

## Aerobic scope and its optimum temperature: clarifying their usefulness and limitations – correspondence on *J. Exp. Biol.* 216, 2771-2782

Clark and colleagues (Clark et al., 2013) have set people straight on how to make high quality measurements of maximum and minimum oxygen uptake rates in fishes. They correctly state that great care and understanding are needed to properly measure a fish's aerobic scope (=maximum metabolic rate–standard metabolic rate). Indeed, such challenges probably contributed to the slow acceptance of the concept of aerobic scope and  $T_{opt}$  (the temperature for maximum aerobic scope) after their introduction in the 1940s by a Canadian, Fred Fry. However, while doing so, Clark et al. take some misguided sideswipes at the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis.

Clark et al. have an obvious error in their fig. 1B (see Clark et al., 2013). They mislabel the peak of the Fry aerobic scope curve as 'onset of loss of performance' such that  $T_{opt}$  (they use  $T_{optAS}$ ) is not the temperature when aerobic scope is maximal. As a result,  $T_{opt}$  is labelled at a lower temperature and reduced aerobic scope. Here, I have assumed the independent variable in their fig. 1 ('scope for aerobic performance') is aerobic scope as the text correctly states '...aerobic scope continues to increase until temperature approaches lethal levels...'. This mistake apparently created a somewhat slippery slope. They then say, '...recent data suggest that  $T_{optAS}$  provides little insight into the preferred temperature or performance of aquatic ectotherms...', without appropriate literature citations. They even ignore a previous study (Clark et al., 2011) where the authors posit aerobic scope at high temperatures may be important for pink salmon in a global warming situation.

Instead, perhaps their fig. 1B (see Clark et al., 2013) was primarily intended to point out that a Fry aerobic scope curve isn't always bell-shaped (see their fig. 1A). But surely such a point is unnecessary given the various curves illustrated by Fry's original works, many of which were recently reproduced alongside newer data for Pacific salmon (Farrell, 2009). [I trust they were not disrespectfully targeting the single cartoon allowed in a *Science* Perspective (Pörtner and Farrell, 2008).] Equally curious is why Clark and colleagues do not also consider a Fry aerobic scope curve for a representative eurythermic fish. Killifish, for example, maintain aerobic scope over an acute temperature range of almost 30°C (Healey and Schulte, 2012). As a result, rather than having a specific  $T_{opt}$ , killifish have a broad  $T_{opt}$  window where absolute aerobic scope varies very little over most of the fish's thermal limit.

To be absolutely clear, for a given temperature, aerobic scope is the maximum amount of oxygen available for any aerobic activity above routine. A Fry aerobic scope curve defines the temperature dependence of aerobic scope, from which one can derive  $T_{opt}$  and the temperature when aerobic scope disappears ( $T_{crit}$  or  $T_c$ ). The concept cannot be simpler. What may be less clear, and a point of ideological difference, is that aerobic scope is a fundamental capacity; an animal must be at  $T_{opt}$  (or within a  $T_{opt}$  window) to maximize this potential. It says nothing about when and how it is realized, which involves competing factors such as food availability and species competition. Clearly,  $T_{opt}$  maximizes the potential to deliver oxygen to tissues, but growth cannot be maximized without high quality food, for example.

In the context of life history, Clark and colleagues should not suggest '... $T_{optAS}$  has little relevance...'.  $T_{opt}$  and  $T_{crit}$  have been given ecological relevance for a life history bottleneck – a once-in-a-lifetime spawning migration up a high-flowing river at peak summer temperatures for adult sockeye salmon (Farrell et al., 2008). It is true, juvenile and adult sockeye salmon typically inhabit lakes, rivers and oceans colder than  $T_{opt}$  (Lee et al., 2003; Eliason et al., 2011; Chen et al., 2013). Therefore, while El Niño oceanic warming provides sockeye salmon with a potential for better growth, this potential is not necessarily realized for the population because predatory tuna invade northward as they are no longer biogeographically constrained by the

cold northeast Pacific (e.g. Block et al., 1997). Conversely, lake-rearing juvenile sockeye salmon behaviourally exploit their Fry aerobic scope curve to manage oxygen allocation and maximize growth by using a diurnal vertical migration. At dawn and dusk, they feed in warm surface water, which maximizes foraging (swimming) activity, but they then relocate to deep, cooler water to maximize food conversion by lowering routine metabolic rate (Brett, 1971). Moreover, by suggesting that maximum metabolic rate for ambush predators should be measured post-exercise, Clark et al. clearly acknowledge that maximum oxygen delivery is required to recover as quickly as possible after escaping a predator. Thus, they imply that  $T_{opt}$  has ecological relevance for recovery. The ecological and evolutionary relevance of the OCLTT is further discussed in the accompanying commentary by Hans-Otto Pörtner and Folco Giomi (Pörtner and Giomi, 2013).

