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OPINION

Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms

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Abstract

Some recent modelling papers projecting smaller fish sizes and catches in a warmer future are based on erroneous assumptions regarding (i) the scaling of gills with body mass and (ii) the energetic cost of ‘maintenance’. Assumption (i) posits that insurmountable geometric constraints prevent respiratory surface areas from growing as fast as body volume. It is argued that these constraints explain allometric scaling of energy metabolism, whereby larger fishes have relatively lower mass-specific metabolic rates. Assumption (ii) concludes that when fishes reach a certain size, basal oxygen demands will not be met, because of assumption (i). We here demonstrate unequivocally, by applying accepted physiological principles with reference to the existing literature, that these assumptions are not valid. Gills are folded surfaces, where the scaling of surface area to volume is not constrained by spherical geometry. The gill surface area can, in fact, increase linearly in proportion to gill volume and body mass. We cite the large body of evidence demonstrating that respiratory surface areas in fishes reflect metabolic needs, not *vice versa*, which explains the large interspecific variation in scaling of gill surface areas. Finally, we point out that future studies basing their predictions on models should incorporate factors for scaling of metabolic rate and for temperature effects on metabolism, which agree with measured values, and should account for interspecific variation in scaling and temperature effects. It is possible that some fishes will become smaller in the future, but to make reliable predictions the underlying mechanisms need to be identified and sought elsewhere than in geometric constraints on gill surface area. Furthermore, to ensure that useful information is conveyed to the public and policymakers about the possible effects of climate change, it is necessary to improve communication and congruity between fish physiologists and fisheries scientists.

Keywords: aerobic scope, gill surface area, growth, metabolism, oxygen consumption, respiration, scaling

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Introduction

Global change has become alarmingly rapid and the scientific community has a responsibility to provide society with valid and reliable information about potential consequences. For a planet whose surface is overwhelmingly oceans, the threats to marine ecosystems are particularly worrying, with negative impacts on fishes and fisheries that could become a pressing concern for humans (Brander, 2015). Physiology can provide a mechanistic, cause and effect, understanding of how animals might respond to a changing environment, which can be used to improve the predictive capacity of models (Jørgensen *et al.*, 2012; Peck *et al.*, 2016). We argue, however, that physiologists must play

a more active role in developing such models, to ensure that they are based upon valid underlying mechanistic assumptions.

One major projection, of obvious significance for ecosystem productivity and human food security, is that oceanic warming will lead to a systematic global decline in the size of fishes (Cheung *et al.*, 2013a). The modelling in that particular study predicted that over 2000 fish species would become up to 24% smaller by 2050. In an earlier paper based upon similar modelling, Cheung *et al.* (2011) estimated that there would be severely reduced fish catch potentials in 2050 relative to 2005. These projections have been used to explain empirical observations that adults of some marine fishes are indeed becoming smaller (Baudron *et al.*, 2014), and to suggest that climate warming will drive evolution towards smaller body sizes in fishes (Waples & Audzijonyte, 2016), and they have recently been

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enshrined in a report from the International Union for Conservation of Nature (IUCN) (Cheung & Pauly, 2016). These model projections are, however, based on the assumption that 'growth and maximum body size in marine fish and invertebrates are determined primarily by availability of oxygen; the latter is related partly to the availability of respiratory surfaces'. We are now obliged to explain, beyond any further debate (Brander *et al.*, 2013; Cheung *et al.*, 2013b), why the physiological principles on which the modelling is based are erroneous. Most physiologists would be surprised by the suggestion that increases in oxygen demand, due to elevated future water temperatures, would constrain fishes to smaller adult sizes because their gills could not supply enough oxygen for a larger body. Here, therefore, we aim to clarify the physiological principles of gill function, metabolic rate and growth in fishes.

Gills are folded surfaces, not spheres

The key physiological assumptions about gills and metabolic rate adopted by Cheung *et al.* (2011, 2013a) were originally posited by Pauly (1981, 1998, 2010), who stated that 'Geometric constraints prevent surfaces to grow as fast as volumes' and that 'Gills, being a surface area, cannot grow, for insurmountable geometric reasons, as fast as the volume they are meant to supply with oxygen' (Pauly, 1998). As we will demonstrate, the second statement is not true: fish gills do not adhere to the geometric surface-area-to-volume relationship that is referred to in the first statement. That faulty assumption is then used to argue that gill surface areas cannot grow as fast as body mass, and that this results in lowered food conversion efficiency, when body mass increases. In fact, it is proposed that geometric constraints on the gills are what underlie the well-known allometric decrease in mass-specific oxygen uptake in relation to body mass in fishes.

The geometric relationship that prevents the surface area of an object from growing as fast as its volume would, for example, apply to oxygen uptake over a body surface. The underlying reason for this geometrical relationship is that the volume of objects like spheres increases with the cube of their radius (volume $\propto r^3$), while their surface area only increases with the square (area $\propto r^2$). The same applies to structures similar to spheres, which includes many animal bodies. As a consequence, the surface area of an animal's skin scales to the volume (or mass) of that animal with an exponent (b) approximating 0.67 (i.e. 2/3), or -0.333 ($b - 1$) for the scaling of mass-specific surface area to mass ratio (Fig. 1a). This relationship was already known to biologists by the 19th century (reviewed by Schmidt-Nielsen, 1984) and Rubner (1883) used it in a

famous attempt to explain why smaller dogs have higher mass-specific metabolic rates than larger ones, ascribing it to greater heat loss over the skin.

