

# Rapid cardiac thermal acclimation in wild anadromous Arctic char (*Salvelinus alpinus*)

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## Abstract

Migratory fishes commonly encounter large and rapid thermal variation, which has the potential to disrupt essential physiological functions. Thus, we acclimated wild, migratory Arctic char to 13°C (~7°C above a summer average) for an ecologically relevant period (3 days) and measured maximum heart rate ( $f_{Hmax}$ ) during acute warming to determine their ability to rapidly improve cardiac function at high temperatures. Arctic char exhibited rapid compensatory cardiac plasticity similar to past observations following prolonged warm acclimation: They reduced  $f_{Hmax}$  over intermediate temperatures (-8%), improved their ability to increase  $f_{Hmax}$  during warming (+10%), and increased (+1.3°C) the temperature at the onset of an arrhythmic heartbeat, a sign of cardiac failure. Consequently, this rapid cardiac plasticity may help migrating fishes like Arctic char mitigate short-term thermal challenges. Furthermore, by using mobile Arctic research infrastructure in a remote field location, the present study illustrates the potential for field-based, experimental physiology in such locations.

**Key Words:** thermal acclimation; acclimation rate; Arctic char; climate change; thermal tolerance; cardiac function

## Introduction

Many fishes, including many Arctic species, can experience rapid and large spatiotemporal thermal variation. Such rapid variation occurs with movement through thermally heterogeneous environments (e.g. -2 to 10°C over minute to hours; Harris et al. 2020b), as well as with diurnal or weather-related fluctuations (e.g. >10°C fluctuation within a day; Gilbert et al. 2016; Gilbert and Tierney 2018). Anadromous Arctic char (*Salvelinus alpinus*) are a remarkable example in this regard because, after spending the summer in the Arctic Ocean at ~6°C, their upriver migration to their spawning and overwintering areas requires passage through rivers with temperatures that range from 0 to 21°C (Gilbert et al. 2016; Harris et al. 2020a; Harris et al. 2020b). Such abrupt thermal variation is likely to challenge the physiological functions and thus whole-organism performance of any migratory fish including Arctic char.

Heart rate ( $f_H$ ) is one critical function that is strongly influenced by temperature in fishes (Farrell and Smith 2017). Warming typically drives an exponential increase in routine  $f_H$  ( $f_{H\text{routine}}$ ) to support an exponential rise in routine oxygen consumption (Eliason and Anttila 2017; Farrell 2016). Correspondingly, maximum heart rate ( $f_{H\text{max}}$ ) must also increase with temperature to maintain any ability to elevate  $f_H$  above  $f_{H\text{routine}}$  (i.e. scope for heart rate) in support of functions like digestion and exercise. However, acute warming only increases  $f_{H\text{max}}$  until a peak  $f_{H\text{max}}$  is reached, beyond which,  $f_{H\text{max}}$  typically declines and the heartbeat ultimately loses its rhythmicity (Casselman et al. 2012; Eliason and Anttila 2017; Farrell 2009; Vornanen 2016). Prolonged warm acclimation (weeks) for many fish species, including Arctic char, can help compensate by reducing  $f_H$  ( $f_{H\text{routine}}$  and  $f_{H\text{max}}$ ) over moderate temperatures and improving its stability at high temperatures (Aho and Vornanen 2001; Badr et al. 2016; Eliason and Anttila 2017; Gilbert and Farrell 2021; Vornanen 2016). Yet, the extent to which such cardiac thermal plasticity occurs more rapidly (Ekström et al. 2016) and in phase with natural acute thermal variation remains much less clear. Recently, juvenile lab-reared rainbow trout (*Oncorhynchus mykiss*) were shown to improve their ability increase  $f_{H\text{max}}$  during acute warming with a warm-acclimation of just 24h, and by 72h they exhibited a significant thermal compensation (i.e. reduction) of  $f_{H\text{max}}$  (Gilbert et al. 2022). Likewise, Sutcliffe et al. (2020a) observed a resetting of intrinsic  $f_H$  after only 1h of warm acclimation in lab-reared rainbow trout. Thus, in the absence of field studies, it seems plausible that rapid cardiac plasticity in wild fishes such as anadromous

Arctic char could help mitigate natural acute thermal warming challenges experienced during river migrations.

Consequently, we examined if wild sea-run adult Arctic char could rapidly adjust the thermal performance of their heart during a brief (~72h) acclimation to 13°C, which is ~7°C above their typical summer, marine average. We hypothesized that Arctic char could rapidly acclimate cardiac function to a warmer temperature. If our hypothesis was correct, we expected three specific results: 1) Arctic char would lower  $f_{Hmax}$  over cool and intermediate temperatures, counteracting the positive chronotropic effect of warming, 2) they would improve their ability to increase or maintain  $f_{Hmax}$  at high temperatures, and 3) they would increase the temperatures at which peak  $f_{Hmax}$  and cardiac arrhythmia first occurred. The logistical challenges of performing such physiological measurements on wild Arctic char in the central Canadian Arctic were solved by using innovative mobile research infrastructure. Thus, a secondary aim of our study was to demonstrate the utility of and need for mobile research infrastructure to address pressing research priorities in remote regions.

## Methods

We established an ecologically relevant duration for warm acclimation by tracking the duration of the upriver migration for 19 Arctic char at Halokvik, Nunavut (69.175°N 107.104°W) in August 2017 as part of a longer-term Arctic char tracking program in the region (Moore et al. 2016). At the start of their upriver migration, these fish were implanted with acoustic tags (V16, InnovaSea, Bedford, NS) as previously described (Moore et al. 2016). An acoustic receiver (VR2AR, InnovaSea) was deployed at Pangniktok (South Lake, NU; 69.272°N 108.065°W; Fig S1) the first lake Arctic char encounter during their upriver migration, although some fish continue further from there at presumably cooler temperatures. Thus, the minimum individual migration duration was taken as the difference between time of release and time of the first detection at Pangniktok. Temperature was recorded (HOBO pendant logger; Onset, Bourne, MA) in the lower 1km of the river every 15 min for the duration of this migration period. Temperature data (recorded every 5 min) was also available from the same location for 2013 from related research (Gilbert 2020; Harris et al. 2020a). The Halokvik upriver migration is one of the longest (>50km) in the central Canadian Arctic and among the most thermally variable

(Gilbert 2020). Based on the observed migration durations and temperature profiles we selected three days (68-75h) and  $\sim 13^{\circ}\text{C}$  as a conservative acclimation duration and temperature.

