
Upper Thermal Tolerance Indicated by CT_{max} Fails to Predict Migration Strategy and Timing, Growth, and Predation Vulnerability in Juvenile Brown Trout (*Salmo trutta*)

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ABSTRACT

Partial migration is common in a variety of taxa and has important ecological and evolutionary implications, yet the underlying factors that lead to different migratory strategies are not clearly understood. Given the importance of temperature in serving as a cue for migration, along with its role in regulating metabolism, growth, reproduction, and survival, we examined how intraspecific variation in critical thermal maximum (CT_{max}) values influenced migratory strategy (residency vs. migration), timing of migration, growth, and predation vulnerability in a wild population of partially anadromous juvenile brown trout (*Salmo trutta*). Using passive integrated transponder telemetry and mark-recapture techniques, we identified individuals that out-migrated to sea, assumed residency, and were predated by cormorants several months later. Acute thermal stress induced by conducting CT_{max} trials did not affect the final fate of assayed fish compared with controls. We found that mass and body condition predicted CT_{max} and migration timing, but CT_{max} failed to predict migratory strategy or timing, growth (of resident fish), or predation vulnerability. Although there may be links between mass, thermal tolerance, and migration strategy, the relationship between CT_{max} and migration remains unclear. The role of upper thermal tolerance in influencing life-history strategies should not be neglected, however, as alternative indicators of thermal tolerance could be further explored. The high degree of variation in CT_{max}

estimates warrants additional investigation of how increasingly prevalent high-temperature events might drive selection toward thermally tolerant extremes, which is particularly relevant in a rapidly warming world.

Keywords: *Salmo trutta*, brown trout, critical thermal maximum (CT_{max}), intraspecific upper thermal tolerance, partial migration, resident, migrant.

Introduction

Over the past century, temperature has been identified as one of the most influential factors involved in regulating growth, survival, metabolism, and reproduction in ectotherms (e.g., Fry 1971). As such, there has been much interest in determining optimal temperatures that enhance fitness in addition to identifying critical thermal limits where performance is impacted (sometimes to the extent where fitness is zero). The critical thermal maximum (CT_{max}) was originally defined by Cowles and Bogert (1944, p. 277) for ectotherms as “the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death.” Although this definition gave rise to much variation among protocols over time, CT_{max} typically involves acute thermal ramping from acclimation temperatures to an endpoint where either loss of equilibrium (LOE) or the onset of muscle spasms is reached. The relative simplicity of this experimental design has led to a wealth of publications where CT_{max} is applied in the context of environmental science to identify regulatory guidelines for thermal pollution originating from anthropogenic sources (Lutterschmidt and Hutchison 1997).

However, there has been a shift in the applications of CT_{max} in the literature over the past few decades as researchers recognize the need to predict individual-, population-, and species-level responses to climate change (e.g., Deutsch et al. 2008; Sandblom et al. 2016; Comte and Olden 2017). Several studies have demonstrated range shifts in response to increases in temperature, indicating the importance of temperature in species distribution (Thomas et al. 2001; Brander et al. 2003; Parmesan and Yohe 2003; A. L. Perry et al. 2005; Sunday et al. 2012, 2019; Pinsky et al. 2019). CT_{max} , among other methods, has been used to infer thermal tolerance in relation to changes in behavior and distribution induced by a warming environment in a variety of ectotherms (e.g., Sandblom et al. 2016; Comte and Olden 2017)

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and may therefore serve as a tool to identify variation in thermal tolerance within populations.

As novel applications of CT_{max} estimates emerge in recent literature, a number of studies have identified concerns regarding the ecological relevance of such metrics, specifically with regard to variations in protocols, rapid rates of experimental temperature increase that rarely reflect natural conditions, and failure of physiological systems, such as the heart, before LOE occurs (Becker and Genoway 1979; Lutterschmidt and Hutchison 1997; Clark et al. 2008; Bates and Morley 2020). Despite these concerns, several recent publications present evidence that validates the use of carefully considered CT_{max} protocols in an ecological context. In particular, CT_{max} has been found to be repeatable within individuals over both short (weeks; Morgan et al. 2018; Grinder et al. 2020) and long (months; O'Donnell et al. 2020) periods of time. The positive correlation between repeatability and heritability suggests that upper thermal tolerance is a heritable trait, as many studies have previously shown (e.g., G. M. Perry et al. 2005; Anttila et al. 2013; Muñoz et al. 2014, 2015; Morgan et al. 2018), with the potential to drive selection under particular conditions. Additionally, Åsheim et al. (2020) recently demonstrated that thermal tolerance to rapid warming rates positively correlates with thermal tolerance evaluated under a more natural, slow warming rate, implying that CT_{max} values derived using rapid temperature increases provide an ecologically relevant proxy for upper thermal tolerance. Moreover, the behavioral response to critical temperatures (LOE or onset of muscle spasms) has been found to be consistent throughout a diversity of taxa, suggesting that it is a highly conserved trait (Lutterschmidt and Hutchison 1997). The long history of CT_{max} , along with recent attempts to validate its use in ecology, warrants further applications to continue making advances in the field of thermal biology.