This simple geometric relationship does not, however, apply to fish gills. These have evolved into very large surface areas of delicate respiratory epithelium, where gas exchange takes place over many small sheets (called lamellae) attached to gill filaments that, in turn, are attached to the gill arches. Thus, gills have folded surfaces (e.g. J. W. Price, 1930) and are one of many examples in nature where the 2/3-exponent relationship between surface area and volume is overcome by folding the surface. Other examples include lungs, intestinal membranes and inner mitochondrial membranes. As each single lamella is a sheet with a half-circle to rectangular shape that grows by increasing the radius or length of the sides, rather than the thickness, it has a surface-to-mass scaling exponent (b) that approaches 1.0 ($b - 1 = 0$ for mass-specific exponent; Fig. 1a, green line). When gills grow by adding more and more lamellae, the surface-to-mass scaling exponent essentially becomes 1.0 (Fig. 1a, blue line; Fig. 1c). Thus, in morphometric studies where both total lamellar area and gill mass have been measured, a linear scaling relationship (scaling exponent of 1.0) has been found in fishes (Gehrke, 1987) as well as bivalves (Scott, 2005). Consequently, there is no geometric constraint that prevents an increase in body size (mass or volume) from being accompanied by a corresponding increase in gill mass and hence respiratory surface area. In other words, gill surface area can scale proportionally with body mass and, if it does not do so, it is because oxygen demands are reduced with body size, as discussed further below.

A simple way to explain the geometry of gills is by analogy to a book, where pages correspond to lamellae. It is easy to grasp that if you double the thickness of a book (thereby doubling its volume and mass), you can fit in twice the number of pages and, therefore, the total surface area of the pages is also doubled. Moreover, increasing the number of books (analogous to increasing the number of gill filaments) leads to a corresponding increase in page area (analogous to respiratory surface area). Thus, with the structural arrangement of books and gills, the surface area will scale to volume with an exponent of 1.0, a linear correlation. The analogy can be expanded by considering the height or width of the book, where any increase will lead to a corresponding increase in total page area. So, increasing the area of each lamella will lead to a corresponding increase in the volume occupied by the gills: still a scaling exponent of 1.0 (Fig. 1c).

An important prerequisite of the book analogy is that the distance between the lamellae, determining the

