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REVIEW

The role of mechanistic physiology in investigating impacts of global warming on fishes

Sjannie Lefevre^{1,*}, Tobias Wang² and David J. McKenzie³

ABSTRACT

Warming of aquatic environments as a result of climate change is already having measurable impacts on fishes, manifested as changes in phenology, range shifts and reductions in body size. Understanding the physiological mechanisms underlying these seemingly universal patterns is crucial if we are to reliably predict the fate of fish populations with future warming. This includes an understanding of mechanisms for acute thermal tolerance, as extreme heatwaves may be a major driver of observed effects. The hypothesis of gill oxygen limitation (GOL) is claimed to explain asymptotic fish growth, and why some fish species are decreasing in size with warming; but its underlying assumptions conflict with established knowledge and direct mechanistic evidence is lacking. The hypothesis of oxygen- and capacity-limited thermal tolerance (OCLTT) has stimulated a wave of research into the role of oxygen supply capacity and thermal performance curves for aerobic scope, but results vary greatly between species, indicating that it is unlikely to be a universal mechanism. As thermal performance curves remain important for incorporating physiological tolerance into models, we discuss potentially fruitful alternatives to aerobic scope, notably specific dynamic action and growth rate. We consider the limitations of estimating acute thermal tolerance by a single rapid measure whose mechanism of action is not known. We emphasise the continued importance of experimental physiology, particularly in advancing our understanding of underlying mechanisms, but also the challenge of making this knowledge relevant to the more complex reality.

KEY WORDS: Critical thermal maximum, CT_{max} , Metabolism, Scope for activity, Temperature tolerance

Introduction

Global warming is accelerating at an alarming rate, causing progressive elevations of seasonal temperatures and also wider thermal variation, with increased frequency of extreme heatwaves (Frölicher et al., 2018; Collins et al., 2019). The responses to climate warming by animal populations are commonly divided into three ‘universal’ phenomena. Firstly, there is a seasonal change in timing of life cycle events, for example earlier spawning or longer reproductive seasons (Poloczanska et al., 2013; Crozier and Hutchings, 2014; Myers et al., 2017; Rogers and Dougherty, 2019). Secondly, there are latitudinal shifts in species distributions, notably a poleward invasion by temperate and sub-tropical species

(Parmesan and Yohe, 2003; Perry et al., 2005; Hickling et al., 2006; Poloczanska et al., 2013). The third phenomenon is a reduction in average body size, due to a decline in final adult size and increases in the proportion of younger and smaller individuals (Daufresne et al., 2009; Gardner et al., 2011; Audzijonyte et al., 2020). The increased frequency, intensity and duration of heatwaves is, however, considered to be the major challenge for the survival and fitness of aquatic ectotherm fauna (Vasseur et al., 2014; Buckley and Huey, 2016; Williams et al., 2016; Stillman, 2019). Indeed, mortality events of fishes after unusually high summer temperatures and heatwaves are increasingly documented in freshwater and marine habitats (Gunn and Snucins, 2010; Hinch et al., 2012; Pearce and Feng, 2013; Till et al., 2019). The mechanisms underlying all of these phenomena are not understood, but will be based on physiological functions and responses by individual animals, so experimental biology holds much promise in advancing the understanding of global warming impacts on fishes (Wang and Overgaard, 2007; Pörtner and Farrell, 2008; Pörtner and Peck, 2010; Huey et al., 2012; Seebacher and Franklin, 2012; Seebacher et al., 2015; Stillman, 2019).

The study of fish thermal physiology has a long history and much is now understood about fundamental mechanisms underlying biochemical and physiological responses to temperature changes (Fry, 1958; Cossins and Bowler, 1987; Prosser and Heath, 1991; Schulte, 2011; Currie and Schulte, 2014; Little et al., 2020). There are relatively long-standing theories about the universal principles that would define how water temperature influences the physiology of fishes and, consequently, determines their performance in their environment. Two theories in particular have been actively promulgated to the scientific community, decision makers and media. These are the ‘gill oxygen limitation’ (GOL; Pauly, 1981) and ‘oxygen- and capacity-limited thermal tolerance’ (OCLTT; Pörtner, 2001; 2010) hypotheses. Fishes are valuable resources, from food to tourism, and negative effects of global warming on their populations threaten many ecosystem services globally. Research into the thermal physiology of fishes has therefore intensified, with particular focus on evaluating how temperature affects physiological performance and on defining thermal tolerance. This research has contributed greatly to our knowledge and understanding, but has also provoked vivid controversy about the validity and universality of the GOL and the OCLTT paradigms, and animated discussions on proper experimental methods and strategies, particularly regarding the design of protocols to evaluate thermal tolerance in fishes. Here, the evidence is reviewed for and against the GOL and OCLTT models, with emphasis on the latter. Experimental physiologists have focused heavily on the use of aerobic scope to develop thermal performance curves (TPCs), in the specific context of the OCLTT. We consider the value of TPCs that use traits of physiological energetics, to broaden future experimental research. The limitations of the critical thermal protocol are reviewed, considering the various mechanisms that

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can be involved in morbidity and mortality from thermal stress on different time scales. The review concludes by considering the value of laboratory and field studies, in understanding mechanisms of thermal tolerance in fishes and the physiological impacts of global warming on natural populations.

Universal patterns – universal explanations?

The GOL paradigm has been proposed as a universal physiological mechanism to explain the global decline in adult size of many fish species (Pauly, 1981; Cheung et al., 2012). The OCLTT hypothesis has a much broader scope; it seeks to explain all elements of thermal tolerance in fishes, by defining their ability to perform over their natural thermal range (or when exposed to future warming scenarios), as well as their absolute upper and lower tolerance boundaries (Pörtner, 2010). Both paradigms focus on cardiorespiratory physiology and the capacity to supply oxygen for aerobic metabolism when fishes are warmed. The basic premise is that, because water is relatively poor in oxygen, meeting requirements for aerobic metabolism may become challenging when metabolic rate is raised by warming. There are, however, distinct mechanistic physiological details to each model, and distinct reasons why they are the focus of controversy.

The gill oxygen limitation paradigm

That adult body size decreases in fish grown at warm temperatures is fairly well established based on laboratory and field measurements (Audzijonyte et al., 2019; Hume, 2019; Loisel et al., 2019), and is referred to as the temperature–size rule (TSR; Atkinson, 1994). The mechanisms underlying the TSR remain to be understood and have been carefully reviewed (Verberk et al., 2021). Although initial theories focused on life history traits (Angilletta and Dunham, 2003; Angilletta et al., 2004; Arendt, 2011), there has been growing interest in a potential role for oxygen supply in fishes, stimulated to some extent by the GOL paradigm (Hoefnagel and Verberk, 2015; Leiva et al., 2019; Rubalcaba et al., 2020; Verberk et al., 2021). The GOL model proposes that, as fishes grow, body volume increases proportionally more than gill respiratory surface area, due to geometric volume-to-surface scaling of spherical bodies. Fishes would therefore become increasingly less able to meet their oxygen requirements as they grow and are proposed to reach maximum size when their gills can only meet oxygen demands of basal metabolism. That is, larger fish would eventually have no aerobic scope (AS), which is defined as the capacity to provide oxygen for all aerobic activities beyond basal maintenance (Fry, 1971). Such activities include tissue anabolism and growth (Pauly, 1981; Cheung et al., 2011). As warming raises basal oxygen demands, the GOL model predicts that the limited branchial capacity for oxygen uptake would occur at smaller maximum sizes, and has therefore been used to project global declines in fish size in a warmer future (Cheung et al., 2011, 2012; Pauly and Cheung, 2017).