The thermal acclimation experiments were conducted at Palik (Byron Bay at the mouth of Lauchlan River, Nunavut;  $68.945^{\circ}\text{N}$ ,  $108.532^{\circ}\text{W}$ ; Fig. S1) during July 2019 ( $n=12$ ) and August 2021 ( $n=12$ ), using mobile research infrastructure (Arctic Research Foundation, Winnipeg, MB) which has been previously described (Gilbert et al. 2020). Palik is a remote field location  $>140$  km by water from the nearest settlement and  $>1500$  km from the nearest aquatics research facility, but just  $\sim 70$  km west of Halokvik by water, and Arctic char commonly move between the two locations while feeding in the ocean over summer (Moore et al. 2016; Moore et al. 2017). The present study is the first to use a mobile laboratory for a multi-day thermal acclimation study in the Arctic.

Wild anadromous adult Arctic char ( $3245 \pm 726$  g; mean  $\pm$  SD) were caught through angling or continuously watched gill nets (139 mm). Arctic char were immediately transferred to submerged mesh holding pens ( $\sim 1 \text{ m}^3$ ) and then some were transferred by cooler ( $\sim 100$  l) to the temperature-controlled holding system ( $\sim 500$  l) in the near shore mobile laboratory. Up to four adult Arctic char were held in the holding system at a time; they were transferred to the system at their ambient water temperatures ( $7-9^{\circ}\text{C}$ ) and were warmed at  $1-2^{\circ}\text{C h}^{-1}$  to the acclimation temperature of  $\sim 13^{\circ}\text{C}$ . Fish were held at  $\sim 13^{\circ}\text{C}$  ( $13.3 \pm 0.2^{\circ}\text{C}$ ) for  $\sim 3$  days (68-75h; hereafter referred to as ‘warm acclimated’), during which time water temperature was continuously recorded. Dissolved oxygen was maintained at  $>70\%$  air saturation and large ( $\sim 50\%$ ) water exchanges were performed, and Prime water conditioner was added (as per manufactures instructions, Seachem, Madison, GA) 1-2 times daily depending on ammonia levels. Most warm-acclimated fish performed well in the thermal performance assessments and were vigorous during handling immediately prior to testing. Two mortalities occurred during holding at  $13^{\circ}\text{C}$  in both years, possibly from a combination of confinement stress and water quality related issues. Thus, future holding studies in remote, space-limited systems such as ours might benefit from the use of smaller sized fish at the same life-stage, more frequent water exchanges and additional filtration.

We examined the extent of cardiac plasticity following the brief warm acclimation, by measuring the response of  $f_{\text{Hmax}}$  to acute warming as previously described (Gilbert et al. 2020) in non-acclimated (i.e. control fish;  $n=15$ ) and warm acclimated ( $n=9$ ) Arctic char. Briefly, we

anaesthetized (150 mg L<sup>-1</sup> tricaine methane sulfonate (TMS) buffered with 225 mg L<sup>-1</sup> NaHCO<sub>3</sub>) individual fish at ambient water temperature (~7-9°C) and then transferred them to the experimental bath containing a well-aerated maintenance anesthetic solution (75 mg L<sup>-1</sup> TMS buffered with 1.5x NaHCO<sub>3</sub>) at 5°C. We continuously irrigated their gills with the bath solution, fitted them with subdermal electrodes and delivered intraperitoneal injections of atropine (1.2 mg kg<sup>-1</sup>) and isoproterenol (4 µg kg<sup>-1</sup>) saline solutions (0.8% NaCl; total volume of 1ml kg<sup>-1</sup>) to elicit their  $f_{Hmax}$  (Anttila et al. 2014; Casselman et al. 2012; Gilbert et al. 2020). We recorded and analyzed an electrocardiogram (ECG as previously described (Gilbert et al. 2020)). The  $f_{Hmax}$  was allowed to stabilize for at least 20min before the bath was warmed at 5-6°C h<sup>-1</sup> in 1°C increments until the heartbeat became arrhythmic and the experiment was terminated. We made minor adjustments to electrode placement as needed throughout the protocol as ECG quality can change with warming. The  $f_{Hmax}$  was recorded over the final minute of each 1°C warming increment. In all cases,  $f_{Hmax}$  increased with acute warming, reached a peak, and then began to decline prior to the onset of arrhythmia. Cardiac arrhythmias at high temperatures were apparent as entirely missing or delayed QRS-complexes (ventricular depolarizations) within the ECG trace, and as such, resulted in a further and more dramatic collapse of  $f_{Hmax}$  (Fig. S2). Among all observed arrhythmias, 35% were classified as a severe AV-block type arrhythmia, defined as one or more P-waves (indicating atrial depolarization) with missing QRS-complexes (indicating an absence of ventricular depolarization; Fig. S2a and b). The rest were characterized by either completely missing, severely delayed heartbeats (no P-wave or QRS-wave; Fig S2c and d). These large gaps in the ECG traces (Fig. S2c and d) generally at least halved the instantaneous  $f_{Hmax}$  (i.e., doubling of the R-R interval).

