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Intraspecific variation in tolerance of warming in fishes

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Abstract

Intraspecific variation in key traits such as tolerance of warming can have profound effects on ecological and evolutionary processes, notably responses to climate change. The empirical evidence for three primary elements of intraspecific variation in tolerance of warming in fishes is reviewed. The first is purely mechanistic that tolerance varies across life stages and as fishes become mature. The limited evidence indicates strongly that this is the case, possibly because of universal physiological principles. The second is intraspecific variation that is because of phenotypic plasticity, also a mechanistic phenomenon that buffers individuals' sensitivity to negative impacts of global warming in their lifetime, or to some extent through epigenetic effects over successive generations. Although the evidence for plasticity in tolerance to warming is extensive, more work is required to understand underlying mechanisms and to reveal whether there are general patterns. The third element is intraspecific variation based on heritable genetic differences in tolerance, which underlies local adaptation and may define long-term adaptability of a species in the face of ongoing global change. There is clear evidence of local adaptation and some evidence of heritability of tolerance to warming, but the knowledge base is limited with detailed information for only a few model or emblematic species. There is also strong evidence of structured variation in tolerance of warming within species, which may have ecological and evolutionary significance irrespective of whether it reflects plasticity or adaptation. Although the overwhelming consensus is that having broader intraspecific variation in tolerance should reduce species vulnerability to impacts of global warming, there are no sufficient data on fishes to provide insights into particular mechanisms by which this may occur.

KEYWORDS
adaptation, critical thermal maximum, phenotypic plasticity, size effects, thermal performance curve, vulnerability

1 | INTRODUCTION

Current models of global warming predict increases in seasonal temperatures by up to 4°C by 2100, along with an increase in the frequency of localized acute and extreme warming events (Collins & Sutherland, 2019; Frölicher & Laufkötter, 2018; IPCC, 2014). These changes are likely to cause population declines, local extirpation or even extinction when species characteristics are poorly suited to the novel environments (Bennett *et al*., 2019; Burggren, 2019; Pacifici *et al*., 2015). Fishes may be especially vulnerable to global warming because, as ectotherms, their physiology is determined by thermodynamic effects of the surrounding water temperature, which sets their

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body temperature (Cossins & Bowler, 1987; Currie & Schulte, 2014; Fry, 1971; Schulte, 2011). General principles of the thermal physiology of fishes and their responses to water temperature and thermal stress have been widely reviewed (*e.g.*, Cossins & Bowler, 1987; Currie & Schulte, 2014; Little *et al.*, 2020), and therefore they are not revisited here. Instead, the authors of this study focus on intraspecific variation in tolerance of warming and its significance for predicting species' responses to climate change.

Intraspecific variation exists both within and among individuals and populations of a species (Bolnick *et al.*, 2011; Killen *et al.*, 2016a; Mimura *et al.*, 2017; Spicer & Gaston, 2000). One element of within-individual variation refers to ontological and physiological changes that occur across life stages and with body size, such that particular life stages may be weak links in overall species sensitivity (Dahlke *et al.*, 2020; Pörtner & Peck, 2010; Righton *et al.*, 2010). A second element is phenotypic plasticity, the ability of a given genotype to produce different phenotypes in response to the environment within an individual's lifetime (Stearns, 1989), which can be a source of variation both within and among individuals. A capacity for plasticity in tolerance can buffer against the immediate impacts of thermal stress, thereby reducing population sensitivity. Thirdly, there is genetically based heritable variation among individuals, either within or between populations. Possessing a broad range of heritable tolerance genotypes will influence population adaptability and the capacity to adjust to new conditions over generational time scales (Bennett *et al.*, 2019; Moran *et al.*, 2016; Pacifici *et al.*, 2015). These collective effects of individual variation in thermal tolerance can, therefore, have important implications for vulnerability of populations and species to both short-term extreme heatwaves and long-term gradual warming (Bennett *et al.*, 2019). This then has far-reaching consequences. If broad functional variation among individuals increases the stability and resilience of a species in the face of environmental stressors, such as warming, this can stabilize the species' ecological functions and, in turn, stabilize overall community and ecosystem function (Bolnick *et al.*, 2011; Mimura *et al.*, 2017; Pacifici *et al.*, 2015).

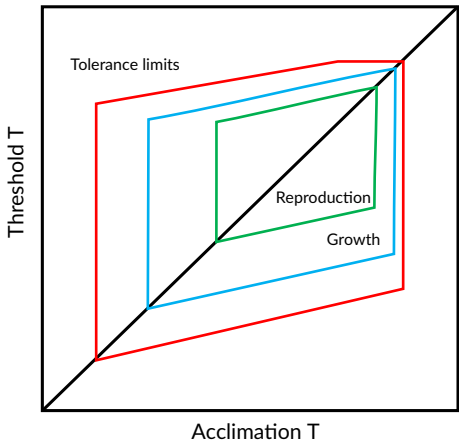

FIGURE 1 Fry thermal tolerance polygon. The polygon is bounded by the minimum and maximum temperatures that can be tolerated for a relatively short period of time before they threaten life (outer red polygon). Boundaries are measured using acute thermal ramping protocols. In particular, the critical thermal (CT) protocol where a fish is progressively heated for the CT maximum (CT_{max}) or cooled for the CT minimum (CT_{min}) until it exhibits a loss of equilibrium (LOE) (Beitinger & Lutterschmidt, 2011; Lutterschmidt & Hutchison, 1997). The critical threshold temperature for fatigue from swimming (CT_{swim}) is an alternative and potentially more ecologically relevant protocol. It involves imposing a fixed level of steady and sustained aerobic exercise upon a fish, in a swim flume, then warming (or cooling) the fish in steps until it fatigues (Blasco *et al.*, 2020b; Steinhausen *et al.*, 2008). Maximum CT_{swim} occurs at a lower temperature than CT_{max} (Blasco *et al.*, 2020b) so a Fry-TTP derived with a CT_{swim} protocol would lie inside of one derived by classic CT protocol. These two boundary temperatures delineate the absolute range of thermal tolerance for a given acclimation temperature, and by making similar determinations as fishes are acclimated in the laboratory (or acclimatized in nature) to temperatures over their natural thermal range, the Fry-TTP also displays how these boundaries change by phenotypic plasticity. The inner polygons denote the temperature limits for major components of fitness such as growth (blue) and reproduction (green) (Brett, 1971). These are typically inferred from thermal performance curves that measure rate functions such as growth or, most commonly, aerobic scope over a range of acclimation temperatures (Figure 2)

2 | HOW TO MEASURE TOLERANCE OF WARMING

Before the nature and extent of these three types of intraspecific variation in thermal tolerance in fishes are considered, how tolerance is typically measured should be briefly reviewed. The methods for assessing thermal tolerance in fishes are well established (Cossins & Bowler, 1987; Currie & Schulte, 2014; Lutterschmidt & Hutchison, 1997; Schulte *et al.*, 2011), and only a brief summary is provided here, for the convenience of the reader. The Fry thermal tolerance polygon (Fry-TTP, Figure 1) is the standard framework to display tolerance boundaries in fishes and how these are influenced by acclimatization (or more often acclimation) to temperatures across a species' natural range (Cossins & Bowler, 1987; Currie & Schulte, 2014). The Fry-TTP boundaries are measured using acute thermal ramping protocols, especially the critical thermal (CT) methodology that uses loss of equilibrium (LOE) as tolerance endpoint (Figure 1). The protocol is simple and defines the temperature where survival is threatened because at LOE the fish cannot escape the conditions (Beitinger & Lutterschmidt, 2011). An alternative is the critical threshold temperature for fatigue from swimming (CT_{swim}), which may have greater ecological relevance because it defines the temperature where fish can no longer perform an ecologically essential activity (Figure 1), but this protocol has not yet been applied widely (Blasco *et al.*, 2020b). Lying inside a Fry-TTP are more restricted zones (Figure 1) that are delimited by temperature-dependent effects on the performance of activities that are essential for growth and reproduction (Brett, 1971; Cossins & Bowler, 1987; Currie & Schulte, 2014; Schulte *et al.*, 2011).