The GOL model is not, however, supported by physiological knowledge or data. Fish gills are folded surfaces, and there is no theoretical support for the notion that they suffer from surface-to-volume constraints of spherical bodies (Lefevre et al., 2017, 2018). Data on multiple fish species show that AS does not decline with mass (Killen et al., 2016; Lefevre et al., 2017; Audzijonyte et al., 2019; Blasco et al., 2020a preprint). The model also disregards universal allometric scaling of basal metabolic rate with mass in animals (Schmidt-Neilsen, 1982; Killen et al., 2010). Many studies focus on food limitation as the causative factor for declining fish sizes in the field (Morita et al., 2015; Myrvold and Kennedy, 2015; Dantas et al., 2019; Huret et al., 2019; Queiros et al., 2019).

Reduced size with warming may also reflect changes to life history traits that cause an earlier shift from investment in somatic growth to investment in reproduction, resulting in smaller asymptotic size (Audzijonyte et al., 2016; Audzijonyte and Richards, 2018).

Although the GOL model is fundamentally flawed, this does not mean that oxygen supply as such might not be one factor underlying the TSR in water-breathing ectotherms (Atkinson et al., 2006; Hoefnagel and Verberk, 2015; Leiva et al., 2019; Rubalcaba et al., 2020; Verberk et al., 2021). The theory of ‘maintain aerobic scope and regulate oxygen supply’ (MASROS) proposes that evolution has modified growth trajectories to avoid oxygen limitation at warm temperatures. If warming causes standard metabolic rate (SMR; basal metabolic rate at the temperature) to rise more steeply with mass than maximum metabolic rate (MMR; maximum rate of oxygen consumption at the temperature), this will reduce AS (calculated as MMR–SMR) with increasing mass. If AS is lower at high temperatures, fishes may limit some oxygen-demanding activities, like foraging and growth, if these would constrain their ability to face transient demanding conditions such as disease, episodes of hypoxia or predator attack (Atkinson et al., 2006; Verberk et al., 2021). Modelling provides some support for this, indicating that oxygen supply capacity might decline with body mass in aquatic ectotherms at warm temperatures (Rubalcaba et al., 2020). Such modelling is, however, largely based on metabolic data that were collated from separate studies. Datasets that include several temperatures and a sufficiently large range of body masses for a single species, to determine the scaling exponents for metabolic traits accurately, are very rare. In Atlantic cod *Gadus morhua*, Tirsgaard et al. (2015) found that SMR rose more steeply than MMR with mass at warm temperatures (15 and 20°C) but not at cooler ones (2, 5 and 10°C), but the slope for MMR did not decline at higher temperature. In European perch *Perca fluviatilis*, the slopes for MMR and AS did appear to be lower at 28°C compared with 20°C, and Christensen et al. (2020) concluded that a reduction in AS at the optimal temperature ($AS_{T_{opt}}$) with body size was due to limitations of gas transfer. Messmer et al. (2017) found that the slope for MMR was significantly higher at 33°C than at 28.5°C, while the slope for AS did not differ. Although more studies of this nature are clearly needed, the examples illustrate that caution is warranted when using cross-species data to model the response of individual species. Overall, the MASROS theory still awaits concrete evidence.

If constraints on oxygen supply do occur with increasing size in aquatic ectotherms, this might render larger animals less able to perform aerobic activities at warm temperatures (Rubalcaba et al., 2020). It is interesting, therefore, that acute thermal tolerance declines with body size in many fish species (reviewed by McKenzie et al., 2020). Blasco et al. (2020a preprint) evaluated the capacity of Nile tilapia *Oreochromis niloticus* to perform intense aerobic exercise when acutely warmed and found a negative relationship between body mass and the temperature at which animals fatigued. This was linked to a very significant mass-related decline in MMR achieved at fatigue, which may indicate that the warming challenge revealed constraints on capacity for oxygen supply in larger animals (Blasco et al., 2020a preprint). Effects of mass on oxygen supply capacity, and potential links to tolerance of warming, are therefore topics for further research.

The oxygen- and capacity-limited thermal tolerance paradigm

Although the OCLTT paradigm has been proposed as a universal explanation for the influence of temperature on performance in fishes (Pörtner, 2010), the hypothesis is intensely debated with

various reviews and experimental studies voicing major criticisms (Clark et al., 2013; Pörtner, 2014; Farrell, 2016; Jutfelt et al., 2018). The OCLTT paradigm is directly based on the Fry paradigm that describes a TPC for AS in fishes (Fry, 1947, 1971). Briefly, fishes are exposed (either acutely, acclimated or acclimatised) to a range of temperatures, then SMR and MMR are measured by respirometry, to calculate AS (Fry, 1971). In the Fry and OCLTT paradigms, a unimodal curve for AS is expected due to the assumed differential thermal responses of SMR and MMR: SMR would increase exponentially due to direct kinetic effects, while the increase in MMR is assumed to increase up until a maximum extent defined by cardiorespiratory capacity, beyond which it increases no further [Fry, 1971; see explanatory figures in McKenzie et al. (2016) and Pörtner (2010)]. This would then reveal the temperature where AS is maximal, which would presumably be the optimal temperature ($T_{opt,AS}$) for physiological performance. The TPCs for AS have been reported in many species, with MMR measured either in a swimming respirometer or by chasing to exhaustion. Indeed, swimming or chasing fish to exhaustion has become the norm to describe AS for most fish physiologists.

It seems intuitive that aerobic capacity is linked to Darwinian fitness, as fish will die if unable to escape from predators or unable to forage and feed. Moreover, although fish can survive for some time without allocating energy to growth and reproduction, both are essential for fitness. Fitness is, however, the outcome of a complex interplay among physiology, behaviour and ecology. Thus, while it may seem straightforward to assume that any reduction in AS will reduce fitness (Fry, 1971; Pörtner and Farrell, 2008), direct evidence is lacking. Furthermore, different species have different life histories and many may rarely utilise their full AS, making it a complex task to predict how short- or long-term reductions in AS affect fitness in the wild. In addition to the problems of linking AS to fitness, the

universality of the OCLTT hypothesis is questioned by empirical data. Many species do not show a unimodal TPC for AS, and maintain high AS until very close to critical temperatures (Lefevre, 2016; see Table S1). Within a large diversity of species (Fig. 1) it is clear that, in some, AS does decrease at high temperatures, but in others, AS increases across the entire thermal tolerance range, while numerous species maintain AS over a broad range of biologically relevant temperatures. The shape of the TPC for AS could depend on many factors, such as life stage, climatic region and abiotic habitat characteristics. Methodological issues may also be significant. We explored these possible variables using a multiple correspondence analysis (MCA; Fig. 2) and, although there are major disparities among studies (Fig. 2A), there are some interesting tendencies.