An incremental Q<sub>10</sub> temperature coefficient for  $f_{Hmax}$  was calculated over each 2°C increase (Anttila et al. 2013; Anttila et al. 2014) because the relative thermal sensitivity of  $f_{Hmax}$  commonly decreases with increasing temperature (Fig. 1). This decline in Q<sub>10</sub> with warming is contrary to the simple exponential rise implied when calculating a single Q<sub>10</sub> value over a 10°C range of temperature. A declining incremental Q<sub>10</sub> can be interpreted as a declining ability to increase  $f_{Hmax}$  with further acute warming (Anttila et al. 2013).

We used three indicators of cardiac thermal performance, the temperature when the incremental Q<sub>10</sub> fell below 1.5 ( $T_{Q10<1.5}$ ), the temperature at peak  $f_{Hmax}$  ( $T_{peak}$ ), and the temperature when a cardiac arrhythmia first appeared ( $T_{arr}$ ). The peak  $f_{Hmax}$  attained during

warming and the total change in  $f_{Hmax}$  ( $\Delta f_{Hmax} = \text{peak } f_{Hmax} - f_{Hmax} \text{ at } 5^{\circ}\text{C}$ ) were also assessed as indicators of the peak and total ability to increase  $f_{Hmax}$  to support acute warming. Two warm-acclimated fish were excluded from the data analysis because post-experiment dissection of one revealed a severe cardiac parasitic infection, and the other was lethargic during acclimation and heart rate was unstable prior to the start of the test. Fish capture and procedures were approved by the Fisheries and Oceans Canada Freshwater Institute (FWI-ACC AUP-2021-48 and 2019-37).

Data presentation was completed with Prism v.9 (GraphPad Software, San Diego, USA) and data analysis with R Studio ( $\alpha=0.05$ ; R Core Team 2014). Changes in  $f_{Hmax}$  and the incremental  $Q_{10}$  during acute warming were characterized using linear mixed effects models (LME4 Package; Bates et al. 2007) with each modelled as a function of acclimation status, acute temperature, and fish ID as a random effect (Table S1). The fixed-factor interaction was excluded in both cases because there was limited or no evidence ( $p>0.05$ ) that it improved the model fit (i.e. lowered AIC). The increase in  $f_{Hmax}$  was modelled from 5-17°C as  $f_{Hmax}$  stopped increasing above 17°C in some individuals. Body mass was log-transformed and included as a covariate to account for any potential negative allometric scaling of  $f_H$  (Clark and Farrell 2011). Coefficients of determination ( $R^2$ ) were calculated for the each model with (conditional  $R^2$ ) and without (marginal  $R^2$ ) the random effect included using the MuMIn: Multi-Model Inference package (Barton 2015). Differences in response variables ( $f_{Hmax}$  at 5°C, peak  $f_{Hmax}$ ,  $\Delta f_{Hmax}$ ,  $T_{Q10<1.5}$ ,  $T_{peak}$ , and  $T_{arr}$ ) between the two acclimation treatments were assessed with an analysis of covariance which included  $\log_{10}(\text{body mass})$  as a covariate. If there was limited evidence ( $p>0.05$ ) for an effect of body mass a Student's t-test was performed to assess the treatment effect with a one-tailed specific to our directional, *a priori* predictions for each metric (see Introduction). Assumptions of normality and homogeneity of variance were verified using Shapiro-Wilk and Levene tests respectively. We used a Fisher's exact test to assess if there was a difference in the prevalence of severe AV block type arrhythmias (Fig. S2) between the treatment and control groups. Data are presented as mean  $\pm$  SEM unless otherwise noted.

## Results

### *Migration duration and river temperatures*

Of the 19 Arctic char implanted with acoustic tags, 14 were detected upriver after completing their migration. Their migration duration was  $7.1 \pm 2.9$  d ( $\pm$  SD; range: 3-13 d). In 2017, the maximum, minimum and mean ( $\pm$  SD) temperatures during the migration period in the lower reaches of the river at Halokvik were  $16.0^{\circ}\text{C}$ ,  $6.6^{\circ}\text{C}$ , and  $10.8 \pm 2.3^{\circ}\text{C}$  with a maximum three-day average of  $14.1 \pm 1.1^{\circ}\text{C}$  (Fig.1). In August 2013, during related research (Harris et al. 2020a), the maximum, minimum and mean ( $\pm$  SD) temperatures were  $21.2$ ,  $-0.8$ , and  $7.3 \pm 5.3^{\circ}\text{C}$  with a maximum three-day mean of  $17.1 \pm 2.3^{\circ}\text{C}$  (Fig.1).

### *The response of maximum heart rate to acute warming*

The  $f_{\text{Hmax}}$  increased with acute warming in all individuals (Fig 2a). As predicted,  $f_{\text{Hmax}}$  was reset to a lower rate in warm-acclimated fish (an overall decrease of 8%; Fig. 2a; Table S1;  $t_{22} = -2.459$ ,  $p\text{-value} = 0.023$ ) over the intermediate temperatures (from 5 to  $17^{\circ}\text{C}$ ). For example, at the start of acute warming,  $f_{\text{Hmax}}$  at  $5^{\circ}\text{C}$  was 9% lower with warm acclimation compared with controls ( $34.7 \pm 1.3$  vs.  $38.2 \pm 0.6$  beats  $\text{min}^{-1}$ ,  $t_{22} = 2.80$ ,  $p = 0.005$ ; Fig 3a).