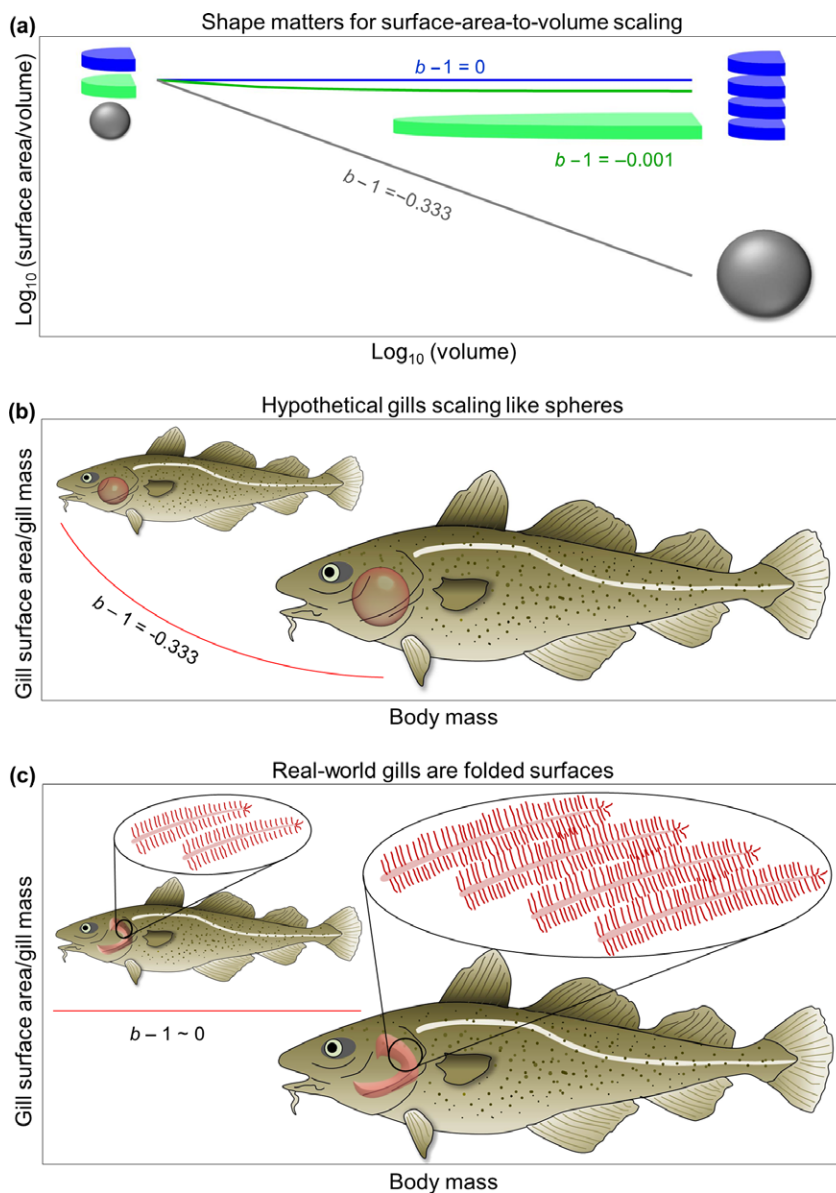


Fig. 1 Scaling of relative surface area with volume of different shapes. The volume-specific surface area (SA) of different shapes is shown as a function of volume (V) in (a). The relative surface area of the sphere (grey line) decreases fast, due to the geometry ($SA_{\text{sphere}} = 4\pi r_{\text{sphere}}^2$ and $V_{\text{sphere}} = \frac{4}{3}\pi r^3$, where r increases linearly). In a disc of the same volume as the sphere (with larger radius than height, resembling the shape of a gill lamella; green line), but with unchanging thickness and increasing radius ($r_{\text{disc}} = \sqrt{\frac{0.5V_{\text{sphere}}}{\pi h}}$), the rate of decrease in surface area ($SA_{\text{disc}} = 2\pi r_{\text{disc}}h + 2\pi r_{\text{disc}}^2$) actually falls as the radius grows. In the third scenario (blue line), when the volume is increased by increasing the number of discs, and maintaining the original thickness and radius, the surface-area-to-volume ratio is constant. For both the single disc and multiple discs, it has been taken into account that only half of the volume will be occupied (as the secondary lamellae of gills have some space between them). In (b), as the fish and, hence, the volume of the gill and the radius of the sphere grow, the surface-area-to-mass ratio decreases, assuming that the volume of the gills relative to the body mass is the same in a big compared to a small fish (at least it is not bigger). This means that larger fish have a relatively smaller respiratory surface area at their disposal, if the gills are assumed to be shaped like spheres. In (c), it is assumed, for simplicity, that as the fish grows, so does the number of respiratory 'units', the lamellae, because the thickness and distance between lamellae does not change consistently with body size (see text). This means that a larger fish could in fact have a relative surface area that is roughly the same as a smaller fish. But because there are trade-offs associated with having large respiratory surfaces, the gill surface-area-to-mass ratio scales to body mass with a mass-specific exponent ($b - 1$) slightly less than 0, guided by the oxygen demand of the fish, rather than the other way around. The curves in (a) were created using GRAPHPAD PRISM 6 (GraphPad Software Inc., La Jolla, CA, USA) after calculation of values according to the equations above, and drawings of shapes and fish were made in Microsoft PowerPoint 2010.

number of lamellae per mm of filament, is not forced by physical constraints to increase with increasing body size. There is good evidence for this assumption: Gray (1954) found no clear relationship between body mass and number of lamellae per mm filament in 31 species of marine fishes ranging in mass from 71 to 6392 g, while lifestyle had a clear influence on how lamella were packed, with 31 lamellae per mm of filament in mackerel *Scomber scombrus* compared to only 11 in the sluggish toadfish *Opsanus tau*. Likewise, there was no increase in lamellar spacing with mass in carp *Cyprinus carpio* ranging from 2 to 2000 g (Oikawa & Itazawa, 1985), and similar results were reported for porgy *Pagrus major*, a marine teleost (Oikawa *et al.*, 1999). In Nile tilapia *Oreochromis niloticus*, a small increase in lamellar spacing with body mass was associated with a relatively minor decrease in gill surface area per gill mass in larger individuals, but the scaling exponent was approximately 0.88 (Kisia & Hughes, 1992), which is far from the 0.67 predicted if a sphere-like surface-area-to-volume relationship was at play. Furthermore, there were either no, or very minor, intraspecific increases in lamellar spacing over a tenfold increase in body size in several species of tunas and billfishes (Wegner *et al.*, 2010), and Palzenberger & Pohla (1992) saw a similar pattern in freshwater fishes. In species where the interlamellar distance does increase with body mass, it could be one of the mechanisms by which gill surface area is matched to metabolic needs, but there is no evidence that it is due to physical constraints. It should also be pointed out that the thickness of the cell layers making up the diffusion barrier between water and blood does not change with body mass in ectothermic vertebrates such as fishes (most recently reviewed by Gillooly *et al.*, 2016).

Finally, if there were an upper limit for gill surface area that was reached as fishes grew, one would expect that the gill mass in relation to body mass would increase with body mass until this limit was reached, to compensate for the increasing 'geometric constraints' of the respiratory surface area. As far as we can see there is no support for this in the literature, rather the opposite. Thus, there is some evidence that gill mass, in relation to body mass, is generally smaller in larger individuals: in Nile tilapia gill mass falls from 5.8% to 2.9% of the body mass when the fish grows from 1 to 1000 g (Kisia & Hughes, 1992), and similar data have been obtained for carp (Oikawa & Itazawa, 1984) and tunas (Brill *et al.*, 2001) while, in the porgy, gill mass scales nearly linearly with body mass (Oikawa *et al.*, 1992). A likely explanation for relatively smaller gills in larger fishes is the general reduction in metabolic demands with body mass, which we will discuss further below.

