The thermal limits of cardiorespiratory performance in anadromous Arctic char (*Salvelinus alpinus*): a field-based investigation using a remote mobile laboratory

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Despite immense concern over amplified warming in the Arctic, physiological research to address related conservation issues for valuable cold-adapted fish, such as the Arctic char (*Salvelinus alpinus*), is lacking. This crucial knowledge gap is largely attributable to the practical and logistical challenges of conducting sensitive physiological investigations in remote field settings. Here, we used an innovative, mobile aquatic-research laboratory to assess the effects of temperature on aerobic metabolism and maximum heart rate ($f_{\text{Hmax}}$) of upriver migrating Arctic char in the Kitikmeot region of Nunavut in the central Canadian Arctic. Absolute aerobic scope was unchanged at temperatures from 4 to 16°C, while $f_{\text{Hmax}}$ increased with temperature ($Q_{10} = 2.1$), as expected. However, $f_{\text{Hmax}}$ fell precipitously below 4°C and it began to plateau above ~16°C, reaching a maximum at ~19°C before declining and becoming arrhythmic at ~21°C. Furthermore, recovery from exhaustive exercise appeared to be critically impaired above 16°C. The broad thermal range (~4–16°C) for increasing $f_{\text{Hmax}}$ and maintaining absolute aerobic scope matches river temperatures commonly encountered by migrating Arctic char in this region. Nevertheless, river temperatures can exceed 20°C during warm events and our results confirm that such temperatures would limit exercise performance and thus impair migration in this species. Thus, unless Arctic char can rapidly acclimatize or alter its migration timing or location, which are both open questions, these impairments would likely impact population persistence and reduce lifetime fitness. As such, future conservation efforts should work towards quantifying and accounting for the impacts of warming, variable river temperatures on migration and reproductive success.

Key words: Arctic char, Arctic fisheries, cardiorespiratory, climate change, fish physiology, thermal tolerance

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Introduction

The Canadian Arctic has warmed at close to three times the average global rate, raising concern among northerners, scientists, and policymakers alike (Galappathithi et al., 2019; Zhang et al., 2019). Despite this concern, we know little about the environmental physiology of many Arctic species, even though such knowledge is fundamental to a mechanistic understanding of the ecological impacts of climate change (Cooke and O’Connor, 2010; Cooke et al., 2012; Cooke et al., 2013; Patterson et al., 2016). Indeed, knowledge regarding thermal limitations to metabolism, growth, and exercise performance is increasingly being used to develop evidence-based management strategies for many fishes (Cooke et al., 2012; DFO, 2012; Patterson et al., 2016). For instance, the allowable harvest of Pacific and Atlantic salmon is now adjusted based on river temperatures, in part, using knowledge that high temperatures, by impairing salmon cardiac performance, capacity for aerobic exercise, and recoverability, can reduce survival during migration (Farrell et al., 2008; Eliason et al., 2011; DFO, 2012; Patterson et al., 2016). Equivalent knowledge for use in management decisions remains sparse for Arctic fishes, largely due to the exorbitant cost of northern research (Mallory et al., 2012; DFO, 2012; Patterson et al., 2016). The overall goal of the study is to provide insight into how and thermal challenges in their lives (Gilbert et al., 2016). Their up-river return migrations are among the greatest physical and thermal challenges in their lives (Gilbert et al., 2016). They can encounter conditions ranging from high-flow rapids to water so shallow that they are only partially submerged, and temperatures that can vary dramatically from ∼0 to 21°C (present study; Gilbert et al., 2016; Gilbert and Tierney, 2018).

