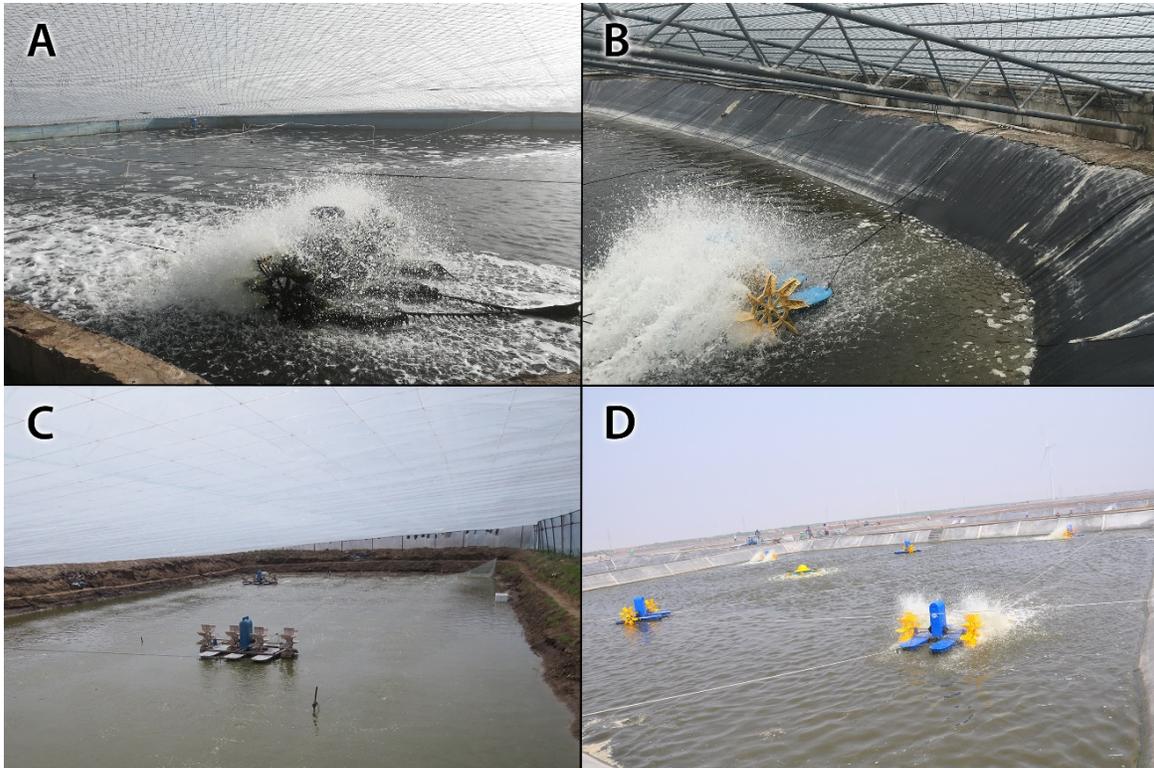
### The scope of the GOLT

If one can agree with the above definitions and constraints, the various predictions of the GOLT (Table 1) follow logically, while being empirically verified. Indeed, most natural scientists other than some fish physiologists, once informed of the points above, tend to accept the elements of Table 1 as straightforward corollaries. This is important given two massive challenges related to the respiration of WBE in an age of global warming, i.e., the accelerating deoxygenation of the oceans and freshwater bodies and the increasing role of aquaculture in supplying global seafood markets.

Studying the effect of temperature increases and deoxygenation requires a robust theory of why WBE, particularly old/large (and hugely fecund) individuals, are as sensitive as they are to such changes (see, e.g., Johansen *et al.* 2014; Messmer *et al.* 2017; Rodnick *et al.* 2004). Similarly, for the insights of physiologists to be able to assist in increasing aquaculture production, the theory that guides them has to be compatible with the fact that the aquaculture industry spends large sums to aerate the ponds in which WBE are raised (Figure 2).

**Table 1.** Some physiological and related differences between young/small and older/larger WBE of the same species, with item number (1) being the cause of all others. 'Relative' stands for 'per unit weight'.

No.	Young/small WBE	Older/larger WBE	Source(s)
1	Relative gill surface area is high.	Relative gill surface area is low.	See text
2	Thus, relative O <sub>2</sub> supply is high.	Thus, relative O <sub>2</sub> supply is low.	See text
3	Growth in weight is accelerating	Growth in weight is decelerating	See Figure 1C and 3B
4	High temperatures and thus shallower habitats are preferred.	Low temperatures and thus deeper habitats are preferred.	Heincke (1913); Messmer et al. (2017).
	In <i>C. macularius</i> , a temperature of 30 °C is “optimal only up to an age of 22-28 weeks”.	In older <i>Cyprinodon macularius</i> , “the temperature optimum shifts gradually to 22-26 °C”.	Kinne (1960); see text for other species.
5	Relative food consumption is high.	Relative food consumption is low.	Palomares and Pauly (1998)
6	Food conversion efficiency is high.	Food conversion efficiency is low, trending toward zero.	Gerking (1952, 1975); Pauly (1986)
7	Young adult fish may skip spawning, but spawn during the next season.	Adults do not skip spawning; large adults may spawn repeatedly in a spawning season.	Morbey and Shuter (2013) ; Rideout et al. (2005); Jørgensen et al. (2006); Pauly (2019c)
8	Enzymes in tissues are mainly oxidative.	Enzymes in tissues are mainly glycolytic.	Davies and Moyes (2007); also see text.
9	Fish otoliths contain proteinaceous substances.	The external layers of fish otoliths are purely crystalline.	Morales-Nin (1986a, 1986b)
10	Clear daily ‘rings’ are formed in otoliths of fish and statoliths of invertebrates.	Daily ‘rings’ in otoliths or statoliths are blurred, later disappear altogether.	Pannella (1971, 1974); Ralston (1985); Pauly (2019c)
11	Extensive seasonal migrations are not undertaken.	Extensive, often temperature-driven seasonal migrations are undertaken	Pauly and Keskin (2017);
12	Fat content is low	In fish, fat content is high, particularly when seasonal temperature oscillations are high.	Shul'man (1974), Pauly (2019c, p. 79-81)



**Figure 29.** Aerating systems add oxygen to the water of fish farming ponds. Such systems are common wherever intensive aquaculture is practiced. **A-C:** Photos by Mr. You Zhou, Ningbo University, 2019; near Ningbo, China (by permission); **D:** Photo by Ms. Liping Zhang, Lijin Ocean and Fishery Bureau, July 2019; near Dongying, China (by permission).

## COUNTERARGUMENTS TO THE GOLT

### The terms of the debate

So, what are the objections? They are presented here in a series of tables briefly stating the objections and their sources and providing a brief refutation, along with a reference to one or several articles presenting the evidence cited as refutation.

Each table addresses a different class of arguments, i.e.:

- I. The gill surface area of WBE either does (or could) grow as required to keep up with a growing volume, i.e., with body weight;
- II. Some WBE contradict key tenets of the GOLT ( $d_G > 1$ , or large size in tropical waters);
- III. What is the cause of the decline in metabolic rates, and what is the effect?
- IV. Different definitions of ‘anabolism’ and ‘catabolism’; and
- V. Miscellaneous discipline-related and/or philosophical objections.

### Gill lamellae versus book pages

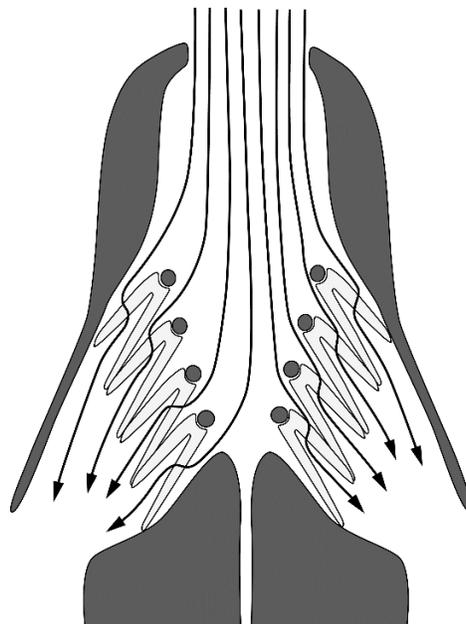
The first group of objections (Table 2) is also the most important. In fact, if any of these objections were tenable, then the GOLT would be eviscerated. These objections refer to gills functioning as a surface, and thus being limited by the geometric constraint that they cannot keep up with the 3-dimensional growth of the bodies that they supply with oxygen.

<sup>9</sup> This figure was deemed “gratuitous” by a reviewer, and was replaced by two references on the need for fish pond aeration.

Some authors believe that this is a simple problem, i.e., that if their gill surface area is too small, WBE can simply enlarge it, i.e., grow bigger gills. However, these authors do not perceive the underlying geometric problem. So far, only Lefevre et al. (2017) have tackled this problem head-on, based on two arguments, and stated that:

1. The surface area of gills is similar to the surface area of the pages of a book, which can increase in proportion to its volume. Thus, gill surface area can always keep up with body weight; and
2. The oxygen requirement of fish declines as they grow older/larger, and thus, these fish do not need to maintain the gill surface area/body weight ratio occurring in young/small fish.

The *raison d'être* of books is to be read, i.e., opened. The transfer of knowledge from their pages through the readers' eyes to the brain is analogous to the transfer of oxygen from the water flowing past the gills to the blood of a WBE. In a 3-dimensional context, only one layer of paper can be read at a time. Similarly, despite appearances to the contrary, in fish, only one 'layer' of gill lamellae stands in the path of a flow of water across gills (Figure 3).



**Figure 3. Schematic representation of water flows across the gills of a fish.** Note that once water has flown between lamellae (which extracted most of  $O_2$  it contained), there is no point for this water to flow through another set of lamellae. Hence gills function as a surface, even though their arrangement in 3-D space may suggest otherwise.

Given the efficiency of gills at extracting oxygen from flowing water, there would be little to be gained by putting subsequent layers (i.e., 'pages') of lamellae behind the first one. Hence, gill surface area, as complex as it may appear, functions like a sieve, perpendicular to the water flowing through the gill chamber. This implies that in a WBE, gill surface area cannot grow in 3 dimensions and thus cannot keep up with the 3-dimensional body that it supplies with oxygen.

The entire argument of Lefevre et al. (2017), who claim that the GOLT assumes gills to behave like spheres, is **strange**. It becomes even **stranger** when one notes that their argument that WBEs are able to maintain the same gill surface area/body weight ratios as their weight increases is backed up with only two **astonishing** references. The first is a contribution on the gill area of spangled perch, *Leiotherapon unicolor*, with a scaling factor of  $d_G=1.04$  (Gehrke 1987) and, second, the bivalve, *Solemya velum*, with

reported scaling factors of 1 between gill surface area and gill mass and  $d_G = 0.85$  between gill surface area and body weight (Scott 2005).

The choice of the Gehrke (1987) citation is **suspicious**, as there are several reviews, jointly covering over 150 species, showing that typical scaling factor for fish gill surface area range from  $d_G = 0.6$  to  $0.9$  (Muir 1969; Muir and Hughes 1969; Hughes 1970; De Jager and Dekker 1975; Palzenberger and Pohla 2002). Indeed, for “medium-sized” fish (200 g), De Jager and Dekker (1975), based on data from well over 200 papers covering 121 fish species, computed a mean value of  $d_G = 0.811$ , very close to their mean estimate of the scaling factor of metabolic rate vs. body weight,  $d_{O_2} = 0.826$ , which confirmed the classical results of Winberg (1960). They then averaged these two values to obtain a robust estimate of  $d_G = d_{O_2} = 0.82$ , assuming that  $d_G$  causes  $d_{O_2}$ . This was based on Fick’s Law of Diffusion, which states that the total amount of oxygen which can diffuse into the circulatory system of a WBE is

$$Q = dP \cdot U \mu G \cdot WBD^{-1} \quad \dots 6)$$

where  $Q$  is the oxygen uptake ( $\text{ml} \cdot \text{h}^{-1}$ ). Here,  $dP$  is the difference between the oxygen partial pressure on either side of the membrane (in atm);  $U$  is Krogh’s diffusion constant, that is, the amount oxygen (in ml) which diffuses through an area of  $1 \text{ mm}^2$  in one minute for a given type of tissue (or material) when the pressure gradient is one atmosphere of oxygen per  $\mu$  (micron);  $G$  is the surface area of the gills (total area of the secondary lamellae); and  $WBD$  is the Water-Blood Distance, or the “water-capillary distance” of Graham (2006), i.e., the thickness of the tissue between water and blood in  $\mu$  (De Jager and Dekkers 1975).

By contrast, Lefevre et al. (2017) argue that, while fish could grow gill surface area such that  $d_G = 1$  is maintained, they do not need to do so because, they suggest, *the activity of oxidative enzymes falls with body mass in fishes (Davies and Moyes 2007)*. This argument is problematic, for two reasons, the first obvious, the second less so:

- i) It begs the question why growing fish -- if not forced by a declining relative  $O_2$  supply -- should have evolved to reduce their  $O_2$  consumption and shift from relying on oxidative to glycolytic enzymes, the latter catalyzing metabolic processes that are far less efficient than the former; and
- ii) It attributes to fish biological features (i.e., gill lamellae) that they could multiply but whimsically choose not to, making its claims about fish physiology unfalsifiable. Thus, Lefevre et al. (2017) can assert that  $d_G < 1$  in the overwhelming majority of fish species so far studied does not refute their claim that gill surface areas can grow according to  $d_G = 1$ . At the same time, single (and questionable) cases with  $d_G = 1$  (e.g., Gehrke 1987) ‘confirm’ that gill surface area can keep up with body weight.

Argument (i) mistakes cause and effect (Pauly and Cheung 2018). The physiologists who documented that the preponderance of oxidative enzymes in the tissues of small/young fish is replaced in large/old fish by a preponderance of glycolytic enzymes were well aware that this shift contradicts standard hypotheses about fish physiology (Burness *et al.* 1999; Davies and Moyes 2007; Norton *et al.* 2000; Somero and Childress 1980). Thus, Somero and Childress (1980) titled the report of their findings: “A violation of the metabolism-size scaling paradigm: activities of glycolytic enzymes in muscles increase in larger size fish”. Note, however, that this feature is not only compatible with the GOLT, but is one of its inescapable consequences.

Argument (ii) evidently points to Karl Popper's 'decision criterion,' that claims which cannot be falsified in principle are not part of science (Popper 2002).

Regarding the bivalve *Solemya velum*, the fact that Scott (2005) reports a value of  $d = 1$  for the scaling factor between gill surface area and gill mass misses the point. What matters here is the scaling factor between gill surface area and the weight of the entire body, which at  $d_G = 0.85$  (Scott 2005) is relatively high for a bivalve, but well under 1, as required by the GOLT. Other bivalves have values of  $d_G$  and  $d_{O_2}$  ranging between 0.5 and 0.8 (see Vakily 1992) and thus suffer from "ontogenic anaerobiosis" (Lutz and Roads 1977. An exception may be the giant clams of the family Tridacnidae, which are phototrophic and thus produce their own oxygen (Klumpp and Griffiths 1994).

Note that despite the argument that gill surface area grows under the constraints of a surface, it does not mean that this growth should be proportional to length squared, i.e., isometric growth, with  $d_G = 2/3$ , though von Bertalanffy (1964) thought so. Indeed, he erroneously referred to instances of  $2/3 < d < 1$  as growth that is "intermediate between surface and weight proportionality".

However, values of  $d_G \approx 0.67$  seem to occur only in very small fish such as the guppies von Bertalanffy (1951, 1964) used to illustrate his theory of growth. An even lower estimate of  $d_G = 0.60$  was obtained for *Mistichthys luzonensis*, in which an adult does not reach more than 25 mm and a weight of about 0.5 g (Te Winkel 1935; Pauly 1982). The other extreme appears to occur in bluefin tuna (*Thunnus thynnus*), in which a well-documented value of  $d_G = 0.90$  for adult specimens has been published (Muir and Hughes 1969).

### **The matter with exceptions, or exceptions matter**

As stated above, the GOLT is falsifiable, i.e., it would be refuted if well-founded estimates of  $d_G \approx 1$  or worse  $d_G > 1$  were shown, for example, via a meta-analysis, to routinely occur in the *adult* stages of WBE (and excluding air-breathing taxa).

So far, credible estimates of  $d_G \gg 1$  have been found to occur only in teleost larvae (De Sylva 1974; Bochdansky and Legget 2001; Oikawa and Itazawa 1985), while estimates of  $d_G \approx 1$  have been reported from juvenile fish transiting from the high  $d_G$  values in larvae to the values of  $d_G < 1$  typical of the adults (Bochdansky and Legget 2001; Oikawa and Itazawa 1985).

There will be a tendency for published estimates of  $d_G$  to be on the high side when, as is often the case, only the small representative of a species is studied. In the case of Gehrke (1987), the published estimate of  $d_G = 1.04$  pertained to juvenile fish reaching at most 30 % of the maximum weight typically attained by the species in question (see Table 3). This was similar to the specimens of icefish (*Chaenocephalus aceratus*) collected by Holeton (1976), who also published a value of  $d_G \approx 1$  (after correction from 1.09 due to the inappropriate use of a 'Type II' regression; Ricker 1973). Pauly (2018) discusses a few more cases of this sort.

Thus, while this may appear as special pleading, in view of their theoretical importance, it may be recommended that  $d_G$  values should preferably pertain to adults (i.e., larger than a third of the maximum weight typically reached by the species in question). In the future, it would be fair to expect criticisms of the GOLT to take account of existing meta-analyses rather than search for isolated estimates that differ from the results of meta-analyses but seem to support one's point.