Despite the abundance of CT_{max} applications, there has been very little focus on how intraspecific variation in upper thermal tolerance estimates contribute to the fitness of individual animals. Understanding how variation in CT_{max} among individuals contributes to variation in fitness will enable us to predict whether animals are capable of rapid adaptation in response to thermal stress while simultaneously providing insights into the underlying factors that lead to differences in life-history strategies.

Here, we used CT_{max} as a proxy for relative upper thermal tolerance in 294 brown trout (*Salmo trutta*), following an adapted version of the protocol described in Morgan et al. (2018), to assess the role of upper thermal tolerance in promoting the fitness of individual fish. We tested whether differences in CT_{max} would lead to differences in migration strategy or timing given that stream temperatures are typically warmer than ocean temperatures, and thus individuals with lower CT_{max} may be driven to migrate to stay within optimal thermal limits. Although stream temperatures in our study system rarely exceed CT_{max} estimates for brown trout provided in the literature, the fast warming rates correlate with ecologically relevant slow warming rates (Åsheim et al. 2020). Thus, CT_{max} is a sufficiently sensitive measure to infer differences in thermal stress below sublethal temperatures. Once these estimates were obtained, we used passive integrated tran-

sponders (PITs) to determine the timing of out-migration toward the sea. After the migration period, mark-recapture techniques were used to resample the instream population to assess the proportion of individuals that assumed residency in the natal stream. A control treatment with temperatures kept at ambient levels was used to assess whether acute thermal shock influenced migration, survival, and growth.

Brown trout are freshwater salmonids native to various regions of Europe that display partial migration; they can either reside within their natal streams or migrate out to sea. Partial migration is a fascinating phenomenon that represents extreme trade-offs (Chapman et al. 2011a). Migration is energetically costly and associated with high mortality due to predation, but migrants can exploit a wider range of resources, often leading to similar or better lifetime fitness than residents as a result of increased size and thus increased reproductive output (Gross 1987; Jonsson and Jonsson 1993; Chapman et al. 2011a). While it is considered one of the most common types of migratory strategy in a variety of taxa, partial migration has critical evolutionary and ecological consequences (Jonsson and Jonsson 1993; Nilsson et al. 2008; Grayson and Wilbur 2009; Hebblewhite and Merrill 2009; Chapman et al. 2011b). Despite this importance, the factors underpinning the decision to migrate or assume residency remain unclear. The decision is thought to be linked to both genetics and environmental factors (Ferguson et al. 2019; Lemopoulos et al. 2019), suggesting that temperature and genetic traits that underlie the mechanisms for coping with thermal stressors may impact these decisions. Moreover, individual condition, gill Na/K-ATPase activity, and energetic status have also been shown to play roles in the decision and timing of migration (Aarestrup et al. 2000; Nielsen et al. 2004, 2006; Wysujack et al. 2009; Boel et al. 2014; Peiman et al. 2017). Given the documented importance of temperature in regulating migration timing and success in salmonids (e.g., Jonsson 1991; Aarestrup et al. 2002; Sloat and Reeves 2014), we tested the hypothesis that individual CT_{max} would predict the decision to either migrate or assume residency and also be linked to the timing of migration, survival, and growth.

Phenotypic variation has been shown to account for variation in migration timing in wild sea-run brown trout (Bohlin et al. 1996), although mechanisms underlying these differences are still poorly understood. Temperature is a key environmental factor that is known to modulate physiological functions, such as growth, metabolism, reproductive success, and migration (Ficke et al. 2007; Jonsson and Jonsson 2009; Sloat and Reeves 2014). Factors that affect physiological functions (both directly and indirectly), such as food availability, temperature, and increased discharge, may affect the decision to migrate or assume residency (Aarestrup et al. 2002; Archer et al. 2020). For example, high temperatures may lead to higher metabolic rates such that fish require more food to sustain adequate growth rates and meet higher metabolic demands. If there is insufficient food available to sustain these demands, fish could have lower body condition and may migrate to sea in search of additional resources (Armstrong et al. 2010). The interactions between temperature, food availability, metabolism, and condition

have been shown to influence the decision to migrate or assume residency (Økland et al. 1993; Boel et al. 2014; Sloat and Reeves 2014).