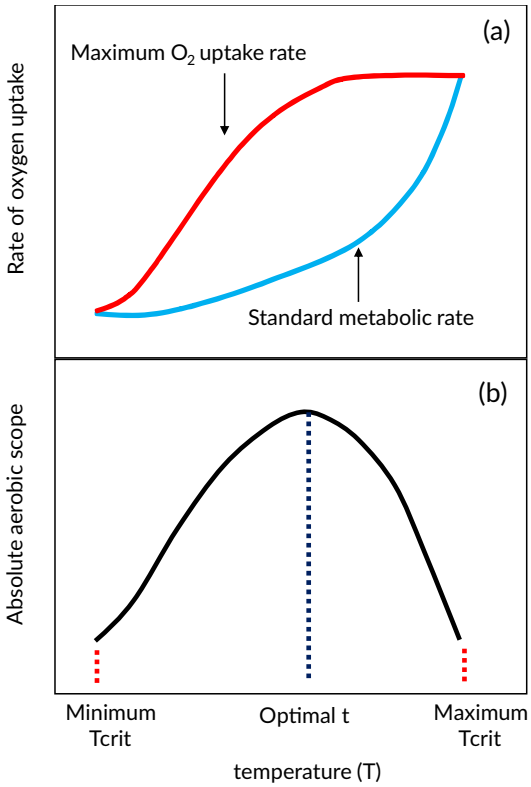

FIGURE 2 The Fry paradigm and how it describes a thermal performance curve (TPC) for absolute aerobic scope (AAS) in fishes. To develop a TPC for AAS, fish are exposed (whether acutely, acclimated or acclimatized) to a range of temperatures and their standard metabolic rate (SMR, the basal metabolic rate at the prevailing temperature) and maximum metabolic rate (MMR, the maximum capacity for oxygen uptake at that temperature) are measured by respirometry. The AAS is the net difference between SMR and MMR (MMR–SMR) (Claireaux *et al*., 2006; Eliason *et al*., 2011; Fry, 1971; Schulte, 2015) and represents the capacity to provide oxygen for all energetic fluxes such as swimming exercise and so forth. Nonetheless, many studies replace SMR with a slightly higher routine metabolic rate (RMR) where there is some contribution to metabolic rate from routine activity (Lefevre, 2016). The theoretical basis of the Fry paradigm is that temperature controls all metabolic processes in ectothermic fishes. In (a), the blue line shows how SMR (or RMR) and MMR vary as a function of water temperature and resultant effects on AAS. The SMR is expected to increase exponentially with temperature because of direct thermodynamic effects on all respiring body tissues. At low temperatures MMR is also low, because the cold inhibits all processes that underlie performance, so AAS is small. As temperatures rise, AAS increases because warming accelerates all metabolic processes and provides for increased MMR and performance. Nonetheless, eventually the effects of temperature on SMR make it rise to the point where it coincides with the fish's absolute maximum capacity for oxygen uptake, so AAS is again very small. The resultant AAS is shown in (b), with a clear optimal temperature (T_{opt}) where AAS is greatest and critical thermal limits (T_{crit}) where AAS is zero. Various researchers define an optimal range of AAS based on the temperatures where it is, *e.g*., at least 90% of the maximum AAS at T_{opt}. TPCs for AAS are time-consuming and labour-intensive to develop. A cardiac TPC can be generated much faster by measuring heart rate (f_H) from the ECG of anaesthetised fish that have been pharmacologically treated to abolish all autonomic control and then incrementally warmed to follow the response of maximum heart rate (f_{Hmax}) (Anttila *et al*., 2013; Casselman *et al*., 2012; Chen *et al*., 2015; Ferreira *et al*., 2014). This can reveal thresholds for f_H that closely parallel those of AAS with temperature, *i.e*., the Arrhenius break temperature (T_{AB}) when f_{Hmax} is reaching its upper asymptote, which coincides closely with T_{opt} for AAS. Beyond that, the warm temperature that triggers cardiac arrhythmia (T_{arr}) coincides closely with T_{crit} (Anttila *et al*., 2013; Casselman *et al*., 2012; Chen *et al*., 2015; Ferreira *et al*., 2014)

These inner zones are typically defined with a thermal performance curve (TPC) that measures a trait of organismal performance over a range of temperatures. A TPC can then identify a thermal optimum, the thermal range over which performance is near to optimal (thermal breadth), and temperature thresholds for alterations in performance (Figure 1) (Currie & Schulte, 2014; Pörtner *et al*., 2010; Schulte *et al*., 2011; Wang & Overgaard, 2007). The prevailing theories for what defines thermal tolerance in fishes, the Fry Paradigm (Fry, 1947, 1957, 1971) and the oxygen and capacity-limited thermal tolerance (OCLTT) hypothesis (Pörtner, 2010), both focus on fish cardiorespiratory physiology and the capacity to meet the oxygen requirements of aerobic metabolism when a fish is subjected to the thermodynamic effects of water temperature (Figure 2). The most common TPC is, therefore, for absolute aerobic scope (AAS), which measures how much a fish can raise its rate of oxygen uptake above standard metabolic rate (SMR, the basal metabolic rate at acclimation temperature) to reach its maximum metabolic rate (MMR, the maximum capacity for oxygen uptake at that temperature) (Fry, 1971; Claireaux *et al*., 2006; Eliason *et al*., 2011; Schulte, 2015; explained in Figure 2). The AAS is proposed to be of ecological significance because it defines the upper limit for oxygen allocation by a fish to sustain aerobic activities such as foraging, digestion, tissue deposition, migration, reproduction (Claireaux & Lefrançois, 2007; Farrell, 2009; Fry, 1971; Pörtner, 2010; Schulte, 2015).

The Fry paradigm and OCLTT hypothesis predict a unimodal curve where AAS rises as a fish is warmed towards its optimal temperature (T_{opt}), followed by a rather steep decline after T_{opt} is exceeded and the animal approaches its critical upper thermal tolerance limit (T_{crit}, Figure 2). The authors describe the Fry paradigm and OCLTT hypothesis here because they are the reason that so many studies have used a TPC for AAS to investigate the effects of temperature on fish performance (see below). In fact, many fish species do not exhibit a unimodal TPC for AAS with a clear T_{opt} (Lefevre, 2016) and, most notably, many show no decline in AAS as they are warmed towards their upper thermal tolerance limit (Gräns *et al*., 2014; Lefevre, 2016; Norin *et al*., 2014; Poletto *et al*., 2017; Verhille *et al*., 2016). That is, based on the available evidence, the Fry paradigm and OCLTT cannot be assumed to be universal principles and are currently a topic of debate in the literature (Clark *et al*., 2013; Farrell, 2016; Jutfelt *et al*., 2018; Pörtner *et al*., 2017).

The fish heart assures oxygen delivery to all tissues in response to their demands, so cardiac performance is considered a central

mechanism determining upper thermal tolerance in fishes (Eliason & Anttila, 2017; Farrell, 2009). TPCs for cardiac performance have been generated for various fish species (Anttila *et al*., 2013; Casselman *et al*., 2012; Chen *et al*., 2015; Ferreira *et al*., 2014), defining a series of threshold temperatures for performance and tolerance of the heart such as the Arrhenius break temperature (T_{AB}) and the temperature that triggers cardiac arrhythmia (T_{arr}). In the species studied to date, these cardiac thresholds are correlated with T_{opt} and upper T_{crit} for AAS, respectively (Casselman *et al*., 2012; Anttila *et al*., 2013; Ferreira *et al*., 2014; Chen *et al*., 2015, see Figure 2). The approach has a number of advantages over a TPC for AAS, in particular that its relatively rapid and easy easy to apply to wild fish under field conditions and the data can be used to develop Fry-TTPs (Chen *et al*., 2015; Drost *et al*., 2016).

Comprehensive Fry-TTPs that include TPCs for underlying traits have only been developed for a few fish species (Brett, 1971; Currie & Schulte, 2014; Ferreira *et al*., 2014). Nonetheless, CT maximum (CT_{max}) and minimum (CT_{min}) have been used to interpret global warming impacts on fishes, such as range shifts (Sunday *et al*., 2011) or vulnerability to extreme warming events (Pinsky *et al*., 2019). Performance curves based on AAS have been used to interpret declines in species population abundance (Pörtner & Knust, 2007), failures of reproductive migrations (Eliason *et al*., 2011), how optimal habitats change with warming (Deutsch *et al*., 2015), and why particular species may be invading new areas (Marras *et al*., 2015). Cardiac TPCs have yet to be applied widely but have revealed population differences and also variation within populations (Anttila *et al*., 2014; Chen *et al*., 2015). These various methodologies to measure heat tolerance have also been used to reveal considerable intraspecific variation in thermal tolerance in fishes.

3 | INTRASPECIFIC VARIATION IN THERMAL TOLERANCE BECAUSE OF THE EFFECTS OF LIFE STAGE

Life stage can have a profound effect on tolerance of warming, reflecting how the physiology of all fishes changes as they grow, from embryos to reproducing adults. A meta-analysis of thermal tolerance thresholds for 694 species (Dahlke *et al*., 2020) concluded that embryos and spawning adults have lower CT_{max} and a narrower thermal range (the difference in °C between CT_{min} and CT_{max}) than larvae or adults (these latter defined as all animals post-metamorphosis, so from juveniles to mature adults that are not spawning). This would indicate that the thermal tolerance of reproducing adults and their immediate offspring is a bottleneck in determining the sensitivity to ongoing global warming (Dahlke *et al*., 2020). Nonetheless, much of the data in this analysis were generated by the technique of phylogenetic data imputation, which is based on reconstruction of an ancestral state and missing data are then estimated by a likelihood-based phylogenetic imputation approach. That is, actual tolerance measures are only available for a sub-set of life stages in a sub-set of the 674 species (Dahlke *et al*., 2020). Very few studies have, in fact, directly compared tolerance thresholds across life stages. Komoroske *et al*. (2014) found that CT_{max} was the highest in larvae and lowest in post-spawning adults of the delta smelt *Hypomesus transpacificus* (McAllister 1963). Drost *et al*. (2016) used a cardiac TPC to find that the temperature of maximum heart rate was lower in larval compared to adult Arctic cod *Boreogadus saida* (Lepechin 1774), indicating a lower T_{opt}, although the life stages did not differ in their T_{AB} or T_{arr} (see Figure 2).

Within the larval stage, thermal tolerance may increase with age because of progressive development of physiological systems, notably the cardiorespiratory system (Wieser, 1985), and the ensuing capacity to meet metabolic challenges imposed by warming. This may be exacerbated if the metabolic costs of growth and development already require a large proportion of a larva's oxygen supply capacity, leaving little scope for anything else (Rombough, 1988). Although various studies have measured CT_{max} in larvae, few have considered how tolerance is affected by larval development (Moyano *et al*., 2017; Illing *et al*., 2020). Larvae of temperate European sea bass *Dicentrarchus labrax* L. 1756 show increased CT_{max} as they develop towards metamorphosis, and the same is true for two tropical species, cinnamon anemonefish *Amphiprion melanopus* Bleeker 1852 and the barramundi *Lates calcarifer* Bloch 1790 (Moyano *et al*., 2017; Illing *et al*., 2020). On the contrary, larvae of the herring *Clupea harengus* L. 1758 (temperate) and the spiny chromis damsel *Acanthochromis polyacanthus* Bleeker 1855 (tropical) show no change in CT_{max} as they age (Moyano *et al*., 2017; Illing *et al*., 2020). Chen *et al*. (2013) found that CT_{max} of fry from four populations of sockeye salmon *Oncorhynchus nerka* (Walbaum 1787) was strongly positively related to their mass. The thermal sensitivity of Antarctic ploughfish *Gymnodraco acuticeps* Boulenger 1902 larvae declined as they developed, measured as the Q_{10} temperature coefficient for oxygen uptake rate (Flynn & Todgham, 2018). Thus, within various fish larvae and a salmonid fry, evidence provides support for a general principle whereby tolerance increases as development proceeds towards metamorphosis.

