OPINION

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Sound physiological knowledge and principles in modeling shrinking of fishes under climate change

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Abstract

One of the main expected responses of marine fishes to ocean warming is decrease in body size, as supported by evidence from empirical data and theoretical modeling. The theoretical underpinning for fish shrinking is that the oxygen supply to large fish size cannot be met by their gills, whose surface area cannot keep up with the oxygen demand by their three-dimensional bodies. However, Lefevre et al. (*Global Change Biology*, 2017, 23, 3449–3459) argue against such theory. Here, we re-assert, with the Gill-Oxygen Limitation Theory (GOLT), that gills, which must retain the properties of open surfaces because their growth, even while hyperallometric, cannot keep up with the demand of growing three-dimensional bodies. Also, we show that a wide range of biological features of fish and other water-breathing organisms can be understood when gill area limitation is used as an explanation. We also note that an alternative to GOLT, offering a more parsimonious explanation for these features of water-breathers has not been proposed. Available empirical evidence corroborates predictions of decrease in body sizes under ocean warming based on GOLT, with the magnitude of the predicted change increases when using more species-specific parameter values of metabolic scaling.

KEYWORDS
body size, fish, gill, growth, oxygen, physiology, warming

1 | INTRODUCTION

Apart from shifts in distribution and phenology, one of the main responses of poikilothermic organisms to warming is decrease in body size (Baudron, Needle, Rijnsdorp, & Marshall, 2014; Daufresne, Lengfellner, & Sommer, 2009; Forster, Hirst, & Atkinson, 2012; Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Ohlberger, 2013; Sheridan & Bickford, 2011). A fundamental factor that cuts across the mechanisms relating warming and decrease in body size is biological constraints on size-related physiological and ecological processes (Atkinson, 2004; Ohlberger, 2013; Pauly, 1997). In the case of water-breathing ectotherms, we suggest that it is the geometric limitation of the growth of gills, and the responses of metabolism to temperature, that lead to a decrease in maximum body size under warming.

Physical constraints (see Table 1) of this sort may not be apparent when we see the animals surrounding us in the wild or in beautiful wildlife movies, which are all wonderfully adapted to their environment, within which they thrive and run and swim with effortless grace. This, however, is a superficial impression, as many of the occurrences we perceive as expressions of these animals' behavior are, in fact, responses to physical constraints that even millions of years of evolution could not circumvent. Given these constraints, when environmental conditions change, the biology of organisms is forced to change, especially in the case of poikilotherms.

Approaching maximum physiology capacity imposed by physical constraints is costly to the fitness of the animals, thus the evolution of biological processes and ecological behavior will avoid capacity maxima. As a result, the biological implications of the physical constraints are often not directly interpretable from physiological measurements over a very short timeframe relative to the lifespan of animals. The cost for animals to approach their maximum physiological capacity is that their survivorship, growth and fecundity are

TABLE 1 Glossary of important technical terms used in this paper

| Terms	Definition
Active metabolism	[a]Maximum metabolic capacity
Allometry	A term coined by Julian Huxley (1887–1975) to characterize the growth an organism's part when it proceeds at a rate different ("allo" = other) from that of the organism's body as a whole (see also [a]Hyper- and [a]Hypoallometry)
d_G	The power linking gill surface area with body weight in water-breathers. The value of d_G appears to vary between about 0.2 ([a]hypoallometry) and $\gg 1$ ([a]hyperallometry), but is limited between 0.7 and 0.9 in most postlarval teleost and adult elasmobranchs, for reasons discussed in the text
Dimensional tension	Our term for the interactions of biological (and other) processes wherein the growth of a process in a certain dimension (typically a surface) limits the growth of a related process unfolding at a higher dimension (typically a volume). Dimensional tensions strongly impact the architecture of growing organisms because they cannot easily be circumvented by evolutionary adaptation
Gill-oxygen limitation theory	An ensemble of mutually compatible hypotheses about the respiration of water-breathing animals (fishes and aquatic invertebrates) based on the fact that the rate of oxygen supply by the gills of (at least the adult form of) these animals constrains their activities and performance
GOLT	See [a]Gill-oxygen limitation theory
Hyperallometry	A form of growth wherein a dimension (length, surface areas, or volume) of a body part or organ increase in size faster than the rest of the body. Here used mainly to characterize the increase of the surface area of the gills of fish, relative to their weight. Note that [a]Isometry: [a]d_G = 2/3, Hypoallometry: d_G < 2/3, and [a]Hyperallometry: d_G > 2/3
Isometry	A term characterizing the growth of an organism's organs when it proceeds at the same ("iso" = same) rate as the body as a whole, or at the expected rate (e.g., for a surface to grow with a power of 2/3 of the corresponding volume, or [a]d_G = 0.667). The converse is [a]Allometry (see also [a]Hyper- and [a]Hypoallometry)
Limiting factor	A variable which, when increased, causes the performance of a system to increase. The concept is understood since Julius von Liebig (1803–1973) demonstrated that increasing agricultural productivity, at any time, was a matter of providing more of the *single* element that constrained productivity (e.g., phosphorus), and not more of *all* the nutrients that are required overall
Maintenance metabolic rate	The weight-specific consumption of oxygen by fish that allows their survival under natural conditions (i.e., in habitats with prey and predators, and other stressors), or in simulated natural conditions, but not allowing for somatic growth. See also [a]Standard (or basal) metabolic rate and [a]Maximum metabolic capacity
Maximum metabolic capacity	Here the highest performance, metabolic or otherwise (e.g., a displayed in flight from a predators) that can be exhibited by an animal. Such performance, also known as "active metabolism", can generally be sustained only for a short time because it reduces the long-term fitness of the animal in question (see Figure 1). Thus, comparison of performance between different animal species should not be based on maximum metabolic capacity
Metabolism	In general, the interactions of chemicals inside a living organism; here more narrowly defined as its consumption of oxygen. Note that this consumption reflects the *supply* of oxygen to the organism cells, and not the amount of oxygen these cells could process or actually need to perform their normal activities, i.e., their *demand*. Not differentiating between *supply* and *demand* makes it difficult to understand the metabolism of fish under stress, e.g., when they suffer from tissue hypoxia due to elevated water temperature
Open surfaces	The surface of a body organ (e.g., the skin or the gills) that is in direct contact with an outside medium. Open surfaces can be used for the transfer of heat, or gas (O_2, CO_2), or liquid (sweat). In this, open surfaces differ from the outer surfaces of internal organs (e.g., the liver), which only separate them from other organs
Physical constraints	The nonbiological processes or features that have shaped the evolution of organisms and still shape their performance (see also [a]Limiting factors). Examples are the gravitational force, or the dissolubility of oxygen in water
Routine metabolic rate	The weight-specific consumption of oxygen by fish under laboratory conditions roughly similar to those in their natural habitat (minus predators to avoid and prey to chase). See also [a]Standard (or basal) metabolic rate and [a]Maximum metabolic capacity
Standard metabolic rate	The weight-specific consumption of oxygen by fish under laboratory conditions that only allow from the fish to survive (while remaining unfed); roughly similar to "basal" metabolism. See also [a]Routine metabolic rate and [a]Maximum metabolic capacity

[a]Refer to another entry.
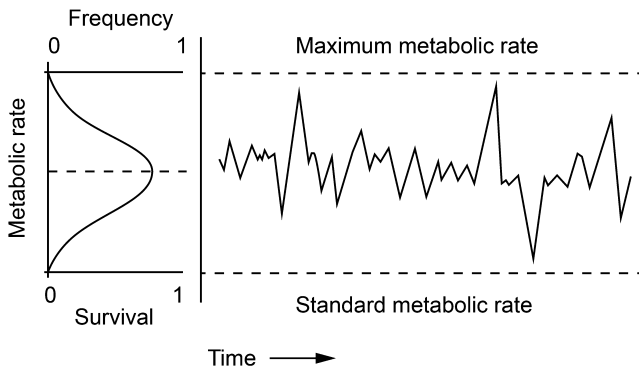
FIGURE 1 Schematic representation of the inter-relationships between maximum and standard metabolic rate (see Table 1), survival and the frequency distribution of metabolic rate through time (modified from Priede, 1985)

reduced (Figure 1), and thus their overall fitness as well (Priede, 1985). For example, although a plaice (*Pleuronectes platessa*) can swim (rather than rest on the sea floor), they will not be that active frequently, to search for food for example, because they have to be close to their maximum physiological capacity to do so, which is energetically costly and will reduce their fitness over the longer term through reduction in survivorship from decrease in growth and increase in predation mortality (Bakun, 2010; Fonds, Cronie, Vethaak, & Van der Puyl, 1992). Indirect effects of physical constraints of this sort are difficult to identify in physiological experiments lasting for a few minutes, hours, or even days. In the wild, the biological limits imposed by physical constraints generally are well below the maximum physiological capacity as identified in physiological experiments (Pörtner, Bock, & Mark, in press).