Geometric constraints do not explain scaling of metabolic rate

The idea that insurmountable geometric constraints on the size of the gills could determine the metabolic rate of fishes has never, as far as we know, been pursued as a valid hypothesis among respiratory physiologists. It is, for example, not mentioned in Schmidt-Nielsen's book 'Animal Physiology: Adaptation and Environment' (1997) or in Evans and Claiborne's 'The Physiology of Fishes' (Evans & Claiborne, 2006), two books widely used as sources for overviews of animal and fish physiology. In our field, it is generally accepted that a species' oxygen demand determines the size of their respiratory surface area, not the other way around. Moreover, as mentioned by Pauly (2010), there are trade-offs involved in having large surface areas, such as passive losses of water or ions, or risk of infections. Therefore, the respiratory surface areas of fishes are in fact smaller than geometric constraints would allow. For example, maintaining acid-base and ion homeostasis will be easier for a fish with smaller gill area, because the rate of passive exchange of ions is directly proportional to the area of the surface over which the exchange occurs. The cost may be in the range of 4–10% of resting metabolic rate (Ern *et al.*, 2014). It will also cost more to ventilate a larger surface area, because of a larger resistance. The cost of ventilation is estimated to be 5–15% under resting, normoxic conditions (e.g. Holeton, 1980; Steffensen & Lomholt, 1983; Scheid, 1987; Steffensen, 1993). Still, none of these factors would be expected to increase disproportionately to gill size as a fish grows. There is, instead, very good evidence that fishes have gills sizes that are matched to their metabolic needs, which in turn are determined by factors such as habitat and life style (Gray, 1954; Kisia & Hughes, 1992; Palzenberger & Pohla, 1992; Chapman *et al.*, 2000; Killen *et al.*, 2016). Thus, fast-swimming pelagic fishes have much larger gills than sluggish benthic ones, and hypoxia-tolerant species have larger gills than less hypoxia-tolerant ones with a similar activity level. It is now also clear that gills are quite dynamic structures where the physical size of the respiratory surface can be regulated within days to months, in response to ambient factors such as oxygen levels and temperature (Chapman *et al.*, 2000; Nilsson *et al.*, 2012; Bowden *et al.*, 2014). This comes in addition to the immediate physiological responses that are available to fishes to boost oxygen uptake when required, including upregulating ventilation and cardiac output, and increasing blood oxygen affinity, the number of perfused lamellae and the number of circulating red blood cells (Perry & Gilmour, 2010). Such minute-to-minute adjustments allow fishes

to at least double their oxygen uptake, usually much more than that, with some species capable of greater than tenfold increases in uptake (Killen *et al.*, 2016; see also Fig. 2d).

Another striking argument against the suggestion that geometric constraints on gill surface area make fishes in warm water smaller than fishes in cold water

is the fact that the very largest teleosts, rays and sharks occur in tropical waters (masses given below are from fishbase.org). These are the sunfish *Mola mola*, the giant manta ray *Manta birostris* and the whale shark *Rhincodon typus*, weighing up to 2300, 3000 and 34 000 kg, respectively. The latter two are almost exclusively tropical. When it comes to highly active fishes with a great

