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Jenni L. McDermid , Friedrich A. Fischer , Mohammed Al-Shamlih , William N. Sloan , Nicholas E. Jones & Chris C. Wilson

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NOTE

Variation in Acute Thermal Tolerance within and among Hatchery Strains of Brook Trout

Jenni L. McDermid*

Wildlife Conservation Society Canada, Trent University, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada

Friedrich A. Fischer

Ontario Ministry of Natural Resources, Aquatic Research and Development Section, Trent University, 2140 East Bank Drive, Peterborough, Ontario K8J 7B8, Canada

Mohammed Al-Shamlih

Environmental and Life Sciences Graduate Program, Trent University, 2140 East Bank Drive, Peterborough, Ontario K8J 7B8, Canada

William N. Sloan

Ontario Ministry of Natural Resources, Codrington Fisheries Research Facility, 15 Fish Hatchery Road, Codrington, Ontario K0K 1R0, Canada

Nicholas E. Jones and Chris C. Wilson

Ontario Ministry of Natural Resources, Aquatic Research and Development Section, Trent University, 2140 East Bank Drive, Peterborough, Ontario K8J 7B8, Canada

Abstract

The ability of coldwater species and populations to respond to temperature increases associated with climate change will depend on the existing adaptive potential within and among populations. Brook trout *Salvelinus fontinalis* is a valued coldwater species that has been widely stocked across its native range as well as extensively introduced in western North America. We investigated the thermal tolerance of the three primary brook trout hatchery strains used in Ontario (Dickson Lake, Lake Nipigon, and Hill's Lake strains) and the thermal tolerance of a brook trout subspecies, Aurora trout *S. fontinalis timagamiensis*; all strains were reared in a common hatchery environment. In addition to comparing the strains' responses to acute thermal stress, we also examined variability in temperature tolerance among families within several of these strains. Evidence for significant differences in temperature tolerance was observed both within and among the strains, with Aurora trout showing the least capacity to cope with higher temperatures. The results of this study suggest that thermal performance of brook trout populations will be under substantial selective pressure as water temperatures increase and that strains with existing tolerances for warmer

conditions will be better equipped to handle these anticipated changes.

Climate change is a significant concern to ectotherms, as temperature directly influences the physiological processes of metabolism, scope for activity, and gas exchange (Fry 1947, 1957; van der Have and de Jong 1996; Gunther et al. 2007). Coldwater fish species, particularly inland populations with finite adaptive resources, may be particularly vulnerable to warmer temperatures (McCullough et al. 2009) because the ability of populations and species to respond to changing ecological and climatic conditions is limited by their local and regional adaptive resources (Stockwell et al. 2003; Willi et al. 2006; Latta 2008). Warmwater species, such as smallmouth bass *Micropterus dolomieu*, are predicted to respond more favorably to climate change than cold-adapted groups, such as salmonids (e.g., brook trout *Salvelinus fontinalis*; Parmesan 2005). Furthermore, the adaptive potential of a species or population requires sufficient variability in the trait under selection to enable an

*Corresponding author: jmcdermid@wcs.org

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TABLE 1. Location, lake size, and maximum depth of the source water bodies for brook trout and Aurora trout strains in the Ontario hatchery system. The numbers of individual fish and families used for critical thermal maximum tests are shown.

Strain	Source water body	Location	Lake size (ha)	Maximum depth (m)	Individuals	Families
Dickson Lake	Dickson Lake	45°48'N, 78°13'W	1,000	18.6	287	12
Lake Nipigon	Lake Nipigon	49°50'N, 88°30'W	484,800	165	288	13
Hill's Lake	Hill's Lake Fish Culture Station	44°57'N, 77°00'W	NA	NA	288	NA
Aurora trout	Whirligig Lake	47°22'N, 80°38'W	11	9.1	284	12
	Whitepine Lake	47°23'N, 80°38'W	77	21.3		

adaptive response (Stockwell et al. 2003). In general, northern species may have an additional adaptive disadvantage due to reduced genetic resources stemming from finite ancestral populations in glacial refugia and postcolonization limits on local population sizes (Bernatchez and Wilson 1998) as well as historical bottlenecks (e.g., Aurora trout *S. fontinalis timagamiensis*).