An important benefit of the OCLTT hypothesis is that the Fry aerobic scope curve offers a framework for a mechanistic understanding of thermal responses. All fishes studied to date increase heart rate ( $f_H$ ) with warming, which is the primary driver to increase cardiac output and arterial oxygen transport (e.g. Cech et al., 1976; Steinhausen et al., 2008; Farrell, 2009; Mendonça and Gamperl, 2010; Eliason et al., 2013). However, warming eventually triggers an arrhythmic heartbeat, a cardiac collapse that occurs at a temperature lower than  $T_{crit}$  and  $CT_{max}$  (the upper critical temperature when a fish can no longer maintain a righting reflex) (Casselman et al., 2012; Anttila et al., 2013). The Arrhenius breakpoint temperature (ABT) for  $f_H$  was recognized nearly a century ago (Crozier, 1926) and is now informing biogeographic distributions of intertidal ectotherms (Somero, 2010). Thus, mechanisms underlying thermal responses can be related back to a Fry aerobic scope curve.

To close, Clark and colleagues provide guidance for measuring metabolic rate in fishes, a field where techniques vary widely (sometimes unavoidably). Thus, readers must be circumspect because these technicalities may mean that all values for aerobic scope are not necessarily exactly comparable among studies. Unfortunately, this important guidance is marred by some poorly supported statements, which mislead rather than advance the field. Hopefully, they will better explain (and defend) at some time their new proposition: multiple performance–multiple optima [see their fig. 7B (Clark et al., 2013)]. I suspect that if a common dimension can be found for the proposed 'physiological performances', summing all these curves may produce a single curve like that in their fig. 1A. The OCLTT remains a valuable conceptual framework around which the various competing factors for oxygen allocation can be examined, with the Fry aerobic scope curve defining  $T_{opt}$ . Nowhere do Pörtner and Farrell (Pörtner and Farrell, 2008) suggest that a fish must operate at  $T_{opt}$ . Indeed, suboptimal temperatures may be exploited to obtain food and avoid predation. Such are the choices in life.

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## Nothing in experimental biology makes sense except in the light of ecology and evolution – correspondence on *J. Exp. Biol.* 216, 2771-2782

'Nothing in biology makes sense except in the light of evolution' is a much cited message from a paper by Dobzhansky (Dobzhansky, 1973). It emphasizes that identifying the principles, similarities and differences of structures and functions between organisms, their families, phyla and domains leads to an understanding of the pathways of evolution. Of course, biology encompasses experimental animal biology, which includes the comparative study of functions within or across phyla to identify the principles maintained and their potential and special modifications. Knowledge of unifying functional principles provides the foundation when addressing the sensitivities of species to environmental change, considering their phylogeny and mode of life. As experimental biology presently aims at becoming involved in conservation science, one question also is how to shape research to obtain the most powerful contributions to this field.

In this context, the recent paper by Clark and colleagues (Clark et al., 2013) discusses high quality measurements of respiratory rates in fishes but does not fully appreciate the ecological and evolutionary framework within which relevant concepts have been developed and applied. The text by Clark et al. is suggestive that the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis [including aerobic scope, see parallel Correspondence by Anthony Farrell in this issue (Farrell, 2013)] as well as associated constraints may only work in some but not all fish species. Does this mean that for other species (to be identified), OCLTT needs to be replaced with alternative concepts? Are there any? Here, the authors may have overlooked the fact that OCLTT addresses a unifying ecological and evolutionary principle in (aquatic) animals: the specialization on temperature and the first lines of thermal limitation are set at the highest level of biological organization, and involve oxygen supply systems and their capacities in relation to oxygen demand. Such constraints have been identified in representative species from key animal phyla and one wonders whether (and how) individual species can be exempt from such principle? A conceivable way out might be through a secondary reduction of environmental constraints or through exceptional evolutionary adaptations. Following OCLTT principles, the movement of species into highly oxygenated environments such as air might have triggered the alleviation of such constraints. Such evidence is in fact emerging for the recurrent evolution of breathing air in crustaceans and fishes (F.G., M. Fusi, A. Barausse, B. Mostert, H.-O.P. and S. Cannicci, unpublished results). In cold polar oceans, oxygen availability in excess of demand may also have led to the relaxation of oxygen constraints and to losses of associated functions as discussed for polar fishes (Pörtner et al.,

2013). Exceptional adaptations may exist in insects due to the use of tracheal rather than convective oxygen supply systems. Interestingly, OCLTT principles apply to insect aquatic larvae (Verberk and Bilton, 2011), leading to relevant perspectives concerning insect evolution. So Clark and colleagues have missed out on the question of what OCLTT can contribute to addressing the role of oxygen and capacity limitations as early constraints in animal evolution in the aquatic realm.

