

Relationship between cardiac performance and environment across populations of Atlantic salmon (*Salmo salar*): a common garden experiment implicates local adaptation

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Abstract Cardiac performance in fishes is predicted to be shaped by environmental factors such as temperature and river flow rate through natural selection for local adaptations, but few studies have explored these relationships. Using a common garden breeding design, we collected heart rate data from three populations of Atlantic salmon (*Salmo salar*) to measure peak heart rate and estimate optimal and upper critical temperatures for cardiac performance. We found that peak heart rate across populations matched the variation in natural river flow rates, such that the population that experienced the highest flow rate had the highest peak heart rate. Moreover, all populations showed evidence of local adaptation to summer water temperatures, with optimal temperatures (inferred from the Arrhenius

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breakpoint temperature) consistently falling 2.2–3.8 °C below the water temperature averaged for the summer months for each population. Also, upper critical temperatures (inferred from the temperature at which heart rates became arrhythmic) were nearly identical to peak summer water temperatures (0–0.3 °C above the peak). These results are consistent with heritable differences in cardiac performance among populations and suggest local adaptation to temperature and river flow.

Keywords Cardiac performance · Heart rate · Local adaptation · Temperature · Climate change · Atlantic salmon

Introduction

Cardiac performance, the capacity of the heart to supply blood to other tissues, is a key determinant of fitness in many animals because of its central role in oxygen transport and its linkage to the capacity to perform exercise (Fry 1971; Claireaux et al. 2005; Clark et al. 2005). In ectotherms, it has been widely shown that heart rate increases with temperature, rising quickly at low temperatures before reaching an inflection point (the Arrhenius breakpoint temperature; T_{AB}) after which heart rate either increases more slowly or begins to decrease; if temperature continues to increase heart rate eventually becomes arrhythmic (the arrhythmia temperature; T_{arr}) (Fry 1971; Claireaux et al. 2005; Clark et al. 2005). These measures have been proposed as useful indicators of the thermal optima for cardiac performance (T_{AB}) and the upper thermal limit for normal cardiac function (T_{arr}) (Caselman and Farrell 2012). Indeed, these measures (heart rates, T_{AB} , T_{arr}) have previously been used to assess the thermal dependence of cardiac performance in ectotherms and have shown that heart rate can predict temperature-related mortality in the wild (Clark et al. 2005; Farrell et al. 2008; Muñoz et al. 2015).

Given the sensitivity of ectotherms to environmental temperature, there is considerable interest in understanding intraspecific variation and local adaptation to thermal conditions (Angilletta et al. 2002; Clarke 2003). Local adaptation has been implicated in many studies. For example, the upper thermal tolerance of rolled-leaf beetles (*Chrysomelidae* spp.) is related to temperature differences associated with both latitude and elevation (García-Robledo et al. 2015). In *Drosophila* species, differences in thermal tolerance among populations generally follow differences in environmental temperatures (Hoffmann et al. 2003). In green turtles (*Chelonia mydas*), populations from sites with warmer black sand can tolerate higher and more variable temperatures than populations from sites with cooler white sand (Weber et al. 2012). Among lizards, *Takydromus wolteri* sprints fastest at 30 °C, whereas the closely related *T. sexlineatus* sprints fastest at 34 °C, mirroring differences in native temperatures (Chen et al. 2003; Zhang and Ji 2004). In marine porcelain crabs (genus: *Petrolisthes*), lethal temperatures (LT_{50}) are positively correlated with maximum habitat temperatures (Somero 2010). Thermal tolerance has been found to covary with local temperatures in populations of brook trout (*Salvelinus fontinalis*) (Stitt et al. 2014), populations of Sockeye salmon (*Oncorhynchus nerka*) (Eliason et al. 2011), subspecies of temperate killifish (*Fundulus* spp.) (Fangue et al. 2006), closely related species of tropical killifish (*Aphyosemion* spp.) (McKenzie et al. 2013), and among *Danio* species (Sidhu et al. 2014). However, few studies have used “common garden” experimental approaches to infer heritable (genetic) differences in thermal performance, which in

turn are required to infer adaptation (Kawecki and Ebert 2004). Furthermore, a critical outstanding question is whether local adaptation of cardiac performance reflects the alignment of cardiac optima to typical temperatures experienced by a population, the alignment of cardiac maximums to extreme temperatures experienced by a population, or both (Eliason et al. 2011).

