Pragmatic perspective on aerobic scope: peaking, plummeting, pejus and apportioning

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A major challenge for fish biologists in the 21st century is to predict the biotic effects of global climate change. With marked changes in biogeographic distribution already in evidence for a variety of aquatic animals, mechanistic explanations for these shifts are being sought, ones that then can be used as a foundation for predictive models of future climatic scenarios. One mechanistic explanation for the thermal performance of fishes that has gained some traction is the oxygen and capacity-limited thermal tolerance (OCLTT) hypothesis, which suggests that an aquatic organism’s capacity to supply oxygen to tissues becomes limited when body temperature reaches extremes. Central to this hypothesis is an optimum temperature for absolute aerobic scope (AAS, loosely defined as the capacity to deliver oxygen to tissues beyond a basic need). On either side of this peak for AAS are pejus temperatures that define when AAS falls off and thereby reduces an animal’s absolute capacity for activity. This article provides a brief perspective on the potential uses and limitations of some of the key physiological indicators related to aerobic scope in fishes. The intent is that practitioners who attempt predictive ecological applications can better recognize limitations and make better use of the OCLTT hypothesis and its underlying physiology.

Key words: critical temperature; maximum heart rate; metabolic rate; optimum temperature; oxygen consumption; pejus temperature.

INTRODUCTION

Shelford’s (1931) extensive and pioneer works on the biogeographic distributions of plants and animals culminated in his law of thermal tolerance. One of his predictions was that animals would be more sensitive than plants as indicators of unfavourable temperatures. This is because animals can relocate to avoid unfavourable environments both in the short term (Elliott, 2000) and long term. Such avoidance behaviours may help explain why dozens of studies encompassing a wide range of aquatic animals (plankton, intertidal invertebrates and fishes) have documented extensive modifications in biogeographic patterning (range expansions and contractions) in association with recent climate changes. For example, in 60 years or less, certain North Atlantic Ocean plankton species have shifted northward by >1000 km (Beaugrand et al., 2002), while fish species such as Atlantic cod Gadus morhua L. 1758, whiting Merlangius
merlangus (L. 1758) and anglerfish *Lophius piscatorius* L. 1758 have shifted northward in the North Sea by 50–800 km (Walther *et al.*, 2002; Perry *et al.*, 2005; Rose, 2005). Similarly, the blue mussel *Mytilus edulis* has contracted its southern range on the shores of the western Atlantic Ocean by over 350 km during the past half century in association with increased air and water temperatures (Jones *et al.*, 2010). Likewise, range shifts for native bay mussel *Mytilus trossulus* and invasive Mediterranean mussel *Mytilus galloprovincialis* are evident on the shores of the eastern Pacific Ocean (Hilbish *et al.*, 2010). Terrestrial ectotherms, such as lizards and toads, are also showing distributional modifications (Huey *et al.*, 2009).

Fish biologists who are interested in developing predictive models for the effects of global climate change on a particular species are especially in need of reliable information on the effects of a changing environment on fish physiology (acclimation and acclimatization), on behaviour and on genetic adaptation (through natural selection). While all three compensatory responses contribute to setting thermal tolerance limits, the exact mixture that contributes to distribution shifts in aquatic ecosystems is not easy to unravel. This is not the intent of this article. Instead, it primarily concerns the thermal physiology of fishes, an area where a significant and rapid growth in knowledge has lead to a conceptual mechanistic understanding, from which useful and ecologically relevant predictions will continue to emerge.

A recent unifying concept, the oxygen and capacity-limited thermal tolerance (OCLTT) hypothesis, suggests that a fish’s capacity to supply oxygen to tissues becomes limited at temperature extremes (Pörtner, 2001, 2010; Pörtner & Farrell, 2008). The foundation of this hypothesis is a fish’s basic need for oxygen at its cells (termed standard metabolic rate, SMR; Chabot *et al.*, 2016a) and its capacity to deliver additional oxygen to support specific activities beyond this basic need. Fry (1947) introduced the term ‘scope for metabolic activity’ to define this capacity in fishes, a term now contracted to aerobic scope (Eliason & Farrell, 2016). Beyond a sound theoretical basis, the concept of aerobic scope is increasingly being applied to fishes because of the new technologies that can more precisely track the movement of oxygen from water through the circulatory system and to needy mitochondria. In fact, the upsurge in temperature studies examining fish cardiorespiratory physiology is impressive (Gollock *et al.*, 2006; Blank *et al.*, 2007a, b; Sandblom & Axelsson, 2007; Steinhausen *et al.*, 2008; Farrell *et al.*, 2009; Gamperl & Driedzic, 2009; Eliason *et al.*, 2011, 2013a, b, c). Moreover, studies have solidly bridged fish ecology and physiology. For example, the niche expansion of the salmon shark *Lamna ditropis* Hubbs & Follett 1947 in the Pacific Ocean has been linked with cardiac physiology (Weng *et al.*, 2005) and failed river migrations of adult sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) have been linked to an exposure to supra-optimal temperature for aerobic scope (Farrell *et al.*, 2008). Other studies have provided good evidence to reject the notion that an *O. nerka* suffocates (can’t extract sufficient oxygen from the water) when the oxygen content of water decreases with increasing temperature (*i.e.* by measuring the oxygen saturation of arterial blood when fish are warmed; Steinhausen *et al.*, 2008; Eliason *et al.*, 2013a).