Cardiac heat tolerance and the ability to increase  $f_{\text{Hmax}}$  during acute warming were also improved following warm acclimation. As expected, the incremental  $Q_{10}$  declined during acute warming in all individuals (Fig 2b, Table S1). However, the decrease with temperature was less pronounced with warm acclimation (Table S1;  $t_{22} = 3.343$ ,  $p\text{-value} = 0.003$ ). Consequently, warm-acclimated fish had a greater overall  $Q_{10}$  from  $5\text{--}15^{\circ}\text{C}$  ( $2.27 \pm 0.04$  vs.  $2.16 \pm 0.03$ ,  $t_{22} = -2.01$ ,  $p\text{-value} = 0.029$ ) and  $T_{Q_{10} < 1.5}$  ( $+1.7^{\circ}\text{C}$ ,  $F_{1,22} = 5.027$ ,  $p = 0.036$ ; Fig. 3b). Peak  $f_{\text{Hmax}}$  did not significantly increase ( $+3\%$ ,  $t_{21} = -1.036$ ,  $p = 0.156$ ) after warm acclimation and we found only weak evidence of an increase in  $T_{\text{peak}}$  ( $+1.2^{\circ}\text{C}$ ,  $t_{22} = -1.527$ ,  $p = 0.071$ ; Fig 3a and b). However, as expected the total  $\Delta f_{\text{Hmax}}$  achieved during acute warming and the  $T_{\text{arr}}$  were significantly greater ( $\Delta f_{\text{Hmax}}$ :  $+10\%$   $f_{1,22} = 4.780$ ,  $p = 0.040$ ;  $T_{\text{arr}}$ :  $+1.3^{\circ}\text{C}$ ,  $t_{22} = -2.18$ ,  $p = 0.015$ ; Fig 3a and b). Notably, we found weak evidence that AV block may be less prevalent (Fisher's exact test;  $p = 0.086$ ) in warm acclimated (1 of 8; One fish was excluded because of an ambiguous p-wave prior to the onset of arrhythmia) relative to control Arctic char (8 of 15).



## Discussion

Over the summer alone, anadromous Arctic char in the Kitikmeot region of Nunavut can experience a drastic range of temperatures from  $-1$  to  $>21^{\circ}\text{C}$  (Fig. 1 of the present study; Gilbert 2020; Gilbert et al. 2016; Harris et al. 2020a; Harris et al. 2020b). Furthermore, we demonstrated that peak temperatures encountered by Arctic char during their physically demanding upriver migration can reach  $21^{\circ}\text{C}$  with sustained temperatures (3-day average) as high as  $\sim 17^{\circ}\text{C}$ , while the migration can take  $>7\text{d}$ . Thus, our acclimation duration ( $\sim 3\text{d}$ ) and temperatures ( $\sim 13^{\circ}\text{C}$ ) are not only ecologically relevant but a conservative rather than extreme scenario, and rapid thermal plasticity could help mitigate such thermal challenges. Indeed, after just 3 days of warm acclimation, wild, migrating Arctic char in the present study exhibited significant thermal compensation of  $f_{\text{Hmax}}$  cardiac thermal sensitivity, and an improvement in cardiac heat tolerance.

During prolonged (weeks) warm exposure, many fishes, including Arctic char and other salmonids, decrease  $f_{\text{Hmax}}$  at a given temperature to counteract the effect of warming. For instance,  $f_{\text{Hmax}}$  was 12% lower at  $12^{\circ}\text{C}$  in Atlantic salmon (*Salmo salar*) acclimated to  $20^{\circ}\text{C}$  rather than  $12^{\circ}\text{C}$  for three months (Anttila et al. 2014). Likewise,  $f_{\text{Hmax}}$  when measured at  $6^{\circ}\text{C}$  was 19% lower in hatchery-reared Arctic char acclimated for  $>6$  weeks to  $14^{\circ}\text{C}$  compared to those acclimated to  $6^{\circ}\text{C}$  (Gilbert and Farrell 2021). Thus, our observation of an  $\sim 8\%$  reduction in  $f_{\text{Hmax}}$  over intermediate temperatures ( $5$ - $17^{\circ}\text{C}$ ) following just a 3 day warm acclimation period suggests that this cardiac thermal compensation begins rather quickly when wild Arctic char encounter warm temperatures. Congruently, Gilbert et al. (2022) recently showed that roughly half of the total thermal compensation of  $f_{\text{Hmax}}$  ( $\sim 8\%$ ) in laboratory reared rainbow trout acutely transferred from  $10$  to  $18^{\circ}\text{C}$ , occurred within the first 3 days; further compensation then occurred more gradually over the following 25d ( $\sim 17\%$  total over 28d). In other fishes, the thermal compensation of the pacemaker rate during warm acclimation is thought, in large part, to be achieved through a reduction in the delayed rectifier  $\text{K}^{+}$  current ( $\text{I}_{\text{Kr}}$ ), which reduces  $f_{\text{H}}$  by lengthening the pacemaker action potential duration (Haverinen and Vornanen 2007; Vornanen 2016). A reduction in  $\text{I}_{\text{Kr}}$  could also account for the resetting of  $f_{\text{Hmax}}$  seen here. Consequently, the time course for warm acclimation of  $\text{I}_{\text{Kr}}$  and its association with  $f_{\text{Hmax}}$  warrants further investigation.



Our findings for a field study with wild Arctic char are generally consistent with the rapid increase in peak  $f_{Hmax}$  and  $\Delta f_{Hmax}$  seen in rainbow trout (+15 and 28% respectively) within 24 h of transfer from 10 to 18°C (Gilbert et al. (2022)). Arctic char, however, did not increase peak  $f_{Hmax}$  with warm acclimation, but the combined reduction of  $f_{Hmax}$  (i.e., compensation) and maintenance or slight improvement in peak  $f_{Hmax}$  meant that the total  $\Delta f_{Hmax}$  was improved by 10%. This increase in  $\Delta f_{Hmax}$  stems from maintaining acute thermal sensitivity (i.e., delaying cardiac failure) after warm acclimation, as indicated by the elevations in incremental  $Q_{10}$  and  $T_{Q10<1.5}$ . Indeed, much longer warm acclimation periods for lab-reared Arctic char, rainbow trout, chinook salmon (*O. tshawytscha*) and Atlantic salmon (Anttila et al. 2014; Gilbert et al. 2022; Gilbert and Farrell 2021; Muñoz et al. 2014) have produced similar changes. All the same, the 10% improvement in  $\Delta f_{Hmax}$  after 3 days of warm acclimation found here is modest compared with the 45% change seen for hatchery-reared Arctic char after a longer acclimation period from 6°C to 14°C (+45%; Gilbert and Farrell 2021). As such, wild migrating Arctic char may show further cardiac plasticity warm acclimation if the migration exposure is longer.