This variable thermal history, the rapid warming of the Arctic and inter-study differences in thermal tolerance provide the impetus for field-based research on the thermal physiology of Arctic char. To this end, we used innovative mobile Arctic research infrastructure and simplified physiological techniques to allow for a field-based assessment of the thermal limits to cardiorespiratory performance for migrating Arctic char in the central Canadian Arctic. Based on their range of encountered migration temperatures, we predicted that Arctic char in this region should have a relatively broad cardiorespiratory thermal performance and would tolerate temperatures warmer than those found in the only other comparable study of wild Arctic char (Hansen et al., 2016). The overall goal of the study is to provide insight into how current and future thermal regimes may impact Arctic char cardiorespiratory physiology and thus migration success in the face of rapid warming.

Methods

Study animals and mobile research laboratory

All sampling and animal use was approved by Fisheries and Oceans Canada Freshwater Institute (AUP 2016-033, AUP 2017-039, LFSF S-16/17 1028-NU, LFSF S-17/18 1023-NU). In the summers of 2016 and 2017, anadromous Arctic char (2016: n = 20 length = 385 ± 13 mm (mean ± SEM), mass = 605 ± 61 g; 2017: n = 12 length = 407 ± 27 mm, mass = 711 ± 209 mm) were caught by angling with barbless hooks at the mouth or in the lower reach (850 m) of Freshwater Creek, NU, Canada (69°07’N, 104°59’W; Fig. 1), where there is an important subsistence fishery for Inuit from the community of Cambridge Bay. Captured fish were transported in an aerated 90-L cooler by all-terrain vehicle...
Figure 1: Study area around the hamlet of Cambridge Bay in the Kitikmeot region of Nunavut, Canada. Anadromous Arctic char were captured at the mouth or in the lower 850 m of Freshwater Creek, which drains the Greiner watershed into the Arctic Ocean.

(Arctic Research Foundation, Winnipeg, CAN; Fig. S1) equipped with a 450-L temperature-controlled fish holding system (Aqua Logic Inc., San Diego, USA), where they were held at commonly encountered river temperatures (10–12°C). The mobile laboratory was constructed out of a standard 6.1 x 2.4 x 2.4 m (20 x 8 x 8 feet) shipping container and equipped with 15 x 305 W solar panels, 2 x 1.1 kW wind turbines, a backup 10 kW diesel generator, 24 x 2 V batteries and 2 x 6.8 kW inverter and charging systems (Fig. S1). The laboratory was also fitted with bench space (~2 m²), equipment storage and a composting toilet.