Cardiac performance may also be adapted to other aspects of local environments, most notably to exercise requirements. For example, species with higher exercise demands are known to have increased cardiac performance, driven largely by differences in heart rate (Farrell 1991). Consequently, any environmental factor that affects exercise demands may in turn affect cardiac performance. For animals living in rivers, flow rate may represent such a selection pressure, and indeed flow rate is known to underlie local differences in morphology in many species (e.g. Rivera 2008; Langerhans and Reznick 2010). However, the role of stream flow rate in shaping cardiac performance remains largely unresolved, with only a single comparison of sockeye salmon populations showing that flow rate during upriver migration affects cardiac performance (Eliason et al. 2011).

Here we used a common garden experiment to tease apart environmental and heritable effects on juvenile cardiac performance for three captive populations of Atlantic salmon (*Salmo salar*), which originated from geographically isolated ancestral sources that differ in water temperature and flow regimes. Atlantic salmon have a long juvenile stream residency period (2–4 years), during which there is high mortality (Hutchings and Jones 1998). Thus, juveniles should be under strong selection to optimize cardiac performance at this life stage (Garcia de Leaniz et al. 2007). The strong natal philopatry of Atlantic salmon should also facilitate genetic divergence among populations and adaptation to local environments (Garcia de Leaniz et al. 2007). We expected cardiac performance to be shaped by summer water temperatures (June–September), as this is the most thermally challenging period for juvenile salmon (Breau et al. 2007). Specifically, we predicted that T_{AB} would be close to average summer water temperatures and T_{arr} would be greater than maximum summer water temperatures (so that some level of cardiac performance is able to be sustained on extremely warm days). Furthermore, we predicted that peak heart rate (f_{Hpeak}) would reflect flow rate, such that populations that encounter a faster flow rate as juveniles would be able to sustain faster heart rates.

Materials and methods

Study populations

Atlantic salmon from three locations were examined in this study: LaHave River (NS, Canada; 44.4°N, 64.5°W), Lac Saint-Jean (QC, Canada; 48.6°N, 72.0°W) and Sebago Lake (ME, USA; 43.9°N, 70.6°W). Atlantic salmon from the LaHave population have been maintained in Ontario Ministry of Natural Resources and Forestry (OMNRF) hatcheries for five generations, and the other two populations for two generations (OMNRF, unpubl. data). Experimental fish from each population were produced by crossing gametes from five males and five females in all pairwise combinations (full factorial breeding design: $n = 25$ families per population; $n = 75$ families total). Families within the LaHave and Sebago populations were made using adults at the OMNRF Harwood Fish Culture Station (Harwood, ON) and transferred to the OMNRF Codrington Research Facility within 6 h of fertilization. Crosses from the Lac Saint-Jean population were made at the OMNRF

Codrington Research Facility. Families from all three populations were reared from the egg stage at the Codrington Research Facility in identical thermal regimes. Eggs were placed in subdivided Heath incubation trays until they hatched (~ 3 months post-fertilization), with each family randomly assigned to two egg tray partitions. As the water supply to the rearing facility and incubation trays was from a spring-fed stream (Marsh Creek), the water temperature during incubation mimicked ambient natural conditions. At approximately 5 months post-fertilization, individuals transitioned from endogenous feeding (yolk sac) to exogenous feeding, and were fed ad libitum using organic fish pellets (EWOS Commercial Feeds, Bergen, Norway). In May 2013, individuals were transferred to the University of Western Ontario and reared in 650 L tanks with individual families kept in ‘fry cups’. These tanks were supplied with freshwater flow of approximately 1 L min^{-1} and maintained at $9.5\text{--}13 \text{ }^\circ\text{C}$ for the remainder of the experiment. Once fish were large enough, they were tagged using Visible Implant Elastomers (Northwest Marine Technology, WA, USA). Of the 25 families produced for each population (75 families total), all fish died in 7 LaHave families, 3 Sebago families, and 3 Lac Saint-Jean families.