Cardiac heat tolerance of Arctic char can also markedly improve with warm acclimation. With prolonged acclimation, hatchery-reared Arctic char (from an anadromous source population only ~75km from our study site) can progressively increase  $T_{arr}$  and  $T_{peak}$  with acclimation temperatures from 2 to 14°C (Gilbert and Farrell 2021). Specifically,  $T_{arr}$  and  $T_{peak}$  increased by ~4 and 6°C following a >6 week acclimation to 14°C when compared to a 6°C acclimation temperature. With,  $T_{arr}$  increased by 1.3°C after just 3 days of warm exposure such acclimatory changes can certainly occur rapidly but may require longer to reach their full extent. Such a rapid initiation of warm acclimation agrees with a previous study on sheepshead minnows (*Cyprinodon variegatus*), in which ~50% of the total observed increase (~6.3°C) in whole-animal thermal tolerance occurred within 48-72h following a transfer from 11 to 18°C (Fangue et al. 2014).

Mechanisms of prolonged cardiac thermal acclimation have received significant attention (Keen et al. 2017; Klaiman et al. 2011; Vornanen 2016), but further research is needed to resolve the extent to which they contribute to the rapid plasticity in cardiac heat tolerance seen here. Heat induced bradycardia and subsequent severe arrhythmias can be, at least in part, attributed to a mismatch in excitability among cardiac tissues (i.e. a source-sink mismatch) at high temperatures (Vornanen 2016; Vornanen 2020). Changes in the underlying ion currents (namely

Na<sup>+</sup> and K<sup>+</sup>) are thus an important aspect of cardiac thermal acclimation but the time course for such changes is not well established (Sutcliffe et al. 2020b). A change in  $\beta$ -adrenergic receptor sensitivity or density, could have also been a factor.  $\beta$ -adrenergic stimulation can facilitate cardiac heat tolerance,  $\beta$ -adrenergic control can change with warm acclimation (Aho and Vornanen 2001; Eliason et al. 2011; Gilbert et al. 2019), and we pharmacologically activated  $\beta$ -adrenergic receptors in the present study. While these types of acclimatory processes were likely at play here, given the short time frame of our acclimation, short term heat stress responses may have also contributed to improving heat tolerance. Indeed, both wild-migrating and lab-reared Arctic char induce a rapid and pronounced heat shock response (e.g. induction of heat shock proteins) (Gilbert 2015; Quinn et al. 2011) at sub-lethal temperatures, which could help stabilize cardiac function at higher temperatures. By improving or stabilizing ventricular excitability at high temperatures any of these mechanisms could also account for a reduction in the prevalence of AV block type arrhythmias (Vornanen 2016), which we found weak evidence for in warm-acclimated Arctic char.

### *Conclusions*

We show for the first time that wild Arctic char, despite being considered a cold-water specialist, can rapidly adjust their cardiac thermal performance during warm acclimation, well within a timeframe that could help them cope with thermal challenges during migration. While these changes were modest relative to those possible with prolonged warm acclimation, any improvement in performance at warm temperatures could improve to the proportion of fish able to complete their essential upriver migration to spawn and overwinter. Such rapid plasticity could also be important for other fishes such as Pacific salmon (*Oncorhynchus* spp.) which also encounter temperatures that constrain their cardiorespiratory performance during their upriver migrations to their spawning areas (Eliason et al. 2011; Farrell 2016). Thus, together with past research on thermal acclimation rates in fishes (Ekström et al. 2016; Fanguie et al. 2014; Gilbert et al. 2022), we emphasize the need to consider relevant time-courses for natural thermal variation when investigating the conservation or ecological implications of thermal acclimation. Here, we considered a natural time-course for acclimation but if cold-water refugia are available, migrating Arctic char, like other salmonids, may behaviorally thermoregulate (Ebersole et al. 2003; but see Barrett and Armstrong 2022). Such regulation could blunt the

stimulus for warm acclimation. Thus, further research should examine how cardiac thermal plasticity manifests in fish migrating through thermally heterogeneous environments, and how acclimation rates and associated mechanisms are influenced by temperature parameters, fish health, life-history stage, population, and species. Our remote field study (>1500km away from the nearest aquatics facilities without road access), would not have been possible without innovative mobile Arctic research infrastructure, illustrating that investing in the development and deployment of such infrastructure can greatly expand basic and applied research possibilities in the north.

### Acknowledgements

Quana (thank you) to Beverly and Rose Maksagak, and the Ekaluktutiak Hunters & Trappers Organization for their help in facilitating this research. This research was funded by Polar Knowledge Canada through the Science and Technology Program (JSM) and the Northern Scientific Training Program (MJHG), the Natural Sciences and Engineering Research Council (NSERC) through Discovery (APF and BSR) and Canada Research Chair grants (APF), the Weston Foundation through the Weston Family Fellowship in Northern Research (MJHG), and EarthRangers through a research grant (MJHG). Extensive in-kind support and equipment was provided by the Arctic Research Foundation and Fisheries and Oceans Canada.