Table 2. Arguments raised against the GOLT: claims by S. Lefevre and associates

No	Arguments	Refutations
2.1	Fish could, if needed, grow new gill lamellae to maintain the ratio gill surface area/body weight constant. However, they don't need to, i.e., <i>“gill surface area can scale proportionally with body mass, and if it does not do so, it is because oxygen demands are reduced with body size...”</i> (Lefevre et al. 2017, particularly their Figure 1A).	It is actually impossible, <b>as any book on geometry will confirm</b> , for gill lamellae, which must function as 2-D surfaces (Figure 3), to keep up with the growth of the 3-D bodies they supply with O <sub>2</sub> (Pauly and Cheung 2017b). Also, the suggestion that large fish could increase their gill surface if they wanted, but somehow don't, makes the claims of Lefevre et al. (2017) effectively unfalsifiable.
2.2	<i>“Weatherley and Gill (1987) [...] had already concluded that there was no evidence that capacity for gas exchange or gill surface area could limit growth performance in fishes...”</i> (Lefevre et al. 2017).	Weatherley and Gill (1987) actually wrote that: <i>“[t]here is little doubt that the relative size of the gills may be important in influencing growth and size of fish, but Pauly's claim that his hypothesis 'offers a single, simple explanation to a whole set of growth-related phenomena...' seems extravagant.”</i> Thus, Weatherley and Gill (1987) disputed the <u>scope</u> of gill limitation, not the idea itself.
2.3	Here is another version of the above citation: <i>“...Blier et al. (1997) had already concluded that there was no evidence that capacity for gas exchange or gill surface area could limit growth performance in fishes, and their analysis remain valid today”</i> .	No, it is no longer valid. Following an exchange with P.U. Blier, he agreed that <i>“under natural conditions, particularly when fish have to move at the same time as they feed or digest, it is very probable that aerobic scope, i.e., the oxygen supply through the gills, acts as a limiting factor”</i> (pers. comm., March 16, 1998, translated from French; Pauly 2010, p. 150).
2.4	Lefevre et al. (2018) asserted that <i>“Pauly and Cheung [2017a] seem to suggest that when the gill area grows, it will eventually deplete the water of oxygen, and more surface area will be useless. However, an increase in body and gill size will of course coincide with a proportional increase in water and oxygen movement, so a doubling of surface area effectively doubles the capacity for oxygen uptake”</i> .	They didn't. Pauly and Cheung (2017a) suggested that the growth of gill surface area can proceed only by making the gill 'sieve' higher and wider (2-D) but not deeper (3-D), as this would put the new gill lamellae <i>behind</i> the first 'layer' of lamellae. Lamellae that were so placed would indeed be “useless”, as the first layer of lamellae would reduce the water flowing across the gills of O <sub>2</sub> , leaving the second layer (and any subsequent layer) with little to nothing to do (see Figure 3, and Figure 2.14 in Pauly 2019c).
2.5	<i>“...a fundamental pillar of the GOLT – that geometrical constraints hinder the gills and their surface from growing at the same pace as the fish body – is not supported by existing data and knowledge”</i> . (Lefevre et al. 2018).	On the contrary, the GOLT has the support of an immense amount of data, stemming from numerous anatomical studies, physiological experiments and ecological surveys. The points are that this evidence had never been assembled into the coherent picture that the GOLT provides, and that this picture requires a rethinking of old assumptions.

Table 3. Arguments raised against the GOLT: issues regarding gill surface areas

No	Arguments	Refutations
3.1	Leferve et al. (2017) assert that “in morphometric studies where both total lamellae area and gill mass have been measured, a linear scaling relationship (scaling exponent of 1.0) has been found in fishes (Gehrke 1987) as well as bivalves (Scott 2005). Consequently, there is no geometric constraint that prevents an increase in body size (mass or volume) from being accompanied by a corresponding increase in gill mass and hence respiratory surface area. In other words, gill surface area can scale proportionally with body mass and, if it does not do so, it is because oxygen demands are reduced with body size”.	Several meta-analyses of gill surface area covering hundreds of fish species exist; they report scaling exponents ranging overwhelmingly from 0.7 to 0.9 (e.g., De Jager and Dekker 1975; Palzenberger and Pohla 1992 and see text) and mention the difficulties in obtaining accurate values when a small range of body sizes are included (see also Hughes 1984). Thus, the value of 1.04 reported by Gehrke (1987) is not representative of fish in general and a likely overestimate, due to the largest specimen considered being only 12% of the maximum weight reported in <i>Leiopotherapon unicolor</i> (see <a href="http://www.fishbase.org">www.fishbase.org</a> ).  The scaling exponent between gill surface area and bivalve body weight appears to range from 0.51 to 0.80 (Franz 1993; Vakily 1992, Table 5.2), with 0.85 in <i>Solemya velum</i> (Scott 2005). The scaling exponent of 1.0 linking gill surface area to gill mass in <i>S. velum</i> is irrelevant to the O <sub>2</sub> supply to its <i>body</i> . Also note that the last sentence of the argument precludes falsification.
3.2	The presence of very large fish in warm tropical waters, e.g., Goliath groupers ( <i>Epinephelus itajara</i> and <i>E. quinquefasciatus</i> ), sunfishes ( <i>Mola mola</i> ), billfishes and other scombroids, giant manta ray ( <i>Manta birostris</i> ) and especially the largest extant fish, the whale shark ( <i>Rhincodon typus</i> ) refutes the GOLT, which postulates that high temperatures tend to reduce the size of fish (Lefevre et al. 2017). [This issue was a genuine challenge to the GOLT, and its successful resolution (see adjacent column and main text) widened its scope]	Pauly (2019c), following an extensive review of the biology of the species in question, concluded that rather than being invalidated by large fishes occurring in the tropics, the GOLT can be used to classify their response to the challenge that high temperatures pose to their metabolism. Thus, in addition to breathing air, as often occurs in tropical freshwater fishes, three types of increasingly complex adaptations occur, none mutually exclusive: i) Placid behavior, combined with ambush predation (e.g., groupers) or filter-feeding (e.g., whale shark); ii) Yo-yo-type swimming between the warm surface and colder, deeper water layers and feeding mainly near the surface (bluefin tuna, whale shark), or at depth (swordfish, billfish), the latter cases involving heating systems to keep their huge eyes and brain <i>warm</i> ; and iii) Huge anatomical changes from the ancestral fusiform shape, turning the body into a shell around a cavernous mouth and oversized gills (giant manta ray) or a mass of inert jelly surrounding specialized locomotory muscles ( <i>Mola mola</i> ).
3.3	O’Dor and Hoar (2000) believe that squid respire through their skin, and that by having tubular bodies, squid have such large respiratory area that they cannot be O <sub>2</sub> -limited. Also, their changed shape as they grow increases the surface area of their body hyperallometrically.	Squid do not breathe through their skin (Birk et al. 2018), and even if they did, it would not matter, because their body surface (even when multiplied by 2 because of their tubular nature and even after changing from roundish to lanceolate in the course of their ontogeny) is much smaller than that of their gill surface area.
3.4	The demonstrably asymptotic growth of <i>Growing Sealife</i> <sup>TM</sup> plastic squids implies that asymptotic growth does not require a limiting surface (Lipinski and Roeleveld (1990).	A detailed analysis of what occurs in plastic squids which ‘grow’ when placed in water shows that, actually (and surprisingly), it is a surface that limits their growth (Pauly 1998, 2019c).

## TWO MAJOR CHALLENGES TO THE GOLT

### Fish growth vs. reproduction

One of the main issues in ichthyology, though it is not often perceived as such, is the relationship between growth and reproduction. The majority of authors writing on this topic repeat the usual belief that the relationship between growth and reproduction is explained by stating that “the growth of fish slows down upon reaching maturity because their energy is redirected from growth to reproduction”, or a variant of this phrase (Hubbs 1926; van Oosten 1923; Jones 1976; Lagler et al. 1977; Sebens 1987; Day and Taylor 1997; Charnov 2008; Quince et al. 2008). This notion implies a “*biphasic growth*” (Quince et al. 2008) with a rapid growth phase before the length at first maturity is reached and a slower phase thereafter, as illustrated by Figure 4A.

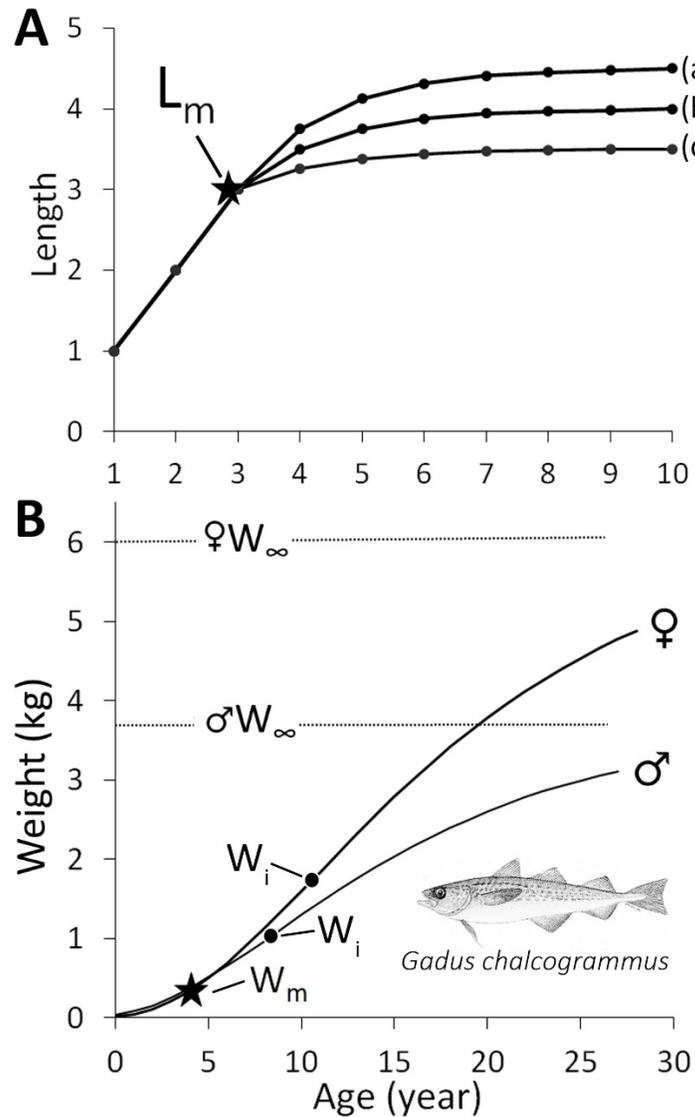
What is not realized, however, is that this phrase, like all statements about complex phenomena, is a hypothesis. Moreover, this hypothesis is contradicted by 4 sets of observations:

1. Fish kept in aquaria and that never mature and spawn also have asymptotic growth curves;
2. In most fish species, the females are larger than the males, although they devote more ‘energy’ to reproduction;
3. Growth in weight is more rapid after maturity is reached than before, and
4. Mean length at first maturity correlates tightly with the maximum length that can be reached in a given environment.

Regarding item (1), many of the salt or freshwater fish kept by home aquarists never mature and spawn. Yet, even though they are fed *ad libitum*, they stop growing at some point. Also, triploid and thus sterile fish exhibit growth patterns largely similar to those of their diploid brethren (Maxime 2008). This should suffice to kill the notion that it is reproduction that causes growth to cease. However, it has become a zombie idea: it does not die.

Similarly, regarding item (2), in over 80% of fish families where females and males look alike, it is the females that eventually reach larger sizes (Figure 4B), even if this growth dimorphism can become attenuated in certain circumstances (Morbey 2018). This strong female dimorphism should lead to a rethink of the notion that the cost of reproduction causes growth to decline. However, some authors, when confronted with this evidence, have doubled down and suggested that males have the higher reproductive cost.

One such case was Ursin (1967; see Table 5, No. 5.2). Also, Marshall & White (2019) suggested, in an effort to refute Pauly (2019b), that males had the higher reproductive effort, citing in support of this claim a figure from an unpublished thesis that did not even compare male and female reproductive *output* (see Table 6, No. 6.2). In reality, females are, by definition, the sex with the higher reproductive output, which also can be shown empirically in almost all groups of animals reproducing sexually (see, e.g., review by Parker et al. 2018). There are a few exceptions (e.g., parental care by male seahorse), but they are not pertinent here.



**Figure 4. Two views of the relationship between size at first maturity and maximum size.** **A:** the traditional view, where 'linear' growth slows down when length at first maturity ( $L_m$ ; black star) is reached, with growth then continuing at a reduced pace depending on circumstances (i.e., a, b or c; redrawn from Quince et al. 2008). **B:** a more appropriate but uncommon view, with growth expressed as change in body weight (in line with Equation 1). This shows not only that weight at first maturity in females and males ( $W_m$ ; black star) is reached when growth is still accelerating (i.e.,  $W_m < W_i$ , the inflexion point of the curve), but also that females grow faster and reach larger weights than the males despite investing more in reproduction (see also text and Table 6). Graph based on length growth parameters, a length-weight relationship and lengths at first maturity for Alaska pollock (*Gadus chalcogrammus*) in FishBase ([www.fishbase.org](http://www.fishbase.org)), which contains hundreds of similar data sets.

Table 5. Arguments raised against the GOLT: different definitions of anabolism and catabolism

No	Arguments	Refutations
5.1	Von Bertalanffy's hypothesis of a surface limiting fish growth (which is a key element of the GOLT) is wrong because the absorptive surface area of the gut is not in permanent contact with food. See Beverton and Holt (1957, p. 32), Ricker (1958, p. 196; 1975, p. 224).	Von Bertalanffy (1934, 1938, 1949, 1951, 1960, 1964) did not state that the surface limiting growth was that of the gut. He thought that " <i>the actual surface responsible for growth of an organism is in general unknown</i> " (von Bertalanffy 1938). However, he clearly favored a link to respiration (albeit without explicitly mentioning gill surface area).
5.2	Ursin (1967, p. 2359) suggested that " <i>Apparently, it was overlooked that although catabolic processes are going on all over the body, the necessary oxygen supply has to be introduced through some surface or the other, mainly the gills. With our basic assumption of isometric growth, this 2/3 means that catabolism is proportional to <math>w^{2/3}</math></i> ".	This was not overlooked. In the GOLT, the catabolic processes 'going on all over the body' do not require oxygen. They consist of the (temperature dependent) spontaneous denaturation (=loss of the quaternary structure) of protein molecules. This process is proportional to weight; the denatured proteins must be re-synthesized, which requires ATP and hence O <sub>2</sub> . However, this is part of anabolism, not catabolism.
5.3	Morais and Bellwood (2018) " <i>...anabolism is proportional to the area of the circulatory network rather than to gill surface area (West, Brown and Enquist, 1997)</i> ".	If this were correct, the scaling factor of anabolism to weight in fish and invertebrates would always be 0.75. This, however, is emphatically not the case (Glazier 2006; Pauly 2010, p. 132; Pauly 2019c, p. 140).
5.4	Brander et al. (2013), critique of Cheung et al. (2013a) included: <i>Methodological shortcomings include (i) assimilated consumption (the 'anabolic' part of the growth equation) is assumed to be proportional to oxygen, but oxygen is only a limiting factor for growth not a controlling factor, i.e. it only affects growth if the oxygen concentration is below a critical value (Brett 1979), and the equation is not documented in their reference, which is an unrefereed book</i> ".	Cheung et al. (2013b) wrote that "[w]hile Brander et al. cite Brett (1979) to suggest that oxygen is a limiting factor for growth, and not a controlling factor, there is abundant theoretical and empirical support in the peer-reviewed literature for oxygen being both a limiting and controlling factor for the growth of fish and aquatic invertebrates (Pauly 1981; Peck and Chapelle 2003; Kolding et al. 2008; Pörtner 2010; Pörtner and Peck 2010; Verberk and Bilton 2011; Verberk et al. 2011)".

Regarding item (3), Figures 1C and 4B show that, in fish, the ratio of weight at first maturity ( $W_m$ ) to asymptotic weight ( $W_\infty$ ) is much lower than the corresponding ratio for length ( $L_m/L_\infty$ ), which is frequently not realized because the overwhelming majority of growth curves drawn reflect growth in length (Figure 4A).

From length growth curves, one can indeed get the impression that spawning strongly affects growth, and hence the name "*reproductive load*" for the  $L_m/L_\infty$  ratio (Cushing 1975). However, growth is a process primarily involving mass (see Equation 1), as reflected in weight growth curves. Weight growth curves have marked inflection points in which growth rate ( $dw/dt$ ) is highest (at  $W_i$ ), and thus the question may be asked if  $W_m > W_i$  or, on the contrary,  $W_i > W_m$ . Taking the 2<sup>nd</sup> derivative of generalized VBGF for

weight growth (Equation 5) and setting it equal to zero allows identifying  $W_i$ , where the growth rate changes from increasing to decreasing:

$$W_i = W_\infty(1-(D/b))^{b/D} \quad \dots 7)$$

As may be seen from Figure 1C and Figure 4B, the weight at the inflection point of these curves is higher than the mean weight at first maturity of the population in question (i.e.,  $W_i > W_m$ ). This result, which can easily be reproduced for multiple species of (larger) fish, implies that as fish reach maturity, their growth in weight is still accelerating, which refutes the reproductive load hypothesis.

The question thus arises: if the reproductive load concept does not hold, i.e., if reproduction does not cause growth to decline, what then is the relationship between reproduction and growth in fish, and by extension, in other WBE?

Equation (1) with  $d < 1$  implies that the heavier fish get, the less  $O_2$  per unit weight they will get, which should imply – other things being equal – more frequent occurrences of respiratory stress. All we need to assume, therefore, is the existence of a threshold weight ( $W_m$ ) at which the high frequency of respiratory stress events triggers the hormonal cascade that leads to maturation (Pauly 1984). Thus, one can define

$$A = (W_\infty^{1/b}/W_m^{1/b})^D \quad 8)$$

From which  $W_m = W_\infty(1/A)^{b/D} \quad \dots 9)$

with  $A$  being the ratio of gill surface area (or  $O_2$  supply) at  $W_\infty$  over the gill surface area (or  $O_2$  supply) at  $W_m$  (Pauly 1984, 2019c).

