



HAL
open science

Tolerance of an acute warming challenge declines with body mass in Nile tilapia: evidence of a link to capacity for oxygen uptake

F.R. Blasco, E.W. Taylor, C.A.C. Leite, D.A. Monteiro, F.T. Rantin, David J Mckenzie

► To cite this version:

F.R. Blasco, E.W. Taylor, C.A.C. Leite, D.A. Monteiro, F.T. Rantin, et al.. Tolerance of an acute warming challenge declines with body mass in Nile tilapia: evidence of a link to capacity for oxygen uptake. 2021. hal-03097440v1

HAL Id: hal-03097440

<https://hal.science/hal-03097440v1>

Preprint submitted on 5 Jan 2021 (v1), last revised 22 Nov 2022 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Tolerance of an acute warming challenge declines with body mass in Nile**

2 **tilapia: evidence of a link to capacity for oxygen uptake**

3

4 F.R. Blasco^{1,2}, E.W. Taylor^{1,3}, C.A.C. Leite¹, D.A. Monteiro¹, F.T. Rantin¹ and D.J.

5 McKenzie^{1,4}

6

7 ¹Department of Physiological Sciences, Federal University of São Carlos, 13565-905,

8 São Carlos (SP), Brazil

9 ²Joint Graduate Program in Physiological Sciences, Federal University of São Carlos –

10 UFSCar/São Paulo State University, UNESP Campus Araraquara, 14801-903, Araraquara

11 SP, Brazil.

12 ³School of Biosciences, University of Birmingham, B15 2TT, UK.

13 ⁴MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, 34095 Montpellier, France.

14

15

16 **Abstract**

17 It is proposed that larger individuals within fish species may be more sensitive to global
18 warming, due to limitations in their capacity to provide oxygen for aerobic metabolic
19 activities. This could affect size distributions of populations in a warmer world but evi-
20 dence is lacking. In Nile tilapia *Oreochromis niloticus* (n=18, mass range 21-313g), ca-
21 pacity to provide oxygen for aerobic activities (aerobic scope) was independent of
22 mass at acclimation temperature (26°C). Tolerance of acute warming, however, de-
23 clined significantly with mass when evaluated as critical temperature for fatigue from
24 aerobic swimming (CT_{swim}). The CT_{swim} protocol challenges a fish to meet the oxygen
25 demands of constant intense aerobic exercise while their demands for basal metabo-
26 lism are accelerated by incremental warming, culminating in fatigue. CT_{swim} elicited
27 pronounced increases in oxygen uptake but maximum rates achieved prior to fatigue
28 declined very significantly with mass. Mass-related variation in CT_{swim} and maximum
29 oxygen uptake rates were positively correlated, which may indicate a causal relation-
30 ship. When faced with acute thermal stress, larger fishes within populations may be-
31 come constrained in their ability to swim at lower temperatures than smaller con-
32 specific. This could affect survival and fitness of larger fish in a world with more fre-
33 quent and extreme heatwaves, with consequences for population productivity.

34

35 Introduction

36 There is evidence that ongoing global warming is associated with a progressive decline
37 in final asymptotic body size in many fish species (Audzijonyte et al., 2020; Baudron et
38 al., 2014; Daufresne et al., 2009; Gardner et al., 2011). This phenomenon may have a
39 physiological mechanism, understanding this could improve the ability to predict
40 effects of future warming (Audzijonyte et al., 2019; Lefevre et al., 2017; Lefevre et al.,
41 2018). There has been major focus upon respiratory gas-exchange in relation to size
42 and temperature in fishes, because water is relatively poor in oxygen and meeting
43 requirements for aerobic metabolism can be challenging (Audzijonyte et al., 2019;
44 Cheung et al., 2011; Lefevre et al., 2017).

45 The Gill Oxygen Limitation (GOL) model proposes a physiological mechanism to
46 explain declining adult fish sizes. The model posits that, as fishes grow, gill respiratory
47 surface area declines in relation to body volume, due to surface to volume
48 relationships of spherical bodies. As fishes grow, therefore, their capacity to meet the
49 oxygen demands of their body volume, and hence body mass, would decrease
50 progressively. At a certain body size, the gills would only be able to meet the oxygen
51 requirements of basal metabolism. At that size, the fish would have no aerobic
52 metabolic scope (AS) to provide oxygen for aerobic activities, including anabolism, so
53 growth would no longer be possible (Cheung et al., 2011; Pauly, 1981). Fishes are
54 ectotherms so, when warmed, their metabolic rate and associated oxygen demand
55 increase (Fry, 1957; Fry, 1971). In the GOL model, increased basal metabolic demands
56 would cause the limitation in gill oxygen uptake capacity to occur at smaller maximum
57 sizes. The model has, consequently, been used to project widespread global declines in
58 fish size due to environmental warming (Cheung et al., 2011; Cheung et al., 2012; Pauly
59 and Cheung, 2017). Numerous major physiological precepts of the GOL model are not,
60 however, supported by current knowledge or data (Audzijonyte et al., 2019; Killen et
61 al., 2016; Lefevre et al., 2017).

