

1 The aerobic scope protection hypothesis: a mechanism explaining
2 reduced growth of ectotherms in warming environments?

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17 **Abstract**

18 Temperature has a dramatic effect on the physiology of ectothermic animals, impacting most
19 of their biology. When temperatures increase above optimal for an animal, their growth rate
20 tends to decrease. The mechanism behind this growth rate reduction is unknown. Here, we
21 suggest the aerobic scope protection hypothesis as a mechanistic explanation for the reduction
22 in growth. After a meal, metabolic rate, and hence oxygen consumption rate, transiently
23 increases in a process called specific dynamic action (SDA). At warmer temperatures, the SDA
24 response becomes temporally compressed, leading to a higher peak oxygen consumption rate.
25 This peak in oxygen consumption rate takes up much of the animal's aerobic scope (the
26 difference between maximum and resting rates of oxygen consumption), leaving little residual
27 aerobic scope for other functions. We propose that animals will actively protect their
28 postprandial residual aerobic scope by reducing meal sizes in order to regulate the peak SDA
29 response. This hypothesis is consistent with the published literature and we suggest further
30 predictions to test it.
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43 Temperature and oxygen delivery capacity

44 The body temperature of ectothermic animals generally follows the ambient temperature. As
45 biochemical reaction rates are temperature sensitive, biological rates in these animals are partly
46 under the control of the environment. Animals have evolved to function across a finite range of
47 suitable temperatures, above and below which physiological functions can suffer. Climate
48 warming is causing increased temperatures worldwide and is threatening the function of
49 ectothermic animals (Pinsky et al., 2019). One common observation is that when temperatures
50 increase above suitable, growth rate and other performance metrics gradually or abruptly
51 decline (Huey and Stevenson, 1979); Gräns et al., 2014). The precise mechanisms behind these
52 decreases in performance are, however, subject to active debate (Clark et al., 2013; Jutfelt et
53 al., 2014; Jutfelt et al., 2018; Pörtner et al., 2017; Schulte, 2015).

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55 Thermal constraint on oxygen delivery to the body has been proposed as a function that can
56 limit performance, particularly in water-breathing animals (Brett, 1972; Fry, 1947; Pörtner and
57 Knust, 2007; Pörtner and Farrell, 2008), a hypothesis called the ‘Fry paradigm’ or ‘oxygen- and
58 capacity-limited thermal tolerance’ (OCLTT). As temperatures increase above suitable, the
59 standard (maintenance) metabolic rate (SMR) is suggested to increase faster than the aerobic
60 maximum metabolic rate (MMR) leading to a reduction in the difference between them (i.e. the
61 aerobic scope). Animals without sufficient aerobic scope are faced with trade-offs in their
62 allocation of energy to activity, digestion, growth, and reproduction (Weiner, 1992), and may
63 even be forced into unsustainable anaerobic metabolism when aerobic scope is most
64 compromised, which is suggested to cause unfavourable downstream consequences in
65 functions such as growth (Pörtner and Farrell, 2008; Pörtner and Knust, 2007).

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67 As the OCLTT hypothesis has been suggested to explain the mechanisms of climate change
68 impacts on water-breathers (Pörtner and Farrell, 2008), it has received great interdisciplinary
69 interest. Several tests of predictions derived from the hypothesis have, however, failed to find
70 support for it (Jutfelt et al., 2018; Verberk et al., 2016). One prediction, that tissue hypoxia
71 restricts growth (Pörtner and Farrell, 2008; Pörtner and Knust, 2007) and therefore that markers
72 of anaerobic metabolism should be detectable at supra-optimal temperatures, has only limited
73 support, as markers for hypoxia generally only appear at or close to lethal temperatures (Pörtner
74 and Knust, 2007; Verberk et al., 2016). Tissue hypoxia is therefore unlikely to explain growth
75 reductions that appear at temperatures far below lethal (Clark et al., 2013; Jutfelt et al., 2018).
76 This mismatch between hypothesis and empirical data remains a major impediment in thermal
77 biology, hampering our ability to model and predict the impacts of climate change on
78 ectothermic animals.