Concentrating on the physical constraints to which fish are exposed made it possible to explain the basic patterns of size, growth and reproduction and their relationship with environmental changes (Pauly, 2010). For fish, the growth of the primary respiratory surface area (gills) is the geometrical/physical constraint that explains a wide range of biological and ecological patterns (Gillooly, Gomez, Mavrodiev, Rong, & McLamore, 2016; Pauly, 2010). Based on this, a theory, hereafter called Gill-Oxygen Limitation Theory (GOLT, Table 1), can be derived (Pauly, 2010) which provides the conceptual basis for models and projections of the effects of ocean warming on fish body sizes (Cheung and Pauly, 2016; Cheung et al., 2013). However, Lefevre, McKenzie, and Nilsson (2017) argue against the GOLT, based on ad hoc arguments from misinterpreted physiological experiments. Specifically, Lefevre et al. (2017) argue that respiratory surface areas in fishes reflect metabolic needs instead of a constraint to metabolism because gill surface area can increase linearly in proportion to gill volume and body mass. By arguing that the oxygen consumption of fish reflects their demand, rather than the supply that their gills can provide, Lefevre et al. (2017) eliminate, per definition, the possibility of an undersupply of oxygen to the body of fishes. However, we must maintain the distinction between oxygen supply through the gill and oxygen demand by a living body's cells, if only to understand the

effects on water-breathers of a scarcity of oxygen in the water surrounding them (Kramer, 1987).

Here, based on the distinction between oxygen supply and demand, we present a new summary outline of the GOLT and explain why the argument provided by Lefevre et al. (2017) do not refute it. We examine the validity of GOLT in light of the followings criteria: (1) the hypothesis must be testable in principle, and (2) the ability of the hypothesis to predict observations different from those used to derive them in the first place. Also, a given hypothesis will be preferred over an alternative if it is (3) more parsimonious; (4) explains observations in widely different subfields or fields; and (5) is consistent (or "consilient") with related, well-corroborated theories. Finally, we suggest that fish physiology needs to be connected to fish ecology and evolution, as exemplified by Pauly (1981, 2010), Pörtner, Peck, and Hirse (2006) and Cheung et al. (2013), if we are to explain and project the expected responses of marine fishes to global change.

2 | BIOLOGICAL SURFACES AS A UBIQUITOUS CONSTRAINT

An uncircumventable constraint occurs across all animal groups when various surfaces of animals limit the size of the three-dimensional bodies that these surfaces (S) are features of. The cross-section of the legs in terrestrial animals, or the respiratory epithelium of water-breathers would be strongly limiting to the growth of the organisms in question if they grew isometrically, i.e., as the square of their length (L) or $S_{iso} = a \cdot L^2$. Thus, they grow faster, or hyperallometrically, as $S_{all} = a \cdot L^n$, with $2 < n < 3$, the latter limit referring to the fact that volumes and hence mass (or here: weight), generally grows in proportion to L^3 (see Froese, 2006).

One vivid example of the limitation of three-dimensional bodies of an organism would be the cross-section of the eight filiform legs of harvester spiders, also known as "daddy longlegs" (e.g., *Leiobunum rotundum*), compared to the elephantine legs of some tarantulas (e.g., the giant birdeater *Theraphosa blondi*), whose body is orders of magnitude heavier than that of harvestmen. This hyperallometric growth occurred, over evolutionary time, because in terrestrial systems, gravity is often the limiting factor for the size of animals, which experience this constraint as a "dimensional tension" between the cross area of their legs and the volume of their bodies. Evolution has responded to this via a hyperallometric increase of the cross-section of their legs, which means that the filiform legs of the harvester spiders would prevent them from growing a heavy body.

The respiratory system of insects also involves such dimensional tension, i.e., one that limits their growth (Verberk et al., 2016). The body space occupied by their trachea and tracheoles, which supplies oxygen (O_2) to their cells, becomes, in larger species, so large that there is little space left for other organ systems, e.g., muscles to propel the insect in question. This results in the theoretical maximum length of beetle-shaped insects (stick insects have other limitations)

being estimated as about 17 cm, which is the size of *Titanus gigan-teus*, a longhorn beetle from tropical South America (Kaiser et al., 2007), and the largest living beetle on record. The singular limitation that the bauplan and trachea/tracheoles of insects impose on their size is lifted when the ambient oxygen system is elevated, and hence the giant dragonfly (*Meganeuropsis permiana*) of the Permian (Ward, 2006).

In the water, where gravity is irrelevant and where trachea/tra-cheoles would not work, the dimensional tension alluded to above takes other forms. In large marine mammals such as whales, whose body is insulated against heat loss by a thick layer of blubber, dump-ing the heat that is produced by the massive muscles within the body can become difficult. Nonfeeding whales can dump excess heat via their flukes and flippers (Castellini, 2000), which, like the tongue used for the same purpose by many terrestrial mammals, can be insufficient when a chase is prolonged. This was well known to wha-lers chasing wounded whales, to San hunters in Botswana, who run antelopes to near death (Liebenberg, 2013), and even to wolves chasing caribou.

3 | DIMENSIONAL TENSION IN FISH

Fishes are constrained neither by gravity nor excess heat. In fact, several species of very active fish have found ways of turning excess heat into resources (Carey, Teal, Kanwisher, Lawson, & Beckett, 1971). In water-breathing fishes and invertebrates (henceforth "fish"), the dimensional tension (see Table 1) to which all life on Earth (and elsewhere, as we might see when we begin to study extraterrestrial life) manifests itself in the need to extract O_2 from a highly viscose medium (compared to air), which does not contain much O_2 (again, compared to air), in which diffusion is 300,000 times slower than in air (Forster et al., 2012; Pauly, 2010).

Moreover, there is no escaping Fick's Law, implying that the amount of O_2 that can diffuse into a body of a fish per unit time is proportional only to the O_2 partial pressure difference between its blood and the surrounding water (which had a clear upper limit), the inverse of the water-blood distance (WBD, i.e., the thickness of the respiratory epithelium, which must have an upper limit), and the respiratory surface (Fick, 1855; Gillooly et al., 2016), which is also limited. Thus, an experiment that ablated enough gill filaments of rainbow trout (*Oncorhynchus mykiss*) to reduce their gill area by approximately 30% led to decrease in oxygen uptake and critical swimming speed by 27% and 22%, respectively (Duthie & Hughes, 1982). The effects of gill ablation on fish' activities correspond clo-sely to expectations from GOLT. Note that it is difficult to "add" gill area experimentally to test for the effects of more gills. Thus, an alternative way of testing the effects of gill area on body activi-ties of fishes is through comparisons between related species (Pauly, 2010); the results of which also matching expectation from GOLT.

Even though GOLT predicts that they are ultimately gill-area lim-ited (see Diaz-Pauli, Kolding, Jeyakanth, & Heino, 2017), fish such as guppies, whose diminutive size implies inherently high surface/vol-ume ratios have little difficulty extracting the little oxygen they require from the water surrounding them. This is consistent with the fact that their gills grow isometrically (see Table 1), or nearly so (Table 2). Indeed, gills growing hypoallometrically occur in the Philip-pine goby (*Mistichthys luzonensis*), one of the smallest fish (and verte-brate) of the world, whose gill surface grows with a weight exponent (d_G, see Table 1) of about 0.60 (See Table 2 and Pauly, 1982, based on Te Winkel, 1935).

This is also the reason why von Bertalanffy (1938, 1951), work-ing with guppies where $S \approx a \cdot L^2$, erroneously thought that his equa-tion, based on the exponent ($n = 2$) for the surface limiting metabolic rate, was "physiologically" correct: he did not realize that a surface could grow hyperallometrically (i.e., with $n < 2$, see above). This error can be remedied, and a generalized von Bertalanffy growth function (VBGF) defined which allows for $n \neq 2$ (Pauly, 1981, 2010), but this is not followed upon here.