Heart rate measurements

Heart rates measurements followed Casselman and Farrell (2012), who showed that pharmacologically stimulated maximum heart rates were similar to in vivo maximum heart rates observed after exercising salmon to exhaustion. Juvenile cardiac performance was measured as the response of maximum heart rate (f_{Hmax}) to warming, using an average of 6.6 fish from each surviving family (range = 1–17). Test fish were anaesthetized using a 1:1 ratio of MS-222 and sodium bicarbonate (to prevent activity from influencing f_{Hmax}), and measured for body mass ($\pm 0.1 \text{ g}$) and fork length ($\pm 0.1 \text{ cm}$). A single test fish was then placed into a holding reservoir and maintained at the acclimation temperature of $11 \text{ }^\circ\text{C}$ by a recirculating temperature controlled water bath (VWR, Edmonton, AB, Canada), with a digital temperature probe used to record the temperature experienced by the fish. The test fish was ram-ventilated to supply oxygenated water that contained a maintenance dose of anesthetic (75 mg L^{-1} of MS-222 buffered with 75 mg L^{-1} sodium bicarbonate). The caudal fin of the test fish was loosely fed through a metal cylinder to maintain dorsal–ventral orientation on electrodes that were positioned on the bottom of the holding reservoir, which allowed non-invasive electrocardiogram (ECG) recordings. Electrodes were connected to a data acquisition system (PowerLab 26T, AD Instruments, Dunedin, New Zealand) including a ground, which converted the analog input from the electrodes to digital input. The output from the PowerLab system was processed and recorded using LabChart v.7.2.5 (AD Instruments, Dunedin, New Zealand).

Each test fish was given 30 min for their heart rate to stabilize, after which the fish was pharmacologically stimulated to reach maximum heart rate using an intraperitoneal injection of 2.4 mg kg^{-1} atropine sulphate (Sigma-Aldrich, St. Louis, MO, USA) to block vagal tone and $8.8 \text{ } \mu\text{g kg}^{-1}$ isoproterenol (Sigma-Aldrich, St. Louis, MO, USA) to fully stimulate β -adrenergic receptors. Both agents were dissolved in 0.9 % NaCl and the injection was followed by a 15 min equilibration period to allow heart rate to stabilize at f_{Hmax} . After the equilibration period, temperature was increased continuously at the rate of $1 \text{ }^\circ\text{C}$ every 6 min and f_{Hmax} measurements were taken every 6 min until the heart became arrhythmic. When arrhythmia was observed, the individual was removed from the apparatus and euthanized with an overdose of MS-222. Heart rates were then calculated by manually identifying peaks of the ECG and determining the number of peaks in a 15 s continuous heartbeat series.

We conducted ECG measurements from October 21, 2013 to August 22, 2014. In total, electrocardiograms were obtained for 410 fish (117 LaHave fish, 127 Sebago fish, and 166 Lac Saint-Jean fish). The body mass (mean \pm SD) of the fish at the time of the heart rate measurements was 12 ± 3 g for LaHave, 10 ± 3 g for Sebago and 12 ± 3 g for Lac Saint-Jean. An additional 21 fish were not included in the analyses because the electrocardiogram signals were of insufficient quality (e.g. a low signal to noise ratio meant that individual heart beats could not be clearly identified) or the pharmacological injections had atypical effects (e.g. an arrhythmia was observed during the equilibration period).