Working with the goldfish *Carassius auratus* (L. 1758), Fry (1947) and Fry & Hart (1948) were the first to provide a mechanistic explanation of the tolerance ‘factors’ (as proposed by Shelford, 1931) that limit an animal’s biogeographic distribution. They discovered that SMR, on which long-term survival depends, increased exponentially with temperature in *C. auratus* essentially up to a fish’s upper incipient lethal temperature. Where this work stood apart from that of their contemporaries, who had
filled the literature with marvellous examples of Arrhenius plots (the natural logarithm of a rate function $v$ the reciprocal of temperature $^\circ$K) for chemical reaction rates and physiological rate functions such as heart rate, velocity of muscle contraction, heat liberation during muscle contraction and ventilation rate for invertebrates, fishes, amphibians, reptiles and mammals (Crozier, 1926; Stier & Wolf, 1932), is that they also examined and integrated the thermal dependence of maximum metabolic rate (MMR). A key discovery was that MMR peaked at a lower acclimation temperature than SMR. Then, the difference between MMR and SMR was calculated, which was called the scope for metabolic activity but is now called absolute aerobic scope (AAS). When considered over a range of acclimation temperatures, the resulting curve for AAS provides a clear, definitive and quantitative description of aerobic capacity and has been termed the Fry aerobic-scope curve to honour this important, integrative relationship (Farrell, 2009).

In essence, the Fry aerobic-scope curve is a graphic illustration of the thermal dependence of the absolute aerobic capacity to perform activities (such as movement, feeding, growth and reproduction). Also, the Fry aerobic-scope curve shows the temperature when AAS reaches a peak value (termed the optimal temperature, $T_{opt}$), which is the temperature when a fish has its maximum aerobic capacity to perform activities. Consequently, it is not surprising that AAS has a long history of being used to make general predictions about a fish’s capacity to perform activities with respect to environmental temperature (Fry, 1947; Brett, 1971; Claireaux & Lefrançois, 2007; Farrell et al., 2008; Elliott & Elliott, 2010). Fry (1971) also formalized the paradigm that other environmental factors beyond temperature can either raise a fish’s SMR (a load) or reduce its MMR (a limit). While Fry’s (1971) general paradigm has not changed, some of the details have. The devil lies in the details.

Collaborations with fisheries managers have revealed pragmatic difficulties when trying to apply AAS in real-life situations (unpubl. obs.). A good example is the difficulty of properly estimating SMR if a fish is maturing, or to properly acclimate fish to respirometers under trying field conditions. Conversely, managers can rightly ask: Is a wild fish ever at its SMR in nature and would a fish ever thermally acclimate if they vertically migrate through a thermocline even once a day? Moreover, some literature has not accepted the ecological relevance of aerobic scope or the validity of the OCLTT hypothesis when examining thermal effects in various ectotherms (Overgaard et al., 2012; Clark et al., 2013a; Ern et al., 2014; Norin et al., 2014), although counterviews have been provided (Farrell, 2013; Pörtner & Giomi, 2013). Such controversy is not new in biology. In fact, in reference to the interest of biologists in the idea of a temperature optimum, Fry (1947) stated that ‘a very significant means of classification … (is) … sought’, but added that while $T_{opt}$ was ‘not completely barred from the biologist’s vocabulary … (it) … can scarcely be uttered without some mumbled qualification’.

Therefore, the primary purpose of this commentary is to consolidate the conceptual reasoning behind the use of aerobic scope in the context of the thermal physiology of fishes, and then work through some of the pragmatic difficulties and potential solutions for its application to real-life ecological scenarios. The intent is to build from other contributions to this volume (Chabot et al., 2016a, b; Claireaux & Chabot, 2016; Clark & Norin, 2016; Nelson, 2016) and elsewhere (Clark et al., 2013a) that have provided important guidance on how to properly measure oxygen uptake by a fish (i.e. oxygen removal from the water), which is used as a reliable index of metabolic rate under most but not all situations.
THE FRY AEROBIC-SCOPE CURVE

PEAKING

AAS has its maximum at $T_{\text{opt}}$. Thus, $T_{\text{opt}}$ is the acclimation temperature where a fish has a peak absolute capacity for aerobic activity (Brett, 1971; Fry, 1971). Consequently, by definition, peak AAS must decrease above and below $T_{\text{opt}}$. When AAS is zero, a critical temperature ($T_{\text{crit}}$) is reached, beyond which a fish is forced into an anaerobic and time-limited lifestyle (Pörtner, 2001; Pörtner & Farrell, 2008). Aerobic scope can also be expressed as a proportion, factorial aerobic scope (FAS = MMR:SMR), which decreases with on either side of $T_{\text{opt}}$ (Clark et al., 2011, 2013a; Overgaard et al., 2012) and at $T_{\text{crit}}$ FAS reaches a value of 1.

Fry (1971) showed that, depending on the fish species, the curve for AAS can take a variety of shapes (Farrell et al., 2008; Eliason & Farrell, 2016). Thus, a bell-shaped curve (Pörtner & Farrell, 2008) is the simplest to model and conceptualize. Independent of shape, the Fry aerobic-scope curve does a good job of distinguishing stenotherm and eurythermal fishes: a eurytherm has a broader thermal range for AAS than a stenotherm. For example, fishes living in polar waters are often thermal specialists that have adapted to a thermally stable environment (−1.9 to +8°C, with daily temperature fluctuations of only c. 1°C; Franklin et al., 2013). In contrast, eurythermal species have a wide critical thermal (CT; $T_{\text{C}}$) range, e.g. $T_{\text{C}}$ 2 to 37°C for 12°C-acclimated C. auratus (Ferreira et al., 2014) and −1 to 34°C for 12°C-acclimated killifish Fundulus heteroclitus (L. 1758) (Fangue et al., 2006). Eurythermal fishes also have a high capacity to thermally acclimate and this is reflected in the wide thermal range over which they can maintain maximum AAS (Healy & Schulte, 2012). Thus, although stenotherms and eurytherms can be distinguished using CT limits, a much more informative distinction is known that a eurytherm can maintain its maximum AAS over a much wider acclimation temperature range than a stenotherm.