Respirometry and critical thermal maxima

In 2017, respirometry was conducted at temperatures from 3.7 to 20.0°C (n = 12). Arctic char were allowed to recover overnight (>12 h) following capture prior to these experiments. To begin, fish were warmed at 2°C h⁻¹ to the test temperature and held at that temperature for 1 h. They were then chased to fatigue (time to fatigue: 4.4 ± 0.2 min), given 1.3 ± 0.1 min air exposure, during which a ~200 µL caudal blood sample was drawn, and the fish was rapidly sealed in a 30-L respirometer (90 cm long x 20.3 cm diameter). Fatigue was defined as the fish being refractory to a tail and mid-body grab for > 5 s. Fish were then allowed to recover for a minimum of 18 h in the respirometer after which they were warmed at rate of 5°C h⁻¹ until they reached their critical thermal maximum (CTMax), the temperature at which they could no longer maintain dorsoventral equilibrium. This protocol allowed us to reliably estimate maximum (MO2Max) and minimum (MO2Min) oxygen consumption rates, calculate absolute and factorial aerobic scope (AAS: MO2Max - MO2Min; FAS: MO2Max/MO2Min), record MO2 during acute warming and estimate CTMax. AAS serves as a measure of the net aerobic capacity available above rest while FAS is a measure of the capacity to increase MO2 above MO2Min in a multiplicative manner. Whether an aerobic function is constrained by AAS or FAS as temperature increases will depend on how its aerobic cost scales with temperature relative to the available scope (see Farrell, 2016; Hasley et al., 2018). Hematocrit (Hct), haemoglobin (Hb) content (HB 201, HemoCue, Ängelholm, SWE), blood glucose (Accu-Chek Aviva, Roche, Basel, CHE) and blood lactate concentration (Lactate Pro, Arkray KDK, JPN) were measured in duplicate immediately following the chase and at CTMax. Hb values were adjusted as previously described for fish (Clark et al.,...
Cardiac thermal tolerance was assessed in 2016 on anaesthetized fish fitted with electrocardiogram (ECG) electrodes in a manner similar to previous studies on other salmonids (Casselman et al., 2012; Anttila et al., 2014; Chen et al., 2015) and notably, in Greenlandic Arctic char (Hansen et al., 2016) and Arctic cod (Drost et al., 2016). To begin each experiment, two fish were anesthetized in 150 mg L\(^{-1}\) buffered tricaine methanesulphonate (TMS; 1:1.5 sodium bicarbonate) at 10°C until ventilation slowed, almost to a stop and was only intermittent. Fish were then weighed and transferred to a well-aerated anaesthetic bath containing 65 mg L\(^{-1}\) buffered TMS where they were placed supine, their gills were irrigated with a pump. Stainless steel electrodes were inserted into the skin over the heart on the right side of the ventral midline and just posterior to the left pectoral fin, and an ECG was acquired and processed as previously described (Gilbert et al., 2019). The fish were then given an intraperitoneal injection in a total volume of 1 mL kg\(^{-1}\) of isoproterenol (Isotemp II, Fisher Scientific, Hampton, USA), and a flow-through aquarium chiller (Tr15, Teco, Ravenna, ITA). The experiment continued until the heartbeat became arrhythmic or the bath began to freeze at which point the fish was euthanized with an overdose of anaesthetic (150 mg/L buffered TMS) followed by spinal pithing. The ECG was analyzed using automated heartbeat detection as in Gilbert et al. (2019). The temperature at the first Arrhenius break point \((T_{\text{warmAB}})\), peak \(f_{\text{Hmax}}\), temperature at peak \(f_{\text{Hmax}}\) \((T_{\text{peak}})\) and temperature at arrhythmia \((T_{\text{arr}})\) were identified for each individual as previously described (Casselman et al., 2012; Chen et al., 2015; Hansen et al., 2016). We also identified an Arrhenius break point temperature \((T_{\text{coldAB}})\) for each fish that was acutely cooled from 10°C. Briefly, Arrhenius break point temperatures were identified using a segmented linear regression and indicate a temperature at which there is a notable transition in the thermal sensitivity of a given rate with further warming or cooling. \(T_{\text{peak}}\) and peak \(f_{\text{Hmax}}\) are the temperature and \(f_{\text{Hmax}}\) at which \(f_{\text{Hmax}}\) ceased to increase or began decreasing with further warming and thus indicate the \(f_{\text{Hmax}}\) and temperature at which a cardiac performance limitation occurred. \(T_{\text{arr}}\) is the temperature at which the heart began skipping beats (became irregular), thus indicating severe cardiac dysfunction.

**Results**

**Respirometry and \(CT_{\text{Max}}\)**

River temperatures ranged from 8.9 to 14.5°C (mean ± SD: 11.0 ± 1.4°C; recorded every 15 min) during the period when fish were captured for the respirometry experiments. Arctic char were acutely brought (2°C h\(^{-1}\)) to their test temperature \((T)\) before being chased to fatigue, which lasted 4.4 ± 0.2 min, independent of temperature \((f_{1,10} = 0.49, P = 0.50, R^2 = 0.05)\). \(MO_{2\text{Max}}\) increased linearly with increasing test temperature \((\text{Eq. } 2a, f_{1,8} = 8.3, P = 0.02, R^2 = 0.51)\), while \(MO_{2\text{Min}}\) increased exponentially \((\text{Eq. } 2a, f_{2,7} = 19.9, P = 0.001), the temperature and \(f_{\text{Hmax}}\) at which \(f_{\text{Hmax}}\) ceased to increase or began decreasing with further warming and thus indicate the \(f_{\text{Hmax}}\) and temperature at which a cardiac performance limitation occurred. \(T_{\text{arr}}\) is the temperature at which the heart began skipping beats (became irregular), thus indicating severe cardiac dysfunction.
Figure 2: The effect of environmentally relevant temperatures on (a) minimum (\(\dot{MO}_2\)\(_{\text{Min}}\); open circles; \(n = 10\)) and maximum oxygen uptake (\(\dot{MO}_2\)\(_{\text{Max}}\); closed circles; \(n = 12\)) and aerobic scope of migratory Arctic char following a chase to exhaustion and air exposure. (b) Absolute aerobic scope (AAS) and (c) factorial aerobic scope (FAS). Two individuals at warm temperatures died after being exhausted (orange ‘x’) and were excluded from all regression analyses. A linear model and a second-order polynomial model were compared for each variable. The model with the lowest AICc is presented (blue lines) with its 95% confidence interval (shaded area), \(R^2\) and \(P\) value.