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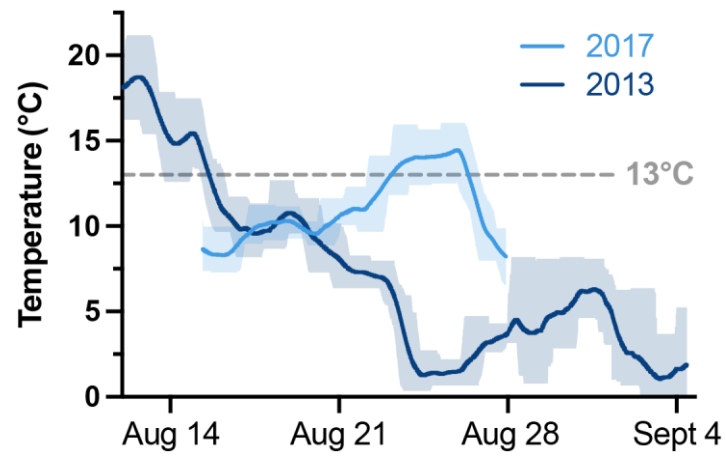
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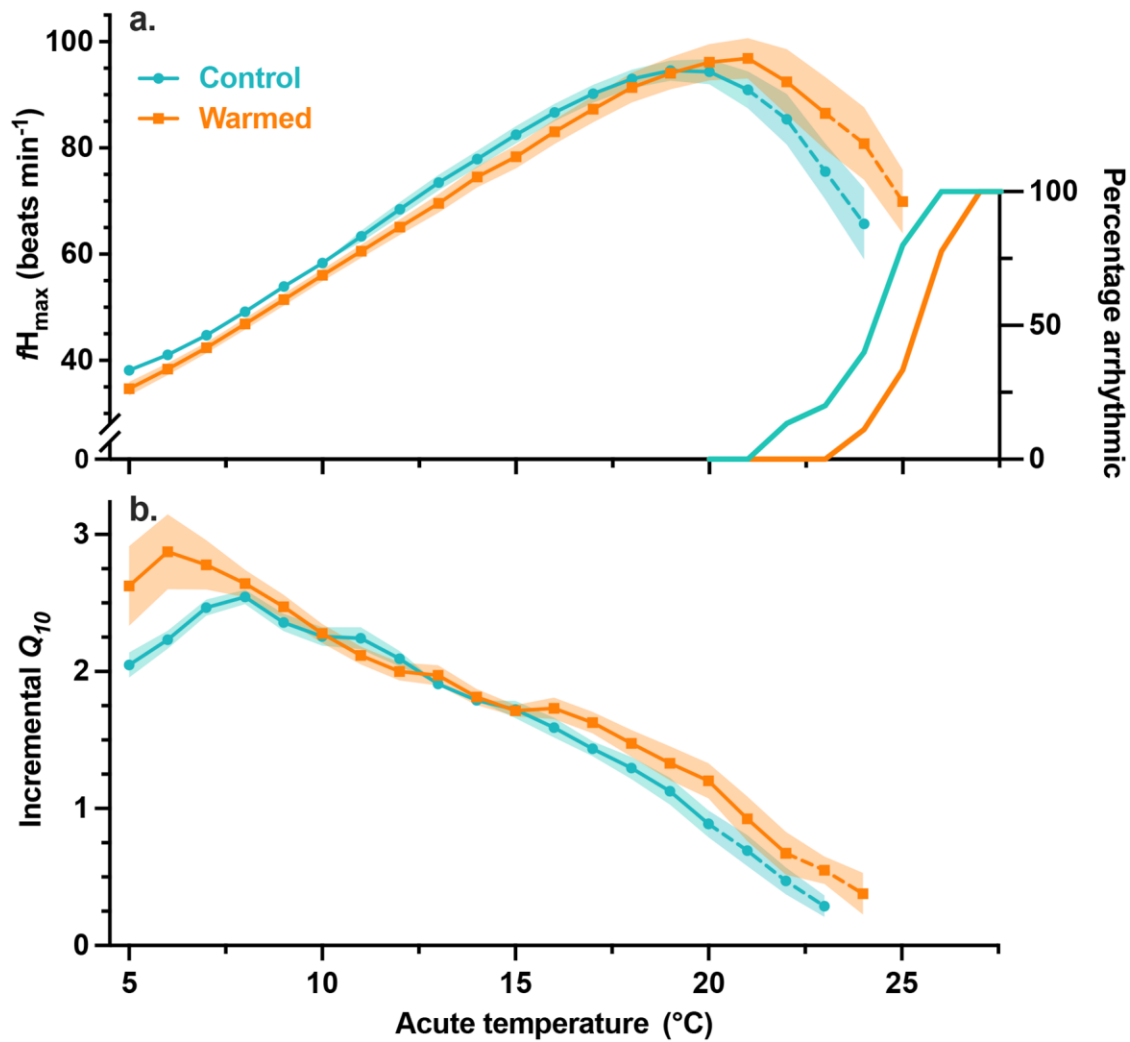
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## Figures