Therefore, these various studies together highlight the importance of intraspecific variation in tolerance of warming because of life stage in fishes. This intraspecific variation in tolerance to warming, and the resulting sensitivity of particular life stages, must be considered when making projections regarding the potential effects of climate change on fish species.

4 | INTRASPECIFIC VARIATION IN THERMAL TOLERANCE TO BODY SIZE

One of the major effects of global warming on fishes may be a widespread progressive decline in final adult body size in many species, which has been correlated with rising temperatures in both freshwater and marine habitats (Audzijonyte *et al*., 2020; Baudron *et al*., 2014; Daufresne *et al*., 2009). In laboratory studies, final adult size after rearing at different temperatures has a negative relationship with temperature, the so-called temperature-size rule (TSR, Atkinson, 1994). These phenomena, the TSR and a global decline in fish size that correlates with global warming, may reflect, at least in part, a decline in tolerance of warming as fishes increase in mass (Audzijonyte *et al*., 2019; Hoefnagel & Verberk, 2015). Furthermore, although the mechanisms

TABLE 1 Dependence on body length or mass of critical thermal maximum and critical thermal maximum for swimming

Species	SL (mm)	M (g)	T_{acc} (°C)	Δ_T (°C min^{-1})	Relationship	*N*	R^2	*P*	Reference
CT_{max}									
Apache trout *Oncorhynchus apache*	40–220	NA	18	0.3	$CT_{max} = -0.0049(SL) + 30.7$	40	0.13	**0.028**	(Recsetar *et al.*, 2012)
Caribbean goby *Elacatinus lobeli*	19–36	0.2–0.7	20	0.37	$CT_{max} = -2.540(M) + 35.9$	8	0.554	**0.034**	(Di Santo & Lobel, 2017)
E. lobeli	25–29	0.4–0.5	24	0.33	$CT_{max} = -2.883(M) + 38.0$	8	0.076	0.509	(Di Santo & Lobel, 2017)
E. lobeli	20–34	0.2–0.6	28	0.32	$CT_{max} = -2.883(M) + 38.0$	8	0.738	**0.006**	(Di Santo & Lobel, 2017)
Channel catfish *Ictalurus punctatus*	50–270	NA	25	0.3	$CT_{max} = -0.0006(SL) + 40.0$	40	<0.01	0.54	(Recsetar *et al.*, 2012)
Cutthroat trout *Oncorhynchus clarkii*	36–188	NA	14	0.3	$CT_{max} = -0.0076(SL) + 30.0$	49	0.412	**<0.001**	(Recsetar *et al.*, 2012)
Largemouth bass *Micropterus salmoides*	72–266	NA	25	0.3	$CT_{max} = 0.0002(SL) + 34.9$	40	<0.01	0.93	(Recsetar *et al.*, 2012)
Leopard coral grouper *Plectropomus leopardus*	350–600	450–2820	26.5–29	0.1	$CT_{max} = \exp.(3.636) \times M^{-0.0117}$	16	0.604	**<0.001**	(Messmer *et al.*, 2017)
Neon goby *Elacatinus oceanops*	37–45	0.5–1.8	20	0.34	$CT_{max} = -0.892(M) + 32.8$	8	0.538	**0.03**	(Di Santo & Lobel, 2017)
E. oceanops	39–49	2.0–2.2	24	0.30	$CT_{max} = -4.519(M) + 43.3$	8	0.388	**0.098**	(Di Santo & Lobel, 2017)
E. oceanops	27–38	0.2–1.1	28	0.24	$CT_{max} = -4.199(M) + 38.1$	8	0.757	**0.005**	(Di Santo & Lobel, 2017)
Nile tilapia *Oreochromis niloticus*	35–206	NA	25	0.3	$CT_{max} = 0.0012(SL) + 40.3$	40	<0.05	0.33	(Recsetar *et al.*, 2012)
O. niloticus	NA	21–313	25	0.033	$CT_{max} = -0.0019(M) + 40.9$	18	0.090	0.22	(Blasco *et al.*, 2020a)
Rainbow trout *Oncorhynchus mykiss*	45–200	NA	18	0.3	$CT_{max} = -0.0002(SL) + 31.2$	40	<0.01	0.75	(Recsetar *et al.*, 2012)
O. mykiss	NA	73–395	12	0.008	$CT_{max} = -0.012(M) + 30.2$	39	0.65	**<0.05**	(Roze *et al.*, 2013)
CT_{max} for swimming (CT_{swim})									
O. niloticus	NA	21–313	25	0.033	$CT_{swim} = -0.873\ln(M) + 41{,}9$	18	0.510	**0.001**	(Blasco *et al.*, 2020a)

Note: Δ_T: rate of temperature increase; CT_{max}: critical thermal maximum; M: mass; SL: standard length; T_{acc}: acclimation temperature. Bold indicates a significant regression, $P<0.05$.

underlying the decline in adult fish size and the TSR remain to be clarified, a reduced capacity to supply oxygen to tissues in larger fishes has repeatedly been evoked (Atkinson & Sibly, 1997; Audzijonyte *et al*., 2019; Cheung *et al*., 2011; Hoefnagel & Verberk, 2015; Leiva *et al*., 2019), a possibility that should be comprehensively tested.

When comparing across fish species, CT_{max} can decline with body and consequent cell size (Leiva *et al*., 2019). There is also evidence that, within some species, CT_{max} declines with fish size or mass (Table 1). In freshwater, cutthroat trout *Oncorhynchus clarkii* (Richardson 1836) or apache trout *Oncorhynchus apache* (Miller 1872) show a very modest, albeit significant, decline with mass, whereas others such as Nile tilapia *Oreochromis niloticus* (L. 1758) and channel catfish *Ictalurus punctatus* (Rafinesque 1818) show no relationship between mass and CT_{max} (Table 1; Blasco *et al*., 2020a; Recsetar *et al*., 2012). In sea water, tropical species such as Caribbean neon goby *Elacatinus lobeli* Randall & Colin 2009, neon goby *Elacatinus oceanops* Jordan 1904 and leopard coral grouper *Plectropomus leopardus* (Lacipède 1802) show quite profound negative relationships between CT_{max} and mass, such that larger individuals do indeed have lower acute tolerance (Table 1; Di Santo & Lobel, 2017; Messmer *et al*., 2017). In marine tropical damselfishes, CT_{max} declined with size in spiny chromis *Acanthochromis polyacanthus* Bleeker 1855 and white damsel *Dischistodus perspicillatus* Cuvier 1830, but not in humbug *Dascyllus aruanus* L. 1758 (Clark *et al*., 2017). In some species like rainbow trout *Oncorhynchus mykiss* (Walbaum 1787) results differ between studies (Table 1). For example, Recsetar *et al*. (2012) found no dependence, whereas, in two rainbow trout strains with either rapid or slow growth, Roze *et al*. (2013) found a clear negative relationship between body mass and "time to loss of equilibrium" (TLOE, measured with a ramping protocol with initial rapid steps and then in lower steps, until LOE).

Thus, with limited data, it can be concluded that whenever a relationship exists between CT_{max} and size or mass in post-metamorphic fishes, it is consistently negative. It is not known how body size affects TPCs and T_{opt} for AAS in fishes as they grow, although optimal temperature for growth declines with increasing body mass in various species (*e.g*., Björnsson & Tryggvadóttir, 1996). In terms of whether declining size is due to problems with providing oxygen for metabolism, mass-specific MMR does in fact decline with increasing mass in many fishes due to allometric scaling phenomena whose mechanisms are still not understood (Glazier, 2020; Killen *et al*., 2016b; Lefevre *et al*., 2017). Nonetheless, because mass-specific SMR also declines with mass, AAS and capacity to perform aerobic activities are maintained independent of mass (Lefevre *et al*., 2017). Blasco *et al*. (2020a) found that CT_{swim} declined significantly with increasing mass in Nile tilapia (Table 1), and this was correlated with a decline in the highest rate of oxygen uptake achieved before fatigue at CT_{swim} (Blasco *et al*., 2020a). Interestingly, CT_{max} showed no relationship to mass in the same individuals (Table 1) and was not correlated with CT_{swim} (Blasco *et al*., 2020a). Thus, tolerance of warming declines with mass in many fish species, but more research is required to establish whether this is because of a reduced capacity of larger fishes to meet the oxygen demands of metabolism when water temperature rises. Further research is also required to understand whether this might be a mechanism underlying ongoing declines in fish body size globally (Audzijonyte *et al*., 2019; Blasco *et al*., 2020a).

Taken together, these data point to body size as another important factor that can lead to intraspecific variation in tolerance of warming in fishes. Such potential effects of fish body size, in combination with the known effects of fishing pressure on body size (van Wijk *et al*., 2013), should be considered when making predictions regarding the likely effects of climate warming on fish populations.

5 | INTRASPECIFIC VARIATION IN THERMAL TOLERANCE DUE TO PHENOTYPIC PLASTICITY

Phenotypic plasticity can be classified into three main types: reversible, developmental and transgenerational (Angilletta, 2009; Donelson *et al*., 2018). Reversible plasticity is also called acclimatization or acclimation and refers to flexible changes in physiological phenotypes as a result of environmental exposures in the time range of days to months, *e.g*., seasonal acclimatization in temperate fishes (Schulte *et al*., 2011). Developmental plasticity occurs when conditions during early development cause the expression of a phenotype that is then fixed for the remainder of the animal's lifetime. Transgenerational plasticity occurs when the environment experienced by the parent affects the phenotype of the offspring and can be mediated by epigenetic responses that affect gene expression and therefore the phenotype, but not the underlying genetic code (Donelson *et al*., 2018; Mimura *et al*., 2017; Moran *et al*., 2016). Epigenetic responses can contribute to immediate plastic responses but may also be heritable over a few generations (Donelson *et al*., 2018; Mimura *et al*., 2017; Moran *et al*., 2016). A vast majority of studies of the effects of plasticity on tolerance of warming in fish have focused on reversible phenomena, and far fewer have examined developmental or transgenerational effects.