\[\dot{MO}_2\]\(_{\text{Max}}\) = 9.6 ± 3.0 • \(T\) + 231.9 ± 35.0 (1)

\[\dot{MO}_2\]\(_{\text{Min}}\) = 1.2 ± 0.4 • \(T^2\) − 12.4 ± 8.1 • \(T\) + 80.5 ± 40.9 (2)

AAS = −3.0 ± 3.9 • \(T\) + 265.9 ± 45.6 (3)

FAS = −0.34 ± 0.06 • \(T\) + 7.71 ± 0.65 (4)

Figure 3: Oxygen uptake (\(\dot{MO}_2\)) of anadromous Arctic char during acute warming to loss of equilibrium (CT\(_{\text{Max}}\)). Individual \(\dot{MO}_2\) values at their measured temperatures (grey circles; \(n = 8\) individuals and 111 data points) and mean ± sem values in 1°C bins (blue circles and grey shading) are presented. Mean values were calculated at all points where data were available for three or more individuals. The dashed line indicates temperatures where individuals were removed after reaching CT\(_{\text{Max}}\). For reference, the models for maximum \(\dot{MO}_2\) and \(\dot{MO}_2\)\(_{\text{Min}}\) (Fig. 1) are presented with their upper or lower 95% confidence intervals, respectively (light blue lines with shaded areas).

Importantly, two of the three fish exercised to exhaustion above 15°C died during recovery and had a lower \(\dot{MO}_2\)\(_{\text{Max}}\) than would be predicted based on the linear model for the remaining fish (Fig. 2a). The individual that did recover after being chased at > 15°C exhibited the lowest AAS and CT\(_{\text{Max}}\) and had the highest blood lactate concentration (15.1 mM) post-CT\(_{\text{Max}}\). Whether this elevated lactate was a result of the notably elevated \(\dot{MO}_2\)\(_{\text{Min}}\) (Figs 1a and 2) or a more severe degree of exhaustion is unclear.

Acute warming following the post-chase recovery period doubled \(\dot{MO}_2\) (LMM: \(f_{1,8.9} = 145.1, P < 0.001\), marginal \(R^2 = 0.50\), conditional \(R^2 = 0.83\)) from 138.8 ± 37.2 mg O\(_2\) h kg\(^{-1}\) at 10°C to 277.7 ± 22.0 mg O\(_2\) h kg\(^{-1}\) at 20°C (\(Q_{10} = 2.0\)). Peak \(\dot{MO}_2\) during acute warming was 319.1 ± 33.6 mg O\(_2\) h kg\(^{-1}\) (at 19.8 ± 1.1°C), a value similar to that measured immediately after exhaustive exercise at warm temperature (Figs 2a and 3). Likewise, a similar \(\dot{MO}_2\) (291.1 ± 42.7 mg O\(_2\) h kg\(^{-1}\)) also was seen immediately prior to reaching CT\(_{\text{Max}}\) (23.0 ± 0.6°C; range 19.0 to 25.2; Fig. 5).

