ECOLOGY

The gill-oxygen limitation theory (GOLT) and its critics

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The gill-oxygen limitation theory (GOLT) provides mechanisms for key aspects of the biology (food conversion efficiency, growth and its response to temperature, the timing of maturation, and others) of water-breathing ectotherms (WBEs). The GOLT's basic tenet is that the surface area of the gills or other respiratory surfaces of WBE cannot, as two-dimensional structures, supply them with sufficient oxygen to keep up with the growth of their three-dimensional bodies. Thus, a lower relative oxygen supply induces sexual maturation, and later a slowing and cessation of growth, along with 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 refutation of objections to the GOLT. This theory still needs to be put on a solid quantitative basis, which will occur after the misconceptions surrounding it are put to rest.

INTRODUCTION

The need for a theory

To make sense of scientific data and their patterns, robust theories are required, which can provide an interpretative context for new findings, or which cannot, in which case the new findings are either problematic or very interesting (*1*). However, a situation can emerge where the practitioners of a given scientific discipline have forgotten Darwin's dictum "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!" (*2*). They not only publish articles that do not test anything but also, 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, and habitat modification (*3*, *4*) and by global changes with its attendant ills, ocean and freshwater warming (*5*–*9*), and acidification and deoxygenation (*10*–*12*).

This is why the gill-oxygen limitation theory (GOLT) is being reintroduced here, and the case made for it to be seriously (re-)examined. Despite it being counterintuitive to the air-breathing mammals that we are, the GOLT is coherent in its content and the range of 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, even before it has become widely known.

To counter the tendency to discredit proposed hypotheses (rather than test them), here, 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 (*13*) 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 biases onto WBE has resulted in a misunderstanding of many features and life histories of fish and marine invertebrates.

These are strong claims, especially because the framework of an alternative vision of the lives of WBE, i.e., the GOLT (*14*, *15*), has, to date, not found many adherents. Recent extensive (*16*) and shorter elaborations (*17*, *18*) of the GOLT exist. Each parsimoniously explains several biological features of, behaviors of, and experimental results with WBE that mostly have no other (simple) explanations (Table 1).

The 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 (*19*–*24*), who built on earlier work by Pütter (*25*), and whose main feature is that organic growth (dw/dt) can be seen as the difference between two processes, i.e.

$$dw/dt = Hw^{d} - kw \qquad (1)$$

where the two terms on the right are usually called anabolism and catabolism, respectively, and where $d < 1$. Here, 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 is degraded (see below). As simple as Eq. 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 adenosine triphosphate (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 (*26*).

Thus, the process of anabolism requires oxygen, which must enter the body through some permeable surface. Therefore, in WBE, the parameter d in Eq. 1, is equivalent to the exponent (d_G) of a relationship linking gill (or another respiratory) surface area (G) to

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Table 1. Some physiological and related differences between young and older WBE. Here, item (1) is 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_2 supply is high.	Thus, relative O_2 supply is low.	See text
3	Growth in weight is accelerating.	Growth in weight is decelerating.	See Figs. 1 and 3
4	High temperatures and thus shallower habitats are preferred.	Low temperatures and thus deeper habitats are preferred.	(*38*, *140*)
	In *Cyprinodon macularius*, a temperature of 30°C is "optimal only up to an age of 22-28 weeks."	In older *C. macularius*, "the temperature optimum shifts gradually to 22-26°C."	(*92*); see text for other species
5	Relative food consumption is high.	Relative food consumption is low.	(*141*)
6	Food conversion efficiency is high.	Food conversion efficiency is low, trending toward zero.	(*108*, *109*, *142*)
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.	(*16*, *143–145*)
8	Enzymes in tissues are mainly oxidative.	Enzymes in tissues are mainly glycolytic.	(*53*); also see text
9	Fish otoliths contain proteinaceous substances.	The external layers of fish otoliths are purely crystalline.	(*146*, *147*)
10	Clear daily "rings" are formed in otoliths of fish and statoliths of invertebrates.	Daily "rings" in otoliths or statoliths are blurred and, later, disappear altogether.	(*16*, *148*, *150*)
11	Extensive seasonal migrations are not undertaken.	Extensive, often temperature-driven seasonal migrations are undertaken.	(*151*)
12	Fat content is low.	In fish, fat content is high, particularly when seasonal temperature oscillations are high.	(*16*, *97*)

body weight of the form $G = a \cdot W^{d_G}$, which determines how much anabolism can occur. For this reason, the oxygen consumption of WBE scales with body weight with a factor (d_{O2}) that should be and is near d_G (*27*). As we shall see below, d_G—and hence d_{O2} 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 keep their native quaternary structure, usually maintained by weak H-bonds (*28*). In the long term, they cannot maintain that structure because they are constantly subjected to Brownian motion (*29–31*). Thus, all such molecules have half-lives that become shorter when temperature increases (*28*, *32*).

Spontaneous loss of quaternary structure by protein 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 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 Eq. 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

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

where L_t is the mean length (however measured) at age t of the WBE in question, L_∞ is their asymptotic length, i.e., the mean length they would attain after an infinitely long time, K is a growth coefficient (of dimension 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, as the growth rate of fish larvae and early juveniles is usually more rapid than predicted by the VBGF) (*33*).

Combining this equation with a length-weight relationship of the form $W = a \cdot L^b$ leads to a version of the VBGF that can express growth in weight, i.e.

