

Choosing source populations for conservation reintroductions: lessons from variation in thermal tolerance among populations of the imperilled redbside dace¹

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Abstract: Reintroduction is an increasingly common conservation tool used to recover populations of imperilled species, but its success depends on the suitability of the introduced animals' phenotype for their new habitat. For fishes, thermal tolerance may be a key trait in urbanized habitats. We compared thermal tolerance (CT_{max}) among three lineages (western, central, eastern) of imperilled redbside dace (*Clinostomus elongatus*). CT_{max} of eastern adults was 3–4 °C lower than that of the other lineages, but adults of each lineage had similar thermal acclimation responses. In contrast, the acclimation response of juveniles differed by ~80% between the central and western lineages. Using these data, we predicted how each lineage would fare in a hypothetical reintroduction to relatively warm urbanized habitats. Owing to the differences in juvenile acclimation responses, predicted thermal safety margins for the central lineage were double those predicted for the western lineage. Overall, we suggest that CT_{max} is a useful trait to incorporate into the source population selection process; however, there is an urgent need for the establishment of captive experimental research populations of imperilled species to address remaining uncertainties.

Résumé : Si la réintroduction est un outil de conservation de plus en plus utilisé pour soutenir le rétablissement de populations d'espèces menacées, il faut, pour assurer son succès, que le phénotype des animaux introduits convienne à leur nouvel habitat. Pour les poissons, la tolérance à la chaleur pourrait être un caractère clé dans les habitats urbanisés. Nous avons comparé la tolérance à la chaleur (CT_{max}) de trois lignées (de l'Ouest, centrale et de l'Est) de menés longs (*Clinostomus elongatus*), une espèce menacée. La CT_{max} d'adultes de l'Est est de 3–4 °C plus basse que celle des autres lignées, mais les adultes des trois lignées présentent des réactions d'acclimatation thermique semblables. En revanche, une différence de ~80 % est relevée entre les réactions d'acclimatation des juvéniles des lignées centrale et de l'Ouest. En utilisant ces données, nous prédisons comment chacune des lignées répondrait à la réintroduction hypothétique dans des habitats urbanisés relativement chauds. En raison des différences de réaction d'acclimatation des juvéniles, les marges de sécurité thermique prédites pour la lignée centrale sont deux fois plus grandes que les marges prédites pour la lignée de l'Ouest. Globalement, nous suggérons que la CT_{max} est un caractère important à incorporer au processus de sélection de populations sources; toutefois, il existe un besoin urgent d'établir des populations de recherche expérimentale en captivité d'espèces menacées pour étudier les sources d'incertitude qui demeurent. [Traduit par la Rédaction]

Introduction

Fisheries management has a long history of using translocations (moving wild fish from one place to another) and captive breeding programs to augment and expand natural populations of commercially and recreationally important fishes (Jachowski et al. 2016). These approaches have since been expanded to include imperilled fishes impacted by habitat alteration and other threats (Lamothe et al. 2019). In many cases, the translocation of individuals

of wild origin, or the reintroduction of captive bred imperilled fishes, is warranted because restoration efforts have resulted in substantial improvements to habitat quality; however, natural recolonization is virtually impossible because of limited dispersal ability, the presence of natural or anthropogenic barriers, or extremely small population sizes (Zwick 1992; Albanese et al. 2009; McManamay et al. 2016). For other species, supplementing wild populations may maintain long-term population viability (e.g., Marsh et al. 2005; Kronenberger et al. 2018; but see Cucherousset

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and Olden 2020). The introduction of individuals from one part of a geographic range to another is one more possible, though contentious, use of translocation to reduce the risk of local extirpation in the face of changing environmental conditions (McLachlan et al. 2007; Hewitt et al. 2011). In each scenario, selecting the source populations most likely to become established after reintroduction remains a major uncertainty (reviewed in Houde et al. 2015).

Many factors determine the suitability of source populations when implementing conservation programs. To minimize harm, source populations should ideally be abundant and not of conservation concern, though the use of highly imperilled populations is sometimes justified if extinction is imminent (e.g., Snucins et al. 1995; Lamothe et al. 2021). Another consideration is the likelihood of survival and successful establishment after release, which can vary owing to phenotypic and genetic variation among source populations (Cochran-Biederman et al. 2015). Two main approaches often used to select source populations for translocation are (1) an adaptive potential strategy that focuses on maximizing genetic variation to allow natural selection to act on as broad a range of phenotypes as possible and (2) a local adaptation strategy that focuses on fitness-related phenotypic traits that are best suited to environmental conditions in the receiving habitat (Houde et al. 2015). Evidence from experimental translocations of fishes suggests that the latter approach may be more successful (reviewed in Houde et al. 2015); however, it is often unclear how to best evaluate local adaptation (Hereford 2009).