Analysis of cardiac performance

Electrocardiograms were used to calculate three cardiac performance measures for each fish: Arrhenius breakpoint temperature (T_{AB}), arrhythmia temperature (T_{arr}), and peak heart rate (f_{Hpeak}). To calculate T_{AB} , a measure of thermal optimum, the performance curve of f_{Hmax} across temperatures was analyzed using a Q_{10} (temperature sensitivity) plot. The Q_{10} of f_{Hmax} (how much f_{Hmax} increased in response to a 10 °C increase in temperature) was calculated between each temperature increment as $(f_{Hmax\ n+1}/f_{Hmax\ n})^{(10/[T_{n+1}-T_n])}$ where $f_{Hmax\ n}$ is the maximum heart rate at temperature step n and T_n is the temperature at step n . The Q_{10} plots were input into SigmaPlot (Systat Software, San Jose, CA, USA) and two regression lines were fit to the biphasic curve by comparing all pair-wise possibilities of residuals of f_{Hmax} at high versus low temperatures, identifying the point at which temperature-induced increases in f_{Hmax} shift to a lower exponent (see Casselman and Farrell 2012). This point was taken as T_{AB} . The T_{arr} , a measure of upper critical temperature, was identified as the first time point when an arrhythmia developed in the continuous ECG. The f_{Hpeak} , a measure of maximum cardiac output, was calculated as the highest maximum heart rate observed for an individual across temperatures. For each cardiac performance measure, a one-way ANCOVA was used to test for differences among populations with body mass included as a covariate and family ID as a random factor nested with population.

Temperature

The natural (ancestral source) water temperatures experienced by each population while in freshwater were compared to T_{AB} and T_{arr} . For Sebago Lake, water temperature data were provided by the Portland Water District, ME, USA (43.3°N, 70.1°W) and were collected at several sites in Sebago Lake between 1990 and 2010 at 10:00 AM EST at a depth of 2 m. For the LaHave River, water temperature data were provided by the Population Ecology Division of Fisheries and Oceans Canada and were collected at the Morgan Falls Fishery, New Germany, NS, Canada (44.3°N, 64.4°W), between 1997 and 2011 at 11:00 AM AST at an average depth of 1 m. For Lac Saint-Jean, water temperature data were provided by the Ministère des Ressources naturelles et de la Faune and were collected at the city of Roberval QC, Canada (48.5°N, 72.2°W) between 1994 and 2012 at 12:00 PM EST at an average depth of 3 m. For each location we calculated the water temperatures averaged over the summer months of June through to September for all recorded years. We also calculated the average water temperature of the 10 warmest days observed across all years as a measure of peak summer water temperatures.

Flow rate

Similarly, the natural (ancestral source) flow rates experienced by each population while in freshwater were compared to f_{Hpeak} . For the LaHave River, flow rate data were collected by Environment Canada at West Northfield, NS, Canada (44.3°N, 62.4°W). For Sebago, flow rate data were collected by U.S. Geological Survey at Crooked River, ME, US (44.0°N, 70.6°W). For Lac Saint-Jean, flow rate data were collected by the Centre d'expertise hydrique Quebec at River Aux salmons, QC, Canada (48.4°N, 72.3°W). Flow rate data were collected between 1995 and 2000 for all locations, and daily flow rates were averaged and used to calculate average flow rate for each site. We also calculated annual peak flow rate by averaging the 10 highest flow rates observed across all years.

Results

All of the cardiac performance measures for juvenile salmon showed significant differences among the three populations (Table 1). The Arrhenius breakpoint temperature (T_{AB}) was significantly different across all populations, with Sebago having the highest T_{AB} followed by LaHave and lastly Lac Saint-Jean. The arrhythmia temperature (T_{arr}) was significantly higher in both LaHave and Sebago than in Lac Saint-Jean. Peak heart rate (f_{Hpeak}) was significantly higher in LaHave than in either Sebago or Lac Saint-Jean, which matched the patterns of average and peak stream flow rates (average: LaHave: 32.2 m³/s; Sebago: 9.4 m³/s; Lac Saint-Jean: 8.4 m³/s; peak: LaHave: 205 m³/s; Sebago: 74 m³/s; Lac Saint-Jean: 71 m³/s; Supplementary Figure S1). Body mass was included as a covariate in each of the ANCOVA models, and was not significantly related to T_{AB} ($F_{2,347} = 3.1, p = 0.07$), T_{arr} ($F_{2,348} = 1.2, p = 0.27$) or f_{Hpeak} ($F_{2,348} = 1.1, p = 0.30$). Family ID was included as a random nested factor within population, and was not significantly related to T_{AB} ($F_{2,347} = 1.6, p = 0.06$), but was significantly related to T_{arr} ($F_{2,348} = 1.5, p = 0.01$) and f_{Hpeak} ($F_{2,348} = 2.0, p < 0.001$).