\(f_{\text{Hmax}}\) and cardiac thermal tolerance

River temperatures ranged from 9.7 to 12.4°C (mean: 10.6 ± 0.24) at the site of capture of fish used for the cardiac thermal tolerance experiments. \(f_{\text{Hmax}}\) in Arctic char acutely transferred to 5°C was 47.7 ± 1.3 beats min\(^{-1}\). Acute warming of these fish increased their \(f_{\text{Hmax}}\) (LMM: \(f_{1,9.6} = 807.5, P < 0.001\), marginal \(R^2 = 0.92\), conditional \(R^2 = 0.98\)), attaining a peak \(f_{\text{Hmax}}\) of 115.4 ± 4.7 beats min\(^{-1}\) at 19.4 ± 0.5°C (\(T_{\text{peak}}\); Figs 4 and 5). Above \(T_{\text{peak}}\), \(f_{\text{Hmax}}\) declined to 99.0 ± 5.9 beats min\(^{-1}\) and became arrhythmic at 21.4 ± 0.5°C (\(T_{\text{arr}}\); Figs 4 and 5) before the experiment.
was terminated. The temperature of the first Arrhenius break point in $f_{H_{\text{max}}}$ during warming ($T_{\text{warmAB}}$) was $12.5 \pm 0.3^\circ\text{C}$ (Fig. 4a and b), which was similar to common ambient river temperatures (Fig. 5). The instantaneous $Q_{10}$ for $f_{H_{\text{max}}}$ decreased progressively with warming (Fig. 4c), falling below 2.0 at $\sim 11^\circ\text{C}$; the $Q_{10}$ of 1.0 at $\sim 19^\circ\text{C}$ indicated that, on average, $f_{H_{\text{max}}}$ had peaked or plateaued (Fig. 4c). With acute cooling from 10 to $0^\circ\text{C}$, $f_{H_{\text{max}}}$ progressively decreased from $76.3 \pm 1.3 \text{ beats min}^{-1}$ to $16.1 \pm 1.2 \text{ beats min}^{-1}$ (LMM: $f_{1,7} = 1273.9$, $P < 0.001$, marginal $R^2 = 0.93$ conditional $R^2 = 0.97$) and exhibited a clear break point at $\sim 3.3 \pm 0.5^\circ\text{C}$ (Fig. 4d), below which the thermal dependence of $f_{H_{\text{max}}}$ increased sharply with an instantaneous $Q_{10} > 10$ (Fig. 4c).

**Blood properties**

The MCHC decreased (Fig. 6a; $f_{1,7} = 33.3$, $P < 0.001$, $R^2 = 0.83$) and blood lactate concentration increased (Fig. 6b; $f_{1,8} = 6.6$, $P = 0.03$, $R^2 = 0.45$) with test temperature when measured immediately after Arctic char were chased to exhaustion. Blood lactate measured immediately after CTMax was negatively correlated with CTMax (Fig. 6c; $f_{1,8} = 21.2$, $P = 0.001$, $R^2 = 0.76$). Additional blood parameters were correlated with each other, but not with the test temperature or CTMax (Fig. S2).

**Discussion**

Anadromous Arctic char can encounter a broad range of temperatures from $\sim 0$ to $21^\circ\text{C}$ during their physically demanding, upriver migrations in the Canadian Arctic (Fig. 5; Gilbert et al., 2016) and even lower when at sea (Harris et al., 2020). Here we show that wild migrating Arctic char can impressively maintain absolute aerobic scope and a high regular heart rate over a large proportion ($\sim 4–16^\circ\text{C}$) of this thermal range. However, factorial aerobic scope (FAS), their ability to recover from exhaustive exercise and their $f_{H_{\text{max}}}$ can become critically limited $> 16^\circ\text{C}$, temperatures that are well within current extremes (Fig. 5). Moreover, and
unexpectedly, $f_{H_{\text{max}}}$ was greatly depressed with acute cooling to 0°C. As we discuss below, these traits may be intimately linked to the need for Arctic char to repeatedly perform prolonged swimming bouts over a wide range of temperatures in order to complete their migrations and successfully reproduce. Importantly, our findings were made possible by the use of innovative mobile research infrastructure (Fig. S1). Thus, the present study demonstrates the critical importance of such infrastructure and logistical support in any effort to understand pressing conservation and management issues in remote Arctic locations.