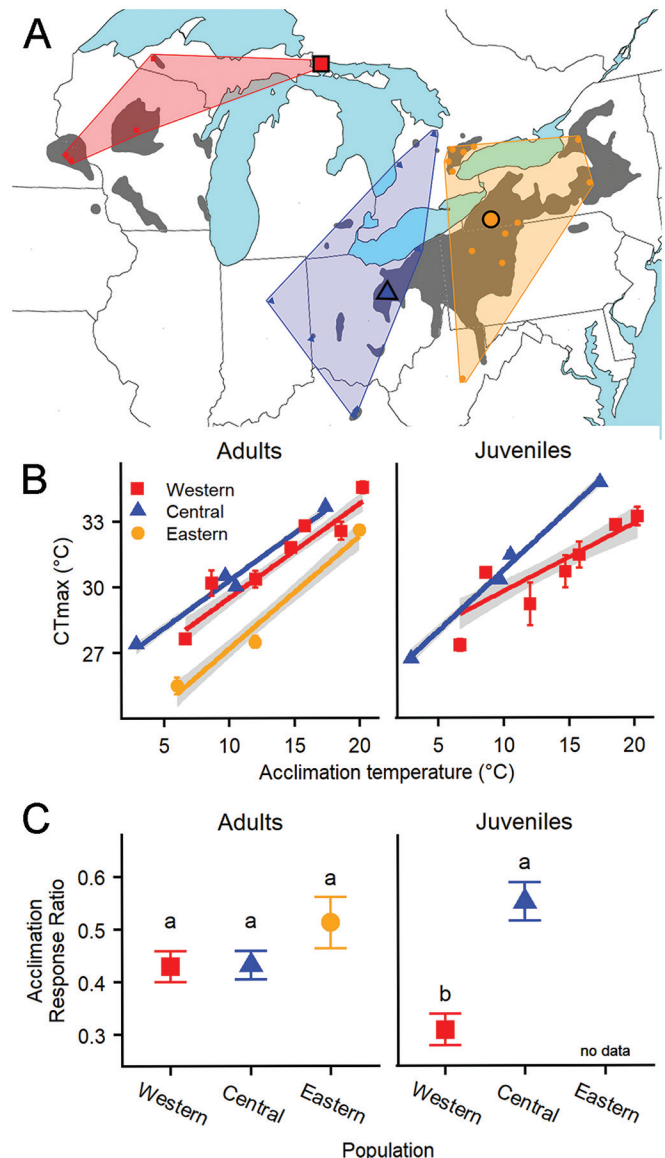
There are several major uncertainties when implementing the local adaptation strategy for imperilled fishes. For example, it is often unknown which fitness-related traits (e.g., growth rate, fecundity, tolerance of abiotic conditions) are most important and whether the most important traits differ between life stages or at certain times of year. Furthermore, most research to date has taken place in the field because of logistical difficulties that limit the possession of many imperilled fishes in captivity for research (e.g., regulatory restrictions, unknown or strict husbandry requirements). While these field studies are useful for understanding species ecology in natural conditions, assessing local adaptation of populations is difficult because it is not clear whether variation in key fitness-related traits is the result of genetic or environmental differences.

In this perspective, we discuss these challenges and their implications using our experience with multiple populations of the imperilled reidside dace (*Clinostomus elongatus*) as a case study. We show how field research has been used to assess population differences in thermal tolerance, an important fitness-related trait (Sunday et al. 2012) that may constitute a component of local adaptation. We then illustrate the utility of these data for evaluating how source population selection might impact success if reidside dace were to be reintroduced where it is currently endangered. However, we also highlight that the interpretation of field data both for traditional conservation programs and for guiding future reintroduction efforts requires caution. Finally, we argue that the establishment of captive experimental research populations is a critical next step to better understand the biology of imperilled fishes and their threats, provided that wild populations are not further harmed.

Conservation of reidside dace

Reidside dace is a small, brightly coloured stream fish with a discontinuous distribution across eastern North America (Scott and Crossman 1998; COSEWIC 2017). Its distribution is the result of postglacial colonization following the last ice age, during which time there were probably three glacial refugia that gave rise to genetically and geographically distinct lineages (Serrao et al. 2018). Populations in the western lineage currently exist in Minnesota, Wisconsin, and northern Michigan in the United States and in northern Ontario in Canada (Fig. 1A). Populations in the central lineage are found in Indiana, Kentucky, Ohio, Michigan,

Fig. 1. Thermal tolerance and thermal acclimation capacity of three reidside dace (*Clinostomus elongatus*) lineages. (A) Range of reidside dace in North America (dark grey). Coloured polygons delineate the range of each of the three lineages identified by Serrao et al. (2018) based on genetic samples collected from sites indicated by the small symbols (red squares, western clade; blue triangles, central clade; yellow circles, eastern clade). Enlarged symbols within each range denote sampling locations of fish used for thermal tolerance measurements. Locations sampled for genetic analyses and resultant population information redrawn from Serrao et al. (2018); base map and overall reidside dace geographic range modified from COSEWIC (2017). (B) Acute upper thermal tolerance (CT_{max}) of reidside dace adults and juveniles as a function of acclimation temperature. (C) Acclimation response ratio ($\Delta CT_{max}/\Delta$ acclimation temperature) of reidside dace, which is derived as the slope of the lines in (B). Different letters represent significant differences ($p < 0.05$) between groups. Data were compared using a simple linear model that included subpopulation, temperature, age, and all interactions as factors, followed by post hoc Tukey's comparison of slopes (see text for details). [Colour online.]



and the Lake Huron watershed of southwestern Ontario, while populations in the eastern lineage exist in Pennsylvania, New York, West Virginia, and the Lake Ontario drainage of southern Ontario (Fig. 1A). Redside dace is of widespread conservation concern, and Ontario, Michigan, Indiana, and West Virginia have placed the species in their highest conservation category (COSEWIC 2017). Canadian populations, particularly those near the Greater Toronto Area, have experienced rapid declines, with several watershed-level extirpations occurring in the last decade (COSEWIC 2017; Lebrun et al. 2020).

