

LEARNING FROM PEER-REVIEWS: THE GILL-OXYGEN LIMITATION THEORY AND THE GROWTH OF FISHES AND AQUATIC INVERTEBRATES*

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Abstract

Peer review is the cornerstone of modern science, but except for complaints by colleagues about unfair reviews of their submissions, not many personal accounts are available of peer review, and even less on peer reviews actually improving papers. This contribution is based on the comments provided by three anonymous referees to the authors of the paper, later published as Pauly and Cheung (2017; *Global Change Biology*), which defended the Gill-Oxygen Limitation Theory (GOLT) from a critique by Lefevre *et al.* (2017, *Global Change Biology*). The back and forth of arguments between referees and authors, which led to the discovery of a new growth pattern in the common thresher shark (*Alopias vulpinus*) and probably in other elasmobranchs as well, is presented in detailed fashion, and thus represent a case study of peer review performing well. This contribution concludes by making a case for theories (such as the GOLT, whose validity was assessed here) that provide constraints on the expected results of experiments, or sampling surveys. Without such constraints, scientific disciplines such as ichthyology or physiology will not enter the age of ‘big data,’ from which strong inferences can be drawn, but remain tied to ‘small data,’ multiple meaningless small heaps of unstructured numbers and observations.

Introduction

The way science is done in the 21st century is rapidly moving away from the way it was done in the second half of the 20th century, notably with regards to big data at the ‘meta’ level (Pauly 2017), and to peer-review at the practical, 9 to 5 level.

Indeed, an entire industry, which may be called “Predatory Publishing” has recently emerged which resembles scientific publishing but is not, because it omits peer-reviews. The reasons for its relative success, notably in emerging countries (India, Iran...) are many, but one might be the obscenely large fees charged by ‘open journals’ or to bring single articles across the paywall of other journals. Indeed, one could also speak here of predatory behavior, with ‘only’ peer review marking the difference between the two business models.

Peer review, which may thus be seen as a service provided freely by scientists to scientific publishers to help them distinguish themselves from “predatory publishers” is, however, also a great help to scientists, as it usually helps improve their papers.

As individual scientists tend to only complain about incompetent and/or malevolent reviews, and editors tend to be mum about reviews, there are relatively few good examples of the review process that make clear, in practical terms, why peer review is good for science, or at least for many individual papers.

What peer review can add to a manuscript is illustrated here, in some details, by a case study whose antecedents are as follows:

- 1) In 1981, the author published, based on his dissertation, the basic elements of what will be called below the Gill-Oxygen Limitation Theory (GOLT), i.e., why the gills of fishes and other water-breathers (e.g., crustaceans and mollusks) cannot grow as fast as the bodies they must supply with oxygen (the scaling factor in question, d_G , is assumed to always be < 1), and hence must limit their growth rate, maximum size, food conversion, etc. Subsequent contributions (notably Pauly 1984, 1998a, 1998b, 2010) added empirical evidence to the GOLT;

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- 2) Based on the GOLT, Cheung *et al.* (2013) estimated, using a single generic values of $d_G = 0.7$, a decline of the maximum size that fish can be expected to reach in the future, given ocean warming;
- 3) Three physiologists, Lefevre *et al.* (2017), published a critique of the paper in (2), asserting that the Cheung *et al.* (2013) paper was fundamentally flawed, because gill respiratory area grows in response to the oxygen demand of fish, and that this growth can keep up with the 3-dimensional growth of a fish body. Moreover, they also accused Cheung *et al.* (2013) - without evidence - to have deliberately chosen the value of $d_G = 0.7$, in the model they developed to predict the effects of temperature, such that it would generate a large decrease of size from a modest ocean warming.
- 4) Pauly and Cheung (2017) rebutted these claims, notably demonstrating that using more detailed values of d_G , ranging from 0.7 to 0.9 generated stronger size decreases than reported in the 2013 paper.

This contribution consists, in the main, of the reviewers' comments (all numbered, in italic and starting with @) and the responses to the peer review of Pauly and Cheung (2017), in form of a letter to the editor of *Global Change Biology*, drafted by this author, and which dealt with the constructive comments of three anonymous reviewers of the submission, now published as Pauly and Cheung (2017). This contribution, thus, is best read along with the paper by Pauly and Cheung (2017) at hand, lest things may get confusing. Also, the start of the letter is very tedious. However, as the arguments go back and forth, the stakes become higher, and the reviewers' questions more incisive. This is where the benefits of peer review manifest themselves.

The text below was minimally edited for typographical errors and flow; notably, all references to line numbers were replaced by in-text locations. The text in square brackets was inserted later for better comprehension and/or to provide additional information. The figures with Arabic numerals (1, 2, 3...) are those included in the draft whose reviews are discussed here, or related papers; the figures with Roman numerals (I, II, III) are those included here to illustrate key concepts. Also note that 'fish', in the following, refers to finfishes (Pisces) as well as invertebrates breathing water through gills.

A letter responding to reviewers' comments

Dear Editor, Please find attached the manuscript "*Sound physiological knowledge and principles in modelling shrinking of fishes under climate change*" which we revised based on the comments from three thoughtful reviewers. In the following, their comments are addressed individually; our responses indicate how the comments were accommodated in the revised text. We believe that the revised manuscript addresses all the comments raised by the reviewers and you. Thank you for your attention. Best wishes.

Editors' comment

@1) This is clearly a very important topic and one that has consequences beyond biological knowledge. We therefore want to ensure that the submission is the best it can be as we have no doubt it will bring forth a lot of discussion. In the main, we do feel the authors have tackled the key issues but there are still some outstanding points and some of the claims need to be more firmly supported by evidence and examples. These points are very clearly articulated by, in the main, supportive reviews. We ask the authors to address all these issues or if they disagree with any, that they clearly state their reasoning. We also agree with reviewers that this MS does offer an excellent opportunity to really further understanding and knowledge and ask the authors to consider this point when choosing the language they use to layout their key arguments. We do feel that a constructive approach would be best. We look forward to seeing the revised version.

We fully agree with this assessment and we document, in the text below, how we implemented the reviewers' suggestions.

Reviewer #1

@2) I agree with the authors that a response was needed to Lefevre et al. (2017) who challenged both the physiological basis and the resulting predictions of theory that predicts body size changes with warming, especially in fish. These size changes are scientifically and socioeconomically important aspects of global change biology. The response by Pauly and Cheung provides lots of useful support for the oxygen-limitation hypothesis, its underlying mechanisms, and its consistency with a variety of other observations. It rebuts many of the assertions of Lefevre et al. and provides novel predictions based on matching the allometric scaling exponent of gill surface area more closely to that of the fish.

We are delighted about this overall assessment.

@3) However, the responses to two important arguments of Lefevre et al. – relating to the scaling of surface area of folded gills, and the mass invariance of 'maintenance' metabolic rate – were not entirely convincing, and would benefit from more fleshing out.

We agree, and have amplified and differentiated our responses; see below.

@4) Also, the response sometimes over-concludes beyond the evidence presented, and sometimes distracts with text that is inappropriate to a logical, evidence-based scientific discourse.

These issues are discussed below. We have adjusted our text as suggested; see below.