Both AAS and FAS are capacities, not activities. In fact, Fry (1947) emphasized the distinction between how an organism works (metabolism) and what it does (activities) by pointing out that $T_{\text{opt}}$ has two widely different meanings: ‘conditions under which an animal can perform a certain activity best, as judged by objective measurements’, as well as ‘conditions that are best for the animal, whoever may be the judge of that’. Fry (1947) largely concerned himself with the former meaning of $T_{\text{opt}}$ and used the currency of oxygen uptake to define the scope for metabolic activity. Consequently, the Fry aerobic-scope curve says nothing about what activity will occur at a particular temperature, or what is the best temperature for any specific activity. It is interesting that using his distinction between activity and capacity, an untested argument can be built that the broad thermal range for AAS of a eurythermal fish is advantageous because different activities can be performed best at different temperatures. Thus, one activity does not necessarily compete against another (Peter is not being robbed to pay Paul, so to speak). Furthermore, if scope for activities is indeed spread across different temperatures, the need for a eurytherm to invest in the construction of biochemical and anatomical support systems for faster oxygen transport is relaxed. Perhaps, Darwin was hinting at these types of advantages when he suggested: ‘It is not the strongest of the species that survives but the most adaptable’ because a highly stenothermal fish will be more likely to prioritize oxygen usage among important activities (e.g. salmonids with a full gut cannot swim as fast; Farrell et al., 2001).
Given that fishes can prioritize activities to apportion oxygen among competing tissues, knowledge of AAS and FAS can help to understand how a sub-optimal environment limits activities. For example, FAS is useful when considering the transient increase in oxygen uptake that follows feeding in all animals (termed specific dynamic action, SDA, or heat increment). During SDA, peak oxygen uptake in a fish is often two- or three-fold higher than its SMR, depending on the environmental temperature and meal size (McCue, 2006; Chabot et al., 2016b). Thus, if a sub-optimal condition limits FAS to say 1.5, then growth must slow down for several reasons, e.g. peak SDA cannot be realized, SDA takes longer, food intake is reduced to match the capacity for SDA (or ceases if appetite fails), or the meal is regurgitated. Conversely, AAS has significance for life-or-death events (e.g. when absolute athletic performance is of paramount importance, say, for a predator–prey competition or to overcome a hydraulic obstacle). A fish that can swim fast for a longer time (using aerobic swimming) or fastest (using glycolytic swimming) may be favoured for survival or reproductive fitness. Despite many excellent studies on fish energetics (Jobling, 1981), however, the current difficulty with rigorously applying AAS and FAS to ecologically relevant situations lies with the on-going inability to assign precise numbers to how oxygen, when it is in short supply, is prioritized among various tissues and organs. Unfortunately, beyond swimming and digestion, the oxygen cost of a particular activity is poorly understood. For example, while ecologists have recognized the importance of dominant and competitive behaviours, their associated oxygen cost is largely conceptual. Likewise, physiologists have a vast knowledge of ionoregulatory mechanisms, but the oxygen cost of life in fresh water v. salt water is still debated. At supra-optimal temperatures, activities are certainly prioritized and may be turned down or switched off, perhaps in a similar manner as conceptualized for a hypoxic fish (Farrell & Richards, 2009). For example, reproductive development and spawning often cease well before an environmental extreme is reached (Wu, 2009), but the associated metabolic saving is unclear. Nevertheless, broad generalities are emerging. For example, if it is accepted that an active lifestyle (e.g. foraging and migrating) requires more oxygen to be periodically allocated to the locomotory muscles, it appears reasonable to assume that peak MMR (and peak AAS and perhaps SMR when viewed as a maintenance cost) will be higher for fishes capable of high levels of sustained locomotion (Brill, 1996; Farrell, 1996; Korsmeyer et al., 1996; Clark et al., 2011). Whether or not a fish can have a high AAS and be a eurytherm is an interesting question that still needs careful study. On one hand, a lower AAS is certainly associated with the broad Fry aerobic-scope curve in eurytherms such as C. auratus (Ferreira et al., 2014) and F. heteroclitus (Fangue et al., 2006) when compared with stenothermic salmonids (Farrell, 2009). Similarly, brown trout Salmo trutta L. 1758 have a lower and broader Fry aerobic-scope curve than O. nerka (Farrell et al., 2008). Thus, a trade-off between athleticism and eurythermy is evident among species. Intraspecific comparisons, however, require more care. For example, the Chilko population of O. nerka stands out by having a higher and broader Fry aerobic-scope curve compared with other populations from the same catchment (Lee et al., 2003a; Eliason et al., 2011), whereas the difference for northern and southern populations of F. heteroclitus is quite subtle (Healy & Schulte, 2012). Also, tunas (and other partial endothermic fishes) are fascinating in this regard because their cardiac muscle operates at ambient water temperature but pumps blood to much warmer red locomotor muscles. Indeed, appreciation of the different life-history traits used by tunas to exploit variable temperatures in the water column, in search of food,
is much fuller because of insightful studies of tuna cardiorespiratory physiology and cardiac molecular biology (Shiels et al., 1999, 2011; Blank et al., 2002, 2007a, b; Landeira-Fernandez et al., 2012; Clark et al., 2013b; Jayasundara et al., 2013).