62 Tolerance of acute warming does, nonetheless, decline with mass in some fish
63 species (Leiva et al., 2019; McKenzie et al., 2020). Although some studies have
64 considered whether size-dependent tolerance might be linked to capacity for oxygen
65 uptake (Christensen et al., 2020; Messmer et al., 2017), this remains to be tested

66 explicitly. This study represents an experimental test of the GOL model and the
67 potential effects of body mass on tolerance of acute warming in a teleost fish. The Nile
68 tilapia *Oreochromis niloticus* is a relatively eurythermal teleost (natural thermal range
69 14-33°C) that provides important fisheries in tropical and sub-tropical countries across
70 the globe (De Silva et al., 2004; Schofield et al., 2011). We performed a series of tests
71 on tilapia that ranged over one order of magnitude in body mass, to (1) how tolerance
72 of acute warming challenges varied with mass and (2) whether this could be related to
73 variation in capacity for oxygen uptake with mass.

74 In order better to interpret any effects of mass on thermal tolerance, we first
75 measured key traits of respiratory metabolism and performance at acclimation
76 temperature (26°C), by swimming respirometry. We then investigated effects of mass
77 on tolerance of warming using two thresholds. The critical thermal maximum (CT_{max})
78 protocol is the standard method to evaluate tolerance, fish are warmed incrementally
79 and loss of equilibrium (LOE) is the tolerance endpoint (Beitinger and Lutterschmidt,
80 2011). The critical temperature for aerobic swimming (CT_{swim}) protocol warms fish
81 incrementally while they perform intense steady aerobic exercise in a swimming
82 respirometer, with fatigue as tolerance endpoint (Blasco et al., 2020b). The CT_{swim}
83 evaluates capacity for oxygen uptake because it challenges a fish to meet the
84 combined oxygen demands of aerobic exercise (constant metabolic load) plus
85 progressive warming (incremental metabolic load). Warming causes a progressive and
86 profound increase in oxygen uptake up to a maximum rate, where the fish transitions
87 to unsustainable anaerobic swimming that presages imminent fatigue (Blasco et al.,
88 2020b). We therefore investigated whether variation in CT_{swim} with mass was
89 correlated with maximum oxygen uptake at fatigue, as evidence of a causal
90 relationship between the variables.

91 **Material and Methods**

92 Experimental animals came from populations of Nile tilapia of different size/age
93 classes, reared in recirculating biofiltered water at 25±1°C in multiple outdoor tanks
94 (vol. 1000L) at the Department of Physiological Sciences, UFSCar, São Carlos (SP),
95 Brazil. Individuals (n=18, mass range 20.6g to 313.0g) were selected in three sequential
96 groups of six relatively size-matched individuals, tagged for identification (PIT under

97 benzocaine anaesthesia) then recovered for at least 96h in an indoor tank (vol. 100L) in
98 the same biofiltered water system and with routine feeding. Animals were fasted 24h
99 prior to experimentation, and weighed prior to overnight recovery in an experimental
100 apparatus. Animals did not change mass between sequential tests. Experimental
101 protocols were approved by CEUA/UFSCAR, number CEUA 3927151016.

102 Metabolic and performance phenotype at acclimation temperature was
103 measured with a Steffensen-type swim-tunnel (volume 13.4L) supplied with vigorously
104 aerated, biofiltered water at $26 \pm 0.1^\circ\text{C}$, as described in (Blasco et al., 2020b). Briefly,
105 fish were placed in the tunnel and left overnight at a low swimming speed equivalent
106 to 1 bodylength·s⁻¹ (BL·s⁻¹, corrected for solid blocking effect) (Blasco et al., 2020b). The
107 following morning swimming speed was increased each 30 min in steps of either 1 BL
108 (mass range 20.6 to 86.5 g, n=12) or 0.5 BL (204 to 313 g, n=6), up to either 5 or 2.5
109 BL·s⁻¹, respectively (Blasco et al., 2020a). All fish engaged steady aerobic body-caudal
110 swimming at all these speeds (Blasco et al., 2020b). Measurements of oxygen uptake
111 ($\dot{M}O_2$, mmol·kg⁻¹·h⁻¹) were made by stopped-flow respirometry at each speed, to
112 derive standard metabolic rate (SMR) (Chabot et al., 2016) and active metabolic rate
113 AMR (Norin and Clark, 2016), and calculate AS as AMR-SMR (Blasco et al., 2020b).
114 Subsequently, the swimming speed was increased by 0.1 BL every 10s to identify gait
115 transition speed (U_{GT}), where fish first engaged an unsteady anaerobic 'burst-and
116 coast' gait, which then increased in intensity until maximum swimming speed (U_{max})
117 and fatigue (Blasco et al., 2020b; Marras et al., 2013). Speed was then immediately
118 reduced to 1 BL·s⁻¹ and, after 30 min, fish were returned to a second holding tank for at
119 least 96h under normal rearing conditions, prior to testing thermal tolerance (50%
120 tested for CT_{swim} or CT_{max} first).