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

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

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

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

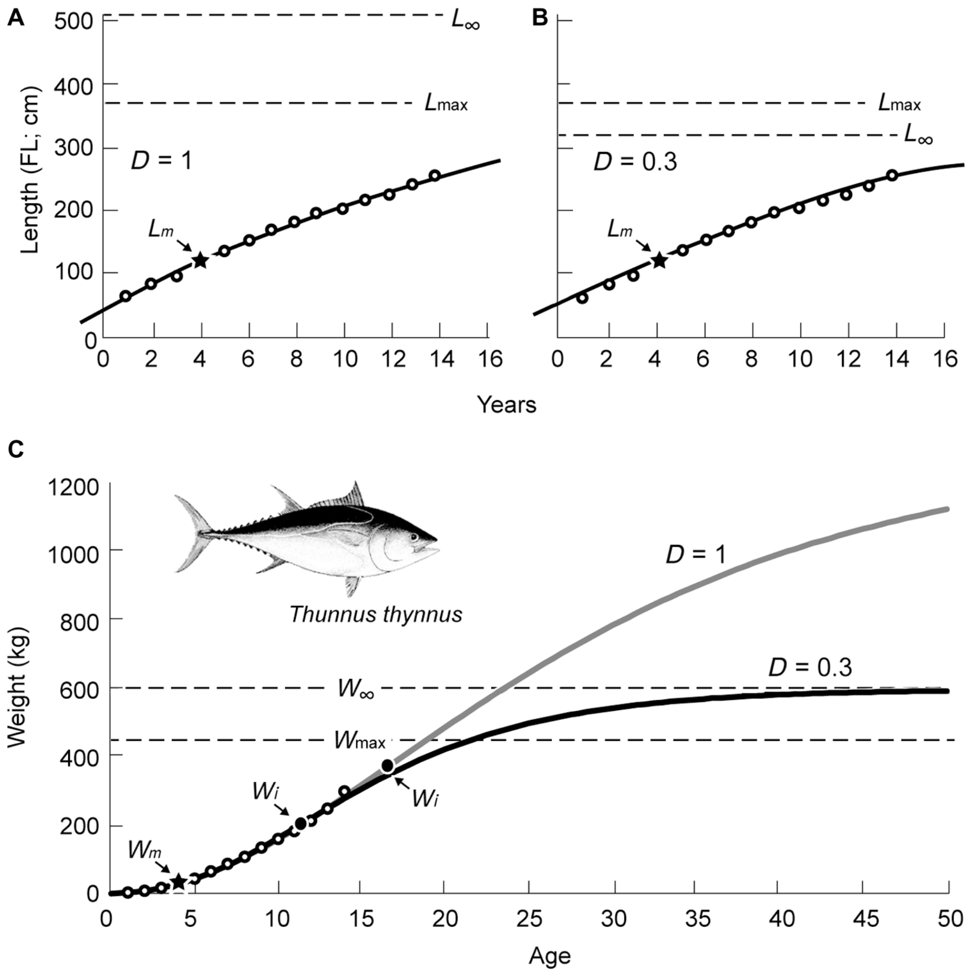

Fig. 1. Different forms of the von Bertalanffy growth function. The VBGF fitted to bluefin tuna (*T. thynnus*) length-age data pairs (*137*). (**A**) Standard VBGF (Eq. 2), which assumes $d = 2/3$, and hence $D = 1$ (which can thus be omitted). (**B**) Same length-at-age data, fitted by Eq. 4, with $b = 3$ and $D = 0.3$, corresponding to $d = 0.9$ (*46*). (**C**) Two versions of the generalized VBGF for weight (Eq. 5), with $D = 1$ and $D = 0.3$, with weights converted from lengths using $W = 0.0182 \cdot L^3$ (from FishBase; www.fishbase.org), where W is in g and (fork) length is in cm. Note the position of L_m [from (*138*)] relative to L_{max}, L_∞, W_m relative to W_{max} and W_∞, 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.

where $D = 3(1 - d)$. Note that here, the exponent of the length-weight is equal to 3, as is (nearly) the case in the overwhelming majority of fish (*34*) (see also www.fishbase.org for fishes and www.sealifebase.org for invertebrate species).

For weight, the generalized VBGF is

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

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

When $d = 0.75$ (and thus, $D = 0.75$), Eq. 4 is equivalent to what was called a "general model" of growth (*35*), which, however, is not general because the value of d does vary between taxa (*14*, *16*). Note that whether one uses the standard VBGF or its generalized versions [including versions that account for ubiquitous seasonal growth oscillations (*16*)], a reasonably good fit to length/age data pairs is obtained, including estimates of asymptotic lengths (L_∞) 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_∞ that are obtained are much higher than L_{max} (compare Fig. 1A with Fig. 1B), with W_∞ being also overestimated (Fig. 1C).

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. 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 (*36*–*39*). 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 large sums are spent by in the aquaculture industry to aerate the ponds in which WBE are raised (*40*, *41*).

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) identifying the cause of the decline in metabolic rates with increasing weight; (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 three-dimensional (3D) growth of the bodies that they supply with oxygen (Fig. 2).

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 one contribution (*42*) has tackled this problem head-on and advanced the following two fundamental arguments:

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. Similarly, gill surface area, which can be seen as equivalent to book pages, can always keep up with body weight.

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

No	Arguments	Refutations
2.1	Fish could, if they needed it, grow new gill lamellae to maintain the ratio gill surface area/body weight constant, but they do not need to, i.e., "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…" (*42*)	It is actually impossible, for gill lamellae, which must function as 2D surfaces (Fig. 2), to keep up with the growth of the 3D bodies they supply with oxygen (*152*). In addition, the suggestion that large fish could increase their gill surface if they wanted, but somehow do not, makes these claims effectively unfalsifiable.
2.2	"Weatherley and Gill (*153*) […] had already concluded that there was no evidence that capacity for gas exchange or gill surface area could limit growth performance in fishes…" (*42*).	The quote in question (*153*) was actually "[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." Thus, it is the scope of gill limitation that was disputed, not the idea itself.
2.3	Here is another version of the above citation: "…Blier *et al.* (*154*) 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".	No, it is no longer valid. Following an exchange with P. U. Blier, he conceded that "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" (pers. comm., 16 March 1998, translated from French) (*15*).
2.4	Lefevre *et al.* (*155*) asserted that "Pauly and Cheung (*17*) 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."	They did not. What was suggested (*17*) is that the growth of gill surface area can proceed only by making the gill "sieve" higher and wider (2D) but not deeper (3D), as this would put the new gill lamellae behind the first layer of lamellae. Lamellae that were so placed would be "useless," as the first layer of lamellae would reduce the water flowing across the gills of O_2, leaving the second layer (and any subsequent layer) with little to nothing to do (see Fig. 2).
2.5	"…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" (*155*)	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 rethink of old assumptions.

