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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

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 fish 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

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,

82   due to elevated future water temperatures, would constrain fishes to smaller adult sizes,

83   because their gills could not supply enough oxygen for a larger body. Here, therefore, we aim

84   to clarify the physiological principles of gill function, metabolic rate and growth in fishes.

85

86   **Gills are folded surfaces, not spheres**

87   The key physiological assumption about gills and metabolic rate adopted by Cheung *et al.*

88   (2011, 2013a) were originally posited by Pauly (1981, 1998, 2010), who stated that

89   "*Geometric constraints prevent surfaces to grow as fast as volumes*" and that "*Gills, being a*

90   *surface area, cannot grow, for insurmountable geometric reasons, as fast as the volume they*

91   *are meant to supply with oxygen*" (Pauly, 1998). As we will demonstrate, the second

92   statement is not true: fish gills do not adhere to the geometric surface-area-to-volume

93   relationship that is referred to in the first statement. That faulty assumption is then used to

94   argue that gill surface areas cannot grow as fast as body mass, and that this results in lowered

95   food conversion efficiency, when body mass increases. In fact, it is proposed that geometric

96   constraints on the gills are what underlie the well-known allometric decrease in mass specific

97   oxygen uptake in relation to body mass in fishes.

98   The geometric relationship that prevents the surface area of an object from growing as

99   fast as its volume would, for example, apply to oxygen uptake over a body surface. The

100   underlying reason for this geometrical relationship is that the volume of objects like spheres

101   increases with the cube of their radius (volume $\propto r^3$), while their surface area only increases

102   with the square (area $\propto r^2$). The same applies to structures similar to spheres, which includes

103   many animal bodies. As a consequence, the surface area of an animal's skin scales to the

104   volume (or mass) of that animal with an exponent (b) approximating 0.67 (i.e. 2/3), or -0.333

105   (b-1) for the scaling of mass-specific surface-area-to-mass ratio (Fig. 1a, grey line; Fig. 1b).

106   This relationship was already known to biologists by the 19th century (reviewed by Schmidt-

107   Nielsen, 1984) and Rubner (1883) used it in a famous attempt to explain why smaller dogs

108   have higher mass-specific metabolic rates than larger ones, ascribing it to greater heat loss

109   over the skin.

110   This simple geometric relationship does not, however, apply to fish gills. These have

111   evolved into very large surface areas of delicate respiratory epithelium, where gas exchange

112   takes place over many small sheets (called lamellae) attached to gill filaments that, in turn, are

113   attached to the gill arches. Thus, gills have folded surfaces (e.g. Price, 1930) and are one of

114   many examples in nature where the 2/3-exponent relationship between surface area and

115   volume is overcome by folding the surface. Other examples include lungs, intestinal

116   membranes and inner mitochondrial membranes. Since each single lamella is a sheet with a

117   half-circle to rectangular shape that grows by increasing the radius or length of the sides,

118   rather than the thickness, it has a surface-to-mass scaling exponent that approaches 1.0 (Fig.

119   1a, green line). When gills grow by adding more and more lamellae, the surface-to-mass

120   scaling exponent essentially becomes 1.0 (Fig. 1a, blue line; Fig. 1c). Thus, in morphometric

121   studies where both total lamellar area and gill mass have been measured, a linear scaling

122   relationship (scaling exponent of 1.0) has been found in fishes (Gehrke, 1987) as well as

123   bivalves (Scott, 2005). Consequently, there is no geometric constraint that prevents an

124   increase in body size (mass or volume) from being accompanied by a corresponding increase

125   in gill mass and hence respiratory surface area. In other words, gill surface area can scale

126   proportionally with body mass and, if it does not do so, it is because oxygen demands are

127   reduced with body size, as discussed further below.

128   A simple way to explain the geometry of gills is by analogy to a book, where pages

129   correspond to lamellae. It is easy to grasp that if you double the thickness of a book (thereby

130   doubling its volume and mass), you can fit in twice the number of pages and, therefore, the

131   total surface area of the pages is also doubled. Moreover, increasing the number of books

132   (analogous to increasing the number of gill filaments) leads to a corresponding increase in

133   page area (analogous to respiratory surface area). Thus, with the structural arrangement of

134   books and gills, the surface area will scale to volume with an exponent of 1.0, a linear

135   correlation. The analogy can be expanded by considering the height or width of the book,

136   where any increase will lead to a corresponding increase in total page area. So, increasing the

137   area of each lamella will lead to a corresponding increase in the volume occupied by the gills:

138   still a scaling exponent of 1.0 (Fig. 1c).