Brook trout are native to coldwater streams and lakes in eastern North America and have been widely introduced in western North America and Europe (Scott and Crossman 1973). Brook trout actively seek out groundwater upwellings as thermal refugia (Biro 1998) and are dependent on coldwater seeps for multiple life stages and developmental events (Ridgway and Blanchfield 1998; Ridgway 2008). The distribution of brook trout will be limited by coldwater habitat loss or disruption associated with climate change (Meisner 1990a, 1990b). Thermal habitat loss can result in sublethal effects, including reduced feeding, conversion efficiency, and growth (Brett 1971; Selong et al. 2001; Wehrly et al. 2007), and has even led to mortality events in wild brook trout populations (Gunn and Snucins 2010). Several studies have investigated thermal performance of brook trout (McCauley 1958; Benfey et al. 1997; Galbreath et al. 2004) and Aurora trout (Sale 1962), with evidence that upper temperature tolerances in brook trout range from 28°C to 30°C (Lee and Rinne 1980; Benfey et al. 1997; Selong et al. 2001). Most of these studies were focused on investigating interspecific differences in thermal tolerance among salmonid species rather than intraspecific variation. McCauley (1958) examined performance differences between two geographically distant strains of brook trout but failed to find differences between the strains.

Recently, population-specific responses in thermal performance have been observed across geographically proximate populations of grayling *Thymallus thymallus* (Haugen and Vøllestad 2000; Kavanagh et al. 2010) and sockeye salmon *Oncorhynchus nerka* (Eliason et al. 2011), whereas other studies have failed to find evidence of intraspecific variation in thermal performance (brown trout *Salmo trutta*: Jensen et al. 2000; Atlantic salmon *Salmo salar*: Jonsson et al. 2001; Arctic char *Salvelinus alpinus*: Larsson et al. 2005). An understanding of fishes' ability to cope with and adapt to a changing climate has been identified as a significant knowledge gap (Wilson and Mandrak 2004; McCullough et al. 2009) and will be essential information for the sustainable management of fishes (Latta 2008).

Lacustrine brook trout populations are ideal candidates for investigations of population-specific differences in thermal response. Within Ontario, three hatchery strains of brook trout are used for stocking across the province to provide angling opportunities and for introductions and rehabilitative stocking (Table 1; Kerr 2006). These strains originated from different native environments and were bred for different purposes (OMNR 2005; Kerr 2006). The Hill's Lake strain is considered domesticated after an unknown number of generations in captivity at Pennsylvania hatcheries followed by approximately 30 generations at the Ontario Ministry of Natural Resources (OMNR) Hill's Lake Fish Culture Station (OMNR 2005). The Lake Nipigon strain was established over 10 generations ago from a wild collection in Lake Nipigon, one of largest and deepest inland lakes in northern Ontario (OMNR 2005). The Dickson Lake strain was established less than a decade ago (2002–2004) as a regionally representative wild strain from Dickson Lake, a moderately large, shallow lake in Algonquin Park (OMNR 2005). Aurora trout have also been maintained in the provincial hatchery system for over half a century as part of an effort to prevent their extirpation (Scott and Crossman 1973; Aurora Trout Recovery Team 2006). Aurora trout are considered severely inbred, as all contemporary fish are descended from nine individuals that were captured after acidification of their native lakes in the 1950s (Balon 1995; Aurora Trout Recovery Team 2006). These last nine wild Aurora trout were rescued from two small, shallow south-central Ontario lakes to which they were native (Table 1), and their gametes were used to establish a broodstock at the Hill's Lake Fish Culture Station. After liming and lake rehabilitation to mitigate acidification, subsequent generations of Aurora trout were stocked back into their native lakes and other nearby lakes (Snucins et al. 1995; Aurora Trout Recovery Team 2006), including Alexander Lake. To prevent domestication of the Aurora trout broodstock, the hatchery population is maintained by using biannual spawn collections of Aurora trout from Alexander Lake (OMNR 2005).