Although there may be an interplay between temperature, metabolism, and food availability, our focus here was to understand whether individual differences in CT_{max} can predict migration strategy and timing given that warmer stream temperatures may induce stress in fish with lower CT_{max}. There is already evidence demonstrating intraspecific differences in thermal tolerance in different populations of salmonids that undergo migrations of variable difficulty (Eliason et al. 2011). Thus, thermal tolerance may be linked to various aspects of migration; it may drive migration in individuals with lower thermal tolerance if stream temperatures rise above optimal temperatures. By using CT_{max} as a relative measure of upper thermal tolerance, we explored the role of upper thermal tolerance in mediating life-history strategies. In turn, this can highlight the importance of phenotypic variation in the distribution of animals in a progressively warming climate.

Material and Methods

Study Site

Wild brown trout were obtained from Gudsø stream, which is located in the southern region of Jutland, Denmark (fig. 1). The stream is home to an abundant population of partially migrant brown trout (Birnie-Gauvin et al. 2017; Peiman et al. 2017). The stream flows for 6 km and is 1–4 m wide, allowing

for efficient mark-recapture electrofishing. The Gudsø stream reaches Kolding Fjord, which exits into the southern end of the Kattegat Sea. Two PIT stations are located roughly 500 and 600 m from the outlet of the stream. Migrant brown trout in this population often spend between 0.5 and 2 yr in freshwater, after which they migrate to sea, where they typically spend 1–2 yr (Birnie-Gauvin and Aarestrup 2019). Although this population is home to migrants and residents, the majority consists of migratory individuals (10:1 ratio), as is the trend for most brown trout populations with access to sea (e.g., Jonsson 1985; Midwood et al. 2015; Birnie-Gauvin et al. 2017). Over the past two decades or so, summer temperatures ranged from 9.7° to 19.5°C, averaging around 13.8°C. Although brown trout are known to tolerate these temperatures quite well (Forseth et al. 2009), individual variation in thermal tolerance may result in some conspecifics being more sensitive to fluctuations in temperatures and may account for differences in behavior, condition, and migratory phenotypes.

Capturing, Measuring, and Tagging

From February 11–15, 2020, a total of 614 brown trout ranging from 11.0 to 22.7 cm were captured from a stretch of the stream approximately 1 km upstream of the PIT stations (fig. 1) using single-pass electrofishing gear (Scubla ELT60 II G, running at 300 V). The use of electrofishing as a method to collect wild trout for this study was justified by a previous study that found that electrical shocks did not have an effect on CT_{max} results (Carline