121 CT_{max} was measured on groups of tilapia that had acclimated overnight in a 68L
122 tank containing vigorously aerated water at 26°C. The following morning, water was
123 warmed 1°C every 30 min until loss of equilibrium (LOE) (Blasco et al., 2020b).
124 Individual CT_{max} was then recorded as the highest temperature step fully completed
125 plus the proportion of the last step that the fish endured prior to LOE (25).
126 Immediately upon LOE, fish were recovered at 26°C for at least 30 min, in a 68L tank of
127 aerated water, then returned to a holding tank for at least 96h prior to further

128 experimentation.

129 For CT_{swim} each individual recovered overnight in the swim-tunnel at $1 \text{ BL}\cdot\text{s}^{-1}$
130 then, the next day, speed was increased over 30 min until 85% of its own U_{GT} (Blasco et
131 al., 2020b). After 30 min at that speed, temperature was increased by 1°C every 30 min
132 until fish fatigued, resting against the rear screen (Blasco et al., 2020b). The CT_{swim} was
133 calculated as for CT_{max} but using fatigue as endpoint (Blasco et al., 2020b). The fish was
134 immediately placed in a recovery tank at 26°C for 30 min, then returned to holding
135 tank for at least 96h prior to further experimentation. Measurements of $\dot{M}O_2$ were
136 made over the last 20 min at each temperature, the highest rate achieved was $\dot{M}O_{2max}$
137 (Blasco et al., 2020b). Nile tilapia acclimated to 26°C can swim at a steady elevated
138 $\dot{M}O_2$ without fatiguing for at least 9h at 85% of U_{GT} , exceeding the duration of the
139 CT_{swim} (Blasco et al., 2020b).

140 Statistics were performed with SigmaPlot 11. Relationships with body mass, of
141 metabolic, performance and tolerance variables, were assessed by least squares
142 regression of log-transformed data. Correlations between variables (CT_{max} vs CT_{swim} ;
143 CT_{swim} vs $\dot{M}O_{2max}$) were assessed by Pearson product-moment. Mean CT_{max} and CT_{swim}
144 were compared by paired T-test. $P < 0.05$ was the limit for statistical significance.

145 Results

146 At 26°C , log mass-specific SMR and AMR both showed a significant negative
147 relationship with log body mass (Table 1, Figure 1A). Log mass-specific AS did not
148 change with mass (Table 1, Figure 1A). Note that the negative slopes of these log:log
149 relationships for the metabolic variables (Table 1, Figure 1A) were the reciprocals of
150 the positive log:log slopes of mass independent scaling exponents for each variable
151 (Fig. S1, Electronic Supplementary Material). Log U_{GT} and U_{max} both fell significantly
152 with mass but the difference between them ($U_{max} - U_{GT}$), a potential indicator of
153 anaerobic swimming capacity, was independent of mass (Table 1).

154 As fish were warmed during CT_{max} they first exhibited erratic behaviour, rolling
155 sideways, followed by complete LOE. During CT_{swim} , fish swam using a steady aerobic
156 gait up to a certain temperature, beyond which they progressively engaged unsteady
157 burst and coast anaerobic swimming that led to fatigue. No fish lost equilibrium during
158 CT_{swim} ; all fish from both protocols recovered normal swimming behaviour within 10

159 min at 26°C. The two thermal thresholds were not correlated ($r=0.371$, $P=0.129$) but
160 overall mean (\pm SEM) CT_{max} , at $40.7\pm 0.23^\circ\text{C}$, was significantly higher than CT_{swim} , at
161 $38.1\pm 0.29^\circ\text{C}$.

162 Log CT_{max} had no relationship with log body mass whereas log CT_{swim} declined
163 significantly with mass (Figure 1B, Table 1). The decline in CT_{swim} with mass was
164 associated with a highly significant negative log:log relationship between mass-specific
165 $\dot{M}O_{2max}$ and mass (Figure 2A, Table 1, see Figure S1 for the reciprocal allometric scaling
166 exponent). The $\dot{M}O_{2max}$ always occurred at the penultimate or ultimate temperature of
167 the CT_{swim} except for one individual (mass 204g, see data in (Blasco et al., 2020a)).
168 There was a significant positive correlation between log $\dot{M}O_{2max}$ and log CT_{swim} (Figure
169 2B).