Adults tend to reduce AS, while juveniles tend to maintain or increase AS (Fig. 2B). A greater resilience of juveniles in terms of sustaining AS under exposure to environmental stressors has also been observed for the effect of elevated CO_2 (Lefevre, 2019), although interpretation is complicated by the limited number of studies on different life stages of the same species. In sockeye salmon *Oncorhynchus nerka*, reduced AS with warming has been reported regardless of life stage (Brett, 1964; Lee et al., 2003; Eliason et al., 2011); in common triplefin *Forsterygion lapillum*, AS is reduced in juveniles (McArley et al., 2018), but effects were mixed in adults (Khan and Herbert, 2012; Khan et al., 2014).

Regarding region and temperature range (Fig. 2C), some polar species tend to reduce AS (Lowe and Davison, 2006; Seth et al., 2013) while others maintain it (Seth et al., 2013; Drost et al., 2016; Kunz et al., 2018). Sub-tropical species more often maintain (Marras et al., 2015; Fu et al., 2018; Laubenstein et al., 2018; Frenette et al., 2019; Mohammadi et al., 2019) or increase AS (Fry, 1947; Claireaux et al., 2006; Tu et al., 2012; Pang et al., 2016; Zhou

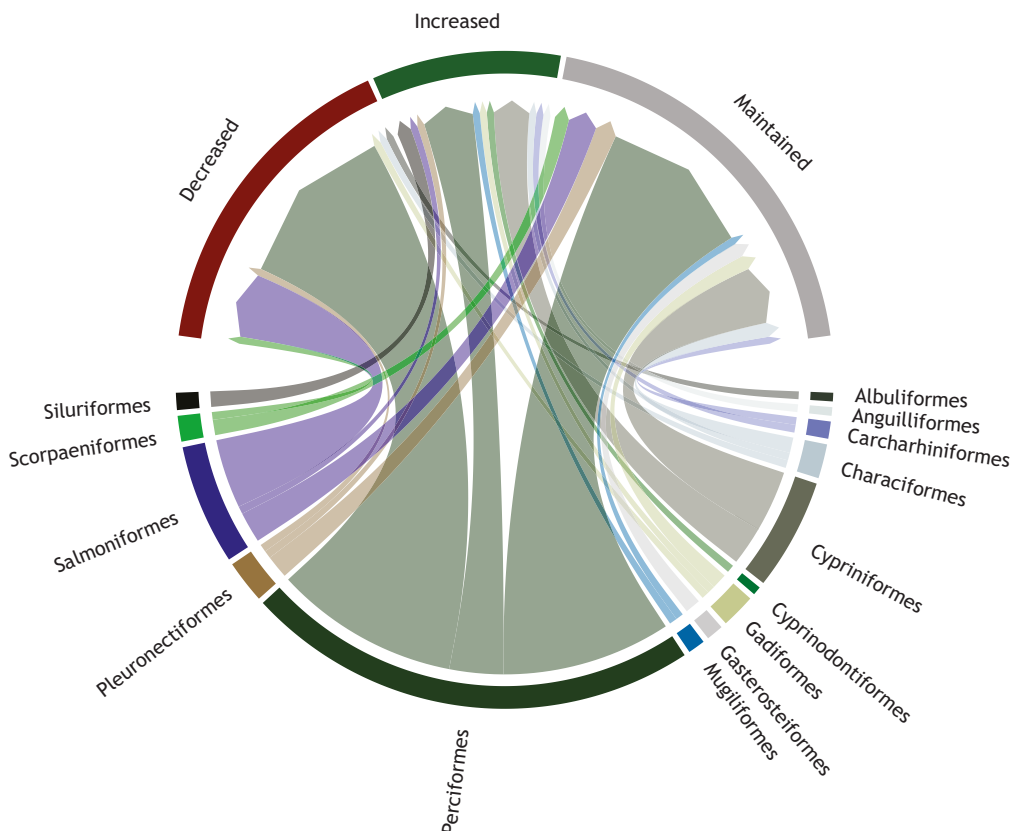


Fig. 1. Taxonomic orders to which species in different studies belong. For each study, it was determined whether the aerobic scope at the highest temperature used was decreased, increased or maintained compared with the temperature at which it was maximised. Compared with the number of species in the order, salmonids stand out as having been studied particularly often. The large number of studies on Perciformes is not surprising given that the order comprises almost a third of all fish species. The plot was generated using *circulize* (v.0.4.12; Gu et al., 2014; <https://cran.r-project.org/package=circulize>) with R (v.4.0.2; <https://www.r-project.org/>) in RStudio (v.1.3.1093; <https://rstudio.com/>). All collected details and references are available in Tables S1 and S2.