139   An important prerequisite of the book analogy is that the distance between the

140   lamellae, determining the number of lamellae per mm of filament, is not forced by physical

141   constraints to increase with increasing body size. There is indeed evidence for this

142   assumption: Gray (1954) found no clear relationship between body mass and number of

143   lamellae per mm filament in 31 species of marine fishes ranging in mass from 71 to 6392 g,

144   while lifestyle had a clear influence on how lamella were packed, with 31 lamellae per mm of

145   filament in mackerel *Scomber scombrus* compared to only 11 in the sluggish toadfish

146   *Opsanus tau*. Likewise, there was no increase in lamellar spacing with mass in carp *Cyprinus*

147   *carpio* ranging from 2 to 2,000 g (Oikawa & Itazawa, 1985), and similar results were reported

148   for porgy *Pagrus major*, a marine teleost (Oikawa *et al*., 1999). In Nile tilapia *Oreochromis*

149   *niloticus*, a small increase in lamellar spacing with body mass was associated with a relatively

150   minor decrease in gill surface area per gill mass in larger individuals, but the scaling exponent

151   was approximately 0.88 (Kisia & Hughes, 1992), which is far from the 0.67 predicted if a

152   sphere-like surface-area-to-volume relationship was at play. Furthermore, there were either

153   no, or very minor, intraspecific increases in lamellar spacing over a 10-fold increase in body

154   size in several species of tunas and billfishes (Wegner *et al.*, 2010), and Palzenberger and

155   Pohla (1992) saw a similar pattern in freshwater fishes. In species where the interlamellar

156   distance does increase with body mass, it could be one of the mechanisms by which gill

157   surface area is matched to metabolic needs, but there is no evidence that it is due to physical

158   constraints. It should also be pointed out that the thickness of the cell layers making up the

159   diffusion barrier between water and blood does not change with body mass in ectothermic

160   vertebrates like fishes (most recently reviewed by Gillooly *et al.*, 2016).

161   Finally, if there were an upper limit for gill surface area that was reached as fish grew,

162   one would expect that the gill mass in relation to body mass would increase with body mass

163   until this limit was reached, to compensate for the increasing 'geometric constraints' of the

164   respiratory surface area. As far as we can see there is no support for this in the literature,

165   rather the opposite. Thus, there is some evidence that gill mass, in relation to body mass, is

166   generally smaller in larger individuals: in Nile tilapia gill mass falls from 5.8 % to 2.9 % of

167   the body mass when the fish grows from 1 g to 1000 g (Kisia & Hughes, 1992), and similar

168   data have been obtained for carp (Oikawa & Itazawa, 1984) and tunas (Brill *et al.*, 2001)

169   while, in the porgy, gill mass scales nearly linearly with body mass (Oikawa *et al.*, 1992). A

170   likely explanation for relatively smaller gills in larger fish is the general reduction in

171   metabolic demands with body mass, which we will discuss further below.

172

Geometric constraints do not explain scaling of metabolic rate

174   The idea that insurmountable geometric constraints on the size of the gills could determine the

175   metabolic rate of fishes has never, as far as we know, been pursued as a valid hypothesis

176   among respiratory physiologists. It is, for example, not mentioned in Schmidt-Nielsen's book

177   "Animal Physiology: Adaptation and Environment" (1997) or in Evans and Claiborne's "The

178   Physiology of Fishes" (2006), two books widely used as sources for overviews of animal and

179   fish physiology. In our field, it is generally accepted that a species' oxygen demand

180   determines the size of their respiratory surface area, not the other way around. Moreover, as

181   mentioned by Pauly (2010), there are trade-offs involved in having large surface areas, such

182   as passive losses of water or ions, or risk of infections. Therefore, the respiratory surface areas

183   of fishes are in fact smaller than geometric constraints would allow. For example, maintaining

184   acid-base and ion homeostasis will be easier for a fish with smaller gill area, because the

185   passive diffusive loss of ions is directly proportional to the area of the surface over which the

186   exchange occurs. The cost may be in the range of 4 – 10% of resting metabolic rate (Ern *et*

187   *al.*, 2014). It will also cost more to ventilate a larger surface area, because of a larger

188   resistance. The cost of ventilation is estimated to be 5-15% under resting, normoxic

189   conditions (e.g. Holeton, 1980; Steffensen & Lomholt, 1983; Scheid, 1987; Steffensen, 1993).

190   Still, none of these factors would be expected to increase disproportionately to gill size as a

191   fish grows. There is, instead, very good evidence that fishes have gills sizes that are matched

192   to their metabolic needs, which in turn are determined by factors such as habitat and life style

193   (Gray, 1954; Kisia & Hughes, 1992; Palzenberger & Pohla, 1992; Chapman *et al.*, 2000;

194   Killen *et al.*, 2016). Thus, fast swimming pelagic fishes have much larger gills than sluggish

195   benthic ones, and hypoxia tolerant species have larger gills than less hypoxia tolerant ones

196   with a similar activity level. It is now also clear that gills are quite dynamic structures where

197   the physical size of the respiratory surface can be regulated within days to months, in

198   response to ambient factors like oxygen levels and temperature (Chapman *et al.*, 2000;

199   Nilsson *et al.*, 2012; Bowden *et al.*, 2014). This comes in addition to the immediate

200   physiological responses that are available to fishes to boost oxygen uptake when required,

201   including up-regulating ventilation and cardiac output, and increasing blood oxygen affinity,

202   the number of perfused lamellae, and the number of red blood cells (Perry & Gilmour, 2010).

203   Such minute-to-minute adjustments allow fishes to at least double their oxygen uptake,

204   usually much more than that, with some species capable of greater than 10-fold increases in

205   uptake (Killen *et al.*, 2016; see also Fig. 2d).