Unifying physiological principles find validation in an ecological context, for a specific life stage, season or in a biogeographical context. Field studies provide evidence that OCLTT sets southern distribution limits in European eelpout (Pörtner and Knust, 2007) or is the key constraint during a critical life cycle period such as the spawning migration of Pacific salmon (Farrell et al., 2008). In both cases, species operate at the limits of their warm acclimatization capacity. These examples also make clear that animals do not continuously exploit the functional capacity associated with OCLTT and do not experience the respective limitations everywhere in their natural range. However, OCLTT defines not only thermal specialization of species and their performance breadths but also the potential to allocate aerobic energy and associated functional tradeoffs. Aerobic scopes for exercise, growth or reproduction are high level proxies for this potential, with the suitability of a proxy depending on the lifestyle and lifestage of a species. Such proxy should be determined in a stress-free situation. Enforced studies of excess post-exercise oxygen consumption (EPOC) are clearly not suitable to measure the subtleties of oxygen and energy allocation in the sense of OCLTT. If EPOC studies are used nonetheless to determine thermal limits, the data need to be tested against ecological realities. In this context, Clark et al. seem to misinterpret the OCLTT concept: it does not assume optimum and preferred temperatures of a species to be similar. Several examples of a mismatch between optimal and preferred temperature are known for fish (Angiletta, 2009).

The unfounded criticism of the OCLTT concept comes with the request that more and more individual species (of fishes) should be studied to see whether it works or not in each individual case. In an evolutionary context, a relevant approach would rather be to ask what the concept can do for understanding differences between species with respect to performance, specific lifestyle, thermal limitations and underlying mechanisms. OCLTT links levels of biological organization and places apparently disconnected mechanisms into a larger context. OCLTT casts new light on the differential energy costs of various processes and their role in thermal limitation, for example the cost of oxygen supply depending on oxygen availability (Mark et al., 2002) or

depending on the functioning of blood pigments (Giomi and Pörtner, 2013). Furthermore, the OCLTT framework contributes to an integrated view of climate-related stressors, their role in evolutionary crises in Earth history, and their functional consequences for animal evolution (Pörtner et al., 2005; Knoll et al., 2007; Clarke and Pörtner, 2010). Unfortunately, apart from their criticism of OCLTT and the present uses of aerobic scope, Clark and colleagues do not even attempt to suggest alternative concepts that would be equally relevant in ecology and evolutionary biology and equally suitable to explain the shape and position of performance curves on the temperature scale.

Stepping back from the present debate, we should put an evolutionary time scale on what experimental findings mean for each species or group in its ecological situation. Such wider context always requires consideration when elaborating what is unifying and what has become specific for the species studied. Finally, in light of climate change it is urgent that we develop a consensus on a concept representing climate-related physiology, for a solid cause and effect understanding and to convincingly voice the contributions of the experimental community. If existing concepts are not convincing enough then alternative ones should be proposed or present ones should be developed further, especially those backed by strong evidence across phyla such as OCLTT. It seems more promising to fill the existing framework than to reinvestigate the wheel for each animal species.

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## Response to Farrell and to Pörtner and Giomi

From the outset, we would like to thank Farrell, Pörtner and Giomi (Farrell, 2013; Pörtner and Giomi, 2013) for their thoughts on our previous publication (Clark et al., 2013), and we acknowledge their valuable contributions to science as well as their desire to find unifying principles to help understand the evolutionary pathways of animals. Of course, we share their desire to bring simplicity to complex biological systems and processes.

The oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis explicitly states that thermal tolerance, physiological performance, climate change sensitivity and field distribution of ectothermic animals are causally determined by oxygen transport capacity, concisely summarised by Pörtner and Farrell (Pörtner and Farrell, 2008): 'Direct effects of climatic warming can be understood through fatal decrements in an organism's performance in growth, reproduction, foraging, immune competence, behaviors and competitiveness. Performance in animals is supported by aerobic scope, the increase in oxygen consumption rate from resting to maximal. Performance falls below its optimum during cooling and warming. At both upper and lower pejus temperatures, performance decrements result as the limiting capacity for oxygen supply causes hypoxemia'. While we agree that increasing temperatures negatively affect the mentioned variables, we disagree on the generality of the proposed mechanism (tissue hypoxaemia at pejus temperatures leading to secondary losses of performance). Furthermore, we propose that different processes ('performances') can be thermally limited by factors unrelated to oxygen transport, by known and unknown mechanisms, and that the way forward is to test these contrasting perspectives experimentally. We fail to see how this could be viewed as taking 'misguided sideswipes', and instead we see it as encouraging scientific progress.