@5) The first issue of Lefevre et al. is that because of the 'folded' nature of fish gills, it is possible, in principle, for their surfaces to increase directly with body mass by just adding to the radius of lamellae, to the length or number of filaments (hence numbers of lamellae), or both. In response, the authors (after a discussion about

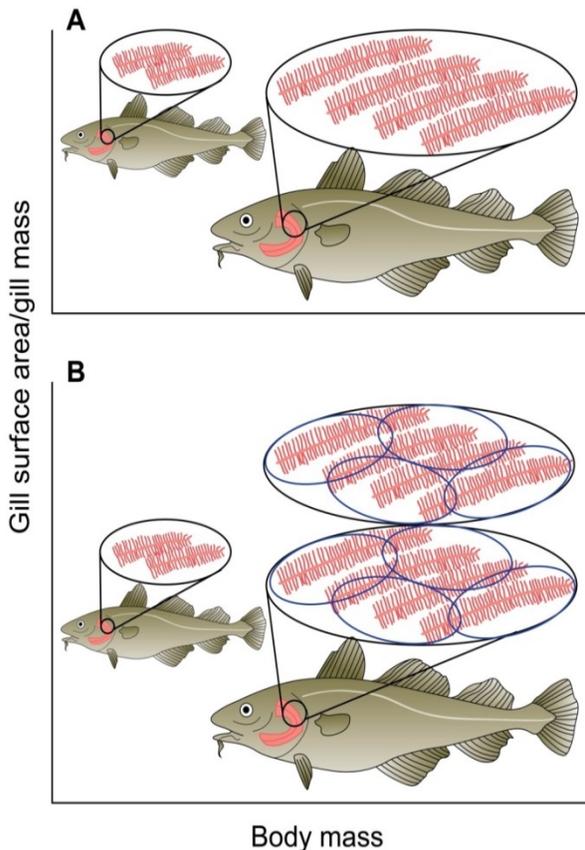


Figure 1. Unmasking a grave error in a schematic graph meant to explain that fish can always grow gills as required for maintaining the same gill area per unit weight. Panel A, copied from Lefevre et al. (2017) is supposed to illustrate that a fish, when growing, simply acquire more gills, as illustrated by the fish on the right. Note that this fish, which is 2 times longer, is $2^2 \times 2^2 = 8$ times heavier than the fish on the left. Panel B shows the approximate gill area (symbolized by the red feather-like drawings) that would be needed by the heavier fish to maintain the same gill area/body weight as the small fish. Panel B would have been honest; however, the readers of Lefevre et al. (2017) would have seen that it did not make sense.

surface area constraints that could be largely culled as it skirts around this specific issue) eventually argue that the gills just don't have enough room in the gill cavities to achieve this. But this argument implies that the gill cavity volume does not scale isometrically with body volume. And so this begs the question why doesn't the gill cavity volume scale in direct proportion with body volume (or mass)? This issue needs to be taken to a more convincing and satisfying conclusion.

We agree that we skirted around the claim of Lefevre *et al.* that gill lamellae can be compared to pages in a book, i.e., disembodied two-dimensional entities that can be stacked at will and will keep up with a growing volume (we initially thought that the flaws of this argument would be immediately obvious to any reader). We now respond to this argument in the revised text, where we point out that if the analogy with pages can keep up with a volume holds only if a book is not read, i.e., if no space between the pages is required. Similarly, gill lamellae are 3-D objects that not only must accommodate capillaries of sufficient diameters for red blood cell to pass through, but also require space because water must be able to flow along their surfaces. We thought this was self-explanatory, but realize now it must be explicit, given the subtlety of the error in the pages-in-a-book analogy. Thus, text to this effect was added. [See also Figure I].

@6) *The second important issue of Lefevre et al. is that mass-specific metabolic rate for 'maintenance' may not be constant with increasing body mass. They refer to studies in which the standard metabolic rate has a scaling exponent less than 1 (importantly this should be during ontogeny, not interspecifically). An important consequence of this for predictions of body size shrinkage with warming is that if this scaling exponent is less than 1, it will lessen the reductions in body size with warming predicted by the von Bertalanffy growth model used by Cheung et al. (2013).*

Agreed. In the original submission, we alluded to this issue in passing, when referring to the insert in Figure 2 [of Pauly and Cheung 2017], which illustrates, via two examples (dotted lines), two possible trajectories (i.e., scaling factors) for the relationship between maintenance metabolism and body weight. We have now amplified our comments on this issue. However, we also point out the difference between the trajectories is large only to young/small individual, while size reduction would show up in old/big individuals. Also, there are two other factors that work against this bias (see below). In addition, we added to the revised manuscript that having a scaling exponent less than 1, given the constraint that fish stop growing at asymptotic size (when anabolism = catabolism), does not affect the use of the Gill-Oxygen Limitation Theory to infer that fish maximum body size decreases with warming. We also noted that if the difference between the trajectories is large, then the shrinkage that Cheung *et al.* (2013) will be overestimated.

@7) *Because the value of this exponent affects their model predictions, it should be discussed earlier in the paper. The authors acknowledge that a change in the scaling of standard metabolic rate is reasonable, but do not then make it sufficiently clear why maintenance metabolism should still be considered directly proportional to body mass. In other words, the authors need to justify why standard metabolic rate is not a measure of maintenance metabolism, and provide evidence of how these two scale differently with body mass. The authors do say that a '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).' Thus, the authors appear to be implying that standard metabolic rate is not maintenance metabolic rate.*

We thank this reviewer for pointing out that we did not define all our terms, notably standard metabolic rate and maintenance metabolic rate, the difference of which is crucial to our argument. We now explain this earlier in the main text in the revised manuscript. We also added a short glossary to explain key terms [see Table 1 in Pauly and Cheung 2017].

@8) *[The authors] also should give a fuller description of what may be problematic at high temperatures besides just protein denaturation (e.g. membrane permeability, ion pumping costs).*

Agreed. We now mention some of the added costs of high temperature. However, we maintained our emphasis on protein denaturation, because its major consequence is that the denatured proteins must be re-synthesized, which require ATP, which itself requires oxygen that comes from the gills.

@9) *Table 1 gives illustrative values of mass-scaling exponents for gill surface area and metabolism. Isn't a more thorough analysis possible with available data?*

We agree that a more thorough analysis of data such as those in [now] Table 2 [of Pauly and Cheung 2017] could be performed. The point of this table, however, was to document both the central tendency (for most teleost fish past metamorphosis) and extremes values (tuna, gobies, fish larvae) to define the terrain within which the discussion occurs, and provide key references in context.

@10) How can the reader be convinced that these examples are illustrative of general trends among the teleosts, rather than selected to support the authors' thesis?

If our readers assume bad faith or chicanery on our part, then even a table 10 times larger could not convince them that we are not cherry-picking. Moreover, the syntheses cited in this table are classics which were, at the time that were published, the most comprehensive studies available on the topics in question.

@11) Which metabolic rate is used? It should be maximum metabolic [rate], to be related to oxygen supply limits. If it isn't MMR, the data should not be included in the table.

Here, we must respectfully disagree. Maximum metabolic rate can be, in nature, sustained only at a high cost to general fitness (a point made by Priede 1985, and which we illustrated with Figure 1 [in Pauly and Cheung 2017]), and cannot be used for such comparisons. Our explanation is now elaborated in the text.