In this study, we examined the acute thermal tolerances and responses of Ontario hatchery strains of brook trout and Aurora trout. We assessed the variability in thermal tolerance among and within strains to investigate coping and potential adaptive capacity within and among populations of this ecologically and economically significant coldwater species. If thermal tolerance

is linked to local environmental conditions, it is reasonable to expect that the different origins and histories of these hatchery strains will result in population-specific differences in thermal performance, although their shared recent thermal history in a common hatchery environment may homogenize ancestral differences. Furthermore, the potential adaptive capacity within Aurora trout may be hampered by their historical population bottleneck and potential inbreeding.

METHODS

Strains and family rearing.—All brook trout strains included in this study (Hill's Lake, Lake Nipigon, and Dickson Lake strains and Aurora trout broodstock) are maintained at the OMNR Hill's Lake Fish Culture Station but were brought to the OMNR Fisheries Research Facility (Codrington, Ontario) for the temperature experiments. Families of brook trout and Aurora trout were produced during the 2006 fall spawning season from strains at the OMNR Fisheries Research Facility. Each family was derived from single-pair matings within each strain; families were held separately except for Hill's Lake fish, which were received as pooled juveniles from the Hill's Lake Fish Culture Station and thus could not be identified to family. After hatching, age-0 fish were reared in family units at equivalent densities. All fish were reared at ambient surface water temperature and were fed to satiation several times per day.

Experimental design.—Acute temperature tolerance experiments were conducted with yearling brook trout and Aurora trout in the winter of 2008. The critical thermal maximum (CTM) method involves exposing experimental fish to progressively higher water temperatures until a behavioral or physiological endpoint, such as loss of equilibrium (LE) or death, is reached (Becker and Genoway 1979). We used a slight modification of the CTM method, Elliott's (1981) hybrid CTM challenge, in which the acute temperature tolerance of each fish was defined as the amount of time to LE while in the zone of thermal resistance (Fry 1947). The temperature for the zone of thermal resistance was estimated in a pilot study by using a mixed sample of individuals from all of the strains to be compared. This pilot sample was exposed to a steady increase in temperature at a rate of 0.15°C per minute. The temperature at which the first fish in the sample exhibited LE (26°C) was defined as the zone of thermal resistance and was then used in all subsequent CTM trials. Temperature was steadily increased to the zone of thermal resistance and was held static until the final fish experienced LE. Use of the time to LE allowed for a greater ability to differentiate between fish within a trial (Galbreath et al. 2004, 2006).

The tolerance experiments were carried out in a 172-L tank, where the temperature was increased to 26°C over the course of 1.5 h. Dissolved oxygen concentrations were monitored and maintained above 6 mg/L by aeration. The thermal tolerance time was recorded for each fish as the time spent in the zone of thermal resistance prior to LE. Upon reaching LE, fish were

removed from the tank and euthanized with tricaine methanesulfonate (MS-222; Sigma-Aldrich, St. Louis, Missouri), and the time spent at 26°C was recorded.

For each strain, 12–13 families representing approximately 285 fish were tested (Table 1). Each trial consisted of eight yearlings from each strain that were placed together in the experimental tank at ambient temperature and were starved for 24 h to allow acclimation and to eliminate differences in responses due to metabolic state. In each trial, the eight fish from each strain (except Hill's Lake) were identified to family. Fish from individual families were generally included in three different trials. Families were randomly assigned to trials to minimize confounding of family and trial effects.

Statistical analyses.—An ANCOVA was used to examine differences in CTM between strains, with body size as a covariate. In total, 36 trials containing each of the four strains were conducted. The time to LE was averaged by stock for each trial to prevent pseudoreplication, and these averages were used in the ANCOVA. To examine adaptive potential in thermal tolerance within strains, we explored existing variation among families by examining the CTM of the different families within strains when this information existed. The Hill's Lake strain was excluded from this comparison, since the pooling of individuals prevented the assessment of performance differences among families. For the other strains, family-level variability was examined with an ANOVA among families within each separate strain. Relationships between strains and between families were explored post hoc by use of the Tukey–Kramer honestly significant difference comparison of means (at $P < 0.05$), which corrects for multiple comparisons.

All statistical analyses were performed using JMP software version 4.0 (SAS Institute, Inc., Cary, North Carolina); the data met the individual assumptions (independence and normality) of the statistical analyses.