It is apparent from recent literature that the OCLTT hypothesis is treated as a confirmed theory by many scientists. Indeed, if we were new to the field of thermal physiology and read the literature on OCLTT, we would probably form the conclusion that the physiological mechanism underlying thermal performance and tolerance in

ectotherms has been discovered in the form of OCLTT. This is worrying, as it implies that aerobic scope measurements over a relevant temperature range will provide a thorough understanding of the thermal ecology and climate-related responses of ectotherms, and it may lead researchers to downplay and overlook important results that do not fit the OCLTT hypothesis. We also raise the point that the OCLTT literature often extrapolates acute thermal exposures to global warming, despite the fact that we know even relatively short thermal acclimation can have profound effects on aerobic scope (Norin et al., 2013). Different rates of heating, from minutes in the lab to decades on a global scale, should not be assumed to affect animal physiology by identical mechanisms.

Our original paper was not intended to provide a thorough evaluation of the ecological and evolutionary framework for OCLTT, as we feel this topic has been addressed thoroughly in a string of papers by Pörtner and colleagues. Moreover, we were cognisant of the fact that a discussion in this direction would necessarily rely on speculation and hypothetical models as empirical data are lacking. Indeed, Pörtner and Giomi question our focus on aerobic scope and  $T_{optAS}$  (the temperature eliciting maximum aerobic scope) while they promote OCLTT as a powerful framework to universally explain broad-scale evolutionary constraints and climate-related effects on aquatic ectotherms [and terrestrial ectotherms (Pörtner, 2002)]. In doing this, they essentially transition away from the fundamental principles of the hypothesis (that oxygen transport limitations induce tissue hypoxaemia at pejus temperatures) and move towards a complex hypothetical framework that does not easily lend itself to experimental testing. The fact remains that the underlying assumptions of OCLTT rely on aerobic scope and its thermal dependence. We argue that individual performance *in vivo* is a fundamental level at which to test oxygen limitation. As these measurements have been most accessible and relevant to the broader scientific community in the context of OCLTT, our paper was targeted in this direction.

We do not agree with the assertion by Farrell that we have an 'obvious error' in fig. 1B (see Clark et al., 2013). We suspect that this



criticism has arisen because some scientists misleadingly use the term  $T_{\text{opt}}$  (without any qualifier) to describe the temperature where aerobic scope is maximal. We strongly recommend that the term  $T_{\text{opt}}$  should be reserved as an abbreviation for the optimal temperature of the animal, which will be context dependent and governed by interacting optimal temperatures of different physiological and ecological performance metrics. Any use of the term  $T_{\text{opt}}$  in the context of a particular performance metric should include a qualifier. We use the term  $T_{\text{optAS}}$  to describe the temperature that is optimal for maximising aerobic scope.  $T_{\text{opt}}$ , not  $T_{\text{optAS}}$ , is what we have annotated in fig. 1B (see Clark et al., 2013), highlighting that aerobic scope may not set the optimal temperature of the animal. Indeed, we propose that the 'onset of loss of performance' of the animal can occur at the peak of the Fry curve where aerobic scope is maximal. In other words, performance metrics like growth and reproduction can be markedly reduced at  $T_{\text{optAS}}$ , as highlighted in the study on killifish cited by Farrell (Healy and Schulte, 2012), which we discussed in our original paper.

Farrell refers to a previous study on pink salmon (Clark et al., 2011), of which the take-home messages are (1) the breadth of acute thermal tolerance of pink salmon is exceptional, (2) aerobic scope across a broad temperature range is higher than has been reported for other Pacific salmon, and (3) the  $T_{\text{optAS}}$  of 21°C is a temperature that causes death within days in captivity (Jeffries et al., 2012) and one that most individuals in the population would never experience in their lifetime (i.e. a clear mismatch between  $T_{\text{opt}}$  and  $T_{\text{optAS}}$ ). This provides evidence that aerobic scope is not tailored to the mean river migration temperature encountered by the population (16–17°C), and instead aerobic scope simply increases with temperature up to (and often beyond) the highest temperature historically encountered by the species.