A first estimate of  $A = 1.365$  was obtained by Pauly (1984; and see Figure 5C), whose 95 % confidence interval is C.I = 1.218 – 1.534, as estimated using the method of Fieller (1940) applied to the data of Table S1. These data covered 56 pairs of  $L_m$  and  $L_\infty$  in 34 different fish species ranging from guppies to tuna and raised to the power  $3/(1-d)$ , which here substitutes for weights (see Supplementary Material). Since  $A^{-1} = 0.733$ , combining with Equation (7) and rearranging (see Liang 2021; Supplementary Material) leads to the conclusion that  $d > 0.733$  implies  $W_i > W_m$ ;  $d \approx 0.733$  implies  $W_i \approx W_m$  and  $d < 0.733$  implies  $W_i < W_m$ . Thus, in small fishes, which usually had small values of  $d$  (e.g., 0.6 in the diminutive goby *Mistichthys luzonensis*; Pauly 1982, 2019c),  $W_m > W_i$ , while the opposite,  $W_m < W_i$ , applies to larger fishes (e.g., bluefin tuna, see Figure 1C and 3B).

This also aligns with the result of Froese and Binohlan (2000), who investigated the relationships between  $L_m$  and  $L_\infty$  (with and without additional variables) in 265 fish species in FishBase ([www.fishbase.org](http://www.fishbase.org)), covering 88 Families and 27 Orders, with an average scaling factor of  $\approx 0.9$  emerging. Thus, the simplest of their empirical relationships is:

$$\log(L_m) = 0.898 \cdot \log(L_\infty) - 0.0782 \quad \dots 10)$$

when  $L_m$  and  $L_\infty$  are in cm.

Equation (9) implies that fish with an asymptotic length of 10 cm reach maturity at a length of 6.6 cm, while fish with asymptotic lengths of 100 and 1000 cm reach maturity at 52 and 412 cm, respectively. These values, when converted to weights, are well within the confidence interval of the value of  $W_m$  predicted by Equation 7 (Table 7).

Table 7. Theoretical vs. empirical predictions of weight at fish maturity. Comparing ‘theoretical’ predictions of  $W_m$  based on the GOLT (Equation 9) to the empirical equation of Froese and Binohlan (2000; Equation 10) and their relationship to growth curves’ inflexion point ( $W_i$ ; Equation 7).

#	$L_\infty$ (cm)	$L_m$ (cm)	$W_\infty$ (g) <sup>a</sup>	$d$ <sup>b</sup>	$W_m$ (% of $W_\infty$ ) <sup>c</sup> Equation 10	$W_m$ (% of $W_\infty$ ) <sup>a</sup> Equation 9	$W_i$ (% of $W_\infty$ ) Equation 7
1	2	≈ 2	0.08	0.6	47	46 (34 - 61)	28
2	10	6.6	10	0.7	29	35 (24 - 52)	30
3	100	52	10 <sup>4</sup>	0.8	14	21 (11 - 37)	33
4	1000	412	10 <sup>7</sup>	0.9	7	4 (1 - 14)	34

a) Assuming the length-weight relationship  $W = 0.01 \cdot L^3$ , corresponding to a trout-like (i.e., ‘average’) fish when cm and g and used for L and W, respectively;  
b) Estimated from  $W_\infty$  (g) and  $d \approx 0.6742 + 0.03574 \cdot \log W_{\max}$  in Pauly (1981, 2019c), with  $W_\infty \approx W_{\max}$ ;  
c) The error term corresponds the 95 % confidence interval of  $A = 1.365$ , i.e., 1.218 - 1.534 (see text).

Unfortunately, Equation (9) does not work below 1.3 cm, i.e., it predicts  $L_m > L_\infty$ . Indeed, it can be hypothesized that such small fish are semelparous, i.e., will spawn only once before they die, as documented in minute gobies (Caputo et al. 2003). It doesn’t work either with large semelparous species such as Pacific salmon (*Oncorhynchus* spp.), whose reproductive strategy, however, is a derived trait connected with their diadromous life history (Crespi and Teo 2002).

Finally, regarding item 4 above, there is the huge environmental plasticity of fish, which can manifest itself both in individuals used for aquarium experiments (Kinne 1960; Kolding et al. 2008) and in the wild. Thus, Randall et al. (1993) noted that “*tropical fishes living near the limit of their tolerance for low temperature grow to larger size at such temperatures.*” In such cases, i.e., when the maximum length ( $L_{\max}$ ) or the computed asymptotic length ( $L_\infty$ ) changes, the mean length at first maturity ( $L_m$ ) also changes in the same direction, such that the ratio  $L_m/L_{\max}$  or  $L_m/L_\infty$  remain approximately constant.

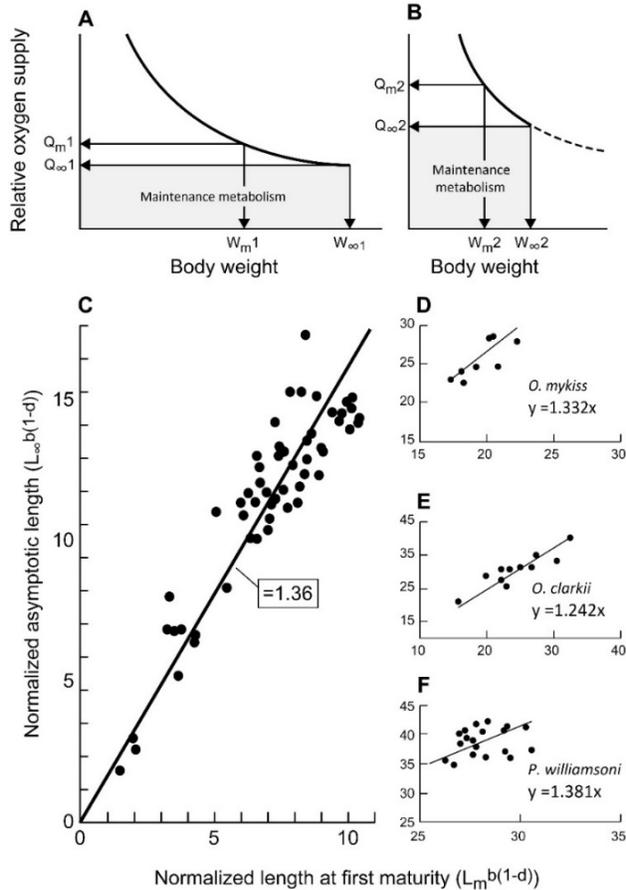
The GOLT provides an explanation for the near constancy of  $L_m/L_{\max}$  or  $L_m/L_\infty$  by postulating that spawning is induced by the same mechanism that also causes growth to decline (i.e., with asymptotic growth). As fish grow in weight, their gills, whose surface area has grown with the scaling factor  $d < 1$ , deliver less O<sub>2</sub> per unit of body weight (Figure 5A).

Thus, growing fish will gradually experience more respiratory stress, and a stress level is finally reached that initiates the hormonal cascade leading to maturation (Bass 1993; Bhattacharya 1999; Pauly 1984). Thus, gonadal products are elaborated, often by using fat accumulated in the summer and fall as energy sources (Shul’man 1974). In spring, the gonadal products are released, the gill surface area/body weight ratio increases again, and summer growth can resume, etc.

With time, however, the fish grow heavier despite generating an increasing reproductive output and the ratio of gill surface area/body weight declining further (Figure 5A). Thus, growth gradually ceases, but life (and reproduction) does not need to, as exemplified by adult whitefish (*Coregonus* spp., Salmonidae) that can live a decade or more after they have ceased to grow (Johnson 1976). The same occurs in a number of coral reef fishes, for example, in the families Acanthuridae and Scaridae (Choat and Axe 1996; Choat et al. 1996).

The threshold gill surface area and hence the relative metabolic rate at which spawning is initiated is similar among different fish families (see Figure 5C and Supplementary Material) because such a critical

threshold would be conserved through evolutionary time. Thus, when the growth of teleosts causes their metabolic rate to drop to about 1.3 to 1.4 times their maintenance metabolic rate (i.e., something that fish can monitor in real time), then sexual maturation is initiated. Figures 5D-F provide further examples of this generalization (see also Meyer and Schill (2020).



**Figure 5. Growing fish mature when their relative gill surface area reaches a threshold.** **A:** In the ontogeny of fish, when their relative gill surface area declines, their oxygen supply declines as well; when the latter reaches 1.3-1.4 times the oxygen supply required for maintenance and routine activities, i.e., as fish increasingly get ‘out of breath’, they initiate the hormonal cascade leading to gonad maturation and spawning. **B:** if the same fish are in a stressful, e.g., warmer environment, causing oxygen demand to be elevated, the same 1.3-1.4 threshold will cause them to mature and spawn at smaller sizes. **C:** The plot, whose 56 point represents the 34 fish species ranging from guppies to tuna (see Supplementary Material) that Pauly (1984) used to estimate the average threshold value of 1.36 (with 95% confidence interval: 1.218-1.534). **D:** the same plot, but for different populations of redband trout (*Oncorhynchus mykiss*); **E:** ditto for Yellowstone cutthroat trout (*Oncorhynchus clarkii*); **F:** ditto for Mountain whitefish (*Prosopium williamsoni*).

Table 6. Arguments raised against the GOLT: spawning vs. growth and vice-versa

No	Arguments	Refutations
6.1	Old/large adult fish do not stop growing because of a declining O <sub>2</sub> supply, but because all their ‘energy’ goes to reproduction (see, e.g., Charnov et al. 2001).	Well-fed, non-reproducing fish (e.g., in aquaria) stop growing at some point. Also, the females of >80% of fish species grow to be larger than the males (see <a href="http://www.fishbase.org">www.fishbase.org</a> and section on ‘Fish growth vs. reproduction’).
6.2	<p><i>“Pauly’s assumption that female fish have higher reproductive output than male fish is unsupported by data. There is no pattern of female fish investing more in reproduction than males in fish (or other water-breathing ectotherm [Parker et al. 2018]”.</i></p> <p><i>Indeed, for the species given by Pauly [2019a], 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). (Marshall and White 2019).</i></p> <p>Note that “figure 5.5” is a plot of ova stages vs. body weight in female (only) black bream (<i>Acanthopagrus butcheri</i>), which does not deal with the female-to-male comparison at hand; it is likely that the authors meant figure 5.6, which compare the gonosomatic index (GSI) of females and male black breams. Also, Ursin (1979), in a context similar to that above, claimed in a funny <i>ad hoc</i> hypothesis that the greater reproductive investment of the female is more apparent than real, i.e., “[t]he male gonad often weighs less than the female gonad. This does not mean smaller spawning loss in males because sperm, consisting almost entirely of DNA, RNA and lipoids, is likely to be the most expensive substance in the fish body.”</p>	<p>Hayward and Gillooly (2011) in a review of 168 mammal, 97 bird, 3 reptile, 100 amphibian, 98 fish and 16 invertebrate species concluded that, overall, the cost of egg production was up to 3 orders of magnitude higher than the cost of sperm production. This confirms Gould (1985, p. 59), who wrote “[s]perm is small and cheap, easily manufactured in large quantities by little creatures. A sperm cell is little more than a nucleus of naked DNA with a delivery system. Eggs, on the other hand, must be large, for they provide the cytoplasm (all the rest of the cell) with mitochondria [...]), and all other parts that a zygote needs to begin the process of embryonic growth...”.</p> <p>Parker et al. (2018) state in their abstract that sessile invertebrates (not “fish”) are “subject mainly to selection on gamete selection and gamete success and so high gonad expenditure is expected in both sexes. [...] We review the literature on gonadosomatic index (GSI) [...], which we use as a proxy for gonad expenditure. [...] When GSI is asymmetric, female GSI usually exceeds male GSI, as least in echinoderms. [...] Intriguingly, higher male GSI also occur in some species [...] of gastropod molluscs”. If these authors had found that male investment routinely matches that of females, they would not have used the word ‘intriguingly’. As for figure 5.6 in G.A. Sarre’s unpublished thesis, it shows male GSI to be occasionally higher than female GSI. However, GSI is an index relating the gonads <i>weight a given time</i> to the weight of the body, not the <i>rate of production</i> of gonad tissue, which alone relates to reproductive costs, which are always much higher in females (see above).</p>
6.3	Brander et al. (2013), critique of Cheung et al. (2013a) included: “the bioenergetic model assumes that the term scaling directly with weight is due to catabolism, but there is a strong case that reproductive investment is the principal factor (Day and Taylor, 1997; Charnov et al. 2001; West et al. 2001)”.	Cheung et al. (2013a) replied: “Brander et al. argue that fish growth is inversely proportional to reproductive investment. However, this [...] cannot explain why female fish (which have a much larger reproductive investment than male fish) reach larger sizes than male in the majority of fish species, and why sterile fish [...] grow asymptotically. Moreover [...] diploid (reproductively active) and triploid (sterile) fish show very similar growth patterns despite large differences in reproductive investment (Maxime 2008)”

### Temperature and maximum sizes

To compensate for Lefevre *et al.* (2017), who critiqued the contribution of Cheung *et al.* (2013a), but did not propose their own hypothesis as to why fish should remain smaller at higher temperatures, the contribution of Audzijonyte *et al.* (2018) is examined in some detail here, as these authors attempt to answer the question of whether “*oxygen limitation in warming waters is a valid mechanism to explain decreased body size in aquatic ectotherms*” (Figure 6A).

Answering this question would also solve the riddle posed by Kinne (1960), who was baffled by his observation, based on guppies raised at different temperatures, that *[t]he results indicate that the differences in growth rate established in young fish do not persist throughout life. Initially slow-growing fishes may surpass initially fast-growing fishes, and finally reach a greater length-at-age*”, as reported and illustrated earlier by Pütter (1920; Figure 6B).

Audzijonyte *et al.* (2018) presented and discussed six potential explanations, as documented in their figure 1 (with the quotes all extracted from its caption), which are here summarized and commented upon. All but the first of these potential explanations can be viewed as implicit alternatives to the GOLT:

#### a) The GOLT (or ‘GOL hypothesis’ in Audzijonyte *et al.* 2018).

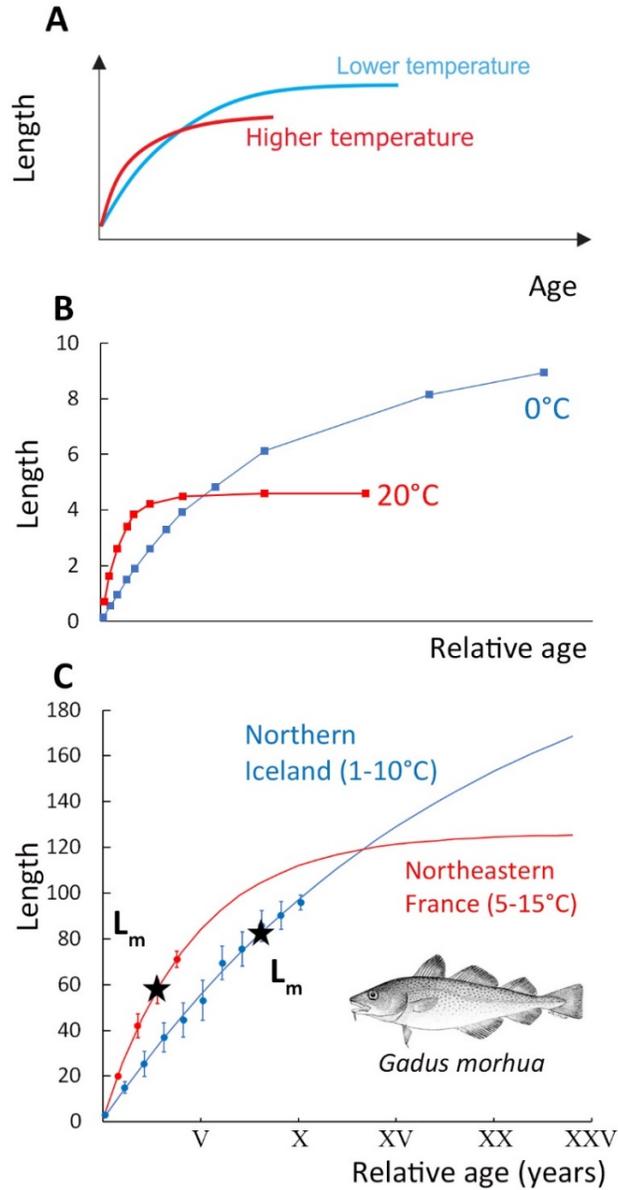
The GOLT, based on the inherent properties of gills as 2-D surface that must remain exposed to an oxygen-laden water flow, assumes that they will provide decreasing amount of oxygen per unit weight to the bodies of growing WBE. Hence, increased temperatures, which increase oxygen demand, will force them to remain smaller (Figures 6C; see also Cheung *et al.* 2013a). However, the fish kept at higher temperature may at first experience a more rapid growth than those kept at low temperature, which also explains the above quote from Kinne (1960).

Note also that many inferences on the growth of fish and other WBE are based on juveniles, whose growth is usually accelerated by temperature increases, and not on adults, whose growth is often depressed by increased temperature (Table 1). The preference of researchers for working with juvenile fish is understandable (they require smaller aquaria, require less food, etc.), but it often leads to more confusion, as illustrated by the above quote of Kinne (1960), one of the few aquatic biologists who raised fish (albeit small ones) under different temperatures from larvae to adults.

#### b) “Different temperature dependence of DNA replication (development) results in smaller cells and faster division at warmer temperatures.”

Fish that remain smaller at higher temperatures have, to the author’s knowledge, never been shown to possess smaller cells. And if they did, this would be the reason for their smaller size in warm water only if they had the same number of cells, as do, e.g., tardigrades and small nematodes. This, as well, has never been demonstrated.