206   Another striking argument against the suggestion that geometric constraints on gill

207   surface area make fishes in warm water smaller than fishes in cold water is the fact that the

208   very largest teleosts, rays, and sharks, occur in tropical waters (masses given below are from

209   fishbase.org). These are the sunfish *Mola mola*, the giant manta ray *Manta birostris* and the

210   whale shark *Rhincodon typus*, weighing up to 2,300, 3,000 and 34,000 kg, respectively. The

latter two are almost exclusively tropical. When it comes to highly active fishes with a great

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.*, 2004; 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 versus 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 fish 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 hours, 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 (post-absorptive, 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

237   consumption at different swimming speeds down to a notional swimming speed of zero

238   (Brett, 1964). This is particularly useful for obligatory ram-ventilating fishes, like tunas and

239   several sharks, which ventilate their gills by swimming with their mouth open (e.g. Brown &

240   Muir, 1970; Wegner *et al.*, 2013). The rates of oxygen uptake obtained by these methods are

241   considered to reflect the basal amount of oxygen needed simply to stay alive, which

242   comprises the costs of ventilation, circulation, neuronal activity, membrane transport –

243   generally speaking the processes that contribute to homeostasis (e.g. Chabot *et al.*, 2016). The

244   minimum oxygen uptake would therefore be considered, by physiologists, to be equivalent to

245   maintenance metabolism as defined by Pauly (1979, 2010). Maximum capacity for oxygen

246   uptake, on the other hand, is typically estimated during swimming at high speed in a swim-

247   tunnel or immediately after exhaustive exercise (e.g. Norin & Clark, 2016), possibly in

248   combination with feeding (Jourdan-Pineau *et al.*, 2010). The difference between the

249   maximum and minimum oxygen uptake is commonly referred to as the net or absolute aerobic

250   scope (AAS), which is a measure of the oxygen that can be provided to support activities

251   beyond basal maintenance, such as swimming, growth and reproduction.

252   An average interspecific scaling exponent for resting metabolism of fishes between 0.8

253   and 0.9 (= a mass-specific scaling exponent of -0.1 to -0.2) has now been obtained by various

254   authors for more than half a century (e.g. Winberg, 1960; White *et al.*, 2006). We have taken

255   the meta-data on both minimum and maximum oxygen uptake, absolute aerobic scope, and

256   factorial aerobic scope (FAS, i.e. maximum oxygen uptake divided by resting oxygen uptake)

257   collected by Killen *et al.* (2016) and Lefevre (2016) to illustrate how these measures scale

258   with body mass (Fig. 2). As expected, minimum oxygen demand scales with an exponent of

259   0.87 (Fig. 2a), while maximum demand scales with an exponent of 0.88 (Fig. 2b), and AAS

260   scales with an exponent of 0.89 (Fig. 2c). Consequently, FAS is maintained with increasing

261   body mass because maximum oxygen uptake scales with virtually the same exponent as

262   minimum oxygen demand (Fig. 2d). At the same time, it is clear that there is profound

263   variation in FAS among species, which was shown by Killen *et al*. (2016) to correlate with

264   ecology and life style. If there were insurmountable geometric constraints on the size of the

265   gills that limited oxygen uptake in larger fishes, this would by necessity show up as a drop in

266   FAS with increasing body mass. While the present analysis includes different species, a

267   similar pattern has also been observed within species (Killen *et al.*, 2007; Norin & Malte,

268   2011; Clark *et al.*, 2012; Norin & Malte, 2012; Huang *et al.*, 2013; Mager *et al.*, 2014; Zhang

269   *et al.*, 2014; Luo *et al.*, 2015; Tirsgaard *et al.*, 2015; Messmer *et al.*, 2016).

270   In contrast to these observed scaling values, the model presented in the IUCN report

271   (Cheung & Pauly, 2016), which ultimately derives from Pauly (1979), assumes that

272   maintenance metabolism, or more specifically the oxygen needed for maintenance, scales in

273   direct proportion to body mass. That is, the mass-specific 'cost of living' is assumed to be the

274   same for a small fish and a big fish. This is clearly not the case, as shown by the negative

275   scaling exponent of mass-specific minimum oxygen demand, which we would argue reflects

276   the maintenance metabolism of fishes (Fig. 2a). Pauly (1979, 2010) offers no explanation for

277   assuming a constant mass-specific cost for maintenance, merely stating that "*The amount of*

278   *body substance degraded per unit of time, however, increases in direct proportion to body*

279   *weight*", and that "'*oxygen demand' refers to the amount* required *or 'needed' by a fish body,*

280   *not to the* observed *O_2 consumption (or 'metabolism') which is here referred to as 'supply'*".

281   There is no mention of fishes' ability to increase their oxygen uptake in response to their

282   demand, which of course they can do when required, as revealed by their aerobic scope.