170 Discussion

171 The results demonstrate that the ability to perform sustained aerobic exercise, while
172 being warmed (CT_{swim}), declines significantly with body mass in a teleost fish. This
173 decline was significantly correlated with a decline in mass-specific $\dot{M}O_{2max}$ with mass,
174 suggesting a causal relationship. This decline in $\dot{M}O_{2max}$ with mass during the CT_{swim} did
175 not reflect differences in AS at acclimation temperature; AS was independent of mass.
176 This latter finding is in direct opposition to the core precept of the GOL model, which
177 predicts that AS will decline with increasing size (Cheung et al., 2011; Pauly, 1981).
178 Nonetheless, there were declines in mass-specific SMR and AMR with mass at
179 acclimation temperature, which were a direct reflection of allometric mass scaling
180 relationships. These latter relationships occur in all fish species but their underlying
181 mechanisms remain a matter of debate (Glazier, 2020; Killen et al., 2010; Killen et al.,
182 2016).

183 The finding that CT_{max} did not decline with increasing body mass is consistent
184 with a previous study on Nile tilapia (Recsetar et al., 2012). In studies that have
185 investigated whether CT_{max} depends upon size in fishes, some report no effect but
186 others report a significant decline with size (McKenzie et al., 2020). The physiological
187 mechanisms underlying LOE at CT_{max} in fishes are unknown but it is notable that, when
188 there is a dependence upon size in post-larval fishes, it is consistently negative
189 (McKenzie et al., 2020). Given the absence of any dependence of CT_{max} upon mass, it

190 was interesting to find such a strong negative dependence of CT_{swim} .

191 It is intriguing that $\dot{M}O_{2max}$ declined so profoundly with body mass during
192 CT_{swim} , if we assume that it represents the maximum capacity for oxygen uptake during
193 acute warming (Blasco et al., 2020b). The significant correlation of $\dot{M}O_{2max}$ with CT_{swim}
194 is evidence that capacity for oxygen uptake is a mechanism underlying size-
195 dependence of CT_{swim} . This is worthy of further investigation. The fact that size-related
196 variation in $\dot{M}O_{2max}$ only accounted for about 60% of the variation in CT_{swim} indicates,
197 however, that other mechanisms must also contribute to fatigue. The tilapia engaged
198 unsustainable anaerobic swimming prior to fatiguing (Blasco et al., 2020b) and capacity
199 for anaerobic exercise varies among individuals in fish species (Marras et al., 2010;
200 Marras et al., 2013). At acclimation temperature, both U_{GT} and U_{max} fell significantly
201 against mass, because mass was related to length in the tilapia (Blasco et al., 2020a)
202 and relative swimming performance declines with length in most fish species
203 (Bainbridge, 1958; Beamish, 1978). If the difference between them ($U_{max}-U_{GT}$) is
204 considered an indicator of anaerobic metabolic capacity in fishes (Marras et al., 2013),
205 this was independent of mass.

206 The decline in $\dot{M}O_{2max}$ with mass presumably reflects, in some degree, the size-
207 related constraints on mass-specific oxygen uptake capacity, AMR, at acclimation
208 temperature. Such constraints were rendered very visible by the profound challenge to
209 oxygen uptake that the CT_{swim} protocol imposed. Interestingly, the scaling exponent (1-
210 b) for the decline in log mass-specific $\dot{M}O_{2max}$ with log mass, of -0.33, is exactly the
211 exponent that the GOL model posits for the decline in capacity for oxygen uptake as a
212 function of mass in fishes, based upon surface to volume geometric constraints
213 (Cheung et al., 2011; Cheung et al., 2012; Glazier, 2020; Pauly, 1981). In the tilapia, a
214 regression coefficient of 0.92 on 18 fish indicates that estimated mass exponents are
215 unlikely to be spurious. One constraint revealed by CT_{swim} may be gill functional
216 respiratory surface area, which declines with mass in Nile tilapia with an exponent of -
217 0.30 (Kisia and Hughes, 1992). This decline in gill surface area with mass may be linked
218 to the decline in mass-specific SMR, whereby basal metabolic costs decline and the fish
219 gills are then 'tailored' to maintain a constant AS at any given mass, as observed in this
220 study. Maintaining a greater gill respiratory surface area than is needed for AS, at any

221 given acclimation temperature, could have costs in terms of, for example, regulating
222 water and ion balance (Lefevre et al., 2017; Taylor, 1998). There may be other surface
223 to volume constraints that emerge as fishes grow and this is an interesting topic for
224 further study, including on other fish species.