Many studies have investigated the effects of seasonal acclimatization or acclimation on CT_{max} in the laboratory (Beitinger & Lutterschmidt, 2011; Lutterschmidt & Hutchison, 1997). These latter effects are delineated in the Fry-TTP by the increases in thermal tolerance boundaries as temperature rises along the *x*-axis (Figure 1). Given that the mechanisms which underlie LOE at CT_{max} in fishes are unknown, the reasons why CT_{max} is plastic are also unclear but may involve a number of processes that are involved in thermal acclimation or acclimatization (Currie & Schulte, 2014). Nonetheless, one common pattern is that a given increase in acclimation temperature is not linked to an equivalent increase in CT_{max}, such that the thermal safety margin, the difference between acclimation temperature and CT_{max}, narrows as a fish is acclimated to progressively warmer temperatures across its thermal range (*e.g*., Habary *et al*., 2017; McArley *et al*., 2017; McDonnell *et al*., 2019; Spinks *et al*., 2019). This effect is exemplified by an extensive data set on rainbow trout relating acclimation temperature to CT_{max} (Table 2, Figure 3), where there is a clear asymptote in CT_{max} as animals are acclimated to increasingly higher temperatures

TABLE 2 Critical thermal maximum (CT_{max}) comparisons for various strains of *Oncorhynchus mykiss* under different acclimation temperatures

T_{acclim} (°C)	CT_{max} (°C)	Heating rate (°C min^{-1})	Mass (g)	Length (cm)	Strain source	Reference
7.4	23.7 ± 0.7	0.3 ± 0.03	30 ± 2		British Columbia	(Zhang *et al*., 2018)
7.4	24.8 ± 0.5	0.3 ± 0.03	18 ± 2		British Columbia	(Zhang *et al*., 2018)
7.4	26.6 ± 0.2	0.3 ± 0.03	24 ± 2		British Columbia	(Zhang *et al*., 2018)
8	26.9 ± 0.12	0.1		11.0–18.0	Washington	(Dale Becker & Wolford, 1980)
9.8	27.9 ± 0.05	0.3		15.3 ± 0.25	Pennsylvania	(Carline & Machung, 2001)
10	28.5 ± 0.28	0.02		15.0–20.0	Arizona	(Lee & Rinne, 1980)
10	28.0 ± 0.12	0.3	~15.0	~10.0	Missouri	(Currie *et al*., 1998)
10	27.7 ± 0.08	0.3	12.9 ± 0.6		California	(Myrick & Cech, 2000)
10	25.3 ± 0.25	0.03	1175.0 ± 42.0	41.1 ± 0.4	Newfoundland	(Motyka *et al*., 2017)
10	26.3 ± 0.3	0.08/0.05	487 ± 34	33.2 ± 0.6	Alingsås Sweden	(Ekström *et al*., 2014)
19	25.9 ± 0.2	0.05	683 ± 136		Alingsås Sweden	(Ekström *et al*., 2014)
11	~27.5	0.3	8.0 ± 1.6		California	(Myrick & Cech, 2005)
12[a]	28.73 ± 0.08	0.3	2.4 ± 0.05		Blackwater	(Scott *et al*., 2015)
12[a]	29.14 ± 0.09	0.3	2.4 ± 0.05		Tzenzaicut	(Scott *et al*., 2015)
12[a]	29.11 ± 0.09	0.3	2.4 ± 0.05		Pennask	(Scott *et al*., 2015)
13	27.9 ± 0.14	0.33		21.8 ± 0.4	Ontario	(LeBlanc *et al*., 2011)
14	28.5 ± 0.11	0.3	13.8 ± 0.8		California	(Myrick & Cech, 2000)
14	29.4 ± 0.1	0.033[b]	41.0–140.0		Oregon	(Rodnick *et al*., 2004)
15	29.4 ± 0.08	0.3				(Strange *et al*., 1993)
15	29.1 ± 0.09	0.3	~15.0	~10.0	Missouri	(Currie *et al*., 1998)
15	27.7 ± 0.03	0.0014[c]	89.9 ± 5.4	11.9–0.3	North Carolina	Galbreath *et al*., 2006
15	~28.4	0.3	9.3 ± 2.0		California	(Myrick & Cech, 2005)
15	~29.65	0.083[d]			Miyazaki, Japan	(Ineno *et al*., 2005)
15	29.0 ± 0.02	0.3/0.1	30.2 ± 0.3	13.0 ± 0.4	Western Australia	(Chen *et al*., 2015)
15	29.1 ± 0.19	0.083	10.8 ± 2.03	8.7 ± 1.9	Nikko	(Ineno *et al*., 2018)
15	29.2 ± 0.17	0.083	8.8 ± 1.5	8.6 ± 0.48	Aomori	(Ineno *et al*., 2018)
15	29.8 ± 0.08	0.3/0.1	2.5 ± 0.2		Little Jacks Creek	(Chen *et al*., 2018a)
15	28.8 ± 0.08	0.3/0.1	2.5 ± 0.2		Fawn Creek	(Chen *et al*., 2018a)
15	29.3 ± 0.07	0.3/0.1	2.5 ± 0.2		Keithley Creek	(Chen *et al*., 2018a)
16	29.0 ± 0.2	0.3	4.6 ± 0.5	8.2 ± 0.2	Turku, Finland	(Anttila *et al*., 2017)
18	~31.2	0.3		4.1–20	Arizona	(Recsetar *et al*., 2012)
19	~29.6	0.3	14.3 ± 2.9		California	(Myrick & Cech, 2005)

Note: This updates the content of table 5 in Chen *et al*., 2015.
[a]Fish held at 10–12°C.
[b]Temperature was increased at 2°C per hour.
[c]Temperature was increased at 2°C per day.
[d]Temperature was increased at 5°C per hour. "~" indicates an estimated or calculated mean by original author. Values separated by "–" represent the range of the traits. Other values were given as mean ± S.E.M.

over their existing thermal range. The fact that fishes show a finite capacity (a ceiling) for their plasticity in upper thermal tolerance may be a major factor in their sensitivity to global warming, including extreme seasonal events (Gunderson & Stillman, 2015). This is argued to be especially true for stenothermal tropical species that already live at temperatures close to their CT_{max} (Comte & Olden, 2017; Gunderson & Stillman, 2015). For temperate species with a broad latitudinal range and panmictic population structure, safety margins are wider but are expected to be lower for populations at the warm edge of their distribution (Bennett *et al*., 2019). Developmental plasticity in CT_{max} has been shown in the zebrafish *Danio rerio* (Hamilton 1822), a tropical eurytherm (Schaefer & Ryan, 2006) and sockeye salmon *O. nerka* (Walbaum 1792), a temperate stenotherm (Chen *et al*., 2013). In both species, exposure of groups of fish to warmer temperatures during embryonic development increased their CT_{max} later in life.

TPCs explicitly measure intraspecific plasticity, how performance varies at different exposure temperatures, within a fish species or across its populations (Currie & Schulte, 2014; Schulte *et al*., 2011).

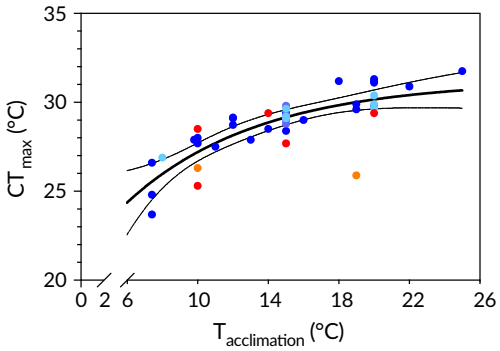

FIGURE 3 Model of the hyperbolic relationship between critical thermal maximum (CT_{max}) and acclimation temperature using various strains of *Oncorhynchus mykiss* Walbaum. CT_{max} was fitted with a one-phase association equation (y = 16.0 + (31.2–16.0)*(1-exp [−0.13*x]) R^2 = 0.66, P = 0.0003). Information on fish size and origins are presented in Table 1. Each point represents a mean value. Colours denote different warming rates. Shaded area represents the 95% confidence interval. (●) 0.001–0.03°C min^{-1}, (●) 0.05–0.065°C min^{-1}, (●) 0.083–0.1°C min^{-1}, (●) 0.2°C min^{-1} and (●) 0.3°C min^{-1}

Effects of temperature on AAS differ among fish species (Lefevre, 2016), indicating much underlying variation in plastic responses to temperature, which remains to be understood. The time of exposure to temperatures also varies widely among studies, from acute (hours) to long-term (months to years), further hindering any analysis of patterns in plasticity of performance (Lefevre, 2016; Schulte *et al*., 2011). If acutely exposed to a range of temperatures, immediate impacts on fish performance represent "passive" plasticity and will expose limitations in sustaining performance (*e.g*., AAS) at temperatures as they diverge from T_{opt} (Eliason *et al*., 2011; Munday *et al*., 2017). Long-term acclimation to the temperatures is expected to provide adequate time for active plastic compensation of metabolic traits, presumably towards optimizing performance at the new temperature (Claireaux *et al*., 2006; Ferreira *et al*., 2014; Healy & Schulte, 2012; Norin *et al*., 2014; Sandblom *et al*., 2014, 2016; Slesinger *et al*., 2019).