283   The two assumptions - (1) that oxygen needed for maintenance, referred to as

284   maintenance metabolism (Pauly, 2010; Cheung *et al.*, 2013a; Cheung & Pauly, 2016) or

285   routine metabolism (Pauly, 1998), is the same for big and small fish (as described by the

286   hypothetical, horizontal line in Fig. 3a), and (2) that the ability to supply oxygen falls with

287   body mass due to mass-dependent geometric constraints on the gills - led to the conclusion

288   that oxygen supply becomes limiting as fish grow. Apparently the claim that maintenance

11

289   (routine) metabolism scales to body mass with an exponent of 1.0 comes from the theories of

290   von Bertalanffy, stating that "*catabolism occurs in all living cells of a fish and is therefore*

291   *directly proportional to the mass of the fish's body*" (quoted by Pauly, 2010). This idea,

292   however, has been completely discarded, as already noted by Enberg *et al.* (2008) and

293   Brander *et al.* (2013). The oxygen consumption of different tissues in an animal vary by more

294   than one order of magnitude and fishes are no exception (e.g. Vernberg, 1954; Itazawa &

295   Oikawa, 1983), and the relative sizes of the various tissues and organs differ in small and

296   large animals. Moreover, cells from small animals have higher rates of oxygen uptake than

297   those from large ones (at least in mammals, see Porter & Brand, 1995) and, even if such

298   measurements have yet to be made for fishes, the activity of oxidative enzymes falls with

299   body mass in fishes (Davies & Moyes, 2007). Most importantly, the primary function of

300   catabolism (i.e. the breakdown of proteins, fat and carbohydrates) in resting, unfed animals is

301   to provide energy for maintenance metabolism and, as we have already explained,

302   maintenance metabolism measured as mass specific oxygen consumption falls with body size

303   in resting, unfed fish (Fig. 2a).

304   It bears pointing out that Weatherley and Gill (1987) and Blier *et al.* (1997) had

305   already concluded that there was no evidence that capacity for gas exchange or gill surface

306   area could limit growth performance in fishes, and their analysis remains valid today.

307   Feeding leads to a transient increase in oxygen demand in fishes (and other animals), the so-

308   called specific dynamic action (SDA) response, which reflects the metabolic costs of

309   digesting and assimilating the meal, hence 'growing' (McCue, 2006). In most fishes,

310   maximum rates of oxygen uptake exceed the highest metabolic rate observed during an SDA

311   response (Blier *et al*., 1997; Fig. 2b). In salmonids, for example, peak SDA when feeding at

312   maximum ration is about half the maximum metabolic rate during sustained aerobic exercise

313   (Brett & Groves, 1979; McKenzie *et al.*, 2007). The database is limited; therefore the peak

314   SDA response in species that consume infrequent large meals may, conceivably, approach

315 their maximum capacity for oxygen uptake (Soofiani & Hawkins, 1982; Blier *et al.*, 1997;

316 Wang *et al.*, 2012). There is no reason to believe, however, that such constraints would

317 become more severe as individuals increase in body mass.

318   The claims that there is a direct proportional increase in oxygen demand for

319 maintenance metabolism with body mass (Fig. 3a), and that oxygen supply, in turn, cannot

320 keep up, are the two critical assumptions that underpin the conclusion by Cheung & Pauly

321 (2016) and Cheung *et al.* (2013a): that fishes will be smaller in warmer future. None of these

322 assumptions are supported by current data and the principles generally recognized by

323 physiologists. On the contrary, the evidence shows that both mass-specific minimum oxygen

324 uptake (i.e. for maintenance) and maximum oxygen supply scale with the same exponent (ca.

325 -0.12), and that the relative scope for activity and growth is independent of body size. In

326 conclusion, fishes with large bodies have no less capacity to increase their rate of oxygen

327 consumption and meet the costs of growth than small fishes. Therefore, based on their

328 respiratory capacities, we would not predict a change in the size of fishes in a warmer world

329 (as summarised in Fig. 3b).

330

331 **The importance of exponents and coefficients**

332 In the modelling exercises by Cheung *et al.* (2011, 2013a), a scaling exponent of 0.7 for

333 anabolic metabolism (i.e. -0.3 for the mass-specific relationship) underlying growth is used,

334 after referring to Pauly (1981, 2010). This exponent appears to have been derived from the

335 scaling of respiratory surface area to mass, which mirrors the exponents for minimum and

336 maximum oxygen uptake (discussed above). A low value of this exponent in the equations

337 underlying the model will lead to a large effect of temperature on growth and future body size

338 (Fig. 3a). As we have argued, oxygen supply by the gills is unlikely to put constraints on

339 metabolism and growth but, nonetheless, we would like to point out that a scaling exponent of

340 0.7 is considerably lower than those reported in the literature. Muir (1969) put the average

341   exponent at 0.8-0.9 for the scaling of gill area, and subsequent estimates range from 0.76 to

342   0.9 (see Nilsson & Östlund-Nilsson, 2008). We expect that, had an exponent of 0.8-0.9 been

343   used in the modelling in Cheung *et al.* (2011, 2013a), rather than 0.7, it would have

344   significantly reduced the future temperature effects proposed in those studies.