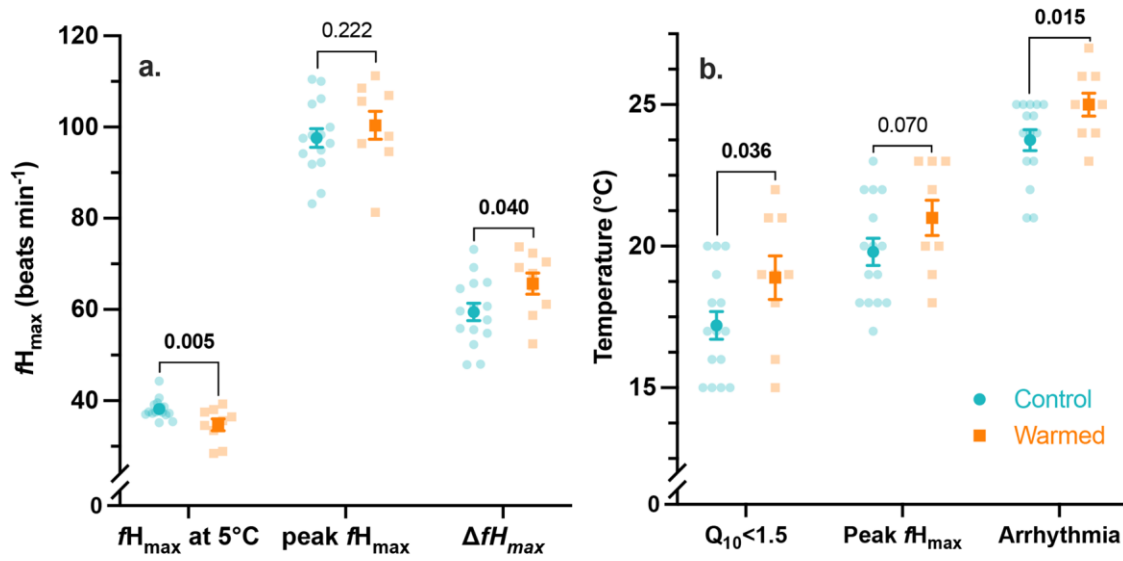


**Fig. 1.** River temperatures at Halokvik, Nunavut, during research on the upriver Arctic char migration in 2013 and 2017. Data are presented as the daily mean (solid line), minimum and maximum (upper and lower semi-transparent bounds).

