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'Aerobic scope protection' reduces ectotherm growth under warming

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Abstract

1. Temperature has a dramatic effect on the physiology of ectothermic animals, impacting most of their biology. When temperatures increase above optimal for an animal, their growth gradually decreases. The main mechanism behind this growth rate reduction is unknown.

2. Here, we suggest the 'aerobic scope protection' hypothesis as a mechanistic explanation for the reduction in growth.

3. After a meal, metabolic rate, and hence oxygen consumption rate, transiently increase in a process called specific dynamic action (SDA). At warmer temperatures, the SDA response usually becomes temporally compressed, leading to a higher peak oxygen consumption rate. This peak in oxygen consumption rate risks taking up much of the animal's aerobic scope (the difference between resting and maximum rates of oxygen consumption), which would leave little residual aerobic scope for other aerobic functions.

4. We propose that water-breathing ectothermic animals will protect their postprandial residual aerobic scope by reducing meal sizes in order to regulate the peak SDA response during times of warming, leading to reductions in growth.

5. This hypothesis is consistent with the published literature on fishes, and we provide predictions that can be tested.

KEYWORDS
climate change, ecophysiology, fish physiology, thermal biology, thermal performance

1 | INTRODUCTION

In this article, we compile data on the effect of temperature on appetite in aquatic ectothermic animals, with a focus on fish, and find

that appetite sharply declines at temperatures above optimal. We propose a hypothesis for the mechanism causing this reduction in appetite: that animals reduce their food intake to protect oxygen transport capacity in warm conditions when constraints on oxygen transport limit the capacity for digestion and assimilation. We call

this the 'aerobic scope protection' hypothesis, and it appears consistent with the published literature. Hypotheses are only as useful as their ability to predict future observations; we therefore present 15 predictions derived from the hypothesis, and we encourage the field to critically test them.

2 | TEMPERATURE AND OXYGEN DELIVERY CAPACITY

The body temperature of ectothermic animals generally follows the ambient temperature. As biochemical reaction rates are temperature-sensitive, biological rates in these animals are partly under the control of the environment and increase with temperature. Animals have evolved to function across a finite range of suitable temperatures, above and below which physiological functions can suffer. Climate warming is causing increased temperatures worldwide and is threatening the physiological performance of ectothermic animals, particularly in water-breathing ectotherms (Pinsky et al., 2019). One common observation is that when temperatures increase slightly above suitable, growth rate and other performance metrics gradually or abruptly decline (Baldwin, 1957; Gräns et al., 2014; Kinne, 1960).

Oxygen delivery to the body has been proposed as a physiological process that can limit performance of various bodily functions when animals are exposed to high temperatures, particularly in water-breathing ectotherms where lower oxygen concentration and higher ventilatory effort in water compared to air cause a reduction in oxygen availability (Dejours, 1989; Verberk et al., 2016). This oxygen limitation hypothesis, linked with temperature-dependent energy metabolism (Ege & Krogh, 1914), has been implicated in the 'Fry paradigm' (Fry, 1947; Fry & Hart, 1948) and the 'oxygen- and capacity-limited thermal tolerance' (OCLTT) hypothesis (Pörtner, 2010). As temperatures increase above suitable, the aerobic standard (maintenance) metabolic rate ($\dot{M}O_{2min}$) is suggested to increase faster than the aerobic maximum metabolic rate ($\dot{M}O_{2max}$), leading to a reduction in the difference between them (i.e. the aerobic scope). Animals without sufficient aerobic scope are faced with trade-offs in their allocation of energy to activity, digestion, growth and reproduction (Weiner, 1992). When aerobic scope is most compromised, animals may even be forced into unsustainable anaerobic metabolism, which is suggested to cause unfavourable downstream consequences in functions such as growth (Pörtner & Farrell, 2008; Pörtner & Knust, 2007).

As the OCLTT hypothesis has been suggested to explain the mechanisms of climate change impacts on water-breathers (Pörtner & Farrell, 2008), it has received great interdisciplinary interest. Some tests of detailed predictions derived from the hypothesis have, however, failed to find support for it (outlined in Jutfelt et al., 2018; Verberk et al., 2016). One prediction, that tissue hypoxia restricts growth (Pörtner & Farrell, 2008; Pörtner & Knust, 2007) and therefore that markers of anaerobic metabolism should be detectable at supra-optimal temperatures, has mixed