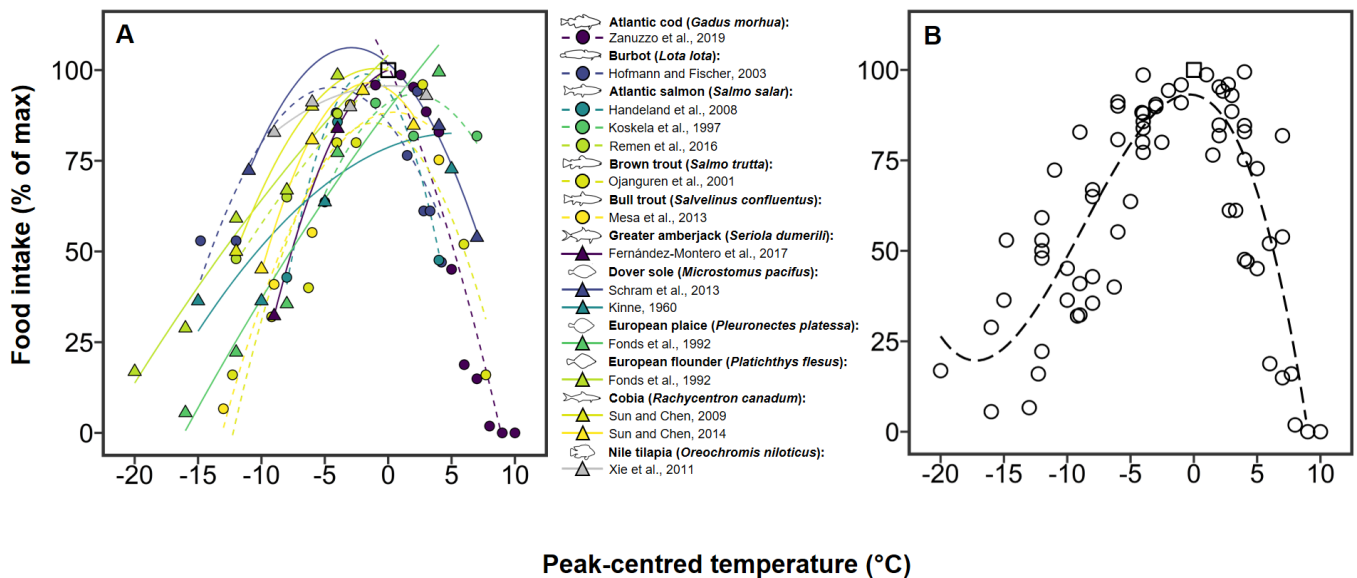
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80 Here, we propose a possible resolution to the mismatch between the OCLTT hypothesis and
81 the lack of empirical support for some of its predictions about growth. In fishes, reductions in
82 growth at supra-optimal temperatures have long been ascribed to increases in SMR combined
83 with reduced appetite (Jobling, 1997). We hypothesise that this reduction in appetite occurs
84 voluntarily in order to conserve a portion of the aerobic scope that is available to the animal on
85 top of the cost of digestion and assimilation. This ‘aerobic scope protection hypothesis’ has

86 been briefly alluded to in the literature (e.g. Jobling, (1997); Norin and Clark, (2017)), but it
87 has not been fully articulated or explored.

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90 Aerobic scope protection by reduction of food intake