The capacity of fishes to engage active compensation of thermal effects on SMR and MMR and the resultant effects on AAS (Figure 2) have been investigated, in particular, by comparing the Q_{10} for the traits after acute and chronic exposure at common temperatures. This is typically for a single temperature, insufficient to generate a TPC but informative all the same. For example, when a temperate marine species, the shorthorn sculpin *Myoxocephalus scorpius* L. 1758, acclimated to 10°C was warmed to 16°C, SMR rose with a Q_{10} of 2.7 at 1 week, leading to a decline in AAS, but AAS was restored after 16 weeks by a progressive decline in SMR to achieve perfect thermal compensation and a Q_{10} of 1 (Sandblom *et al*., 2014). In the tropical barramundi *Lates calcalifer* (Bloch 1790) acclimated to 29°C, acute exposure to 38°C caused an increase in SMR, MMR and AAS; nonetheless, after 5 weeks acclimation at 38°C, MMR and SMR had both declined such that AAS was now similar again to the fish at 29°C (Norin *et al*., 2014). In the temperate black sea bass *Centropristis striata* (L. 1758) acclimated to 22°C, acute exposure to 30°C raised SMR and MMR but AAS remained constant, whereas, after 1 month at 30°C, SMR had not changed but MMR and AAS had declined significantly (Slesinger *et al*., 2019). Sandblom *et al*. (2016) compared two populations of European perch *Perca fluviatilis* L. 1758 in the Baltic sea, one that lived in the sea itself (Baltic perch) and one that lived inside a man-made enclosure that had been warmed for 30 years by thermal effluent from a nuclear power station (Biotest Perch). When Baltic perch acclimated to 18° were acutely exposed to 23°C, both SMR and MMR rose and AAS did not change. In the Biotest perch at 23°C, AAS was higher than the Baltic fish that had been acutely exposed but this was achieved by lowering SMR, with MMR being similar in the two populations. This respiratory response was mirrored in cardiac performance, in terms of resting and maximum cardiac output and the resultant cardiac scope (Sandblom *et al*., 2016). Collectively, these studies show a range of different thermal acclimation responses for AAS, over different time scales, with no generalized pattern.

Studies have investigated how a TPC for AAS, measured over a range of acute temperature exposures, varies with thermal acclimation (Ferreira *et al*., 2014; Healy & Schulte, 2012; Poletto *et al*., 2017). Such studies are technically demanding but can reveal whether active plasticity in SMR, routine metabolic rate (RMR) and MMR (Figure 2), and resultant AAS with temperature acclimation, has the potential to change T_{opt} and the form of a TPC, *e.g*., shifting T_{opt} to higher temperatures with warm acclimation and potentially changing the breadth of performance. The most in-depth study is on the Atlantic killifish *Fundulus heteroclitus* (L. 1766), a small topminnow that inhabits intertidal salt marshes along the east coast of North America from the Gulf of the St. Lawrence River to northern Florida (Taylor, 1999). These habitats are very thermally dynamic over diurnal and seasonal time scales (Fangue *et al*., 2008; Schulte, 2007), and Atlantic killifish are extreme eurytherms that can withstand acute temperature changes greater than 30°C and can be acclimated to temperatures ranging from 2 to 35°C (Fangue *et al*., 2006). The species is a model for studies of intraspecific variation in thermal physiology of fishes because, over its biogeographic range, it is divided into two sub-species – a northern form, *F. heteroclitus macrolepidotus* (Walbaum 1792) and a southern form, *F. heteroclitus heteroclitus* (Morin & Able, 1983), which differ in genetics, physiology, morphology and behaviour (Schulte, 2007, see below).

TPCs for AAS have been determined for both sub-species, comparing acute exposure and longer term acclimation (Healy & Schulte, 2012). The most striking feature of the curves following acute temperature exposure is that they are extremely broad, with AAS maintained at a similar level from 10 to 30°C. This insensitivity of AAS was not due to reduced thermal sensitivity of metabolic processes in general, because both RMR and MMR were thermally sensitive with Q_{10} between 2 and 3. Thus, the insensitivity of AAS to an acute temperature change was a result of essentially parallel changes in RMR and MMR with temperature. A somewhat different picture emerged for TPCs determined for *F. heteroclitus* tested at their acclimation temperatures. These reveal a much narrower TPC for AAS, with a plateau

for T_{opt} between 25 and 30°C (Healy & Schulte, 2012). The shape of the curve is strongly left-skewed, increasing gradually with temperature up to the T_{opt} plateau, and then dropping sharply at temperatures above 30°C (Healy & Schulte, 2012). The differences between the AAS TPCs of acutely exposed *vs*. acclimated killifish were largely because of changes in the RMR of warm-acclimated fish, with RMR at higher temperatures being depressed relative to that of acutely exposed animals (Healy & Schulte, 2012).

Performance curves for AAS were also evaluated in another extreme eurytherm, the goldfish *Carassius auratus* L. 1756, acclimated to 12, 20 or 28°C (Ferreira *et al*., 2014). In this species, peak AAS was rather insensitive to acclimation temperature and again was sustained by parallel increases in RMR and MMR, although both of these traits showed significant thermal compensation, with a Q_{10} between 1 and 1.5. The T_{opt} shifted to be centred on the acclimation temperature; a notable finding was that the AAS curve at 12°C was extremely broad and narrowed with progressive warm acclimation. Therefore, these two eurytherms maintained thermal performance across a wide range of temperatures by maintaining parallel thermal sensitivities of both routine and maximum aerobic performance up to the failure temperature, rather than having MMR constrained at a temperature lower than that for RMR.

Another study is for a stenothermal species, the chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792), that is found on the Pacific coast of North America from Alaska to southern California. A Californian population from the Mokelumne River Hatchery (Clements, CA, U.S.A.) can survive widely fluctuating rearing temperatures (13–16, 17–20 or 21–24°C) and grow at temperatures up to 24°C, albeit at significantly reduced rates (Marine & Cech, 2004). Poletto *et al*. (2017) found that O_{2max} and AAS of this strain of Chinook salmon when acclimated to either 15 or 19°C was mostly insensitive to test temperatures from 12 to 23°C, despite a marked increase in RMR with warming.

The only study that, to the best of the authors' knowledge, has investigated plasticity in the TPC for AAS during seasonal thermal acclimatization is on the temperate European seabass *D. labrax* L. 1756 (Claireaux *et al*., 2006). A cohort was measured for their SMR, MMR and AAS at seven temperatures over a seasonal thermal range from 7 to 30°C, and SMR rose progressively with an average Q_{10} of 1.76 and MMR with a Q10 of 1.69 such that thermal compensation was not perfect, but AAS nonetheless rose progressively across the natural thermal range (Claireaux *et al*., 2006).

Overall, although there is a strong evidence of reversible plasticity in TPCs in fishes, there are very few studies on very few species to draw firm conclusions about general patterns of plasticity in AAS with thermal acclimation. Nonetheless, one response that appears to be observed in multiple species is that when acclimated chronically, the capacity to raise MMR appears to be finite so that plastic adjustments to maintain AAS are often linked to a capacity offset Q_{10} effects on SMR (Ferreira *et al*., 2014; Healy & Schulte, 2012; McArley *et al*., 2017; Norin *et al*., 2014; Sandblom *et al*., 2014, 2016; Slesinger *et al*., 2019). That is, the fishes recruit mechanisms to compensate for the thermodynamic effects of increased temperature on basal metabolic processes and their associated oxygen demand. Known thermal compensation mechanisms associated with warm acclimation in eurythermic fishes, which might enable them to offset thermodynamic effects on basal or routine metabolism, could include decreases in the amount (or density) of mitochondria and perhaps the efficiency of generating ATP (Johnston, 1982), of sarcoplasmic reticulum (Penney & Goldspink, 1980), of capillaries (Egginton & Sidell, 1989) and of red muscle (Johnston & Lucking, 1978). Such compensations are thought to partially compensate for changes in cytoplasmic viscosity, diffusion rate and membrane fluidity (Egginton & Sidell, 1989; Pörtner, 2001; Tansey & Brock, 1972) and should result in Q_{10} values nearer to unity when comparisons are made between acclimation temperatures (Ferreira *et al*., 2014; Jayasundara & Somero, 2013).

Le Roy *et al*. (2017) investigated developmental plasticity in thermal performance in guppies *Poecilia reticulata* Peters 1859 bred and raised at either 23 or 29°C (a thermal extreme in their natural range in Australia). After two generations of rearing at a common temperature of 26°C, they were tested for their AAS at a range of acute temperature exposures (18, 26, 32 and 36°C). The temperature at which grandparents had been held had little effect on the TPC. Nonetheless, the same study reported transgenerational plasticity over three successive generations for the two temperature groups. Both temperature groups increased in AAS across the acute test temperatures, but guppies held at 29°C tended to have higher AAS at all test temperatures aside from 18°C and especially at 36°C. There were complex differences between the sexes whereby in females such effects were strongest in the F2 generation and had tended to diminish by the F3, whereas in males they continued to become more pronounced across successive generations (Le Roy *et al*., 2017). In both sexes and at all temperatures, swimming performance was poor at 36°C despite a high AAS (Le Roy *et al*., 2017). Thus, this study shows complex potential effects of transgenerational plasticity and, although such studies are technically very difficult to perform, more research is required in this area (Donelson *et al*., 2018).

Reversible, developmental and transgenerational plasticity all contributes to intraspecific variation in tolerance of warming in fishes and has the potential to buffer species against the negative effects of climate warming. In essence, "buying time" by allowing a species to persist as the environment changes. This may enable long-term evolutionary responses by populations, if it protects population size and underlying genetic diversity in the face of initial warming (Crispo, 2008). By contrast, a buffering effect of plasticity can also hinder adaptation by shielding a population from natural selection. Thus, the question of whether intraspecific variation generated by plasticity will help or hinder long-term persistence of a species in the face of climate change remains far from settled (Fox *et al*., 2019).

6 | INTRASPECIFIC VARIATION IN THERMAL TOLERANCE DUE TO HERITABLE GENETIC VARIATION WITHIN POPULATIONS

CT_{max} is a heritable trait (Doyle *et al*., 2011; Meffe *et al*., 1995; Perry *et al*., 2005) that shows familial variation in Atlantic salmon *Salmo salar*

L. 1756 and Atlantic cod *Gadus morhua* L. 1756 grown under common garden conditions (Anttila *et al*., 2013; Gradil *et al*., 2016; Muñoz *et al*., 2014, 2015; Zanuzzo *et al*., 2019). Within individuals of a few species such as European sea bass, zebrafish or guppies *P. reticulata* Peters 1859, CT_{max} is a repeatable trait over quite extended periods (Claireaux *et al*., 2013; Grinder *et al*., 2020; Mauduit *et al*., 2019), which is a prerequisite for it to be subject to selection (Killen *et al*., 2016a).