Urban development is thought to be the overarching factor leading to redside dace population declines, because of the combined effects of changes in stream morphology and hydrology, sedimentation, decreased food supply, invasive species, and thermal stress (COSEWIC 2017). To mitigate these issues, restoration actions in some redside dace habitat such as riparian restoration and improvement of stormwater management infrastructure have reduced the severity of multiple hypothesized stressors simultaneously (e.g., reductions in water temperature and suspended sediment inputs, increased food supply). However, natural recolonization of these restored sites is highly unlikely for small-bodied fishes such as redside dace, as such species would have to disperse through inhospitable conditions within large rivers — often between watersheds through the Laurentian Great Lakes — to reach suitable habitats in headwater streams (COSEWIC 2017). To address these issues, developing methods for reintroduction of redside dace to restored habitat has been identified as a high-priority conservation action (DFO 2019). To date, however, there has been no explicit consideration of which redside dace lineages should be used as source populations for these efforts.

Temperature is the fundamental factor that governs the rate of virtually all physiological processes in fishes and other ectotherms (Fry 1947; Huey and Stevenson 1979; Schulte 2015), and pervasive thermal stress due to urbanization and global climate change is hypothesized to be an important threat to many fishes including redside dace (Somero 2005; COSEWIC 2017; Sunday et al. 2012). The thermal sensitivity of physiological processes is an important component of local adaptation for many fishes (Huey and Stevenson 1979; McKenzie et al. 2020). For example, brown trout (*Salmo trutta*) embryos from populations that inhabit relatively cold streams develop faster at cold temperatures than embryos from populations adapted to warmer streams, but at warm temperatures, development is slowest in cold-adapted embryos (Jensen et al. 2008). In mummichog (*Fundulus heteroclitus*), which are geographically and genetically divided into a cold-adapted northern subspecies and a warm-adapted southern subspecies, thermal tolerance (i.e., critical thermal maximum, CT_{max}) and growth rates at high temperatures are higher in the southern subspecies (Healy and Schulte 2012). In sockeye salmon (*Oncorhynchus nerka*) and redband trout (*Oncorhynchus mykiss gairdneri*), the temperature at which different populations can maximally increase heart rate and aerobic metabolism closely matches historic water temperatures experienced by each population (Eliason et al. 2011; Chen et al. 2018). Given this widespread importance of local thermal adaptation for fishes, we suggest that population-level differences in thermal physiology should be a key consideration when selecting source populations for reintroduction efforts.

While temperature affects the performance of nearly all aspects of fish physiology, the maximum temperatures that fishes can tolerate is thought to be one of the most important factors determining population persistence and thus the geographical distribution of many species (McCullough et al. 2009; Payne et al. 2021). The ability of fishes to tolerate high temperatures can be measured relatively easily in the field using well-established and nonlethal protocols to evaluate CT_{max} , defined as the temperature at which fish can no longer maintain an upright orientation during acute warming (typically $0.3\text{ }^{\circ}\text{C}\cdot\text{min}^{-1}$; Becker and Genoway 1979; Lutterschmidt and Hutchison 1997). For these reasons, we have focused on thermal

tolerance as a key fitness-related trait that may be useful for identifying redside dace source populations. Importantly, the sensitivity of fishes to thermal stress depends on life stage, and in general across many other species, early life stages (eggs, larvae, juveniles) are more sensitive than adults (Pankhurst and Munday 2011). For example, juveniles of the endangered longfin dace (*Agosia chrysogaster*) are more thermally sensitive and show reduced thermal acclimation ability compared with adults (Troia et al. 2015). Furthermore, population modelling for redside dace suggests that survival of immature individuals (i.e., young-of-year and one-year-old fish) is the most important factor governing population growth (van der Lee et al. 2020). Given the potential differences between juvenile and adult fish for understanding population-level responses to thermal stress, we have prioritized this comparison in our research to date. Unfortunately, we still lack data on the earliest life stages (i.e., embryos and larvae) — this is because redside dace is an obligate spawner in the nests of other cyprinids such as creek chub (*Semotilus atromaculatus*; Koster 1939), leading to mixed-species assemblages of larvae that are difficult to identify nonlethally.

Thermal tolerance among populations of redside dace

Until recently, the only thermal tolerance (i.e., CT_{max}) measurement for redside dace was a single study of laboratory-acclimated fish from the eastern lineage in New York State (Novinger and Coon 2000). However, recent studies on wild redside dace from the two other lineages (western lineage, Leclair et al. 2020; central lineage, Turko et al. 2020) at the opposite ends of its latitudinal range now allow us to compare thermal tolerance among all three genetic lineages. Here, we synthesize the data from these three studies to address three main questions. First, does thermal tolerance (CT_{max}) differ among populations? Second, are there differences between adult and juvenile thermal tolerance? Finally, do redside dace populations differ in their capacity for thermal acclimation?

Full thermal tolerance data sets are available for both the western (Leclair et al. 2020) and central (Turko et al. 2020) lineages. Unfortunately, raw data were not available for the eastern population (D. Novinger, personal communication). Therefore, for statistical comparisons, we used the means, standard deviations, and sample sizes reported in the original study (Novinger and Coon 2000). Importantly, these three studies employed nearly identical CT_{max} experimental protocols (Bates and Morley 2020). Adult and juvenile redside dace within the central lineage were determined by dissection and evaluation of gonad development, as these experiments were performed in Ohio, USA, where redside dace is not of conservation concern (Turko et al. 2020). However, thermal tolerance of the western population was evaluated in Ontario, Canada, where redside dace is listed as endangered both provincially and federally, and thus terminal sampling to confirm reproductive status was not possible (Leclair et al. 2020). To assign these fish as juveniles or adults, we used a threshold of 70 mm total length, which represents the juvenile–adult body-size threshold previously reported for redside dace (Dieterman et al. 2018; Turko et al. 2020). All fish studied by Novinger and Coon (2000) in New York, USA, exceeded 70 mm total length and were assumed to be adults.