RESULTS

Yearling brook trout and Aurora trout showed significant differences in thermal tolerance among strains ($F_{3,138} = 35.95$, $P < 0.001$). These differences were independent of fish mass ($F_{1,138} = 0.59$, $P = 0.45$); inclusion of body length or Fulton's condition factor as covariates also was not significant (data not shown). All populations differed from one another, except the Aurora trout and Lake Nipigon strains, which did not differ significantly based on the Tukey–Kramer honestly significant difference comparison. The Hill's Lake and Dickson Lake strains (mean time to LE = 127 and 116 min, respectively) were able to endure elevated temperatures significantly longer than the Lake Nipigon strain (mean time to LE = 87 min), whereas Aurora trout (mean time to LE = 76 min) were least able to withstand elevated temperatures (Figure 1).

Within-strain variability as measured by the CV (SD/mean) was similar among strains (CV = 0.18–0.20) except the Lake Nipigon strain, which had greater variation (CV = 0.25;

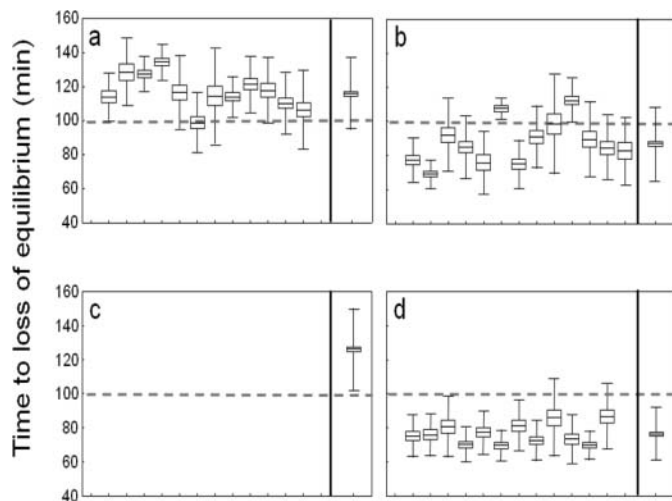


FIGURE 1. Box-and-whisker plots of time to the loss of equilibrium at 25°C for brook trout: (a) Dickson Lake strain, (b) Lake Nipigon strain, (c) Hill's Lake strain, and (d) Aurora trout (line within box = mean; ends of box = \pm SE; ends of whiskers = \pm SD). Values for individual families within a strain are shown to the left of the vertical line in each panel; pooled data for the strain are shown to the right of the vertical line. The grey dashed horizontal line at 100 min is included for reference only.

Figure 1). Despite this greater variation, the Lake Nipigon strain still had lower overall temperature tolerance than the other brook trout strains (mean time to LE = 87 min). Examination of within-strain variability for the Dickson Lake, Lake Nipigon, and Aurora trout strains showed that there was statistically significant variation among the families tested within each strain ($P < 0.05$; Figure 1). The Dickson Lake and Lake Nipigon strains showed greater within-strain variation than Aurora trout, in which only two families were responsible for the statistically significant within-strain differences (Figure 1). Mean CTM values for the Lake Nipigon and Dickson Lake families varied by as much as 43 and 36 min to LE, respectively, whereas Aurora trout families exhibited less than half the variation observed in the brook trout strains (17 min to LE; Figure 1). Family-level variability also differed among strains, as some families exhibited a narrow range of temperature tolerances, whereas other families had broader ranges (Figure 1).

DISCUSSION

This study adds to the growing body of evidence for intraspecific variation in thermal performance (Fields et al. 1987; Haugen and Vøllestad 2000; Myrick and Cech 2004; Kavanagh et al. 2010; Eliason et al. 2011). In contrast to other studies that have shown only limited intraspecific variation in thermal biology for temperate freshwater fishes (Elliott and Klemetsen 2002; Larsson et al. 2005; Forseth et al. 2009), our study reveals that brook trout and Aurora trout exhibit strain-specific temperature tolerance. Because all of the study strains were maintained in a common hatchery environment, they may have responded to the rearing temperatures in the hatchery; if so, we would expect all strains to perform similarly to the Hill's Lake strain.