@12) Figure 2 needs better labelling or explanation. Is the curve fitted by eye to gill area/body weight (y-axis label), and then assumed to be directly proportional to maximum metabolic rate?

We agree to the need for a better caption. There are two bivariate graphs in Figure 2 [of Pauly and Cheung 2017]. The main one shows straight regression lines fitted by least squares to gill area/body weight data pairs. It shows, for carp, that gill surface area can grow faster than body weight in in very small and small individuals (as in Table 2). Then, the expected post-metamorphosis scaling ($d_G < 1$) establishes itself at about 1 g. The smaller bivariate graph (insert) presents the same data, but as gill area per body weight. Therein, the two dotted lines are hypothetical examples of possible alternative trajectories for the maintenance metabolism. We have modified the caption to make this clear, and now mention 'hyperallometric' growth, as requested.

@13) The scope for growth is derived from comparing this curve with a horizontal line, but see Point above, about whether a horizontal line is justified. Also, the line is not measured in units of gill area/body weight, so the axis labelling is incomplete.

Agreed; we have expanded and clarified the caption of Figure 2 [in Pauly and Cheung].

@14) The application of a size-specific value for the scaling exponent d_G for uptake, produces a very interesting result – that body size shrinkage with warming is expected most in larger species. If this is borne out with data, it would extend to larger species the finding of Forster et al. (2012) that warming reduces adult size of larger aquatic ectotherm species more than that of smaller species.

We agree with this assessment. Forster et al. (2012) is now cited. Note that this effect would also strongly counteract the overestimation of shrinkage that we conceded earlier.

@ 15) Text [in the Introduction, referring various examples of surface/volume tensions] inappropriate to a concise, logical, evidence-based paper. All of it!

We respectfully disagree. As mentioned by Reviewer #2, in this paper, we must be didactic, to draw readers in. Nothing is better for this than powerful imagery. Moreover, an important point is being made: near-perfect adaptations even to difficult conditions have the effect of masking the underlying challenge. This is later elaborated upon with regards to the extraction of oxygen from water, which, we argue, is a challenge for water-breathing animal such as fish.

@16) While [the content of the section titled "Biological surfaces as a ubiquitous constraint"] is correct, it is not directly addressing the particular issue raised by Lefevre et al., which is concerned with how the specific folded geometry of gills enables the usual surface area constraints to be potentially overcome (see above).

The section on 'Biological surfaces as a ubiquitous constraint' presents the fundamental elements of what will be called 'Gill-Oxygen Limitation Theory' (GOLT), which is a special case of 'dimensional tension' (see new glossary). Without this section, our argument would be nothing but special pleading, i.e., for fish being 'different'

from other organisms just because we study them. [The glossary defines ‘dimensional tension’ as “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”].

@17 [Text to be removed] *‘and elsewhere, as we will see when we begin to study extraterrestrial life.’*

We have modified this to read “...as we might see...” The point here is that the GOLT is built from first (geometric) principles, and is meant to be ‘substrate-independent’, just as gravity is. There is no reason why we should accept that physical or chemical ‘laws’ should work on other worlds, but not biological one (e.g., Natural Selection). This is important here because near the end, Lefevre *et al.* appear to argue that different principles apply even to different rivers. Here we claim the exact opposite.

@18) [Statement] *‘This is due to something called scientific progress’ This sounds like something called condescension. Just remove the ‘something called’.*

Agreed. This is now edited as suggested.

@19) *Over-concluding beyond the evidence presented [several examples] ‘This is the reason...’ (or similar). More appropriate would something like ‘this is consistent with...’*

Agreed; changed as suggested.

@20) *What is the specific nature of the constraints [to gills growing as fast as a volume]? [Asserting that] Lefevre et al.’s argument about folds and number of lamellae does not hold [is not enough]. No evidence is presented for why fish ‘cannot’ grow gills whose surface remains proportional... Also, you say ‘Indeed, if they could, they would’ Who can know this?! The authors need to write for a critical scientific readership, not one who shares the authors’ beliefs.*

We see now that we should have dealt with the gill-lamellae-as-pages-in-books analogy of Lefevre *et al.* in our original submission, because refuting this misleading analogy also explains why fish cannot grow gill whose surface remains proportional to their weight. This is now done [See also Figure I in this contribution].

@21 *For ‘comes along with understanding that’ I suggest ‘emerges from the theory that...’*

Agreed; changed as suggested.

@22 *While the argument of Lefevre [regarding catabolism] is correctly identified as being incorrect, the quotation of von Bertalanffy is not quantitatively logical: because all living cells catabolise doesn’t mean that catabolism is directly proportional to body mass. In principle, the proportion of different tissues or structures with different metabolic intensities may scale allometrically during ontogeny, so that overall, metabolic rate is not directly proportional to body mass (as has been observed recently in insects by Maino and Kearney).*

We agree that one can easily conceive of post-metamorphosis fish whose gross morphology (and proportions of cell and protein types) would change (say due to acquisition of an armor, from rapidly denaturing muscle cell proteins to more slowly denaturing bone cell proteins), which would change the overall denaturation rate. Indeed, in the book by Pauly (2010), cited in the paper, two such cases are discussed: the seasonal deposition of visceral fat, marked in fish exposed to strong summer-winter temperature differences, and the gradual ‘jellification’ in some species of flatfish (Pleuronectiformes), where big/old specimens can reduce their metabolic requirements by converting part of their bodies to acellular ‘jelly.’ However, dealing with these exceptions (which do not lead to contradictions anyway) in the context of our paper would make it exceedingly long. We believe, moreover, that in the spirit of parsimony, there is no need to assume in the absence of supporting evidence that radical changes in tissue composition routinely occur in fishes. [This contradicts the findings of Maino and Kearney (2014, 2015) of massive changes in tissue composition and metabolic rate in the ontogeny of insects, but then, young fish do not differ from older fish the way insect larvae differ from the adult forms; we forgot to make this point and thus to cite “Maino and Kearney”].

@23) Wording/meaning unclear [in the caption of Figure 4: 'Average' - Is this the mean or median? The value for the latter on Fig.4 seems to be greater than 30%. Does the figure show the median and the text describe the mean?]

The median values are now reported in the revised manuscript, which is consistent with the figure.

@24) Typographical errors [list followed].

Thanks for pointing out these errors; they are now all fixed.

Reviewer #2

@25) This manuscript is a response to a rebuttal (Lefevre et al. 2017 *Global Change Biology*) that argued against the idea and model results from Cheung et al. (2011, *ICES J. mar. Sci.*; 2013, *Nature Climate Change*) that fish body sizes will become smaller in the future under ocean warming conditions. These original papers (Cheung et al. 2011; 2013) based their models and underlying assumptions that Lefevre et al. (2017) challenged. In turn, this current manuscript responds to the challenges Lefevre et al. (2017) lays out. This series of papers highlights the current tension between physiologists and ecologists, in which physiologists generally believe that metabolic rate constrains gill area and ecologists generally believe that gill area constraints metabolic rate.

The last sentence of this paragraph is very well put, though we do not believe that there are many aquatic ecologists who think about gills, unfortunately.