Cardiac performance measures for f_{Hmax} were compared with seasonal water temperatures for each population in Fig. 1. In all three populations, the average T_{AB} value was lower than the water temperature averaged for the summer months by 2.2–3.8 °C, and the rank order of T_{AB} among populations matched the order of averaged summer water temperatures. The average T_{arr} values were essentially the same as the peak summer water temperatures for each population (the difference was 0–0.3 °C), and the rank order of T_{arr} among populations matched the order of peak summer water temperatures. Interestingly, 43 % of the individuals we examined had a T_{arr} that was less than the peak summer water temperatures (LaHave: 46 %, Sebago: 37 %, Lac Saint-Jean: 46 %).

Table 1 Cardiac performance measures for three populations of Atlantic salmon (*Salmo salar*)

Measure	Sebago	LaHave	Lac Saint-Jean	F	df	p
T_{AB} (°C)	17.0 ± 0.1 ^A	16.4 ± 0.1 ^A	14.7 ± 0.1 ^B	32.0	2, 347	<0.001
T_{arr} (°C)	26.4 ± 0.2 ^A	26.1 ± 0.1 ^A	23.5 ± 0.2 ^B	30.1	2, 348	<0.001
f_{Hpeak} (beats min ⁻¹)	167 ± 2 ^A	176 ± 1 ^B	164 ± 2 ^A	5.0	2, 348	<0.001