345   Moreover, we would question the use of a single temperature coefficient (Q_{10}) by

346   Cheung *et al.* (2011, 2013a). The Q_{10} describes the factorial increase in metabolic rate with

347   temperature. A Q_{10} of 2 means that metabolic rate doubles with a 10 °C increase in

348   temperature, a Q_{10} of 1 means that there is no temperature effect, and values lower than 1

349   imply that metabolism falls with temperature. The models of Cheung and co-workers adopt a

350   single Q_{10} of 2.4, based on the median Q_{10} of 14 studies reported in a review of Q_{10} values in

351   fishes by Clarke and Johnston (1999). Q_{10} of many more fishes are now available, not least

352   because of the current focus on climate change. Clarke and Johnston (1999) pointed out that

353   Q_{10} varied from 0.45 to 3.41 among species, and they did not report how long the fishes had

354   been allowed to acclimate. Many fishes have the ability to acclimate to a rise in temperature if

355   given enough time, which will reduce their Q_{10} considerably. For example, in shorthorn

356   sculpin *Myoxocephalus scorpius* exposed to a rise in temperature from 10 to 16 °C, Q_{10} fell

357   from 2.7 to 1.0 when the acclimation time was extended from 1 to 8 weeks (Sandblom *et al.*,

358   2014). That is, acclimation completely abolished any temperature effect on aerobic metabolic

359   rate. Although all fishes may not show such perfect compensation, it illustrates the problem

360   of using a single, high Q_{10} of 2.4, since it will cause all species to have elevated metabolic

361   rates at warmer temperatures, causing an exaggeration of unknown magnitude in the model,

362   for an unknown number of species. For models that include Q_{10} in the parameterisation, it

363   would be pertinent to make an up-dated survey of published Q_{10} values, to at least estimate

364   what proportion of species are likely to show an elevation of metabolic rate, or not, when

365   exposed to warmer water.

366

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, since 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 other 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, like 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

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393 fields collaborate to identify and understand the underlying causes, to then search for relevant

394 solutions.

395

396 **Author contributions**

397 All authors contributed equally.

398

399 **Conflict of interests**

400 The authors declare no conflicts of interest.

401

402 **Acknowledgement**

407

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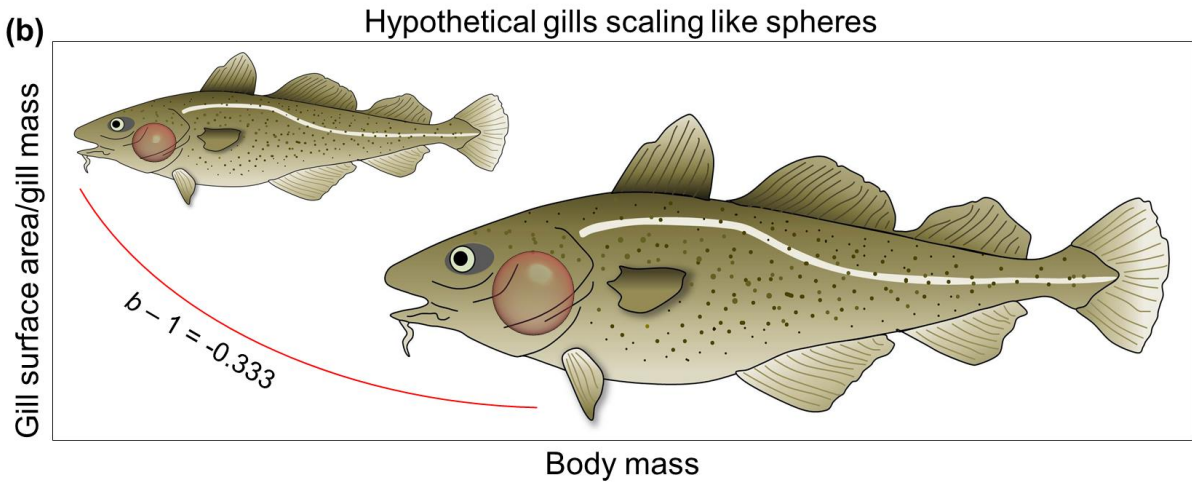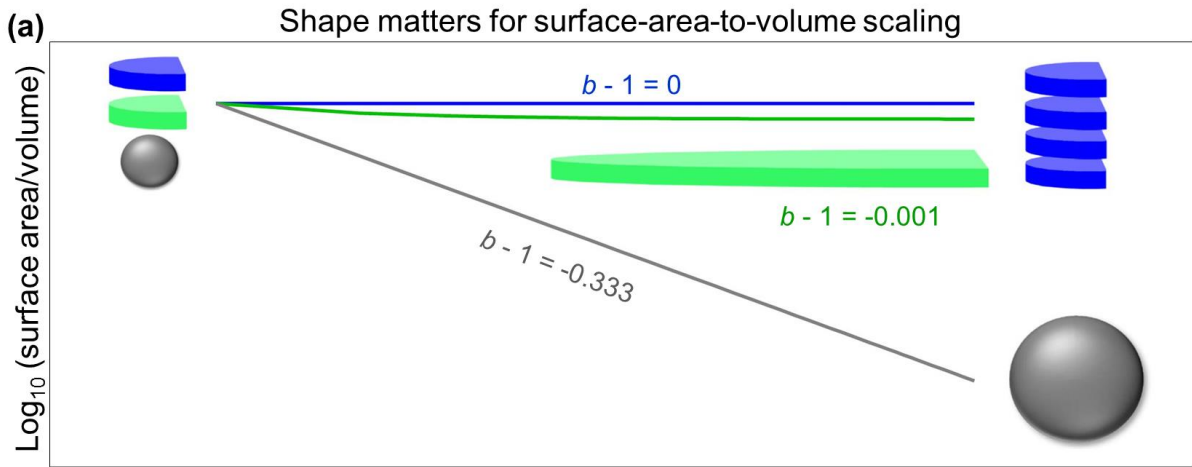
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Figures