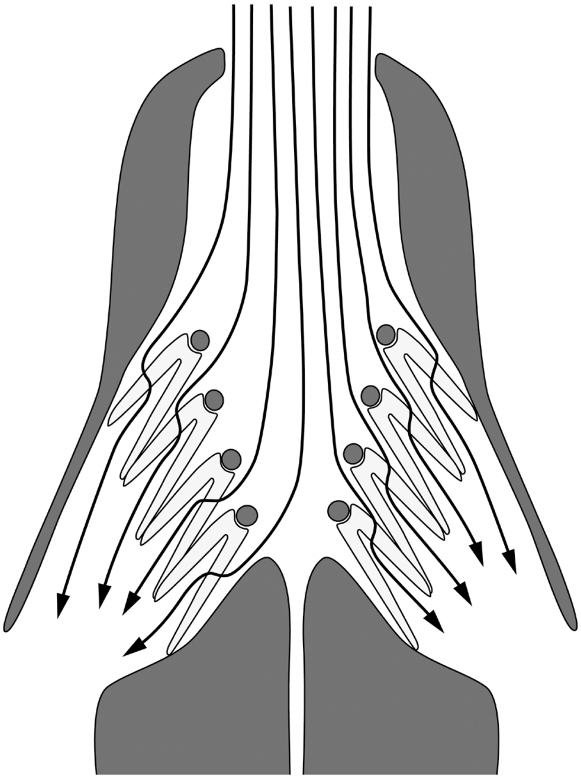

Fig. 2. Schematic representation of water flows across the gills of a fish. Note that once water has flown between lamellae (which extracted most of the O_2 it contained), there is no point for this water to flow through another set of lamellae. Hence, gills function as a surface, although their arrangement in 3D space may suggest otherwise.

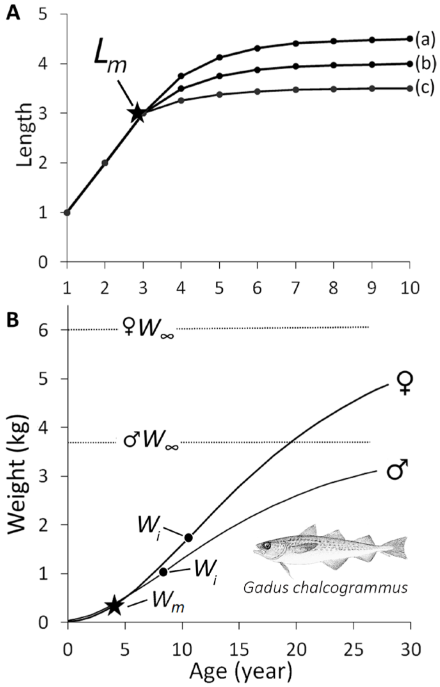

Fig. 3. Two views of the relationships between size at first maturity and maximum size. (**A**) Traditional view, where "linear" growth slows down when length at first maturity (L_m; black star) is reached, with growth then continuing at a reduced pace, depending on circumstances [i.e., a, b, or c; redrawn from (*77*)]. (**B**) More appropriate, but uncommon, view, with growth expressed as change in body weight (in line with Eq. 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 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 length at first maturity for Alaska pollock (*Gadus chalcogrammus*) in FishBase (www.fishbase.org), which contains hundreds of similar datasets.

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 our 3D world, 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 is in the path of a flow of water across gills (Fig. 2).

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 three dimensions and thus cannot keep up with the 3D body that it supplies with oxygen. Note that the improvements of gas exchange performance that may be achieved by changing the pattern of perfusion of the lamellae or reducing blood residence time by altering branchial blood flow would not overcome the "dimensional tension" occurring when a surface limits the rate of a process required to by a growing volume (*17*).

The disconcerting argument in (*42*), that the GOLT assumes gills to behave like spheres, becomes even more disconcerting when one notes that the argument that WBE are able to maintain the same gill surface area/body weight ratios as their weight increases is backed up with only two very questionable references. The first is a contribution on the gill area of spangled perch, *Leiopotherapon unicolor*, with a scaling factor $d_G = 1.04$ (*43*) 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 (*44*) (see also Table 3).

The choice of (*43*) is unfortunate, as there are several reviews, jointly covering more than 150 species, showing that typical scaling factor for fish gill surface area ranges from $d_G = 0.6$ to 0.9 (*27*, *45*–*48*). For "medium-sized" fish (200 g), it was shown (*27*), on the basis of data from well over 200 papers covering 121 fish species, that the mean value of $dG = 0.811$ is very close to the mean estimate of the scaling factor of metabolic rate versus body weight, $d_{O2} = 0.826$, which confirmed the results of an earlier comprehensive review (*49*); thus, these two values were averaged to obtain a robust estimate of $dG = d_{O2} = 0.82$, assuming that *dG causes* d_{O2}. This was based on Fick's law of diffusion, which states that the total amount of oxygen that can diffuse into the circulatory system of a WBE is

$$Q = \mathrm{dP} \cdot U \cdot G \cdot \mathrm{WBD}^{-1} \qquad (6)$$

where Q is the oxygen uptake (ml hour^{-1}). Here, dP is the difference between the oxygen partial pressure on either side of the membrane

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

No	Arguments	Refutations
3.1	It was asserted (*42*) 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 (*43*) as well as bivalves (*44*). 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 (*27*, *58*) and mention the difficulties in obtaining accurate values when a small range of body sizes are included (*156*). Thus, the value of 1.04 mentioned here 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 *L. unicolor* (see www.fishbase.org). The scaling exponent between gill surface area and bivalve body weight appears to range from 0.51 to 0.80 (*58*, *157*), with 0.85 in *S. velum* (*44*). The scaling exponent of 1.0 linking gill surface area to gill mass in *S. velum* is irrelevant to the O_2 supply to its body. 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 (*Epinephelus itajara* and *Epinephelus quinquefasciatus*), sunfishes (*Mola mola*), billfishes and other scombroids, giant manta ray (*Manta birostris*), and especially the largest extant fish, the whale shark (*Rhincodon typus*), refutes the GOLT, which postulates that high temperatures tend to reduce the size of fish (*42*). [This issue was a genuine challenge to the GOLT, and its successful resolution (see adjacent column and main text) widened its scope.]	Following an extensive review of the biology of the species in question (*16*), it 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 and whale shark) or at depth (swordfish and billfish), the latter cases involving heating systems to keep their huge eyes and brain warm; 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 (*M. mola*).
3.3	Squid respire through their skin; moreover, by having tubular bodies, squid have such large respiratory area that they cannot be O_2-limited (*158*). In addition, their changed shape as they grow increases the surface area of their body hyperallometrically.	Squid do not breathe though their skin (*159*), 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 Growing Sealife plastic squids implies that asymptotic growth does not require a limiting surface (*160*).	A detailed analysis of what occurs in plastic squids that "grow" when placed in water shows that, actually (and surprisingly), it is a surface that limits their growth (*16*, *33*).