Hypothesis (b) is probably another case of cause and effect being inverted (similar to the case documented above; Table 4), as often happens when things correlate (Pearl and Mackenzie 2018). Some of the largest fish, e.g., tuna, have very small cells, while the much smaller lungfish have large cells (Hinegardner and Rosen 1972; Thompson 1972; Cavalier-Smith 1991). Indeed, it seems that, in fish at least, cell size is linked with DNA content and activity level but not with size (Pauly *et al.* 2000). On the other hand, the higher cellular turnover implied by “*faster cell division at warmer temperatures*” would be associated with a higher rate of protein denaturation, which is a central tenet of the GOLT (see above).



**Figure 6. Fish, at higher temperatures, tend to grow fast toward smaller maximum sizes.** A: The “Observed phenomenon” that needs to be explained (adapted from an insert in Figure 1 of Audzijonyte et al. 2018); B: A simplified version of figure 1 in Pütter (1920), who derived it from principles later elaborated upon by von Bertalanffy (1934 and beyond); C: Atlantic cod (*Gadus morhua*) has wide geographic and temperature ranges; in Eastern Iceland (1-10 °C), they reach much larger sizes than in French waters (8-18 °C); based on data in Saemundsson (1923) and Le Franc (1966).

Table 4. Arguments raised against the GOLT: mistaking cause and effect

No	Arguments	Refutations
4.1	Lefevre <i>et al.</i> (2017) suggested that since “ <i>the activity of oxidative enzyme falls with body mass in fishes (Davies and Moyles 2007)</i> ” larger/older fish need less oxygen anyway. Thus, it is not necessary to maintain a high O <sub>2</sub> supply.	This is mistaking cause and effect: fish shift from oxidative to glycolytic enzymes <i>because</i> their relative O <sub>2</sub> supply declines. This was understood by Somero and Childress. 1980), who attributed the shift from oxidative to glycolytic enzymes, if tentatively, to “[ <i>l</i> ]imitation on aerobic metabolism [ <i>which</i> ] may derive from surface-volume relationships...”
4.2	Lefevre et al (2017) write: “ <i>In our field, it is generally accepted that a species’ oxygen demand determines the size of their [sic] respiratory surface area, not the other way around</i> ”.	Something being “ <i>generally accepted</i> ” within one’s field is not evidence of its validity. Thus, e.g., Plate Tectonics was not mentioned in geology textbooks and generally not accepted by geologists... until it was (Oreskes 2013).
4.3	In their abstract, Lefevre et al. 2017) claimed that there is “ <i>a large body of evidence demonstrating that respiratory surface areas in fishes reflect metabolic needs, not vice versa, which explains the large interspecific variation in scaling of gill surface areas</i> ”.	There is no such body of evidence; rather, the O <sub>2</sub> consumption of fish is generally <i>assumed</i> to reflect their ‘needs’. What is missing are tests of whether the <i>supply</i> of O <sub>2</sub> by the gills to the body (always) satisfies the O <sub>2</sub> <i>demand</i> of the fish tissues. It does not in large adult fish, which is the reason that they switch from oxidative to glycolytic enzymes

c) “Decreasing growth efficiency at higher temperatures means that less energy is converted to growth.”

This is not an explanation because it shifts that which must be explained from ‘reduced growth when temperature is high’ to ‘decreased growth efficiency’, which is a restatement of the issue at hand. The GOLT explains ‘decreased growth efficiency’ (i.e.,  $K_1$  = growth increment/food ingested; Gerking 1952, 1971) by pointing out that when WBE are exposed to higher temperatures, more of their oxygen supply is diverted to basal metabolism, leaving less available to assimilate food. Hence, the amino acid pool of fish spills over and “*is excreted by the gills and kidney as incompletely oxidized nitrogenous compound*” – the latter point quoted from Webb (1978), who cites the works of Forster and Goldstein (1969); Savitz (1969, 1971); Olson and Fromm (1971) and Niimi and Beamish (1974); see also Kajimura *et al.* (2004).

d) “Higher size-specific allocation to reproduction at higher temperatures [...] leaves less energy for growth.”

No evidence is presented by Audzijonyte *et al.* (2018) that fish and/or aquatic invertebrates devote more resource to reproduction at high temperatures. Besides<sup>21</sup>, the argument is irrelevant because the effects of temperature on growth manifest themselves well before fish mature (see Figure 6A-C).

e) “Faster increases in energy demand (metabolism, activity cost, etc.) compared with food availability leaves [less] energy for growth and reproduction in [...] warmer environments.”

This complex hypothesis, which implies that tropical ecosystems make less food available to consumers than colder ecosystems, would be hard to test. Fortunately, there is no need to test it, because experiments can be and have been conducted *in vitro* in which food is provided *ad libitum* and in which fish kept at

<sup>21</sup> Deleted at the suggestion of a reviewer.

cooler temperatures grow to be larger than those at higher temperatures (Kinne 1960; Liu and Walford 1966, 1970).

The only reason this point is perhaps not obvious is that laboratory growth experiments are difficult to run with large/old fish, and thus are mostly conducted with juvenile fish, with the initial growth acceleration due to higher temperatures leaving the strongest impression. Only when small, short-lived fishes are monitored over their entire life-spans does the phenomenon, which so puzzled Kinne, appear (1960; see above quote).

f) *“Increased predation mortality at higher temperatures drives an evolutionary response of higher net energy allocation to reproduction versus growth.”*

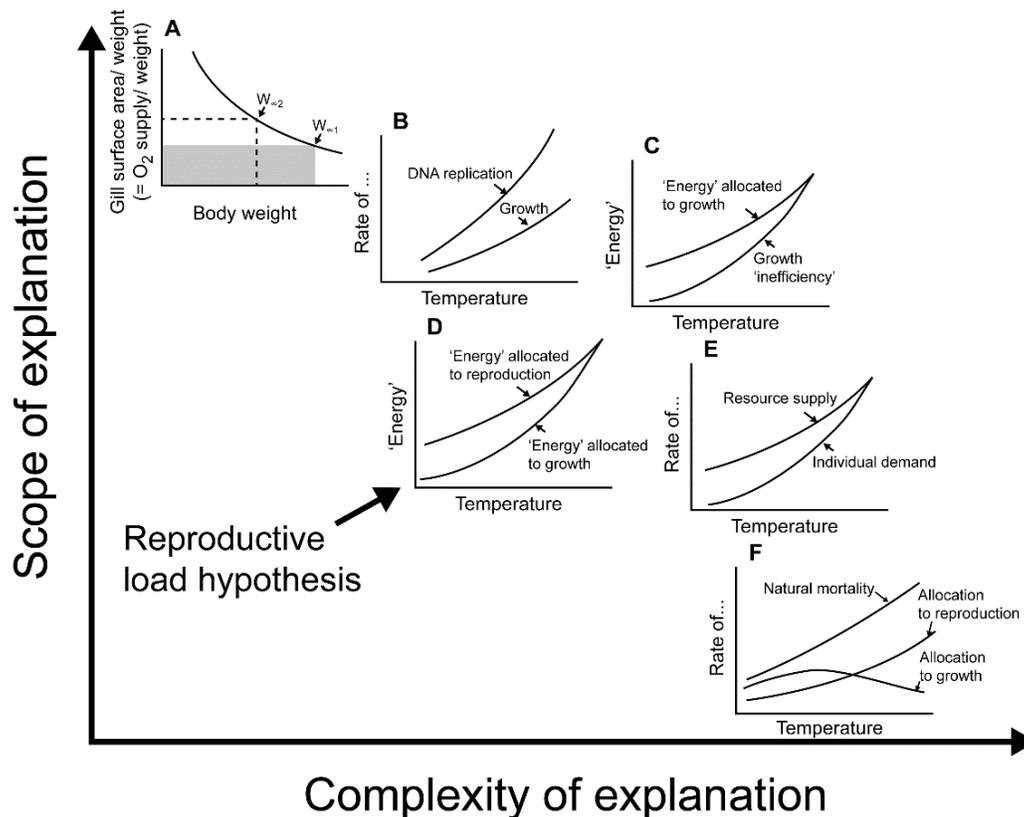
This is hypothesis (d) in another guise. Evoking a complex “evolutionary response” is not an explanation of anything because, as was said so elegantly, “*nothing in biology makes sense except in the light of evolution*” (Dobzhansky 1973). The point, rather, is to identify the mechanism in question. However, it will be quite difficult, given that, as stated for (d), fish grown under experimental conditions and without opportunity to spawn remain smaller at higher temperatures (Kinne 1960; Liu and Walford 1966, 1970). The critique of items (b) to (f) is serious: proposed hypotheses should be able to withstand a confrontation with common-sense observations. Moreover, several of these hypotheses were only complex restatements of the issue at hand (Figure 7).

In contrast, the GOLT proposes a mechanism for the reduced body size of fish and invertebrates under global warming that is simpler than what needs to be explained and that is based on consensual knowledge – including that gills cannot be perceived as Escher-like objects *à la* Lefevre et al. (2017). Also, the GOLT makes numerous predictions pertaining to domains that, at first glance, appear to be unrelated to temperature affecting the size of fish.

This is because the constraints on the surface area of gills are real: their surface area was optimized in the course of evolution to allow their owners to reach first maturity relatively fast, after which growth can gradually slow down.

The notion that gill surface area cannot be limiting because lamellae can be added as required, as suggested by Lefevre et al. (2017), is false because gills function similar to a sieve, i.e., and must be perpendicular to the flow of water that flows through them. This means that they can grow in height and in breadth but not in depth – they cannot grow in the 3<sup>rd</sup> dimension, and thus 3-D bodies must experience a declining oxygen supply as they grow. Moreover, as Audzijonyte et al. (2018) emphasize, gills are a favorite site for parasite infestation, and thus fish and aquatic invertebrates have good reasons to keep them as small as possible (see also Nilsson et al. 2012). Thus, gill surface area is not limiting to young/small fish, but they are limiting to big adults.

The GOLT offers a coherent framework for exploring these phenomena and a vast number of related observations. This is not the case for just-so hypotheses.



**Figure 7. Simplicity vs. scope in explaining why higher temperatures lead to smaller sizes.** The 6 explanatory models are adapted from Audzijonyte et al. 2018), who presented them in two columns, as 'intrinsic mechanisms' (A, B, C and D), and 'extrinsic mechanisms' (E and F). Here, they are arranged according to the perceived complexity of the mechanism(s) they require its (or their) generality or 'scope' (see text).

## DISCUSSION

### The nature of explanations

The physicist Wolfgang Pauli is supposed to have said, “*God made the bulk; surfaces were invented by the devil*” (Jamtveit and Meakin 1999, p. 21). When thinking about the explanations provided by the GOLT, which is concerned primarily with the ‘tension’ between volumes and surfaces (and the arguments denying such tensions that have been advanced against the GOLT’s explanations), it is appropriate to recall what is meant by an ‘explanation’. Rather than pedantry, an exercise is required to define the terms of the debate and the criteria that are applied below.

To become widely accepted, scientific explanations, in addition to being (obviously) congruent with the facts at hand, must be:

1. Consilient with underlying scientific disciplines;
2. Parsimonious, i.e., as simple as possible;
3. Independent from the observer and/or standpoint; and
4. Productive, i.e., make unexpected predictions.

The first of these, building on Wilson (1998), is the notion that the different scientific disciplines, while autonomous in their investigations of the phenomena upon which they focus, cannot accept explanations that violate constraints established by other scientific disciplines (or by logic and mathematics). Thus,

biological organisms must comply with physical laws, and the processes comprising their metabolism must comply with constraints studied by chemists.

An explanation consists, therefore, of ‘mapping’ a phenomenon observed by the practitioners of a given discipline onto constraints, rules, or ‘laws’ that are parts of an underlying discipline. For example, ‘Bergmann’s Rule’ (Bergmann 1847) explains why high-latitude mammals and birds tend to have bigger bodies and shorter appendages (ears, limbs, tails) than their congeners in more temperate climes. It states that, while they generate heat in their bodies (a volume, which tends to grow according to length *cubed*), mammals and birds radiate (i.e., lose) heat through their body surface (proportional to length *squared*). Hence, increasing body weight and reducing the size of appendages through evolutionary time will reduce heat loss by reducing body surface per unit volume. Bergmann’s Rule relies on consilience, specifically on facts of geometry and physics, to make a case concerning the biology of homeotherms.

The key feature of this type of explanation is that it avoids infinite regress: an observation is explained once it is mapped onto a more basic framework i.e., there is no need to map the basic framework onto an even more basic one. Thus, in the example above, there is no need for biologists to explain why heat loss is proportional to a surface – though it has been, for a while at least, a legitimate research question for physicists (Boltzmann 1884).

Parsimony is the requirement that an explanation should be ‘small’ relative to the ‘size’ of what needs to be explained (Dawkins 2006). Parsimony is another term for ‘Ockham’s razor’, the rule that among competing hypotheses, the simplest one is (generally) to be favored (Kelly 2004).

The third requirement of a scientific explanation is that it must be non-local, i.e., it must not favor a privileged observer, or standpoint (Feynman 1985). For example, we should not project our homeotherm biases (notably our mammalian preoccupation with the food we require to maintain our elevated temperature) onto WBE, which require far less food, but to which the extraction of oxygen from their surrounding medium is a challenge that air-breathers often find difficult to imagine.

Finally, a successful hypothesis should not only explain the facts at hand, and map them parsimoniously onto the fabric of a more basic discipline, but it should also make successful predictions, i.e., make sense of facts that it was not designed to explain.

### **Some real issues with the GOLT**

While the GOLT can obviously deal with objections that are beside the point (Table 8), there are several areas in which this theory is deficient. One of these issues is that the GOLT is still largely a qualitative theory, frequently unable to make quantitative predictions. For example, while the GOLT met the challenge posed by whale shark – the largest extant fish – occurring in warm tropical waters by evoking their yo-yo type “cooling dives” (Table 3, No. 3.2), it would at present provide no quantitative constraints for a model that could predict the duration of such dives as a function of whale shark size and depth-temperature gradients. Such a model could be tested using the data on whale sharks occurring in the Persian Gulf (which is both warm and shallow; Chao et al. 1992) and the Red Sea (whose deeper waters are very hot and briny; Swift et al. 2012).

At present, it can only be stated that the GOLT is not refuted by the presence of whale shark in these extreme environments, even though cooling dives are not possible because these whale sharks are

juveniles and young adults below 10 m in the Gulf and below 7 m in the Red Sea (Berumen et al. 2014; Cochran et al. 2016; Rezzolla and Storai 2010; Robinson et al. 2017). Fully grown whale sharks, those assumed to require frequent cooling dives, are reported to exceed 18 m (McClain et al. 2015).

Another example is the experiment explicitly conducted by Kolding et al. (2008) as a test of the GOLT, which predicts that fish raised in (mildly) hypoxic conditions should reach maturity at a smaller size than fish raised in normoxia. The GOLT passed this test while alternative hypotheses did not (Kolding et al. 2008), but its prediction concerned only the type of response and not its strength.

Another deficiency of the GOLT is assuming that the WBE in question always get enough food to grow (i.e., the converse of most studies that deal with food limitation) but tacitly assuming the oxygen needed to turn ingested food into ‘energy’ is always available, and at no cost. This issue is obviously related to the investment required to produce ova and sperms by mature WBE, whose reproduction can be understood only by considering seasonal growth oscillations, a topic not considered here (but see Pauly 2019c).

Clearly, the GOLT will have to be assimilated into a bioenergetics model or vice versa. However, the intellectual effort this represents will be undertaken only if oxygen supply to the bodies of WBE is perceived as the constraint that it is, and hence this contribution.

### **The GOLT and Evolution**

How a further elaboration of the GOLT would look cannot be anticipated, at least not by the author. However, such elaboration, if successful, may influence the way we view the evolutionary process. It may lead to a realization that evolution has two ways of handling challenges, depending on their nature. In the first, the challenge is met head-on by an adaptation (for example when its grazers neutralize a toxic substance in the leaves of a plant, or when a parasite gradually becomes a symbiont). In the second, the challenge (e.g., gravity, oxygen requirements, heat buildup) cannot be overcome by a metabolic or behavioral trick. In the latter case, all that can occur is what may be called a set of ‘accommodations.’

The ‘dimensional tension’ (Pauly and Cheung 2017a) between the gill (or other respiratory) surface of a WBE and its body weight results in the accommodations that are made explicit by the GOLT. These should not be perceived as adaptations. Indeed, when the challenge posed by geometric or physical constraints cannot be accommodated, the corresponding region of morphological space remains unoccupied. This is why neither the huge spiders stalking Frodo and Sam in *Lord of the Rings* nor even beetle-shaped insects of more than 18 cm (Kaiser et al. 2007) can exist. As for fish, this is why the megatooth (*Megalodon*) could not reach more than twice the length of the great white shark (i.e., 20 m), implying a weight nearly 10 times greater, as claimed in a Discovery Channel ‘documentary’ film.

The GOLT requires that these two types of evolutionary challenges be recognized and distinguished, lest colleagues continue to believe that if fish suffer from warmer temperature and deoxygenation, they will just grow larger gills.