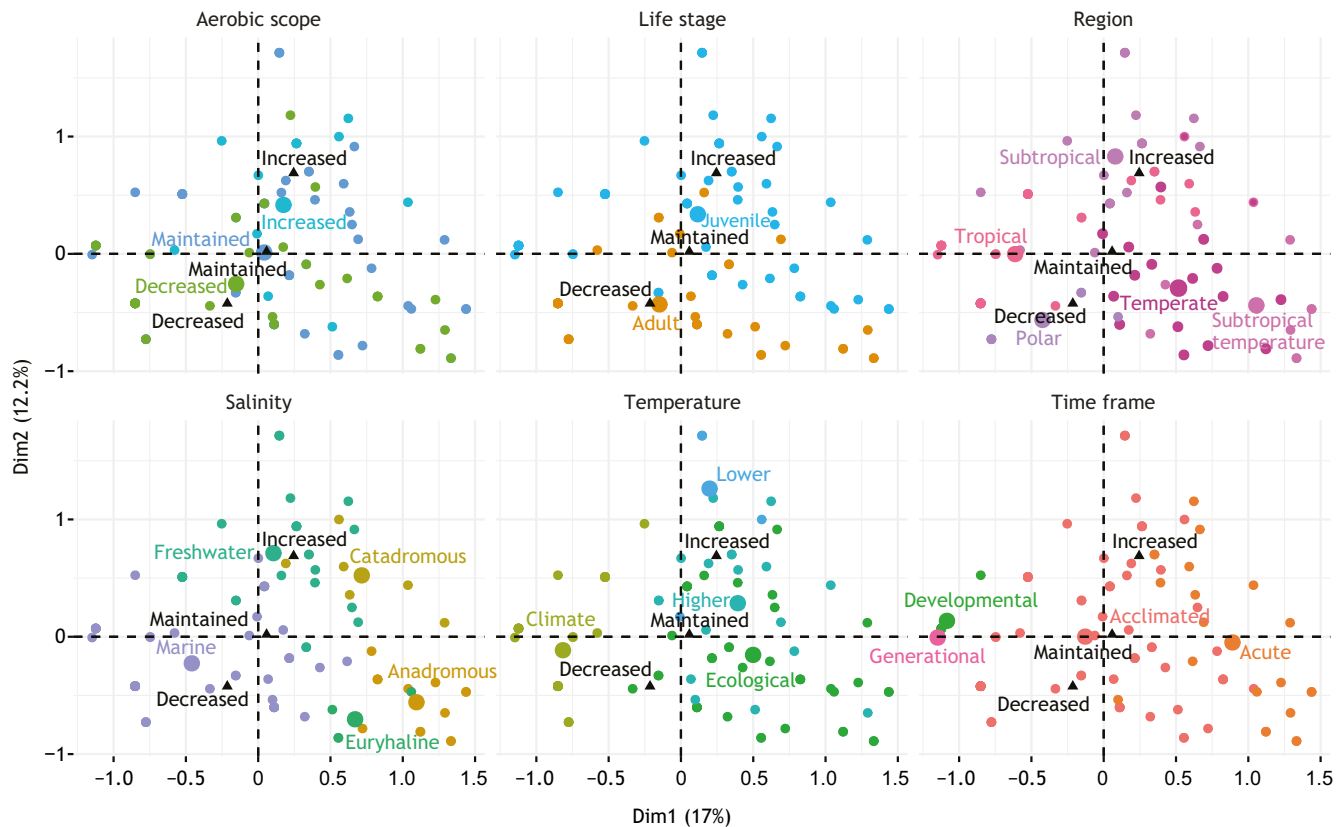


Fig. 2. Multiple correspondence analysis bi-plot. Plots showing the aerobic scope response as a supplementary variable (triangles) and individual study/species data points coloured by (A) whether AS was decreased, maintained or increased in response to elevated temperature, (B) life stage, (C) region, (D) salinity, (E) temperature treatment regime and (F) treatment time frame. Data were analysed and plotted using factoextra (v.1.0.7; <https://cran.r-project.org/package=factoextra>), FactoMineR (v.2.4; Le et al., 2008; <http://factominer.free.fr/>) and ggplot2 (v.3.3.3; Wickham, 2016; <https://ggplot2.tidyverse.org>) with R (v. 4.0.2) in RStudio (v.1.3.1093). All collected details are available in Tables S1 and S2.

et al., 2019; Crear et al., 2019, 2020). This pattern may reflect that sub-tropical species are more likely to occur over a broad temperature range with larger variations and thus be eurythermal, while polar and tropical species are adapted to a more narrow temperature range and are typically considered stenothermal. A cross-species analysis found that species with higher $T_{opt,AS}$ also tended to have a relatively higher $AS_{T_{opt}}$, but there was no correlation, and hence no trade-off, between this $AS_{T_{opt}}$ and breadth of the thermal range (Nati et al., 2016).

While one might not expect salinity itself to play a major role in how temperature affects AS, the majority of freshwater fishes studied maintain or increase AS, while AS is reduced in half the marine species studied (Fig. 2D; Table S1). This may be a result of many freshwater species living in more variable thermal environments (i.e. lakes or rivers) than most marine species. Some of the most heat-tolerant freshwater species, in terms of AS, are the barramundi *Lates calcarifer* that maintain AS from 23 to 38°C (Norin et al., 2014, 2016; Gomez Isaza et al., 2019), the hot-springs population of lake Magadi tilapia *Alcolapia grahami* with highest AS at 39°C (Wood et al., 2016), and central stoneroller *Campostoma anomalum* and Southern redbelly dace *Chrosomus erythrogastrer* that maintain AS from 10 to 30°C (Frenette et al., 2019). Most of the marine species that decrease AS are tropical coral reef cardinalfishes (Apogonidae) and damselfishes (Pomacentridae) (Nilsson et al., 2009; Gardiner et al., 2010; Rummer et al., 2014; Motson and Donelson, 2017; Laubenstein et al., 2019). Other marine species seem more resilient (Duthie, 1982; Mallekh and Lagardere, 2002; Marras et al., 2015; Mazloumi et al., 2017; Laubenstein et al., 2018; Crear et al., 2019, 2020; Bouyoucos et al., 2020; Table S1).

In addition to biological factors inherent to each species, there are methodological factors that may influence study outcomes. There is a problem of researchers using poor experimental methods, despite numerous papers describing best-practices (Clark et al., 2013; Norin and Clark, 2016; Rummer et al., 2016; Svendsen et al., 2016). Studies with flawed respirometry are obviously unsound and pollute the literature with invalid data, irrespective of how highbrow the hypothesis and impactful the journal. Common flaws include very short recovery times after handling, no mixing devices in respirometers, and very short measurement periods to estimate metabolic traits. Ideally, fish should not be air-exposed when transferred, given at least 4 h recovery (overnight is best), then measured for at least 24 h.

Beyond these methodological faux pas, the form of an AS curve may be affected by the choice of exposure temperatures, especially how these relate to the acclimation (or acclimatisation) temperature and the natural thermal range of the species. The number of test temperatures is often limited, due to the labour-intensive and lengthy nature of respirometry, and criteria for selecting the highest temperature vary among studies. In roughly a third of studies, upper temperature was based on climate change projections, while in another large group, upper temperature was based on current average maxima. A limited number of studies used temperatures that are either lower or higher than the ecologically relevant range (Table S1). Not surprisingly, in studies where the highest chosen temperature is lower than the maximum of the natural thermal range, AS increases with temperature, although this pattern can also be observed for some species exposed to temperatures that exceed their ecologically relevant maximum (Fig. 2E).