639 **Fig. 1: Scaling of relative surface area with volume of different shapes.** The volume-

640 specific surface area (SA) of different shapes is shown as a function of volume (V) in a). The

641 relative surface area of the sphere (grey line) decreases fast, due to the geometry

642 ($SA_{sphere} = 4\pi r_{sphere}^2$ and $V_{sphere} = \frac{4}{3}\pi r^3$, where r increases linearly). In a disc of the same

643 volume as the sphere (with larger radius than height, resembling the shape of a gill lamella;

644 green line), but with unchanging thickness and increasing radius ($r_{disc} = \sqrt{\frac{0.5 V_{sphere}}{\pi h}}$), the rate of

645 decrease in surface area ($SA_{disc} = 2\pi r_{disc} h + 2\pi r_{disc}^2$) actually falls as the radius grows. In the

646 third scenario (blue line), when the volume is increased by increasing the number of discs,

647 and maintaining the original thickness and radius, the surface area

648 ($SA_{disc} = \frac{0.5 SA_{1disc}}{V_{1disc}} 0.5 V_{sphere}$) to volume ratio is constant. For both the single disc and multiple

649 discs, it has been taken into account that only half of the volume will be occupied (as the

650 secondary lamellae of gills have some space between them). In b), as the fish and, hence, the

651 volume of the gill and the radius of the sphere grow, the surface-area-to-mass ratio decreases,

652 assuming that the volume of the gills relative to the body mass is the same in a big compared

653 to a small fish (at least it is not bigger). This means that larger fish have a relatively smaller

654 respiratory surface area to their disposal, if the gills are assumed to be shaped like spheres. In

655 c), it is assumed, for simplicity, that as the fish grows, so does the number of respiratory

656 'units', the lamellae, because the thickness and distance between lamellae does not change

657 consistently with body size (see text). This means that larger fish could in fact have a relative

658 surface area that is roughly the same as a smaller fish. But because there are trade-offs

659 associated with having a large respiratory surfaces, the gill surface-area-to-volume ratio scales

660 with an exponent between 0.5 and 1, guided by the oxygen demand of the fish, rather than the

661 other way around. The curves in a) were created using Graphpad Prism 6 after calculation of

26

662 values according to the equations above, and drawings of shapes and fish were made in

663 Microsoft PowerPoint 2010.

(a) Shape matters for surface-area-to-volume scaling

Log$_{10}$ (surface area/volume)

$b - 1 = 0$

$b - 1 = -0.001$

$b - 1 = -0.333$

Log$_{10}$ (volume)