@26) The assumptions that Lefevre et al. (2017) question and this manuscript attempts to provide evidence for are in regard to how gill surface area increases with increasing body mass (i.e. the scaling exponent of the relationship of gill surface area and body mass, d_G). Specifically, these assumptions made originally by Cheung et al. (2011 and 2013) and upheld in this manuscript suggest that geometric constraints on gills result in the gill surface area not growing as quickly as body mass (i.e. gills can only grow as fast as surface area to volume ratios allow, resulting in a scaling exponent of 2/3) and thus, limit the growth and metabolic rate of an individual.

We agree almost completely with the content of the above paragraph, except that gills, while functioning as 'surfaces' for the exchange of gases (see below) do not need to grow with a scaling exponent of 2/3. In fact, we show (e.g., in Table 2) that this exponent can range in fish between 0.55 and 0.95. The point we make is that, in post-metamorphosis water-breathing fish, the scaling exponents cannot be equal to unity for long, and pertain to functioning gills (see below).

@27) Pauly and Cheung draw heavily on the original Pauly papers from the 1980s and a recent synthesis published as a book in 2010. Furthermore, Cheung et al. (2011, 2013) and this manuscript argue that this constraint on growth and metabolic rate imposed by gill allometry results in a decrease in fish size. This is because the amount of available oxygen will decrease for a given depth and location as ocean temperatures increases, and the gill area will not be able to keep up with the oxygen demand of the fish species, as indexed by the maximum, asymptotic weight [W_∞]. The core feature of the Lefevre et al. (2017) argument is that gills, specifically the surface area, are not under geometric constraints and thus can grow proportionally to body mass [M]. Specifically, they argue that gill filaments, like book pages, can be added in a manner that is proportional to overall surface area, i.e. the scaling of Gill Area $\sim M^{d_G}$, where d_G can be = 1.

We agree with every word in this paragraph. In our original submission, we avoided dealing with gill-lamellae-as-pages-in-a-book comparison, mainly because it seemed like a digression, but now realize that we must bite the bullet, and explain why this analogy doesn't work, or rather, why it lacks a key element. The *raison d'être* of books is to be read, and hence they have to allow for 3-D space above their pages. Similarly, the *raison d'être* of gill lamellae is to pick up O_2 from the surrounding water, and to release CO_2 into it. Moreover, this water must be passing by the lamellae, i.e., old water must replace by new water. None of this can occur in 3-D. We have attempted to express in a new paragraph on why 3-D gill lamellae would not work. [A graph explaining this via an analogy to a car's radiator is provided here as Figure II].

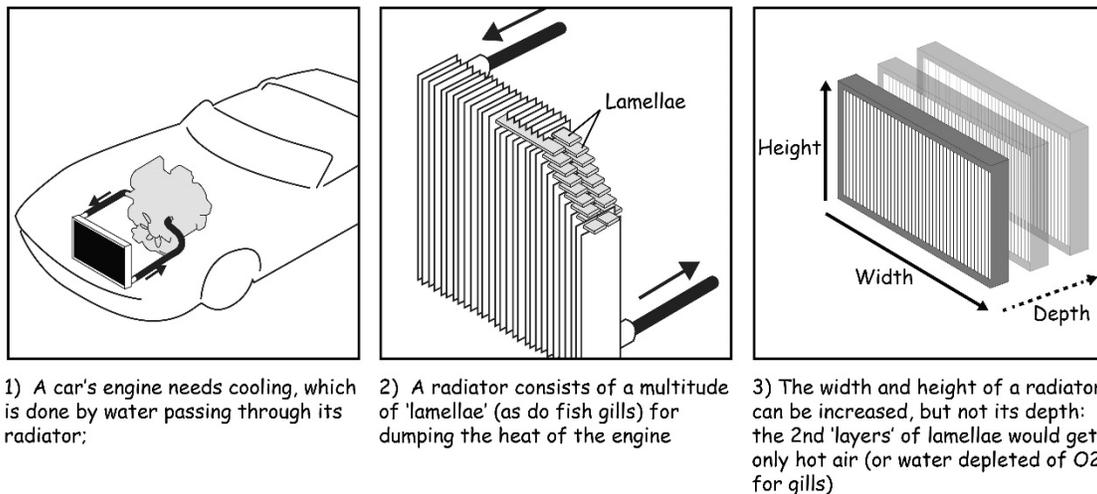


Figure II. Illustrating, in form of a 'comic strip,' that cars' radiators fulfil their function by exposing their lamellae to an airflow that warms the water circulating through the radiator. After air has flown across lamellae, it is hot. Thus, putting a radiator behind a radiator does not make sense, and radiators can grow in width and height (2-D), but not in width and height and depth (3-D). This is similar to gills, whose lamellae extract oxygen from the water passing through them.

@28) Furthermore, as Cheung *et al.* (2013) document in the supplementary material, Lefevre *et al.* (2017) state that the scaling exponent resulting from the relationship of gill surface area and body mass, and used in Cheung *et al.* (2011, 2013) will have a great influence on model results that attempt to estimate the decrease in fish growth in response to ocean warming.

Yes, and the shrinking effect is much stronger when variable and higher scaling exponents are considered (See Figure 4 in Pauly and Cheung 2017) [These findings are based on simulations designed by William Cheung, and whose mathematical background is documented in https://docs.google.com/viewerng/viewer?url=http://www.nereusprogram.org/wp-content/uploads/2017/08/Short-notes-on-body-size-calculation.pdf&hl=en_US. These facts contradict Lefevre *et al.*'s allegation that we chose a low scaling factor so as to boost our case. (Accusing people of such shenanigans without a shred of evidence is not very professional, incidentally).

@29) While Pauly and Cheung thoughtfully argue that Lefevre *et al.* (2017) are incorrect in refuting the original assumptions made by Cheung *et al.* (2011, 2013), this manuscript is not likely to be influential in successfully arguing against the core of Lefevre *et al.* (2017) rebuttal. This is largely for two reasons that, if tackled, would greatly improve the manuscript. The first improvement is to reframe this paper in terms of constructive rather than destructive criticism. The authors can win the battle by dismissing Lefevre *et al.*, but they have a wonderful opportunity to didactically lay out their theory to a larger audience. After all, disagreeing with other scientists' ideas, analyses, results, etc. and thoughtful discussion of these disagreements is what moves the field forward.

We agree that the Lefevre *et al.* paper offers a good opportunity to elaborate on the ideas in Cheung *et al.* (2013), and the underlying theory in Pauly (2010), and this is the reason, indeed, why we responded in the first place, even though we viewed the arguments of Lefevre *et al.* (2017) as so deeply flawed that we first thought a response was superfluous. However, their paper is a direct attack on the fundamentals of a theory which could allow us to understand the effect of warming on water-breathing animals, and this attack cannot be dealt with without their authors being contradicted and their argument refuted one by one. If we do not refute their points, the readers will think that we have no arguments. The important thing, however, is to use proper language, and thus we accepted all the reviewers' suggestions for avoiding provocative language.