The thermal conditions experienced by redside dace varied among each of the three studies synthesized here. We therefore analyzed CT_{max} as a function of acclimation temperature, which was either uniformly maintained in the laboratory (Novinger and Coon 2000) or calculated as the mean stream temperature (measured by data loggers in the field) over the 14-day period prior to thermal tolerance experiments (Leclair et al. 2020; Turko et al. 2020). The slope of the relationship between CT_{max} and acclimation temperature, known as the acclimation response ratio (ARR), provides a standardized measure of how much CT_{max} changes for every degree of change in acclimation temperature.

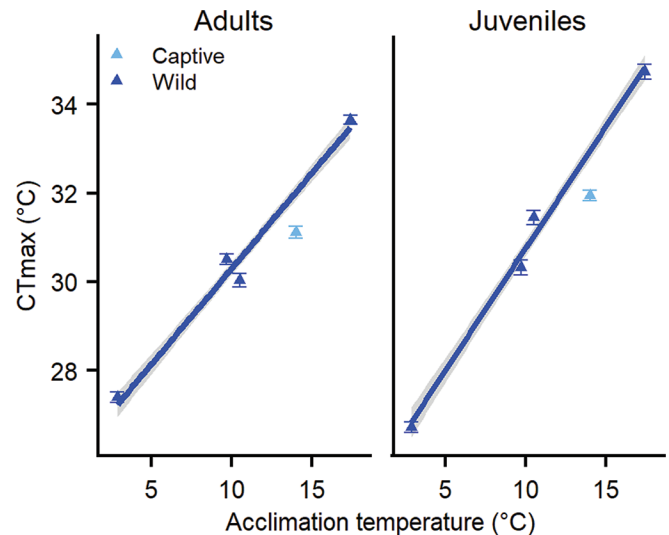
From this overall model (i.e., $CT_{max} \sim \text{acclimation temperature} \times \text{population} \times \text{maturity}$), post hoc comparisons of slopes (i.e., ARR) and intercepts were conducted using the R package emmeans (Lenth et al. 2020). The script used for these analyses is available in the Supplementary material².

Overall, we found a positive relationship between acclimation temperature and CT_{max} of reidside dace (Fig. 1B). However, the slope of this relationship (ARR) depended on the statistical interaction between the maturation stage and population ($F = 15.1$, $p = 0.00012$; Fig. 1C). In the western population, juveniles were less thermally responsive (lower ARR) than western adults (post hoc $t = 2.91$, $p = 0.044$; Fig. 1C). Western juveniles also had a significantly lower ARR than juveniles from the central population (post hoc $t = 5.12$, $p < 0.0001$; Fig. 1C). In contrast, central juveniles tended to have a higher ARR than central adults (by ~20%), although this result was not statistically significant (post hoc $t = 2.61$, $p = 0.097$; Fig. 1C). Consistent with this trend, a similar analysis in our previous study (Turko et al. 2020) found that juvenile fish had significantly higher CT_{max} than adults in the summer, but lower CT_{max} in the winter, indicating a higher ARR in juveniles. These population-level differences in the ARR of juvenile fish could have major consequences for how reidside dace demographics will be affected by thermal stress, particularly because population growth is highly dependent on juvenile survival (van der Lee et al. 2020). We note, however, that a low ARR in western reidside dace may not necessarily have negative fitness consequences, as temperatures in these habitats may never approach CT_{max} (Leclair et al. 2020) and the capacity for thermal acclimation may carry other physiological costs (Seebacher et al. 2015; Comte and Olden 2017; Loughland and Seebacher 2020). For example, northern populations of reidside dace grow faster, perhaps owing to a shorter growing season (Dieterman et al. 2018), and sustained rapid growth can reduce the amount of energy that can be allocated to other physiological processes (Norin and Clark 2017), possibly including thermal acclimation.

Adult reidside dace from the eastern population had a significantly lower CT_{max} (by 3.1–4.7 °C) at any given acclimation temperature than adults or juveniles from the other populations (all intercepts $t \geq 3.90$, $p \leq 0.0016$; Fig. 1B). Given that the eastern population represents the majority of the reidside dace distribution, increased thermal sensitivity of these fish could have major implications for species persistence. A 3–4 °C difference in CT_{max} is substantial, as even small differences in CT_{max} can be associated with much larger differences in the thermal sensitivity and thermal optima of other fitness-related traits. For example, a difference in CT_{max} of ~1 °C (~29 versus 30 °C) between populations of redband trout was correlated with a 50% difference in maximum aerobic scope (the ability to increase aerobic metabolism) and a 30% difference in maximum heart rate under warm (24 °C) conditions (Chen et al. 2018).