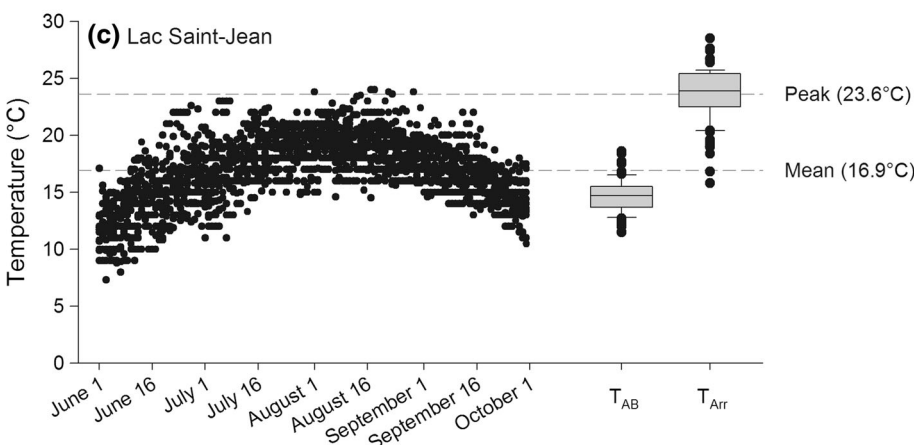
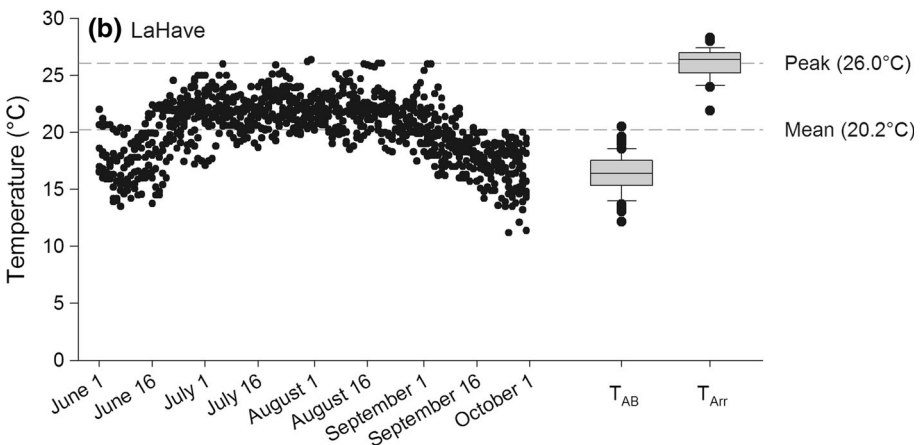
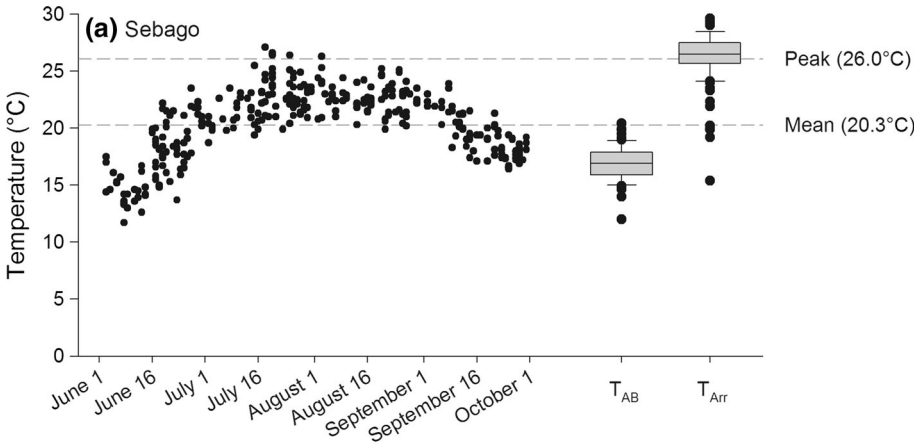
Presented are means ± 1 SEM for each population, as well as the F-stats, degrees of freedom and p values for the population term in the ANCOVA models. Significant differences among population pairs are indicated by different letters

Discussion

In ectotherms, differences in thermal environments are predicted to drive local adaptation, with selection for individuals to perform best at the temperatures that they typically experience. For example, local adaptation was observed in green turtles, such that developing embryos were adapted to the temperature of their nesting beach (Weber et al. 2012). Thermal adaptation has similarly been found in Fraser River sockeye salmon populations, such that optima for aerobic scope correlated with the median water temperature experienced during upstream spawning migration (Eliason et al. 2011). Here, we found that thermal optima, as measured by the Arrhenius breakpoint temperature (T_{AB}), were significantly different across three populations of Atlantic salmon, with Sebago having the highest T_{AB} , LaHave having an intermediate T_{AB} , and Lac Saint-Jean having the lowest T_{AB} , which mirrored the average summer water temperatures in these environments. Because we used a common garden design, our results implicate heritable differences in T_{AB} among populations, which would be consistent with genetic (or epigenetic) effects. A study of European Atlantic salmon similarly found that T_{AB} tended to be higher for a southern (warmer) population compared to a northern (cooler) population, albeit the difference between populations was not statistically significant (Anttila et al. 2014). Our data thus provide some of the first evidence that suggests local adaptation of thermal performance in Atlantic salmon.