@30) Secondly, this manuscript greatly suffers from the logical fallacy "false cause," or using a simple correlative relationship between two variables to prove causation. In this manuscript, the authors' state that "Indeed, the very fact that in most fish, gills grow with a positive allometry is an indication that the O₂-supply that these fish experience is a limiting factor for them, and does not meet their demand." An allometric

relationship between gill surface area and body mass (to be clear, an exponent $> 2/3$) does not prove causation. The causation question of which constrains which (i.e., gill surface area constraining metabolic rate or metabolic rate constraining gill area) has not been directly tested, and examining the mass-scaling of each does not test the causation, only the correlation. While the mathematical elements and implications of the scaling of gill area and body mass are elegant, the authors should take the time to be more didactic in order to reveal their reasoning behind the proposed causality to the reader, especially to readers who might be more used to experimental approaches.

Here, we must respectfully disagree, because we are well aware that “correlation doesn’t prove causation”. Indeed, we would put it more precisely: correlation, while a *necessary* condition for causation, is not a *sufficient* condition. For sufficient conditions, we must look for corroborations, i.e., alternative lines of evidence. And we must also realize that, strictly speaking, we never will get the evidence to convince a determined skeptic, because he or she could argue that each alternative line of evidence is also questionable, and so on *ad infinitum*. We have to stop (if temporarily) at some point, i.e., when there is clearly more evidence on one side than on the other. This is why we listed, near the end, a list of scientific problems that are resolved if we assume the causation arrow to go our way, and which cannot be explained if the arrow goes the other way. Indeed, we think that this was the best way “*to didactically lay out [our] theory to a larger audience.*”

@31) *Furthermore, in addition, much of this manuscript suffers from unclear writing.*

We agree that our writing can be improved and hope to have done so, thanks to the reviewers. We note, however, that Reviewer #3 suggested that “[t]he manuscript is clearly written and easy to read.”

@32) *[This manuscript suffers], as well [from] poor examples that do not corroborate the authors’ intended point.*

Here, we are at a loss: what other kind of examples are being suggested?

@33) *The authors seem to be so convinced of the point they are trying to make (that geometric constraints on gill area limits growth) that the oversimplification of explanations hinders the audiences’ ability to understand just what is so convincing. This includes the supporting examples; although the authors try to substantiate their ideas with examples, these examples need to be expanded upon or changed to ensure that the writing is clear and that examples are corroborating intended points (see major concerns below).*

We cannot follow up on this point, as no example is given of how our examples fail to convey what they are intended to.

@34) *Major Concerns: Reframe from destructive language to constructive language: This includes seemingly trivial instances (e.g. the word “huge”).*

Agreed. The word ‘huge’ has been twice replaced by ‘wide.’ We have also revised the text to turn destructive language into constructive language.

@35) *The authors claim that there are no other major hypotheses to explain a huge range of biological features of fishes. For example, the metabolic theory of ecology offers a plausible alternative without even needing to consider respiration. As Pauly himself claimed back at the FSBI meeting two decades ago that these constraints should equally apply to mammals.*

There must be some misunderstanding: [the author] would never have claimed that respiration is a limiting factor to the growth of mammals and other air breathers. Claiming this would instantly invalidate the reason given for the claim actually made, i.e., that gill growth and hence oxygen supply limits the growth of water breathers. As for the explanatory power of (i) the metabolic theory of ecology and (ii) the theory of West *et al.* (1997, 2001, 2003) of branching distribution networks, I have not seen any attempts by their practitioners to actually explain simple phenomena, such as why fish grow larger when they are in colder water, of why size at first maturity is a simple function of the maximum size reached in a given population, etc. (I am certain that they can represent these phenomena, but how many new parameters do they need to introduce for this?). Lack of space prevents us from dealing with alternative theories. However, we have now mentioned in the revised text that Pauly (2010) discusses both the metabolic theory of ecology and the theory of West *et al.* (1997, 2001, 2003) of branching distribution networks.

@36) One major point that refutes Lefevre et al. (2017)'s main argument that gills are not limited by geometric constraints and can in fact scale with body size to an exponent of > 1 is not mentioned in this manuscript. This point is that in some fishes, particularly highly active obligate ram ventilators, gill area is not increased by reducing space between individual lamellae (Lefevre's book pages) and instead, is achieved by lengthening the gill filaments (see Wegner et al. 2010 *Journal of Morphology*).

This is a good point and we have now mentioned lengthening of gill filaments and cited Wegner et al. (2010). We were aware of papers on ram ventilation, but opted to 'not go there,' because even in specialized ram-ventilator such as tuna, the gills scale with body mass with 0.9 and not unity, which is sufficient for our point to be valid.

@37) Revise writing to ensure that it is clear and explanations are fully explained with supporting examples; specific instances to this comment below as line-by-line comments: Despite the term "physical constraints" being used several times throughout the manuscript, it was not defined and the meaning remains unclear.

Now clarified via the added glossary. [The glossary defines physical constraints as "the non-biological processes or features that have shaped the evolution of organisms and still shape their performance. Examples are gravity or the dissolubility of oxygen in water].

@38) What is meant by "open surfaces"?

See new glossary. [The glossary defines open surfaces as "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 (O₂, CO₂), 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."]

@39) Authors are not consistent throughout document in regards to what they are calling their theory; here, it is "gill area limitation; it is "Gill-Oxygen Limitation Theory.

Agreed. We now call it Gill-Oxygen Limitation Theory (GOLT) throughout.

@40) [In the introduction], what are the "different mechanisms" relating warming and decrease in body size? The authors should explain to support their claim that "biological constraints on size-related physiological and ecological processes."

We agree that the sentence in question was messy. We have rephrased it, to better introduce the constraints in question.

@41) [Paragraph in the introduction dealing with animals in nature misleadingly suggesting they are free of constraints]. This is not relevant to the paper and does not support the authors' argument.

We respectfully disagree and kept this paragraph unchanged (see also above, item 15).

@42) What is the "maximum capacity imposed by physical constraints"? Is "maximum capacity" the same as the term used 4 lines later, i.e., "maximum physiological capacity"? These sentences are uncited and need citations; one could use the argument against symmorphosis here to corroborate point.

Yes, it refers to maximum physiological capacity. We have clarified this in the revised manuscript. [And we have not dealt with symmorphosis].

@43) The plaice example does not support the point that it is costly to fitness to approach the maximum physiological capacity.

We think that the plaice is a relevant example to explain and support our point. The authors of the paper from which it was drawn [Fonds et al. 1992] explicitly state that "for a given supply, the energy spent in active (swimming) metabolism is the main variable component in the energy budget: a very active fish will grow less." We know that "less growth" results in more predation and smaller egg production, both fitness-reducing factors. This is what is behind Figure 1 [in Pauly and Cheung 2017]. Therefore, if plaice is more active in feeding, it is energetically costly and its growth is limited. This is now clarified in the revised manuscript.

@44) *[The text dealing with physiological limits in the wild] needs a citation here so reader can go back to original citation to further understand point that the authors' are attempting to make.*

Agreed; we added a citation.

@45) *What do the authors mean by "strongly limiting"?*

A definition of 'limiting factor', going back to Justus von Liebig was added to the glossary. [This definition is: "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." We forgot to define 'strongly limiting', but it should be obvious.]