However, and here we are directly confronting the critique of Lefevre et al. (2017), we are well aware that for most fish larger than guppies, gills do grow hyperallometrically (see Table 2), i.e., that "[g]ills are folded surfaces, not spheres" (Lefevre et al., 2017). Indeed, the very fact that in most fish, gills grow hyperallometrically is an indication that the O_2–supply that these fish experience is a limiting factor (Table 1) for them, and does not meet their demand. Although catabolism may scale with body mass with an exponent of <1, it does not affect the constraints of gill respiratory surface area on growth (Figure 2).

4 | LETTERS IN AN UNREAD BOOK VERSUS GILL LAMELLAE

Lefevre et al. (2017) attempt to demonstrate that the metabolic rate of fish cannot be limited by the overall respiratory surface of their gills by arguing that gill lamellae are analogous to the letters making up the words in a book, and whose number per unit of a book's vol-ume can remain constant, whatever its three linear dimensions (i.e., height, width, and depth).

However, just as books are meant to be opened and their let-ters and words apprehended sequentially, gill lamellae must have oxygen-rich water flowing through them to fulfill the function for which they have evolved (see Hughes, 1966 and Hughes and Mor-gan, 1973 for details on the blood circulation across gill lamellae). This function is achieved either by pushing a "sieve" of gill lamellae against the water (ram-ventilation, similar to a car's radiator; Ste-ven, 1972) or by a buccal pump which pulls water across that sieve (Brainerd & Ferry-Graham, 2005).

Once the water has crossed that sieve, it is largely depleted of O_2 (Johansen, 1982; Park, Kim, & Kim, 2014; Steven, 1972), and thus they would be no point to direct it into another sieve. Thus, while lamellae can be stacked along the height and width dimensions, they cannot be stacked in depth. That the depth dimension cannot be accessed is why the overall respiratory surface of the gill cannot keep up with a

TABLE 2 Illustrative values of the powers of weight in proportion to gill surface area (d_G) and metabolism (d_{O2}) increase with the body weight of individual fishes

Taxa	d_G	d_{O2}	Reference(s) and remarks
Mystichtys luzonensis	0.601	–	Pauly (1982), based on Te Winkel (1935), pertaining to one of the smallest vertebrates in the world, reading a maximum length of 1.5 cm and a weight of 0.03 g
Gambusia affinis	–	0.63	Winberg (1960), based on Maksudov (1940)
Poecilia reticulata	–	0.667	von Bertalanffy (1951) working with guppies, and erroneously believing that they validated his "2/3 rule" for all fishes
Cyprinus carpio	0.794	–	Oikawa and Itazawa (1985), for carp <1 g (see bottom of this table and Figure 1)
Various marine fishes	–	0.80	Winberg (1961), based on a classic review on the then extent literature
Various freshwater fishes	–	0.81	Winberg (1961), based on a classic review on the then extant literature
Various fishes	0.811	0.826	De Jager and Dekkers (1975), based on species whose gill surface area was estimated and whose metabolic rate was measured, both as a function of body weight. De Jager and Dekkers (1975) assumed that d_G and d_{O2} were necessarily identical, and averaged the two values to $d = 0.82$
Katsuwonus pelamis	0.85	–	Muir and Hughes (1969), based on 4 skipjack tuna
T. thynnus + T. albacares	0.88	–	Muir and Hughes (1969), based on 5 bluefin + 2 yellowfin tuna
Thunnus thynnus	0.90	–	Muir and Hughes (1969), based on 19 bluefin tuna
Teleostean fish larvae (until metamorphosis)	≥1.0[a]	≥1.0	De Sylva (1974), Oikawa and Itazawa (1985; see also Figure 2), Giguère, Côté, and St-Pierre (1988), Bochdansky and Leggett (2001). Teleost larvae can grow with d_G and d_{O2} ≥1.0 because their fast-growing gills complement the important contribution (at this stage) of the body and primordial median fin fold

[a]The respiratory surface here includes the primordial median fin fold and the body.

FIGURE 2 Respiratory area of carp (*Cyprinus carpio*), redrawn from Oikawa and Itazawa (1985), illustrating its fast hyperallometric growth in teleost larvae ($d_G \gg 1$) and early fingerlings ($d_G > 1$), and the slower, but still hyperallometric growth of its gills in juveniles and adults ($d_G = 0.794$). The inset shows the gill area in juvenile and adults, divided by the corresponding body weight and plotted against that same body weight. The resulting scope for growth (which requires O_2) declines with body weight, down to a level (at $W_{\infty 1}$, or $W_{\infty 2}$) where all the available O_2 is used for maintenance. Higher temperatures, by increasing metabolic rate, will shift the asymptotic weight from $W_{\infty 2}$ to $W_{\infty 1}$, irrespective of assumptions or data on the shape of the maintenance metabolism (dotted lines, see Table 1)
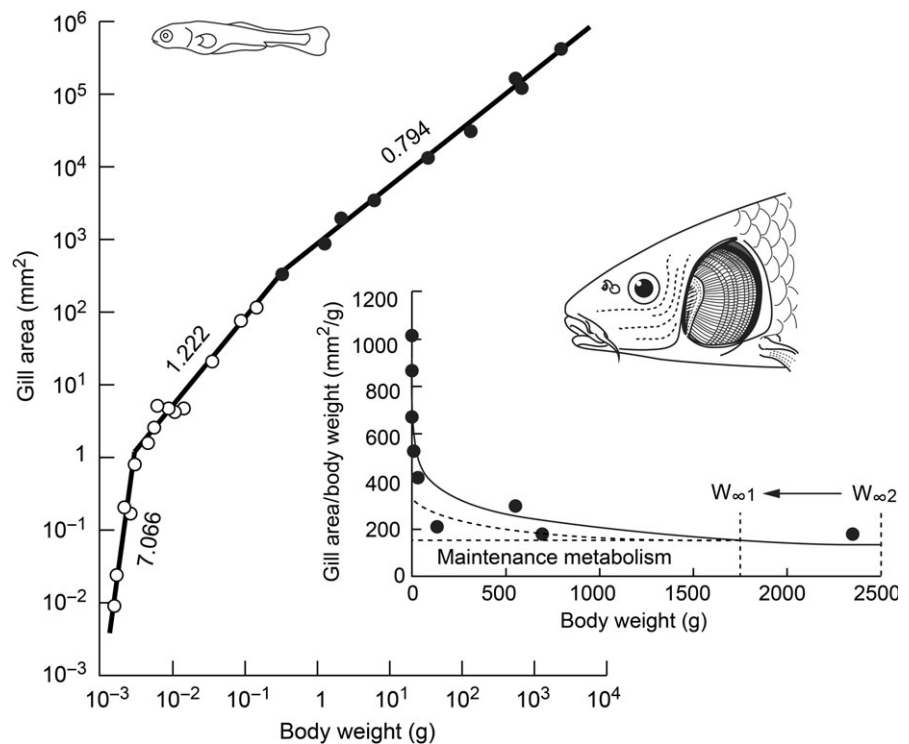
growing volume (the growing body of the fish, and the head space available for its gills), and why growing fish cannot simply add gill lamellae to maintain their weight-specific gill area.

Note that this argument is independent of the shape of the lamellae, which may be triangular, rectangular or filiform (Wegner,

Sepulveda, Bull, & Graham, 2010), or their thickness, which determines the "WBD" (De Jager & Dekkers, 1975; Graham, 2006), or the interlamellar distance, which is small in ram-ventilators such as tuna, and larger in other fishes (Hughes, 1966; Park et al., 2014).

5 | THE USE OF GOLT FOR EXPLAINING ANOMALIES

A test to GOLT is provided by the fact that it provides explicit constraints to the values of certain parameters, and thus provides criteria to re-examine results that do not conform to expectations, and to identify anomalies.

5.1 | Exponential growth of fish larvae

Because of geometrical/physical constraints, adult fish cannot grow gills whose surface remains proportional to their weight. Indeed, if they could, they would. Teleost larvae can (see how in De Sylva, 1974; Bochdansky & Leggett, 2001) and this is consistent with the fact that their bodies grow exponentially, usually as a function of their food intake and temperature (Overnell & Batty, 2000). In this, they differ radically from postmetamorphosis teleosts, which cannot, simply by adding gill lamellae, keep up with the body weight they are supposed to supply with O_2 (Figure 2).

Another perceived anomaly of GOLT is the case of the rainbow trout (*O. mykiss*), in which d_G is 3.443 (Morgan, 1971; Satora & Wegner, 2012) . These estimates of d_G, at first sight, may appear incompatible to prediction from GOLT. However, the range for body weights to which this high value applies is 0.068–0.100 g, which corresponds to larval rainbow trout.