(in atm); U is Krogh's diffusion constant, that is, the amount of oxygen (in ml) that diffuses through an area of 1 mm^2 in 1 min for a given type of tissue (or material) when the pressure gradient is 1 atm of oxygen per μ (μm), and G is the surface area of the gills (total area of the secondary lamellae). Last, WBD is the water-blood distance or the "water-capillary distance" (*50*), i.e., the thickness of the tissue between water and blood in μ (*27*) that cannot be reduced much without risks to the structural integrity of the gill lamellae.

Note also that Eq. 6 also applies to WBE that lack gills and blood, as part of a closed system for distributing oxygen to the tissues (*51*). One such example is provided by the arrow worms (Chaetognatha), in which, in the absence of gills, the body integument serves as respiratory organ (*52*) and whose thickness cannot be reduced as they grow.

However, the authors of (*42*) argue that, while fish could grow gill surface area such that $d_G = 1$ is maintained, they do not need to

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

No	Arguments	Refutations
4.1	It was suggested (*42*) that because "the activity of oxidative enzyme falls with body mass in fishes (*53*)," larger/older fish need less oxygen anyway. Thus, it is not necessary to maintain a high O_2 supply.	This is mistaking cause and effect: Fish shift from oxidative to glycolytic enzymes because their relative O_2 supply declines. This was well understood by earlier authors (*57*), who attributed the shift from oxidative to glycolytic enzymes, if tentatively, to "[l]imitation on aerobic metabolism [which] may derive from surface-volume relationships…"
4.2	Lefevre *et al.* (*42*) wrote "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."	Something being "generally accepted" 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 (*163*).
4.3	There is "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" (*42*).	There is no such body of evidence. Rather, the O_2 consumption of fish is generally assumed to reflect their "needs." What is missing are tests of whether the supply of O_2 by the gills to the body (always) satisfies the O_2 demand of the fish tissues. It does not in large adult fish, which is the reason why they switch from oxidative to glycolytic enzymes

do so because they suggest that "the activity of oxidative enzymes falls with body mass in fishes" and cited (*53*) as source. 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. (ii) It attributes to fish biological features (i.e., gill lamellae) that they could multiply and use but somehow choose not to, which makes its claims about fish physiology unfalsifiable. Thus, the authors of (*42*) 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 $d_G = 1$ (*43*) "confirm" that gill surface area can keep up with body weight.

Argument (i) mistakes cause and effect (*54*) (Table 4). 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 (*53*, *55*–*57*). Thus, the authors of (*57*) titled the report of their findings: "A violation of the metabolism-size scaling paradigm: Activities of glycolytic enzymes in muscle increase in larger-size fish." Note, however, that this feature not only is compatible with the GOLT but also is one of its consequences. Argument (ii) evidently points to Popper's "decision criterion" that claims that cannot be falsified in principle are not part of science (*1*).

Regarding the bivalve *S. velum*, the fact that a value of $d = 1$ is reported (*44*) 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 $d_G = 0.85$ is relatively high for a bivalve, but well under 1, as required by the GOLT. Other bivalves have values of d_G and d_{O2} ranging between 0.5 and 0.8 (*58*) and thus suffer from "ontogenic anaerobiosis" (*59*). An exception may be the giant clams of the family Tridacnidae, which are phototrophic and thus produce their own oxygen (*60*).

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 $d_G = 2/3$, although von Bertalanffy (*24*) thought so. He erroneously referred to instances of $2/3 < d < 1$ as growth that is "intermediate between surface and weight proportionality" (Table 5).

However, values of $d_G \approx 0.67$ seem to occur only in very small fish such as the guppies which von Bertalanffy (*22*, *24*) 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 0.05 g (*61*, *62*). The other extreme appears to occur in bluefin tuna (*Thunnus thynnus*), where a well-documented value of $d_G = 0.90$ for adult specimens has been published (*46*).

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 $d_G >> 1$ have been found to occur only in teleost larvae (*63*–*65*), which also breathe through their integument and fins (*66*), 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 (*64*, *65*).

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 representatives of a species are studied. In the case of spangled perch (*43*), the published estimate of $d_G = 1.04$ pertained to juvenile fish reaching at

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 (*162*, *163*).	Von Bertalanffy (*19*–*24*) did not commit himself to stating that the surface-limiting growth was that of the gut. He thought that "the actual surface responsible for growth of an organism is in general unknown" (*20*). However, he clearly favored a link to respiration (albeit without explicitly mentioning gill surface area).
5.2	The claim was also made that "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 $w^{2/3}$" (*82*).	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 (equal to loss of the quaternary structure) of protein molecules. This process is proportional to weight; the denatured proteins must be resynthesized, which requires ATP and hence O_2. However, this is part of anabolism, not catabolism.
5.3	Another claim (*164*) was "…anabolism is proportional to the area of the circulatory network rather than to gill surface area (*35*)."	If this were correct, then the scaling factor of anabolism to weight in fish and invertebrates would always be 0.75. This, however, is emphatically not the case (*15*, *16*, *165*).
5.4	A critique (*166*) of (*7*) included "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 affect growth if the oxygen concentration is below a critical value (*167*)."	The response (*7*) was that "[w]hile Brander et al. cite Brett (*167*) 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." (*14*, *93*, *168*–*172*).

most 30% of the maximum weight typically attained by that species (see Table 3). This was similar to the specimens of icefish (*Chaenocephalus aceratus*) (*67*), for which $d_G \approx 1$ [after correction from 1.09 due to the inappropriate use of a "type II" regression (*68*)]. More cases of this sort have been documented (*69*).