225 Extreme warming events are predicted to increase in frequency and severity in
226 aquatic habitats worldwide due to accelerating global climate change (Field et al.,
227 2012; Frölicher et al., 2018; Stillman, 2019). Swimming is an essential activity for most
228 fishes, including Nile tilapia, so there are clear ecological implications to the fact that, if
229 their populations experience an acute warming event, the ability of larger fishes to
230 swim aerobically would be constrained at lower temperatures than that of smaller
231 conspecifics. The law of averages would predict that larger fishes are more likely to
232 encounter temperatures sufficiently warm to limit their performance (Field et al.,
233 2012; Stillman, 2019). Therefore, stochastic extreme warming events could threaten
234 fitness and survival of fishes in a size-dependent manner, including by limiting the
235 ability of larger individuals to seek thermal refuges (Habary et al., 2017; Stillman,
236 2019). If fitness and survival of larger animals is compromised more frequently, this
237 could have important consequences for Nile tilapia fisheries, an important source of
238 dietary protein in many countries (De Silva et al., 2004).

239 Overall, the data indicate that global warming could indeed ‘favour the small’
240 for fishes (Daufresne et al., 2009). Further work is required to understand if this size-
241 dependence in temperature tolerance might be linked to ongoing declines in
242 maximum body size of fishes globally (Audzijonyte et al., 2019; Baudron et al., 2014;
243 Daufresne et al., 2009). The rate of global warming is too fast for adaptive evolutionary
244 responses by most fish species, so survival and resilience will depend upon the options
245 for migration, the prevailing plasticity in tolerance, and the existence of tolerant
246 genotypes (Bell, 2013; Gunderson and Stillman, 2015; Habary et al., 2017; Stillman,
247 2019). The current data indicate that capacity for migration is more likely to be
248 impaired in larger fish, and that smaller animals are more tolerant. The potential
249 downstream consequences, for future populations, may indeed be a decline in
250 maximum body size.

251 **Acknowledgements**

252 We are grateful to Cesar Poletini, of Piscicultura Poletini, for donating the tilapia.

253 **Funding Statement**

254 FRB was supported by a doctoral bursary from Coordenação de Aperfeiçoamento de
255 Pessoal de Nível Superior (CAPES).

256 **References**

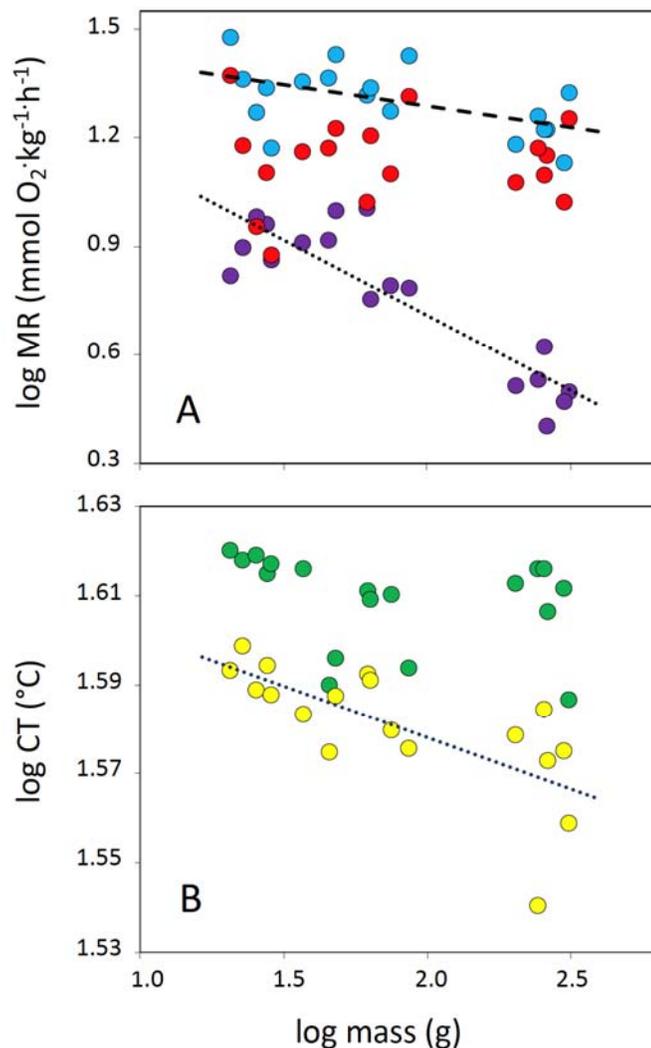
- 257 **Audzijonyte, A., Barneche, D. R., Baudron, A. R., Belmaker, J., Clark, T. D., Marshall,**
258 **C. T., Morrongiello, J. R. and van Rijn, I.** (2019). Is oxygen limitation in warming
259 waters a valid mechanism to explain decreased body sizes in aquatic ectotherms?
260 *Glob. Ecol. Biogeogr.* **28**, 64–77.
- 261 **Audzijonyte, A., Richards, S. A., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N.**
262 **S., Payne, N. and Blanchard, J. L.** (2020). Fish body sizes change with temperature
263 but not all species shrink with warming. *Nat. Ecol. Evol.* **1**, 1–6.
- 264 **Bainbridge, R.** (1958). The speed of swimming of fish as related to size and to the
265 frequency and amplitude of the tail beat. *J. Exp. Biol.* **35**, 109–133.
- 266 **Baudron, A. R., Needle, C. L., Rijnsdorp, A. D. and Tara Marshall, C.** (2014). Warming
267 temperatures and smaller body sizes: Synchronous changes in growth of North
268 Sea fishes. *Glob. Chang. Biol.* **20**, 1023–1031.
- 269 **Beamish, F. W. H.** (1978). Swimming capacity. In *Fish Physiology Volume 7* (ed. Hoar,
270 W. S.) and Randall, D. J.), pp. 101–187. New York: Academic Press.
- 271 **Beitinger, T. and Lutterschmidt, W.** (2011). Temperature | Measures of thermal
272 tolerance. In *Encyclopedia of Fish Physiology: From Genome to Environment* (ed.
273 Farrell, A. P.), pp. 1695–1702. Elsevier Ltd.
- 274 **Bell, G.** (2013). Evolutionary rescue and the limits of adaptation. *Philos. Trans. R. Soc. B*
275 *Biol. Sci.* **368**,.
- 276 **Blasco, F. R., Taylor, E. W., Leite, C. A. C., Monteiro, D. A., Rantin, F. T. and McKenzie,**
277 **D. J.** (2020a). Data from: Tolerance of an acute warming challenge declines with
278 size in Nile tilapia: evidence of a link to capacity for oxygen uptake. Dryad Digital
279 Repository.
- 280 **Blasco, F. R., Esbaugh, A. J., Killen, S., Rantin, F. T., Taylor, E. W. and McKenzie, D. J.**
281 (2020b). Using aerobic exercise to evaluate sub-lethal tolerance of acute warming
282 in fishes. *J. Exp. Biol.* **223**, jeb218602.