A key methodological constraint for laboratory experiments is the difficulty of replicating the time scale at which climate change is occurring, which questions their ecological validity. The general expectation is that longer acclimation should be beneficial, giving the fish time to make compensatory physiological modifications that enable AS to be maintained over a broad range of temperatures, i.e. reduced SMR and/or increased MMR in acclimated versus non-acclimated individuals. In other words, longer acclimation periods make it less likely to find a decline in AS at upper temperatures (Lefevre, 2016). The number of studies using an acclimation period of several weeks and even months has now increased (Habary et al., 2017; Motson and Donelson, 2017; Slesinger et al., 2019; Vagner et al., 2019; Zhou et al., 2019), although studies using transgenerational and developmental acclimation remain quite rare. In three coral reef wrasses (Labridae), AS at elevated temperature did not improve with developmental exposure, and the same was the case for spiny chromis damselfish *Acanthochromis polyacanthus* (Laubenstein et al., 2019), although in this case AS at elevated temperature was restored with transgenerational acclimation (Munday et al., 2017). Transgenerational studies on reproduction, growth and size (Salinas and Munch, 2012; Shama et al., 2014; Donelson and Munday, 2015; Donelson et al., 2016; Loisel et al., 2019) indicate that there is potential for adaptation of these traits, even in the most sensitive species. In addition to exploring the role of transgenerational acclimation on whole-animal performance, epigenetics and gene expression analyses are increasingly being probed to gain insights into underlying mechanisms (Veilleux et al., 2015; Bernal et al., 2018; Chen et al., 2018; Metzger and Schulte, 2018; Ryu et al., 2018, 2020). Another means of making temperature treatments more realistic is to use a fluctuating regime; in lake trout *Salvelinus namaycush* the AS of fish held and measured at 10°C was significantly improved by daily short exposures to 17°C (Guzzo et al., 2019). When considering the data collectively, the inclusion of more long-term studies does not, however, reveal a clear effect of time scale of acclimation (Fig. 2F). That is, among studies that compared acute and longer acclimation periods, there are several cases where AS at high temperatures is lower after longer acclimation. For example, barramundi increased MMR and AS with an acute temperature increase from 23°C and were highest at the highest temperature of 38°C, largely due to a faster increase in MMR than SMR. However, after 5 weeks of acclimation, AS at 29 and 38°C was similar, mainly due to a reduction in MMR (Norin et al., 2014). A very similar pattern was observed in black sea bass *Centropristis striata* (Slesinger et al., 2019). In common triplefin, there was a reduction in AS after 12 weeks at 24°C, but AS was higher after 4 weeks of acclimation (Khan et al., 2014; McArley et al., 2017). Looking at an even longer perspective, in populations of three-spined stickleback (*Gasterosteus aculeatus*) with different evolutionary thermal histories, fish from warmer lakes often had lower AS than fish from colder lakes, and the response to acclimation was more consistent across populations from warmer lakes (Pilakouta et al., 2020). More studies are necessary to confirm this pattern, but it raises a question regarding AS and MMR as measures that are assumed to be set by limitation. If it is beneficial to have higher AS at higher temperature, and it is evidently physiologically possible for fishes to achieve a higher AS (i.e. the cardiorespiratory system is capable of delivering the oxygen needed), then why, in some cases, does MMR decline with time? Perhaps there are costs of having a high MMR (e.g. a large respiratory surface area increases infection risk and need for ion regulation), which may be higher at high temperature, such that if

the achievable maximum is not actually needed to achieve sufficient oxygen supply, it is more beneficial to reduce MMR slightly.

Recently it has been argued that AS, as measured in most of the studies discussed above, is not an appropriate measure of aerobic capacity and that 'Analyses of the OCLTT should mimic natural conditions and consider routine activities displayed by the animal in the field, as well as minimising stress phenomena that would transiently mobilise functional reserves' (Pörtner et al., 2017). In other words, the MMR and AS measured during exercise in the laboratory over-estimate the aerobic capacity a fish would have under 'routine' conditions, for their activities in the wild. Pörtner et al. (2017) suggest 'functional capacity' and 'functional scope' as more relevant terms, although it is unclear how this performance should be measured in the laboratory to allow for experimentation and hypothesis testing. The boundaries for AS, as it is most commonly measured, are easy to interpret. The maximum (MMR) is the maximum oxygen supply rate, whether this reflects limitation or optimisation of cardiorespiratory systems. The minimum (SMR) is set by the minimum oxygen uptake needed to sustain basal life functions. That routine oxygen demand or 'functional scope' would be supply limited is not intuitive, given the knowledge we have of both the long-term plasticity (acclimation) and ability to increase, e.g. respiratory surface area. It should also be noted that in the above analyses (Figs 1 and 2), for simplicity, the degree of reduction in AS has not been taken into account, but obviously varies (Lefevre, 2016). According to the OCLTT hypothesis, any reduction would represent a reduction in fitness, but this mechanistic link remains hypothetical.

Overall, it is clear from the growing number of papers that AS, measured by traditional means using enforced exercise, is not universally limited at warm temperatures, even if the OCLTT paradigm holds true for some salmonids and coral reef species (Table S1). There has been further debate on the hypothesis and its underlying principles (Pörtner et al., 2017; Jutfelt et al., 2018), but the current empirical data represent incontrovertible evidence that the OCLTT paradigm is not a universal principle underlying heat tolerance in fishes.

Using the OCLTT paradigm in modelling

If, however, the OCLTT paradigm holds for a species, and there is a clear $T_{opt,AS}$ within the ecologically relevant temperature range, then it can be a very useful tool for predicting impacts of global warming (Eliason et al., 2011), although an explicit link between AS and fitness remains to be demonstrated for any fish species. The form of AS curves has been used to explain ongoing effects of warming such as changes in fish population abundance (Pörtner and Knust, 2007), failure of reproductive migrations (Eliason et al., 2011) and the spread of invasive species (Marras et al., 2015). The OCLTT has also been used as a basis for modelling, for example of growth in the field. Moyano et al. (2020) measured the Arrhenius breakpoint temperature and critical temperature for heart rate of Atlantic herring *Clupea harengus* in the laboratory, and showed that the number of days that temperature had been above this temperature over the past 20 years correlated with growth in the field over that period. The authors argue that these traits can therefore project further changes expected from ocean warming.

That aerobic capacity can be limiting is theoretically conceivable, given that ATP production must be aerobic to be sustainable. Whether this is limiting in practice for fish in the wild is another question, considering all the other factors that affect energy budgets and survival. Modelling distribution based on a TPC and projected temperature, regardless of which performance measure is used, may

indicate the absolute theoretical physiological limit for the distribution of a species, which can then reveal that certain areas may become uninhabitable. Dahlke et al. (2017) measured egg survival for polar cod *Boreogadus saida* and Atlantic cod at various temperatures in the laboratory, and then mapped potential egg survival (PES) across the seas in the North, using information about known spawning sites from 1985 to 2004 as a baseline. They then projected changes in the PES across the region, concluding that suitable spawning habitat would shrink. The authors also measured oxygen uptake of the eggs over the same temperature range as egg survival was measured, but while egg survival dropped from 80% at 6°C to 40% at 9°C, oxygen uptake was highest at 9°C, and maintained at 12°C, where egg survival was almost zero. In this case, a limitation in oxygen supply would not seem to explain the reduced survival at 9°C. It could be contributing at 12°C, but without other measurements (e.g. anaerobic end-products, oxygen) it is difficult to separate cause and effect. As spawning is a crucial event in the life history of fishes, constraints on this stage are obviously important. The problem of spawning habitat contraction expected from ocean warming was recently emphasised using a multi-species analysis (Dahlke et al., 2020), where the patterns were attributed directly to OCLTT although it is not clear why, based on the information provided.