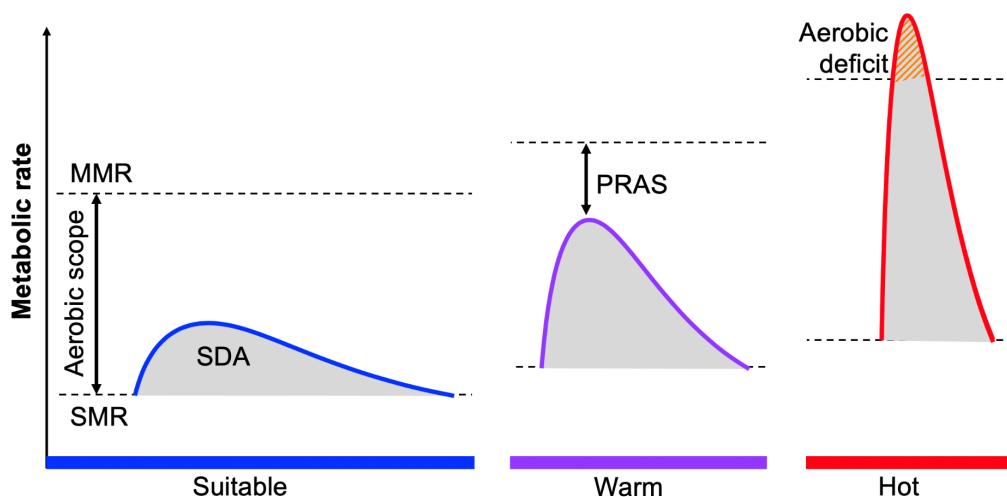
91 At supra-optimal acclimation temperatures, most fishes exhibit a decrease in food consumption
92 (Figure 1), likely due to a loss of appetite. The reduced food intake, combined with elevated
93 SMR at high temperatures, results in reduced growth (Jobling, 1997). To investigate the nature
94 of this temperature–appetite relationship, we compiled data from studies investigating the
95 thermal effect on voluntary food intake in fishes. The emerging pattern revealed large
96 interspecific variation in thermal sensitivity (Figure 1), likely related to different acclimation
97 capacities of the different species. However, there was a clear pattern of slowly increasing food
98 intake up to an optimum temperature, reflecting the species’ maximum food intake, followed
99 by sharply reduced food intake at temperatures above optimal. While the increasing food intake
100 can be attributed to a temperature-induced increase in maintenance metabolism (i.e. SMR), the
101 reason for the loss of appetite at supra-optimal acclimation temperatures is likely a deficit or
102 declining functioning of one or several physiological systems, but the precise system or
103 mechanism has remained elusive.
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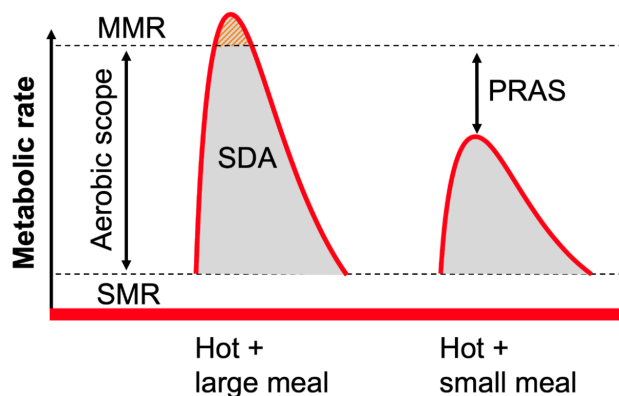
Figure 1. Food intake as a function of temperature. Food intake temperature profiles normalised as percent of maximum intake, compiled from 14 studies on 11 species of fish from tropical to cold temperate thermal environments (A). To be able to compare shapes of the food intake temperature profiles between species, all profiles were centred around the temperature of peak food intake (highest data point for each species) for each species (A and B). Overlapping points at maximum food intake are replaced with a black square. Data for each species were fitted with a second-degree polynomial regression in (A). In (B) all data are combined, and a third-degree polynomial regression shows the shape of the influence of temperature on food intake. Data are from (Fernández-Montero et al., 2017; Fonds et al., 1992; Handeland et al., 2008; Hofmann and Fischer, 2003; Kinne, 1960; Koskela et al., 1997; Mesa et al., 2013; Ojanguren et al., 2001; Remen et al., 2016; Schram et al., 2013; Sun and Chen, 2009; Sun and Chen, 2014; Xie et al., 2010; Zanuzzo et al., 2019).