A major uncertainty in the interpretation of the apparent differences in adult CT_{max} among lineages results from different acclimation protocols among studies. Eastern fish were acclimated to constant temperatures under laboratory conditions (Novinger and Coon 2000), while CT_{max} of western and central fish was measured in wild fish that experienced natural thermal fluctuations. Fluctuating thermal conditions are known to enhance thermal tolerance (Feldmeth et al. 1974; Corey et al. 2017; Hall and Warner 2020). To assess the potential magnitude of this effect for reidside dace, we compared our CT_{max} data for fish from the central population in the field to additional measurements we made in this population under controlled laboratory conditions at a constant temperature (14 °C for 12 weeks; all data from Turko et al. 2020). CT_{max} of both adult and juvenile captive reidside dace was ~1 °C lower than would be expected based on

Fig. 2. Acute thermal tolerance (CT_{max}) of reidside dace (*Clinostomus elongatus*) from the wild (dark blue) or after 6 months in captivity (light blue) under constant thermal conditions (14 °C). All fish are from the central lineage and were captured in the Kokosing River, Ohio, USA. Wild fish were collected to establish a captive experimental research population at the Freshwater Restoration Ecology Centre, University of Windsor. Shaded grey region around the wild fish indicates the 95% confidence interval; error bars show standard error. [Colour online.]

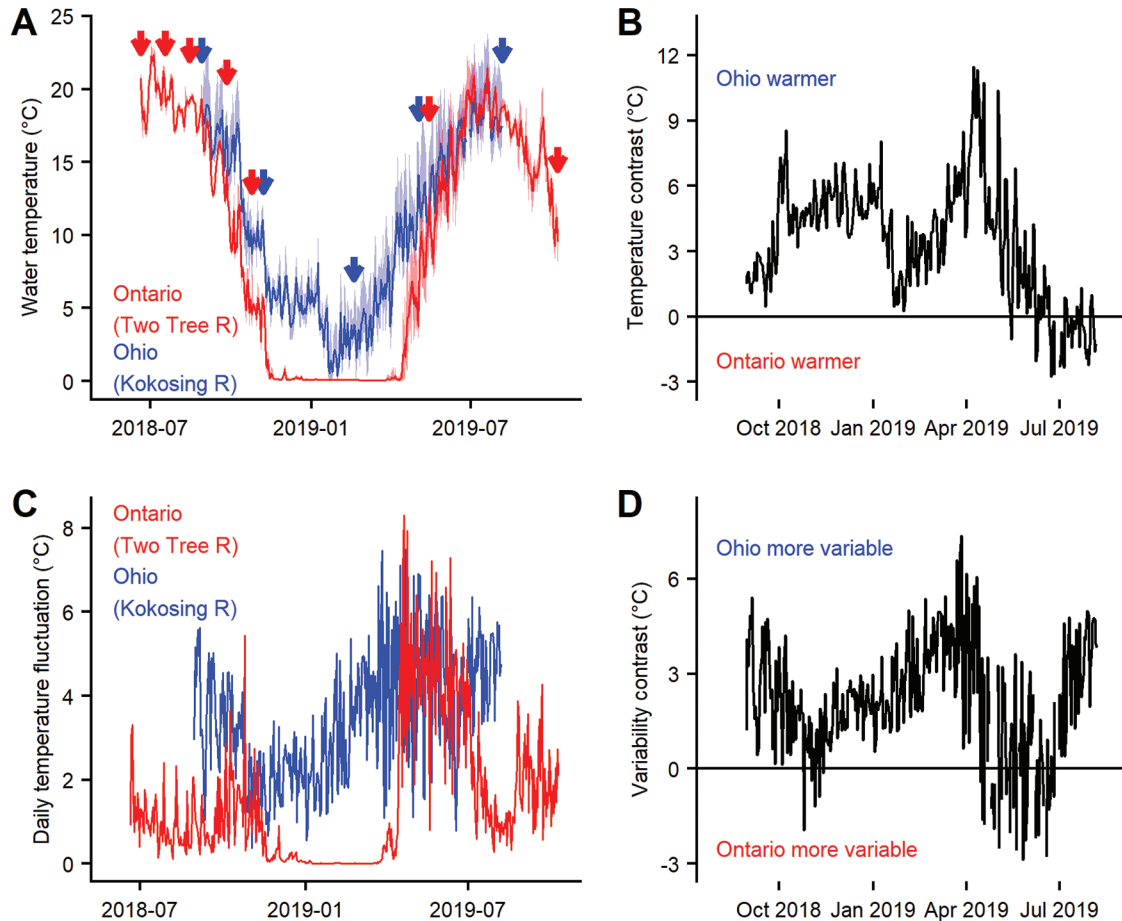


measurements of wild fish (Fig. 2), representing a much smaller difference in CT_{max} than is exhibited between populations (Fig. 1). Thus, captive housing under uniform thermal conditions probably accounts for some, but not all, of the differences in thermal tolerance that were found among populations. These results, combined with our data showing that ARR is similar among lineages in adult fish, suggest that warming may be a particularly important threat for the eastern lineage of reidside dace, including endangered populations in southern Ontario, Canada. Furthermore, these results indicate that conservation translocations of reidside side from the more thermally tolerant western and central lineages may increase the chance of species persistence in the eastern part of the range, assuming thermal stress is a major cause of population decline.

We found no difference in CT_{max} of wild adult reidside dace between the western and central populations after controlling for stream temperature ($t = 1.42$, $p = 0.71$; Fig. 1B). This result was surprising, as the central fish generally experience warmer and more variable thermal conditions than fish from the western population (Fig. 3) and might therefore have been expected to have evolved higher CT_{max} . Regional intraspecific variation in thermal tolerance has been reported for a number of fishes, with populations from warmer habitats generally having higher CT_{max} (Fangue et al. 2006; Healy and Schulte 2012; Rooke et al. 2017; Nyboer et al. 2020). However, differences in thermal tolerance among populations do not always evolve in response to different thermal environments (e.g., Wells et al. 2016; Yu et al. 2018), or even in rigorous artificial selection experiments (Baer and Travis 2000; Morgan et al. 2020), and it has been suggested that upper thermal tolerance of many fishes may have a fixed “concrete ceiling” (Sandblom et al. 2016). We speculate that a similar limit to CT_{max} might exist in reidside dace, given the similarity in CT_{max} that we found between fish sampled near the

²Supplementary material is available with the article at <https://doi.org/10.1139/cjfas-2020-0377>.