Rather than temperature effects on capacity for oxygen supply itself, Deutsch et al. (2020) argue that a metabolic index, which includes hypoxia tolerance, may explain boundaries of the geographical ranges of species, somewhat similar to the 'oxygen- and temperature-limited metabolic niche' framework proposed by Ern (2019). Although these examples illustrate that it is certainly possible to model and project changes in distribution ranges using physiological traits, wider applicability is less certain. For many species, a 1–2°C increase in temperature would probably not restrict the theoretical physiological maximum for the distribution but, rather, expand it. Whether a species will actually be able to take advantage and expand its range depends on many other factors in addition to physiological performance, such as habitat and food requirements (e.g. Feary et al., 2014). For many species, the adaptation capacity is unknown, as is the relative importance of different selection pressures (Crozier and Hutchings, 2014).

Thermal performance curves based on physiological energetics

Despite the controversy surrounding OCLTT, the TPC is a valuable concept in understanding thermal tolerance in fishes, towards predicting future effects of global warming. TPCs do require significant manpower, infrastructure and time, but it seems clear that long-term studies are essential for climate change research. For ectothermic fishes, all TPCs may share some common features, notably that performance and scope for activity are low at the cold end of the thermal range, but they then increase with warming due to thermodynamic effects of water on biochemical and physiological reactions (Schulte et al., 2011; Currie and Schulte, 2014). Why (and if) different performance measures decline beyond an optimum is a more complex question, and mechanisms may differ depending upon the trait in question (Clark et al., 2013). Furthermore, life history, morphological and physiological differences among species are likely to determine the ecological relevance of a given trait and therefore the usefulness of its TPC in investigating responses to climate warming at the population level (Clark et al., 2013). There are TPCs based upon traits of cardiorespiratory physiology other than AS. Aerobic locomotor performance curves may be interesting for active species (Bennett, 1990; Claireaux

et al., 2006; Pang et al., 2013; Pang et al., 2016). Cardiac performance curves (Casselman et al., 2012; Anttila et al., 2014; Ferreira et al., 2014) are quick to perform but focus on a single organ and results are always interpreted in relation to the OCLTT. Here we consider TPCs for traits of physiological energetics, which rely on the integrated function of multiple organ systems, have an outcome that is readily related to fitness, and may apply to fishes of all lifestyles.

Specific dynamic action

The specific dynamic action of food (SDA) response is the ubiquitous and transient rise in metabolism during digestion, and probably has both ecological and evolutionary relevance because it reflects processes and costs of nutrient handling, tissue turnover and deposition, hence growth (Jobling, 1994; McCue, 2006; Wang et al., 2006). The response requires the integrated performance of multiple organs, including digestion and absorption by the gut, nutrient and oxygen transport by the cardiovascular system, nutrient handling by the liver, nutrient turnover and deposition in all body tissues, plus gas exchange at the gills to support the rise in aerobic metabolism as well as nitrogen excretion (McCue, 2006; Wang et al., 2006). The SDA can occupy a sizable proportion of AS in fishes (Sandblom et al., 2014; Steell et al., 2019) and is considered, along with locomotor activity, to represent a major component of the overall cost of living (Jobling, 1994). In some species, AS measured in digestion may exceed that measured in activity (Steell et al., 2019). The SDA response is measured by respirometry on animals that either feed spontaneously or are force-fed (Chabot et al., 2016). Measures of performance include the peak rate of oxygen uptake, duration of the response, and the SDA coefficient, which is the proportion of the SDA response to the amount of energy in the meal, i.e. how much of the meal's energy is used to digest it (McCue, 2006; Chabot et al., 2016). There are theoretical reasons to assume that warming should increase the peak, reduce the duration but not affect the coefficient, and this has some empirical support (Jobling and Davies, 1980; Jobling, 1994; McCue, 2006; Wang et al., 2006; Luo and Xie, 2008; Steell et al., 2019). The SDA performance can also, however, have a T_{opt} in some species such that warming can cause declines in performance, which can reflect local adaptation to thermal regimes (McKenzie et al., 2013; Tirsgaard et al., 2014). The response has been used to investigate the functional consequences of exposure to future warming scenarios (Sandblom et al., 2014) and the invasion potential of species and how this will be affected by warming (Steell et al., 2019). As such, the SDA response seems to hold promise as a means of investigating thermal tolerance in fishes and predicting responses to future warming, and is not that much more challenging to perform than a TPC for AS.

Growth

Like the SDA, growth depends on multiple physiological systems and behaviours including appetite, but with a temporal dimension that can provide much greater insight into how fishes are affected by temperature. Growth rate is a major component of life history strategies in fishes and global warming has been shown to affect growth (Metcalfe et al., 1995; Réale et al., 2010; Morrongiello et al., 2012; Audzijonyte et al., 2020). Growth TPCs have been developed extensively in aquaculture, where the objective is to maximise growth potential under farming conditions, so feed is provided *ad libitum* (Jobling, 1994; Imsland and Jonassen, 2001; Volkoff and Rønnestad, 2020). The overall pattern of a growth TPC in farmed fishes is a progressive increase in rate with temperature up to a

maximum that is the optimum temperature for growth ($T_{opt,G}$); this is followed by a decline beyond $T_{opt,G}$ that can be very steep (Brett, 1979; Imsland and Jonassen, 2001; Volkoff and Rønnestad, 2020). Scope for growth is determined by the balance of energy supply and demand, namely the difference between energy consumed in feed and energy dissipated to sustain metabolism (Brett, 1979). As temperatures rise to $T_{opt,G}$, thermal acceleration of metabolism provides for increased rates of feed intake, capacity for processing food, and the efficiency with which it is assimilated and deposited as tissue (Brett, 1979; Brett and Groves, 1979; Imsland and Jonassen, 2001; Volkoff and Rønnestad, 2020). This provides for increased scope for growth, up to a maximum at $T_{opt,G}$. Beyond this, growth rates and scope for growth decrease because, while metabolic costs continue to increase with temperature, there is a progressive decline in feed conversion efficiency and appetite (Imsland and Jonassen, 2001; Volkoff, 2020; Volkoff and Rønnestad, 2020). The reduced conversion efficiency may just reflect a changing balance of energy supply and demand, while the mechanisms that cause the decline in appetite are not yet understood (Volkoff and Rønnestad, 2020). One proximate cause of the decline in appetite may be impaired mitochondrial function as temperatures rise beyond the optimum (Salin et al., 2016), although the neural or endocrine pathways by which such sub-cellular effects are transduced into the observed feeding response remain to be explored (Volkoff and Rønnestad, 2020).