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.

TWO MAJOR CHALLENGES TO THE GOLT

Fish growth versus 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 (*70*–*77*). This notion implies a "biphasic growth" with a rapid growth phase before the length at first maturity is reached, and a slower phase thereafter, as illustrated by Fig. 3A.

What is not realized, however, is that this phrase, like all statements about complex phenomena, is a hypothesis. Moreover, this hypothesis is contradicted by four sets of observations: (i) Fish kept in aquaria and that never mature and spawn reach maximum sizes that are similar to those of reproducing conspecifics in the wild. (ii) In most fish species, the females are larger than the males, although they devote more energy to reproduction. (iii) In most fish species, growth in weight is more rapid after maturity is reached than before. (iv) Mean length at first maturity, in fish, correlates tightly with the maximum length that can be reached in a given environment.

Regarding item (i), popular aquarium fish such as clown loach (*Chromobotia macracanthus*) do not breed in captivity but still approach a common maximum length of about 16 cm (*78*). Similarly, most saltwater aquarium fish such as damsels or butterfly fish do not breed in tanks but again reach a common maximum length similar to the one in the wild (*79*); many of the saltwater or freshwater fish kept by home aquarists never mature and spawn. However, although they are fed ad libitum, they stop growing at some point. In addition, triploid (and thus sterile) fish exhibit growth patterns largely similar to those of their diploid brethren (*80*). 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 (ii), in over 80% of fish families where females and males look alike, it is the females that eventually reach larger sizes (Fig. 3B), even if this growth dimorphism can become attenuated in certain circumstances (*81*). 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 is (*82*) (see also Table 6, number 6.2); it was suggested (*83*), in an effort to refute the claim above (*84*), that males had the higher reproductive effort. This was backed with a graph 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

Table 6. Arguments raised against the GOLT: Spawning versus growth and vice versa.

No	Arguments	Refutations
6.1	Old/large adult fish stop growing because all their energy goes to reproduction (*70*–*77*)	Well-fed, non-reproducing fish (e.g., in aquaria) stop growing at some point. In addition, the females of >80% of fish species grow to be larger than the males (see www.fishbase.org and section on "Fish growth vs. reproduction").
6.2	"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*. (*85*). Indeed, for the species given by Pauly (*84*), females invest relatively less in reproduction than males as a proportion of body mass (see figure 5.5 in Sarre's doctoral dissertation (*173*)" (*83*). Note that "figure 5.5" is a plot of ova stages versus body weight in female (only) black bream (*Acanthopagrus butcheri*), 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. In addition, in a context similar to that above, an author (*174*) proposed the ad hoc 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."	A review of 168 mammal, 97 bird, 3 reptile, 100 amphibian, 98 fish, and 16 invertebrate species (*175*) concluded that, overall, the cost of reproduction, in female was up to three orders of magnitude higher than for males. This confirms Gould (*176*), 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…." Parker *et al.* (*85*) state in their abstract, that sessile invertebrates (not "fish") are "subject mainly to selection on gamete production and gamete success and so high gonad expenditure is expected in both sexes. […]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 GSI routinely matches that of females, they would not have used the word 'intriguingly'. They also note that their "limited data also suggest that higher male GSI may be the prevalent pattern in sperm casters (where only males release gametes)." As for figure 5.6 in Sarre's unpublished thesis, it shows male GSI to be occasionally higher than female GSI, but GSI is an index relating gonad weight a given time to the weight of the body, not the rate of production of gonad tissue, which alone relates to reproductive costs.
6.3	A critique (*166*) of (*7*) included "the bioenergetic model assumes that the term scaling directly with weight is due to catabolism, but the there is a strong case that reproductive investment is the principal factor (*75*, *177*, *178*)."	The answer to this (*7*) was that "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 (*80*)."

can be shown empirically in almost all groups of animals reproducing sexually [reviewed in (*85*)]. There are a few exceptions (e.g., parental care by male seahorse), but they are not pertinent here.

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

From length growth curves, one can get the impression that spawning strongly affects growth, hence the name "reproductive load" for the L_m/L_∞ ratio (*86*). However, growth is a process primarily involving mass (see Eq. 1), as reflected in weight growth curves. Weight growth curves have marked inflection points, where growth rate (dw/dt) is highest (at W_i), and thus, the question may be asked whether $W_m > W_i$ or, on the contrary, $W_i > W_m$. Taking the second derivative of generalized VBGF for weight growth (Eq. 5) and setting it equal to zero allow us to identify W_i, where the growth rate changes from increasing to decreasing