Sprint, burst and exhaustive exercise are activities that have enormous ecological relevance. Yet, all three activities largely defer their oxygen cost until after the activity has ceased (it is measured as excess post-exercise oxygen consumption; EPOC). Thus, although long-term survival ultimately depends on a steady delivery of oxygen to mitochondria (paying on demand, if you like), survival periodically requires an oxygen debt (perhaps equivalent to a credit card that needs to be paid off at a later date). Consequently, the rate at which EPOC can be repaid (i.e. recovery) potentially has life-saving consequences (e.g. escaping from a predator just once may be insufficient if the predator can recover faster and try again). Moreover, if EPOC is cleared faster because of a higher AAS, AAS is then a useful index of the speed of recovery. Missing, however, is information on the exact relationships between AAS, EPOC and rate of recovery, even though it is known that EPOC is directly dependent on temperature (Lee et al., 2003b; Zeng et al., 2010), just like SMR. This type of important information could be generated easily by new technologies for fish respirometry. Also, the information might help reinforce the case that a useful way (and certainly easier and faster way) to estimate MMR is to exhaust a fish and measure peak oxygen uptake during recovery. When MMR was measured immediately after a sprint, it was found to be slightly higher compared with MMR measured during prolonged swimming in G. morhua (Reidy et al., 2000). This small discrepancy is probably explained because during recovery oxygen flow from the water to mitochondria is not in a steady state: oxygen uptake progressively decreases with time after exhaustion and burst swimming would have temporarily depleted venous oxygen content beyond that seen during prolonged swimming (Farrell & Clutterham, 2003). Measuring oxygen uptake during prolonged swimming is not without its limitations either. For example, locomotion is progressively powered by anaerobic glycolysis as a fish nears its critical swimming speed in a prolonged swimming test. This means that the oxygen uptake measured near the critical swimming speed underestimates the true metabolic cost of swimming unless EPOC is added to the cost of transport (Lee et al., 2003b; Farrell, 2007). Thus, oxygen removal from the water is not always a reliable index of metabolic rate.

The shape of the Fry aerobic-scope curve (hence $T_{opt}$) is not necessarily fixed during a fish’s life history. For example, a lower quality diet of insects reduced $T_{opt}$ for AAS (Elliott, 1975, 1995, 2000; Elliott & Elliott, 1995, 2010). Furthermore, the daily feeding behaviour of a fish can take advantage of a thermal gradient in its habitat by making vertical movements in the water column. Thus, it could prefer a water temperature that either speeds up digestion of a meal (SDA duration is inversely proportional to temperature), or reduces SMR and hence the need to feed. In fact, adult Pacific salmonids that have stopped eating prior to river migration will seek cool water if it is available, to conserve fat stores for subsequent activities (Eliason & Farrell, 2016). Consequently, just because a $T_{opt}$ exists for AAS, this does not mean that a fish spends its whole life, or even a whole day at $T_{opt}$. To reiterate, $T_{opt}$ for AAS represents a peak aerobic capacity and this capacity may not be needed to be used very often during a fish’s life history. While the mechanistic basis of any ontogenetic flexibility in aerobic scope needs thorough study, it is clear that a fish’s ability to swim to a new location provides an opportunity for it to express a preferred body temperature, provided they have physical access to the preferred
water temperature and there is sufficient aerobic scope to power swimming to get there.

PLUMMETING AEROBIC SCOPE

In an era of global warming, it would appear that the upper $T_{\text{crit}}$ (when AAS is zero) should be of greater interest to fishery managers than critical thermal maximum for loss of equilibrium ($T_{\text{Cmax}}$). Both are indices of the upper thermal tolerance, which is when time-limited survival begins. Yet, rather than the temperature when a fish rolls over because it has no righting reflex, the more conservative index for a fishery manager should be the temperature when a fish must remain immobile with zero AAS. Nevertheless, the data on $T_{\text{Cmax}}$ and incipient lethal temperatures continue to build for fish species and to be highly cited (Vinagre et al., 2015). Even though $T_{\text{Cmax}}$ will continue to be used for species comparisons, $T_{\text{Cmax}}$ measurements also have their difficulties. The debate on how $T_{\text{Cmax}}$ is best measured (Jobling, 1981; Chown et al., 2009) primarily revolves around the need to standardize the rate of change in temperature and the sensitivity of $T_{\text{Cmax}}$ to the rate of warming, as well as the influence of body mass on thermal inertia during rapid heating. Ecologically relevant heating rates would appear to be the most useful, but they can be incredibly complex. Tidepool fishes, for example, deal with complex daily changes in ambient air and sea surface temperature, as well as, for example, variable tidal height, wind, CO$_2$, pH, salinity and cloud cover. Also, the importance of daily oscillations in temperature is increasingly being recognized (Niehaus et al., 2012). Cellular survival mechanisms in tidepool fishes are turned on better in the wild than after steady-state thermal acclimation in the laboratory (Todgham et al., 2006). Therefore, the ecological significance of $T_{\text{Cmax}}$ may have more to do with being a potential trigger for cellular ‘repair, demolition and reconstruction’ functions (Somero, 2010, 2011).

The difficulty with using $T_{\text{Cmax}}$ and resting physiology to examine thermal performance was exemplified in a recent study that tested the idea that anaemia should alter $T_{\text{Cmax}}$ because of a cardiorespiratory constraint (Wang et al., 2014). Instead, anaemia (halving haematocrit) did not alter the $T_{\text{Cmax}}$ of sea bass *Dicentrarchus labrax* (L. 1758) to any great degree. This result would not be a surprise to Fry (1947) given that he found SMR peaks near the upper incipient lethal limit, where it intercepts with MMR. In fact, Wang et al. (2014) showed that routine heart rate and cardiac output both increased with temperature up to just 31$^\circ$C in anaemic and normocythaemic fish, a temperature $>4^\circ$C lower than the measured $T_{\text{Cmax}}$ values (both $>35^\circ$C), much like Fry (1947) had shown earlier for maximum heart rate. As routine oxygen uptake continued on an upward trajectory up to 33$^\circ$C (supported now by increased tissue oxygen extraction), the study indicates that the heart’s capacity to continue increasing heart rate (to keep pace with the thermally induced increase in routine oxygen demand) failed well before these fish lost their righting reflex.