**Cold performance**

Early research on cold-adapted fish species suggested that they may exhibit elevated metabolic rates at cold temperatures to allow elevated growth and activity when compared to related species that were not cold-adapted (Scholander et al., 1953; Wohlschlag, 1960). This idea, which was termed ‘metabolic cold adaptation’, has largely been disproven and currently has limited support (Holeton, 1973; Holeton, 1974; Steffensen et al., 1994; Steffensen, 2002; White et al., 2012). Indeed, when Holeton (1973) tested this hypothesis on wild juvenile Arctic char in the Canadian Arctic, he found that their resting $\dot{O}_{2}$ was no higher than would be predicted for more temperate salmonids despite the Arctic char being adapted and acclimatized to a cold environment. However, Holeton’s measurements of resting $\dot{O}_{2}$ measurements at ambient temperatures (2°C) were technically limited by available equipment, facilities and technology. Although our $\dot{O}_{2}$ data do not extend to 0°C, our $\dot{O}_{2}$ data for cool temperatures similarly indicate that Arctic char do not exhibit elevated metabolism when compared with other salmonids (e.g. Hvas et al., 2017). Instead, $f_{H_{\text{max}}}$ clearly and sharply declined (high $Q_{10}$ at $< 3.3^\circ$C), suggesting the potential for Arctic char to undergo metabolic rate suppression rather than elevation metabolism at frigid temperatures. Further, we propose this transition in $f_{H_{\text{max}}}$ may be part of a suite of behavioural and physiological overwintering strategies that
conserves energy during a period of limited food availability. Indeed, other species display an active depression of metabolic rate (Guppy and Withers, 1999), fasting and suppression of activity (Speers-Roesch et al., 2018). However, we did not directly characterize acute or prolonged responses of MO2 to cold temperature (<3°C), this possibility remains to be tested.

While the observed limitation in fHmax at cold temperatures could be part of an adaptive energy conservation strategy, it would likely limit maximum cardiac output and thus aerobic exercise capacity. This cold limitation could, in turn, impact performance during demanding activities such as river migrations or diving down to frigid waters to forage. Indeed, telemetry data suggest that dives to colder, deeper ocean waters are typically very brief (Spares et al., 2012; Harris et al., 2020). If this is indeed an issue, cold acclimation could help mitigate the observed effects of acute cold exposure. Fish in the present study were presumably acclimated to near the ambient river temperatures at which they were caught (≈11°C), while Arctic char at sea (e.g. ≈5–8°C, Harris et al., 2020) or overwintering (e.g. 0.5–2°C; Mulder et al., 2018) would be acclimated to colder water. Indeed, the only other comparable study of fHmax which focused on ocean-caught Arctic char, did not find such a pronounced change in fHmax at cold temperatures (Hansen et al., 2016). Furthermore, cold acclimation has previously shown to increase intrinsic and maximum fH in many fishes, which helps counteract rate limitations inherently associated with cold exposure (Aho and Vornanen, 2001; Drost et al., 2016; Eliason and Anttila, 2017).