support, as markers for hypoxia generally only appear at or close to lethal temperatures (Pörtner & Knust, 2007; Verberk et al., 2016). Tissue hypoxia is therefore unlikely to explain growth reductions that appear at temperatures far below lethal (Clark et al., 2013; Jutfelt et al., 2018; Lefevre et al., 2021). A related OCLTT prediction is that aerobic scope determines the performance of aerobic bodily functions during warming, with higher aerobic scope allowing more aerobic energy to processes such as growth. This prediction was not confirmed in Atlantic halibut *Hippoglossus hippoglossus* acclimated for 4 months to a range of temperatures, because, at temperatures close to upper lethal limits, the aerobic scope was high but growth reduced (Gräns et al., 2014). Such mismatches between the hypothesis and empirical data remain an impediment in thermal biology, hampering our ability to model and predict the impacts of climate change on ectothermic animals.

Here, we propose that oxygen limitation causes reductions in growth, but through a different mechanism than proposed by the OCLTT hypothesis. In fishes, reductions in growth at warmer-than-optimal temperatures have long been ascribed to increases in $\dot{M}O_{2min}$ combined with reduced appetite (Jobling, 1997). We hypothesise that this reduction in appetite occurs in order to conserve a portion of the aerobic scope that is available to the animal on top of the cost of digestion and assimilation. An 'aerobic scope protection'-like mechanism relating to feeding has been briefly alluded to in the literature (e.g. Auer et al., 2015; Chadwick & McCormick, 2017; Claireaux et al., 2000; Farrell, 2016; Jobling, 1997; Norin & Clark, 2017; Sandblom et al., 2014; Secor, 2009), but it has not been fully articulated or explored. Protection of aerobic scope has also been implied in the 'MASROS' ('maintain aerobic scope and regulate oxygen supply') hypothesis, which suggests that animals retain their aerobic scope throughout their environmental niche by altering tissue oxygen delivery (Atkinson et al., 2006). Furthermore, the term 'functional hypoxia' has been used to refer to oxygen limitation impacts that can arrive before hypoxia appears in the tissues, causing the animal to reduce functions such as activity and growth (Harrison et al., 2018). While these papers suggest different forms of aerobic scope conservation that resemble our hypothesis, our hypothesis differs in its emphasis on the effects of temperature on food intake and appetite, and it is readily testable through a series of predictions presented later in this paper.

3 | AEROBIC SCOPE PROTECTION BY REDUCTION OF FOOD INTAKE

At supra-optimal temperatures, most ectothermic water-breathers exhibit a decrease in food consumption. This is likely due to a loss of appetite, at least partly mediated by appetite-regulating hormones (Rønnestad et al., 2017; Volkoff, 2016). The reduced food intake, combined with elevated $\dot{M}O_{2min}$ at high temperatures, results in reduced growth (Jobling, 1997). To investigate the nature of this temperature–appetite relationship, we compiled data from studies investigating the thermal effect (using at least three temperatures)

on voluntary food intake in fishes. The emerging pattern revealed large interspecific variation in thermal sensitivity (Figure 1), likely related to different acclimation capacities of the different species as better acclimation may partially counter the thermal effect. However, there was a clear pattern of slowly increasing food intake up to an optimum temperature, reflecting the species' maximum food intake, followed by sharply reduced food intake at temperatures above optimal. The increasing food intake on the way to the optimum can be attributed to temperature-induced increases in digestion, assimilation and maintenance metabolism (i.e. $\dot{M}O_{2min}$). However, the reason for the loss of appetite at supra-optimal acclimation temperatures is likely a deficit or declining functioning of one or more physiological systems, the specifics of which have remained elusive.

When animals eat a meal, their metabolic rate initially increases sharply as part of the digestive response and remains elevated for an extended period (Figure 2a), before eventually returning to baseline levels (i.e. to $\dot{M}O_{2min}$ in a resting ectotherm). This increase in postprandial oxygen consumption rate is termed 'specific dynamic action' (SDA) and is considered a product of increased activity in the gut as well as increased biochemical nutrient processing and tissue assimilation of nutrients (Secor, 2009). The SDA response is temperature-sensitive and is typically 1–3 days in duration at warmer temperatures in animals eating similar-sized meals (Secor, 2009, 2011) but can last a week or two in cold-living Antarctic fishes (Boyce & Clarke, 1997; Johnston & Battram, 1993). As the total amount of energy expended to digest and assimilate a meal of a certain size (the area under the SDA curve) often is independent of temperature (Secor, 2009), the shorter duration of the SDA response at warm temperatures results

in a greater postprandial peak in metabolic rate (Figure 2a; Luo & Xie, 2008; McCue, 2006; Secor, 2011; Wang et al., 2002).