Similarly, Satora and Wegner (2012), based on Hughes (1966) present a d_G estimate of 1.168 for Atlantic horse mackerel *Trachurus trachurus*, ranging in weight from 12 to 135 g. Atlantic horse mackerel reached up to 70 cm, corresponding to slightly above 2 kg (see www.fishbase.org). Thus, the upper limit of the range of sizes studied so far corresponds with the lower 6.7% of the realized range of body weight of Atlantic horse mackerel. Given the previous consideration on initially high d_G values declining with increasing body size, it is not unreasonable to expect that the study of respiratory area in larger specimen would yield a lower estimate of d_G.

Thus, the high d_G in the early ontogenic stages of teleosts (e.g., in rainbow trout and Atlantic horse mackerel) is consistent with the expectation from GOLT, which allows values of d_G to be ≫1 in larval teleosts, which, then gradually transits to a value <1, when the "head space" occupied by the gills becomes crowded, as illustrated here for carp *Cyprinus carpio* (Figure 2). This is consistent with the fact that the growth rate of (postmetamorphosis) fish does not *increase* with length (as is the case with exponential growth) but *decreases* throughout their lives (if one omits seasonal growth oscillations), and why their growth rate in weight starts to decline at about 30% of the maximum weight they are capable of reaching in a given habitat. These features are well captured by the VBGF for length and weight growth (Beverton & Holt, 1957; Pauly, 2010), which is the reason why thousands of authors have used the VBGF to describe the growth of fish and aquatic invertebrates (see www.fishbase.org for the former and www.sealifebase.org for the latter).

5.2 | Hyperallometric growth of gills in adult tunas

The power linking respiratory surface (*S*) and body weight (d_G), which ranges between 0.70 and 0.85 in most (postmetamorphosis) mid-size fish, rarely reaches unity, although it can get close, notably in tuna (Table 2). Indeed, the interlamellar distance of tuna gills is so small that it can be measured in terms of O_2 molecules (Stevens, 1992). Consequently, they must use ram-ventilation to irrigate their gills, and cannot tolerate coastal (i.e., turbid) waters, which can explain why tunas occur only in open oceanic waters. Therein, they occupy, geographically vast habitats which are, however, ecologically and thermally narrow, and which is increasingly being "compressed" because of the expansion of oxygen minimum zones (Prince & Goodyear, 2006).

In other words, while one can easily conceive of gills with an allometry *nearly* equal to 1, the constraints this imposes on actual fish are very hard to overcome, as not all fish, in all habitats, can have gills such as tuna. Indeed, ram-ventilation, such as used by tunas is energetically costly, particularly for larger individuals. For example, the O_2 consumption of swimming tuna scales with body weight with an exponent >1 (Gooding et al., 1981; Graham & Laurs, 1982) . Tuna in the wild spend most of the time swimming well below their maximum sustainable speed and slightly above their minimum swimming speed (Carey & Olson, 1981; Priede, 1985). Thus, oxygen supply through the gill essentially limits the activities and growth of even the fish with the most elaborate gills.

5.3 | The case of the common thresher shark (*Alopias vulpinus*)

Wegner (2016), based on Wotton et al. (2015), lists an estimate of $d_G = 1.03$ for the common thresher shark *Alopias vulpinus*. However, this estimate is based on smaller specimens (7.9–91.5 kg). For larger individuals (60–180 kg), Wegner (2016) provided an estimate of $d_G = 0.41$, along with even lower values of d_G for two rays. All three cases of low d_G were linked to a note stating that they refer to "species not included in scaling exponent means due to low sample size or a limited size range in comparison to other species". Wootton et al. (2015) also suggest that the low estimate ($d_G = 0.41$) is an error "likely due to the limited range of body size sampled".

Yet the sample sizes used for estimating the two slopes are comparable (*n* = 9 vs. 6), while the body size range associated with the "wrong" estimate of d_G is much larger than with the "correct" estimate. Wegner (2016) assumed that d_G was "wrong", then proposed the ad hoc hypothesis that "the high scaling exponent for the gill surface area of the common thresher shark *A. vulpinus* (1.03) may reflect an increased ability for regional endothermy (and hence disproportional increase in oxygen demand)."

However, such anomalies can be readily explained by GOLT. The estimates of gill area for large common thresher sharks, originally published by Emery and Szczepanski (1986), are fully compatible with those for the smaller individuals (Figure 3). It is just that the space available for the growth of gills in thresher sharks had a "head start", and that the volume of the gill apparatus
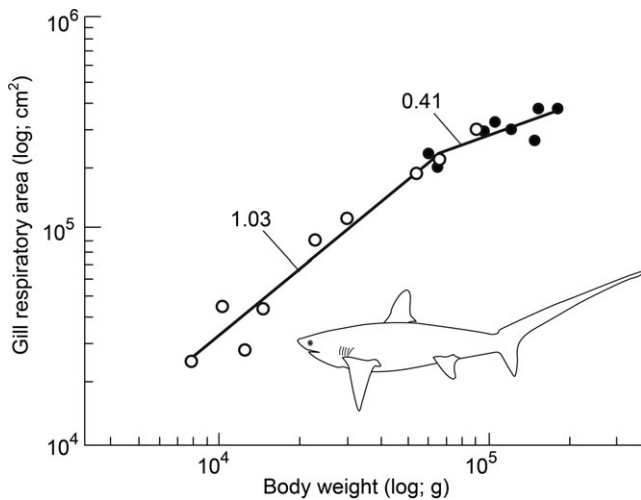
FIGURE 3 Relationship between gill respiratory area and body weight of common thresher shark as reported in Wegner (2016). The data used to estimate the high mean value of d_G, as reported in Wegner (2016), are represented by the open dot, while the perceived anomalous values by Wegner (2016) and Wootton et al. (2015) that result in a lower d_G are represented by the black dot. Note the compatibility between the two datasets

catches up with the available volume in the head of thresher sharks only when they are large (beyond about 40 kg, see Figure 3). From then on, the growth of gill area is strongly hypoallometric, i.e., becomes limiting for the growth of the common thresher shark.

What the resolution of this anomaly documents is that in elasmobranchs, as suggested by the other low values of d_G in Table 3.3 of Wegner (2016), the transition from fast- to slow-growing gill areas may occur at relatively larger sizes than in teleosts, where it appears to occur just after metamorphosis, at the fingerling stage (see Figure 2 and Table 2).

6 | HYPOTHESES THAT EXPLAIN MORE THAN EXPECTED

An important point here is the broad explanatory power that emerges from the theory that gills are limiting for the growth of fish. Notably, this provides an explanation for a suite of questions for which straightforward explanation has been wanting, especially in term of being compatible or "consilient" with each other (Wilson, 1999). Consilience is important for real scientific advances, which usually turn out to be explaining more than the questions they were originally supposed to answer. In our case, some of these questions are:

- Why fish grow as can be described by a simple asymptotic function (with growth rate declining linearly with length), i.e., in the manner described by the von Bertalanffy equation, as demonstrated in thousands of cases (see, e.g., FishBase at www.fishbase.org);

- Why the growth performance of fish, and the maximum size they reach is proportional to the size of their gills, other things being equal (Pauly, 2010);
- Why, within a species and hence similar gill anatomy and O_2 requirements, the fish occurring at higher temperatures remain smaller than those at lower temperatures, as often reported by taxonomists, e.g., Randall, Earle, Pyle, Parrish, and Hayes (1993), who noted that "tropical fishes living near the limit of their tolerance for low temperature grow to larger size at such temperatures." (See also Gunter, 1950; Ricker, 1979; Smith-Vaniz, Collette, & Luckhurst, 1999);
- Why the size at which fish reach first maturity is related to their maximum size in a given environment and both are reduced when its temperature is increased or its ambient O_2 is reduced, as e.g., demonstrated in Nile tilapia (*Oreochromis niloticus*) by Kolding, Haug, and Stefansson (2008) and in guppies by Diaz-Pauli et al. (2017) through explicit tests of the hypotheses in Pauly (1984);
- Why the larger individuals of a given species have a longer spawning season than smaller individuals, which may experience skipped spawning (Jørgensen, Ernande, Fiksen, & Diekman, 2006; Pauly, 2010);
- Why the females in most fish species reach larger sizes than the males, even though they allocate far more energy to their gonads (Pauly, 1989, 2010);
- Why it is that the large fish of a given species are more sensitive to temperature increase such as presently occurring, or can be expected from global warming (Di Santo & Lobel, 2017; Neuheimer, Thresher, Lyle, & Semmens, 2011; Tirsgaard, Behrens, & Steffensen, 2015);
- Why the food conversion efficiency of large individuals of a given species lower than that of smaller individuals (other things being equal; see Gerking, 1971; Pauly, 2010);
- Why stress in fish, which "has been identified as a diversion of metabolic energy from routine, maintenance and anabolic to non-routine activities" (Radull, Kaiser, & Hecht, 2002; citing Barton & Schreck, 1987) reduces their growth (e.g., McCormick et al., 1998);
- Why larger individuals of a given species occur in deeper, cooler water and undertake wider seasonal migrations (Heincke, 1913; Pauly, 2010);
- Why young/small teleost exhibit daily rings on their otoliths (and young squids on their statoliths) which are invisible in older/larger individuals (Pauly, 1998, 2010); and
- Why a number of other phenomena previously considered biological riddles (see Pauly, 2010) can also be explained straightforwardly when following up on the implications of gills being responsible for the O_2 *supply* to the bodies of fish, but not necessarily meeting their *demand*.