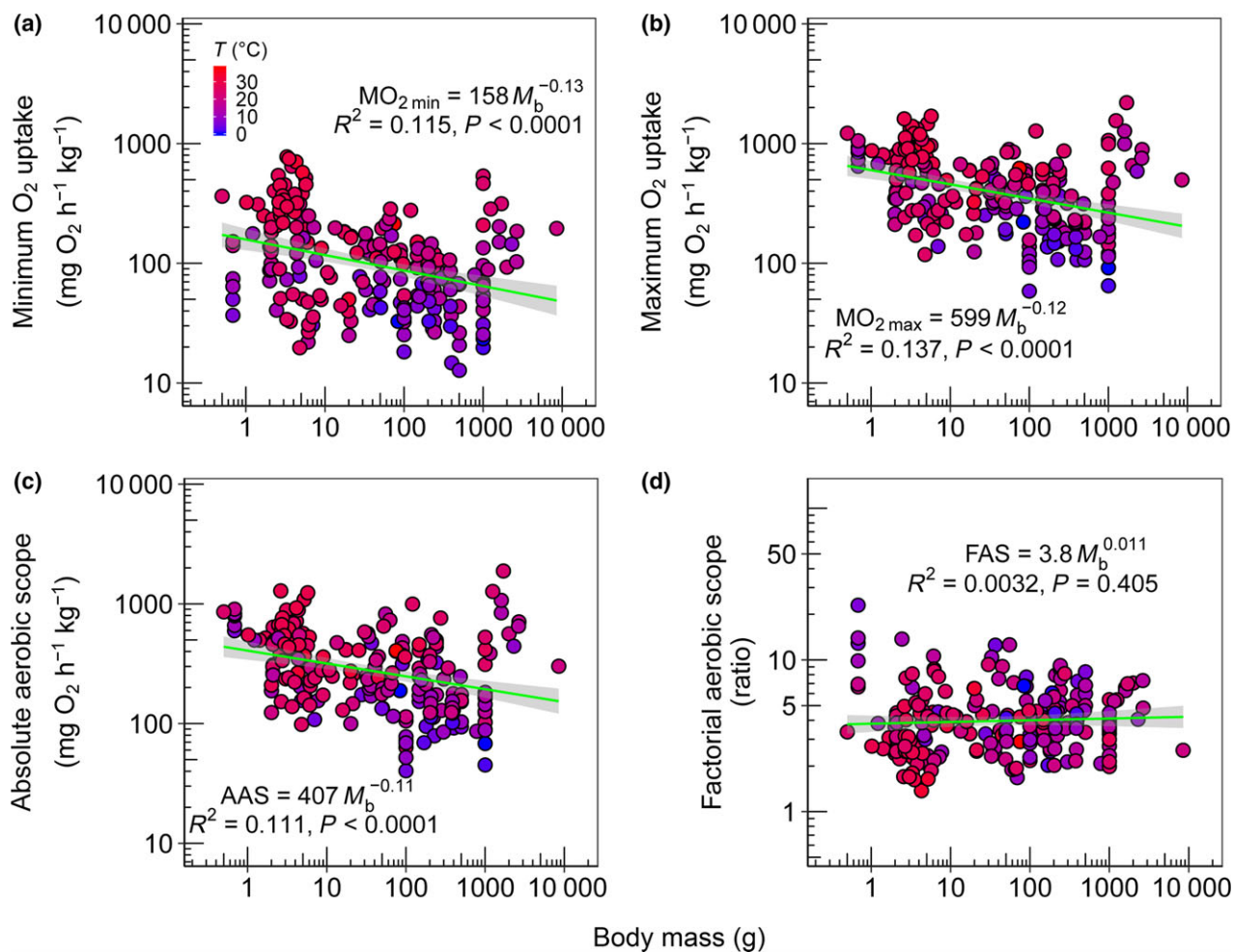


Fig. 2 Scaling of mass-specific oxygen demand to body mass at different temperatures. The mass-specific basal oxygen demand (or 'maintenance metabolism', measured as minimum oxygen uptake (MO_{2min}) (a), decreases with a mass-specific scaling exponent of -0.13 ± 0.05 (95% confidence interval, CI), and fish at warmer temperatures have a higher MO_{2min} , at all body masses. The mass-specific maximum capacity for oxygen supply, estimated as maximum oxygen uptake (MO_{2max}) (b), decreases with body mass with an exponent of -0.12 ± 0.04 (95% CI), and fish at warmer temperatures have a higher MO_{2max} , at all body masses. The absolute scope for activities beyond basic maintenance needs, measured as absolute aerobic scope (AAS) (c) also decreases slightly with body mass, with an exponent of -0.11 ± 0.04 (95% CI). Because MO_{2max} and MO_{2min} both have a similar scaling exponent, the relative ability to increase oxygen uptake, measured as the factorial aerobic scope (FAS) (d), is maintained as body mass increases, showing that the capacity for oxygen supply does not become increasingly limited as a fish grows. Overall, the data indicate that the mass-specific scaling exponent for oxygen uptake and hence aerobic metabolism in fishes is close to -0.1 . Note the large variability in all the measures (approximately a tenfold difference at a given body mass), which is partly due to temperature effects but also to differences in species lifestyle (Killen *et al.*, 2016). The data have been sourced from the supplementary material of Lefevre (2016) and Killen *et al.* (2016), where references for all data points can be found. The colours of the points reflect the acclimation temperature of the individuals used in a given study. Green lines are fitted power relationships, while grey shades indicate 95% confidence interval for the fit, with equations and R^2 indicated in each panel. Graphs were created using the package `GGPLOT2` (Wickham, 2009) in R version 3.3.2 (R Core Team, 2016).

oxygen demand and thereby need for large gills, there are also very large tropical species, including blue marlin *Makaira nigricans* that reaches 636 kg, black marlin *Istiompax indica* (750 kg) and tiger shark *Galeocerdo cuvier* (800 kg). It has been questioned whether marlins really are tropical (Pauly, 1998), but temperature and depth loggers attached to them in tropical waters reveal a preference for warm surface waters at 26–30 °C in both Pacific and Atlantic oceans (Block *et al.*, 1992; Horodysky *et al.*, 2007; Prince *et al.*, 2005). Other gigantic tropical teleosts include the Queensland grouper *Epinephelus lanceolatus* (400 kg) and the Atlantic goliath grouper *E. itajara* (455 kg). The list of very large tropical fishes goes on and, in our view, is impossible to reconcile with any constraints on oxygen uptake as they grow.

Oxygen demand vs. oxygen supply and how they scale with body mass

Before dealing with the second assumption concerning the scaling of ‘maintenance metabolism’, it is necessary to point out some principles that most fish physiologists agree upon. First of all, the ATP used by fishes under steady state conditions is assumed to be derived mainly from aerobic metabolism, and hence, oxygen uptake is used as a proxy for metabolic rate (Nelson, 2016). Traditionally, physiologists consider two boundaries to oxygen uptake: the minimum (basal or standard) oxygen uptake and maximum oxygen uptake. Minimum oxygen uptake in fishes is measured over several hours (ideally 24–48 h, depending on the species) in a respirometer (e.g. Svendsen *et al.*, 2016), and care is taken to ensure that the oxygen uptake has stabilized before measurements are considered reliable. The fish should be in an unfed state (postabsorptive, but not starving), meaning that there is no contribution of direct costs associated with digestion and anabolism (the specific dynamic action response, discussed below), and the fish should display minimal levels of activity. Minimum oxygen uptake can also be estimated using a swim-tunnel respirometer, by extrapolating oxygen consumption at different swimming speeds down to a notional swimming speed of zero (Brett, 1964). This is particularly useful for obligatory ram-ventilating fishes, such as tunas and several sharks, which ventilate their gills by swimming with their mouth open (e.g. Brown & Muir, 1970; Wegner *et al.*, 2013). The rates of oxygen uptake obtained by these methods are considered to reflect the basal amount of oxygen needed simply to stay alive, which comprises the costs of ventilation, circulation, neuronal activity and membrane transport – generally speaking the processes that contribute to homeostasis (e.g. Chabot

et al., 2016). The minimum oxygen uptake would therefore be considered, by physiologists, to be equivalent to maintenance metabolism as defined by Pauly (1979, 2010). Maximum capacity for oxygen uptake, on the other hand, is typically estimated during swimming at high speed in a swim-tunnel or immediately after exhaustive exercise (e.g. Norin & Clark, 2016), possibly in combination with feeding (Jourdan-Pineau *et al.*, 2010). The difference between the maximum and minimum oxygen uptake is commonly referred to as the net or absolute aerobic scope (AAS), which is a measure of the oxygen that can be provided to support activities beyond basal maintenance, such as swimming, growth and reproduction.