For fishes fed meals up to 5% of their body mass, this postprandial peak generally occupies <60% of their aerobic scope at benign temperatures [reviewed by Norin and Clark (2016)]. Several of these species have even been reported to exhibit an additive response (termed 'additive mode') to digestion and exercise, whereby they achieve a higher $\dot{M}O_{2max}$ while digesting and swimming (Dupont-Prinet et al., 2009; Fu et al., 2009; Jourdan-Pineau et al., 2010; Pang et al., 2010; Zhang et al., 2012). Other species cannot increase their $\dot{M}O_{2max}$ while digesting (termed 'priority mode') and many experience reduced swimming performance during the postprandial period (Alsop & Wood, 1997; Fu et al., 2009; Thorarensen & Farrell, 2006; Zhang et al., 2012), indicative of compromised performance even with the retention of a substantial postprandial residual aerobic scope (PRAS; Figure 2a).

As temperature rises, the postprandial peak in metabolic rate occupies an increasing proportion of aerobic scope in southern catfish *Silurus meridionalis* and goldfish *Carassius auratus* feeding at different acclimation temperatures (Pang et al., 2010, 2011). This increase was relatively steep for both the catfish and goldfish when going from a cool 15°C (24% and 31% of aerobic scope occupied, respectively) to an intermediate 21–27°C temperature (36%–40% of aerobic scope occupied). The goldfish were not measured beyond this but, interestingly, further warming of the catfish to a high temperature of 33°C only increased the postprandial peak slightly, occupying 42% of aerobic scope (Pang et al., 2010). As both species were fed ad libitum with an excess of food (that was removed after the feeding session), this suggests that the catfish voluntarily restricted further
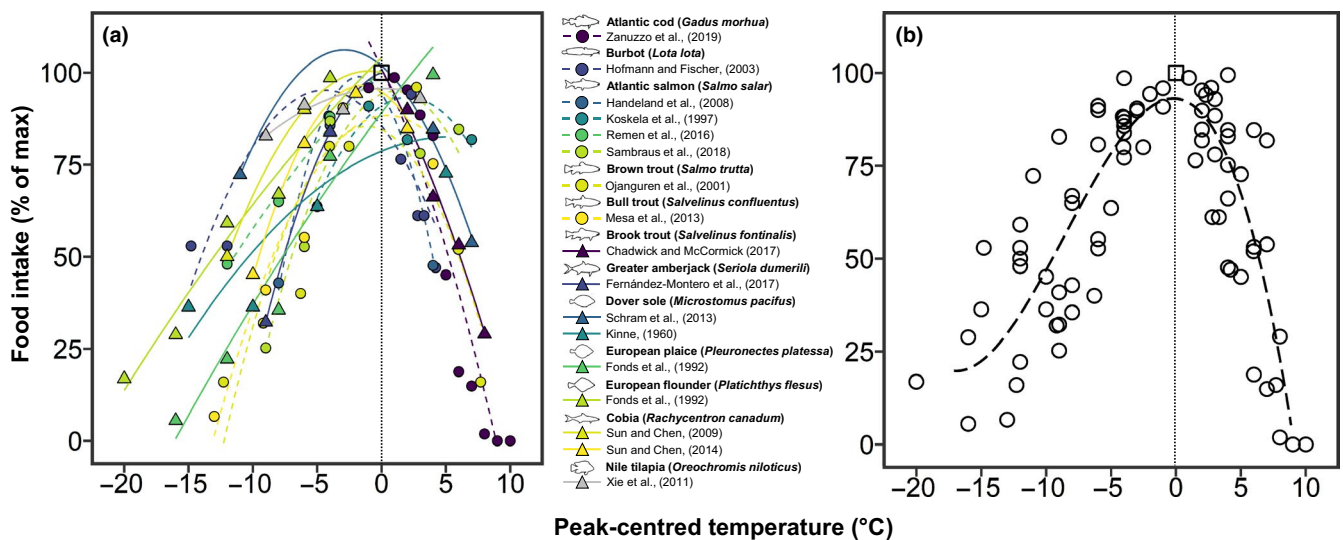
FIGURE 1 Food intake as a function of acclimation temperature. (a) Food intake versus temperature profiles normalised as percent of maximum intake, compiled from 16 studies on 12 species of fish from tropical to temperate thermal environments. To compare shapes of the food intake–temperature profiles between species, all profiles have been centred around the temperature of peak food intake (highest data point, black square) for each species (a and b). Overlapping points at maximum food intake are replaced with the black square. Data for each species are 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: (Chadwick & McCormick, 2017; Fernández-Montero et al., 2017; Fonds et al., 1992; Handeland et al., 2008; Hofmann & Fischer, 2003; Kinne, 1960; Koskela et al., 1997; Mesa et al., 2013; Ojanguren et al., 2001; Remen et al., 2016; Schram et al., 2013; Sambraus et al., 2018; Sun & Chen, 2009, 2014; Xie et al., 2010; Zanuzzo et al., 2019)