- 283 **Chabot, D., Steffensen, J. F. and Farrell, A. P.** (2016). The determination of standard
284 metabolic rate in fishes. *J. Fish Biol.* **88**, 81–121.
- 285 **Cheung, W. W. L., Dunne, J., Sarmiento, J. L. and Pauly, D.** (2011). Integrating
286 ecophysiology and plankton dynamics into projected maximum fisheries catch
287 potential under climate change in the Northeast Atlantic. *ICES J. Mar. Sci.* **68**,
288 1008–1018.
- 289 **Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y., Deng**
290 **Palomares, M. L., Watson, R. and Pauly, D.** (2012). Shrinking of fishes
291 exacerbates impacts of global ocean changes on marine ecosystems. *Nat. Clim.*
292 *Chang.* **2**, 1–5.
- 293 **Christensen, E. A. F., Svendsen, M. B. S. and Steffensen, J. F.** (2020). The combined
294 effect of body size and temperature on oxygen consumption rates and the
295 size-dependency of preferred temperature in European perch *Perca fluviatilis*. *J.*
296 *Fish Biol.* jfb.14435.
- 297 **Daufresne, M., Lengfellner, K. and Sommer, U.** (2009). Global warming benefits the
298 small in aquatic ecosystems. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 12788–12793.
- 299 **De Silva, S. S., Subasinghe, R. P., Bartley, D. M. and Lowther, A.** (2004). Tilapias as
300 alien aquatics in Asia and the Pacific: A Review. *FAO Fish. Tech. Pap.* 453 65.
- 301 **Field, C. B., Barros, V., Stocker, T. F., Dahe, Q., Jon Dokken, D., Ebi, K. L.,**
302 **Mastrandrea, M. D., Mach, K. J., Plattner, G. K., Allen, S. K., et al.** (2012).
303 *Managing the risks of extreme events and disasters to advance climate change*
304 *adaptation: Special Report of the Intergovernmental Panel on Climate Change.*
305 Cambridge and New York: Cambridge University Press.
- 306 **Frölicher, T. L., Fischer, E. M. and Gruber, N.** (2018). Marine heatwaves under global
307 warming. *Nature* **560**, 360–364.
- 308 **Fry, F. E. J.** (1957). The aquatic respiration of fish. In *The Physiology of Fishes Volume 1*
309 (ed. Brown, M. E.), pp. 1–63. New York: Academic Press.
- 310 **Fry, F. E. J.** (1971). The Effect of Environmental Factors on the Physiology of Fish. In
311 *Fish Physiology Volume 6* (ed. Hoar, W. S.) and Randall, D. J.), pp. 1–98. New York:
312 Academic Press.
- 313 **Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L. and Heinsohn, R.** (2011). Declining