Given the evidence that CT_{max} is temporally stable and heritable, there have been attempts to investigate whether variation in acute thermal tolerance is significant for fitness, by exposing fish to challenging conditions in mesocosms. In three studies with European sea bass, upper thermal tolerance (measured as TLOE) was compared to correlates of fitness (survival and growth) in populations of more than 100 individuals stocked into a set of semi-natural tidal ponds for a period of 6 months. Each pond sustained a natural food web with a carrying capacity for 2–3 kg of fish in the spring but much less in autumn, when productivity declined (Claireaux *et al*., 2013; Mauduit *et al*., 2016, 2019). The sea bass showed broad individual variation in thermal tolerance, with a nearly twofold difference in TLOE between the least and most tolerant fish. The relationship of thermal tolerance to individual fitness in the pond depended on the pattern of selection pressure. In years when selection pressure was weak (overall survival >60% over the 6 months), there was no relationship between TLOE and survival or growth (Mauduit *et al*., 2016, 2019). On the contrary, in the year that was characterized by strong selective pressure (survival rate was halved to ≈ 30%), individual TLOE was a predictor of survival (Claireaux *et al*., 2013). These field studies highlight the complexity with which individual variation in tolerance can impact ecological performance, and they illustrate that caution is required when interpreting the significance of tolerance in an evolutionary context. Quite clearly, further research is warranted.

A few studies have started to probe the genetic basis of heritable differences in CT_{max}. Several early studies using quantitative trait locus mapping revealed genomic regions associated with variation in CT_{max} in a variety of salmonids including rainbow trout (Jackson *et al*., 1998; Perry *et al*., 2001, 2005), Arctic charr *Salvelinus alpinus* L. 1758 (Quinn *et al*., 2011; Somorjai *et al*., 2003) and cutthroat trout *O. clarkii* (Richardson 1836) (Robinson, 2010). More recently, in Atlantic killifish, multilocus association mapping showed that 47 single nucleotide polymorphisms (SNPs) could explain 43.4% of the within-population variation in thermal variation in CT_{max} (Healy *et al*., 2018). Several of the SNPs associated with CT_{max} fall within genes coding for transmembrane ion channels, consistent with the suggestion that the temperature-dependent depression of electrical excitability may explain the impaired electrical excitability of ventricular cardiac myocytes (and potentially other excitable cells) at high temperature (Vornanen, 2016) and thus underlie variation in tolerance to acute warming. Similarly, one of the SNPs associated with variation in CT_{max} falls within a gene encoding a ubiquitin E3 ligase, implicating variation in protein degradation and repair processes as potentially important in shaping intraspecific variation in thermal tolerance. In rainbow trout, association mapping identified 207 genomic regions that were strongly associated with either variation in maximum heart rate or rate-limiting temperatures among individuals, with the identification of candidate genes that fall within pathways associated with cardiac function, the neuroendocrine system and the stress response (Chen *et al*., 2018b). Taken together, these studies suggest that intraspecific variation in tolerance to warming in fishes has a strong genetic basis, but that this variation is polygenic – the result of variation at multiple interacting genes. Nothing is known about heritability of variation in TPCs for any trait and may never be, because of the technical challenge of measuring curves on the large numbers of individuals needed to estimate heritability of complex traits that are polygenic (Muñoz *et al*., 2014, 2015). Nonetheless, there is evidence for heritability of traits that may impact upon a TPC, *e.g*., AAS (Munday *et al*., 2017).

Therefore, there is heritable genetic variation in tolerance of warming within fish populations, a substrate upon which natural selection can act. Incorporating the potential evolutionary responses of populations to climate change will be critical for accurately predicting the responses of fish species to ongoing warming (Waldvogel *et al*., 2020).

7 | INTRASPECIFIC VARIATION IN THERMAL TOLERANCE AMONG POPULATIONS: DETAILED CASE STUDIES

In many cases where variation in thermal tolerance is observed among and within fish populations, the relative contributions of plasticity *vs*. adaptation are not known. Distinguishing between plastic and heritable variation requires common garden experiments or pedigree studies, which are technically challenging for fishes that typically have quite long life spans and that cannot be followed easily in their natural environment (*e.g*., Chen *et al*., 2015; Gradil *et al*., 2016; Le Roy *et al*., 2017). Nonetheless, when species exhibit structured variation in tolerance, namely persistent differences among individuals in space or time, these can be of ecological and evolutionary significance (Bennett *et al*., 2019; Moran *et al*., 2016). That is, when comparing among populations at specific sites, phenotypic variation in tolerance will reflect responses to local thermal regimes.

There is extensive evidence of variation among populations in tolerance to warming; evidence is strongest in species where populations have little gene flow, a prime example being semelparous salmonids (Eliason *et al*., 2011; Jensen *et al*., 2008). For widespread marine species with broadcast spawning and panmictic population structures, it has been shown at an oceanic scale (*e.g*., Bradbury *et al*., 2010). Here the authors of this study summarize the results from three study systems where extensive investigations provide particular insights into the extent and nature of among-population variation in tolerance to warming.

7.1 | Atlantic killifish

Substantial phenotypic and genetic variation exists among *F. heteroclitus* populations in salt marshes and estuaries over their

range from the St Lawrence estuary south to Florida, with relatively little gene flow from one habitat to another, providing conditions that are likely to promote local adaptation (Crawford *et al*., 2020). At a larger scale, the two sub-species differ in multiple aspects of tolerance to warming, with the southern sub-species generally being more tolerant than the northern. For example, southern *F. heteroclitus* have greater CT_{max} than do northern, and these differences are maintained across the entire range of temperatures to which the species can be acclimated (Fangue *et al*., 2006) even with relatively modest differences (*c*. 2°C). Southern *F. heteroclitus* also tolerate higher temperatures in long-term thermal exposures, with chronic thermal maxima estimated to be 36.4°C for northern and 38.2°C for southern.

As is the case for upper thermal limits, there are also differences between the sub-species in cold tolerance. Northern *F. heteroclitus* have lower CT_{min} than do southern, although CT_{min} converges at the freezing point of water in fish of both sub-species if they are acclimated to temperatures below 15°C (Fangue *et al*., 2006). This pattern suggests that there may be a trade-off between upper and lower thermal tolerance in *F. heteroclitus*. Nonetheless, chronic thermal minima were not different between northern and southern killifish, with both sub-species surviving down to the freezing point of brackish water (Fangue *et al*., 2006).

Acute AAS curves are similar in both sub-species (Healy & Schulte, 2012). In general, the height of the acute curve is greater in southern than in northern sub-species, and the upper thermal limit (T_{crit}) for AAS of southern fish is modestly shifted to higher temperatures compared to those of northern. These results are generally consistent with trade-offs between upper and lower limits in this killifish but suggest that within this species there may not be trade-offs between the widths and heights of the TPC for AAS.

The shapes of the acclimated AAS curves are also similar between the sub-species (Healy & Schulte, 2012), but in this case the height of the curve is greater in northern than in southern fish, suggesting a slightly greater capacity for thermal acclimation of scope in the northern sub-species. Nonetheless, these differences in acclimation capacity are minor and result from small differences between the sub-species in the effects of acclimation on both RMR and MMR.

These differences in tolerance to warming in adult *F. heteroclitus* are also evident during early development. Northern embryos are more cold-tolerant, and southern embryos are more warm-tolerant (DiMichele & Westerman, 1997), with embryos of northern fish dying at temperatures of 30°C, which embryos of southern *F. heteroclitus* can withstand. Thus, Atlantic killifish provide a clear example of differentiation between populations in tolerance to warming across multiple life stages.

7.2 | Sockeye salmon

O. nerka is an ideal species to examine local adaptation of thermal performance because it forms discrete genetic populations across a broad diversity of environments (Taylor, 1991). Sockeye populations return faithfully to their natal lake or stream to spawn, across their range from eastern Russia *via* Alaska to Oregon in the U.S.A. (Rand *et al*., 2012). Very broad diversity in life-history characteristics exists across populations (Burgner, 1991; Quinn, 2018; Wood, 1995). Eggs are deposited typically in the summer or fall in a gravel nest (redd); the fry usually spend 1–3 years in fresh water in either a lake or river habitat and then migrate out to the ocean for 1–3 years to feed and grow, before returning to their spawning grounds. Environmental characteristics vary enormously across the geographic range (*e.g*., temperature, elevation and river flow) and over the life history of the fish (*e.g*., redd to rearing lake/stream to ocean to return migration). Population differences in morphology, physiology, behaviour and life-history traits have been attributed to local adaptation (Crossin *et al*., 2004; Eliason *et al*., 2011; Fraser *et al*., 2011; Taylor, 1991).

Much of the research on intraspecific variation in *O. nerka* thermal tolerance has focused on the upriver adult spawning migration in the Fraser River watershed (British Columbia, Canada), a once-in-a-lifetime event. Warm river temperatures are associated with elevated mortality in migrating adults (Hinch & Martins, 2011), raising conservation concerns for this iconic and economically important species. Aerobic scope is particularly relevant for adult salmon because fish must swim maximally to reach distant spawning grounds. Studies measuring a TPC for AAS found that T_{opt} corresponds with the typical historical range of temperatures encountered during upriver migration in Fraser River *O. nerka* populations (Eliason *et al*., 2011, 2013; Farrell *et al*., 2008; Lee *et al*., 2003). The T_{opt} varies from 14 to 17°C across populations, and T_{crit} is estimated to be even more variable. Nonetheless, the T_{crit} is essentially irrelevant for a migrating adult salmon because it is impossible for it to swim aerobically upstream for days at T_{crit}. It is estimated that *c*. 90% of the maximum AAS at T_{opt} is required to successfully migrate upstream. Tagging studies confirm that populations facing temperatures outside this range experience elevated mortality en-route (Eliason *et al*., 2011; Farrell *et al*., 2008; Martins *et al*., 2011). A biotelemetry study showed that when one population attempted an upstream migration of <50 km when the river temperature was above the T_{opt} for AAS, many fish did not reach their natal spawning area (Farrell *et al*., 2008). Furthermore, migration mortality rates differ across populations, and this can be attributed to differences in thermal tolerance (Hinch & Martins, 2011). Tagging studies (Martins *et al*., 2011) and management estimates of escapement from fisheries (Hinch & Martins, 2011) show that populations with a broader T_{opt} window for AAS, such as the Chilko population (migration distance 642 km and elevation 1174 m), have higher survival to the spawning grounds.