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

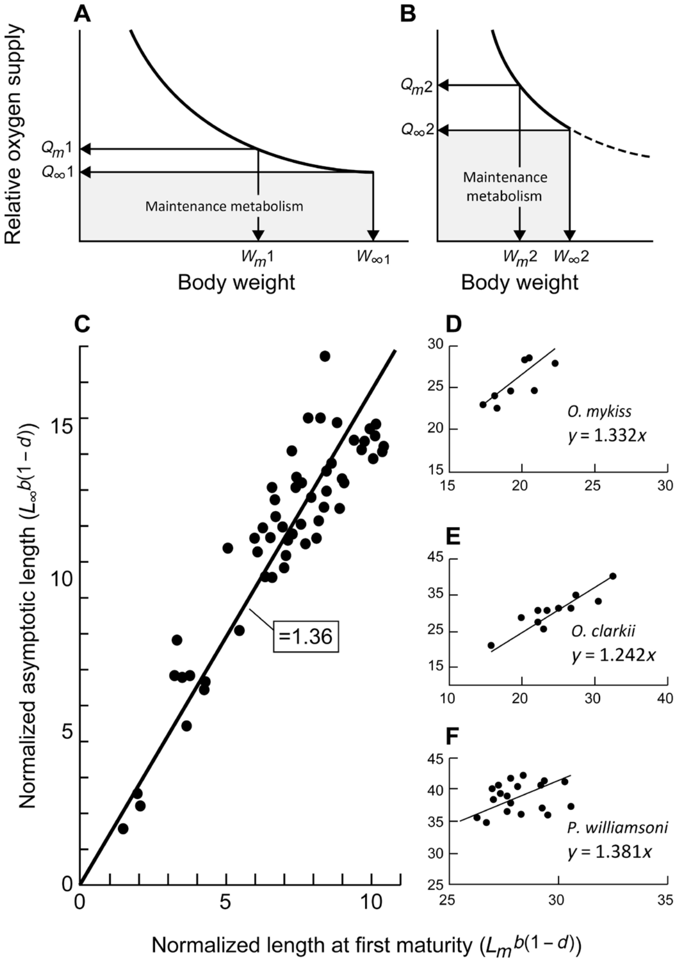

Fig. 4. Growing fish mature when their relative gill surface area reaches a threshold. (**A**) In the ontogeny of fish, when their relative gill surface area declines, their oxygen supply declines as well; when the latter reaches 1.3 to 1.4 times the oxygen supply required for maintenance and routine activities, i.e., as fish increasingly get "out of breath" (and suffer from hypercapnia), the hormonal cascade is initiated that leads 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 to 1.4 threshold will cause them to mature and spawn at smaller sizes. (**C**) Plot, whose 56 points represent the 34 fish species, ranging from guppies to tuna (*87*) (see the Supplementary Materials) used to estimate the average threshold value of 1.36 (with 95% confidence interval of 1.218 to 1.534). (**D**) 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*).

As may be seen from Figs. 1C and 3B, 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 (large) fish (Table 7), 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 and hypercapnia. All we need to 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 (*87*). Thus, one can define

$$A = \left(W_\infty^{1/b} / W^{1/b}\right)^D \tag{8}$$

from which

$$W_m = W_\infty \cdot (1/A)^{b/D} \tag{9}$$

with A being the ratio of gill surface area (or O_2 supply) at W_∞ over the gill surface area (or O_2 supply) at W_m (*16*, *87*).

A first estimate of $A = 1.365$ was published in 1984 (see Fig. 4C) (*87*), whose 95% confidence interval is 1.218 to 1.534, as estimated using the Fieller method (*88*) (see www.graphpad.com/quickcalcs/ErrorProp1.cfm) applied to the data of table S1. These data covered 56 pairs of L_m and L_∞ in 34 different fish species ranging from guppies to tuna and raised to the power of $3/(1-d)$, which here substitutes for weights.

Because $A^{-1} = 0.733$, combining with Eq. 7 and rearranging (see the Supplementary Materials) lead 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 *M. luzonensis*) (*16*, *62*), $W_m > W_i$, while the opposite, $W_m < W_i$, applies to larger fishes (e.g., bluefin tuna; see Figs. 1C and 3B).

This also aligns with the empirical relationships between L_m and L_∞ (with and without additional variables) in 265 fish species in FishBase (www.fishbase.org), covering 88 families and 27 orders, with an average scaling factor of ≈0.9 emerging (*89*). The simplest of these relationships was

$$log(L_m) = 0.898 \cdot log(L_\infty) - 0.0782 \tag{10}$$

when L_m and L_∞ are in cm.

Equation 10 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 Eq. 7 (Table 7).

Unfortunately, Eq. 9 does not work below 1.3 cm, i.e., it predicts $L_m > L_\infty$. It can be hypothesized that all such small fish are semelparous, i.e., will spawn only once before they die, as documented in minute gobies (*90*). Equation 10 does not 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 (*91*).

Last, regarding item (iv) above, there is the huge environmental plasticity of fish, which can manifest itself both in individuals used for aquarium experiments (*92*, *93*) and in the wild. Regarding the latter, it was noted that "tropical fishes living near the limit of their tolerance for low temperature grow to larger size at such temperatures" (*94*). In such cases, i.e., when the maximum length (L_{max}) or the computed asymptotic length (L_∞) 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_∞ remains approximately constant.

The GOLT provides an explanation for the near constancy of $L_m/L_{\max}$ or L_m/L_∞ by postulating that spawning is induced by the same mechanism that also causes growth to decline (i.e., asymptotic growth). As fish grow in weight, their gills, whose surface area has grown with the scaling factor $d < 1$, deliver less O_2 per unit of body weight (Fig. 4A).

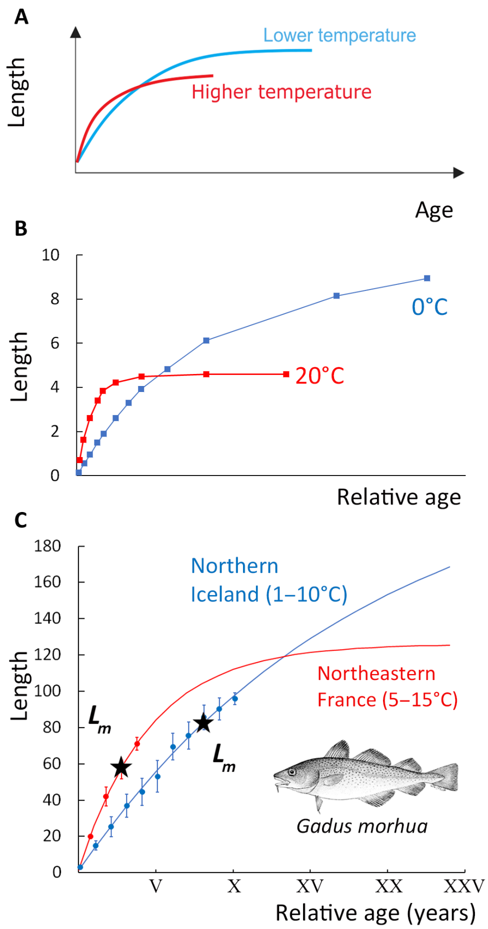

Fig. 5. Fish, at higher temperatures, tend to grow fast toward smaller maximum sizes. (**A**) "Observed phenomenon" that needs to be explained [adapted from an insert in figure 1 of (*102*)]. (**B**) Simplified version of figure 1 in (*25*). (**C**) Atlantic cod (*G. morhua*) has wide geographic and temperature ranges; in Eastern Iceland (1° to 10°C), they reach much larger sizes than in French waters (8° to 18°C), based on data in (*138*, *139*).