@46) *The authors explain isometric and allometric here in an interesting manner, that requires some context for those that work on other forms of allometry. To improve the consistency of the use of these terms in the metabolic and gill mass-scaling literature, I suggest that (hyper-)allometric be defined as a mass-scaling exponent $> 2/3$ and an isometric mass scaling exponent $= 2/3$. The authors fail to make the connection between the length and mass/volume ratio for the reader that the isometric scaling exponent expectation is calculated by dividing L^2/L^3 . The authors should be cognizant that isometry typically means scaling to a power exponent of 1, say for brain mass relative to body mass, but in this field of gill and metabolic scaling, isometry is $2/3$. Please use this term correctly and didactically to enable a broader range of readers to grasp the working hypothesis.*

We agree to use 'isometric' for a scaling exponent of $2/3$, because it implies that volume grows with the 3rd power of length and surface growing with the 2nd power of length, i.e., with the power the 'same' (= 'iso') as the dimension itself. Hyperallometry will then mean $>2/3$, and hypoallometry $<2/3$, i.e., 'different up' and 'different down.' We have added these terms to the glossary.

@47) *The spider example [in the section on 'Biological surfaces as a ubiquitous constraint'] is not clear and does not seem to support the authors' intended point. To keep the reader focused on the main point, please drop the cross-sectional area arguments, the insect trachea and whale flukes. These are great points dealt with in the book, but a sidebar to the issues at hand. Keep the reader focused on the pertinent core points.*

We respectfully disagree. Above, the same reviewer required that we lay our case in didactic fashion, such that it can be understood by a wide range of readers. Analogies help understanding. The specific example is to help explain the concept of allometric growth, which in comparative evolutionary studies, is particularity noticeable in response to a physical constraint, here gravity.

@48) *What [is] allometric growth?*

This term was originally defined as the growth of an organ or body part at a rate exceeding or different (= 'allo') from that of the rest of the body. We define this in the new glossary. [The glossary now defines Allometry as "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."].

@49) *Do not use the word "obvious" when something is not.*

Agreed. We rephrased the sentence in question, and omitted the word 'obvious.'

@50) *It is unclear as to how the whale example of dumping heat relates to the issue of dimensional tension.*

Heat is produced by and in a muscle volume (within 3-D), and can be dumped only via a surface (across 2-D). This is a clear-cut case of dimensional tension, and one which had great practical implications, as many of the whales hunted in previous centuries could be caught only because they overheated after being chased for a while. This is also the reason why the San people in the Kalahari can run down antelopes which don't sweat and must stop running when they become too hot (Liebenberg 2013). Again: we are using example of dimensional tension that a reader can understand, so she or he can appreciate the concept when applied to gills and oxygen supplies to fish.

@51) The fact that gills grow allometrically relative to body mass does not answer the question if gills are limiting growth in terms of O₂ supply. Obtaining a scaling exponent from a relationship of gill area and body mass does not mean causation and is not the correct test to answer the causality question. Again, please consider the scientific method for establishing causality and respect that factorial experimental evidence is the only way to do this.

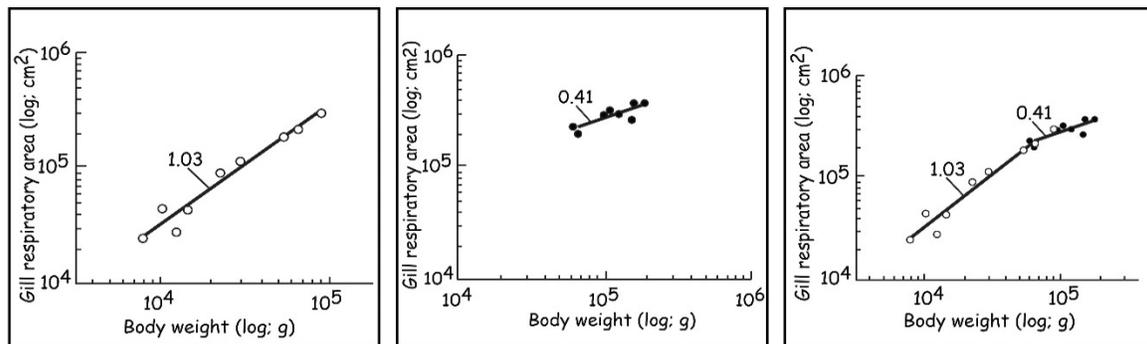
Evidence gained from factorial experiments is not the only evidence suitable to establish causality in science. If this were the case, most of geology, astronomy and cosmology and - for that matter evolutionary biology - would not be scientific. Rather, in science, we test hypotheses which must have two major properties to be interesting: (1) they must be testable in principle (which is the reason why, e.g., string theory is being increasingly challenged by various physicists) and (2) they must predict observations different from those used to derive them in the first place. Also, a given hypothesis will be much preferred over an alternative hypothesis 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 [Wilson 1999]. This is why we give examples of the wide applicability of the GOLT. These are now explained at the beginning of the manuscript.

@52) While the gill ablation experiment is compelling it would clearly be very difficult to 'add' surface area to gills to provide a stronger experimental test. Humor the audience of experimental physiologists by at least framing the narrative in terms of strength of evidence.

Agreed. In fact, it is precisely because it is difficult to experimentally 'add' gill area that we use comparison between related species differing in their gill areas. On the other hand, we did not mention that gill ablation experiments support our case; we now mention this and cite an example.

@53) See the following citations for an example of scaling exponents of gill area to body mass >1 indicating that gills can grow in proportion, or even faster, than body mass in some fishes: (1) Table 3 in Satora and Wegner 2012 Reviews in Fish Biology and Fisheries (2). Table 4.3 [sic] in Wegner 2015, Ch. 4 [sic] in Fish Physiology of Elasmobranch Fishes: Structure and Interaction with Environment, vol. 34A; and (3). Figure 1 in Wootton et al. 2015 Journal of Morphology.

In response to this comment, we added a case study of the common thresher shark, based on Wootton et al. (2015) and Table 3.3 of Wegner (2015), in Chapter 3 of the book in question. While these authors emphasized a scaling exponent of 1.03, pertaining to smaller individuals, they excluded data pertaining to threshers of greater body sizes, which yielded a much lower scaling exponent (0.41), and which they arbitrarily pronounced erroneous (See Table 4.3 in Wegner 2015). However, we show [in the new Figure 3 of Pauly and Cheung (2017); see also Figure III] that this value of 0.41 is in fact neither erroneous nor anomalous, and can be explained by the GOLT [as a necessary transition of an unsustainably high value of d_G to a low value, as should occur if gills surface area is limiting the maximum size of the shark].



1) A slope of 1.03 was estimated from 9 sharks ranging from 7.9 to 91.5 kg.

2) A slope 0.41 was estimated from 6 sharks ranging from 60-180 kg; this was thought to be 'wrong'.

3) But the two datasets are fully compatible, and jointly, they tell us something new about the common thresher shark.

Figure III. Illustrating, in form of a 'comic strip' how two datasets, from Wootton et al. (2015) and Emery and Szczepanski (1986), respectively, on changes in gill surface areas in common thresher shark (*Alopias vulpinus*), previously thought to be incompatible (which implies that one should be 'wrong'), are in fact perfectly compatible and led to a discovery about the growth of *A. vulpinus* and possibly other elasmobranchs (see text).