Fraser River populations such as Chilko and Harrison (migration distance 121 km and elevation 10 m), which have a higher thermal tolerance compared to other co-migrating populations (Eliason *et al*., 2011, 2013), are helping to elucidate the mechanisms that underpin thermal tolerance. Focusing on the central importance of cardiac function for upper thermal tolerance, Chilko had a greater density of adrenaline-binding β-adrenoceptors on their ventricles compared to Nechako (migration distance 958 km and elevation 716 m), a co-migrating population with a lower thermal tolerance. Chilko also had elevated cardiac sarco(endo)plasmic reticulum Ca^{2+}

ATPase (SERCA) activity compared to three other populations. This suggests that the capacity to use adrenaline and cycle Ca^{2+} within the cardiomyocytes at high temperature may support cardiac performance and thus improve thermal tolerance. These ideas require further study, but like the Biotest perch (Sandblom *et al*., 2016) enhancements to cardiac performance can reflect a better thermal performance of AAS.

One study also examined CT_{max} and its relation to cardiac T_{AB} across four populations of *O. nerka* fry (Chen *et al*., 2013). Eggs were collected from nine sockeye salmon spawning grounds, reared in a common garden environment at 10, 14 and 16°C, and the resultant fry were all held at ambient temperatures (5–7°C). Across all populations, CT_{max} was higher for fry reared at the lowest temperature (reflective of natal rearing temperatures) and decreased with warmer, stressful rearing temperatures. CT_{max} also varied among populations, which strongly depended on body size. Interestingly, the T_{AB} was similar across four populations incubated at 10°C but differed across populations incubated at 14°C (a thermally stressful temperature). Chilko fry reared at 14°C had the lowest T_{AB}, but the highest overall f_H across all temperatures. Chilko fry inhabit a glacial lake at high elevation and thus may be locally adapted to cooler temperatures at this life stage.

Thus, there is very strong evidence that thermal tolerance has a genetic component, and that variation in tolerance among sub-species or populations is linked to local adaptation, with *F. heteroclitus* and *O. nerka* providing detailed empirical studies of the physiological manifestations of such adaptation.

7.3 | Rainbow trout

Studies on rainbow trout provide ample evidence of variation in thermal tolerance in populations and strains across different sites. The rainbow trout is a model species for fish physiologists globally, and therefore its thermal and cardiorespiratory physiologies are very well studied. Generally regarded as a cold-water species within its range of Pacific coastal waters and tributary streams from the Kamchatka Peninsula to northern Mexico (Behnke, 2002), rainbow trout have been introduced onto all continents except Antarctica (Crawford *et al*., 2008), suggesting a tremendous physiological plasticity and perhaps adaptability. The inland strain of redband trout *O. mykiss gairdneri* inhabits desert streams where summer daytime highs can approach 30°C (Chen *et al*., 2018a). Three domesticated strains of *O. mykiss* raised and tested in common garden hatchery conditions exhibited differences in CT_{max} (Zhang *et al*., 2018). The strain with the highest CT_{max} also had the best cardiorespiratory performance (highest MMR and AAS). Importantly, the strain with superior CT_{max} and high aerobic capacity also had a lower critical partial pressure for tolerance of hypoxia (P_{crit}). This indicates a potential genetically based link between tolerance of warming and of hypoxia, which is another major stressor associated with global change (Zhang *et al*., 2018). Thus, there are marked differences in thermal tolerance among strains and populations that have a genetic basis, opening up interesting research perspectives and possibilities.

The CT_{max} for *O. mykiss* depends on acclimation temperature (Table 2), increasing from *c*. 27°C for animals acclimated to 8°C to almost 32°C for those acclimated to 25°C (Figure 3). Intraspecific variation in thermal tolerance is revealed by population (or strain) differences in CT_{max}. Similarly, intraspecific differences in thermal sensitivity of growth are evident in Californian *O. mykiss*, where the Mount Shasta strain acclimated to 22–25°C grew 18% faster than the Eagle Lake strain (Myrick & Cech, 2000). An excellent example of thermal adaptation occurred when the *O. mykiss irideus* strain was introduced into the Pemberton Freshwater Hatchery Centre, Western Australia, about 50 years ago (Molony, 2001; Molony *et al*., 2004). A breeding population was maintained at the hatchery despite mass mortalities during high summer temperature events, an example of "hard selection" which resulted in the emergence of a warm-tolerant H-strain (Molony *et al*., 2004) that had less genetic diversity (Ward *et al*., 2003) than its parental stock (the S-strain). When acclimated to 15°C, the H-strain has a CT_{max} in excess of 29°C and can maintain 90% of peak AAS up to 20°C during acute warming, with peak AAS at 18°C (Chen *et al*., 2015). Investigating how the animals acclimate successfully to temperatures higher than the 15°C is an interesting topic for future study because the Pemberton Hatchery staff routinely feed their H-strain at temperatures up to 23°C, a temperature well beyond the U.S. Environmental Protection Agency recommendation of 18°C for the 7 day average for daily maxima when managing *O. mykiss* habitats in the Pacific Northwest (USEPA, 2003).

In contrast to the bell-shaped TPC for AAS for the Australian H-strain, wild *O. mykiss irideus* tested riverside in a mobile laboratory after capturing from the Tuolumne River in central California, with an ambient habitat temperature of 14–24°C, had an unusually flat TPC for AAS during acute warming (Figure 4; Verhille *et al*., 2016). Although peak AAS was at 21.2°C, AAS varied slightly (<5%) between 17.8 and 24.6°C; factorial aerobic scope (FAS, namely MMR/SMR) decreased with test temperature in both of these heat-tolerant *O. mykiss irideus* populations because SMR increased more than MMR (Figure 4). Nonetheless, at 25°C the FAS of the Tuolumne River population (2.1) was slightly greater than that of the H-strain (1.8; Chen *et al*., 2015).

Redband trout are an example of thermal adaptation to warm conditions, with geographically isolated populations that inhabit both desert (*e.g*., Little Jacks Creek) and montane (*e.g*., Keithley and Fawn Creeks) habitats in Idaho, U.S.A., where daily and seasonal temperature oscillations differ considerably (Chen *et al*., 2018b). There are clear indications that the desert population has adapted its physiology to tolerate the warmer temperatures of its habitat (Chen *et al*., 2018a, 2018b); they have a significantly higher CT_{max} (by 1°C) and a broader thermal window for AAS (>3°C) than the montane populations (Figure 3). These phenotypic traits were associated with differential expression of genes involved in stress responses, metabolic activity and the neuroendocrine system. In addition, the desert population has a 20% higher maximum f_H than the montane population (Chen *et al*., 2018b), which again opens up interesting perspectives to investigate the underlying genetic pathways for cardiac function.

With the exception of the growth study of Myrick and Cech (2000), the population comparisons of thermal performance and

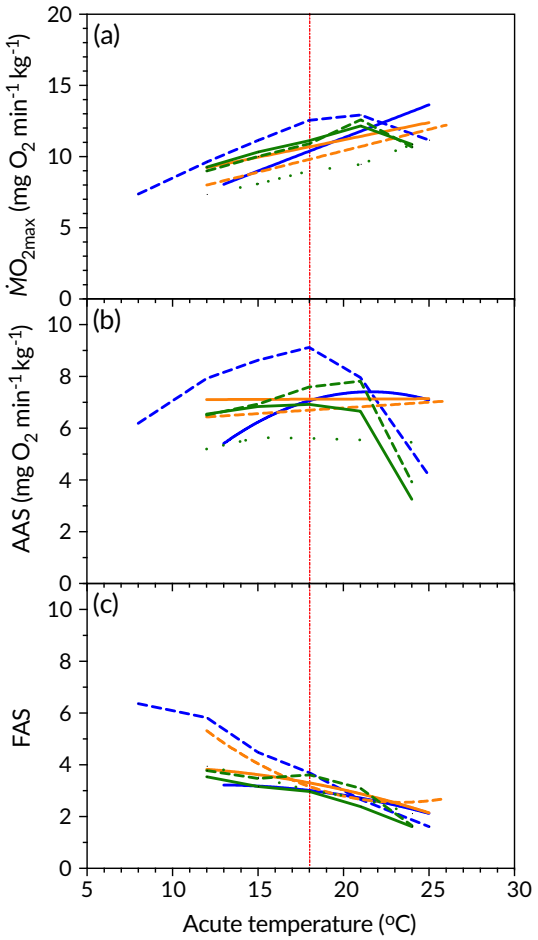

FIGURE 4 Maximum oxygen uptake (O_{2max}; a), absolute aerobic scope (AAS; b) and factorial aerobic scope (FAS; c) over a range of acute temperatures in various studies on *Oncorhynchus* spp. The studies had different settings, testing protocols and analytical techniques, as well as acclimation temperatures (indicated), but not all the differences in the curves can be attributed to these. A red vertical dash line marks 18°C as the 7 Day Average of the Daily Maxima criterion for management of rainbow trout habitat in the Pacific Northwest (U.S. Environmental Protection Agency, 2003). Rainbow trout *Oncorhynchus mykiss*, redband trout *O. mykiss gairdneri* and chinook salmon *O. tshawytscha* are in blue, green and orange, respectively. Patterns of lines differentiate the study groups. As noted by Verhille *et al.* (2016), peak AAS at 15°C for the wild Tuolumne River *O. mykiss* (5.1 mg O_2 kg$^{-0.95}$ min^{-1}) is at the high end of previous laboratory measurements of AAS (1.8–5.8 mg O_2 kg$^{-0.95}$ min^{-1}) for *O. mykiss* at 15°C, but lower than peak AAS (*c.* 7.3 mg O_2 per kg$^{-0.95}$ min^{-1}) at 20°C in Australian *O. mykiss* (Chen *et al.*, 2015). Notably, AAS at 24°C for Tuolumne River *O. mykiss* is greater than other *O. mykiss* populations. Although peak AAS of the Australian *O. mykiss* population was 50% greater than for the other two *O. mykiss* populations, Tuolumne River *O. mykiss* had the broadest and highest thermal window (from 17.8 to 24.6°C) among the group. (——) 13°C *O. mykiss*, Verhille *et al.*, 2016, (– – ·) 15°C *O. mykiss*, Chen *et al.*, 2015, (——) 15°C Fawn *O. mykiss gairdneri*, Chen *et al.*, 2018, (– – ·) 15°C Keithley *O. mykiss gairdneri*, Chen *et al.*, 2018, (·) 15°C Little Jacks *O. mykiss gairdneri*, Chen *et al.*, 2018, (——) 15°C *O. tshawytscha*, Poletto *et al.*, 2017 and (– – ·) 19°C *O. tshawytscha*, Poletto *et al.*, 2017