**Table 8. Arguments raised against the GOLT: miscellaneous, mainly normative arguments**

No	Arguments	Refutations
7.1	O'Dor and Hoar (2000) claimed that <i>“There is a fundamental flaw in examining Pauly’s surface area limited growth scheme by plotting two different sets of units (m<sup>2</sup> and m<sup>3</sup>) on the same graph and then making quantitative conclusions. Not only is [the resulting figure] messy, it violates a rule of physics and engineering (Vogel 1981)”</i> . The rule alluded to here is probably: <i>“For an equation to have any applicability to the real world, not only must the two sides be numerically equal, but they must also be dimensionally equal”</i> (Vogel 1981, p. 6).	The GOLT involves no equation with dimensionally unequal sides. Its presentation, however, may include graphs with two ordinate axes with different units, as in figure 6.8, in Vogel (1981, p. 96), who therefore is not likely to have suggested that such figures violate the rules of physics and engineering. In fact, plots with two (or more) ordinate scales are common in science (see e.g., Crawley 2009, p. 868).  The key issue, in any case, is that anything proportional to the 3 <sup>rd</sup> power of length will outgrow anything that remains proportional to its 2 <sup>nd</sup> power, whatever the units and the starting values (Figure 4b).
7.2	Lefevre et al. (2017) claimed that in Cheung et al. (2013a), the GOLT predicted a strong size reduction of fish with temperature because a key parameter was deliberately set too low (d = 0.7)	When the parameter in question was set at higher values (d = 0.8-0.9), the size reduction caused by increasing temperature actually <i>increased</i> (Pauly and Cheung 2018).
7.3	Ecophysiological arguments should not be used to explain physiological processes, as implied by the title of Jutfelt et al. (2018) which implicitly criticizes H.-O. Pörtner’s ‘Oxygen and Capacity Limited Temperature Tolerance’ (OCLTT) hypothesis (which partly overlaps with the GOLT; Pörtner 2010; Pörtner et al. (2017, 2018).	No biological sub-discipline can assume <i>a priori</i> a monopoly in answering a specific scientific question. In fact, scientific problems are nowadays best tackled using interdisciplinary approaches (Ledford 2015). Pörtner et al. (2018) suggest that <i>“to connect closely to ecological changes, studies need to consider the long-term consequences of subtle functional constraints. [...] Indeed, such requirements are rarely met in purely physiological studies”</i> .
7.4	Jutfelt et al. (2018) suggest that H.-O. Pörtner’s OCLTT hypothesis <i>“incorrectly [considers] aerobic scope or oxygen delivery capacity as the ‘energy’ available to animals, when in fact it is only a permissive factor compared with other constraints (e.g., food availability)”</i> .	Animals – including fish -- deprived of oxygen die within minutes. Also, the chemical energy embodied in their food becomes available to them only when that food is combined with oxygen, i.e., ‘burnt’. Thus, considering oxygen to be one of several ‘permissive’ factors of metabolism in order to score a few points against a colleague takes us back to the times before the discoveries of Lavoisier (1743-1784).
7.5	Here is another argument against H.-O. Pörtner’s OCLTT hypothesis <i>“it is hard to imagine why animals would allow tissue hypoxia to become severe enough to inflict performance decline at moderate levels of activity when possessing the functional capacity to significantly increase oxygen delivery to tissues”</i> (Jutfelt et al. 2018).	That none of the 28 authors of Jutfelt et al. (2018) could imagine why animals can’t operate all the time at peak performance is itself hard to imagine. However, it bears repeating here: peak performance extracts a massive toll on all organ systems and is used only to escape predators or life-threatening situations (Priede 1985; Pauly and Cheung 2017a). Repeated peak performance, as forced in experiments, renders the tested animals unfit for life in the wild.
7.6	Lefevre et al (2017) write: <i>“The idea that insurmountable geometric constraints on the size of the gills could determine the metabolic rate of fishes has never, as far as we know, been pursued as a valid hypothesis among respiratory physiologists. It is for example not mentioned in Schmidt-Nielsen or in Evans and Clairborne, two sources for overviews of animals and fish physiology.</i>	This meta-argument about the authority of textbooks such as Schmidt-Nielsen (1997) or Evans and Clairborne (2006) is a strange one to make in the 21 <sup>st</sup> Century, though it could have been made in the Middle Ages with reference to species not mentioned in Aristotle’s <i>Historia Animalium</i> (Thompson 1910) or in the writings of Plinius the Elder (Cotte 1944).

## ACKNOWLEDGEMENTS

My thanks to the numerous colleagues who, over the years, have variously challenged me to come up with a better framing for my ‘oxygen story’, notably Rainer Froese, William Cheung, and Jennifer S. Bigman. Included also are the critics, to whom I respond in Tables 2-8. They found this story was at least worthy of criticism, rather than simply ignoring it. I thank Mr. Kevin Meyer, Idaho Department of Fish and Game for Figure 5D-F, Dr. Cui ‘Elsa’ Liang for assistance with the equations establishing the relationship between  $W_m$  and  $W_i$  and obtaining photos of aquaculture pond aeration operation in China, and Ms. Evelyn Liu and Elaine Chu for drafting Figures 1 to 7.

## REFERENCES

- Audzijonyte, A., D.R. Barneche, A.R. Baudron, J. Belmaker, T.D. Clark, C.T. Marshall, J.R. Morrongiello and I. van Rijn. 2018. Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? *Global Ecology and Biogeography*, 28: 64–77.
- Bass, A.H. 1993. From brains to behaviour: hormonal cascades and alternative mating tactics in teleost fishes. *Rev Fish Biol Fisheries*, 3: 181–186.
- Bednaršek, N., C.J. Harvey, I.C. Kaplan, R.A. Feely and J. Možina. 2016. Pteropods on the edge: Cumulative effects of ocean acidification, warming, and deoxygenation. *Progress in Oceanography*, 145: 1–24.
- Bergmann, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, 3: 595–708.
- Bertalanffy, L., von. 1934. Untersuchungen über die Gesetzlichkeit des Wachstums. I Allgemeine Grundlagen der Theorie, mathematische und physiologische Geseztlichkeiten des Wachstums bei Wassertieren. *Wilhelm Roux’ Archiv für Entwicklungsmechanik der Organismen*, 131: 613–652.
- Bertalanffy, L., von. 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). *Human Biology*, 10: 81–213.
- Bertalanffy, L., von. 1949. Problems of Organic Growth. *Nature*, 163: 156–158.
- Bertalanffy, L., von 1960. Principles and theory of growth, p. 137-259. In: W.W. Nowinski (ed). *Fundamental Aspects of Normal and Malignant Growth*. Elsevier, Amsterdam and New York.
- Bertalanffy, L. von. 1964. Basic concepts in quantitative biology of metabolism. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, 9: 5–37.
- Bertalanffy, L., von 1951. *Theoretische Biologie. Zweiter Band: Stoffwechsel, Wachstum*. A. Francke Verlag, Bern. 418 p.
- Berumen, M.L., C.D. Braun, J.E.M. Cochran, G.B. Skomal and S.R. Thorrold. 2014. Movement Patterns of Juvenile Whale Sharks Tagged at an Aggregation Site in the Red Sea. *PLOS ONE*, 9(7). [doi.org/10.1371/journal.pone.0103536](https://doi.org/10.1371/journal.pone.0103536)
- Beverton, R.J.H., S.J. Holt. 1957. *On the Dynamics of Exploited Fish Populations*. Fisheries Investigations, Series 2. H.M. Stationary Office, London. 533 p.
- Beverton, R.J.H. 1959. A review of the lifespan and mortality rate of fish in nature and the relation to growth and other physiological characteristics, p. 142-177. In: G.E.W. Wolstenhome and M. O’Connor (eds). *The Lifespan of Animals, volume V: Colloquia on Ageing*. CIBA foundation symposium.
- Beverton, R.J.H. 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *Rapports et Procès-verbaux des Réunions du Conseil permanent international pour l’Exploration de la Mer*, 154: 44–67.
- Bhattacharya, S. 1999. Recent advances in the hormonal regulation of gonadal maturation and spawning in fish. *Current Science*, 76: 342–349.
- Birk, M.A., A.K. Dymowka and B.A. Seibel. 2018. Do squid breathe through their skin? *The Journal of experimental Biology*, 221(Pt19). [doi.org/10.1242/jeb.185553](https://doi.org/10.1242/jeb.185553)
- Blier, P.U., D. Pelletier, and J.-D. Dutil. 1997. Does aerobic capacity set a limit on fish growth rate? *Reviews in Fisheries Science*, 5: 323–340.
- Bochdansky, A.B. and W. Leggett. 2001. Winberg revisited: Convergence of routine metabolism in larval and juvenile fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 220–230.
- Boltzmann, L. 1884. Ableitung des Stefan’schen Gesetzes, betreffend die Abhängigkeit der Wärmestrahlung von der Temperatur aus der electromagnetischen Lichttheorie. *Annalen der Physik*, 258: 291–294.
- Boonstra, W.J., K.M. Ottosen, A.S.A. Ferreira, A. Richter, L.A. Rogers, M.W. Pedersen, A. Kokkalis, H. Bardarson, S. Bonanomi, W. Butler, F. K. Diekert, N. Fouzai, M. Holma, R.E. Holt, K.Ø. Kvile, E. Malanski, J.I.

- Macdonald, E. Nieminen, G. Romagnoni, M. Snickars, B. Weigel, P. Woods, J. Yletyinen and J.D. Whittington. 2015. What are the major global threats and impacts in marine environments? Investigating the contours of a shared perception among marine scientists from the bottom-up. *Marine Policy*, 60: 197–201.
- Bornmann, L. and R. Mutz. 2015. Growth rates of modern science: A bibliometric analysis based on the number of publications and cited references. *Journal of the Association for Information Science and Technology*, 66: 2215–2222.
- Brander, K., A. Neuheimer, K.H. Andersen and M. Hartvig. 2013. Overconfidence in model projections. *ICES Journal of Marine Science*, 70: 1065–1068.
- Brandts, T.F. 1967. Heat effects on Proteins and Enzymes, p. 25-27. In: A.E. Rose (ed). *Thermobiology*. Academic Press, London and New York.
- Breitburg, D., L.A. Levin, A. Oschlies, M. Grégoire, F.P. Chavez, D.J. Conley, V. Garçon, D. Gilbert, D. Gutiérrez, K. Isensee, G.S. Jacinto, K.E. Limburg, I. Montes, S.W.A. Naqvi, G. C. Pitcher, N.N. Rabalais, M.R. Roman, K.A. Rose, B.A. Seibel, M. Telszewski, M. Yasuhara and J. Zhang. 2018. Declining oxygen in the global ocean and coastal waters. *Science*, 359(6371). [doi.org/10.1126/science.aam7240](https://doi.org/10.1126/science.aam7240)
- Brett, J.R. 1979. Environmental factors and growth, p. 599-675. In: W.S. Hoar, D.J. Randall and J.R. Brett (eds). *Fish Physiology*. Academic Press, London.
- Burness, G.P., S.C. Leary, P.W. Hochachka and C.D. Moyes. 1999. Allometric scaling of RNA, DNA, and enzyme levels: an intraspecific study. *The American Journal of Physiology*, 277: R1164–1170.
- Caputo, V, M.L. Mesa, G. Candi, P.N. Cerioni. 2003. The reproductive biology of the crystal goby with a comparison to that of the transparent goby. *Journal of Fish Biology*, 62: 375–385.
- Cavalier-Smith, T. 1991. Covolution of vertebrate genome, cell and nuclear sizes, p. 51-86. In: G. Ghiara (ed). *Symposium on the evolution of terrestrial vertebrates*. Collana UZI selected Symposia and Monographs, Volume 4. Modena, Mucchi.
- Chao, S.-T., W. Kao and K.R. Al-Hajri. 1992. A numerical investigation of circulation in the Arabian Gulf. *Journal of Geophysical Research: Oceans*, 97: 11219–11236.
- Charnov, E.L. 2008. Fish growth: Bertalanffy k is proportional to reproductive effort. *Environmental Biology of Fishes*, 83: 185–187.
- Charnov, E.L., T.F. Turner and K.O. Winemiller. 2001. Reproductive constraints and the evolution of life histories with indeterminate growth. *PNAS*, 98: 9460–9464.
- Cheung, W.W.L., J.L. Sarmiento, J. Dunne, T.L. Frölicher, V.W.Y. Lam, M.L.D. Palomares, R. Watson and D. Pauly. 2013a. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3: 254–258.
- Cheung, W.W.L., R. Watson and D. Pauly. 2013b. Signature of ocean warming in global fisheries catch. *Nature*, 497: 365–368.
- Choat, J.H. and L.M. Axe. 1996. Growth and longevity in acanthurid fishes; an analysis of otolith increments. *Marine Ecology Progress Series*, 134: 15–26.
- Choat, J.H., L. Axe and D. Lou. 1996. Growth and longevity in fishes of the family Scaridae. *Marine Ecology Progress Series*, 145: 33–41.
- Cochran, J.E.M., R.S. Hardenstine, C.D. Braun, G.B. Skomal, S.R. Thorrold, K. Xu, M.G. Genton and M.L. Berumen. 2016. Population structure of a whale shark *Rhincodon typus* aggregation in the Red Sea. *Journal of Fish Biology*, 89: 1570–1582.
- Corriero, A., S. Karakulak, N. Santamaria, M. Deflorio, D. Spedicato, P. Addis, S. Desantis, F. Cirillo, A. Fenech-Farrugia, R. Vassallo-Agius, J.M. de la Serna, Y. Oray, A. Cau, P. Megalofonou and G.D. Metrio. 2005. Size and age at sexual maturity of female bluefin tuna (*Thunnus thynnus* L. 1758) from the Mediterranean Sea. *Journal of Applied Ichthyology*, 21: 483–486.
- Cotte, J. 1944. *Poissons et animaux aquatiques au temps de Pline: commentaires sur le livre IX de l'Histoire naturelle de Pline*. Paul Lechevalier Éditeur, Paris. 286 p.
- Cox, M. and D. Nelson. 2008. *Lehninger Principles of Biochemistry*. W.H. Freeman, New York. 1340 p.
- Crawley, M.J. 2009. *The R Book*. John Wiley & Sons Ltd, West Sussex, U.K. 1076 p.
- Crespi, B.J. and R. Teo. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evolution*, 56: 1008–1020.
- Cushing, D.H. 1975. *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge. 278 p.
- Darwin, C. 1861. *Letter Henry Fawcett*. Available at: <https://www.darwinproject.ac.uk/>
- Davies, R. and C.D. Moyes. 2007. Allometric scaling in centrarchid fish: origins of intra- and inter-specific variation in oxidative and glycolytic enzyme levels in muscle. *The Journal of Experimental Biology*, 210: 3798–3804.
- Dawkins, R. 2006. *The God delusion*. Houghton Mifflin, Boston. 464 p.

- Day, T. and P. Taylor. 1997. Von Bertalanffy's Growth Equation Should Not Be Used to Model Age and Size at Maturity. *American Naturalist*, 149: 381–393.
- De Jager, S. and W.J. Dekkers. 1975. Relations Between Gill Structure and Activity in Fish. *Netherlands Journal of Zoology*, 25: 276–308.
- De Sylva, D.P. 1974. Development of the Respiratory System in Herring and Plaice Larvae, p. 465–485. In: J.H.S. Blaxter (ed). *The Early Life History of Fishes*. Springer, Berlin and New York.
- Dobzhansky, T. 1973. Nothing in Biology Makes Sense except in the Light of Evolution. *The American biology Teacher*, 35: 125–129.
- Evans, D.H. and J.B. Clairborne. 2006. *The Physiology of Fishes*. CRC Press, Boca Raton, FL, USA. 257 p.
- Feynman, R.P. 1985. *QED: The Strange Theory of Light and Matter*. Princeton University Press, Princeton, NJ. 194 p.
- Fieller, E.C. 1940. The Biological Standardization of Insulin. *Supplement to the Journal of the Royal Statistical Society*, 7: 1–64.
- Forster, R.P. and L. Goldstein. 1969. Formation of excretory products, p. 313–350. In: W.S. Hoar and D.J. Randall (eds). *Fish Physiology, Vol. 1*. Academic Press, New York.
- Franz, D.R. 1993. Allometry of shell and body weight in relation to shore level in the intertidal bivalve *Geukensia demissa* (Bivalvia: Mytilidae). *Journal of Experimental Marine Biology and Ecology*, 174: 193–207.
- Froese, R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*, 22: 241–253.
- Froese, R. and C. Binohlan. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology*, 56: 758–773.
- Gehrke, P.C. 1987. Cardio-respiratory morphometrics of spangled perch, *Leiopotherapon unicolor* (Günther, 1859), (Percoidei, Teraponidae). *Journal of Fish Biology*, 31: 617–623.
- Gerking, S.D. 1952. The Protein Metabolism of Sunfishes of Different Ages. *Physiological Zoology*, 25: 358–372.
- Gerking, S.D. 1971. Influence of Rate of Feeding and Body Weight on Protein Metabolism of Bluegill Sunfish. *Physiological Zoology*, 44: 9–19.
- Glazier, D.S. 2006. The 3/4-Power Law Is Not Universal: Evolution of Isometric, Ontogenetic Metabolic Scaling in Pelagic Animals. *BioScience*, 56: 325–332.
- Goldberg, A.L. and A.C. St John. 1976. Intracellular protein degradation in mammalian and bacterial cells: Part 2. *Annual Review of Biochemistry*, 45: 747–803.
- Gould, S.J. 1985. *The Flamingo's Smile: Reflections in Natural History*. W.W. Norton, New York. 476 p.
- Graham, J.B. 2006. Aquatic and aerial respiration, p. 85–117. In: D.H. Evans and J.B. Clairbornes (eds). *The Physiology of Fishes*. Taylor and Francis, Boca Raton, FL, USA.
- Hayward, A. and J.F. Gillooly. 2011. The Cost of Sex: Quantifying Energetic Investment in Gamete Production by Males and Females. *PLOS ONE*, 6: e16557.
- Hawkins, A.J.S. 1991. Protein Turnover: A Functional Appraisal. *Functional Ecology*, 5: 222–233.
- Heincke, F. 1913. *Investigations on the plaice. General Rapport I. Plaice fishery and protective regulations. Part I. Rapports et Procès-verbaux des Réunions du Conseil permanent international pour l'Exploration de la Mer vol 17A*. B. Luno, Copenhagen.
- Hinegardner, R. and D.E. Rosen. 1972. Cellular DNA Content and the Evolution of Teleostean Fishes. *The American Naturalist*, 106: 621–644.
- Holeton, G.F. 1976. Respiratory morphometrics of white and red blooded Antarctic fish. *Comparative Biochemistry and Physiology Part A: Physiology*, 54: 215–219.
- Hubbs, C.L. 1926. The Structural Consequences of Modifications of the Developmental Rate in Fishes, Considered in Reference to Certain Problems of Evolution. *The American Naturalist*, 60: 57–81.
- Hughes, G.M. 1970. Morphological measurements on the gills of fishes in relation to their respiratory function. *Folia Morphol (Praha)*, 18: 78–95.
- Hughes, G.M. 1984. Measurement of gill area in fishes: practices and problems. *Journal of the Marine Biological Association of the United Kingdom*, 64: 637–655.
- Jamtveit, B. and P. Meakin. 1999. Growth, Dissolution and Pattern Formation in Geosystems, p. 1–19. In: B. Jamtveit and P. Meakin (eds). *Growth, Dissolution and Pattern Formation in Geosystems*. Springer, Dordrecht.
- Johansen, J.L., V. Messmer, D.J. Coker, A.S. Hoey and M.S. Pratchett. 2014. Increasing ocean temperatures reduce activity patterns of a large commercially important coral reef fish. *Global Change Biology*, 20: 1067–1074.