Thus, fish physiologists would benefit from collaborating with aquaculture researchers. It is commonplace to couple growth studies with measures of feed intake in aquaculture; this reveals how temperature affects appetite and feed efficiency (Imsland and Jonassen, 2001). Tank respirometry can then provide simple energy budgets on feeding, growing animals (McKenzie et al., 2007, 2012). Variable thermal regimes can be incorporated, to improve ecological realism (Morash et al., 2018; Guzzo et al., 2019). Results can be interpreted further by sampling fish to measure thermal impacts at a cellular level, like oxidative damage, mitochondrial function and expression of heat shock proteins (Khan et al., 2014; Salin et al., 2016; Stillman, 2019). Furthermore, extreme events can be integrated into tank energetics studies, with downstream tissue sampling, for example to investigate whether there is evidence of cellular stress responses, from oxidative damage to expression of heat shock proteins (Williams et al., 2016; Stillman, 2019) in different target organs and tissues (see below).

The advantage of growth rate as a TPC is that the response seems to be universal across fish species, with a definable $T_{opt,G}$ followed by a decline linked to reduced appetite (Volkoff and Rønnestad, 2020). Interestingly, in the Atlantic halibut *Hippoglossus hippoglossus*, the effects of temperature acclimation on growth and AS are not linked: growth declines at high temperatures while AS does not (Gräns et al., 2014). The major drawbacks are the technical challenges of long-term growth studies and their lack of ecological realism. Growth rates of fishes in the wild are not solely driven by effects of temperature on energy demand, feed intake and scope for growth. Factors such as food availability, time and energy spent foraging, and how foraging rates are affected by perceived risks, will all contribute to the capacity of a fish to allocate energy to growth in the wild (Holt and Jørgensen, 2015; Guzzo et al., 2017; Neubauer and Andersen, 2019; van Denderen et al., 2020).

Growth rate seems, nonetheless, to be the most promising alternative TPC to those that focus on the OCLTT. In terms of experimental biology in climate change research, growth rate has been used to investigate mechanisms that define tolerance of warming in fishes (Gräns et al., 2014; Salin et al., 2016) and to

develop dynamic energy budget models and to map habitat suitability (Teal et al., 2012, 2018). Childress and Letcher (2017) modelled a TPC for growth on wild salmonids based on repeated field observations and found that it returned a significantly lower $T_{opt,G}$ than when modelled on data for growth of captive conspecifics, such that TPCs developed in the laboratory may over-estimate $T_{opt,G}$ for wild fishes. Wild fishes also show weaker effects of temperature on growth rates than fish in aquaculture (van Denderen et al., 2020).

Tolerance of extreme events

Not only the slow and long-term change in temperature with global warming impacts fishes. Extreme heatwave events, or thermal pulses, may cause increased morbidity and even direct mortality in fishes, either due to direct effects of temperature or to associated biotic interactions, such as increased susceptibility to parasites, disease and predation (Hinch et al., 2012; Miller et al., 2014; Roberts et al., 2019; Till et al., 2019). Magel et al. (2020) found that heatwaves caused a 50% reduction in abundance and diversity in a coral reef fish community, notably due to emigration of several species, among which coral-dependent species never returned. This example highlights the complexity and severe consequences extreme temperature events can have, and why measures of acute and upper thermal tolerance limits remain ecologically relevant.

The upper limit of thermal tolerance that might be tested by heatwaves is typically estimated in the laboratory using the critical thermal maximum (CT_{max}) protocol. Temperature is increased in increments until the fish loses equilibrium (LOE), an incipient lethal threshold because the moribund animal would be unable to escape the conditions (Lutterschmidt and Hutchison, 1997; Beitinger and Lutterschmidt, 2011). There are quite major limitations to the critical thermal protocol as an experimental tool (Rezende et al., 2014; Blasco et al., 2020b). Notably, the idea that the complexity of thermal tolerance limits can be captured by a single measure is a major oversimplification (Rezende et al., 2014; Rezende and Bozinovic, 2019). There are also methodological issues; particularly that the measured CT_{max} depends upon heating rate (Becker and Genoway, 1979; Lutterschmidt and Hutchison, 1997; Rezende et al., 2014; Vinagre et al., 2015). Furthermore, the mechanism(s) that causes LOE are not known (Currie and Schulte, 2014; Healy et al., 2018; Blasco et al., 2020b) and may differ among species and with warming rate (e.g. Wang et al., 2014; Brijs et al., 2015; Ekström et al., 2016; Ern et al., 2016; Vinagre et al., 2016; Jutfelt et al., 2019). This lack of mechanistic understanding hinders comprehension of essential questions such as why fish species differ in their CT_{max} , or why it is modified by thermal acclimation (Currie and Schulte, 2014; Comte and Olden, 2017b; McKenzie et al., 2020). Also, much of the search for physiological mechanisms underlying acute tolerance has focused on the function of organs that are critical for immediate survival, the heart and brain (e.g. Friedlander et al., 1976; Ekström et al., 2014, 2017; Gilbert et al., 2019; Jutfelt et al., 2019) (Fig. 3) and mechanisms related to oxygen supply, such as mitochondrial function (Chung and Schulte, 2020). This is a problem because dire effects on other organs may limit thermal tolerance during longer exposures to more benign temperature, but will not be identified with the same ease in current protocols. Thus, there is the danger that fast rates of temperature increments to determine CT_{max} will pinpoint the organs with the most immediate effects, namely the brain or the heart, but these organs are merely identified because destruction of their functions leads to immediate death. An equally destructive effect by heat on the intestines or the liver would kill the fish in days, and with