An average interspecific scaling exponent for resting metabolism of fishes between 0.8 and 0.9 (= a mass-specific scaling exponent of –0.1 to –0.2) has now been obtained by various authors for more than half a century (e.g. Winberg, 1960; White *et al.*, 2006). We have taken the metadata on both minimum and maximum oxygen uptake, absolute aerobic scope and factorial aerobic scope (FAS, i.e. maximum divided by minimum) collected by Killen *et al.* (2016) and Lefevre (2016) to illustrate how these measures scale with body mass (Fig. 2). As expected, minimum oxygen demand scales with an exponent of 0.87 (Fig. 2a), while maximum supply capacity scales with an exponent of 0.88 (Fig. 2b), and AAS scales with an exponent of 0.89 (Fig. 2c). Consequently, FAS is maintained with increasing body mass because maximum oxygen supply capacity scales with virtually the same exponent as minimum demand (Fig. 2d). At the same time, it is clear that there is profound variation in FAS among species, which was shown by Killen *et al.* (2016) to correlate with ecology and life style. If there were insurmountable geometric constraints on the size of the gills that limited oxygen uptake in larger fishes, this would by necessity show up as a drop in FAS with increasing body mass. While the present analysis includes different species, a similar pattern has also been observed within species (Killen *et al.*, 2007; Norin & Malte, 2011, 2012; Clark *et al.*, 2012; Huang *et al.*, 2013; Mager *et al.*, 2014; Zhang *et al.*, 2014; Luo *et al.*, 2015; Tirsgaard *et al.*, 2015; Messmer *et al.*, 2016).

In contrast to these observed scaling values, the model presented in the IUCN report (Cheung & Pauly, 2016), which ultimately derives from Pauly (1979), assumes that maintenance metabolism, or more specifically the oxygen needed for maintenance, scales in direct proportion to body mass. That is, the mass-specific ‘cost of living’ is assumed to be the same for a small fish and a big fish. This is clearly not the case, as shown by the negative scaling exponent of mass-specific minimum oxygen demand, which we would argue reflects

the maintenance metabolism of fishes (Fig. 2a). Pauly (1979, 2010) offers no explanation for assuming a constant mass-specific cost for maintenance, merely stating that *'The amount of body substance degraded per unit of time, however, increases in direct proportion to body weight'* and that *'"oxygen demand" refers to the amount required or "needed" by a fish body, not to the observed O₂ consumption (or "metabolism") which is here referred to as "supply"'*. There is no mention of fishes' ability to increase their oxygen uptake in response to their demand, which of course they can do when required, as revealed by their aerobic scope.

The two assumptions – (i) that oxygen needed for maintenance, referred to as maintenance metabolism (Pauly, 2010; Cheung *et al.*, 2013a; Cheung & Pauly, 2016) or routine metabolism (Pauly, 1998), is the same for big and small fishes (as described by the hypothetical, horizontal line in Fig. 3a) and (ii) that the ability to supply oxygen falls with body mass due to mass-dependent geometric constraints on the gills – led to the conclusion that oxygen supply becomes limiting as fishes grow. Apparently the claim that maintenance (routine) metabolism scales to body mass with an exponent of 1.0 comes from the theories of von Bertalanffy, stating that *'catabolism occurs in all living cells of a fish and is therefore directly proportional to the mass of the fish's body'* (quoted by Pauly, 2010). This idea, however, has been completely discarded, as already noted by Enberg *et al.* (2008) and Brander *et al.* (2013). The oxygen consumption of different tissues in an animal vary by more than one order of magnitude and fishes are no exception (e.g. Vernberg, 1954; Itazawa & Oikawa, 1983), and the relative sizes of the various tissues and organs differ in small and large animals. Moreover, cells from small animals have higher rates of oxygen uptake than those from large ones (at least in mammals, see Porter & Brand, 1995) and, even if such measurements have yet to be made for fishes, the activity of oxidative enzymes falls with body mass in fishes (Davies & Moyes, 2007). Most importantly, the primary function of catabolism (i.e. the breakdown of proteins, fat and carbohydrates) in resting, unfed animals is to provide energy for maintenance metabolism and, as we have already explained, maintenance metabolism measured as mass-specific oxygen consumption falls with body size in resting, unfed fishes (Fig. 2a).

It bears pointing out that Weatherley *et al.* (1987) and Blier *et al.* (1997) had already concluded that there was no evidence that capacity for gas exchange or gill surface area could limit growth performance in fishes, and their analysis remains valid today. Feeding leads to a transient increase in oxygen demand in fishes (and other animals), the so-called specific dynamic action (SDA) response, which reflects the metabolic costs of

digesting and assimilating the meal, hence 'growing' (McCue, 2006). In most fishes, maximum rates of oxygen uptake exceed the highest oxygen uptake observed during an SDA response (Blier *et al.*, 1997; Fig. 2b). In salmonids, for example, peak SDA when feeding at maximum ration is about half the maximum rate of oxygen uptake during sustained aerobic exercise (Brett & Groves, 1979; McKenzie *et al.*, 2007). The database is limited; therefore, the peak SDA response in species that consume infrequent large meals may, conceivably, approach their maximum capacity for oxygen uptake (Soofiani & Hawkins, 1982; Blier *et al.*, 1997; Wang *et al.*, 2012). There is no reason to believe, however, that such constraints would become more severe as individuals increase in body mass.