Fig. 3. Daily mean water temperature and water temperature fluctuations at two reidside dace (*Clinostomus elongatus*) study sites from 2018 to 2019. Fish from the western lineage were sampled from Two Tree River, Ontario (red), and fish from the central lineage were sampled from the Kokosing River, Ohio (blue). (A) Thick coloured lines show mean daily temperature, and the shaded region around each line shows the daily temperature range. Coloured arrows indicate critical thermal tolerance (CT_{max}) measurements of reidside dace at each site. (B) Difference between mean daily water temperature between the two reidside dace study sites. Values greater than zero indicate that Kokosing River was warmer than Two Tree River. (C) Daily temperature fluctuations (maximum – minimum recorded temperature) in Two Tree River, Ontario (red), and the Kokosing River, Ohio (blue). (D) Difference between daily water temperature fluctuations at the two reidside dace study sites. Values greater than zero indicate that Kokosing River was more variable than Two Tree River. [Colour online.]



northern and southern limits of the geographic range. This finding suggests that conservation translocations of reidside dace from the southern portion of their geographic range to the endangered range in the north (e.g., “assisted migration”) may do little to improve thermal tolerance of adult fish, although translocations of fish from either the western or central lineage into the range of the eastern lineage (such as the heavily urbanized Greater Toronto Area in Ontario) have the potential to increase thermal tolerance. Carefully executed common-garden and inter-population breeding experiments are necessary to accurately evaluate these possibilities and their possible consequences (e.g., outbreeding depression; Huff et al. 2011).

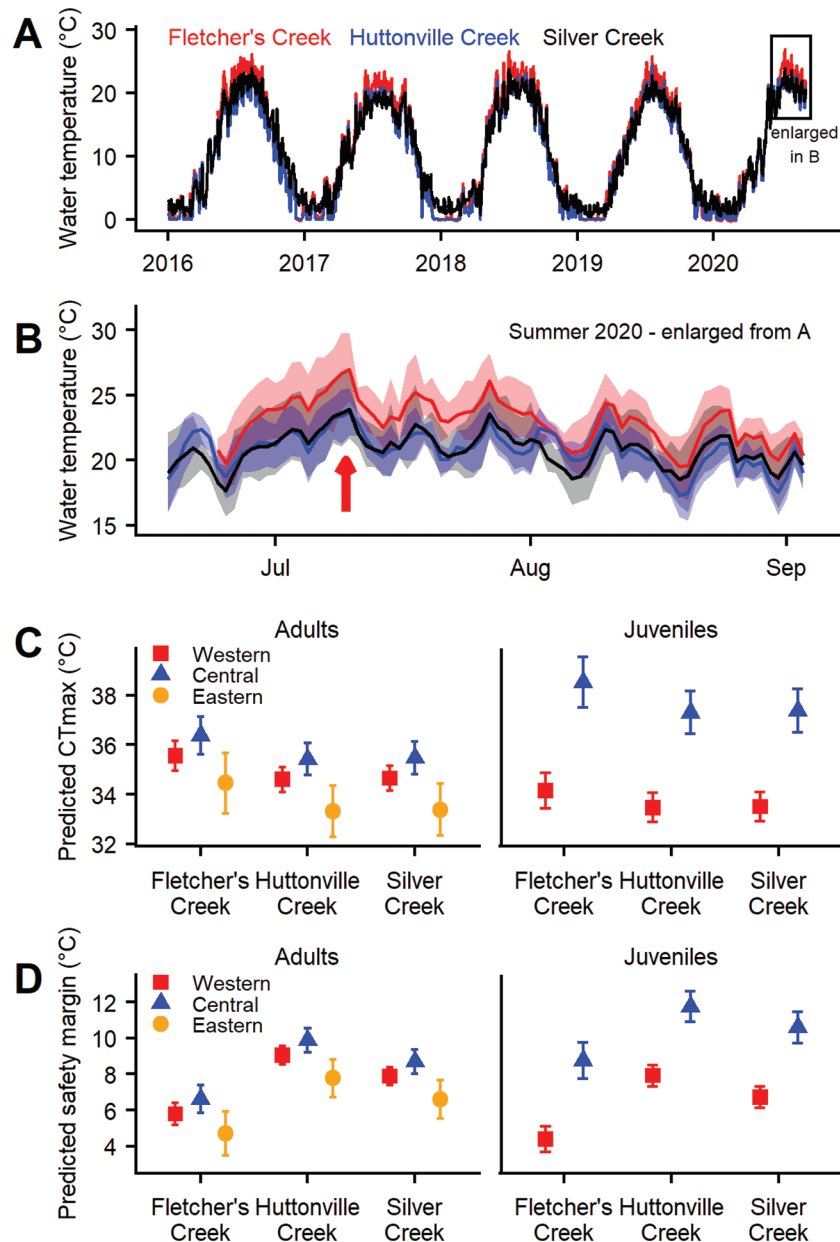
CT_{max} experiments provide a rapid, robust, repeatable, and nonlethal method for assessing thermal tolerance (Morgan et al. 2018; O’Donnell et al. 2020). Despite the utility of CT_{max} measurements for understanding the thermal physiology of fishes, interpreting the overall fitness consequences of differences in CT_{max} and the capacity for thermal acclimation is not straightforward, as there are often trade-offs with other fitness-related traits — and there may even be a trade-off between outright CT_{max} and the capacity of thermal acclimation (Comte and Olden 2017; Armstrong et al. 2019). For example, increased CT_{max} may increase