We suggest that GOLT, which straightforwardly explains these phenomena, is superior to alternative hypotheses, mainly because it offers a parsimonious, coherent explanation for these phenomena, rather than a series of ad hoc reiterations of the problems at hand.

7 | USE OF MORE PRECISE SCALING EXPONENTS EXACERBATE SHRINKING

Scaling between gill surface area or oxygen demand and body weight varies between species (Table 2; Lefevre et al., 2017), which also affects the sensitivity of their growth to warming. The standard VGBF assumes a scaling exponent of 2/3 (Table 2; von Bertalanffy, 1951). Cheung et al. (2013) adopted a scaling exponent close to the value used in the standard VBGF (0.7) in their model to predict the effects of warming on maximum body size, while acknowledging that the exponent can vary. Lefevre et al. (2017) suggested this relatively low value was chosen in order to generate a stronger shrinking effect than—they presume—using higher value would have generated.

We show that this is not the case, first by recalling the key equation of Cheung et al. (2013):

$$\frac{dW_t}{dt} = H \cdot W_t^d - k \cdot W_t^b, \tag{1}$$

where W is body weight, t is time and H and k are coefficients for anabolism and catabolism. In line with Pauly (1981, 2010, and see above), anabolism, i.e., the synthesis of new proteins, was considered to be limited by oxygen supply to the body, and hence by gills that grow in proportion to W^d, with $d < 1$. Catabolism, on the other hand, driven by the spontaneous denaturation of these proteins all over the body, is assumed proportional to its mass, i.e., $b = 1$, if mainly to simplify calculations (We discussed above the implications of $b < 1$ which may be observed in some fishes). At higher temperature, catabolism increases because protein denaturalization increases, along with other added energetic cost to the fish such as increased membrane permeability and ion pumping. From Equation 1, asymptotic body weight (W_∞) is derived from:

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{(1-d)}}. \tag{2}$$

Cheung et al. (2013) predicted a decrease in the value of H/k under warming. However, if d takes a different value, this will also affect W_∞. For example, with $d = 0.7$, a fish population with an initial value of $W_\infty = 10,000$ g and a decrease in H/k under warming by 5% is projected to have a W_∞ of 8,430 g, i.e., a decrease of approximately 16%. However, with $d = 0.85$, the decrease in W_∞ would be of 29%, other things being equal.

Since k is also dependent on d, we re-ran the growth model described in Cheung et al. (2013) for 754 species of exploited marine fishes with two sets of exponent d. We investigated two sets of assumptions: (1) the exponent is 0.7 in all cases (as in Cheung et al., 2013) and (2) the exponent varies with maximum size of fishes: small fishes (maximum length < 30 cm) = 0.7, medium fishes (maximum length 30–60 cm) = 0.8, and large fishes (maximum length > 60 cm) = 0.9 (roughly corresponding to Figure 1.2 in Pauly, 2010). Maximum length estimates were based on FishBase (www.fishbase.org). We then compared the decrease in W_∞ between these two sets of assumption.
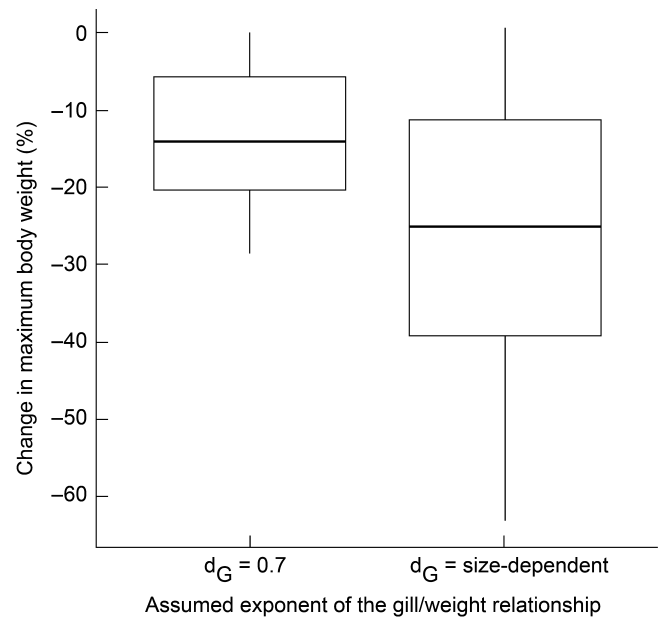

FIGURE 4 Projected changes in asymptotic weight (%) given an increase of water temperature of 1 degree of warming relative to the current (1971–2000) temperature in each species' distribution under two different assumptions for the values of the scaling exponent d, in contrast to the guess in Lefevre et al., 2017). The vertical lines above and below the boxes represent upper and lower limits of the estimates, respectively. The upper and lower boundaries of the boxes represent the 75th percentile and 25th percentile, and the thick black lines represent the median

The projected decrease in W_∞ per degree Celsius warming relative to mean current (1971–2000) water temperature of their range is substantially higher and more variable with the size-dependent exponent compared to a constant value of 0.7 (Figure 4). The median decreases in W_∞ under $d = 0.7$ and $d = 0.7$ to 0.9 under warming were predicted to be 13.9% per °C and 24.9% per °C, respectively, while the standard deviation across species increases by an order of magnitude in the latter case.

The biological implication of these results is that fish whose gills grow almost as fast as their weight (e.g., tuna) are physiologically more sensitive to warming. As discussed earlier, such elaborate gill development enables these fish to have an oxygen-demanding, active life-style. However, it also renders them more sensitive to increased oxygen demand from warming or decrease in oxygen supply. Thus, they move actively to follow specific isotherms and avoid lower oxygen area. Alternative estimate of the coefficient $b < 1$ for the catabolism term in Equation 1 would not alter the conclusion, given the constraint that fish stops growing when anabolism = catabolism (i.e., $H \cdot W_\infty^d - k \cdot W_\infty^b = 0$) where W_∞ is the asymptotic weight of the fish. On the other hand, the shrinkage of body size under warming may be lower with $b < 1$, which needs to be examined in future studies.

Thus, in contrast to the guess of Lefevre et al. (2017) that higher scaling exponents "would have significantly reduced the future temperature effects," we show that the use of higher scaling exponents

exacerbates the projected decrease in maximum body size under warming. To wit: the use of $d = 0.7$ by Cheung et al. (2013) led to conservative results, i.e., to a strong *under*estimation of the effect of global warming on the size of fish. Interestingly, the stronger decreases in body size for larger species predicted by the model is consistent with the meta-analysis conducted by Forster et al. (2012). Future studies should further examine this dimension of the prediction from our model with observations.