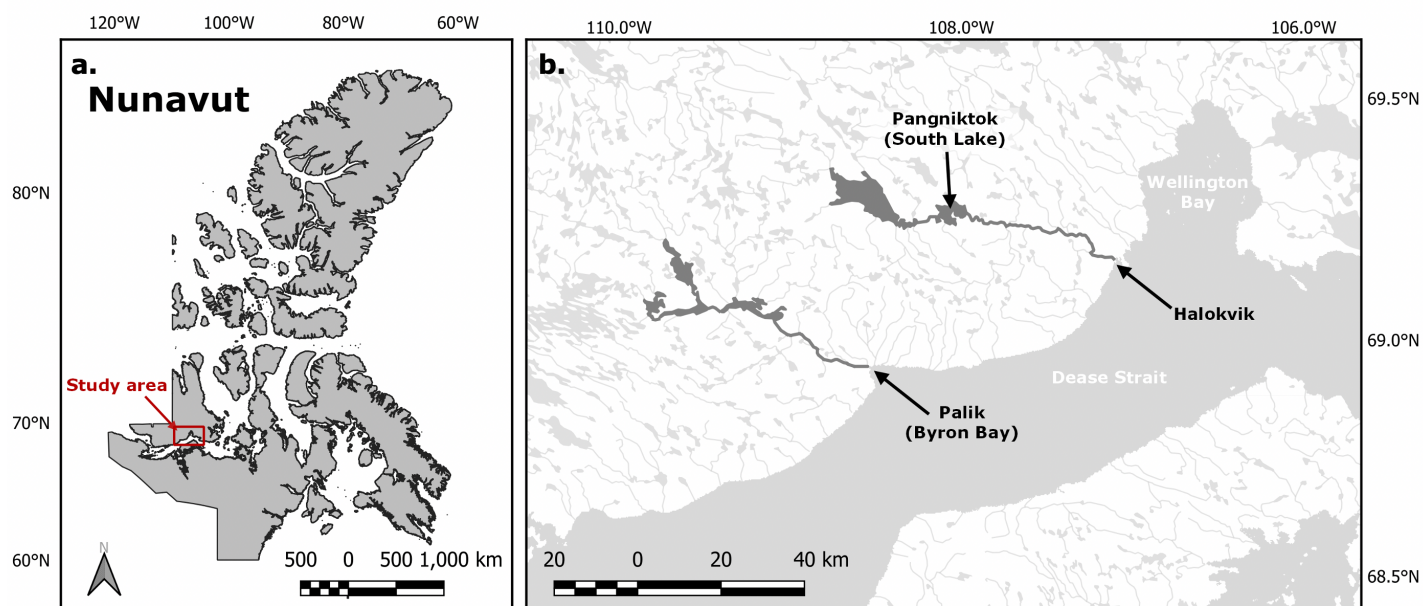




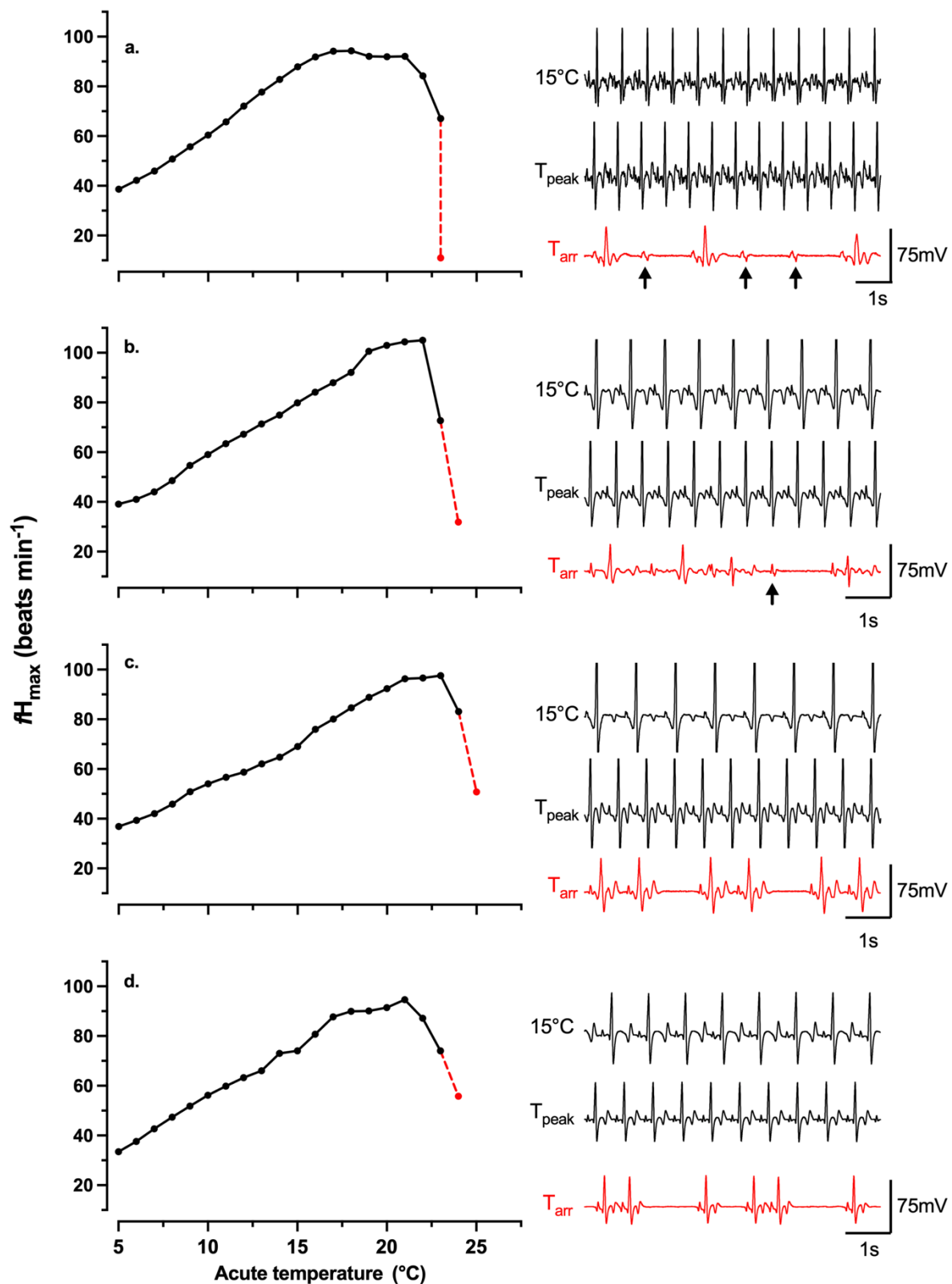
**Fig. 2.** The response of maximum heart rate ( $f_{H_{max}}$ ) to acute warming in wild adult Arctic char with (orange; square;  $n=9$ ) and without (teal; circle;  $n=15$ ) a three-day warm exposure ( $\sim 13^{\circ}\text{C}$ ). The mean ( $\pm$  SEM)  $f_{H_{max}}$  (a) and corresponding incremental  $Q_{10}$  (b) are shown during acute warming with dashed lines indicating temperatures at which individuals were excluded after exhibiting cardiac arrhythmias (proportion of individuals on right y-axis). Model statistics are presented in Table S1. The inset in panel a. shows the progressive increase in the percentage of individual fish showing a cardiac arrhythmia at a supra-optimal temperature.



**Fig. 3.** The effect of a 3day warm acclimation on maximum heart rates ( $f_{H_{max}}$ ; a) and transitional temperatures for  $f_{H_{max}}$  (b) during acute warming. Mean ( $\pm$  SEM) and individual values (semi-transparent) are shown for (a)  $f_{H_{max}}$  at  $5^{\circ}\text{C}$ , the peak  $f_{H_{max}}$ , the difference between the two ( $\Delta f_{H_{max}}$ ), and (b) the temperatures at which incremental  $Q_{10}$  fell below 1.5 ( $T_{Q_{10} < 1.5}$ ), peak  $f_{H_{max}}$  occurred ( $T_{\text{peak}}$ ), and the heart became arrhythmic ( $T_{\text{arr}}$ ). P-values for the effect of warm acclimation (t-test) are presented above each metric with significant differences in bold.



**Fig. S1.** The study area (red box in a, and enlarged in b) in the Kitikmeot Region of Nunavut, Canada. The acoustic telemetry work characterized the migration duration between Halokvik and Pangniktok (b). The cardiac thermal acclimation experiment was performed using a mobile laboratory at Palik.



**Fig. S2.** The response of maximum heart rate ( $f_{Hmax}$ ) to acute warming and representative heat induced changes in the electrocardiograms of four individual Arctic char (a-d). The  $f_{Hmax}$  during warming are shown (black points) with the  $f_{Hmax}$  at the onset of the cardiac arrhythmia indicated by a red point and the drop from the last rhythmic  $f_{Hmax}$  measurement with a dashed red line. Corresponding electrocardiogram traces are shown at 15  $^{\circ}C$  and the temperatures at peak  $f_{Hmax}$  ( $T_{peak}$ ) and arrhythmia ( $T_{arr}$ ). Arrows mark unambiguous P-waves with no QRS complex, which indicates a severe AV-block (a and b).

**Table S1.** Linear mixed effect model statistics for the change in maximum heart rate ( $f_{Hmax}$ ) and incremental  $Q_{10}$  for  $f_{Hmax}$  during acute warming in control and warm acclimated (treatment) wild Arctic char. The  $f_{Hmax}$  was modelled from 5-17°C and  $Q_{10}$  from 5-25°C. Fish ID was included as a random effect.

	Coefficient	SE	Df	t	p
$f_{Hmax}$ (beats min <sup>-1</sup> )					
Intercept	75.737	32.973	1, 21	2.297	0.032
Acute temp. (°C)	4.511	0.033	1, 287	135.077	<0.001
Warm acclimation	-4.908	1.996	1, 21	-2.459	0.023
Log <sub>10</sub> (mass)	-17.421	9.310	1, 21	-1.871	0.075
<i>marginal R<sup>2</sup> = 0.93, conditional R<sup>2</sup> = 0.98</i>					
$Q_{10}$ for $f_{Hmax}$					
Intercept	3.482	0.050	1, 225	69.461	<0.001
Acute temp. (°C)	-0.127	0.003	1, 414	-42.067	<0.001
Warm acclimation	0.138	0.042	1, 22	3.343	0.003
<i>marginal R<sup>2</sup> = 0.80, conditional R<sup>2</sup> = 0.81</i>					