117 When animals eat a meal, their metabolic rate initially increases sharply as part of the digestive
 118 response and remains elevated for an extended period (Figure 2), before eventually returning
 119 to baseline levels (i.e. SMR in a resting ectotherm). This increase in post-prandial oxygen
 120 consumption rate is termed ‘specific dynamic action’ (SDA) and is considered a product of
 121 increased activity in the gut as well as increased biochemical nutrient processing and tissue
 122 assimilation of nutrients (Secor, 2009). The SDA response is temperature sensitive and can last
 123 a week or two in cold-living Antarctic fishes (Johnston and Battram, 1993); (Boyce and Clarke,
 124 1997), but is much shorter in duration at warmer temperatures in animals eating similar-sized
 125 meals (Secor, 2009; Secor, 2011). As the total amount of energy expended to digest and
 126 assimilate a meal of a certain size (the area under the SDA curve) often is independent of
 127 temperature (Secor, 2009), the shorter duration of the SDA response at warm temperatures
 128 results in a greater post-prandial peak in metabolic rate (Figure 2) (Secor, 2009; Secor, 2011).
 129 This peak can occupy the majority of an animal’s aerobic scope. For example, in the short-horn
 130 sculpin (*Myoxocephalus scorpius*), a week of warming from 10 to 16°C did not change the
 131 aerobic scope but elevated the post-prandial peak in metabolic rate up to MMR (Sandblom et
 132 al., 2014), leaving no aerobic scope for activities other than SDA. As these fish were gavage
 133 fed a meal corresponding to 5% of their body mass, they did not have the option to regulate
 134 their meal size.
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 138 **Figure 2. Conceptual illustration of the effect of temperature on metabolic rate and SDA in ectotherms.**
 139 Standard metabolic rate (SMR) and maximum metabolic rate (MMR) increase with temperature. The
 140 metabolic increase after a same-sized meal (SDA) is shown as a time profile at three different temperatures
 141 (‘suitable’ in blue, ‘warm’ in purple, and ‘hot’ in red). Increasing temperature temporally compresses the
 142 SDA response while giving rise to a higher post-prandial peak metabolic rate. At the warm temperature, the
 143 post-prandial residual aerobic scope (PRAS) is reduced compared to the suitable temperature, potentially
 144 limiting other oxygen-demanding processes. At the hot temperature, PRAS is gone and the post-prandial
 145 peak metabolic rate overshoots the maximum oxygen delivery capacity, forcing the animal to exploit its
 146 anaerobic metabolism (hatched area above MMR) and creating a costly oxygen debt. We propose that water-
 147 breathers actively avoid this latter situation by reducing meal sizes to maintain a sufficient PRAS for activities
 148 other than digestion.
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150 Meal size is a primary determinant of the magnitude of the SDA response (Norin and Clark,
151 2017; Secor, 2009), which provides a potential mechanism for fishes and other animals to
152 voluntarily regulate their SDA magnitude by eating relatively large or small meals. Previous
153 research has shown that fish eating larger meals grow more efficiently but also incur a relatively
154 high post-prandial peak in metabolic rate during digestion of the larger meals (Norin and Clark,
155 2017), which reduces the amount of aerobic scope available for other oxygen-demanding
156 activities such as swimming and collective behaviour (McLean et al., 2018). These findings
157 indicate that, ideally, animals should regulate their food intake based on their need to maintain
158 aerobic scope under challenging conditions. However, the interacting effects of temperature
159 and aerobic scope protection on meal size selectivity have not been explored. We propose that
160 animals use this mechanism of reduced food intake at elevated temperatures to conserve their
161 post-prandial residual aerobic scope (PRAS) within a species- and context-specific limit
162 (Figure 3).
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Figure 3. Aerobic scope protection by meal size reduction. At hot temperatures, the SDA after a large meal can comprise the full aerobic scope, and potentially force anaerobic metabolism (hatched area above MMR). By voluntarily reducing meal size, fishes and other ectothermic animals may reduce their post-prandial peak metabolic rate and thus maintain a sufficient post-prandial residual aerobic scope (PRAS) for other aerobic processes.

173 Testing the aerobic scope protection hypothesis

174 The prediction derived from the OCLTT hypothesis, that tissue hypoxia and hypoxic markers
175 should occur at supra-optimal temperatures, has not been clearly supported and is even
176 contradicted by experimental data (Gräns et al., 2014; Pörtner and Knust, 2007). One resolution
177 to the lack of support for this OCLTT prediction may be that fish generally do not allow their
178 aerobic scope to be reduced to the point of insufficient oxygenation of their tissues, and the
179 aerobic scope protection hypothesis presented here could be the mechanism behind this.
180 Avoidance of tissue hypoxia, however, is more difficult to detect experimentally than actual
181 realised tissue hypoxia. Below, we summarise observations consistent with the aerobic scope
182 protection hypothesis, and we suggest paths for experimentally testing it.