[We forgot to respond to the challenge posed the values of $d_G > 1$ for in Satora and Wegner (2012). If we had, if we had, we would have written as follows:

The case of rainbow trout (*Oncorhynchus mykiss*):

Satora and Wegner (2012) present in their Table 3 estimates of d_G for rainbow trout which at first sight may appear incompatible, i.e., $d_G = 3.443$, from Morgan (1971) and $d_G = 0.904$ from several other authors, with the former estimate $\gg 1$. However, the range for body weights to which this high value applies is 0.068 to 0.100 g, which corresponds exactly to the expectation from GOLT. Thus, in larval teleost, d_G is expected to be $\gg 1$, then gradually transits to a value < 1 , when the 'head space' occupied by the gills becomes crowded, as occurs here, and as also illustrated for the carp *Cyprinus carpio* (Figure 2 in Pauly and Cheung 2017).

The case of Atlantic horse mackerel (*Trachurus trachurus*):

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 specimens would yield a lower estimate of d_G .]

@54) Why [do you state that key features of the growth of fishes] are well captured by the VBGF? Need to explain.

The phrase "These features [of fish growth] are well captured by the von Bertalanffy growth function..." was modified to "These features are all properties of the von Bertalanffy growth function..." which should do the job, given the preceding and subsequent text.

@55) A correlation between growth and gills does not prove causation. Again, please acknowledge and reveal your thinking on causality. What are the expectations that flow from this correlation, e.g., ontogenetic variation and ablation? While this is laid out in the book [Pauly 2010] at great length, this MS is an opportunity to summarize the book for a different audience rather than berate physiologists like Lefevre et al.

See above for correlation vs. causation. While we cannot "summarize the book" in the few pages of a paper, our choice of examples is an attempt to convince physiologists to look at the evidence we have marshalled. And we don't 'berate' anyone.

@56) A list of questions that can be answered by the authors' gill area limitation theory does not prove in any way that the GOLT is true. This is especially true for points [indirectly related to respiration, and] for which no explanation by the authors is given for how this question relates at all to the GOLT. These questions could have many other answers that are physiologically relevant that have nothing to do with gills. For example, the effect of temperature on chemical reactions in the body could play a big role in answering many of these questions. If these are to be included then raise the hypothesis flowing from the mathematics of gill isometry and provide a summary of the evidence. I fear that this will be a rewrite of the Pauly 2010 book.

One few paragraphs above, this reviewer suggests we treat this submission as "an opportunity to summarize the book for a different audience." Now, he or she "fear[s] that this will be a rewrite of the Pauly 2010 book." Which is it? What we did [by mentioning questions answered by indirectly the GOLT, indirectly related to respiration] is to present some corollaries of the theory which it explains, and which thus help set the orientation of the causal arrow (see above for 'correlation vs. causation').

@57) Explain the choice of using a smaller scaling exponent for larger-bodied fishes.

We did not use a smaller exponent for larger fishes. [Indeed, fishes that can reach larger sizes usually have higher scaling exponents, i.e., values of d_G ; see also Pauly (2010), and Table 2 in Pauly and Cheung 2017].

@58) Minor Concerns as line-by-line comments. Instead of "oxygen supply to large fish size" do the authors intend "oxygen needed to supply fish to increase in body size."

Agreed. The text now reads “...the oxygen supply to fish of large and increasing size cannot be met by their gills...”

@59) *Do the authors mean “cuts across” instead of “cut-across”*

It means cuts across. This is now corrected.

@60) *Need to put citations [to back certain statements]*

Citations were added.

@61) *Add “or” before “which” and “the scaling exponent ranges” after “which”*

Done.

@62) *Ram ventilation is not the only factor here; see Wegner et al. 2006 Bulletin of Marine Science.*

Sorry, we could not understand what the reviewer suggests we do.

@63) *[Several instances:] “fish” should be “fishes.”*

Corrected.

@64) *See comment above about Wegner et al. 2006 Bulletin of Marine Science.*

Sorry, we could not understand what the reviewer suggests we do.

@65) *[Various typos]*

Agreed; all corrected.

@66) *We do not yet know if whale sharks have large gills RELATIVE to their body size.*

The argument made here does not require the gill of whale shark to be large relative to their body size; in fact, the surface area/body weight in adult whale sharks is probably very low. The issue, rather, is that they live in warm water, which should lead to a high oxygen demand relative to the oxygen supplied by their gills. This is probably the reason why they visit colder deeper waters at regular intervals.

@67) *What is meant by “it must be lower limits below”?*

Thanks for pointing out this error. The sentence, now corrected, should read as follow: “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’s living cells cannot function.”

Reviewer #3

@68) *Comments to the Author: The response of Pauly and Cheung to Lefevre et al. (2017) raises some important points on an issue that is timely and important. Here I summarize the strengths and weaknesses of their response for the authors’ consideration: Weaknesses: The tone of the manuscript is somewhat snarky in places, which takes away from their more objective arguments. For example [near the end], the authors state sarcastically “this is due to something called scientific progress”. Regardless of the tone of Lefevre et al. (2017), I’d recommend removing this sort of commentary.*

Agreed; we removed the ‘snark’ in the above expression by omitting the words “something called.” This leaves the important remark intact that something cannot be rejected (as Lefevre *et al.* do, incredibly) because it is not in major textbooks.

@69) *The authors never adequately summarize the arguments to which they are responding. A few sentences outlining the central arguments would be helpful.*

Agreed. Lefevre *et al.*’s views are now summarized in the Introduction.

@70) *There is too much reliance on specific species' natural histories / morphologies that appear consistent with the authors' arguments. Some are perhaps worthy of mention in a discussion, but themselves provide little hard scientific evidence.*

We respectfully disagree. As stated above, for a hypothesis to be scientifically interesting, it must explain more than the observations from which it was derived. The wide range of “natural histories/morphologies” that are consistent with that hypothesis can all be seen as tests of that hypothesis, which becomes stronger if it survives these tests, and weaker if it does not. This is in fact the reason why this reviewer, quite naturally, also challenges it with “specific species’ natural histories/morphologies”, i.e., fish species in which the gill apparently scale with body weight >1 (see below).

@71) *Related to the last point, the authors' frequently confound correlation for causation in considering the mass-dependence of gill surface area. For example, the relationships they describe between gill surface area and metabolic rate offer corollary support, but do not firmly establish that gill surface area itself is the primary cause of the body mass scaling of oxygen consumption in fishes. As such, their arguments should be tempered a bit.*

“Corollary support,” when it applies to a wide variety of cases, can become so strong that it shifts the burden of proof with regard to the causality arrow (see our previous take on correlation vs. causation).

@72) *The authors' arguments rely heavily on the implicit assumption that limitations on oxygen supply, rather than oxygen demands, drive oxygen usage. This has been a contentious argument in biology, and thus some brief, but explicit discussion of this assumption may be useful.*

Agreed; we have added a paragraph on this (Note that the assumption that “oxygen usage” (nice expression!) corresponds to oxygen supply, not oxygen demand is not “implicit” in the GOLT. It is rather its central tenet).