- 314 body size: A third universal response to warming? *Trends Ecol. Evol.* **26**, 285–291.
- 315 **Glazier, D. S.** (2020). Activity alters how temperature influences intraspecific metabolic
316 scaling: testing the metabolic-level boundaries hypothesis. *J. Comp. Physiol. B*
317 *Biochem. Syst. Environ. Physiol.* **190**, 445–454.
- 318 **Gunderson, A. R. and Stillman, J. H.** (2015). Plasticity in thermal tolerance has limited
319 potential to buffer ectotherms from global warming. *Proc. R. Soc. B Biol. Sci.* **282**,
320 20150401.
- 321 **Habary, A., Johansen, J. L., Nay, T. J., Steffensen, J. F. and Rummer, J. L.** (2017).
322 Adapt, move or die – how will tropical coral reef fishes cope with ocean warming?
323 *Glob. Chang. Biol.* **23**, 566–577.
- 324 **Killen, S. S., Atkinson, D. and Glazier, D. S.** (2010). The intraspecific scaling of
325 metabolic rate with body mass in fishes depends on lifestyle and temperature.
326 *Ecol. Lett.* **13**, 184–193.
- 327 **Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S. T.**
328 **and Halsey, L. G.** (2016). Ecological Influences and Morphological Correlates of
329 Resting and Maximal Metabolic Rates across Teleost Fish Species. *Am. Nat.* **187**,
330 592–606.
- 331 **Kisia, S. M. and Hughes, G. M.** (1992). Estimation of oxygen-diffusing capacity in the
332 gills of different sizes of a tilapia, *Oreochromis niloticus*. *J. Zool.* **227**, 405–415.
- 333 **Lefevre, S., McKenzie, D. J. and Nilsson, G. E.** (2017). Models projecting the fate of fish
334 populations under climate change need to be based on valid physiological
335 mechanisms. *Glob. Chang. Biol.* **23**, 3449–3459.
- 336 **Lefevre, S., McKenzie, D. J. and Nilsson, G. E.** (2018). In modelling effects of global
337 warming, invalid assumptions lead to unrealistic projections. *Glob. Chang. Biol.*
338 **24**, 553–556.
- 339 **Leiva, F. P., Calosi, P. and Verberk, W. C. E. P.** (2019). Scaling of thermal tolerance with
340 body mass and genome size in ectotherms: A comparison between water- And
341 air-breathers. *Philos. Trans. R. Soc. B Biol. Sci.* **374**,.
- 342 **Marras, S., Claireaux, G., McKenzie, D. J. and Nelson, J. A.** (2010). Individual variation
343 and repeatability in aerobic and anaerobic swimming performance of European
344 sea bass, *Dicentrarchus labrax*. *J. Exp. Biol.* **213**, 26–32.