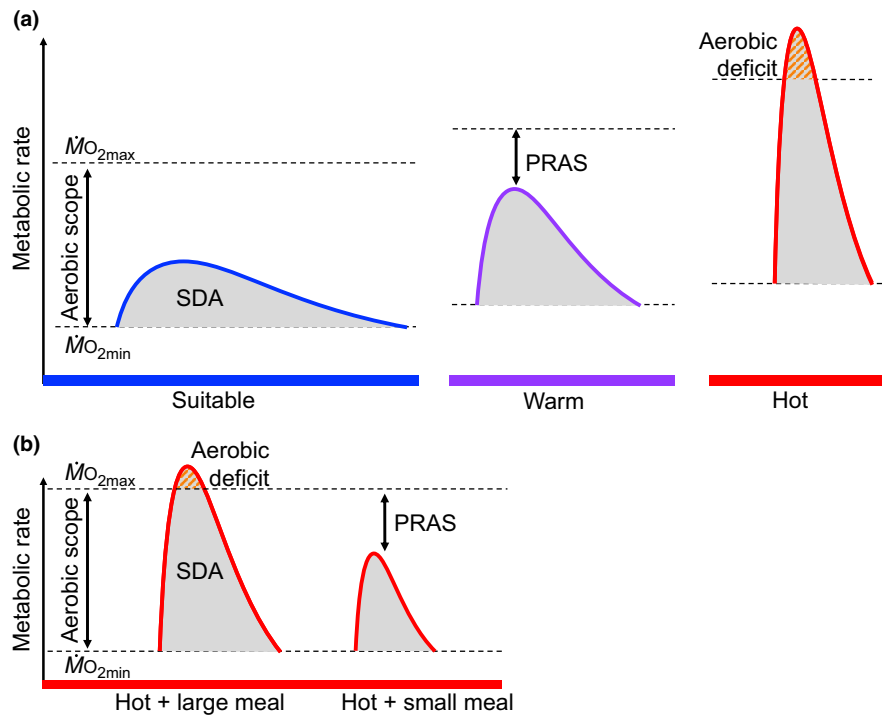
FIGURE 2 (a) Conceptual illustration of the effect of temperature on metabolic rate and specific dynamic action (SDA) in ectotherms. Aerobic standard metabolic rate ($\dot{M}O_{2min}$) and aerobic maximum metabolic rate ($\dot{M}O_{2max}$) increase with temperature. The metabolic increase after a same-sized meal (SDA) is shown as a time profile at three different temperatures ('suitable' in blue, 'warm' in purple and 'hot' in red). Increasing temperature temporally compresses the SDA response while giving rise to a higher postprandial peak metabolic rate. At the warm temperature, the postprandial residual aerobic scope (PRAS) is reduced compared to the suitable temperature, potentially limiting other oxygen-demanding processes. At the hot temperature, PRAS is gone and the postprandial peak metabolic rate overshoots the maximum oxygen delivery capacity, forcing the animal to exploit its anaerobic metabolism (hatched area above $\dot{M}O_{2max}$) and creating a costly oxygen debt that must be repaid at a later time. We propose that water-breathers actively avoid this latter situation by selectively reducing meal sizes at high temperatures to maintain a sufficient PRAS for activities other than digestion. (b) 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 $\dot{M}O_{2max}$). By voluntarily reducing meal size, fishes and other ectothermic animals may reduce their postprandial peak metabolic rate and thus maintain sufficient PRAS for other aerobic processes

food intake at high temperatures, despite increased metabolic demands (increased $\dot{M}O_{2min}$), in line with the aerobic scope protection hypothesis proposed here. The postprandial peak has also been found to occupy the entire aerobic scope of some fish when food ingestion was experimentally manipulated; a week of warming from 10 to 16°C did not change the aerobic scope of gavage-fed short-horn sculpin *Myoxocephalus scorpius* but elevated the postprandial peak in metabolic rate up to $\dot{M}O_{2max}$ (Sandblom et al., 2014), leaving no aerobic scope for aerobic activities other than SDA. As the sculpin were gavage fed a meal corresponding to 5% of their body mass, they did not have the option to regulate their meal size.