8 | PERCEIVED ANOMALIES OF GOLT THAT ARE ACTUALLY NOT ANOMALOUS

Lefevre et al. (2017) mention a number of phenomena which, they suggest, contradict the GOLT. Here, we deal with these alleged anomalies in no particular order, and show that the phenomena in question are consistent with GOLT:

- It is true that tropical groupers (Family Serranidae) can get really large. But when they are adults, they are extremely passive, and feed by ambush, suddenly opening their mouth and sucking in passing fish and invertebrates (Collins & Motta, 2017). Indeed, large species can be expected to be among the fish most affected by the warming of their environmental temperature (Johansen, Messmer, Coker, Hoey, & Pratchett, 2016; Johansen et al., 2015);

- It is true that the sunfish (*Mola mola*) grows to a large size, and occur in tropical waters. However, when adult, sunfish barely move, resting sideways on or near the surface (hence the name) and slurping jellyfish. Young and small sunfish (with relatively larger gill area per unit weight) display a completely different, active behavior (D. Pauly, personal observations, December 29, 1997, Monterey Aquarium);

- It is true that at first sight, the fact that the largest fish on Earth, the whale shark (*Rhincodon typus*), occurs in the tropics is disconcerting. It is, however, well documented that this slow-growing fish (Pauly, 2002) spends only half of its time at the surface, the rest being spent on descending into and ascending from deeper, cooler water (Gleiss, Norman, & Wilson, 2011), as do, incidentally, most large tuna, so that on the average, they experience subtropical or lower temperatures. Indeed, it would be interesting to check if whale sharks use counter-current mechanisms in their large gills to dump heat when they are in cold waters, as whales do through their flukes when they overheat;

- Lefevre et al. (2017) suggest that feeding "leads to a transient oxygen demand [...] which reflect the metabolic cost of digesting and assimilating the meal, hence 'growing'". Not so: growth occurs only when fish (or any other organism) synthesize its own proteins (anabolism), which require ATP, which itself requires O_2 for its own synthesis. Having a stomach full of half-digested prey is not "growing". As illustrated in Figure 1 and confirmed by physiological evidence examined in Pörtner et al. (in press), fish can function at maximum physiological capacity in the short term; however, it is the long-term physiological performance that constraints the growth of fishes over ecologically relevant time frame, a fact not considered in Lefevre et al. (2017).

- Lefevre et al. (2017) state that in "our field, it is generally accepted that a species oxygen demand determines the size of their respiratory area, not the other way round." This can be re-expressed in evolutionary terms, e.g., by stating that a specific individual of given species of fish will inherit a gill size that was sufficient for its ancestors to grow in the appropriate time to a size appropriate for their reproduction. However, this being true does not preclude this very same fish from being O_2 limited in the course of its ontogeny, in specific conditions, e.g., when it is exposed to a temperature increase in a French river;

- That "the oxygen consumption of different tissues in an animal vary by more than one order of magnitude and fishes are no exception" as pointed out by Lefevre et al. (2017). However, it is irrelevant to the argument of von Bertalanffy, quoted in Pauly (2010) that "catabolism occurs in all living cells of a fish, and is therefore directly proportional to the mass of the fish's body"—unless we are willing to assume that the relative contribution of tissues of fish (muscles, integuments, bones, etc.) to their overall body mass changes radically in the course of their ontogeny;

- Figure 2b in Lefevre et al. (2017) implies that maintenance metabolism per unit may be higher than in small fish than in adult of a given species, which is reasonable (Figure 2). However, it is not reasonable to assume that, as body mass increases, the decrease of maintenance metabolism can continue without limit, i.e., it must have a lower limit, below which a fish' living cells cannot function. Thus, O_2 is needed to resynthesize proteins that spontaneously denature, and in the case of the large grouper and sunfish mentioned above, to suck in or slurp prey, and to digest it, etc. This minimum metabolic level, which will occur at smaller sizes when higher temperatures cause protein to be denatured faster, is what limits the size of fish (Figure 2).

9 | DISCUSSION

Lefevre et al. (2017) concede that "global warming may lead to reduction in average body size and size-at-age of fish (see Munday et al., 2008; Daufresne et al., 2009; Baudron et al., 2014)", but suggest that "underlying mechanisms be investigated [...] using sound physiological knowledge and principles". Firstly, we demonstrated here that GOLT provides a parsimonious explanation for the manner that fish growth can be constrained by the physical geometry of the gill respiratory area, and consequently, its ability to take up oxygen from waters. Secondly, GOLT explains a wide range of phenomena and perceived anomalies of fish biology and ecology that are directly or indirectly related to fishes' oxygen needs and growth without the need to invoke different ad hoc hypotheses. Thirdly, through the use of a mathematical model, we demonstrate that GOLT is able to predict the decrease in body size of marine fish under warming, which intensifies when realistic parameters are selected. All of this is also consistent with the evidence presented by physiologists (e.g.,

Pörtner et al., in press), who also demonstrated that fish exposed to high temperatures cannot meet their increased oxygen demand (see, e.g., Bozinovic & Pörtner, 2015; Pörtner & Knust, 2007; Pörtner et al., 2006).

It is often easier to develop ad hoc unconstrained hypotheses that are then used to explain individual cases than to develop generalizable theory capable of explaining perceived anomalies, e.g., the high value of d_G in the common thresher shark reported in Wegner (2016) and Wootton et al. (2015). This is well illustrated by Lefevre et al. (2017), who suggest that it "is essential that the correct underlying mechanisms be investigated and identified, and that projection of the effects on fish populations be modeled using sound physiological knowledge and principles" and that "other mechanisms must be at play in French river fishes" in the context of a study that shows the decrease in body size of fishes in a French river. Thus, instead of developing a different explanation for each instance of these phenomena, for each species, we show that the GOLT can provide a unified explanation. With GOLT, we do not need to assume that the fish of French rivers use physiological mechanisms to respond to temperature increase that are different from those of other fish. In addition, GOLT could be used to predict similar phenomenon for fishes in Spanish rivers, or other European river fishes, without assuming that these fishes are physiologically constrained in a manner fundamentally different from one another.

Finally, it is true, as Lefevre et al. (2017) note, that GOLT is not mentioned in the physiology textbooks of Schmidt-Nielsen (1997) and Evans and Clairborne (2006). Similarly, what we now know as 'plate tectonics' were not mentioned in some geology textbooks until way in the 1970s (Oreskes, 1999). This is due to scientific progress, which requires textbooks to be updated when a new understanding of previously unexplained processes emerges.

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REFERENCES

Atkinson, D. (2004). Temperature and organism size: A biological law for ectotherms. *Advances in Ecological Research*, 25, 1–58.
Bakun, A. (2010). The oxygen constraint. In V. Christensen, & J. L. Maclean (Eds.), *Thinking big about ecosystem approaches to fisheries* (pp. 11–23). Cambridge: Cambridge University Press.
Barton, B. A., & Schreck, C. B. (1987). Metabolic cost of acute physical stress in juvenile steelhead. *Transactions of the American Fisheries Society*, 116(2), 257–263.
Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Marshall, T. C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20(4), 1023–1031.
von Bertalanffy, L. (1938). A quantitative theory of organic growth (Inquiries on growth laws. II). *Human Biology*, 10(2), 181–213.
von Bertalanffy, L. (1951). *Theoretische Biologie - Zweiter Band: Stoffwechsel, Wachstum. A* (418 p). Bern: Francke Verlag.
Beverton, R. J. H., & Holt, S. J. (1957). *On the dynamics of exploited fish populations*. Fisheries Investigations, Series 2 (Vol. 19, 533 p.). London: H.M. Stationary Office.
Bochdansky, A. B., & Leggett, W. C. (2001). Winberg revisited: Convergence of routine metabolism in larval and juvenile fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 220–230.
Bozinovic, F., & Pörtner, H. O. (2015). Physiological ecology meets climate change. *Ecology and Evolution*, 5(5), 1025–1030.
Brainerd, E. L., & Ferry-Graham, L. A. (2005). Mechanics of respiratory pumps. *Fish Physiology*, 23, 1–28.
Carey, F. G., & Olson, R. J. (1981). Sonic tracking experiments with tunas. Call. Sci. Papers, Int. Comm. Cons. Atlantic Tuna, 17(2), 458.
Carey, F. G., Teal, J. M., Kanwisher, J. W., Lawson, K. D., & Beckett, J. S. (1971). Warm-bodied fish. *American Zoologist*, 11(1), 137–143.
Castellini, M. (2000). History of polar whaling: Insights into the physiology of the great whales. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 126(2), 153–159.
Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V., Palomares, M. L. D., ... Pauly, D. (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3, 254–258.
Cheung, W. W. L., & Pauly, D. (2016). Impacts and effects of ocean warming on marine fishes. In J. M. Baxter, & D. Laffoley (Eds.), *Explaining ocean warming: Causes, scale, effects and consequences* (pp. 239–254). Gland, Switzerland: IUCN.
Collins, A. B., & Motta, P. J. (2017). A kinematic investigation into the feeding behavior of the Goliath grouper *Epinephelus itajara*. *Environmental Biology of Fishes*, 100(4), 309–323. https://doi.org/10.1007/s10641-016-0543-4
Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 12788–12793.
De Jager, S., & Dekkers, W. J. (1975). Relations between gill structure and activity in fish. *Netherlands Journal of Zoology*, 25(3), 276–308.
De Sylva, D. P. (1974). Development of the respiratory system in herring and plaice larvae. In J. H. S. Blaxter (Ed.), *The early life history of fishes* (pp. 465–485). Berlin-New York: Springer.
Di Santo, V., & Lobel, P. S. (2017). Body size and thermal tolerance in tropical gobies. *Journal of Experimental Marine Biology and Ecology*, 487, 11–17.
Diaz-Pauli, B., Kolding, J., Jeyakanth, G., & Heino, M. (2017). Effect of ambient oxygen and size-selective mortality on growth and maturation in guppies. *Conservation Physiology*, 5(1), cox010. https://doi.org/10.1093/conphys/cox010
Duthie, G. G., & Hughes, G. M. (1982). Some effects of gill damage on the swimming performance of rainbow trout (*Salmo gairdneri*). *Journal of Physiology (London)*, 327, 21–22.
Emery, S. H., & Szczepanski, A. (1986). Gill dimensions in pelagic elasmobranch fishes. *The Biological Bulletin*, 171(2), 441–449.
Evans, D. H., & Clairborne, J. B. (2006). *The physiology of fishes*. Boca Raton, FL: CRC Press.
Fick, A. V. (1855). On liquid diffusion. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*, 10(63), 30–39.
Fonds, M., Cronie, R., Vethaak, A. D., & Van der Puyl, P. (1992). Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. *Netherlands Journal of Sea Research*, 29(1–3), 127–143.