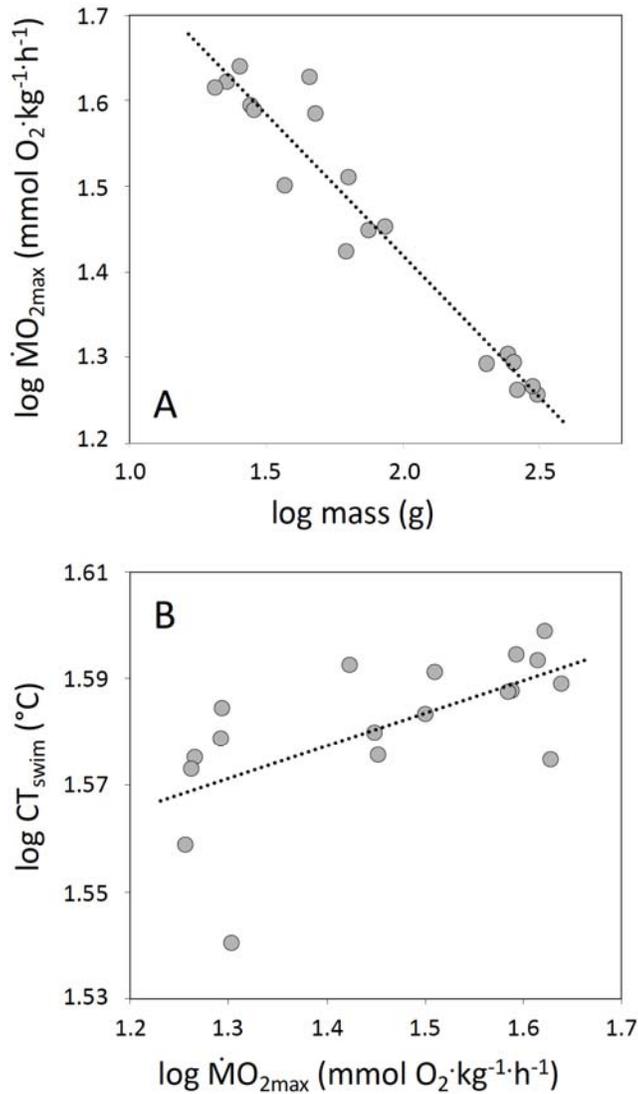
- 345 **Marras, S., Killen, S. S., Domenici, P., Claireaux, G. and McKenzie, D. J.** (2013).
346 Relationships among Traits of Aerobic and Anaerobic Swimming Performance in
347 Individual European Sea Bass *Dicentrarchus labrax*. *PLoS One* **8**, e72815.
- 348 **McKenzie, D. J., Zhang, Y., Eliason, E. J., Schulte, P. M., Blasco, F. R., Claireaux, G.,**
349 **Nati, J. J. H. and Farrell, A. P.** (2020). Intraspecific variation in tolerance of
350 warming in fishes. *J. Fish Biol.* doi.org/10.1111/jfb.14620.
- 351 **Messmer, V., Pratchett, M. S., Hoey, A. S., Tobin, A. J., Coker, D. J., Cooke, S. J. and**
352 **Clark, T. D.** (2017). Global warming may disproportionately affect larger adults in
353 a predatory coral reef fish. *Glob. Chang. Biol.* **23**, 2230–2240.
- 354 **Norin, T. and Clark, T. D.** (2016). Measurement and relevance of maximum metabolic
355 rate in fishes. *J. Fish Biol.* **88**, 122–151.
- 356 **Pauly, D.** (1981). The relationships between gill surface area and growth performance
357 in fish: a generalization of von Bertalanffy's theory of growth. *Berichte der Dtsch.*
358 *Wissenschaftlichen Kommission fur Meeresforsch.* **28**, 32.
- 359 **Pauly, D. and Cheung, W. W. L.** (2017). Sound physiological knowledge and principles
360 in modeling shrinking of fishes under climate change. *Glob. Chang. Biol.* **24**, e15–
361 e26.
- 362 **Recsetar, M. S., Zeigler, M. P., Ward, D. L., Bonar, S. A. and Caldwell, C. A.** (2012).
363 Relationship between fish size and upper thermal tolerance. *Trans. Am. Fish. Soc.*
364 **141**, 1433–1438.
- 365 **Schofield, P. J., Peterson, M. S., Lowe, M. R., Brown-Peterson, N. J. and Slack, W. T.**
366 (2011). Survival, growth and reproduction of non-indigenous Nile tilapia,
367 *Oreochromis niloticus* (Linnaeus 1758). I. Physiological capabilities in various
368 temperatures and salinities. *Mar. Freshw. Res.* **62**, 439.
- 369 **Stillman, J. H.** (2019). Heat waves, the new normal: Summertime temperature
370 extremes will impact animals, ecosystems, and human communities. *Physiology*
371 **34**, 86–100.
- 372 **Taylor, E. W.** (1998). Gills of water-breathers: Structures with multiple functions. In
373 *Principles of Animal Design: The Optimisation and Symmorphosis Debate* (ed.
374 Weibel, E. R.), Taylor, C. R.), and Bolis, C. L.), pp. 186–194. Cambridge: Cambridge
375 University Press.

376 **Figure 1.** Least squares regression of the log:log relationship between (A) body mass
377 and mass-specific metabolic rate (MR) variables, standard metabolic rate (purple
378 symbols, dotted line), active metabolic rate (blue symbols, dashed line) and aerobic
379 metabolic scope (red symbols); and (B) body mass and two critical temperatures (CT)
380 for tolerance, critical thermal maximum (green symbols) and critical temperature for
381 fatigue from swimming (yellow symbols, dotted line). Data are for n = 18 Nile tilapia,
382 mass range 21 to 313g, acclimated to 26°C. Regression lines are for variables where
383 relationship is significant, lines denote best fit, see Table 1.



384

385 **Figure 2.** (A) Least squares regression of the log:log relationship between body mass
386 and mass-specific maximum rate of oxygen uptake achieved during CT_{swim} ($\dot{M}O_{2max}$, see
387 Table 1 for regression information) and (B) Pearson correlation between critical
388 temperature for fatigue from swimming (CT_{swim}) and $\dot{M}O_{2max}$, dotted line is described
389 by $\log CT_{swim} = (\log \dot{M}O_{2max}) \times 0.061 + 1.491$ ($r = 0.637$, $P = 0.004$). Data are for $n = 18$
390 Nile tilapia, mass range 21 to 313g, acclimated to 26 °C.



391