Thus, growing fish will gradually experience more respiratory stress and hypercapnia, and a level of either is finally reached that initiates the hormonal cascade leading to maturation (*95*, *96*). Gonadal products are elaborated, often by using fat accumulated in the summer and fall as a fuel (*97*). When, 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 (Fig. 4, A and B). 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 (*98*). The same occurs in a number of coral reef fishes, for example, in the families Acanthuridae and Scaridae (*99*, *100*).

The threshold gill surface area, and hence the relative metabolic rate at which spawning is initiated, is similar among different fish families (see Fig. 4C and fig. S2) 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. Figure 4 (D to F) provides further examples of this generalization [see also (*101*)].

Temperature and maximum sizes

The major critique (*42*) of a contribution based on the GOLT that predicted that ocean warming would reduce the maximum size of fish (*7*) proposed no alternative explanation as to why fish should remain smaller at higher temperatures. Thus, another contribution (*102*) is examined here, in some detail, as its authors attempt to answer the question whether "oxygen limitation in warming waters is a valid mechanism to explain decreased body size in aquatic ectotherms" (Fig. 5A).

Answering this question would also solve the riddle posed earlier by an author (*92*) who was surprised 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 (Figure 5B) (*25*) and well documented

Table 7. Theoretical versus empirical predictions of weight at fish maturity. The "theoretical" predictions of W_m based on the GOLT (Eq. 9) match the empirical estimates based on Eq. 10 (*90*); the relationship of W_m to the inflexion (W_i; Eq. 7) of weight growth curves is also as predicted (see text).

#	L_∞ (cm)	L_m (cm)	W_∞ (g)*	d†	W_m (% of W_∞) Eq. 10	W_m (% of W_∞)‡ Eq. 9	W_i (% of W_∞) Eq. 7
1§	2	≈2	0.08	0.6	*47*	*46* (*34–60*)	*28*
2	10	6.6	10	0.7	29	35 (*24–51*)	30
3	100	52	10^4	0.8	14	21 (*11–37*)	33
4	1000	412	10^7	0.9	7	4 (1–14)	34

*Assuming the length-weight relationship $W = 0.01 \cdot L^3$, corresponding to a trout-shaped (i.e., "average") fish when in cm and g and used for L and W, respectively. †Estimated from W_∞ (g) and $d \approx 0.6742 + 0.03574 \cdot \log W_{\max}$ in (*14*, *16*), with $W_\infty \approx W_{\max}$. ‡The range (in brackets) corresponds to the 95% confidence interval of $A = 1.365$, i.e., 1.218 to 1.534. §The first row values in italics are meant only to illustrate the behavior of Eqs. 7, 9, and 10 for very small sizes. Such fishes are usually iteroparous, and hence, their $L_m \approx L_\infty$ and their $W_m \approx W_\infty$ (see text).

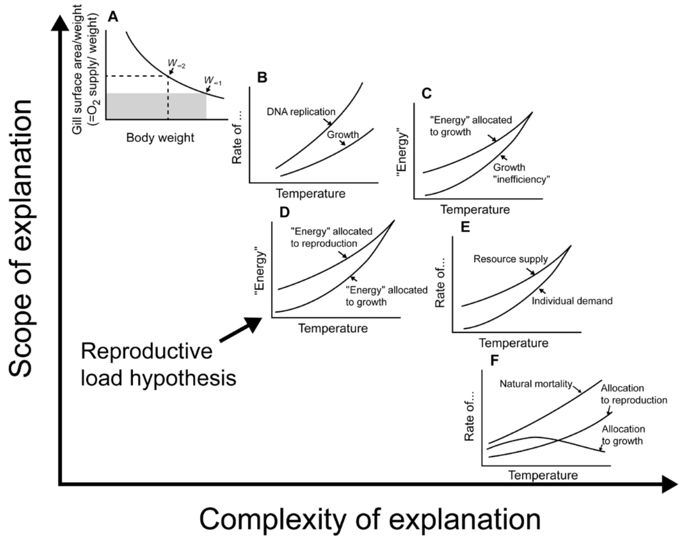

Fig. 6. Simplicity versus scope in explaining why higher temperatures lead to smaller sizes. The six explanatory models are adapted from (*102*) and were presented in two columns, as "intrinsic mechanisms" (**A** to **D**) and "extrinsic mechanisms" (**E** and **F**). Here, they are arranged according to the perceived complexity of the mechanism(s) they require (abscissa) and their generality or "scope" (ordinate).

in the literature, for example, for Atlantic cod (*Gadus morhua*) (Fig. 5C).

Six potential explanations were presented and discussed by these authors (*102*), as documented in their figure 1, from which all quotes below are extracted. These potential explanations are then summarized, illustrated (Fig. 6, A to F), and commented upon. All but the first of these potential explanations can be viewed as alternatives to the GOLT:

1) The GOLT [or "GOL hypothesis" in (*102*)]. The GOLT, based on the inherent properties of gills as 2D 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 (Fig. 6A). Hence, increased temperatures, which increase oxygen demand, will force them to remain smaller [Fig. 5C; see also (*7*)]. 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 (*92*)]. 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 can lead to confusion, as illustrated by one of the few aquatic biologists who raised fish (albeit small ones) under different temperatures from larvae to adults (*92*) and who penned the quote above.

2) "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 have 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 (2) (Fig. 6B) is probably another case of cause and effect being inverted (Table 4), as often happens when things correlate (*103*). Some of the largest fish, e.g., tuna, have very small cells, while the much smaller lungfish have large cells (*104*–*106*). It seems that in fish at least, cell size is linked with DNA content and activity level but not with size (*107*). 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).

3) "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" (Fig. 6C), which is a restatement of the issue at hand. The GOLT explains decreased growth efficiency [i.e., K_1, growth increment/food ingested (*108*, *109*)] 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 from (*110*), which cites (*111*–*115*) [see also (*116*)].

4) "Higher size-specific allocation to reproduction at higher temperatures […] leaves less energy for growth." This argument (Fig. 6D), for which no supporting evidence was presented, is not pertinent in any case because the effects of temperature on fish growth manifest themselves well before size at first maturity is reached (see Fig. 5C).