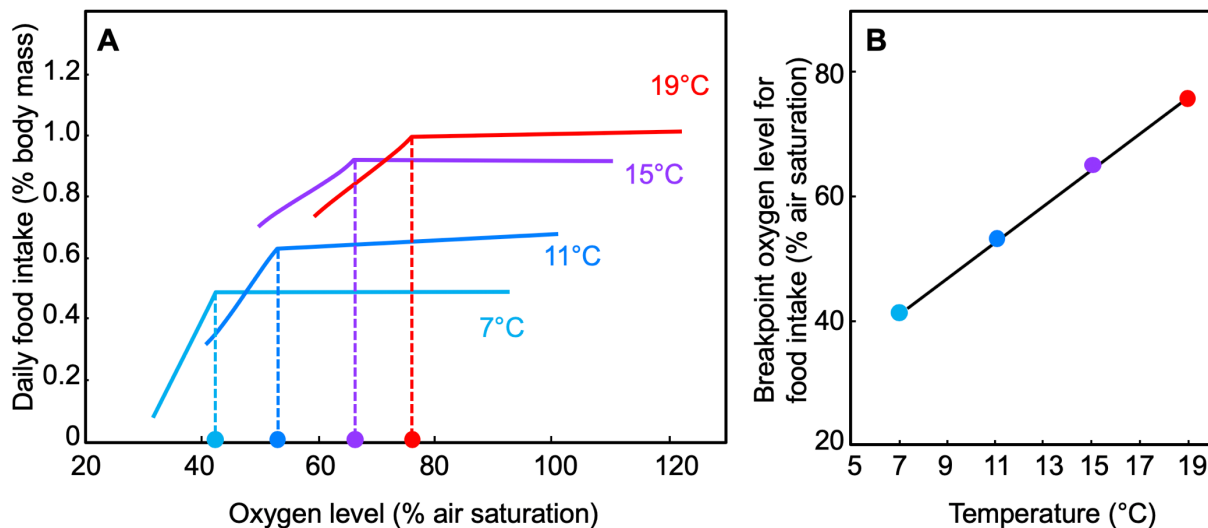
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184 A review of the relationship between growth rate of fishes and their aerobic capacities found
185 no consistent correlation (Blier et al., 1997). This seemingly contradicts our aerobic scope

186 protection hypothesis and indicates that aerobic capacity is not a major constraint to fish growth
187 [but see (Auer et al., 2015)]. The investigation into the relationship between growth rate and
188 aerobic capacity, however, did not include the full temperature range (sub- to supra-optimal)
189 for the species included (Blier et al., 1997). We predict that temperature is a major interacting
190 factor in this correlation due to its effect on the SDA response (cf. Figure 2), and that the benefit
191 of having a higher oxygen transport capacity only becomes apparent at supra-optimal
192 temperatures. This prediction would be interesting to test.

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194 If reductions in growth occur through a voluntary reduction in food intake that is implemented
195 to reserve a portion of the aerobic scope available for activities other than SDA, as proposed
196 here, it is predicted that the appetite of an animal would be more sensitive to water hypoxia in
197 warmer than in colder temperatures, since hypoxia decreases MMR while warmer temperatures
198 increase the post-prandial peak metabolic rate. Indeed, when channel catfish (*Ictalurus*
199 *punctatus*) were exposed to water hypoxia, their food intake was only marginally affected at
200 colder temperatures. However, at the warmest temperatures, even mild hypoxia (80-90% air
201 saturation) caused a large decrease in voluntary food intake, suggesting that the fish were highly
202 attentive to the water oxygen levels (Buentello et al., 2000). Likewise, appetite in hypoxia was
203 highly sensitive to temperature in Atlantic salmon (*Salmo salar*); the fish maintained stable
204 maximum food intake from normoxia down to hypoxia (40% air saturation) at 7°C, but food
205 intake started to decline at oxygen levels of 75% air saturation at 19°C (Figure 4). This
206 demonstrates increasing oxygen limitation on appetite with increasing temperature, which is
207 consistent with our proposed aerobic scope protection mechanism.