- Johnson, L. 1976. Ecology of Arctic Populations of Lake Trout, *Salvelinus namaycush*, Lake Whitefish, *Coregonus clupeaformis*, Arctic Char, *S. alpinus*, and Associated Species in Unexploited Lakes of the Canadian Northwest Territories. *Journal of the Fisheries Research Board of Canada*, 33: 2459–2488.
- Jones, R. 1976. Growth of fishes, p. 251-279. In: E.D. Cushing and J.J. Walsh (eds). *The Ecology of the Seas*. Blackwell Scientific Publications, London.
- Jørgensen, C., B. Ernande, Ø. Fiksen and U. Dieckmann. 2006. The logic of skipped spawning in fish. *Canadian Journal of Fisheries and Aquatic Science*, 63: 200–211.
- Jutfelt, F., T. Norin, R. Ern, J. Overgaard, T. Wang, D.J. McKenzie, S. Lefevre, G.E. Nilsson, N.B. Metcalfe, A.J.R. Hickey, J. Brijs, B. Speers-Roesch, D.G. Roche, A.K. Gamperl, G.D. Raby, R. Morgan, A.J. Esbaugh, A. Gräns, M. Axelsson, A. Ekström, E. Sandblom, S.A. Binning, J.W. Hicks, F. Seebacher, C. Jørgensen, S.S. Killen, P.M. Schulte and T.D. Clark. 2018. Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology. *Journal of Experimental Biology*, 221(1): Article 1. [doi.org/10.1242/jeb.169615](https://doi.org/10.1242/jeb.169615)
- Kaiser, A., C.J. Klok, J.J. Socha, W.-K. Lee, M.C. Quinlan and J.F. Harrison. 2007. Increase in tracheal investment with beetle size supports hypothesis of oxygen limitation on insect gigantism. *PNAS*, 104: 13198–13203.
- Kajimura, M., S.J. Croke, C.N. Glover and C.M. Wood. 2004. Dogmas and controversies in the handling of nitrogenous wastes: The effect of feeding and fasting on the excretion of ammonia, urea and other nitrogenous waste products in rainbow trout. *Journal of Experimental Biology*, 207: 1993–2002.
- Kelly, K.T. 2004. Justification as Truth-Finding Efficiency: How Ockham's Razor Works. *Minds and Machines*, 14: 485–505.
- Kinne, O. 1960. Growth, Food Intake, and Food Conversion in a Euryplastic Fish Exposed to Different Temperatures and Salinities. *Physiological Zoology*, 33: 288–317.
- Klumpp, D. and C. Griffiths. 1994. Contributions of phototrophic and heterotrophic nutrition to the metabolic and growth requirements of four species of giant clam (Tridacnidae). *Marine Ecology Progress Series*, 115: 103–115.
- Kolding, J., L. Haug and S. Stefansson. 2008. Effect of ambient oxygen on growth and reproduction in Nile tilapia (*Oreochromis niloticus*). *Canadian Journal of Fisheries and Aquatic Science*, 65: 1413–1424.
- Lagler, K.F., J.E. Bardach, R.R. Miller and D.R.M. Passino. 1977. *Ichthyology*. 2<sup>nd</sup> edition. John Wiley and Sons, Inc., New York.
- Ledford, H. 2015. How to solve the world's biggest problems. *Nature News*, 525: 308–311.
- Lefevre, S., D.J. McKenzie and G.E. Nilsson. 2017. Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Global Change Biology*, 23: 3449–3459.
- Lefevre, S., D.J. McKenzie and G.E. Nilsson. 2018. In modelling effects of global warming, invalid assumptions lead to unrealistic projections. *Global Change Biology*, 24: 553–556.
- Lefranc, G. 1966. Note préliminaire sur la morue du sud de la mer du nord et de la région du Pas-De-Calais. *Science et Pêche Bull. Inst. Pêches marit*, 154: 1–8.
- Liang, C. 2021. Relationships between  $W_m$  and  $W_i$ . In: Supplementary Materials of D. Pauly. D. Pauly. 2021 The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Science Advances*, 7: eabc6050.
- Liang, C., W. Xian and D. Pauly. 2018. Impacts of Ocean Warming on China's Fisheries Catches: An Application of "Mean Temperature of the Catch" Concept. *Frontier in Marine Science*, 5. [doi.org/10.3389/fmars.2018.00026](https://doi.org/10.3389/fmars.2018.00026)
- Lipinski, M.R. and M.A. Roeleveld. 1990. Minor extension of the von Bertalanffy growth theory. *Fisheries Research*, 9: 367–371.
- Liu, R.K. and R.L. Walford. 1970. Observations on the lifespans of several species of annual fishes and of the world's smallest fishes. *Experimental Gerontology*, 5: 241–246.
- Liu, R.K. and R.L. Walford. 1966. Increased Growth and Life-span with Lowered Ambient Temperature in the Annual Fish, *Cynolebias adloffii*. *Nature*, 212: 1277–1278.
- Lutz, R.A. and D.C. Rhoads. 1977. Anaerobiosis and a Theory of Growth Line Formation. *Science*, 198: 1222–1227.
- Marshall, D.J. and C.R. White. 2019. Aquatic Life History Trajectories Are Shaped by Selection, Not Oxygen Limitation. *Trends in Ecology & Evolution*, 34: 182–184.
- Maxime, V. 2008. The physiology of triploid fish: Current knowledge and comparisons with diploid fish. *Fish and Fisheries*, 9: 67–78.
- McClain, C.R., M.A. Balk, M.C. Benfield, T.A. Branch, C. Chen, J. Cosgrove, A.D.M. Dove, L.C. Gaskins, R.R. Helm, F.G. Hochberg, F.B. Lee, A. Marshall, S.E. McMurray, C. Schanche, S.N. Stone and A.D. Thaler. 2015. Sizing ocean giants: patterns of intraspecific size variation in marine megafauna. *PeerJ*, 3. [doi.org/10.7717/peerj.715](https://doi.org/10.7717/peerj.715)

- Messmer, V., M.S. Pratchett, A.S. Hoey, A.J. Tobin, D.J. Coker, S.J. Cooke and T.D. Clark. 2017. Global warming may disproportionately affect larger adults in a predatory coral reef fish. *Global Change Biology*, 23: 2230–2240.
- Meyer, K.A. and D.J. Schill. 2020. The Gill-Oxygen Limitation Theory and size at maturity/maximum size relationships for salmonid populations occupying flowing waters. *Journal of Fish Biology*, 98(1): 44–49. [doi.org/10.1111/jfb.14555](https://doi.org/10.1111/jfb.14555)
- Mitani, F. 1970. A comparative study on growth patterns of marine fishes. Symposium on growth of fishes. *Bulletin of the Japanese Society of Scientific Fisheries*, 36: 258–265.
- Morais, R.A. and D.R. Bellwood. 2018. Global drivers of reef fish growth. *Fish and Fisheries*, 19: 874–889.
- Morales-Nin, B. 1986a. Chemical composition of the otoliths of the sea bass (*Dicentrarchus labrax* Linnaeus, 1758) (Pisces, Serranidae). *Cybium*, 10: 115–120.
- Morales-Nin, B. 1986b. Structure and composition of otoliths of Cape hake *Merluccius capensis*. *South African Journal of Marine Science*, 4: 3–10.
- Morbey, Y.E. 2018. Female-biased dimorphism in size and age at maturity is reduced at higher latitudes in lake whitefish *Coregonus clupeaformis*. *Journal of Fish Biology*, 93: 40–46.
- Morbey, Y.E. and B. Shuter. 2013. Intermittent breeding in the absence of a large cost of reproduction: Evidence for a non-migratory, iteroparous salmonid. *Ecosphere*, 4(12): 1–18.
- Muir, B.S. 1969. Gill Dimensions as a Function of Fish Size. *Journal of the Fisheries Research Board of Canada*, 26(1): 165–170.
- Muir, B.S. and G.M. Hughes. 1969. Gill Dimensions for Three Species of Tunny. *Journal of Experimental Biology*, 51(2): 271–285.
- Niimi, A.J. and F.W.H. Beamish. 1974. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. *Canadian Journal of Zoology*, 52(4): 447–456.
- Nilsson, G.E., A. Dymowska and J.A.W. Stecyk. 2012. New insights into the plasticity of gill structure. *Respiratory Physiology & Neurobiology*, 184: 214–222.
- Norton, S.F., Z.A. Eppley and B.D. Sidell. 2000. Allometric scaling of maximal enzyme activities in the axial musculature of striped bass, *Morone saxatilis* (Walbaum). *Physiological and Biochemical Zoology*, 73: 819–828.
- O’Dor, R.K. and J.A. Hoar. 2000. Does geometry limit squid growth? *ICES Journal of Marine Science*, 57: 8–14.
- Oikawa, S. and Y. Itazawa. 1985. Gill and Body Surface Areas of the Carp in relation to Body Mass, With Special Reference to The Metabolism-Size Relationship. *Journal of Experimental Biology*, 117: 1–14.
- Olson, K.R. and P.O. Fromm. 1971. Excretion of urea by two teleosts exposed to different concentrations of ambient ammonia. *Comparative Biochemistry and Physiology Part A: Physiology*, 40: 999–1007.
- van Oosten, J. 1923. The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages. *Zoologica*, 2: 380–412.
- Oreskes, N. 2013. Earth science: How plate tectonics clicked. *Nature News*, 501: 27–29.
- Palomares, M.L.D. and D. Pauly. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Research*, 49: 447–453.
- Palzenberger, M. and H. Pohla. 1992. Gill surface area of water-breathing freshwater fish. *Review in Fish Biology and Fisheries*, 2: 187–216.
- Pannella, G. 1971. Fish Otoliths: Daily Growth Layers and Periodical Patterns. *Science*, 173: 1124–1127.
- Pannella, G. 1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes, p. 28–39. In: T.B. Bagenal (ed). *The Ageing of Fish*. Unwin Brothers Ltd, Old Woking, Surrey, England.
- Parker, G.A., S.A. Ramm, J. Lehtonen and J.M. Henshaw. 2018. The evolution of gonad expenditure and gonadosomatic index (GSI) in male and female broadcast-spawning invertebrates. *Biological Reviews of the Cambridge Philosophical Society*, 93: 693–753.
- Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy’s theory of growth. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung*, 28: 251–282.
- Pauly, D. 1982. Further evidence for a limiting effect of gill size on the growth of fish: the case of the Philippine goby (*Mistichthys luzonensis*). *Kalikasan/Philippines Journal of Biology*, 11: 379–383.
- Pauly, D. 1984. A mechanism for the juvenile-to-adult transition in fishes. *ICES Journal of Marine Science*, 41: 280–284.
- Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. *United States Fishery Bulletin*, 4: 827–842.

- Pauly, D. 1998. Why squids, though not fish, may be better understood by pretending they are, p. 47–58. In: A.I.L. Payne, M.R. Lipinski, M.R. Clarke and M.A.C. Roeleveld (eds). *Cephalopod biodiversity, Ecology and Evolution*. South African Journal of Marine Science.
- Pauly, D. 2010. *Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals*. Excellence in Ecology Series vol. 22. International Ecology Institute, Oldendorf/Luhe.
- Pauly, D. 2018. Learning from peer-reviews: The Gill-Oxygen Limitation Theory and the Growth of Fishes and Aquatic Invertebrates, p. 53–70. In: D. Pauly and V. Ruiz-Leotaud (eds). *Marine and Freshwater Miscellanea*. Fisheries Centre Research Reports 26(2).
- Pauly, D. 2019a. A précis of Gill-Oxygen Limitation Theory (GOLT), with some Emphasis on the Eastern Mediterranean. *Mediterranean Marine Science*, 20: 660–668.
- Pauly, D. 2019b. Female Fish Grow Bigger - Let's Deal with It. *Trends in Ecology & Evolution* 34: 181–182.
- Pauly, D. 2019c. *Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals*. 2<sup>nd</sup> edition. Excellence in Ecology Series vol. 22. International Ecology Institute, Oldendorf/Luhe.
- Pauly, D. 2021. The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Science Advances*, 7: eabc6050.
- Pauly, D. and W.W.L. Cheung. 2017a. Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global Change Biology*, 24: e15–e26.
- Pauly, D. and W.W.L. Cheung. 2017b. Is climate change shrinking our fish? *Environmental Science Journal for Teens*, 1–4.
- Pauly, D. and W.W.L. Cheung. 2018. On confusing cause and effect in the oxygen limitation of fish. *Global Change Biology*, 24: e743–e744.
- Pauly, D. and E. Chu. 2021. Key Traits of Amphioxus Species (Cephalochordata) and the GOLT, p. 59-70. In: D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III*. Fisheries Centre Research Report **XX(XX)**.
- Pauly, D. and Ç. Keskin. 2017. Temperature constraints shaped the migration routes of mackerel (*Scomber scombrus*) in the Black Sea. *Acta Adriatica*, 58: 339–346.
- Pauly, D., C. Casal and M.L.D. Palomares. 2000. DNA, cell size and fish swimming, p. 254, Box 34. In: R. Froese and D. Pauly (eds). *FishBase 2000: Concepts, Design and Data*. ICLARM, Los Baños.
- Pearl, J. and D. Mackenzie. 2018. *The Book of Why: The New Science of Cause and Effect*. 1<sup>st</sup> edition. Basic Books, New York. 432 p.
- Peck, L.S. and G. Chapelle. 2003. Reduced oxygen at high altitude limits maximum size. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270: S166–S167.
- Pinsky, M.L., B. Worm, M.J. Fogarty, J.L. Sarmiento and S.A. Levin. 2013. Marine Taxa Track Local Climate Velocities. *Science*, 341: 1239–1242.
- Pörtner, H.-O. 2010. Oxygen-and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, 213: 881–893.
- Pörtner, H.-O., C. Bock and F.C. Mark. 2017. Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. *Journal of Experimental Biology*, 220: 2685–2696.
- Pörtner, H.-O., C. Bock and F.C. Mark. 2018. Connecting to ecology: a challenge for comparative physiologists? Response to 'Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology.' *Journal of Experimental Biology*, 221. [doi.org/10.1242/jeb.174185](https://doi.org/10.1242/jeb.174185)
- Pörtner, H.-O. and M.A. Peck. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of fish biology*, 77: 1745–1779.
- Popper, K. 2002. *The Logic of Scientific Discovery*. 3<sup>rd</sup> edition. Routledge, London.
- Priede, I.G. 1985. Metabolic scope in fishes, p. 33–64. In: P. Tyler and P. Calow (eds). *Fish Energetics: New Perspectives*. Croom Helm, London.
- Prince, E.D. and C.P. Goodyear. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography*, 15: 451–464.
- Pütter, A. 1920. Studien über physiologische Ähnlichkeit VI. Wachstumsähnlichkeiten. *Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere*, 180: 298–340.
- Quince, C., P.A. Abrams, B.J. Shuter and N.P. Lester. 2008. Biphasic growth in fish I: Theoretical foundations. *Journal of Theoretical Biology*, 254: 197–206.
- Ralston, S. 1985. A novel approach to ageing tropical fish. *ICLARM Newsletter*, 8: 14–15.
- Randall, J.E., J.L. Earle, R.L. Pyle, J.D. Parrish and T. Hayes. 1993. Annotated Checklist of the Fishes of Midway Atoll, Northwestern Hawaiian Islands. *Pacific Science*, 47: 356–400.
- Reid, A.J., A.K. Carlson, I.F. Creed, E.J. Eliason, P.A. Gell, P.T.J. Johnson, K.A. Kidd, T.J. MacCormack, J.D. Olden, S.J. Ormerod, J.P. Smol, W.W. Taylor, K. Tockner, J.C. Vermaire, D. Dudgeon and S.J. Cooke. 2019.

- Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94: 849–873.
- Rezzolla, D. and T. Storai. 2010. “Whale Shark Expedition”: Observations on *Rhincodon typus* from Arta Bay, Gulf of Tadjoura, Djibouti Republic, Southern Red Sea. *Cybium*, 34: 195–206.
- Ricker, W.E. 1958. *Handbook of Computations for Biological Statistics of Fish Populations*. Bulletin No. 119. Fisheries Research Board of Canada, Ottawa.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, 191, 382 p.
- Ricker, W.E. 1973. Linear Regressions in Fishery Research. *Journal of Fisheries Board of Canada*, 30: 409–434.
- Rideout, R., G. Rose and M. Burton. 2005. Skipped spawning in female iteroparous fishes. *Fish and Fisheries*, 6: 50–72.
- Robinson, D.P., M.Y. Jaidah, S.S. Bach, C.A. Rohner, R.W. Jabado, R. Ormond and S.J. Pierce. 2017. Some like it hot: Repeat migration and residency of whale sharks within an extreme natural environment. *PLOS ONE*, 12(9): e0185360. [doi.org/10.1371/journal.pone.0185360](https://doi.org/10.1371/journal.pone.0185360)
- Rodnick, K.J., A.K. Gamperl, K.R. Lizars, M.T. Bennett, R.N. Rausch and E.R. Keeley. 2004. Thermal tolerance and metabolic physiology among redband trout populations in south-eastern Oregon. *Journal of Fish Biology*, 64: 310–335.
- Saemundsson, B. 1923. On the Age and growth of the cod *Gadus callarias* L. in Icelandic waters. *Meddelelser fra Kommissionen for Havundersogelser, Series: Fiskeri*, 7(3): 1–35.
- Savitz, J. 1969. Effects of Temperature and Body Weight on Endogenous Nitrogen Excretion in the Bluegill Sunfish (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada*, 26: 1813–1821.
- Savitz, J. 1971. Effects of Starvation on Body Protein Utilization of Bluegill Sunfish (*Lepomis macrochirus* Rafinesque) with a Calculation of Caloric Requirements. *Transactions of the American Fisheries Society*, 100: 18–21.
- Svärdson, G. 1943. *Studien über den Zusammenhang zwischen Geschlechtreife und Wachstum bei Lebistes*. Meddelanden från Statens Undersöknings- och Försöksanstalt för Sötvattensfisket, nr. 21. Mitt. Anst. F. Binnenfischerei bei Drottingholm, Stockholm.
- Schindler, D.W. 1997. Widespread Effects of Climatic Warming on Freshwater Ecosystems in North America. *Hydrological Processes*, 11: 1043–1067.
- Schmidt-Nielsen, K. 1997. Energy metabolism, p. 169–216. In: J.B. Duke (ed). *Animal Physiology: Adaptation and Environment*. Cambridge University Press, Cambridge.
- Scott, K. 2005. Allometry of gill weights, gill surface areas, and foot biomass  $\delta^{13}\text{C}$  values of the chemoautotroph-bivalve symbiosis *Solemya velum*. *Marine Biology*, 147: 935–941.
- Sebens, K.P. 1987. The Ecology of Indeterminate Growth in Animals. *Annual Review of Ecology and Systematics*, 18: 371–407.
- Sella, M. 1929. Migrazioni e habitat del tonno (*Thunnus thynnus* L.) studiati col metodo degli ami, con osservazioni su l'accrescimento, sul regime delle tonnare ecc. *Memoria Reale Comitato Talassografico Italiano*, 156: 511–542.
- Shul'man, G.E. 1974. *Life cycles of fish; physiology and biochemistry*. Wiley, New York. 258 p.
- Somero, G.N. 1995. Proteins and temperature. *Annual Review of Physiology*, 57: 43–68.
- Somero, G.N. and J.J. Childress. 1980. A Violation of the Metabolism-Size Scaling Paradigm: Activities of Glycolytic Enzymes in Muscle Increase in Larger-Size Fish. *Physiological Zoology*, 53: 322–337.
- Swift, S.A., A.S. Bower and R.W. Schmitt. 2012. Vertical, horizontal, and temporal changes in temperature in the Atlantis II and Discovery hot brine pools, Red Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 64: 118–128.
- Te Winkel, L.E. 1935. A study of *Mistichthys luzonensis* with special reference to conditions correlated with reduced size. *Journal of Morphology*, 58: 463–535.
- Thompson, K.S. [Translator] 1910. *The Work of Aristotle. Vol. IV*. Clarendon Press, Oxford.
- Thompson, K.S. 1972. An attempt to reconstruct evolutionary changes in the cellular DNA content of lungfish. *Journal of Experimental Zoology*, 180: 363–371.
- Ursin, E. 1967. A Mathematical Model of Some Aspects of Fish Growth, Respiration, and Mortality. *Journal of the Fisheries Board of Canada*, 24: 2355–2453.
- Ursin, E. 1979. Principles of growth in fishes, p. 63–87. In: P.J. Miller (ed). *Fish Phenology: anabolic adaptiveness in teleosts*. Academic Press, London.
- Vakily, J.M. 1992. Determination and comparison of bivalve growth, with emphasis on Thailand and other tropical areas. *ICLARM Technical Report 36*. 125 p.

- Verberk, W.C.E.P. and D.T. Bilton. 2011. Can Oxygen Set Thermal Limits in an Insect and Drive Gigantism? *PLOS ONE*, 6: e22610.
- Verberk, W.C.E.P., D.T. Bilton, P. Calosi and J.I. Spicer. 2011. Oxygen supply in aquatic ectotherms: Partial pressure and solubility together explain biodiversity and size patterns. *Ecology*, 92: 1565–1572.
- Vogel, S. 1981. *Life in Moving Fluids: The Physical Biology of Flow*. Princeton University Press, Princeton, NJ. 484 p.
- Weatherley, A.H. and H.S. Gill. 1987. *The Biology of Fish Growth*. Academic Press, London. 443 p.
- Webb, P.W. 1978. Partitioning of energy into metabolism and growth, p. 184–214. In: S.D. Gerking (ed). *Ecology of Freshwater Fish Production*. Blackwell Scientific Publications, Oxford.
- West, G.B., J.H. Brown and B.J. Enquist. 1997. A General Model for the Origin of Allometric Scaling Laws in Biology. *Science*, 276: 122–126.
- West, G.B., J.H. Brown and B.J. Enquist. 2001. A general model for ontogenetic growth. *Nature*, 413: 628–631.
- Wilson, E.O. 1998. *Consilience: The Unity of Knowledge*. Alfred A. Knopf, Inc, New York. 384 p.
- Winberg, G.G. 1960. *Rate of metabolism and food requirements of fishes, and New information on metabolic rate in fishes*. Translation Series No.194. Fisheries Research Board of Canada, Dartmouth, NS. 250 p.

## Supplementary Materials

### Relationships between $W_m$ and $W_i$

Given:

$$W_i = W_\infty \cdot (1 - (D/b))^{b/D} \quad \dots(1)$$

$$W_i / W_\infty = (1 - (D/b))^{b/D} \quad \dots(2)$$

$$A^{-1} = (W_m^{1/b} / W_\infty^{1/b})^D \quad (3)$$

$$A^{-1} = (W_m / W_\infty)^{D/b} \quad (4)$$

$$W_m = W_\infty (1/A)^{b/D} \quad (5)$$

By combining equation (2) and (5), we get

$$W_i / W_m = (1 - (D/b))^{b/D} / A^{-b/D} \quad \dots(6)$$

When  $W_i > W_m$ , we also have:

$$(1 - (D/b))^{b/D} > A^{-b/D} \quad \dots(7)$$

which implies

$$(1 - (D/b)) > A \quad \dots(8)$$

Given that  $D = b \cdot (1-d)$ , then:

**$d > A^{-1}$  implies  $W_i > W_m$**

**$d \approx A^{-1}$  implies  $W_i \approx W_m$**

**$d < A^{-1}$  implies  $W_i < W_m$**

Derivation courtesy of Dr. Cui Liang,  
Chinese Academy of Science, Qingdao, China

**Table S1.** Data on 34 fish species (f = female; m = males) used to infer the underlying relationship between their length at first maturity ( $L_m$ ; cm) and their asymptotic length ( $L_\infty$ ; cm); 'a·100' is ; see Figure 5C<sup>a)</sup>

No.	Species	$L_m$	$L_\infty$	a·100	$W_\infty$ (g)	$D^{b)}$	$L_m^D$	$L_\infty^D$	Source
1	<i>Clupea harengus</i>	24	30	0.75	203	0.73	10.2	12.0	B&H'59
2	<i>Clupea harengus</i>	28	34	0.75	295	0.71	10.7	12.2	B&H'59
3	<i>Clupea harengus</i>	25	34	0.75	295	0.71	9.83	12.2	B&H'59
5	<i>Coregonus clupeaformis</i>	27	50	1.7	2125	0.62	7.72	11.3	B&H'59
6	<i>Cottus gobio</i> (f)	5	6.5	1.55	4	0.91	4.33	5.49	B&H'59
8	<i>Cottus gobio</i> (f)	4.6	7.2	1.55	6	0.89	3.89	5.79	B&H'59
7	<i>Cottus gobio</i> (m)	5	6.5	1.55	4	0.91	4.33	5.49	B&H'59
9	<i>Cottus gobio</i> (m)	4.2	7.3	1.55	6	0.89	3.59	5.87	B&H'59
10	<i>Euthynnus affinis</i>	45	100	1.6	16000	0.53	7.52	11.5	M.'70
11	<i>Euthynnus alletteratus</i>	38	102	1.6	17000	0.52	6.63	11.1	B&H'59
12	<i>Gadus chalcogrammus</i>	31.2	55	0.8	1300	0.64	9.04	13	M.'70
13	<i>Gadus microcephalus</i>	55	94	1.3	11000	0.54	8.71	11.6	M.'70
14	<i>Gadus microcephalus</i>	60	105	1.3	15000	0.53	8.76	11.8	M.'70
15	<i>Gadus morhua</i>	85	134	0.85	20450	0.52	10.1	12.8	B&H'59
16	<i>Gadus morhua</i>	70	105	0.85	10000	0.55	10.3	12.9	M.'70
17	<i>Gasterosteus aculeatus</i>	3.6	6.7	1	3	0.93	3.29	5.86	B&H'59
18	<i>Hippocampus erectus</i>	7	14	0.5	14	0.85	5.23	9.42	B&H'59
19	<i>Hippocampus erectus</i>	2	2	0.5	0.04	1.13	2.19	2.19	B&H'59
20	<i>Hippoglossus hippoglossus</i> (f)	132	250	1.8	281250	0.39	6.71	8.61	B&H'59
21	<i>Hippoglossus hippoglossus</i> (m)	95	170	1.8	88434	0.45	7.76	10.1	B&H'59
22	<i>Katsuwonus pelamis</i>	46.5	106	2.6	31000	0.5	6.82	10.3	M.'70
23	<i>Katsuwonus pelamis</i>	70	180	2.5	140000	0.43	6.21	9.33	B&H'59
24	<i>Katsuwonus pelamis</i>	55	157	2.5	95000	0.45	6.07	9.73	B&H'59
25	<i>Labidesthes sicculus</i>	7	9.2	1.2	9	0.88	5.54	7.05	B&H'59
26	<i>Leuresthes tenuis</i> (f)	11.9	18.4	1	60	0.79	7.07	9.98	B&H'59
27	<i>Leuresthes tenuis</i> (m)	11	17.8	1	55	0.79	6.65	9.72	B&H'59
28p	<i>Limanda aspera</i>	23	50	1.2	1500	0.64	7.44	12.2	M.'70
29	<i>Melanogrammus aeglefinus</i>	26	60	0.75	890	0.66	8.59	14.9	B&H'59
30	<i>Merluccius merluccius</i> (f)	27	60	0.75	1620	0.63	7.98	13.2	B&H'59
31	<i>Merluccius merluccius</i> (m)	23	44	0.75	640	0.18	8.43	13.1	B&H'59
32	<i>Phoxinus phoxinus</i>	4	9	1.1	8	0.88	3.39	6.91	B&H'59
33	<i>Pleuronectes platessa</i>	48.5	68.5	1	3200	0.6	10.3	12.6	M.'70)
34	<i>Poecilia reticulata</i>	1.9	2.36	0.9	0.12	1.08	2.00	2.53	U.'69
35	<i>Poecilia reticulata</i> (m)	1.4	1.5	0.9	0.03	1.14	1.47	1.59	S.'43
36	<i>Pollachius virens</i>	71	107	0.95	11640	0.54	9.99	12.5	B&H'59
37	<i>Pseudopleuronectes americanus</i>	32	44	1.6	1365	0.64	9.19	11.3	B&H'59
38	<i>Pungitius pungitius</i>	3.7	4.3	0.5	0.4	1.02	3.8	4.43	B&H'59
39	<i>Rastrelliger brachysoma</i>	17	22	1.2	128	0.75	8.37	10.2	B&H'59
40	<i>Rheinhardtius hippoglossoides</i>	60	90	1.8	13000	0.54	9.12	11.4	M.'70

**Table S1.** (continued)

No.	Species	$L_m$	$L_\infty$	$a \cdot 100^{b)}$	$W_\infty$ (g)	$D^c)$	$L_m^D$	$L_\infty^D$	Source
41	<i>Sardinops sagax</i>	18.5	26	1	176	0.74	8.66	11.1	B&H'59
42	<i>Scomber japonicus</i>	32	40	1	640	0.68	10.6	12.3	B&H'59
43	<i>Scomber japonicus</i>	30.5	46	1	975	0.66	9.54	12.5	B&H '59
44	<i>Sprattus sprattus</i>	13	16	0.7	29	0.82	8.19	9.71	B.'63
45	<i>Sprattus sprattus</i>	10.5	14	0.7	19	0.84	7.21	9.18	B.'63
46	<i>Sprattus sprattus</i>	9	12.5	0.7	14	0.85	6.47	8.56	B.'63
4	<i>Sprattusprattus</i>	10	13	0.7	15.4	0.85	7.08	8.85	B&H'59
47	<i>Thunnus alalunga</i>	90	124	1.9	36000	0.49	9.07	10.6	M.'70
48	<i>Thunnus alalunga</i>	89	136	1.9	48000	0.48	8.62	10.6	M.'70
49	<i>Thunnus alalunga</i>	86	160	1.6	65000	0.47	8.11	10.9	B&H '59
50	<i>Thunnus albacares</i>	100	190	1.6	110000	0.44	7.59	10.1	M. '70
51	<i>Thunnus maccoyii</i>	120	190	2	140000	0.43	7.84	9.55	M.'70
52	<i>Thunnus obesus</i>	95	180	2	120000	0.44	7.42	9.82	B&H'59
53	<i>Thunnus obesus</i>	92	170	2	100000	0.44	7.31	9.58	B&H'59
54	<i>Thunnus tonggol</i>	48	105	1.6	18500	0.52	7.49	11.2	B&H'59
55	<i>Trisopterus minutus</i> (f)	13	24	1	138	0.75	6.85	10.8	B&H'59
56	<i>Trisopterus minutus</i> (m)	11	20	1	80	0.77	6.34	10	B&H'59

a) Data used previously (Pauly 1984), but not publicly available;

b) The  $a$ -values refer to length-weight relationships of the form  $W = a \cdot L^3$ ;

c) The estimates of  $D$  stem from  $D = 3(1-d)$ , with  $d = 0.6742 + 0.03574 \cdot \log(W_\infty)$ ;  $W_\infty$  in grams (Pauly 1981, 2019c)

d) B.'63 = Beverton (1963); B&H'59 = Beverton and Holt (1959); M.'70 = Mitani (1970); S.'43 = Svärson (1943); U.'69 = Ursin (1969)

## RESPONSES TO REVIEWERS

Dear Editor,

Please find below my responses to the two generally positive reviews (*in italics*) that my original submission of ‘The Gill-Oxygen Theory (GOLT) and its critics’ received.

To facilitate your evaluation that I have taken the reviewers’ comment seriously, I have added to the responses new line numbers to the line numbers in the original submission that were mentioned by the reviewers<sup>22</sup>.

Cheers

Daniel Pauly

### Reviewer: 1

*1) General: This is an interesting article that makes several important points and contributes to the debate around size/growth relationships in fishes, especially as it relates to global warming. It provides a detailed, point by point refutation of an important hypothesis. The rebuttal is extremely thorough and detailed. As such, it makes important contributions to the literature.*

I thank the reviewer for this positive assessment.

*2) However, I have a couple of serious concerns. First, the author ignores the blood side of the equation (literally and figuratively). This is exacerbated by the simplistic analogy of the gill as a page of paper in a book. In this analogy, the gills are static, and all that can change about the gills to improve gas exchange is to add more “pages”.*

This is a misunderstanding. The analogy of gills (of rather gill lamellae) with pages in a book was not made by me, but by my critics (Lefevre et al. 2017, p. 3450), who argued that the surface area of the page of a book would increase in proportion of its volume (length x height x depth), that gills, which they claimed behave like the page of a book, could not be limiting oxygen supply. Thus, they wrote “A simple way to explain the geometry of the gills is by analogy to a book, where pages correspond to lamellae. It is easy to grasp that if you double it’s the thickness of a book (thereby doubling its volume and mass), you can fit in twice the number of pages and, therefore, the total surface area of the page is also doubled”.

As this was their only attempt at a coherent argument, I cannot avoid dealing with it, and deal with books as well, by pointing out that you can’t read through a book, but that it must be open to be read and thus used. I have now rephrased this argument so it will hopefully be understood as their, not mine.

As for blood, the volume of blood in fish (and other animals that have blood) scales with the volume of their body, as stated in Schmidt-Nielsen’s classic, which does not mention changes of blood volume during their ontogeny. Thus, blood is not a limiting factor for growth as defined here. The dimensional

---

<sup>22</sup> The line numbers have been left here, although they do not appear in the above version of the article.

tension that is at the heart of the GOLT, moreover, must also apply to WBE which lack gills (despite the first letter of GOLT...) and blood (see also Point # 4).

3) *Nothing is said of how the gill could improve gas exchange performance by changing the pattern of perfusion of the lamellae (e.g. sending more or less blood to peripheral channels) or changing blood residence time by altering branchial blood flow.*

A sentence dealing with these two processes has been added between lines 184 and 185 (now lines 185-188). It states that neither of them scales such that they could offset the dimensional tension between the cumulative surface area of the gill lamellae and the volume of a growing fish (or another water-breathing ectotherm).

4) *...nor is discussion made of longer-term performance changes by actually remodeling to reduce water-blood diffusion distance. To be fair, this has rarely been considered in the GOLT community. Yet, such changes could allow gas exchange to keep pace with body size, even though the morphometric values were not.*

Unfortunately, there is not yet a 'GOLT community' (though hopefully, there will be once this paper is published). Therefore, it is still up to me to argue that reducing the water-blood diffusion distance cannot be reduced at will, and that such reduction wouldn't scale, even if it were possible (see line 209 [now 212] and also argument (3) above).