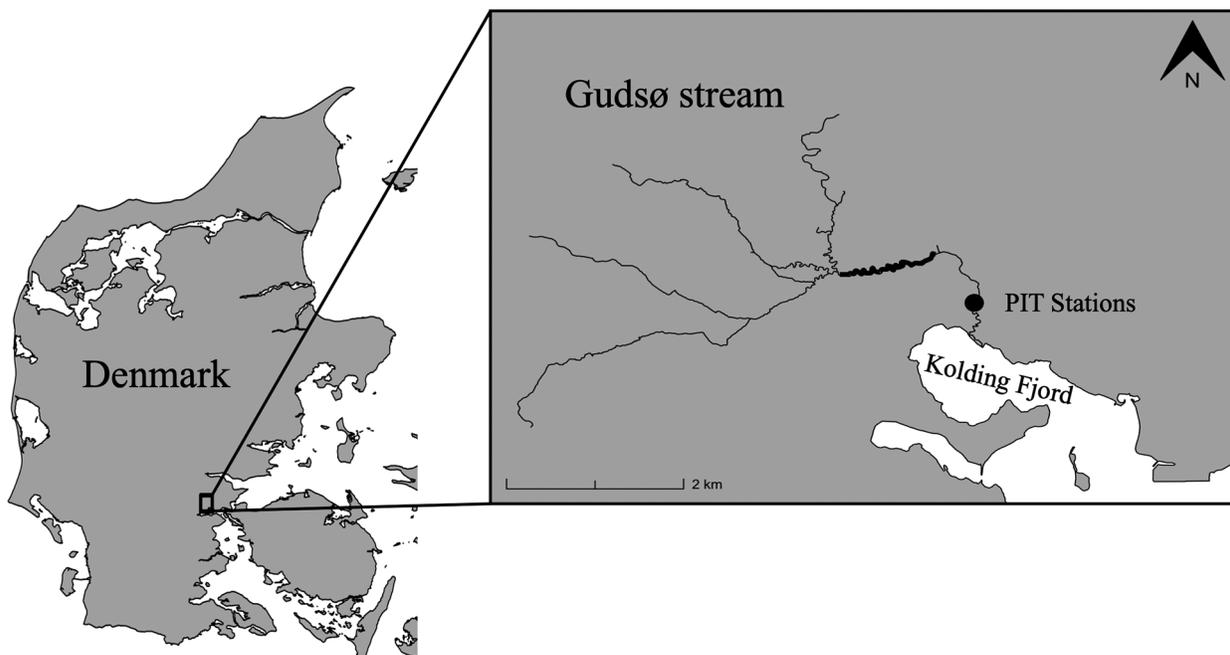


Figure 1. Location of study site, Gudsø stream, Jutland, Denmark. The dot indicates the location of the passive integrated transponder (PIT) stations. Traced lines represent areas where the stream runs and the outflow location of the stream into the Kolding Fjord. The traced bold line represents the location where fish were captured.

and Machung 2001). Fish were netted immediately and placed in a 60-L container of freshly oxygenated stream water, where water was changed frequently. Additional oxygen was provided via air stones to ensure appropriate holding conditions were met. Once fish were captured, they were anesthetized in a 0.3-g L⁻¹ benzocaine solution and measured for total length (± 1 mm) and wet mass (± 0.1 g). Fulton's condition factor (K ; eq. [1]; Ricker 1975) was calculated for each fish using total length and weight measurements:

$$\text{condition factor } (K) = \frac{\text{mass (g)}}{\text{length (cm)}^3} \times 100. \quad (1)$$

The fish were then tagged using a 23-mm PIT tag (RI-TRP-RRHP, Texas Instruments, Plano, TX; 134 Hz, 0.6 g mass in air). PIT tags have been shown to be effective tools to monitor and identify particular individuals while posing virtually no negative impact on the fish, provided that they have the appropriate body size to accommodate the tag (Gibbons and Andrews 2004). Previous studies have also shown good retention rates of PIT tags (97% in a similar species and system; Larsen et al. 2013), providing us with a good method for monitoring fish long-term.

Experimental Design

The experimental tanks consisted of two 60-L opaque containers filled with approximately 17.5 L of well-oxygenated stream water: one for a control group and one for the CT_{max} group that experienced thermal ramping. Each container was supplied with a pump to circulate water at low flow rates (EHEIM Air400 10W), air stones to keep oxygen levels >70% saturation, and a metal mesh separating the fish from the equipment. In the CT_{max} tank, two heaters (EHEIM ThermoControl 250W and EHEIM JÄGER 300W) were included and set to the highest setting to achieve a rate of temperature increase of 0.3°C min⁻¹ (18°C h⁻¹), as suggested in previous studies (see Becker and Genoway 1979; Lutterschmidt and Hutchison 1997; Morgan et al. 2018). Water temperatures were monitored using a recently factory-calibrated thermometer (Traceable 4052 long-stem thermometer S/N, 191869383, $\pm 1^\circ\text{C}$ accuracy), in addition to temperature data loggers (HOBO TidbiT v2) that were set to record temperatures every second for the duration of the trials. Oxygen was monitored using a recently calibrated handheld dissolved-oxygen meter (OxyGuard Handy Polaris).

Before each trial, the tanks were filled with fresh stream water such that the experiment began at the temperatures at which the fish were acclimated in their natural environment, which ranged from 4.5° to 5.7°C during the course of the experiments. Then 20 fish were randomly selected from the holding containers for each group (control or CT_{max}) and placed in the experimental containers, at which point the heaters in the CT_{max} container were turned on and thermal ramping began. Temperatures were kept at ambient levels in the control container. The fish were monitored from a distance to observe changes in behavior and swimming performance and the onset of muscle spasms that

lead to LOE, which we defined as the endpoint in accordance with several studies (e.g., Becker and Genoway 1979; Baroudy and Elliott 1994; Galbreath et al. 2006; O'Donnell et al. 2020). The fish were removed from the experimental container when they lost their ability to maintain dorsoventral orientation, which clearly marks LOE. Once removed from the experimental tank, the brown trout were placed in a recovery container supplied with stream water at ambient temperature. Most fish recovered and displayed normal behavior in less than 5 min, indicating that the thermal challenge did not cause significant trauma. Only five fish were unable to recover from the temperature treatment (98.41% survival). Once the fish recovered, they were released in the stream near the site of capture. Multiple trials were conducted each day until the designated sample size of approximately 300 fish per treatment was reached.