@73) *Strengths: The arguments presented using classic growth equations are the strongest evidence presented by these authors. The specific examples given in Table 2 are also informative and convincing. The authors' general point that there must be some matching between morphology and physiology is a point well-taken in the context of this debate. The small, but specific criticisms of Lefevre et al. (2017) in the concluding paragraphs are worth mentioning, apart from the tone.*

Thanks for this. We have softened the tone of the last paragraph.

@74) *The manuscript is clearly written and easy to read.*

Thanks for this – especially in the light of contrary assessment by another reviewer.

Discussion

The editor to whom this letter was addressed wrote us on the day it was received that it was “[a]n incredibly thorough and considered response to the reviewers and we see no further reason to delay the MS from publication further.” This suggests that taking reviewers seriously, and dealing with the questions they have respectfully and in detail is a winning strategy. However, while we had three largely positive reviews, issues were raised which could have sunk the paper, had we not provided reasonable responses.

The most challenging of these issues, raised by Reviewer #2, was that Table 3.3 of Wegner (2015) reported a scaling factor for the gill area – body mass relationship $d_G = 1.03$ in the common thresher shark (*Alopius vulpinus*). This was definitely a serious challenge for the GOLT, which claims of that the growth of fishes is limited because d_G is ‘always’ < 1 . In fact, it looked like the famous quote attributed to Thomas Huxley, stating that “[t]he great tragedy of Science [is] the slaying of a beautiful hypothesis by an ugly fact.”

However, (and this might be the result of a tendency toward confirmatory bias), I looked very carefully at the table where this extraordinary value of $d_G = 1.03$ was listed. At the bottom of this table, I found another value of $d_G = 0.41$ for the same species, i.e., *Alopius vulpinus*, but linked to a footnote stating that this latter value was “not included [...] due to a limited sample size or a limited body mass size range in comparison to other species.”

Yet the estimate $d_G = 1.03$ was based on 9 fish, not much more than the 6 upon which the estimate of $d_G = 0.41$ was based, while the size range associated with $d_G = 1.03$ (7.9 - 91.5 kg) was actually smaller than the one associated with $d_G = 0.41$ (60 - 180 kg) [See Figure III].

Thus, it is with a large grain of salt that we must take the *ad hoc* hypothesis of Wegner (2015) that “the high scaling exponent for the gill surface area of the common thresher shark, *Alopias vulpinus* (1.03) may reflect an increased ability for regional endothermy (and hence a disproportionate increase in oxygen demand) (Wootton *et al.* 2015).” Within that framework, a value of $d_G = 0.41$ would not have been compatible with regional (?) endothermy, and thus it was declared erroneous, although it was the very “ugly fact” that Huxley warned us about.

Conversely, the GOLT has no problem with gills whose surface grows at first as fast as (or even faster than) a volume, i.e., with $d_G = 1$ (or even $d >> 1$), as long as d_G , in the course of ontogeny, drops below 1. However, that the transition from $d_G > 1$ to $d_G = 1$, then $d_G > 1$, which occurs at in post-larvae/early juveniles in teleosts, should occur at about 1/3 of the maximum sized reached by common thresher shark, *Alopias vulpinus* was not previously known. Moreover, it may apply to other elasmobranchs, as suggested by Table 3.3 in Wegner (2015), which also lists Atlantic stingray (*Dasyatis sabina*) and cownose ray (*Rhinoptera bonasus*) as having ‘wrong’ (=low) scaling values, of $d_G = 0.20$. This discovery, which I will follow up on in a future contribution, is entirely due to peer review.

Another insight attributable to this peer review is that I finally realized, after over 35 years, that I used ineffective arguments in my attempts to convince colleagues (ichthyologists, marine biologists, fisheries scientists...) that gills are limiting to animals that breathe water. Rather than argue abstractly that gill areas as a surface, cannot in principle keep up with a volume, I now use, in my lectures and other presentations, objects which scale as a surface, but are functionally related to a volume. One good example is the radiator of a car, which can grow in width and height, but not in depth (Figure III). Another example is that of sieves, whose meshed surfaces can be increased when there is more material to sort, but whose efficiency cannot be increased by stacking. Now, colleagues understand why an ‘oxygen sieve’ whose meshes are made up of gill lamellae can be made larger by increasing its width and its height, but not its depth, because there is little or no oxygen to be extracted from water that has gone through a first ‘layer’ of gill lamellae.

Once the dimensional problem inherent in, e.g., car radiators is fully understood, one can obviously talk about engineering solutions to mitigate its effect. Thus, a propeller turning a high speed in front of a radiator can increase its efficiency, and to a certain extent, obviate the 2-D vs. 3-D problem.

Similarly, hundreds of millions of years have optimized the design of fish gills (see Figure 7 in Pauly 1981, and Ward 2006), so that their effective surface grows, in most (adult) fish, faster than length², i.e., $d_G > 2/3$. This is particularly true for tuna and other large pelagic fishes, in which $d_G > 0.9$ (or as we have seen above, even $d_G = 1.03$, followed by $d_G = 0.41$).

Finally, I must deal with the issue of ‘big data’ as alluded in the Introduction, in spite of the datasets discussed here being very small in comparison with classically big datasets, such as meteorological or genomic data (Pauly 2017).

Here, the issue is that a huge literature exists of where fish live, descend from, and what they do, which ecology, evolutionary biology, genetics, ethology, etc. attempt to make sense of. These sub-disciplines of biology usually proceed by identifying patterns in the data that their practitioners collect, and from these patterns, they derive ‘mechanisms,’ or causal relationships. Such relationships are often correlative at first, then the direction of causal arrows (if any) are identified, usually by a preponderance of evidence on one side. At this point, the formulation of facile *ad hoc* hypotheses of the type illustrate above (“the high scaling exponent for the gill surface area of *Alopias vulpinus* may reflect an increased ability for regional endothermy...”) has to stop. Rather, the discipline in question must be able to identify constraints, i.e., events that are not supposed to occur, observations that are not supposed to be made, and estimates of parameters that are not above or below certain thresholds.

This is understood by all physicists, and constraints of this sort make their discipline strong, and enable it to progress (Platt 1964). Evolutionary biology also has constraints; a crude example would be the fact that we cannot find a fossil rabbit in Ordovician rocks. A moment of reflection suffices to realize that most of what we

know about fish can be re-expressed as constraints. Thus, the ‘law’ (Heincke, 1913) stating that in the North Sea, small plaice (*Pleuronectes platessa*) are found inshore and large plaice offshore (a fact neatly explained by the GOLT, incidentally), can be re-expressed as “in the North Sea, large plaice do not occur inshore” which is a constraint. Thus, if you find a concentration of large plaice inshore, “Heincke’s Law’ would be in trouble.

The GOLT provides strong constraints, and thus an interpretative framework for physiology and various other biological sub-disciplines, including the fast-growing field of global change studies, as the above presentation of the peer review of Pauly and Cheung (2017) may have illustrated. Indeed, this peer review helped solidify the GOLT more than my 35 years of writing about it.

Acknowledgements

I thank William Cheung for the collaboration which led to the joint paper discussed above, and for his completion of the complex modelling which led to the evaluation of the effect of using a range of d_G values. I also thank Rainer Froese for numerous discussions on the dimensionality of fish gills, Evelyn Liu for Figures 2 and 3, and the three anonymous reviewers whose crucial inputs form the bulk of this contribution.

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