Forster, J., Hirst, A. G., & Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 19310–19314.

Froese, R. (2006). Cube law, condition factor and weight–length relationships: History, meta-analysis and recommendations. *Journal of Applied Ichthyology*, 22(4), 241–253.

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, 26(6), 285–291.

Gerking, S. D. (1971). Influence of rate of feeding and body weight on protein metabolism of bluegill sunfish. *Physiological Zoology*, 44(1), 9–19.

Giguère, L. A., Côté, B., & St-Pierre, J.-F. (1988). Metabolic rates scale isometrically in larval fishes. *Marine Ecology Progress Series*, 40, 13–19.

Gillooly, J. F., Gomez, J. P., Mavrodiev, E. V., Rong, Y., & McLamore, E. S. (2016). Body mass scaling of passive oxygen diffusion in endotherms and ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, 113(19), 5340–5345.

Gleiss, A. C., Norman, B., & Wilson, R. P. (2011). Moved by that sinking feeling: Variable diving geometry underlies movement strategies in whale sharks. *Functional Ecology*, 25(3), 595–607.

Gooding, R. M., Neill, W. H., & DizoN, A. E. (1981). Respiration rates and low-oxygen tolerance limits in skipjack tuna. *Katsuwonus pelamis*. *Fishery Bulletin*, 79(1), 31–48.

Graham, J. B. (2006). Aquatic and aerial respiration. In D. H. Evans, & J. B. Clairborne (Eds.), *The physiology of fishes* (pp. 85–117). Boca Raton, FL: Taylor and Francis.

Graham, J. B., & Laurs, R. M. (1982). Metabolic rate of the albacore tuna *Thunnus alalunga*. *Marine Biology*, 72(1), 1–6.

Gunter, G. (1950). Correlation between temperature of water and size of marine fishes on the Atlantic and Gulf coasts of the United States. *Copeia*, 1950(4), 298–304.

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(1), 153 p.

Hughes, G. M. (1966). The dimensions of fish gills in relations to their function. *Journal of Experimental Biology*, 45, 177–195.

Hughes, G. M., & Morgan, M. (1973). The structure of fish gills in relation to their respiratory function. *Biological Reviews*, 48(3), 419–475.

Johansen, K. (1982). Respiratory gas exchange of vertebrate gills. In D. F. Houlihan, J. C. Rankin, & T. J. Shuttleworth (Eds.), *Gills* (pp. 99–109). Cambridge: Cambridge University Press.

Johansen, J. L., Messmer, V., Coker, D. J., Hoey, A. S., & Pratchett, M. S. (2016). Increasing ocean temperatures reduce activity patterns of a large commercially important coral reef fish. *Global Change Biology*, 20(4), 1067–1074.

Johansen, J. L., Pratchett, M. S., Messmer, V., Coker, D. J., Tobin, A. J., & Hoey, A. S. (2015). Large predatory coral trout species unlikely to meet increasing energetic demands in a warming ocean. *Scientific Reports*, 5, 13830. https://doi.org/10.1038/srep13830

Jørgensen, C., Ernande, B., Fiksen, Ø., & Diekman, U. (2006). The logic of skipped spawning. *Canadian Journal of Fisheries and Aquaculture Sciences*, 63, 200–211.

Kaiser, A., Klok, C. J., Socha, J. J., Lee, W. L., Quinlan, M. C., & Harrison, J. (2007). Increase in tracheal investment with beetle size support hypothesis of oxygen limitation on insect gigantism. *Proceedings of the National Academy of Sciences of the United States of America*, 104(32), 13198–13203.

Kolding, J., Haug, L., & Stefansson, S. (2008). Effect of ambient oxygen on growth and reproduction in Nile tilapia (*Oreochromis niloticus*). *Canadian Journal of Fisheries and Aquatic Science*, 65, 1413–1424.

Kramer, D. L. (1987). Dissolved oxygen and fish behavior. *Environmental Biology of Fishes*, 18(2), 81–92.

Lefevre, S., McKenzie, D. J., & Nilsson, G. (2017). Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Global Change Biology*, https://doi.org/10.1111/gcb.13652

Liebenberg, L. (2013). *The origin of science* (266 p). Cape Town: Cyber-Tracker.

Maksudov, I. Kh. (1940). [Data on the physiology of *Gambusia*, Communication No. 1]. *Bulletin of Experimental Biology and Medicine*, 10, 129–131. [in Russian].

McCormick, S. D., Shrimpton, J. M., Carey, J. B., O'dea, M. F., Sloan, K. E., Moriyama, S., & Björnsson, B. T. (1998). Repeated acute stress reduces growth rate of Atlantic salmon parr and alters plasma levels of growth hormone, insulin-like growth factor I and cortisol. *Aquaculture*, 168(1), 221–235.

Messmer, V., Pratchett, M. S., Hoey, A. S., Tobin, A. J., Coker, D. J., Cooke, S. J., & Clark, T. D. (2016). Global warming may disproportionately affect larger adults in a predatory coral reef fish. *Global Change Biology*, 23(6), 2230–2240. https://doi.org/10.1111/gcb.13552

Morgan, M. (1971). Gill development, growth and respiration in the trout, *Salmo gairdneri*. Ph. D. Dissertation, University of Bristol, UK

Muir, B. S., & Hughes, G. M. (1969). Gill dimensions for three species of tunny. *Journal of Experimental Biology*, 51, 271–285.

Munday, P. L., Jones, G. P., Pratchett, M. S., & Williams, A. J. (2008). Climate change and the future for coral reef fishes. *Fish and Fisheries*, 9(3), 261–285.

Neuheimer, A. B., Thresher, R. E., Lyle, J. M., & Semmens, J. M. (2011). Tolerance limit for fish growth exceeded by warming waters. *Nature Climate Change*, 1(2), 110–113.

Ohlberger, J. (2013). Climate warming and ectotherm body size—From individual physiology to community ecology. *Functional Ecology*, 27, 991–1001.

Oikawa, S., & Itazawa, Y. (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.

Oreskes, N. (1999). *The rejection of continental drift: Theory and method in American earth science*. Oxford: Oxford University Press.

Overnell, J., & Batty, R. S. (2000). Scaling of enzyme activity in larval herring and plaice: Effects of temperature and individual growth rate on aerobic and anaerobic capacity. *Journal of Fish Biology*, 56, 577–589.

Park, K., Kim, W., & Kim, H.-Y. (2014). Optimal lamellar arrangement in fish gills. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 8067–8070.

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(4), 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(2–3), 379–383.

Pauly, D. (1984). A mechanism for the juvenile-to-adult transition in fishes. *Journal du Conseil international pour l'Exploration de la Mer*, 41, 280–284.

Pauly, D. (1989). On the sex of fish and the gender of scientists. *Naga, The ICLARM Quarterly*, 12(2), 8–9 [Reprinted as Essay no. 24, p. 172–175 In: D. Pauly. 1994. On the sex of fish and the gender of scientists: essays in fisheries science. Chapman & Hall, London].