Thus, the attraction to $T_{\text{Cmax}}$ lies less with ecological significance and more with it being a reproducible, high-throughput index of temperature tolerance, one that signals when a highly integrated sensory reflex has been lost and perhaps life-saving cellular compensations have been gained. Therefore, to challenge the ecological relevance of the Fry aerobic-scope curve is rather a moot point if $T_{\text{Cmax}}$ is a replacement. Instead, perhaps it would be better to simply recognize upper $T_{\text{crit}}$ as a more difficult and time-consuming measurement that is restrictive in terms of the volume of data.
AERobic Scope: Uses and Limitations

Fig. 1. Curves for absolute aerobic scope (AAS) after *Carassius auratus* were thermally acclimated to either 12°C (—) or 28°C (—) and acutely tested at each of the temperatures. Values are mean ± s.e. used to statistically model the data with a modified Gaussian four-parameter equation. 95% c.l. for the statistical models. Note that the Gaussian model variably fits the optimal temperature (T_{opt}) and optimal temperature range but cannot intercept the x-axis. Adapted from Ferreira et al. (2014).

that can be generated. Indeed, measuring MMR at supra-optimal temperatures become progressively more difficult if a fish becomes refractory to the stimuli normally used to encourage aerobic exercise. In fact, a fish may be more inclined to escape from the unfavourable thermal conditions rather than remain nearly immobile (as required by their low AAS). Unfortunately, burst swimming at supra-optimal temperatures can be problematic too because aerobic capacity is still required to recover. Recovery might be slowed without sufficient aerobic scope and delayed mortality may be triggered. Thermal acclimation is an additional challenge at supra-optimal temperatures; fishes that have stopped or reduced feeding due to AAS plummeting towards a subsistence level might not survive the required three-week acclimation period. Clearly, increased vigilance and attention to fish husbandry is needed at supra-optimal temperatures. Yet, another difficulty is accurately modelling T_{crit} over a very small thermal range (perhaps just 4–8°C or less) as AAS plummets, something that is greatly hampered by individual variability. In fact, not all statistical models of T_{opt} intercept the x-axis to properly estimate T_{crit} (see Fig. 1).

Nevertheless, when properly measured at supra-optimal temperatures, AAS will reveal an obvious benefit of thermal acclimation. Warm acclimation typically resets SMR and intrinsic heart rate (Tsukuda *et al.*, 1985; Graham & Farrell, 1989; Ferreira *et al.*, 2014) to a lower rate. These are simple compensatory mechanisms to increase upper T_{crit}, provided MMR is not compromised. When a rate function is compared for two acclimation temperatures, thermal compensation during acclimation usually reduces the Q_{10} to between 1.0 and 2.0 (perfect thermal compensation is indicated when Q_{10} = 1.0). If Q_{10} is <1.0, a fish will have entered into a state of metabolic suppression (*e.g.* an aestivating lungfish). Thus, while metabolic compensation does extend upper thermal tolerance, a fish might also move into a specialized and suspended lifestyle when most activities are not supported. Care is needed to identify specialized responses in SMR.

The Fry thermal polygon graphically (and nicely) illustrates the relationship between $T_{\text{Cmax}}$ (or incipient lethal temperatures) and acclimation temperature (Elliott, 1995). Given that Somero (2011) suggested that the most prevalent threats from global change are likely to be long-term sub-lethal effects, looking within the Fry thermal polygon for ecological relevance in the context of global climate change appears a very sensible approach that deserves further attention. For example, other indices of thermal performance can easily be added to a thermal polygon with significant effect (Jobling, 1981). Similarly, Fry et al.’s (1942) original thermal polygon for $C.\text{auratus}$ was used by Ferreira et al. (2014) to insert rate-transition temperatures for aerobic scope and maximum heart rate for three acclimation temperatures. Interestingly, the $T_{\text{crit}}$ and $T_{\text{Cmax}}$ values tended to aggregate (Fig. 2) even though they clearly operate on different time scales and perhaps through different mechanisms. Perhaps, $T_{\text{Cmax}}$ could be substituted for the more difficult to determine $T_{\text{crit}}$ when composing the Fry aerobic-scope curve, just as Fry (1942) used upper incipient thermal limits in his own assessments of AAS.

The OCLTT hypothesis is a very useful conceptual framework for when AAS plummets between $T_{\text{opt}}$ and $T_{\text{crit}}$. This is because the thermal range between $T_{\text{opt}}$ and $T_{\text{crit}}$ is literally the degree ($^\circ$C) of separation between the capacities for maximal performance and subsistence living. This thermal range can thus be viewed as the buffer against future aquatic warming. Consequently, fishes with fewer degrees of separation and a smaller thermal buffer [=$(T_{\text{opt}} - T_{\text{crit}})$ or $(T_{\text{opt}} - T_{\text{Cmax}})$] are at a greater risk. Indeed, certain tropical fishes from the Great Barrier Reef appear to be in this situation (Munday et al., 2008, 2009; Nilsson et al., 2009). Similarly, with some aquatic ecosystems already warmed by $2^\circ$C during the last $c.\, 50$ years, some fishes already may have used up 50% of their thermal buffer. The idea of a small thermal buffer between optimal and subsistence aerobic capacities should not be a foreign concept. Humans succumb when a fever increases their core body temperature from 37 to 45$^\circ$C (i.e. a thermal buffer of $8^\circ$C), but hopefully, anti-pyretic drugs or a hospital are at hand when the fever reaches $c.\, 42$ and $5^\circ$C of the thermal buffer has been used up. Fishes cannot access drugs and hospitals, but they can avoid supra-optimal temperatures, behaviourally, by swimming to cooler regions. Such behaviours may be responsible for some of the population-level shifts in biogeographic patterning noted above. To what degree fishes can rely on adaptation responses within the population to deal with aquatic warming lies outside of this commentary, but remains an open question (Munday et al., 2012; Anttila et al., 2014; Muñoz et al., 2014).

**UPPER PEJUS AND RATE-TRANSITION TEMPERATURES**

Managers should be extremely interested in the rate transition-temperature when AAS first starts to decline. Therefore, this section considers the importance of (and methods to determine) the temperature when a fish’s AAS starts to plummet. The idea of an upper pejus temperature ($T_{\text{pej}}$ = getting worse) was introduced as part of the OCLTT hypothesis to define when AAS progressively (and sometimes abruptly) decreases at supra-optimal temperatures.