sensitivity to cold temperatures (Gutiérrez-Pesquera et al. 2016), and thus juvenile reidside dace from the more thermally tolerant central lineage may be more susceptible to cold overwintering temperatures than juveniles from the western lineage. Evolutionary responses to thermal conditions are also thought to affect life history traits. For example, evolution of increased thermal tolerance in mosquitofish (*Gambusia holbrooki*) was correlated with larger batches of smaller offspring and reduced adult size (Meffe 1990, 1991). The southern subspecies of mummichog has higher CT_{max} than the northern subspecies (Fangue et al. 2006), but a slower growth rate (Schultz et al. 1996). Similarly, zebrafish (*Danio rerio*) acclimated to fluctuating temperatures had higher CT_{max} but lower growth rates than those acclimated to constant temperatures (Schaefer and Ryan 2006). Given these trade-offs, it is critical that we understand the broader fitness consequences of variation in thermal tolerance among life stages before CT_{max} is used to assess the suitability of different source populations for reintroduction efforts.

Using CT_{max} to choose source populations for reintroduction

To illustrate the utility of considering CT_{max} when evaluating potential reidside dace source populations, we conducted a hypothetical evaluation of thermal tolerance at potential future

Fig. 4. Annual variation in mean daily water temperature (2016–2020) and predicted thermal tolerances and thermal safety margins of three reddsides (*Clinostomus elongatus*) lineages in three tributaries of the Credit River, Ontario, Canada, during the warmest two-week period of 2020. (A) Mean daily water temperature in Fletcher’s Creek (red), Huttonville Creek (blue), and Silver Creek (black). (B) Enlarged view of water temperature in summer 2020. Thick coloured lines show mean daily temperature, and the shaded region around each line shows the daily temperature range (minimum – maximum). The red arrow indicates the highest recorded water temperature in all three creeks for 2020, which occurred on 9 July. (C) Predicted critical thermal maximum (CT_{max}) of adult and juvenile reddsides from each subpopulation in each of the Credit River tributaries on the warmest day of 2020. Values were predicted using the relationships between CT_{max} and acclimation temperature for each subpopulation shown in Fig. 1; acclimation temperature was estimated as the mean water temperature of the preceding 14-day period. (D) Predicted thermal safety margins of reddsides subpopulations in each Credit River tributary on the warmest day of 2020. Safety margins were calculated as the difference between predicted CT_{max} (in C) and the warmest temperature recorded at each site. Error bars represent 95% confidence intervals. [Colour online.]



reintroduction sites using the data synthesized in this paper (i.e., Fig. 1). Specifically, we predicted the thermal tolerance and thermal safety margins of each reddsides lineage in three tributaries of the Credit River near Toronto, Ontario (Huttonville Creek, Silver Creek, and Fletcher’s Creek). Each system may be the subject of future reintroduction efforts if current population declines continue. Water temperature data were collected by permanent monitoring stations maintained by the Credit River

Conservation Authority (location of each monitoring station available at <https://cvc.ca/watershed-science/watershed-monitoring/real-time-water-quality/>). We calculated predicted thermal tolerances (CT_{max}) and thermal safety margins of reddsides dace on the day with the highest recorded water temperature of 2020. We note, however, that among-site differences in maximum water temperature were consistent over the past 5 years (Fig. 4A) and thus predicted CT_{max} values would be as well. To predict CT_{max} , we extrapolated

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the acclimation temperature – CT_{max} relationship for each lineage (Fig. 1B), using the mean water temperature from the 14 days preceding the warmest recorded temperature within each creek as the acclimation temperature. Safety margins, which reflect how much water temperatures can rise before a fish reaches CT_{max} , were calculated as the difference between these predicted CT_{max} values and the peak temperature recorded at each site (for R script, see Supplementary material²).

Mean daily water temperature in Fletcher’s Creek was ~ 2 °C warmer than that in Huttonville Creek or Silver Creek in the summer of 2020 (Fig. 4B). Given that we used linear extrapolations of the relationship between acclimation temperature and CT_{max} , our results correspondingly show the highest predicted CT_{max} values in Fletcher’s Creek (Fig. 4C). However, these calculations assume a linear relationship between CT_{max} and acclimation temperature. This was the case up to ~ 20 °C for all three lineages (Fig. 1B), but our predictions assume that Fletcher’s Creek fish were acclimated for 14 days to a substantially higher mean temperature of 24.3 °C. In other fishes, the slope of the CT_{max} – acclimation temperature relationship typically plateaus at high temperatures (e.g., Fanguie et al. 2006; McKenzie et al. 2020). Thus, our predictions of reddsides dace CT_{max} and safety margins in the three Credit River tributaries are likely overestimates. Nonetheless, our results show that within each creek, there were small differences among reddsides dace lineages in CT_{max} (Fig. 4C) and thermal safety margins (Fig. 4D) for adult fish. In contrast, predicted juvenile CT_{max} showed strong divergence (3–4 °C) between western and central populations. This result highlights an important consequence of the differences in ARR between these lineages (Fig. 1C) — as acclimation temperatures increase, so does the divergence in juvenile CT_{max} . Predicted juvenile thermal safety margins also differed dramatically among lineages. Under the warmest conditions in Fletcher’s Creek, the predicted safety margin of juvenile reddsides dace from the central lineage (~ 8 °C) was almost double that of fish from the western lineage (safety margin of ~ 4 °C). Given this dramatic difference in safety margins, the likely association of variation in CT_{max} with greater variation in other growth and performance traits, and the presumed importance of juvenile survival for reddsides dace population growth (van der Lee et al. 2020), the results of our reintroduction application show that the success or failure of a reintroduction effort could depend in large part on the source population selected.