In addition to adaptation to average temperatures, there may also be selection for tolerance to extreme temperatures. For example, lethal temperatures are positively correlated with maximum habitat temperatures in porcelain crabs (Somero 2010). Redband trout (*Oncorhynchus mykiss gairdneri*) are locally adapted to thermal extremes, such that populations that experience extreme heat are better able to tolerate thermal stress without the need to express physiologically costly heat shock proteins (Narum et al. 2015). Here, we found that T_{arr} significantly differed across three Atlantic salmon populations in a way that mirrored peak summer temperatures in their local environments. Specifically, the Sebago and LaHave populations, which experience similar peak temperatures, had T_{arr} values that did not differ from each other, whereas T_{arr} values were significantly lower in the cooler Lac Saint-Jean population. Interestingly, the average T_{arr} values were close to current peak summer temperatures for all populations, with peak summer temperatures falling at or above T_{arr} values for at least 37 % of the sampled individuals within each population. Peak summer temperatures thus represent a potential cardiac stressor for all three populations, although some caution is warranted in extrapolating cardiac performance measured in the laboratory to performance in natural environments. Fish in our experiment were reared at consistent temperatures, and we did not quantify the effects of acclimation or developmental plasticity on cardiac performance. A previous study of Atlantic salmon found significant developmental plasticity associated with cardiac performance, with warmer rearing temperatures leading to higher T_{arr} values (Anttila et al. 2014). The T_{arr} values that we measured may thus be specific to the conditions under which the fish were reared, and may differ from the T_{arr} values that would occur if the fish were reared in their natural environments. Nevertheless, the use of a common garden design suggests that there are underlying heritable differences in T_{arr} among populations of Atlantic salmon.

Environmental features other than temperature may also shape cardiac performance. For example, individuals that swim against stronger water flow are expected to have higher exercise demands and higher overall cardiac performance requirements. Indeed, the cardiac output of Fraser River sockeye salmon was previously found to differ based on the difficulty of a population's upriver migration, such that populations that had to migrate



◀ **Fig. 1** Natural water temperature and cardiac performance measures for three populations of Atlantic salmon (*Salmo salar*). The panels show data for the **a** Sebago, **b** LaHave, and **c** Lac Saint-Jean populations. Individual temperature observations are shown by date on the *left side* of each figure with horizontal *dashed lines* used to display average and peak summer temperatures for each population. *Box plots* on the *right side* of each panel show the Arrhenius breakpoint temperature of maximum heart rate f_{Hmax} (T_{AB}) and the arrhythmia temperature (T_{arr}). The *box plots* display the median, 25th and 75th percentiles, with whiskers indicating the 10th and 90th percentiles and individual points used to show data outside this interval. For details of temperature measurements at each location, see “[Materials and methods](#)” section

through the hydraulically challenging “Hell’s Gate” had greater cardiac scope (Eliason et al. 2011). Heart rate similarly has been shown to differ across species in a manner consistent with exercise demands (Farrell 1991). We found that the LaHave population of Atlantic salmon, which experiences a mean flow rate three-times higher than the Lac Saint-Jean and Sebago populations, had significantly higher peak heart rates. Our findings suggest that aspects of cardiac capacity may be locally adapted to match both temperature and flow rate.

In conclusion, we provide evidence that supports local adaptation of cardiac performance in juvenile Atlantic salmon. Based on our common garden design, the observed population differences in cardiac performance appear to be heritable and to mirror the thermal profiles of the populations’ native environments. However, given that many Atlantic salmon from these populations experience temperatures near the thermal limits measured in this study, these populations may be vulnerable to further increases in temperature associated with global climate change. The effects of climate change may be partially mitigated by developmental plasticity (Anttila et al. 2014) and the utilization of cool-temperature refuges (Breau et al. 2007), but may also require genetic adaptation if Atlantic salmon populations are to persist in their current habitats. A better understanding of these processes will be critical to conserving Atlantic salmon and other ectotherms.

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Author contribution K.J.G., B.D.N., A.P.F. and C.C.W. conceived the design of the project. K.J.G. collected the heart rate data. K.J.G, B.D.N. and S.R.G. analyzed the data and drafted the initial manuscript. All authors contributed to editing the manuscript and gave final approval for submission.

Compliance with ethical standards

Conflict of interest The authors have no competing interests.

Ethics All experiments followed ethical guidelines from the Canadian Council on Animal Care as reviewed and approved by the Animal Use Subcommittee at the University of Western Ontario (protocol no. 2010–214).

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