The claims that there is a direct proportional increase in oxygen demand for maintenance metabolism with body mass (Fig. 3a) and that oxygen supply, in turn, cannot keep up are the two critical assumptions that underpin the conclusion by Cheung & Pauly (2016) and Cheung *et al.* (2013a): that fishes will be smaller in a warmer future. None of these assumptions are supported by current data and the principles generally recognized by physiologists. On the contrary, the evidence shows that both mass-specific minimum oxygen uptake (i.e. for maintenance) and maximum capacity for oxygen supply scale with the same exponent (ca. -0.12) and that relative scope for activity and growth are independent of body size. In conclusion, large fishes have no less capacity to increase their rate of oxygen consumption and meet the costs of growth than small fishes. Therefore, based on their respiratory capacities, we would not predict a change in the size of fishes in a warmer world (as summarized in Fig. 3b).

The importance of exponents and coefficients

In the modelling exercises by Cheung *et al.* (2011, 2013a), a scaling exponent of 0.7 for anabolic metabolism (i.e. -0.3 for the mass-specific relationship) underlying growth is used, after referring to Pauly (1981, 2010). This exponent appears to have been derived from the scaling of respiratory surface area to mass, which mirrors the exponents for minimum and maximum oxygen uptake (discussed above). A low value of this exponent in the equations underlying the model will lead to a large effect of temperature on growth and future body size (Fig. 3a). As we have argued, oxygen supply by the gills is unlikely to put constraints on metabolism and growth but, nonetheless, we would like to point out that a scaling exponent of 0.7 is considerably lower than those reported in the literature. Muir (1969) put the average exponent at 0.8–0.9 for the