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211 **Figure 4. Water oxygen levels required to sustain maximum food intake.** While food intake gradually
212 increased with increasing temperature in Atlantic salmon (*Salmo salar*) within the species' suitable
213 temperature range (A), varying oxygen levels did not markedly affect feeding until a breakpoint oxygen level,
214 which occurred closer to normoxia at higher temperatures (i.e. food intake was more insensitive to water
215 oxygen levels at lower temperatures) (A, B). Redrawn from Remen et al., (2016).

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217 If the reduction in PRAS becomes restrictive to food intake only at higher temperatures, then
218 factors that increase aerobic scope can be predicted to also increase food intake. Hyperoxia has

219 been shown to increase the aerobic scope in fish; oxygen levels of 200% air saturation
220 effectively doubled the aerobic scope (Brijs et al., 2015) and increased venous oxygen partial
221 pressure and cardiac stroke volume in European perch (*Perca fluviatilis*) (Ekström et al., 2016).
222 As a higher aerobic scope would allow for a higher post-prandial peak metabolic rate during
223 the SDA response without markedly restricting PRAS or tissue oxygenation, we predict that
224 water hyperoxia would increase appetite. Additionally, this effect of hyperoxia would be
225 temperature sensitive, with no effect at suitable temperatures and increasing effect with
226 increasing supra-optimal temperatures. Few studies have tested this prediction: Rainbow trout
227 fed various diets at hypoxia (50% air saturation), normoxia (100% air saturation), and hyperoxia
228 (200% air saturation) varied in their weight gain in accordance with the prediction for
229 increasing appetite with increasing oxygen availability (Dabrowski et al., 2004), although
230 another study on rainbow trout did not find the same benefit of hyperoxia (Caldwell and
231 Hinshaw, 1994). Notably, the growth experiment by Dabrowski et al. (2004) was conducted at
232 20-22°C, which is above the temperature range for optimal growth in rainbow trout (Hokanson
233 et al., 1977). This supports our prediction of an increasing effect of hyperoxia at supra-optimal
234 temperatures, but temperature has not yet been systematically included as a factor.

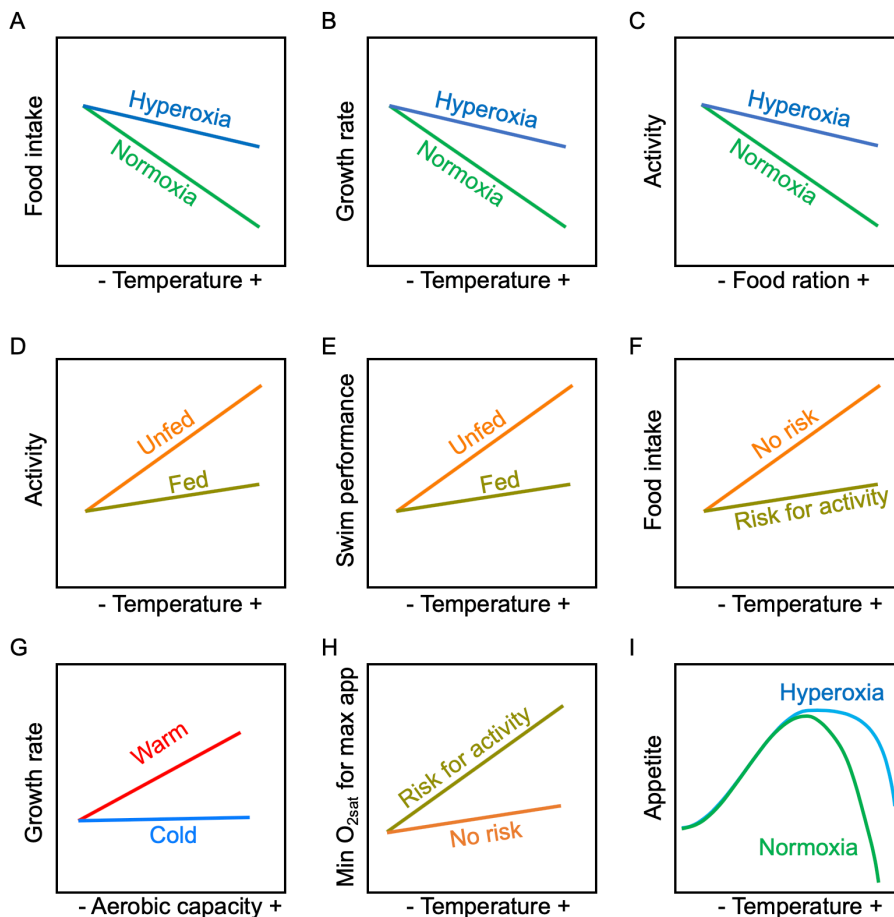
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236 With supra-optimal temperatures and temporal compression of the SDA response, animals may
237 face a trade-off between using their aerobic scope for SDA or for mobility. This trade-off can
238 be quantified and would be predicted to be more obvious at warmer temperatures. The trade-
239 off could be detected as both a decrease in spontaneous activity and/or a decrease in meal size.