Although the term $T_{\text{pej}}$ should be gaining traction as an ecologically relevant thermal index, some difficulties remain to be resolved. Mathematically, $T_{\text{opt}}$ is an inflection point on the curve for AAS, a rate transition-temperature where ASS is greatest and the derivative of the curve is zero. Thus, the lower $T_{\text{pej}}$ and upper $T_{\text{pej}}$ are simply when the derivative of the AAS curve first becomes different from zero (with a positive and
A conceptual conundrum is that \( T_{\text{pej}} \) and \( T_{\text{opt}} \) might be identical for a stenothermal fish with a very sharp peak for AAS, i.e. ASS decreases as soon as the temperature deviates from \( T_{\text{opt}} \). Conversely, eurytherms can probably maintain peak AAS over a wide thermal range, an optimal thermal window (= upper \( T_{\text{pej}} \) – lower \( T_{\text{pej}} \)). Resolving these issues might be as simple as setting the \( T_{\text{pej}} \) as a fixed and high percentage of the maximum AAS at \( T_{\text{opt}} \). Thus, the width of an optimal
thermal window would formally and consistently distinguish stenotherms from eurytherms; some researchers have used 90% of maximum as an arbitrary rate-transition temperature for maximum heart rate (Anttila et al., 2014).

Setting $T_{\text{pej}}$ at a high percentage of AAS does not necessarily get to the issue of ecological relevance (other than being very conservative). Thus, for a sound decision in this regard, it may be necessary to assign different percentages of AAS according to the fish species and the ecological situation. For example, it has been suggested that adult $O. \text{nerka}$ require between 50 and 80% of their AAS to successfully complete a challenging spawning migration up the Fraser River (Farrell et al., 2008; Eliason et al., 2011, 2013c). Very few life histories, however, require a fish to perform such an arduous, once-in-a-lifetime migration. Therefore, more knowledge is needed on how fishes prioritize oxygen to different activities at supra-optimal temperatures. As crucial life support organs, the brain and heart are probably the last to lose their oxygen supply, i.e. one or the other (or both) probably has an insufficient oxygen supply at $T_{C_{\text{max}}}$. Yet, although blood flow distribution is known for some tissues in a few fishes (Bushnell et al., 1992), blood flow distribution to a fish’s brain has not been measured (a guess might be 10% of cardiac output judging by cranial artery diameter). By contrast, the coronary circulation receives just 1–2% of cardiac output (Farrell & Jones, 1992), which might be easier to maintain near a fish’s $T_{C_{\text{max}}}$. Most fishes have no coronary circulation and depend instead on venous blood with a low oxygen partial pressure, which is a precarious oxygen supply for the cardiac mitochondria. Therefore, depletion of venous reserves could easily limit cardiac function (Farrell et al., 2009).

So, until better quality information becomes available, is there a more general rule of thumb for an ecologically relevant $T_{\text{pej}}$, one that might find broad application? Perhaps there is. Growth is considered as a very powerful integrator of environmental, behavioural and physiological influences of a fish’s lifetime fitness. As a result, regulatory agencies such as the U.S. Environmental Protection Agency (EPA) rely heavily on growth studies to set their seven-day average of the daily water temperature maximum (7DADM). For example, the 7DADM of $<18^\circ \text{C}$ (USEPA, 2003) for juvenile $Oncorhynchus \text{mykiss}$ (Walbaum 1792) living in the Pacific Northwest rearing habitats is largely based on a growth study by Hokanson et al. (1977) (USEPA, 2001). Moreover, the oxygen cost of digesting every meal that fuels this growth (protein uptake, turnover and deposition) is reflected in SDA. The gut may be a lower priority circulation in fishes, even though it receives c. 25% of cardiac output in non-digesting animals. For example, gut blood flow can be completely switched off under stressful situations (Farrell et al., 2001) and the post-prandial cardiorespiratory response is blunted by hypoxia (Eliason & Farrell, 2014). Lastly, AAS sets the capacity for SDA. So, if it is assumed that SDA doubles SMR and all other things are equal, digestion still might be fully supported if FAS falls to 2. Thus, $T_{\text{pej}}$ for digestion would be set at 25% of peak AAS at $T_{\text{opt}}$ if, for example, FAS normally reaches 8 at $T_{\text{opt}}$. Clearly, much work is needed before applying this idea (e.g. the considerable species variability in peak AAS means that $T_{\text{pej}}$ for digestion would be a variable percentage of peak AAS). Still, there are encouraging signs. For example, four closely related tropical killifishes from the genus $Aphyosemion$ were shown to differ in the time required to process food at different temperatures (McKenzie et al., 2013). Specifically, while routine oxygen uptake for all four species increased similarly with temperature, the speed with which meals were digested varied between high and low altitude species and there were differential effects of temperature. The authors concluded that ‘exposure to temperatures beyond
the apparent thermal envelope in their habitats caused profound declines in (digestive) function’ because these stenothermal fishes were adapted to discrete altitudinal ranges.