**Warm performance**

While debate continues over the ecological relevance of CTMax and similar acute lethal thermal tolerance measures (Pörtner and Peck, 2010; Sunday et al., 2011), such metrics remain useful, relative indicators of whole-organism heat tolerance and are unarguably the ceiling for thermal performance (Sandblom et al., 2016). Previous measures of CTMax in hatchery-reared (-0.02–0.05 kg) European Arctic char parr (e.g. ≈26–28°C; Baroudy and Elliott, 1994; Anttila et al., 2015) are significantly higher than CTMax for adults in the present study (23°C). In contrast, CTMax for adult Arctic char (0.7 kg) reared in a marine aquaculture in eastern Canada and acclimated to ≈10°C (23°C; Penney et al., 2014) was identical to the present result. By comparison, adult Arctic cod, a classic polar stenotherm and important food source for Arctic char, have a much lower CTMax (~15–17°C, Drost et al., 2016), whereas the CTMax of adult rainbow trout (0.3–0.7 kg) and Atlantic salmon (0.7 kg), both temperate relatives of Arctic char, is notably higher (~26–27°C; Ekström et al., 2014; Penney et al., 2014; Gilbert et al., 2019). In the present study, elevated blood lactate was associated with a lower CTMax, indicating that anaerobic stress prior to or during acute warming may subsequently decrease heat tolerance, which could be particularly important for exercising (migrating)fish.

Sub-lethal thermal limitations to physiological performances, such as a collapse in aerobic scope and heart rate, or cardiac arrhythmia, are arguably of greater ecological relevance than acutely lethal limitations because they occur at lower, more commonly encountered temperatures (Fig. 4). Penney et al. (2014) monitored fH and MO2 in Arctic char during acute warming and found an identical peak fH to that found here (115 beats min⁻¹). This similarity suggests that acutely warmed adult Arctic char reach their physiological maximum fH prior to CTMax, leaving little to no scope for fH available to support further warming. At 10°C the same study (Penney et al., 2014) found that resting fH was ~44 beats min⁻¹ whereas fHmax at 10°C was ~74 beats min⁻¹ in the present study, highlighting a significant scope to increase fH at cooler temperatures. Despite the similarities, Penney et al. (2014) found that the peak MO2 achieved during warming was only 223 mg O2 h kg⁻¹ compared to ~319 mg O2 h kg⁻¹ in the present study, which may indicate a loss of aerobic performance following captive rearing or domestication, as found in Atlantic salmon (Zhang et al., 2016).

Hansen et al. (2016) examined cardiac heat tolerance in sea-run fish from Greenland and found that Twarma: Tpeak, Tar: and peak fHmax were only 7.5, 12.8, 15.2 and 61.8 beats min⁻¹, respectively. All of these thermal performance indicators are all markedly lower (Twarma: ~5.0°C Tpeak: ~6.6°C, Tar: ~6.2°C and peak fHmax: ~53.6 beats min⁻¹) than in the present study, despite similar methodology and fish size. There were, however, key differences between the studies including the life history period (marine vs. upstream fall migration), fish provenance (Greenland vs. central Canadian Arctic) and possibly acclimation temperatures (~7 vs ~11°C). The most parsimonious explanation for these differences is the potential for either thermal acclimation or thermal adaptation among populations (as discussed below).

Gilbert and Tierney (2018) found that acutely warmed wild smolts and lab-reared juvenile Arctic char (~0.1 kg) maintained swimming performance up to 21°C, but their recovery was impaired above ~20°C. This impaired recoverability was associated with highly elevated blood lactate concentrations, which can be indicative of increased anaerobic demand and metabolic acidosis. Here, blood lactate levels also increased with temperature and we observed impaired recoverability following exhaustive exercise albeit in much larger animals at an even lower temperature (~15–16°C). We measured blood lactate immediately following chasing although lactate release from tissues can continue over a longer time course (Milligan, 1996). As such, our results could be a product of increased rate of lactate release into the blood rather than elevated anaerobic metabolism. However, we also observed a decrease in MCHC with increased temperature, which is indicative of red blood cell swelling in response to metabolic acidosis (Nikinmaa et al., 1987). Gilbert and Tierney (2018) also found that a handling challenge in large migrating adult Arctic char (~4 kg) resulted in an increase in reflex impairment above 12°C, which was associated with
early mortality. These post-handling impairments were particularly severe (>50%) above 15°C, which is lower than their observations in smolts (>20°C) and consistent with results for adults in the present study. Together these data suggest that access to cold-water refugia in lakes or pools may be critical for recovery if they encounter and can swiftly pass through warm temperatures during their up-river migration.