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241 Beyond its dependence on meal size, the SDA response is also highly variable between species
242 (Secor, 2009). An animal's lifestyle influences the amount of aerobic scope taken up by its
243 SDA. For example, among fishes, active swimmers tend to show a less pronounced SDA
244 response than sit-and-wait ambush predators (Clark et al., 2013; Fu et al., 2009a; Fu et al.,
245 2009b; Secor, 2009). Therefore, it could be predicted that ambush predators, with their larger
246 SDA, would be more likely to reduce their food intake to conserve PRAS at elevated
247 temperatures, compared to more active fishes. However, ambush predators also require less
248 PRAS than active swimmers (Clark et al. 2013), so, in the absence of experimental work, it is
249 difficult to predict which lifestyle, if any, would show the more pronounced decrease in
250 appetite.

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252 Anecdotal, yet interesting, evidence for immediate PRAS limitation comes from an observation
253 by Claireaux et al. (Claireaux et al., 2000) who placed recently fed Atlantic cod (*Gadus*
254 *morhua*) in respirometers and gradually reduced water oxygen saturation. At the point where
255 the cod's PRAS approached zero, they terminated digestion, as colourfully described by the
256 authors: "*At this point, scope for activity being almost nil, all the fish in the measuring chamber*
257 *simultaneously regurgitated their food, presumably to reduce their immediate oxygen*
258 *requirements. Then, as soon as water SO_2 [water oxygen saturation] was restored to above 45%,*
259 *approximately 5 min later, the fish recovered enough metabolic potential to resume digestion*
260 *and re-swallowed all the food.*" This suggests that fish monitor not only external oxygen levels,
261 but also somehow are attentive to the magnitude of their aerobic scope and SDA, and that they
262 act to avoid an aerobic deficit (cf. Figure 3) by controlling their SDA.

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The predictions derived from the aerobic scope protection hypothesis presented here are similar to what the OCLTT hypothesis predicts, in that oxygen transport is limiting thermal performance. It could even be argued that the mechanism suggested here is inherent to the larger OCLTT framework. The mechanism of voluntary meal size reductions, however, has not previously been explicitly proposed, and there are several differences between OCLTT and the aerobic scope protection hypothesis that can be experimentally tested and therefore used to discriminate between the two hypotheses. The OCLTT hypothesis has a focus on cardiorespiratory function, oxygen delivery to the tissues, and (in extreme conditions) tissue hypoxia as the limiting constraints to performance at higher temperatures. The difference proposed here is that cardiorespiratory oxygen limitations only develop at relatively high temperatures if the animal allows its SDA to occupy the majority of its aerobic scope and, to avoid this, the animal should reduce its appetite at temperatures where the postprandial residual aerobic scope may become limited. This loss of appetite is the main mechanism that can be used to differentiate our aerobic scope protection hypothesis from the OCLTT hypothesis. In Figure 5, we present a range of predictions that would be consistent with voluntary food intake restriction and aerobic scope protection. These can be readily tested, and some of them already have some support in the literature as outlined above. The figures show the main direction of change in a suite of attributes related to feeding or physical activity, but the exact shape of the illustrated relationships will be more complex and context-dependent. A more specific prediction is made in Figure 5I, where the shape of the temperature–appetite function from Figure 1 is used (green line) and the predicted effect of hyperoxic water is added (blue line).