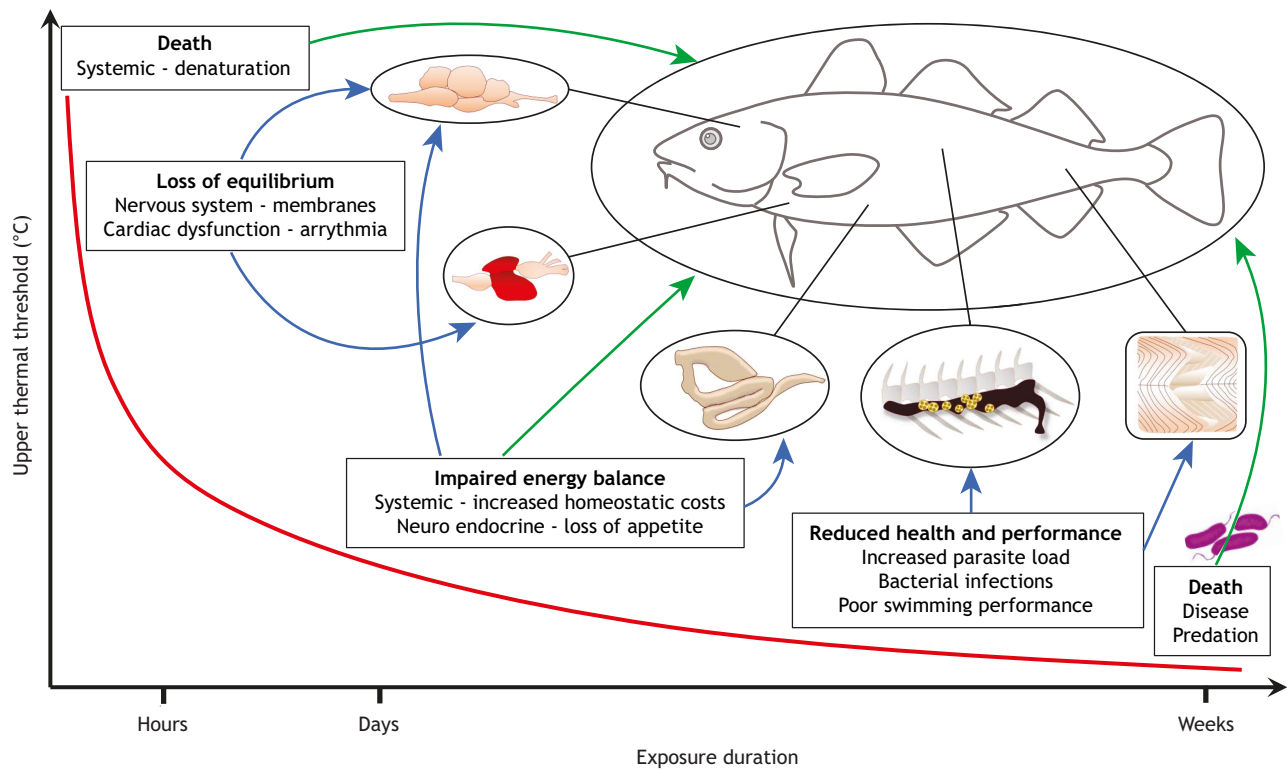


Fig. 3. Upper thermal temperature as a function of time. The upper temperature that causes mortality and morbidity shows an exponential decline with exposure duration in ectotherms (Rezende et al., 2014). Physiologists have focused on acute tolerance over time scales of hours (or less) using the critical thermal maximum protocol, where fish are warmed incrementally until loss of equilibrium due, presumably, to dysfunction of critical organs such as the nervous system and heart. Over longer durations, morbidity and mortality from chronic thermal stress may reflect impaired energy balance due to increased metabolic costs coupled with loss of appetite. The energy imbalance would reduce health, visible as increased parasite and bacterial loads, and reduce performance, in particular swimming ability. Thus, over longer durations at less extreme warm temperatures, major die-offs may occur due to disease and predation.

the same effect on fitness (i.e. no reproduction, no fitness). In other words, we tend to make the mistake that the organs with fastest effects are identified as the culprits for thermal tolerance, while the more correct picture is likely to be that most organs fail at similar temperatures, but the time course of the effects vary. Seeking a single ubiquitous mechanism that explains CT_{max} in all fish species therefore seems an illusion.

Nevertheless, the CT_{max} protocol has provided important knowledge about potential impacts of global warming on fishes, e.g. to demonstrate that tropical fish species live closer to their upper thermal limits and are, consequently, more vulnerable to future warming than temperate species (Comte and Olden, 2017a; Pinsky et al., 2019). Also, the latitudinal range boundaries of fishes and how these are being modified by global warming are related to their limits of thermal tolerance as measured by CT_{max} and the equivalent for cold tolerance (CT_{min}) (Sunday et al., 2011, 2012, 2019). Tolerance thresholds based upon fatigue from exercise performance are, potentially, preferable to LOE at CT_{max} , because fatigue may have a common physiological mechanism across all species (Steinhausen et al., 2008; Blasco et al., 2020a preprint, 2020b). This does not move away from the limitations of having a single value that is expected to define 'tolerance' (Rezende et al., 2014). As argued above, we need to move beyond the heart and brain and must consider other organ systems (osmoregulation, digestion, immune system) that may cause mortality and declines in fitness as a result of extreme events, and thresholds for such effects (Fig. 3).

Mortality, or reduced fitness due to carry-over effects (Stillman, 2019), could depend upon impacts on multiple organ systems that

become significant over time scales of days to weeks, rather than hours in the laboratory (Fig. 3). Coping with thermal stress may have physiological costs and consequences, for example in the increased production of heat shock proteins (Kingsolver and Woods, 2016; Williams et al., 2016) that, coupled with a loss of appetite, would challenge energy balance at warm temperatures. This may weaken fishes and render them more at risk from predation and disease. Warm temperatures, especially pulse heat stress, can increase susceptibility to both parasites and bacterial infections over a time scale of days and weeks (Miller et al., 2014; Bruneaux et al., 2017; Teffer et al., 2019; Claar and Wood, 2020), which can then cause further declines in physiological performance (Bruneaux et al., 2017). Examination of mortalities after heatwaves consistently finds evidence of high tissue bacterial and/or parasite loads, and disease is considered a major factor in die-offs (Miller et al., 2014; Strepparava et al., 2018; Roberts et al., 2019).

Conclusions and perspectives

Our analysis aims to highlight the challenges experimental fish physiologists face when seeking to provide a mechanistic foundation to predict the effects of global warming. While the importance of physiology seems beyond intuitive dispute, we need evidence-based approaches in moving forward. The GOL hypothesis is not based on current knowledge and data. It has been valuable in focusing attention on a possible role for respiratory physiology in size-related differences in thermal tolerance, but should be disregarded as an explanation for why fishes might be shrinking. The evidence collected to date clearly indicates that the OCLTT is not a universal paradigm, so the time seems ripe to move on to different paradigms

for TPCs. Traits of physiological energetics, particularly SDA and growth, seem promising candidates. Growth studies have the advantage of a temporal dimension that can incorporate thermal variation and extreme events.

Laboratory studies can never capture the complexity of real life and the multiple interacting stressors that a fish may face (Currie and Schulte, 2014; Williams et al., 2016; Morash et al., 2018; Stillman, 2019). Technologies for biologging and biotelemetry hold much promise and are advancing (Treberg et al., 2016), but field physiology on fish lags far behind research on mammals and birds, due to the problems with transmitting data through water or recapturing animals to retrieve data from biologgers. Some species, such as smallmouth bass *Micropterus salmoides* that guard nests in lakes (Prystay et al., 2019) or sockeye salmon from populations that spawn and die in a particular mountain stream (Prystay et al., 2017), provide increased likelihood of recovering loggers, which is promising for future studies. Marine species present major technical challenges, but the economic value of species like bluefin tuna may drive advances in the field.

Laboratory studies can continue to be used to investigate mechanisms, especially of thermal tolerance, acclimation and plasticity, but also, conceivably, of evolutionary adaptation to temperature, especially when including genomics. Field studies can reveal mechanisms but also the impacts of thermal stress on fishes, and the consequences for their fitness. We clearly need more knowledge on more species to improve our ability to predict effects of global change, including warming. We hope that advances in techniques for biotelemetry and biologging will provide information about what is happening under natural conditions. If we can understand what has and is happening with populations, this can only improve our ability to predict what may happen in the future.

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Competing interests

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Supplementary information

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