(b) Hypothetical gills scaling like spheres

Gill surface area/gill mass

$b - 1 = -0.333$

Body mass

(c) Real-world gills are folded surfaces

Gill surface area/gill mass

$b - 1 \sim 0$

Body mass

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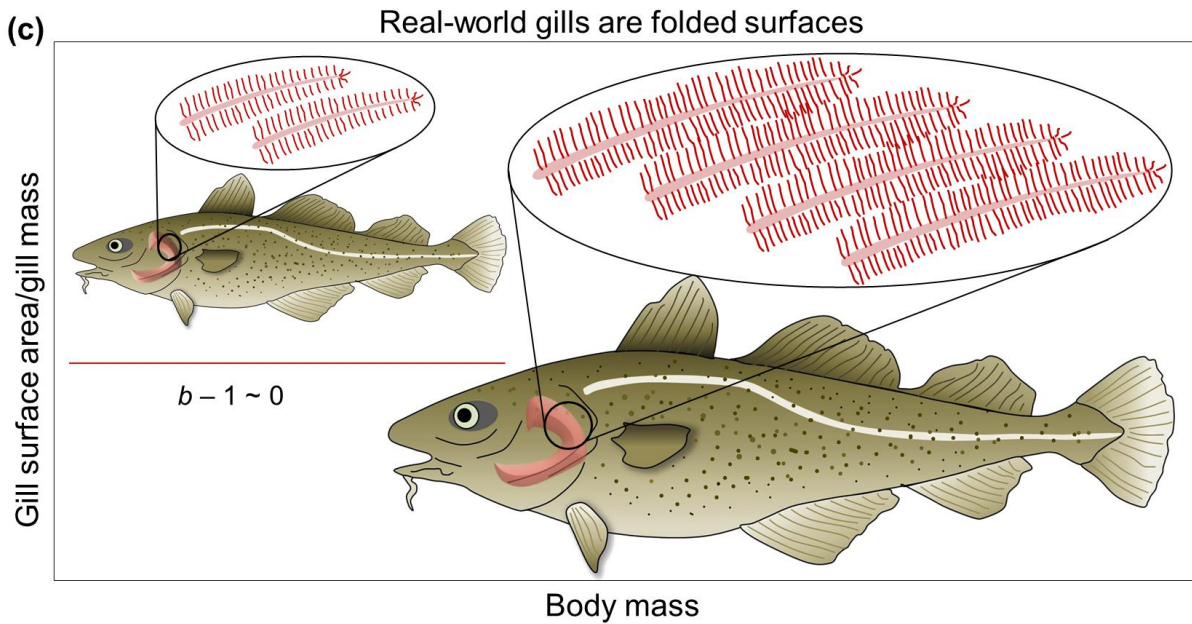
Fig. 2: Scaling of mass-specific oxygen demand with body mass and temperature. The mass-specific basal oxygen demand (or 'maintenance metabolism'), measured as minimum oxygen uptake (MO_{2min}) (a), decreases with a scaling exponent of -0.13±0.05 (95% confidence interval, CI), and fish at warmer temperatures 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 a scaling 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 a scaling factor 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 fish is close to -0.1. Note the large variability in all the respiratory variables (approximately a 10-fold 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 has 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).
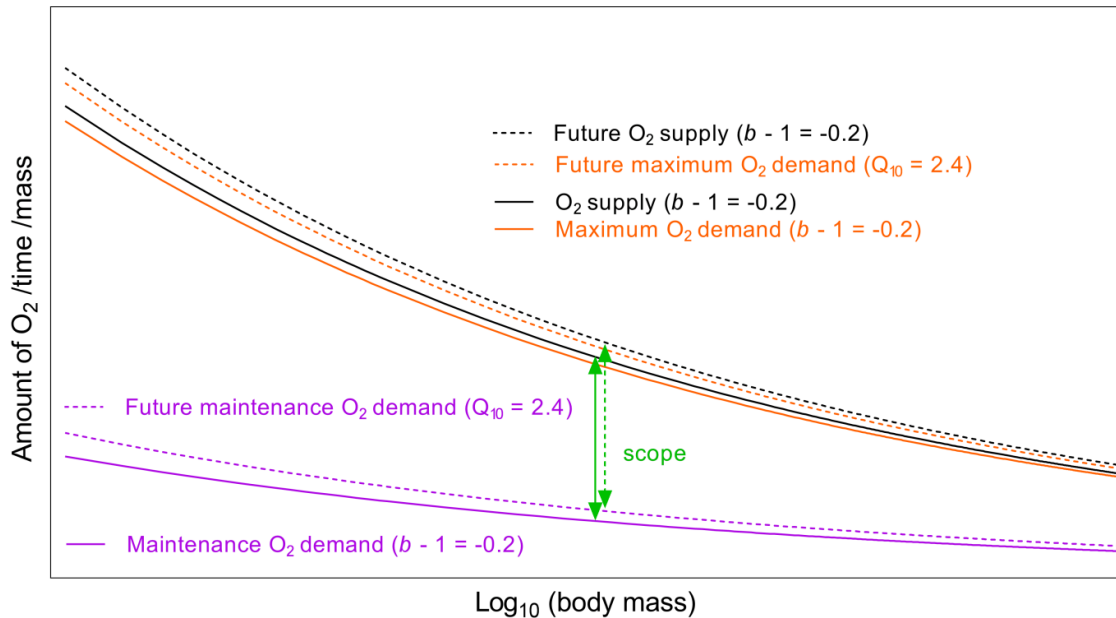
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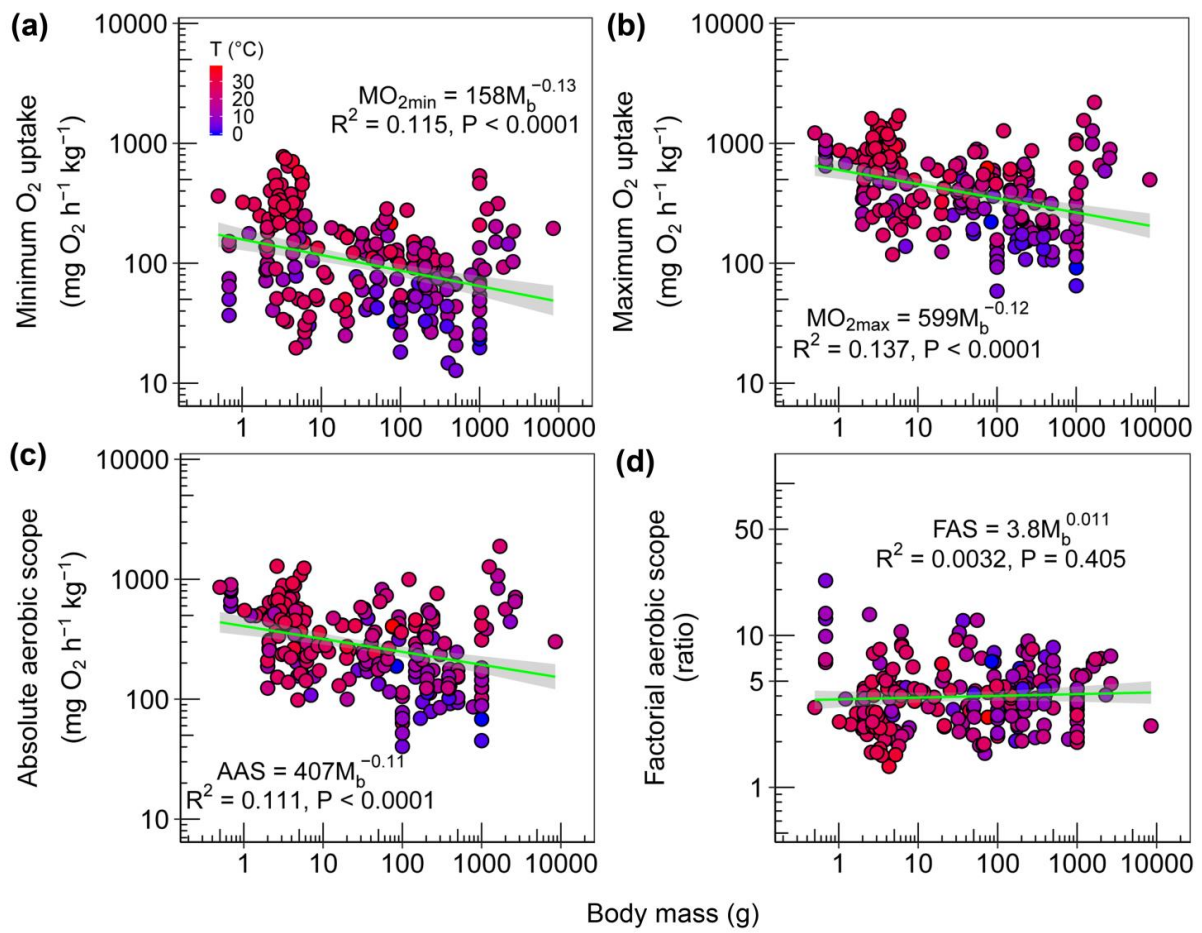
Fig. 3: Predicted scaling of mass-specific oxygen supply and demand with body mass under different assumptions. In a), which is based on the reasoning in Cheung et al. (2013a) and Pauly (2010), it is assumed that mass-specific 'maintenance' metabolism (equal to basal oxygen demand), is maintained with body mass ($MO_2 = a \cdot M_b^0$; solid purple line), while maximum capacity for oxygen supply decreases with an exponent of -0.3 ($MO_{2supply} = b \cdot M_b^{-0.3}$; 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 ($\Delta T = +2°C$), 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 a scaling factor 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 factor ($MO_{2max} = b \cdot M_b^{-0.2}$ 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, hence it is slightly higher but scales with the same factor as MO_{2max} ($MO_{2supply} = (b+c) \cdot M_b^{-0.2}$; 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