\( T_{\text{pej}} \) can be identified using two other time-honoured mathematical approaches. While both are familiar to fish biologists interested in thermal effects, they both require small temperature increments to be of maximum value. An Arrhenius plot will identify an Arrhenius breakpoint temperature (\( T_{\text{AB}} \)), an abrupt change in slope (which is equivalent to the rate being measured). If an Arrhenius plot is applied to AAS, theoretically the first \( T_{\text{AB}} \) with a negative slope might be useful as a lower \( T_{\text{pej}} \), whereas \( T_{\text{opt}} \) (or the start of the optimal thermal window) is the \( T_{\text{AB}} \) when the curve no longer has a slope. Thus, the upper \( T_{\text{pej}} \) for AAS is the \( T_{\text{AB}} \) when the plot takes on a positive slope. There are two drawbacks of using Arrhenius plots: transforming biological rate functions with a natural logarithm does not properly linearize them because very few have a \( Q_{10} \) as high as 2·72, and very few data points limit the resolution of a \( T_{\text{AB}} \) (Fig. 3). More typically \( Q_{10} \) is 2–3, which indicates a two to three-fold increase in the rate of oxygen uptake for a 10° C increment (Lefrançois & Claireaux, 2003). Recently, an incremental \( Q_{10} < 2\cdot0 \) was used with continuous measurements of maximum heart rate from ECG recordings to identify a rate-transition temperature that appears to be close to the upper \( T_{\text{pej}} \) for AAS (Casselman et al., 2012; Anttila et al., 2013; Drost et al., 2014; Ferreira et al., 2014; Chen et al., 2015). Thus, an incremental \( Q_{10} \) approach could be easily be applied more broadly to other key biological processes, provided test temperature increments were 0·5–1·0° C just like the studies of maximum heart rate (for studies of AAS, test temperatures have been more typically 2–4° C apart).

Thus, despite the mechanistic insights that the Fry aerobic-scope curve offers, data generation with this method is inevitably constrained by time and technical considerations (e.g. reliable SMR determinations require several days of measurement; Chabot et al., 2016a). Consequently, it is reasonable to ask whether another biological rate function, one that is more easily measured, can act as a surrogate for AAS. Below, heart rate is considered for this role at supra-optimal temperatures.

**IS HEART RATE A USEFUL SURROGATE FOR AEROBIC SCOPE?**

All fishes examined to date increase their heart rate with temperature (Farrell et al., 2009). Furthermore, the response of AAS to temperature is determined in large part by changes in heart rate, which then reflects cardiac capacity. Indeed, Fry (1947) observed that heart rate in exercising brook trout *Salvelinus fontinalis* (Mitchell 1814) reached a plateau at a supra-optimal temperature below their upper incipient lethal temperature, whereas routine heart rate reached the same maximum value closer to the upper incipient lethal temperature (see Fig. 3; Farrell, 2009). Therefore, a reasonable expectation is that the thermal responses of heart rate might be useful for ecologically relevant predictions, especially if the rate-transition temperatures for heart rate are similar to those for AAS. Arrhenius plots were used over a century ago to examine the thermal dependence of heart rate, but at that time there was a greater interest in the slope of the line than in the \( T_{\text{AB}} \) (terrapin, species not given: Snyder, 1905; *Ambystoma*: Laurens, 1914 and a *Corregonus* species: Crozier, 1926).

An important advance for invertebrates, one that goes well beyond the well-established relationship between resting heart rate and temperature (Crozier, 1926; Stier & Wolf, 1932), is the relationship established between the thermal performance...
Fig. 3. An example of an application of an Arrhenius plot for (a) oxygen uptake data [▲, maximum metabolic rate (MMR); ■, standard metabolic rate (SMR); ●, absolute aerobic scope (AAS)] and (b) heart rate (▲, maximum heart rate; ■, resting heart rate; ●, scope for heart rate). Original data derived from Fry (1947) for Carassius auratus. Note that while the split regression lines generally have high $r^2$ values, the fit of the regression line to the actual data is not that precise because the temperature increments are not that close to each other to generate the necessary precision with breakpoint analysis.
of heart rate (using $T_{AB}$) and the biogeography of marine intertidal invertebrates. For example, when porcelain crab congeners (genus: *Petrolisthes*; Stillman & Somero, 1996) and turbinate snail congeners (genus: *Chlorostoma*, formerly *Tegula*; Stenseng et al., 2005) were warmed, resting heart rate increased with temperature up to an abrupt rate-transition temperature (termed $T_{C_{\text{max}}}$ for the heart), which varied by 6–7°C among species and congeners, and was very closely related to the maximum microhabitat temperature in nature (Tepolt & Somero, 2014). Consequently, a functional index of habitat boundaries for these intertidal invertebrates was the temperature when heart rate no longer increased. Despite the similarity between $T_{C_{\text{max}}}$ for the whole animal and the ‘$T_{C_{\text{max}}}$ for the heart’ (Somero, 2010), the term $T_{C_{\text{max}}}$ for the heart should not be truncated and confused with the more common usage of $T_{C_{\text{max}}}$ for the whole animal. Interestingly, the resting heart rate for other crab species reached a plateau when lactate started to accumulate in their blood, which is indicative of an oxygen delivery problem near to $T_{\text{crit}}$ (Frederich & Pörtner, 2000; Frederich et al., 2009; Storch et al., 2009). The physiological significance, however, of the three distinct rate-transition temperatures for resting heart rate observed in the intertidal snail *Echinolittorina malaiana* (Marshall et al., 2011) remains unclear.

In fishes, resting heart rate was recently used to examine physiological plasticity of cardiorespiratory function in the longjaw mudsucker *Gillichthys mirabilis* Cooper 1864 (Jayasundara & Somero, 2013). The $T_{AB}$ of routine heart rate was identified in lake whitefish *Coregonus* spp. embryos almost a century ago (Crozier, 1926). As noted above, a potential limitation of studying resting heart rate is that it is more likely an indicator of $T_{C_{\text{max}}}$ rather than $T_{\text{opt}}$ for AAS. Therefore, attention probably needs to be switched to a fish’s maximum heart rate rather than the resting heart rate. Casselman et al. (2012) explored the specific relationship between the rate-transition temperatures for AAS and for maximum heart rate, using pharmacological stimulation in an anesthetized fish during acute warming. The results were entirely consistent with the earlier but more limited observations by Fry (1947) and Brett (1971). The findings have been subsequently supported by additional work with salmonid species (Anttila et al., 2013; Chen et al., 2013, 2015; Verhille et al., 2013), Arctic cod *Boreogadus saida* (Lepechin 1774) (Drost et al., 2014), three *Danio* species (Sidhu et al., 2014) and *C. auratus* at different acclimation temperatures (Ferreira et al., 2014; as depicted in Fig. 2). What has emerged is that the temperature range that is bracketed by $T_{QB}$ (when the incremental $Q_{10}$ for maximum heart rate first decreases below and remains below 2-0) and $T_{\text{arr}}$ (the temperature when maximum heart rate first becomes arrhythmic) approximates the same temperature range overwhich AAS is plummeting.