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289 **Figure 5. Predictions derived from the aerobic scope protection hypothesis.** (A) Food intake decreases
 290 with increasing supra-optimal temperature in normoxic water, but less so in hyperoxic water as it can increase
 291 aerobic scope (Brijs et al., 2015) and thus PRAS. (B) Growth rate is suggested to show a similar pattern to
 292 food intake at supra-optimal temperatures, as increased food intake in hyperoxia is assumed to result in higher
 293 growth rate. (C) Voluntary activity is predicted to decline with increasing food rations at high temperatures,
 294 but hyperoxia may ameliorate this decline by increasing aerobic scope and thus PRAS. (D) Voluntary activity
 295 often increases with temperature (up to a point), but activity competes with digestion for the available aerobic
 296 scope, leading to a lower increase in activity with temperature in fed compared to unfed animals. (E) Animals
 297 that are force-fed a large meal should show reduced locomotor performance compared to unfed or voluntarily
 298 feeding animals at supra-optimal temperature but not at sub-optimal temperature. (F) Animals may estimate
 299 their need for activity in the near future (e.g. escaping predators, migrating, navigating currents), and
 300 increased perceived risk for activity may reduce food intake to maintain a larger PRAS at supra-optimal
 301 temperature. (G) Aerobic capacity generally is not considered to correlate with growth rate (but see (Auer et
 302 al., 2015)), although this should be temperature-dependent and a positive correlation is predicted at warmer
 303 temperatures. (H) The minimum oxygen level required for maintaining maximum food intake or appetite
 304 ($\text{Min O}_{2\text{sat}}$ for max app) increases with temperature (cf. Figure 4). If the animal predicts an increased risk of
 305 physical activity, the increase with temperature should be higher than in the absence of risk of activity. (I)
 306 The peak-centred shape of the temperature–food intake relationship (cf. Figure 1) should differ between
 307 normoxia (green line) and hyperoxia (blue line).

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309 Finally, we caution that the aerobic scope protection hypothesis is likely not a silver bullet
 310 mechanism to understand performance limitation at high temperature, but only one potential
 311 explanation among many for the observed patterns of thermal performance in ectothermic

312 animals. For example, it can be assumed that the gastrointestinal tract is adapted to suit the food
313 type and amount associated with the species' niche. With warming, the increased energy
314 expenditure and therefore food throughput requirement may cause the gastrointestinal capacity
315 to limit nutrient uptake and thus growth (McLeod and Clark, 2016). The immune system is
316 tailored to the risk of infection and cell damage (e.g. through oxidative stress or thermal increase
317 in turnover), but these functions may become restrictive at higher temperatures (Dittmar et al.,
318 2014; Miest et al., 2019; Wegner et al., 2008). Nerve function is optimised for a certain thermal
319 range through ion channel function and membrane fluidity (Cossins et al., 1977). Gonads can
320 be more thermally sensitive than other organs (Pankhurst and King, 2010). Mitochondrial
321 proton leak increases with temperature (Leo et al., 2017), meaning more food and oxygen is
322 consumed per unit of ATP produced. Such limitations can likely occur for every physiological
323 organ system. Therefore, oxygen delivery is just one permissive factor that needs to be in place
324 for the organism to function at higher temperatures. There may be many such permissive
325 factors, both physiological and ecological, any of which can become limiting for fitness in
326 certain contexts (e.g. limitations in food, water, ions, refuges). Such permissive factors may
327 become saturated at some high level (e.g. more food will not increase growth over a certain
328 maximum food-handling level). Likewise, oxygen delivery is one permissive factor to tissue
329 performance among many that may or may not become limiting under thermal challenges, and
330 whether it does is context specific. The task for ecophysiologicalists now is to figure out ways of
331 testing which factors are limiting which animals and in which contexts; a task that will likely
332 keep us busy for some time.

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350 Author contribution

351 F.J. conceived of the initial ideas and wrote the first manuscript draft. F.J., B.S.R., L.E.R., and
352 E.R.Å. collected data and produced figures. All authors discussed the ideas and helped write
353 the manuscript.

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