716　aerobic metabolism, depending on the ability of the species to increase oxygen supply

717　($MO_{2supply} = (b+d) \cdot M_b^{-0.2}$). Regardless, the aerobic scope will never become zero - oxygen

718　supply is not limiting and there is no oxygen-constrained growth limit. Graphs were created in

719　Graphpad Prism 6 using the equations above.

(a) O_2 demand is proportional to body mass and O_2 supply is constrained by gill surface area
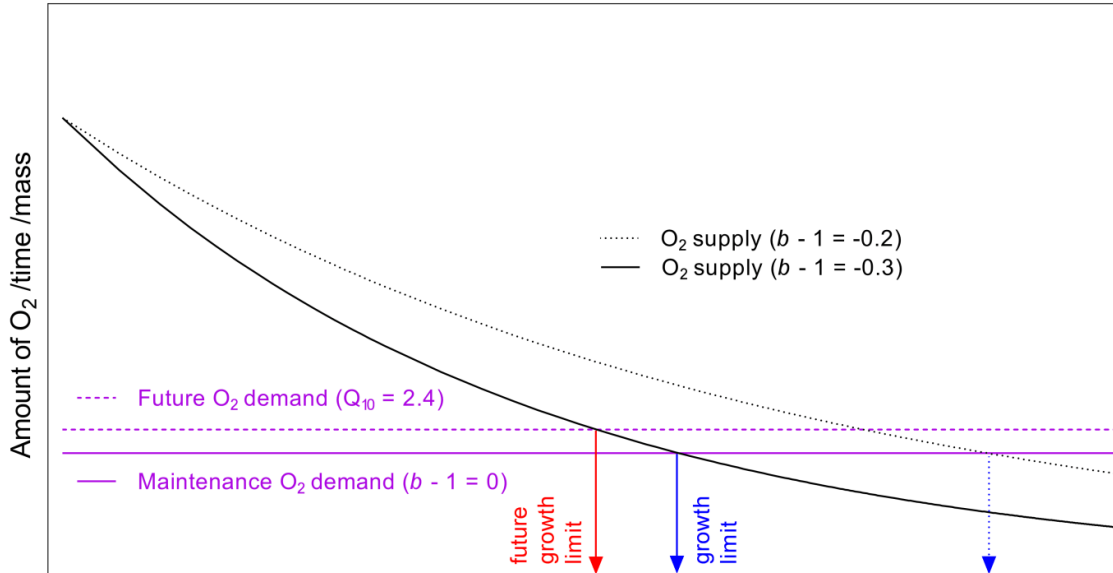
(b) O_2 demand is scaled allometrically to body mass and gill surface area is guided by demand

720