Meal size is a primary determinant of the magnitude of the SDA response (Fu et al., 2005; Norin & Clark, 2017; Secor, 2009), which provides a potential mechanism for fishes and other animals to voluntarily regulate their SDA magnitude by eating relatively large or small meals. Fish eating larger meals can grow more efficiently (higher food conversion ratio) but also incur a relatively high postprandial peak in metabolic rate during digestion of the larger meals (Fu et al., 2005; Norin & Clark, 2017), which reduces the amount of aerobic scope available for other oxygen-demanding activities such

as swimming (McLean et al., 2018). These findings indicate that, ideally, animals should regulate their food intake based on their need to maintain aerobic scope under challenging conditions. However, the interacting effects of temperature and aerobic scope protection on meal size selectivity have not been explored. We propose that animals, in particular water-breathers, use this mechanism of reduced food intake at elevated temperatures to conserve their postprandial residual aerobic scope within a species- and context-specific limit (Figure 2b).

One potential mitigating strategy could be for ectotherms to reduce meal size but increase meal frequency at temperatures above optimal, for example through switching to smaller prey items. That might allow continuous low-level SDA that retains sufficient postprandial residual aerobic scope while still ensuring high nutrient intake. Another potential strategy could be to maintain normal feeding at elevated temperature but induce rapid regurgitation to lower SDA if perceived threat levels increase, as was recently suggested to improve escape kinematics in black carp (Zhao et al., 2020). However, much of the oxygen consumption during SDA is used for supplying energy to cellular biochemistry involved in assimilation (anabolism).
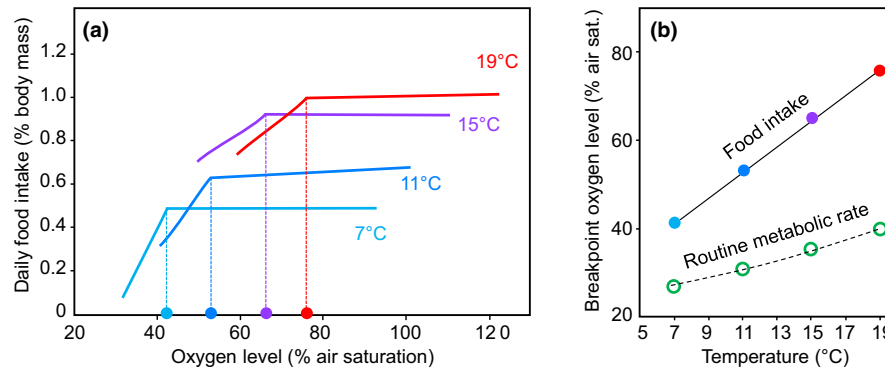
FIGURE 3 Water oxygen levels required to sustain maximum food intake and routine metabolic rate. (a) While food intake gradually increased with increasing temperature in Atlantic salmon *Salmo salar* within the species' suitable temperature range, varying oxygen levels did not markedly affect feeding until a breakpoint oxygen level, which occurred closer to normoxia at higher temperatures (a, b; filled symbols). (b) The breakpoint oxygen level for routine metabolic rate (open green symbols) is always lower than the breakpoint for food intake, suggesting a pre-emptive suppression of appetite rather than a direct physiological limitation. Redrawn from Remen et al. (2016)

As the outcome of many predatory attacks is quickly determined, regurgitation may not cause SDA to drop fast enough to make a difference. It is possible that regurgitation could be advantageous if the threat level is high and prolonged. The regurgitation strategy would be species- and context-specific but may allow testing of the aerobic scope protection hypothesis (see section 'Testing the aerobic scope protection hypothesis').