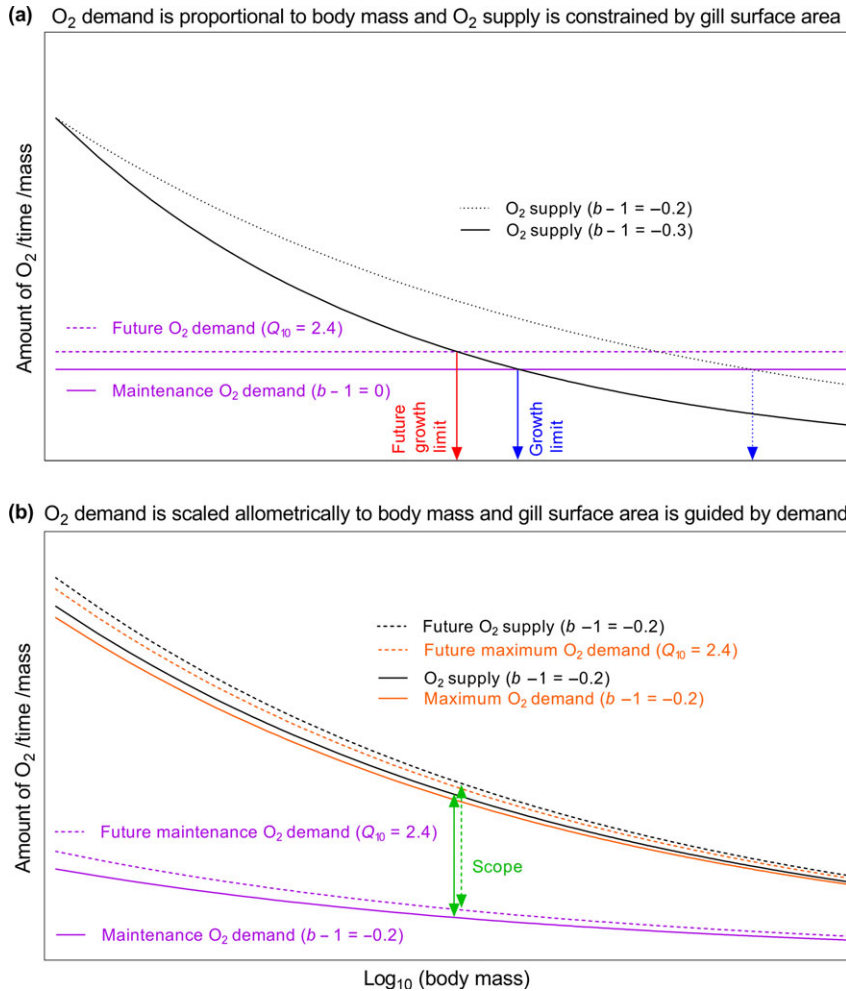


Fig. 3 Predicted scaling of mass-specific oxygen supply and demand to body mass under different assumptions. In (a), which is based on the reasoning in Cheung *et al.* (2013a) and Pauly (2010), it is assumed that mass-specific ‘maintenance’ metabolism (equal to basal oxygen demand), is maintained with body mass ($MO_2 = a \cdot M_b^0$; solid purple line), while maximum capacity for oxygen supply decreases with a mass-specific exponent ($b - 1$) of -0.3 ($MO_{2supply} = c \cdot M_b^{-0.3}$; solid black line). This means that when a certain body size is reached, oxygen demand for maintenance exceeds capacity for supply and the rate of growth is constrained (the growth limit; solid blue arrow). Note that decreasing the exponent from -0.3 to -0.2 (dotted black line) has a pronounced effect on the body mass at which the growth limit is reached (dotted blue arrow). In a warmer future ($\Delta T = +2^\circ C$), MO_2 is assumed to increase with a Q_{10} of 2.4 ($MO_{2future} = MO_2 \cdot Q_{10}^{(\Delta T/10)}$; dashed purple line). It is also assumed that $MO_{2supply}$ remains the same, and hence, maintenance oxygen demand surpasses oxygen supply at a smaller body size (the future growth limit; solid red arrow). In (b) – which we argue is the condition supported by physiological evidence – it is the oxygen demand that determines the capacity for oxygen uptake, not vice versa, as assumed in (a). In (b), the mass-specific minimum oxygen demand is assumed to decrease with an exponent of -0.2 ($MO_{2min} = a_2 \cdot M_b^{-0.2}$; solid purple line) (although it is likely to be closer to -0.1 , see text and Fig. 2a), while maximum oxygen uptake is x times higher and scales with the same exponent ($MO_{2max} = c \cdot M_b^{-0.2}$ or $x \cdot MO_{2min}$; where x = factorial aerobic scope; solid orange line). Here, $MO_{2supply}$ is determined by the respiratory surface area, which in turn is guided by the maximum oxygen demand and, hence, it is slightly higher but scales with the same exponent as MO_{2max} ($MO_{2supply} = (c+d) \cdot M_b^{-0.2}$; solid black line). In this scenario, the oxygen supply that can be allocated to anabolism (growth) is somewhere between basal demands for maintenance (MO_{2min}) and maximum capacity for supply (i.e. within the aerobic scope). In a warmer future (dashed lines), MO_{2min} will increase ($MO_{2min,future} = MO_{2min} \cdot Q_{10}^{(\Delta T/10)}$), and may or may not cause a decrease in the scope for aerobic metabolism, depending on the ability of the species to increase oxygen supply ($MO_{2supply} = (c+e) \cdot M_b^{-0.2}$). Regardless, the aerobic scope will never become zero – oxygen supply is not limiting and there is no oxygen-constrained growth limit. Graphs were created in GRAPHPAD PRISM 6 using the equations above.

scaling of gill area, and subsequent estimates range from 0.76 to 0.9 (see Nilsson & Östlund-Nilsson, 2008). We expect that, had an exponent of 0.8–0.9 been used

in the modelling in Cheung *et al.* (2011, 2013a), rather than 0.7, it would have significantly reduced the future temperature effects proposed in those studies.

Moreover, we would question the use of a single temperature coefficient (Q_{10}) by Cheung *et al.* (2011, 2013a). The Q_{10} describes the factorial increase in metabolic rate with temperature. A Q_{10} of 2 means that metabolic rate doubles with a 10 °C increase in temperature, a Q_{10} of 1 means that there is no temperature effect, and values lower than 1 imply that metabolism falls with temperature. The models of Cheung and co-workers adopt a single Q_{10} of 2.4, based on the median Q_{10} of 14 studies reported in a review of Q_{10} values in fishes by Clarke & Johnston (1999). Q_{10} of many more fishes are now available, not least because of the current focus on global warming. Clarke & Johnston (1999) pointed out that Q_{10} varied from 0.45 to 3.41 among species, and they did not report how long the fishes had been allowed to acclimate. Many fishes have the ability to acclimate to a rise in temperature if given enough time, which will reduce their Q_{10} considerably. For example, in shorthorn sculpin *Myoxocephalus scorpius* exposed to a rise in temperature from 10 to 16 °C, Q_{10} fell from 2.7 to 1.0 when the acclimation time was extended from 1 to 8 weeks (Sandblom *et al.*, 2014). That is, acclimation completely abolished any temperature effect on aerobic metabolic rate. Although all fishes may not show such perfect compensation, it illustrates the problem of using a single, high Q_{10} of 2.4, as it will cause all species to have elevated metabolic rates at warmer temperatures, causing an exaggeration of unknown magnitude in the model, for an unknown number of species. For models that include Q_{10} in the parameterization, it would be pertinent to make an updated survey of published Q_{10} values, to at least estimate what proportion of species are likely to show an elevation of metabolic rate, or not, when exposed to warmer water.

Conclusions

We fully appreciate that large-scale modelling studies have focussed much-needed attention on potential effects of climate change on fishes, and we do not dispute that global warming may lead to reductions in average body size and size-at-age of fishes (see Munday *et al.*, 2008; Daufresne *et al.*, 2009; Baudron *et al.*, 2014). It is essential, however, that the correct underlying mechanisms be investigated and identified and that projections of the effects on fish populations be modelled using sound physiological knowledge and principles. The temperature effects on body size in bacteria and plankton observed by Daufresne *et al.* (2009) may very well relate to the 2/3 exponential relationship between body mass and surface area, as these organisms lack respiratory organs with a folded surface and will rely largely on their body surface for exchange of gasses with the environment. However, other

mechanisms must be at play in the French river fishes (Daufresne *et al.*, 2009) and some marine fishes (Baudron *et al.*, 2014), and this should be food for thought for physiologists and fishery biologists.

Physiologists have failed to take an active role in ensuring that influential reports, such as the current one from IUCN (Laffoley & Baxter, 2016), have a sound basis for what they promulgate as universal, physiological paradigms. This includes not just the incorrect notion that oxygen uptake limits growth in fishes, but also the hypothesis of 'Oxygen- and Capacity-Limited Thermal Tolerance' (OCLTT) (Pörtner, 2010), whose universality is far from accepted (Lefevre, 2016). Incidentally, Cheung *et al.* (2013a) refer to the OCLTT hypothesis to support their claim that '*the capacity for growth is limited by oxygen in aquatic water-breathing ectotherms*', although this hypothesis does not embrace the notion that the size of a fish is relevant for its response to warming. To ensure that accurate and useful information is conveyed to the public, about the possible consequences of climate change, there is an urgent need to improve communication and congruity between fish physiologists and fisheries scientists. If fishes are indeed becoming smaller, it is crucial that researchers from different fields collaborate to identify and understand the underlying causes, to then search for relevant solutions.

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Conflict of interest

The authors declare no conflict of interests.

Author contributions

All authors contributed equally.

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