Interestingly, differences in thermal tolerance persisted despite the generations spent in the hatchery environment; thus, differences in performance are likely attributable to heritable (genetic) differences among strains. The observed differences in temperature tolerance reflect historically different thermal regimes and geographic origins. Strains with more southerly origins (Hill's Lake and Dickson Lake strains) were better able to cope with warmer conditions than brook trout from the more northerly Lake Nipigon strain, suggesting some degree of ancestral local adaptation for temperature tolerance.

Levels of within-strain variability also differed among strains. Brook trout from the Dickson Lake and Lake Nipigon strains showed variability among family groups, whereas the inbred Aurora trout had minimal variability among the family groups. The ability of a population to respond to changing selection increases with its inherent variation for the trait being selected upon, as long as the shift in selection does not exceed the existing expressed range for that trait (Stockwell et al. 2003). As such, wild brook trout from Dickson Lake may have a greater ability to adapt to warmer waters than fish from Lake Nipigon, which in turn may have greater adaptive potential than Aurora trout. Aurora trout not only showed limited within-strain variability but also showed lower overall temperature performance than the Dickson Lake and Hill's Lake strains. Although Aurora trout are considered a subspecies of brook trout, they occupy habitats similar to those of brook trout (Aurora Trout Recovery Team 2006), and a previous study by Sale (1962) concluded that the upper lethal limit for Aurora trout consistently followed that of brook trout. The reduced tolerance of Aurora trout to elevated temperatures and the limited within-strain variability likely resulted from their historical bottleneck and subsequent inbreeding (Balon 1995). This combined evidence indicates that Aurora trout have less potential to adapt to predicted temperature increases and may experience more severe impacts from the reductions in coldwater habitat that are likely to result from climate change.

Adaptation in a species' thermal tolerance is likely an extremely complex process and cannot be evaluated rigorously with a simple test of thermal tolerance as was implemented here. Expressed thermal performance is the phenotypic expression of underlying physiological processes, which are influenced by rearing conditions and acclimation as well as levels of standing genetic variation relating to expression of the trait (Stockwell et al. 2003; Willi et al. 2006). Mapping of quantitative trait loci in other salmonids have identified loci associated with thermal tolerance (Jackson et al. 1998; Perry et al. 2001; Somorjai et al. 2003); as knowledge of the genetic architecture of brook trout improves with mapping homologies (Timusk et al. 2011) and as high-resolution panels of genetic markers become available, future studies may be able to tease out the underlying genetic factors and true adaptive potential within and among brook trout populations.

The observed differences in thermal tolerance among the tested strains appeared to be more strongly linked to their ancestry rather than to recent hatchery history, suggesting that

their differing physiological responses to thermal stress are heritable and slow to change across generations. To some extent, fish are able to behaviorally respond to elevated temperatures by seeking more preferable temperatures (e.g., thermal refuges) but only to the extent that these coldwater areas persist (Meisner 1990a, 1990b; Biro 1998). Brook trout in Ontario have already been observed to suffer mortalities linked with warming waters (Gunn and Snucins 2010). This limited flexibility in thermal performance has management implications for stocking in the face of climate change. For example, supplementation stocking, especially from nonnative sources, is known to slow adaptation to higher temperatures (McCullough et al. 2009). Widespread supplemental stocking is not advocated; however, stocking will continue to be necessary for populations that already rely on supplemental stocking for population maintenance. Fraser (1981, 1989) determined that domesticated fish from the Hill's Lake strain had limited success in comparison with Lake Nipigon and Dickson Lake brook trout. Ashford and Danzmann (2001) suggested that the lower success of the Hill's Lake strain as a stocking source was attributable to the strain's low reproductive success. The Lake Nipigon strain is also not a preferred candidate for supplemental stocking in warmer habitats due to the lower thermal performance of this strain. Climatic or latitudinal differences between Lake Nipigon and southern stocked brook trout populations could lead to a decreased ability to respond to the warmer conditions that are predicted by climate change models (Stefan et al. 1993; De Stasio et al. 1996). Based on the present study and other studies, the Dickson Lake strain is likely the best candidate for stream and lake supplementation in southern Ontario because of its thermal performance and recent wild origin. In general, our results suggest that if brook trout populations decline as water temperatures increase (Meisner 1990a), stocking and rehabilitation plans should incorporate consideration of the thermal performance and adaptive potential of source strains and populations.

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