Some evidence exists not only for thermal oxygen limitation in aquatic invertebrates, especially for acute thermal tolerance (Verberk et al., 2016), but also for growth rates during periods of warm temperatures (Hoefnagel & Verberk, 2015; Verberk et al., 2021). As the majority of the current relevant literature is on fish, most of the examples used in this article refer to fish. However, the aerobic scope protection hypothesis should be applicable to many active invertebrates. Applying Krogh's principle (Krebs, 1975), some of the predictions in Figure 4 could be most efficiently tested in invertebrates, including the possibility that climate-induced aquatic hypoxia could further constrain oxygen delivery, appetite and growth of water-breathing animals in the future (Diaz & Breitburg, 2009).
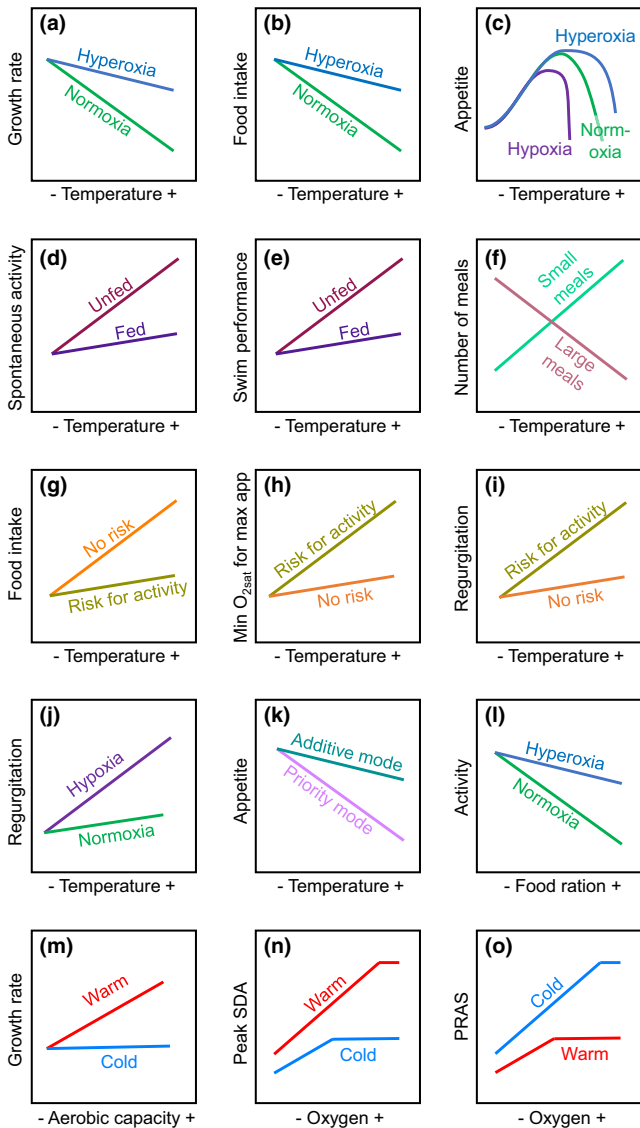
4 | TESTING THE AEROBIC SCOPE PROTECTION HYPOTHESIS

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

aerobic scope protection hypothesis, and we suggest paths for experimentally testing it.

A review of the relationship between growth rate of fishes and their aerobic capacities found no consistent correlation (Blier et al., 1997). This seemingly contradicts our aerobic scope protection hypothesis and indicates that aerobic capacity is not a major constraint on fish growth [but see Auer et al. (2015)]. The investigation into the relationship between growth rate and aerobic capacity, however, did not include the full temperature range (sub- to supra-optimal) for the species included (Blier et al., 1997). We predict that temperature is a major interacting factor in this correlation due to its effect on the SDA response (cf. Figure 2a), and that the benefit of having a higher oxygen transport capacity only becomes apparent at supra-optimal temperatures. This prediction would be interesting to test. An additional mechanism that could hide positive effects of aerobic scope on growth is slightly inflated $\dot{M}O_{2min}$ measurements due to lingering SDA and to continuously elevated $\dot{M}O_{2min}$ during high growth (Van Leeuwen et al., 2012). Such inflated $\dot{M}O_{2min}$ in high-growth individuals could reduce the apparent aerobic scope and potentially obscure correlations between aerobic scope and growth regardless of temperature.

If reductions in growth occur through a reduction in food intake that is implemented to reserve a portion of the aerobic scope available for activities other than SDA, as proposed here, it is predicted that the appetite of an animal would be more sensitive to water hypoxia in warmer than in colder temperatures, since hypoxia decreases oxygen supply capacity while warmer temperatures increase the postprandial peak metabolic rate. Indeed, when channel catfish *Ictalurus punctatus* were exposed to water hypoxia, their food intake was only marginally affected at colder temperatures. However, at the warmest temperatures, even mild hypoxia (oxygen levels at 80%–90% air saturation) caused a large decrease in voluntary food intake, suggesting that the fish were highly sensitive to the water oxygen levels (Buentello et al., 2000). Likewise, appetite in hypoxia was highly sensitive to temperature in Atlantic salmon *Salmo salar*; the fish maintained stable maximum food intake from normoxia down to relatively severe hypoxia