The Fry curve is repeatedly presented as a bell-shaped curve in most studies concerning OCLTT (e.g. Pörtner and Farrell, 2008; Farrell, 2009). That shape gives the false impression that aerobic scope declines gradually as temperature is increased beyond  $T_{\text{optAS}}$ , giving plenty of room for oxygen limitation to progressively affect other physiological systems. In reality, most species that have been investigated using appropriate techniques show high aerobic scope all the way up to lethal temperatures. If there is a general consensus that the Fry curve is not bell-shaped as implied by Farrell, then we see no reason why it should be continually portrayed this way in the literature.

Pörtner and Giomi ask whether there are any alternative concepts and whether OCLTT must be replaced with these alternatives in different ectothermic species. They also wonder how any species can be exempt from the hypothetical principles of OCLTT. Of course, aerobic scope is vital as it provides the capacity for increasing aerobic metabolism, but is  $T_{\text{optAS}}$  important? Must animals have access to maximum attainable aerobic scope in order to perform optimally? As portrayed in fig. 7B of our original paper, we believe that a temperature eliciting sub-maximal aerobic scope can be beneficial to maximise fitness as it may enhance other important performance metrics (e.g. growth rate, food conversion efficiency, reproduction). While a greater aerobic scope may be obtained at higher temperatures, the costs involved to other physiological and biochemical systems may outweigh any potential benefit. If aerobic scope increases with temperature throughout the ecologically relevant range (e.g. Claireaux et al., 2000; Clark et al., 2011), then  $T_{\text{optAS}}$  has limited power to predict the optimal temperature of the organism. If thermal acclimation causes aerobic scope to become temperature independent across most of the ecologically relevant temperature range (e.g. Norin et al., 2013), then any perceived benefit of  $T_{\text{optAS}}$  is lost and OCLTT loses predictive power.

The OCLTT hypothesis has given the broader scientific community the perception that they can answer many of their ecological and climate-related questions by measuring aerobic scope across a relevant temperature range. In this context, Pörtner and Giomi criticise the use of enforced exercise to gain an understanding of maximum aerobic metabolism, yet one wonders how this variable (and thereby aerobic

scope) can be quantified in a 'stress-free situation'. It was the goal of our original paper to stimulate critical thinking around the claimed generality of OCLTT, to find where it may make useful predictions, and to determine where its limitations may lie. We encourage scientists to critically assess their data and the published literature and ask some relevant questions: (1) is there a statistically significant  $T_{\text{optAS}}$ , does it align with data on other performance metrics (e.g. growth efficiency, reproduction) and, if so, how can the direction of causality be established?; (2) does the reported  $T_{\text{optAS}}$  make sense in light of the thermal history, evolution and ecology of the animal?; (3) does aerobic scope progressively approach zero as temperature exceeds  $T_{\text{optAS}}$  towards the upper critical temperature?; (4) did the animals survive the experimental protocols at all temperatures or could any observed reductions in aerobic scope be a consequence (not a cause) of poor health and impending death?; and (5) how does thermal acclimation influence aerobic scope and  $T_{\text{optAS}}$ ? These questions may help to guide more thorough testing of the general relevance of the OCLTT hypothesis across species.

In their concluding paragraph, Pörtner and Giomi seem to suggest that we should stop debating and instead throw our support behind OCLTT to provide a unified voice from the experimental community about climate-related physiology. If we blindly endorse one view without rigorous testing, then we fail in our role as scientists and our perception in society would rightfully suffer. We believe that the OCLTT hypothesis has some major shortcomings in assuming that  $T_{\text{optAS}}$  has significant ecological and evolutionary relevance. Our desire to have a unifying principle should not trump empirical evidence. An increasing number of studies have shown that organisms maintain an excellent capacity for oxygen transport at the temperatures predicted to occur in their environments over the next 100 years (Brett, 1972; Clark et al., 2011; Overgaard et al., 2012; Norin et al., 2013; Gräns et al., in press), yet there are clearly other physiological and/or biochemical processes that may deteriorate, compromise fitness and survival, and explain the shape and position of performance curves on the temperature scale [see 'Conclusions' of our original paper (Clark et al., 2013)].

Our formalisation of the idea of 'multiple performances – multiple optima' [see fig. 7B of our original paper (Clark et al., 2013)] highlights that different performances can have different thermal optima, and the interrelations between these performances govern the thermal preference and fitness of animals. Of course, the challenge for scientists is to pinpoint important performance metrics and determine their thermal dependence in the context of animal fitness. This is likely to differ between organisms, life stages and rates of heating. It is therefore unfortunate that Farrell sees our idea as poorly supported and misleading when our intention is to advance the field by encouraging scientists to test the assertion that thermal performance and resilience to climate warming must be governed by oxygen transport capacity. Our common goal should be to find the causal mechanisms for deteriorations in animal performance and use them to understand the responses of animal populations to environmental perturbations including climate change.

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