The need for captive experimental research populations

A major limitation of the hypothetical evaluation of three candidate source populations for reintroduction was the heavy reliance on thermal tolerance data collected in the field. While field studies of wild fishes are ecologically realistic, common-garden conditions are necessary to determine, with confidence, whether genetically based phenotypic differences exist between lineages (Conover and Baumann 2009; de Villemereuil et al. 2016). Furthermore, the logistical challenges of conducting experiments in the field generally mean that only a few fitness-related traits can be feasibly measured (e.g., CT_{max}), while laboratory experiments using sophisticated equipment and (or) longer time scales are often required to understand the thermal sensitivity of many other important traits such as metabolism, exercise, growth, and reproduction. Acquiring and captive rearing imperilled species involves complex factors that likely have limited laboratory experiments to date. A major consequence is that conservation activities such as habitat restoration targets or reintroductions for reddsides dace and other imperilled species face major uncertainties related to basic natural history, population demographics, physiological tolerances, and population-level differences. To address these challenges, we advocate for the establishment and study of captive experimental research populations (CERPs) of imperilled freshwater fishes. We define a CERP as a population of a species of conservation concern that is obtained from the

wild, typically from an area where the species is least threatened by anthropogenic disturbance and then held in captivity for study. However, in cases where local adaptation or other strong intraspecific differentiation is suspected, or where evaluating possible differences is a major study goal (e.g., for reintroduction source selection), founding CERPs using individuals from the at-risk populations may be justified. A major benefit of establishing imperilled species CERPs is the potential for captive breeding, which allows for controlled experiments on early life stages that are often the most vulnerable to disturbance (e.g., Pankhurst and Munday 2011). Another major benefit to CERPs is the ability to conduct controlled experiments necessary for testing hypotheses about the mechanisms of harm caused by habitat disturbance, which provides critical information for developing effective recovery strategies. Understanding these threats in relation to species biology is also critical for identifying suitable habitat for reintroductions. CERPs are particularly helpful during the feasibility and preparation phases of a reintroduction when little prior knowledge exists.

One example of such a CERP (funded by the DFO Canadian Freshwater Species at Risk Research Network; Castañeda et al. 2021) is a reddsides dace population housed at the Freshwater Restoration Ecology Centre, University of Windsor. To date, this CERP consists of individuals (juveniles and adults) collected from parts of the range where the species is not imperilled (i.e., central lineage, captured in Ohio, USA; see Beausoleil et al. 2012; Turko et al. 2020). This CERP has been used to experimentally determine cause-and-effect relationships between variables found to be correlated in field studies. For example, we used this CERP to experimentally determine that body condition (manipulated by controlling feeding ration) causally influences thermal tolerance of reddsides dace (Turko et al. 2020). Other experiments using this CERP are underway to examine the consequences of a variety of anthropogenic stressors (e.g., light pollution, suspended sediments, hypoxia, thermal stress). Captive-breeding protocols are also being established. However, there is a pressing need to expand this CERP to include the western and eastern reddsides dace lineages to allow for common-garden comparisons of fitness-linked traits important for guiding management actions and reintroduction programs. Housing all three lineages would also allow for experimental evaluation of the consequences of outbreeding among populations (e.g., Huff et al. 2011), an important step before reintroduction programs can begin considering source populations of reddsides dace outside of their historical range. For example, Atlantic salmon (*Salmo salar*) CERPs originating from two potential source populations for reintroduction to Lake Ontario were used to examine whether interbreeding of adults would result in outbreeding depression in offspring (Audet et al. 2017). Similarly, lake trout (*Salvelinus namaycush*) CERPs were used to assess the thermal acclimation capacity of various populations for stocking in the Laurentian Great Lakes (Hébert and Dunlop 2020). Overall, we strongly advocate for the funding and establishment of a network of conservation-oriented CERPs at various research institutions to improve fundamental and applied research outcomes for imperilled freshwater fishes.

Conclusions

Source population selection is an important determinant of the success of fish reintroductions (Cochran-Biederman et al. 2015; Houde et al. 2015). If source populations are to be chosen based on phenotype–environment matching, it must be determined which phenotypic traits are expected to be linked to fitness, and how these traits vary among possible source populations that could be used for reintroduction. For reddsides dace, we have focused on thermal tolerance, as the combined effects of urbanization and climate change will have major impacts on the thermal regime of drainages occupied by this species. We found substantial

differences in thermal tolerance among the three genetically distinct reidside dace lineages, especially in juveniles, highlighting the importance of testing multiple life stages when choosing source populations. However, we emphasize that common-garden experiments using captive populations are needed to confirm that the differences in thermal tolerance reported here are genetically based, a critical assumption of source population selection. Overall, we advocate for the establishment of captive experimental research populations of imperilled fishes to increase the quality and quantity of information used to inform conservation actions, including reintroduction.

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