FIGURE 4 Predictions derived from the aerobic scope protection hypothesis. (a) Growth rate decreases from optimal (left of figure) to increasingly supra-optimal temperatures in normoxic water, but the decline is predicted to be less steep in hyperoxic water as hyperoxia can increase aerobic scope (Brijs et al., 2015) and thus postprandial residual aerobic scope (PRAS), which allows for higher food intake. (b) Food intake is thus predicted to show a similar pattern to growth rate at optimal to supra-optimal temperatures, with hyperoxia increasing food intake at supra-optimal temperatures relative to food intake in normoxia. (c) This more specific prediction uses the peak-centred shape of the temperature–food intake relationship from Figure 1; we predict that the change in appetite with temperature should differ between hypoxia (purple), normoxia (green) and hyperoxia (blue), with no difference at lower temperature but increasing difference at supra-optimal temperatures. (d) Spontaneous activity often increases with temperature around the optimal temperature range, but activity competes with digestion for the available aerobic scope, leading to a lower increase in activity with temperature in fed compared to unfed animals. (e) Animals that are force-fed a large meal should show reduced swim performance compared to unfed or voluntarily feeding animals at supra-optimal temperature, but not at sub-optimal temperature. (f) Meal sizes may decline with increasingly supra-optimal temperatures, but some animals may compensate for that decline by eating smaller prey items more often to keep peak SDA low. (g) Animals may estimate their need for activity in the near future (e.g. escaping predators, migrating, navigating currents), and increased perceived risk for activity may reduce food intake to maintain a larger PRAS at supra-optimal temperature. (h) The minimum oxygen level required for maintaining maximum food intake or appetite ('Min O_{2sat} for max app') increases with temperature (cf. Figure 3); if the animal predicts a risk of elevated physical activity, the increase with temperature should be steeper than in the absence of risk of activity, and this effect should be most apparent at supra-optimal temperatures. (i) Regurgitation of meals could be a strategy to reduce SDA during risk for elevated activity (e.g. increased threat levels from nearby predators) at supra-optimal temperatures. (j) Similar to panel i, hypoxic water could reduce PRAS and increase the frequency of regurgitation at supra-optimal temperatures. (k) In animals where SDA adds to their exercise-induced $\dot{M}O_{2max}$ (termed 'additive mode'), the magnitude of PRAS reduction should be smaller at supra-optimal temperatures than for animals that have to prioritise between SDA and other activities (termed 'priority mode'); animals with an additive mode should therefore show smaller reductions in appetite at supra-optimal temperatures than those with priority mode. (l) Spontaneous activity is predicted to decline with increasing food rations at supra-optimal temperatures, but hyperoxia may ameliorate this decline by increasing aerobic scope and thus PRAS. (m) Aerobic capacity (aerobic scope) is generally not considered to correlate with growth rate [but see Auer et al. (2015), Auer et al. (2015)], although this should be temperature-dependent and a positive correlation is predicted at supra-optimal ('Warm') temperatures. (n) Assuming animals protect their PRAS through voluntary reductions in food intake when PRAS reaches a critical point, a breakpoint in the postprandial peak in metabolic rate (peak SDA) should be apparent when water oxygen is manipulated (from hypoxia over normoxia to hyperoxia), but primarily in the cold. (o) Similarly, PRAS should increase with increasing oxygen availability but plateau at warm temperatures when sufficient PRAS is reached near normoxia, allowing SDA to increase while holding PRAS constant in hyperoxic conditions; in cold conditions, PRAS is not threatened and is thus determined by the increasing $\dot{M}O_{2max}$ as water oxygen increases

(40% air saturation) at 7°C, but food intake started to decline at an oxygen level of 75% air saturation at 19°C (Figure 3). Furthermore, the breakpoint oxygen levels for food intake (Figure 3b) are always higher (by 10%–20% air saturation) than the breakpoint oxygen levels for routine metabolic rate of fed Atlantic salmon (Remen et al., 2016). Thus, Atlantic salmon appear to pre-emptively suppress appetite at oxygen levels higher than those which constrain their routine metabolic rate, inferring a behavioural response to conserve aerobic scope. Together, these data demonstrate increasing oxygen limitation on appetite with increasing temperature, which is consistent with our proposed aerobic scope protection mechanism.