Arctic char are clearly more heat tolerant than classically stenothermal polar fishes, likely as a result of the extreme thermal variability they can encounter over the course of their lives (Janzen, 1967; Verde et al., 2008). Nonetheless, they are among the least heat-tolerant salmonids (Elliott and Elliott, 2010; Penney et al., 2014; Gilbert and Tierney, 2018), yet they are already encountering temperatures warm enough to impair vital physiological functions and impact survival. Given that fish only recapture maximum physiological performances (e.g. MO₂Max and fHmax) during demanding activities (e.g. navigating rapids) and operate at a sub-maximal performance level most of the time, further research is needed to examine temperature effects on sub-maximal performances such as routine swimming, growth, feeding and digestion.

Future directions: examining sources of variation in Arctic char thermal physiology

The inter-study differences in thermal physiology highlighted above suggest that thermal history, ontogeny, and genetic background likely all contribute to thermal performance in Arctic char in a similar manner to other salmonids. For example, in Atlantic salmon warm acclimation can markedly increase cardiac thermal tolerance (Anttila et al., 2014). However, comparable knowledge for Arctic char is almost completely lacking. Ontogeny also has a pronounced effect on thermal physiology (Elliott and Elliott, 2010; Portner et al., 2017; Hines et al., 2019). Such effects have not been well characterized in Arctic char but likely contribute to incongruences between the present and past studies (see Larsson, 2005; Larsson and Berglund, 2005; Mortensen et al., 2007; Mulder et al., 2019; Harris et al., 2020).

In temperate salmonids (e.g. Oncorhynchus spp.), thermal tolerance tends to be higher in strains from warm habitats (Rodnick et al., 2004; Chen et al., 2015; Verhille et al., 2016; Poletto et al., 2017). Based on the current literature, European Arctic char may appear more thermally tolerant than Arctic char from Greenland and the Canadian Arctic. European Arctic char are from a different glacial lineage than Greenlandic and northern Canadian Arctic char and have therefore evolved independently for > 250,000 years (Brunner et al., 2001; Moore et al., 2015). This isolation may provide a genetic basis for regional differences in thermal physiology. Even within a watershed, the cardiorespiratory thermal performance curves of sockeye salmon (O. nerka) appear locally adapted to the conditions they encounter during their upriver migration (Eliason et al., 2011). While a recent study has shown that Kitikmeot Arctic char exhibit genetic differences among populations that are consistent with the hypothesis that they may be locally adapted (Moore et al., 2017), no study to date has examined this at the phenotypic level.

Conclusions: thermal barriers to migration

Extreme heat events have repeatedly been shown to impose thermal barriers on the migration of temperate salmonids (Baisez et al., 2011; Martins et al., 2011; Hinch et al., 2012; Martins et al., 2012) by critically impairing physiological performances (Cooke et al., 2006; Farrell et al., 2008; Farrell, 2009; Eliason et al., 2011). Here we clearly show that, like these temperate salmonids, migrating Arctic char experience limitations in cardiac performance, FAS and recoverability at water temperatures that already occur during their migrations in some Arctic rivers (Fig. 4; Gilbert et al., 2016). Such limitations can critically impair migration, and they are only going to become more common as the Canadian Arctic is among the most rapidly warming regions on our planet (Zhang et al., 2019). The consequences of migration failure and associated reductions in fitness may be particularly dire in regions like the Kitikmeot, NU, where Arctic char are heavily harvested and relied upon as both a subsistence and economic resource (Day and Harris, 2013; Roux et al., 2019). As such, understanding and mitigating the impacts of extreme temperature events should be an urgent priority for fisheries managers, researchers and conservationists alike.

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**Research article**

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