Moreover, $T_{\text{arr}}$ is a very good index of $T_{C_{\text{max}}}$, whereas $T_{QB}$ appears to approximate $T_{\text{pej}}$ (when set at 90% of peak AAS; see Fig. 2). Between $T_{QB}$ and $T_{\text{arr}}$, heart rate reaches its maximum value ($T_{\text{max}}$; the derivative is zero) and heart rate may even decrease before $T_{\text{arr}}$ is reached. Given that this new technique of measuring a fish’s maximum heart rate has a much higher throughput than measuring AAS, maximum heart rate may emerge as a very useful surrogate technique to establish when a fish is in a supra-optimal temperature range. An important physiological implication of this association is that it confirms that the capacity of the heart to beat ever faster with increasing temperature occurs well below the temperature when a fish loses its balance ($T_{C_{\text{max}}}$). Less clear is which rate-transition temperature for maximum heart rate might be a useful index of $T_{\text{opt}}$ or the lower $T_{\text{pej}}$ for AAS. Depending on the fish species and acclimation temperature, $T_{AB}$ or $T_{QB}$ might fit the bill. As more species and

environmental conditions are examined, these nuances may be resolved. Minimally, this high-throughput method has the potential to identify temperatures when AAS is plummeting.

Fry (1947, 1971) expressed concerns about the interaction of environmental factors; laboratory experiments typically change one variable while controlling the others. He noted that nature is not that simple. Therefore, what is measured in the laboratory will always have limited ecological relevance in one way or another. This should not distract from the fact that AAS is a valuable index of the capacity of a fish to remove oxygen from water and fuel metabolic activities, which was Fry’s (1947) original intention. If a fish has less aerobic capacity, it cannot perform as well. What was also evident with Fry’s (1947) earlier work, and something that is even clearer now, is that the ability to increase AAS with temperature is determined primarily by the heart’s capacity to beat faster. Ecologists and fishery managers could take better advantage of these facts. Also, for the more ecologically minded, maximum heart can be tested in the field in acclimatized fishes [this test has been used on the tailgate of a truck in the field (S. Narum, pers. comm.) and at fish hatcheries (Chen et al., 2015; M. Casselman, pers. comm.)]; fishes do not have to be transported to the laboratory and acclimated there. Finally, fishes typically recover after these heart-rate tests, provided $T_{\text{Cmax}}$ is not exceeded, and they could be released after testing. Some fishes have been transported afterwards from the Arctic to the Vancouver Aquarium (Drost et al., 2014).

CONCLUSIONS

Aerobic scope is a fundamental characteristic and its dependence on environmental temperature can be measured. It must be clearly stated that AAS is only a capacity. How a fish exploits this capacity is poorly understood; it involves complex behavioural interactions with the environment, its competitors and its food. Thus, peak AAS may not be realized at any given time. Indeed, AAS and FAS are more likely to contribute to setting a fundamental ecological niche rather than a realized niche, even though changes in biogeographic patterning of fishes and aquatic invertebrates in response to unfavourable environments have been mapped onto the thermal response of aerobic scope and other key physiological rate functions such as heart rate. Consequently, Fry aerobic-scope curves can have great utility for ecologists and fisheries managers provided the difficulty (and associated limitations) of both obtaining (and accurately modelling) aerobic-scope data are recognized and appreciated. Lastly, and unfortunately, obtaining high quality aerobic scope data inevitably takes a considerable amount of experimentation, which then limits the breadth of application.

Therefore, if any appreciable inroad is to be made into understanding the thermal performance of around 30,000 fish species, high-throughput measurements that have functional relevance will need to be developed and validated. Although easy to measure, $T_{\text{Cmax}}$ values alone are rarely used by fish managers. Other metrics with greater ecological relevance show promise, but need to be refined. To streamline the task ahead, educated guesses and prioritizations will be needed to decide on which species to consider first. Criteria could include putting stenotherms ahead of eurytherms, using existing $T_{\text{Cmax}}$ data to target species that are most at risk relative to local changes, giving immediate attention to economically important species that are thermally sensitive and being more knowledgeable on the capacities of invasive species relative to those
that need to be protected. Decisions, however, need to be made at a local level and using the well-honed framework of aerobic scope.

For the sceptics, the closing statements concern the remarkable Antarctic icefishes that are unique in the vertebrate world because they lack haemoglobin and are probably Nature’s best example of the inevitable linkage between temperature, aerobic scope and cardiac activity. What is known for sure is that without haemoglobin, the amount of oxygen these fishes can dissolve in their blood (= plasma) is about one tenth of other fishes. To compensate, they have a hugely enlarged heart (×10 larger than some fishes) that pumps a large volume of blood with each heartbeat. They probably have a limited AAS compared with other fishes and they live at a very stable temperature near 0°C to survive. They are probably intolerant of temperatures much warmer than those they live in, and thermal acclimation may not be an option. Thus, they would probably be a casualty of global warming, just like some coral-reef fish species.

In the end, Newtonian Laws work well for everyday activities, but perhaps travel to the next galaxy should not be taken using them alone. So those who worry about the universal nature of the OCLTT concept and the ecological application of the Fry paradigm should be careful not to throw out the baby with the bath water. Instead, more instructive in the long run may be to ask why empirical data do not quite fit some aspect of a concept and search for a mechanistic explanation of the variance.

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