If the reduction in PRAS becomes restrictive to food intake only at higher temperatures, then factors that increase aerobic scope can be predicted to also increase food intake. Hyperoxia has been shown to increase the aerobic scope in some fishes; oxygen levels of 200% air saturation effectively doubled the aerobic scope in European perch *Perca fluviatilis* (Brijs et al., 2015) and increased their venous oxygen partial pressure and cardiac stroke volume (Ekström et al., 2016). As a higher

aerobic scope would allow for a higher postprandial peak metabolic rate during the SDA response without markedly restricting postprandial residual aerobic scope or tissue oxygenation, we predict that water hyperoxia would increase appetite. Additionally, this effect of hyperoxia would be temperature-sensitive, with no effect at suitable temperatures and increasing effect with increasing supra-optimal temperatures. Few studies have tested this prediction: Rainbow trout fed various diets at hypoxia (50% air saturation), normoxia (100% air saturation) and hyperoxia (200% air saturation) varied in their weight gain in accordance with the prediction for increasing appetite with increasing oxygen availability (Dabrowski et al., 2004), although another study on rainbow trout did not find the same benefit of hyperoxia (Caldwell & Hinshaw, 1994). Notably, the former growth experiment (Dabrowski et al., 2004) was conducted at 20–22°C, which is above the temperature range for optimal growth in rainbow trout (Hokanson et al., 1977), while the latter was conducted at close to optimal (13–15°C). This supports our prediction of an increasing effect of hyperoxia at supra-optimal temperatures, but temperature has not yet been systematically included as a factor.

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

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

Anecdotal, yet compelling, evidence for immediate PRAS limitation comes from an observation by Claireaux et al. (2000) who placed recently fed Atlantic cod *Gadus morhua* in respirometers and gradually reduced water oxygen saturation. At the point where the PRAS approached zero, the cod terminated digestion, as colourfully described by the authors: *At this point, scope for activity being almost nil, all the fish in the measuring chamber simultaneously regurgitated their food, presumably to reduce their immediate oxygen requirements. Then, as soon as water S_{O2}* [water oxygen saturation] *was restored to above 45%, approximately 5 min later, the fish recovered enough metabolic potential to resume digestion and re-swallowed all the food.* This suggests that fish sense not only external oxygen levels but also somehow physiologically monitor the magnitude of their aerobic scope and SDA, and that they act to avoid an aerobic deficit (cf. Figure 2b) by controlling their SDA (Figure 4i,j).

The predictions derived from the aerobic scope protection hypothesis presented here share similarities with other oxygen limitation hypotheses (e.g. OCLTT, MASROS), in that oxygen transport is limiting thermal performance. It could even be argued that the mechanism suggested here is inherent to the larger oxygen limitation or 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 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 on 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. 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 a main mechanism that can be used to differentiate our aerobic scope protection hypothesis from the OCLTT hypothesis. In Figure 4, 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 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 4c, where the shape of the temperature–appetite function from Figure 1 is used (green line) and the predicted effect of hypoxic and hyperoxic water is added.

Finally, we caution that the aerobic scope protection hypothesis is likely not a 'silver bullet' mechanism to understand performance limitations at high temperature, but one potential explanation among many for the observed patterns of thermal performance in ectothermic animals. Such physiological explanations can be oxygen-dependent or oxygen-independent. For example, it can be assumed that the gastrointestinal tract is adapted to suit the food type and amount associated with the species' niche. With warming, the increased energy expenditure and therefore food throughput requirement may cause limitations in gastrointestinal capacity, nutrient uptake and thus growth, although little data exist at supra-optimal temperatures (McLeod & Clark, 2016). The immune system is tailored to the risk of infection and cell damage (e.g. through oxidative stress or thermal increase in turnover), but these functions may become restrictive at higher temperatures (Dittmar et al., 2014; Miest et al., 2019; Wegner et al., 2008). Nerve function is optimised for a certain thermal range through ion channel function and membrane fluidity (Cossins et al., 1977; Jutfelt et al., 2019). Gonads can be more thermally sensitive than other organs (Pankhurst & King, 2010). Mitochondrial proton leak increases with temperature (Leo et al., 2017), meaning that more food and oxygen are consumed per unit of ATP produced. Similar limitations can likely occur for every physiological organ system.

Sufficient oxygen delivery can be considered a permissive factor that needs to be in place for the organism to function at higher temperatures. There may be many such permissive factors, both

physiological and ecological, any of which can become limiting for fitness in certain contexts (e.g. limitations in food, water, ions, refuges). Such permissive factors may become saturated at some high level, for example higher food availability will not increase growth over a certain maximum food-handling level. Likewise, oxygen delivery is one permissive factor to tissue performance among many that may or may not become limiting under thermal challenges, and whether it does is context-specific. The task for ecophysiologists now is to figure out ways of testing which factors are limiting which animals and in which contexts; a task that will likely keep us busy for some time.

AUTHORS' CONTRIBUTIONS

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

DATA AVAILABILITY STATEMENT

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