cardiac tolerance have not considered the potential significance of temperature acclimation, which is so important for CT_{max} (Table 2, Figure 2). The chinook salmon is closely related to *O. mykiss*, and plasticity in thermal performance of the Californian fall-run *O. tshawytscha* from the Mokelumne River Hatchery has been described earlier. The Tuolumne River rainbow trout showed a similar thermal insensitivity (Verhille *et al.*, 2016) (Figure 3). Thus, Californian fall-run *O. tshawytscha* and possibly Tuolumne River *O. mykiss* may have a broad thermal range for peak AAS, but a limited capacity to acclimate to warm temperatures. Muñoz *et al.* (2015) reared *O. tshawytscha* at 10°C, 4°C higher than the present-day rearing at 6°C, and measured f_{Hmax} finding that T_{AB} and the temperature of peak maximum f_H (T_{peakfH}) increased by 2°C, whereas T_{arr} was unchanged. Therefore, *O. tshawytscha* show standing phenotypic variation and perhaps also have underlying genetic variation for T_{AB} and T_{peakfH}, but not for T_{arr}.

The wide geographic distribution of *O. mykiss* shows an impressive capacity for phenotypic plasticity of this species that can have genomic or physiological origins. Studies on the warm-adapted Australian rainbow trout and redband trout provide a perspective on how the selection pressure of warm temperature might shape traits of tolerance. The general pattern that emerges is that a TPC flattens at high temperatures to extend the thermal window and support sufficient scope for activity. This is underpinned by cardiac performance, with maximum f_H sustained at warm temperatures, thereby increasing T_{AB}. These cardiac responses may be mechanisms underlying the higher CT_{max} of trout strains and populations living at warm temperatures.

8 | BROAD-SCALE STRUCTURED VARIATION IN THERMAL TOLERANCE

At a geographic scale, variation in thermal tolerance is expected to be structured by large-scale environmental gradients and may reflect both plastic responses and underlying genetic diversity (Bennett *et al.*, 2019). A well-known example of large-scale structured variation in thermal tolerance is related to the latitudinal range of a species (Bennett *et al.*, 2019; Comte & Olden, 2017), as this defines the range of temperatures that individuals are exposed to annually and over evolutionary time (Payne *et al.*, 2016). At temperate latitudes the thermal variability is higher than in the tropics and polar regions, such that tropical and polar species are typically considered to be stenothermal. Tropical species also live closer to their upper thermal limits (Comte & Olden, 2017), such that there would be less thermal margin for standing variation in tolerance to persist in tropical latitudes. Therefore, an expectation might be that temperate species would have greater variation in CT_{max} compared to tropical or polar counterparts. Nati *et al.* (2020) calculated intraspecific variation in CT_{max} for 203 species (N = 127 fresh water, N = 76 marine), based simply on the standard deviation of the mean. A phylogenetically informed analysis revealed that intraspecific variation in CT_{max} was greater in temperate than in

tropical species, whereas there were very little data on polar species to include them in the analysis. There was a very strong phylogenetic signal in thermal tolerance, at the level of the family. This may indicate, at least in part, that species in many families share a common thermal history over evolutionary time and therefore have a similar thermal physiology (Nati *et al*., 2020

). This is a fertile area for future research.

9 | ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF INTRASPECIFIC VARIATION

The broad arguments about the significance of plasticity and genetic diversity to species vulnerability to global change have been made many times earlier and are now accepted wisdom. Nonetheless, it is interesting to interpret the empirical data of thermal tolerance in the light of specific theories about the ecological and evolutionary significance of intraspecific variation, in particular, to focus on the proposed mechanisms by which the extent of such variation may influence vulnerability to environmental stressors (Mimura *et al*., 2017; Moran *et al*., 2016; Pacifici *et al*., 2015).

Among the various mechanisms by which intraspecific variation in thermal tolerance could influence the sensitivity of a species to the impacts of global warming, the portfolio effect may be of particular significance (Bolnick *et al*., 2011; Moran *et al*., 2016). It is named in analogy to sensitivity to fluctuations in stock markets, where having a broad portfolio reduces the likelihood of losing all your investments. Greater variation within and among populations can buffer negative effects of climactic stressors and reduce the overall risk of negative effects on stability of the species. This effect does not require that variation is heritable, just that structured variation exists (Bolnick *et al*., 2011; Moran *et al*., 2016). An oft-cited example is the Alaskan sockeye salmon fishery which depends on hundreds of discrete salmon runs. Asynchrony in timing among local populations and cohorts reduces annual variability in overall migratory returns more than two-fold compared to if the populations were all synchronous, thereby contributing to long-term sustainability (Schindler *et al*., 2010). For tolerance of warming, one example where a portfolio effect might contribute to differences in vulnerability is latitudinal structuring, with the greater variation in CT_{max} in temperate species compared to tropical species (Nati *et al*., 2020).

The "sampling effect" is linked to the portfolio effect but is more specific, being where possessing a broad range of phenotypes (and genotypes) within a population increases the likelihood that one has a high tolerance (Bolnick *et al*., 2011; Moran *et al*., 2016; Pacifici *et al*., 2015). This would also be relevant to the changes in the extent of variation in CT_{max} with latitude (Nati *et al*., 2020), but may also underlie the response to hard selection for heat tolerance in rainbow trout farmed in Australia (Chen *et al*., 2015). The theory of "increased degree" is where populations themselves may have rather narrow and restricted variation in thermal sensitivity but tolerance differs widely among them, so broadening the overall range of tolerance in the species as a whole (Bolnick *et al*., 2011; Moran *et al*., 2016). This concept might be applied to the Fraser river sockeye populations because their individual thermal ranges for optimal AAS are quite narrow compared to other species, but population differences in T_{opt} exist (Eliason *et al*., 2011). By contrast, one potential negative effect of having low intraspecific variation, or restricted variation within each population, is the risk of a local extinction (Moran *et al*., 2016). Here, the Fraser river sockeye salmon is also a prime example (Eliason *et al*., 2011). It remains a challenge for physiologists to provide data in support of these various hypotheses.

The effects mentioned so far do not distinguish whether diversity is phenotypic or genetic. The other major concept that defines vulnerability of a species to global warming is its adaptability or evolvability, which obviously focuses on heritable genetic variation (Bolnick *et al*., 2011; Mimura *et al*., 2017; Pacifici *et al*., 2015). The concept is simple; having a large degree of heritable variation can provide genotypes for new selections in a changing environment and contribute to populations fitting into the new environment (Bolnick *et al*., 2011; Mimura *et al*., 2017; Pacifici *et al*., 2015). Very little is known about the relative adaptability of species although it would seem self-evident that highly eurythermal species with short generation times, such as Atlantic killifish, would be more adaptable than the more stenothermal and longer-lived salmonids. Ongoing innovations in molecular biology may allow the direct investigation of functional genetic variants responsible for adaptation (Mimura *et al*., 2017; Razgour *et al*., 2019). For example, genomic studies of local adaptations can reveal the extent of molecular genetic diversity and how it relates to tolerance phenotypes and to prevailing environmental conditions at sites across a species' range (Razgour *et al*., 2019).

Overall, the authors of this study are far from understanding how variation in heat tolerance within species can actually contribute to their relative vulnerability to warming, and whether this occurs by any of the mechanisms proposed earlier. Improvements in technologies for rapid phenotyping of fishes, coupled with advances in sequencing, may provide access to testing the theories.

10 | CONCLUSIONS

There are well-established methods to investigate and assess intraspecific variation in tolerance of warming in fishes that can define absolute tolerance boundaries and how temperature affects performance within these. Nonetheless, the knowledge base is limited, and therefore more research is required to establish patterns that hold across multiple species. The evidence that tolerance changes systematically with life stages, and possibly with size as fishes become mature, should definitely be explored further and considered in projections of the sensitivity of species to future warming challenges. Phenotypic plasticity can reduce sensitivity to thermal stress, but there is an evidence that upper thermal tolerance has a "ceiling" in fishes, both in terms of CT_{max} and capacity to raise MMR when warmed. Effective plasticity in aerobic performance may involve maintaining broad thermal breadth in the short term and thermal compensation of basal metabolism by acclimation over the

longer term. Having extensive heritable genetic variation is expected to improve the potential for adaptability; nonetheless, this remains to be demonstrated. Overall, the existing empirical data cannot yet provide any insights into specific mechanisms linking intraspecific variation to vulnerability, such as the portfolio effect or adaptability/evolvability.

Nonetheless, the fact that intraspecific variation in tolerance is such an important component of overall species vulnerability highlights the need for further research into this component of biodiversity. It is also a clear message that such intraspecific variation should be fostered, managed and conserved whenever possible (Mimura *et al*., 2017; Moran *et al*., 2016; Pacifici *et al*., 2015). Promising avenues to evaluate the ecological and evolutionary significance of intraspecific variation include genomics and modelling. Advances in sequencing are opening up means to infer a role for physiological adaptation to the environment by linking genome-wide scans to prevailing environmental conditions (Mimura *et al*., 2017; Razgour *et al*., 2019). There are also methods to incorporate individual variation in physiological tolerance into mechanistic niche models (Kearney & Porter, 2009; Moran *et al*., 2016; Pacifici *et al*., 2015), although this has not yet been achieved for fishes.

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