Pauly, D. (1997). Geometrical constraints on body size. *Trends in ecology & evolution*, 12(11), 442.

Pauly, D. (1998). Why squids, though not fish, may be better understood by pretending they are. South African Journal of Marine Science, 20, 47–58.

Pauly, D. (2002). *Growth and mortality of basking shark* Cetorhinus maximus, *and their implications for whale shark* Rhincodon typus. In S. L. Fowler, T. Reid, & F. A. Dipper (Eds.), Elasmobranch biodiversity: Conservation and management. Proceedings of an International

Seminar and Workshop held in Sabah, Malaysia. Occasional Papers of the IUCN Survival Commission No. 25, Gland, Switzerland. pp. 199–208.

Pauly, D. (2010). *Gasping fish and panting squids: Oxygen, temperature and the growth of water-breathing animals. Excellence in ecology* (Vol. *22*, xxviii + 216 p). Oldendorf/Luhe, Germany: International Ecology Institute.

Pörtner, H.-O., Bock, C., & Mark, F. C. (in press). Oxygen- and capacity-limited thermal tolerance: Bridging ecology and physiology. *Journal of Experimental Biology.*.

Pörtner, H. O., & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science, 315* (5808), 95–97.

Pörtner, H. O., Peck, L. S., & Hirse, T. (2006). Hyperoxia alleviates thermal stress in the Antarctic bivalve, *Laternula elliptica*: Evidence for oxygen limited thermal tolerance. *Polar Biology, 29*(8), 688–693.

Priede, I. G. (1985). Metabolic scope in fishes. In P. Tyler, & P. Calow (Eds.), *Fish energetics: New perspectives* (pp. 33–64). London: Croom Helm.

Prince, E. D., & Goodyear, C. P. (2006). Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography, 15*(6), 451–464.

Radull, J., Kaiser, H., & Hecht, T. (2002). Stress-related changes in the metabolic rate of juvenile spotted grunter, *Pomadasys commersonnii* (Haemulidae, Pisces). *Marine and Freshwater Research, 53*(2), 465–469.

Randall, J. E., Earle, J. L., Pyle, R. L., Parrish, J. D., & Hayes, T. (1993). Annotated checklist of the fishes of Midway Atoll, northwestern Hawaiian Islands. *Pacific Science, 47*(4), 356–400.

Ricker, W. E. (1979). Growth rates and models. In W. S. Hoar, D. J. Randall & J. R. Brett (Eds.), *Fish physiology* (Vol. *8*, pp. 677–743). New York: Academic Press.

Satora, L., & Wegner, N. C. (2012). Reexamination of the Byczkowska-Smyk gill surface area data for European teleosts, with new measurements on the pikeperch, *Sander lucioperca*. *Reviews in fish biology and fisheries, 22*(1), 1–9.

Schmidt-Nielsen, K. (1997). *Animal physiology: Adaptations and environment*. Cambridge: Cambridge University Press.

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change, 1*, 401–406.

Smith-Vaniz, W. F., Collette, B. B., & Luckhurst, B. E. (1999). *Fishes of Bermuda: History, zoogeography, annotated checklist and identification keys*. American Fisheries Society of Ichthyologist and Herpetologists Special Publication No 4 (424 p.). Lawrence, Kansas: Allen Press.

Steven, E. D. (1972). Some apect of gas exchange in tuna. *Journal of Experimental Biology, 56*, 809–823.

Stevens, E. D. (1992). Oxygen molecules as units to dimension the sieve of fish gills. *Environmental Biology of Fishes, 33*, 317–318.

Te Winkel, L. E. (1935). A study of *Mistichthys luzonensis* with special reference to conditions correlated with reduced size. *Journal of Morphology, 58*(2), 463–535.

Tirsgaard, B., Behrens, J. W., & Steffensen, J. F. (2015). The effect of temperature and body size on metabolic scope of activity in juvenile Atlantic cod *Gadus morhua* L. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 179*, 89–94.

Verberk, W. C. E. P., Overgaard, J., Ern, R., Bayley, M., Wang, T., Boardman, L., & Terblanche, J. S. (2016). Comparative biochemistry and physiology, part A does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. *Comparative Biochemistry and Physiology, Part A, 192*, 64–78.

Ward, P. (2006). *Out of thin air: Dinosaurs, birds and Earth's ancient atmosphere*. Washington, DC: Joseph Henry Press, National Academies Press. 296 p.

Wegner, N. C. (2016). Elasmobranch gill structure. In R. E. Shadwick, A. P. Farrell, & C. J. Brauner (Eds.), *Physiology of elasmobranch fishes: Structure and interaction with environment* (pp. 102–153). London: Academic Press.

Wegner, N. C., Sepulveda, C. A., Bull, K. B., & Graham, J. B. (2010). Gill morphometric in relation to gas transfer and ram ventilation in high-energy demand teleosts: Scombrids and billfishes. *Journal of Morphology, 271*, 36–49.

Wilson, E. O. (1999). *Consilience: The unity of knowledge*. New York: Random House.

Winberg, G. G. (1960). *Rate of metabolism and food requirements of fishes*. Translation Series, No. 194, 239 p. Nanaimo: Fisheries Research Board of Canada.

Winberg, G. G. (1961). New information on metabolic rate in fishes. *Voprosy Ikhtiologii, 1*(1), 157–165 [Fisheries Research Board of Canada Translation. Series, (362) 11 p.].

Wootton, T. P., Sepulveda, C. A., & Wegner, N. C. (2015). Gill morphometrics of the thresher sharks (Genus Alopias): Correlation of gill dimensions with aerobic demand and environmental oxygen. *Journal of morphology, 276*(5), 589–600.

Graphical Abstract

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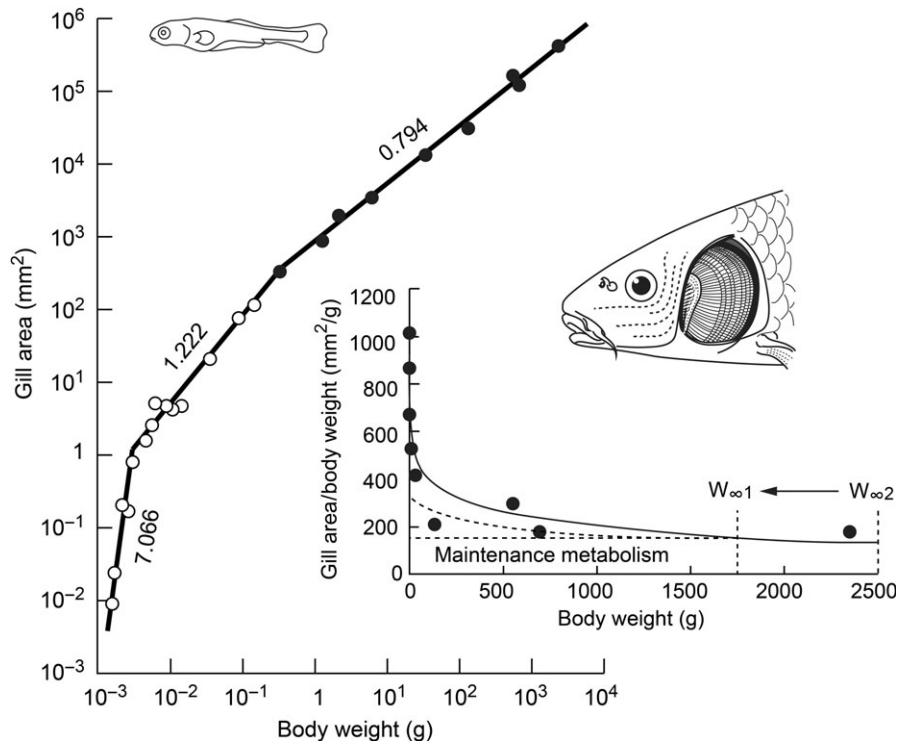
Ocean warming is expected to cause a decrease in body size of marine fishes. Such phenomenon is explained by the Gill-Oxygen Limitation Theory (GOLT)—under warming, the oxygen supply to large fish size cannot be met by their gills, whose surface area cannot keep up with the increased oxygen demand by their three-dimensional bodies. A wide range of biological features of fish can be understood when GOLT is used as an explanation. Available empirical evidence of fish shrinking under warming corroborates predictions based on GOLT. It is important to consider GOLT in understanding responses of fishes to global change.