5) "Faster increases in energy demand (metabolism, activity cost, etc.) compared with food availability leaves [less] energy for growth and reproduction in […] warmer environments." This is a complex hypothesis, implying that tropical ecosystems make less food available to consumers than colder ecosystem (Fig. 6E), which would be hard to test. Fortunately, there is no need to because experiments can be and have been conducted in vitro where food is provided ad libitum and where fish kept at cooler temperatures grow to be larger than those at higher temperatures (*92*, *117*, *118*). 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 appear, which was found so puzzling (*92*).

6) "Increased predation mortality at higher temperatures drives an evolutionary response of higher net energy allocation to reproduction versus growth." This is hypothesis (4) in another guise (Fig. 6F). 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" (*119*). The point, rather, is to identify the mechanism in question. However, it will be quite difficult, given that, as stated for (4), fish grown under experimental conditions and without opportunity to spawn remain smaller at higher temperatures (*92*, *117*, *118*). The critique of items (2) to (6) is serious: Proposed hypotheses should be able to withstand a confrontation with common sense observations. Moreover, several of the hypotheses in Fig. 6 were only complex restatements of the issue at hand.

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 trans-dimensional Escher-like objects (*42*). In addition, the GOLT makes numerous predictions pertaining to domains that, at first

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

No	Arguments	Refutations
7.1	O'Dor and Hoar (*158*) claimed that "There is a fundamental flaw in examining Pauly's surface area limited growth scheme by plotting two different sets of units (m^2 and m^3) on the same graph and then making quantitative conclusions. Not only is [the resulting figure] messy, it violates a rule of physics and engineering (*179*)." The rule alluded to here is probably "For an equation to have any applicability to the real world, not only must the two sides by numerically equal, but they must also be dimensionally equal" (*179*).	The GOLT involves no equation with dimensionally unequal sides. Its presentation, however, may include graphs with two ordinates axes with different units, as illustrated on figure 6.8, p. 96 of the reference cited here (*179*). This reference is therefore 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 (*180*). The key issue, in any case, is that anything proportional to the third power of length will outgrow anything that remains proportional to a lower power of length, whatever the units and the starting values.
7.2	It was claimed (*42*) that in the contribution of Cheung *et al.* (*7*), 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 ($d = 0.8$ to 0.9), the size reduction caused by increasing temperature actually increased (*54*).
7.3	That ecophysiological consideration should not be used to explain physiological processes was asserted in a contribution (*181*) that criticizes Pörtner *et al.*'s "oxygen and capacity limited temperature tolerance" (OCLTT) hypothesis, which partly overlaps with the GOLT (*169*, *182*, *183*).	No biological subdiscipline can assume a priori a monopoly in answering a specific scientific question. In fact, scientific problems are nowadays best tackled using interdisciplinary approaches (*184*). Pörtner *et al.* (*183*) suggest that "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."
7.4	Jutfelt *et al.* (*181*) suggest that Pörtner *et al.*'s OCLTT hypothesis "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)."	Animals, including fish, deprived of oxygen die within minutes. In addition, 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 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 Pörtner *et al.*'s OCLTT hypothesis "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" (*181*).	That none of the 28 authors of that contribution could imagine why animal cannot operate all the time at peak performance is itself hard to imagine, but 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 (*17*, *185*). Repeated peak performance, as forced in experiments, renders the tested animals unfit for life in the wild.
7.6	The closing argument (*42*): "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."	This meta-argument about the authority of textbooks (*186*, *187*) is a strange one to make in the 21st century, although it could have been made in the Middle Ages with reference to species not mentioned in Aristotle's *Historia Animalium* (*188*) or in the writings of Plinius the Elder (*189*).

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 (*42*) is false because gills function similarly to a sieve, i.e., must be perpendicular to the 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 third dimension, and thus, 3D bodies must experience a declining oxygen supply as they grow. Moreover, gills are a favorite site for parasite infestation, and fish and aquatic invertebrates have good reasons to keep them as small as possible (*102*, *120*). Thus, gill surface area is not limiting to young/small fish, but they are 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.

DISCUSSION

The nature of explanations

The physicist Wolfgang Pauli is supposed to have said, "God made the bulk; surfaces were invented by the devil" (*121*). 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, some reflections are 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, should be consilient with related disciplines, parsimonious, independent from the observer, and "productive," i.e., make unexpected predictions.

The first of these 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 (*122*) or by logic, geometry, 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. An example is "Bergmann's rule" (*123*), which explains why high-latitude mammals and birds tend to have bigger bodies and shorter appendages (ears, limbs, and tails) than their congeners in more temperate climes. It is built on the idea 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, although it has been, for a while at least, a legitimate research question for physicists (*124*).

Parsimony is the requirement that an explanation should be "small" relative to the "size" of what needs to be explained (*125*) Parsimony is another term for "Ockham's razor," the rule that among competing hypotheses, the simplest one is (generally) to be favored (*126*).

The third requirement of a scientific explanation is that it must be nonlocal, i.e., it must not favor a privileged observer or standpoint (*127*). For example, we should not project our mammalian preoccupation with the food that 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. Last, a successful hypothesis should not only explain the facts at hand and map them parsimoniously onto the fabric of a more basic discipline but 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 really deficient. One of these 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 cannot, at present, provide 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 (*128*)] and the Red Sea [whose deeper waters are very hot and briny (*129*)].

At present, it can only be stated that the GOLT is not refuted by the presence of whale shark in these extreme environments, although 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 (*130*–*133*). Fully grown whale sharks, those assumed to require frequent cooling dives, are reported to exceed 18 m (*134*), which makes them over 11 times heavier than at 8 m.

Another example is the experiment explicitly conducted as an explicit test of the GOLT (*93*), 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 (*93*). However, this prediction concerned only the direction of the response, and not its strength.

Another deficiency of the GOLT is assuming that the WBEs in question always get enough food to grow (i.e., the converse of most studies that deal with food limitation, but tacitly assume that 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 (*16*)].

Clearly, the GOLT will have to be assimilated into a bioenergetics model or vice versa. However, the intellectual effort this represents will only be undertaken 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 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, and 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 (*17*) 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, which should not be perceived as adaptations. 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 (*135*) 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 gill.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/2/eabc6050/DC1

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