5) *Second, and I admit up front that this is a matter of style rather than content, the author, in an effort to make his (reasonable) points, resorts to hyperbole and unfortunately uses words like "astonishing", "suspicious", "strange", "baffled", and "whimsical" to describe the actions and attitudes of those who oppose the GOLT. In doing so, he only undermines his own credibility.*

Agreed; these words were all replaced by less-charged terms. Thus, 'astonishing' was replaced by 'very questionable', 'suspicious' by 'unfortunate' (as suggested by this reviewer, see below), 'strange' by 'disconcerting', 'baffled' by 'surprised', and 'whimsical' by 'somehow'.

6) *Specific Comments. Line 2. Title: Why emphasize only critics, excluding supporters?*

If the editor insists on a change of the title, I will have to go along. I would do so very reluctantly, however, because at present, the GOLT has fewer supporters than critics. I explain in the Introduction that I think the GOLT will be examined fairly (i.e., rigorously tested) only after scurrilous critiques are dealt with (which this article does). I assume that if it were published, the number of its supporters will begin to outgrow the critics.

7) *Line 12. WBE not defined.*

Thanks for pointing out this oversight. This is now rectified in line 11 (now line 14).

8) *Lines 22-33. This section is largely superfluous, and should be curtailed or eliminated. By defining what "this attitude" is in a phrase, the article could easily start on Line 34.*

Agreed; this section was curtailed, as suggested (see new line 25). Completely eliminating this section doesn't work because it introduces the concept of atheoretical 'ad hoc' hypotheses which are a running theme in this article.

9) *Lines 38. Not clear. Do you mean that the GOLT is being introduced to the readers who don't already know about it?*

This article is meant to introduce the GOLT to colleagues who don't know it and re-introduce it to colleagues who may have casually dismissed it (see new line 38-39). I have slightly modified Line 38 to express this.

10) *Lines 45. Discredit is a better than "knock down"*

Agreed; changed as suggested (see new line 45).

11) *Lines 53-55. This seems to me to be seriously overstated. How is the distribution of almost all marine fishes (or fishes in large lakes, for that matter) dependent on oxygen and (once below the surface waters) temperature? I suggest toning this down.*

Here, I must respectfully disagree, as these lines can be seen as summarizing the whole paper. However, I should have cited here an important review of oxygen as a 'resources' which very much backs claim in Line 53-55 (see Kramer, D.L. 1987. Dissolved oxygen and fish behavior. *Environmental Biology of Fishes* 7: 47-55). This is now done (new line 53).

*Line 158. Point III is a not an argument, as the points in the rest of the list, but rather a question. Rephrase.*

Agreed; done (see new line 158).

12) *Line 170-174. This is an interesting section, but it doesn't address certain aspects of gill remodeling – i.e. more lamellae (definitely not like pages of a book) or even a decrease in the water-blood diffusion distances. Moreover, it doesn't address the perfusion side. What about changes, especially increases, in the rate of blood flow and the residence time of RBCs in the lamellae themselves?*

As explained above (Item 2), the book page analogy was not mine. Equation 6 in Line 202 (now line 205) includes the 3 factors which determine how much O<sub>2</sub> can diffuse through gill lamellae into the blood of fish, or through the integument of a small, gill-less WBE<sup>23</sup>. The water-blood distance (or the integument thickness) cannot continuously decline as the volume of a WBE increases. Accelerating the flow of blood through the gill lamellae would not help either, as the rate of O<sub>2</sub> diffusion is the limiting factor, and not the removal of the O<sub>2</sub> that has diffused through the lamellae. Thus, even if the venous O<sub>2</sub>-free blood entering the gill were flowing at high speed through the gills (i.e., with a small residence time), this fast-flowing blood could still only pick up the oxygen that had diffused across the water-blood distance, and not more.

---

<sup>23</sup> As, e.g., in the case of lancelets (Pauly and Chu 2021) [Note added in January 2021]

13) *Line 175-176. Ditch the analogy, which is weak at best.*

As stated above, the gill-lamellae-as-book-page analogy is not mine. It is however, the most serious attempt by others to refute the core tenet of the GOLT, based on a (flawed) dimensional argument. If I don't deal with it here (new line 175-179), it will continue to haunt all discussions about the GOLT.

14) *Line 188. Replace astonishing with another adjective.*

Agreed; done (new line 192).

15) *Line 192. Replace "suspicious" with "unfortunate".*

Agree; done (new line 196).

16) *Line 259. Not only are larvae small representatives of the species, but they are physiologically different from adults, even deriving some gas exchange across their integument.*

Agreed; it is now stated (new line 264) that teleost larvae breathe through their integument, and a supporting reference was added.

17) *Line 281-287. You mention 4 sets of observation that contradicts the hypothesis. Given the importance of these, you should provide references for each of them.*

Each of these 4 set of observations is commented further below in one or more paragraphs that present the evidence for them (see new lines 297, 306, 319 and 374 for the start of the presentation of the evidence for each of the 4 sets of observations). The presentation of this evidence requires a context; simply adding references after each of the 4 sets wouldn't do them justice.

18) *Line 288-289. Aquarium fish can hardly be held up in any way as representative of broader populations. They don't breed for a myriad of reasons – type of food, photoperiod, temperature, density, etc. etc... and etc. You should be careful of criticizing authors who at least cite references while not similarly supporting your observations the same way.*

Agreed: aquarium fish may not spawn for a variety of reasons. However, the point that was made was not about the reasons they have not to spawn, but about the fact that they stop growing (i.e., reach a maximum size and maintain it) in spite of not having spawned. Given the high frequency of such occurrences (i.e., non-reproducing fish reaching a maximum size similar to that of reproducing fish despite food given to them *ad libitum*), we simply cannot maintain that it is spawning which limits the size of fish.

Two aquarium books are now cited (from the dozens that could be used for such purpose) which report maximum sizes reached in aquarium that are similar to the maximum size of the reproducing conspecifics in the wild. (See new lines 297-301).

19) *Line 445. You criticize by saying “no evidence if presented....”. This places an additional burden upon the author to substantiate with references as many of his points as possible. (E.g. see my comment immediately above.)*

Agreed. The sentence starting with ‘No evidence in presented...’ was deleted because it was not a good argument to make (absence of evidence of not evidence is really not absence of evidence!). Also, the second argument is sufficient to counter the hypothesis in question (See new line 459-460). See response to Point 15 for the “comment immediately above”.

20) *Line 497-503. This takes on the feel of being lectured at. I suggest softening.*

Agreed; this was rewritten in fewer words as a continuous sentence (new lines 510-512).

21) *Figure 2. This figure seems gratuitous to me. What does this add other than fish farms are aerated? Of course they are. Delete figure.*

I agree to delete the figure, but very reluctantly, as I still think that confronting the readers with batteries of (undoubtedly costly) aerating devices would have helped them realize that fish farmers know something that biologists often do not seem to care about, i.e., that oxygen is really needed for growth. I have replaced the nice figure by two references, cause this argument must still be made (new line 148).

22) *Table 2. “It is actually impossible, as any book on geometry will confirm, ...” This subtle ad homonym<sup>24</sup> insult is complete unnecessary. In my opinion there is no place in scientific discourse for such an approach.*

Agreed; I have deleted the words ‘as any book on geometry will confirm’.

## **Reviewer: 2**

23) *The gill oxygen limitation theory has been set up to explain body size limitations during growth in fish, relating it to gill surface area in relation to body size. The backbone is represented by the von Bertalanffy growth equation which has an empirical basis. What is appealing about the theory is its empirical logic, building on patterns observed.*

I thank the reviewer for this positive valuation; and yes, the GOLT relies on patterns in large data sets, for which explanations are presented.

24) *Evidence is mostly indirect. In light of multiple components potentially contributing to oxygen limitations the link to gill surface area may just be correlative or represent one of several system components involved. Opponents have developed their own rationale why such reasoning focusing on gill surface area may not work. I will not go into who is right or wrong and focus on where I see gaps in the storyline of GOLT and where the narrative needs tightening.*

---

<sup>24</sup> Here, I did not dare to mention that insults are never ‘ad homonym’, but rather *ad hominem*.

Agreed; when, as is attempted here, a theory such as the GOLT is to challenge (or overthrow) a set of explanations for various phenomena by another set of explanations thought to be more 'correct' (for lack of a better term), what one does (1) assemble correlative studies that are compatible with the new explanations, (2) hope that these new studies and their interpretation survive successive tests

*25) What is missing on both sides of the argument is a step by step full traceability of the evidence. This leaves the impression of a debate on interpretation of empirical observations.*

This article is indeed part of “*a debate on interpretation of empirical observations*”. A mountain of empirical observations on the growth, respiration distribution, behavior, etc. of fish and other water breathing ectotherms has been accumulated by diligent researchers in the last two centuries, and these observations have tended to be interpreted a certain way. I now propose to interpret these observations in a different way: through the GOLT. If colleagues accept that this new way of interpreting the evidence before us is plausible, they can subject the GOLT to more and more stringent tests. If the GOLT survives these tests, it will gradually seep into textbooks, then be used widely to interpret new empirical observations. If not, the present interpretations will continue to have currency, or a better set of hypotheses will emerge. This is how science progresses.

*26) I fully share the call for a theoretical basis which should be at least somewhat unifying. However, acknowledging deficiencies, limitations and open questions should be part of this and need to be called out to allow the reader to evaluate limits to understanding, the confidence / uncertainties around any conclusions and to formulate open questions. The specific examples discussed (536 to 587) are somewhat illustrative but do not provide such insight to overcome the limits in understanding. In general, the text would need explanatory notes with full traceability to literature reporting underlying evidence.*

I could cite far more references supporting the various claims in this article. However, the number of references already cited exceeds by far the limit suggested in the guidelines of *Science Advances*. Thus, I cited my 2019 book on the GOLT for issues dealt therein at length, and which the present contribution need not duplicate.

*27) While elegantly written this paper is full of assertive statements which would need to be amended / worded differently, e.g. 51 to 57 “...for water-breathing ectotherms (WBE, i.e., most fish and aquatic invertebrates), life is shaped more by the distribution and concentration of dissolved oxygen, and the temperature of the water surrounding them than by the availability of food, which is more important for endotherms (birds and mammals)” A physiologist would clearly say this differently as this comparison is simply inappropriate... Both groups need food and oxygen.*

Agreed, both groups need food and oxygen. However, the whole point of the GOLT and of this paper is that oxygen is far more difficult to extract from water than from air (due to the specific density and viscosity of the two media, and to the latter containing far more oxygen than the former). On the other hand, mammals and birds consume far more food per unit weight than WBE, except perhaps for tuna and some sharks, which can also maintain body temperatures above that of their surrounding medium.

As mentioned in Point 11 of Reviewer 1, I have added to the paragraph in question the reference to a review arguing that oxygen in fish should be treated as a ‘resource’ (like food) and which thus support my point (see new line 53).

*28) As to the basis, 72 to 74: an increase of body mass ( $dw/dt$ ) is the difference between body mass that is newly ( $Hw^d$ ) synthesized and the body mass ( $kw$ ) that becomes unusable.... The term unusable is not defined.*

Agreed; the term ‘unusable’ was replaced by ‘degraded (see new line 73)’ with ‘below’ refereeing to paragraphs immediately following.

*29) 82 to 87: When looking at the energetic basis the paper essentially introduces an allometric exponent but does not discuss the related wider literature and open questions, as well as its value. The background of the allometric coefficient would be worth exploring, also associated energetic patterns which also relate to body size. Such allometric patterns are not only found in water breathers but across the animal kingdom.*

The article introduces a number of exponents, e.g.,  $d$  in equation 1, or  $b$  in equation 3, can be isometric (e.g., when  $d = 2/3$ , or  $b = 3$ ) or allometric. For all the equations presented, the allometric cases is discussed along with the isometric case. Thus, unless the reviewer is asked to specify which ‘allometric coefficient’ is meant, I can’t respond to this comment.

*30) 88 to 93: The description of protein denaturation is not up to speed with the literature.*

The description of denaturation (new lines 87-93) is not meant to be exhaustive. Rather, it only addresses the question whether the loss of the quaternary structure of proteins (which renders protein molecules ‘unusable’) requires ATP (and hence  $O_2$ ) or not. Or put differently, it interprets denaturation as a two-step process: the first, i.e., the loss of quaternary configuration is spontaneous, requires no ‘energy’ input, and is temperature-dependent, while the second, i.e., the breakdown of molecules having lost their quaternary configuration requires ATP.

I have added to the references I originally provided the reference to a biochemistry text which support this two-step interpretation (28; D. L. Nelson, M. M. Cox, *Lehninger Principles of Biochemistry* (Freeman and Company, San Francisco, 7th edition, 2017).

*31) Line 121: the exponent of the length-weight relationship is equal to 3...? so briefly, what is the explanation?*

The explanation is that when its exponent is 3, a fish or other WBE maintains the same relationships between its linear dimensions (length, height and depth), i.e., growth is isometric. When  $b < 3$ , growth is negative allometric (i.e., the WBE gets thinner); when  $b > 3$ , growth is positive allometric (i.e., the WBE gets thicker). The exponent  $b$  in fish differ between species and between their populations, and also seasonally. Overall,  $b$  has a bell-shaped distribution, with  $b = 3$  as the mean and the mode. The reference cited to that effect (34; Froese 2006; new line 121) is the best of which I am aware.

32) 140 to 142: *There is one statement which shows that GOLT is a first and useful but not sufficiently deep grinding approach to explaining the patterns observed: talking about ...“massive challenges related to the respiration of WBE in an age of global warming, i.e., the accelerating deoxygenation of the oceans and freshwater bodies...” leading to the question whether and to what extent reduced oxygen solubility during warming is indeed a constraint at constant oxygen partial pressure. Verberk and Spicer would argue otherwise. This clearly has to be distinguished from a situation where oxygen partial pressure falls.*

Agreed: I also do not believe that the reduction of oxygen solubility with increasing water temperatures is the main problem facing water-breathing ectotherm (WBE). Rather, it is the fact that WBE are ectotherms whose oxygen requirements increase with temperature and their own size. This is the core of this paper and of the GOLT, which, however, must end somewhere. Thus, I can't elaborate here on the physics and chemistry of dissolved oxygen, and the deoxygenation of the ocean. I just show why WBE are so sensitive to it.

33) 214 to 223: *I am supportive here but while I appreciate the effort of the author to counter the arguments of the opponents the question is what counts. Most empirical data clearly show an allometric exponent below 1 and this is what needs to be explained. If the opponents want to construct a hypothetical case, they can do so but should not confuse it with reality. The picture is complex and any one sentence explanation such as the one on glycolytic enzymes becoming more important will be insufficient and will need a wider context, e.g. considering mode of life of the growing adults as well as the allometric scaling of metabolic rate.*

The reason why the exponent  $d$  is below 1 in adult fishes and other WBE is that it pertains to a surface (S), and that surface, even when growing allometrically (i.e.,  $S \propto L^a$ , with  $a > 2$ ),  $d$  cannot come too close to 3 – because a surface can become a solid (i.e.,  $S \propto L^3$ ) and function as a surface, e.g., for gas exchange.

34) 267 to 269 *fully supported.*

Glad we agree on this – the cherry picking is annoying.

35) 327 to 328, 373: *This is one of the cases where the paper operates with educated guesses: .... “more frequent occurrences of respiratory stress and hypercapnia.” An allometric time series of the respective data would be needed for such statements to be made.*

Let's agree that these are at least well-educated guesses. The decline of weight-specific gill area with increasing weight is inescapable if  $d < 1$ . In any WBE, this must result in less  $O_2$  being available, given equation 6. Another line of evidence is provided by the finding of Somero and Childress (1980), Norton et al. (2000) and Davis and Moyes (2007) whom I cite, and who showed, much to their expressed surprise, that the tissue of the larger specimens of a given species contain predominantly glycolytic enzymes (i.e., catalyzing reactions in the absence of  $O_2$ ), while smaller specimens, contain predominantly oxidative enzymes (i.e., catalyzing reactions in the presence of  $O_2$ ). This is the reason why Somero and Childress (1980) concluded that “*Limitation may derive from surface- volume relationships*”, a theme that they did not pursue, but which is at the heart of the GOLT.

36) 328 to 330, ditto: “...assume, therefore, is the existence of a threshold weight ( $W_m$ ) at which the high frequency of respiratory stress or hypercapnia events triggers the hormonal cascade that leads to maturation (79). Thus, one can define...” This comes across as a speculative statement that needs to be tested by measurements of the actual process in relation to size threshold. This gap is glaring, especially, as this hypothesis has been repeated by the author for quite some time... Correlation with a certain fraction of maximum body size is quite natural to expect for different reasons but does not necessarily represent causation.

We all agree that “correlation [...] does not necessarily represent causation”, or more precisely, that it is a necessary, but not a sufficient condition for causation. However, if a growing number of lines of correlative evidence keep pointing to the same relationship, there is a point the burden of proof must shift. The best example of this is the correlative evidence pointing to cigarettes as the cause for cancer, which became compelling long before the cellular mechanism was elucidated which explained, in agonizing details, how the tar from cigarette smoke affects the DNA of lung cells. Similarly, evolution through Darwinian natural selection became widely accepted before population genetic (not to mention genomics) provided the underlying mechanisms. Indeed, if this argument became a reason not to publish this article, there would be no reason for physiologists to search for the trigger of the hormonal cascade that the GOLT requires to exist.

37) *Fig. 5 does not present evidence for the hypothesis described.*

This must be a misunderstanding, as Figure 5 (now Figure 4) is the illustration of the section of “Fish growth vs. reproduction” (starting on new line 280), which is entirely devoted to presenting (and citing) the considerable evidence presented for that very figure. For what it is worth, however, I have added a few words and a citation to a paper just accepted in the *Journal of Fish Biology* which rigorously tested the hypothesis inherent in Figure 5C (new line 401).