Critical Thermal Maximum

CT_{max} was used to quantify relative differences in thermal tolerances among 294 individual brown trout exposed to thermal ramping rates of approximately 18°C h⁻¹ (average: 0.32° \pm 0.02°C min⁻¹) in accordance with previous studies (Becker and Genoway 1979; Lutterschmidt and Hutchison 1997; Morgan et al. 2018). Fluctuations in air and river temperatures both before and during the experimental trials resulted in slight deviations from the desired rate of thermal ramping (0.3°C min⁻¹). This caveat is addressed by accounting for the time exposed to temperatures above acclimation while reporting CT_{max} values. Although maximum water temperature in which fish experience LOE is most frequently used as an endpoint for CT_{max} values (Lutterschmidt and Hutchison 1997; Morgan et al. 2018), a recent study found that using cumulative degree minutes (CDM) provided a more accurate measure, since fish with different start temperatures may experience these changes at relatively similar temperatures but quite some time apart (O'Donnell et al. 2020). Incorporating time to LOE also accounts for imperfect heating rates within experimental trials due to mechanical or electrical malfunctions (Galbreath et al. 2004; O'Donnell et al. 2020). For the purposes of this study, it is more appropriate to use CDM rather than temperature readings, since fish were acclimated to stream temperatures immediately before conducting CT_{max} trials. Stream temperatures varied temporally with each trial (by a maximum of 0.7°C), as water temperature is highly correlated with air temperature. Fish in trials with lower starting temperatures will experience higher temperatures for a longer period of time before reaching LOE and potentially be subjected to a higher degree of thermal stress. Additionally, Galbreath et al. (2004) state that mortality due to thermal stress is an additive process, meaning that the time involved in coping with higher-than-usual temperatures should be accounted for while measuring relative tolerance between fish within an experiment (Kilgour and McCauley 1986; Galbreath et al. 2004). In this case, using CDM as a proxy for CT_{max} provides a more sensitive measure than raw temperature (°C) for comparing thermal tolerance between individual fish across multiple trials.

Migration

Two PIT stations were set to continuously detect the passage of tagged fish as they migrated from the stream to the fjord. The two PIT stations were approximately 100 m apart, with each station consisting of two full-stream-covering antennas spaced 5 m apart. The efficiency of the upstream PIT station was estimated to be approximately 91.2% on the basis of fish that were detected at both PIT stations as well as fish that were detected only at the downstream PIT station (see Zydlewski et al. 2006). For the purpose of this study, we assume that the efficiency of the downstream PIT station is similar to the upstream one, although the specific efficiency of the downstream station cannot be calculated (Zydlewski et al. 2006). The stream was resampled on June 8, 2020, which is considered to be after the typical spring migration period for juvenile brown trout in this system. Fish that were detected at the upstream station then at the downstream station in that order were defined as migrants, while fish that were simply recaptured within the stream in June were defined as residents. For the purpose of this study, we assume that fish that passed both PIT stations—upstream station then downstream station in that order—migrated. While there is a 500-m stretch of stream between the downstream PIT station and the sea, previous samplings found no previously tagged fish in that stretch, as it is highly inhabitable for brown trout (K. Birnie-Gauvin, personal communication). Fish with no detections and that were not recaptured within the river were categorized to be of unknown strategy. Fish that were detected at only one of the PIT stations and not recaptured in the stream were also considered to be of unknown strategy, as directionality of movement could not be confirmed.

Growth

Specific growth rate (SGR; eq. [2]) was calculated for each fish that was recaptured over a 4-mo interval (i.e., all residents) from the day of capture to the day of recapture:

$$\text{SGR} = \frac{\ln(\text{final mass}) - \ln(\text{initial mass})}{\text{days after sampling}} \times 100. \quad (2)$$

Survival and Predation

Survival and predation can be inferred by PIT station detection efficiency, electrofishing recapture efficiency, and detection of PIT tags that were found at cormorant colonies near Gudsø stream. High detection efficiency (91.2%) and high recapture rates achieved in narrow streams (>90%; see Midwood et al. 2015) provide sufficient grounds to assume mortality of fish that were not recaptured or detected at PIT stations. Fish that were detected at cormorant colonies were classified as predated, regardless of their migratory strategy.

Statistical Analyses

Data were first examined for homogeneity of variance, collinearity, and outliers. Among the 614 fish that were sampled

and used in the experiments, five CT_{max} fish (0.8% of all fish) did not recover from the experiment and were thus removed from analyses. Preliminary analysis showed autocorrelation between length and mass; therefore, only mass was considered in the models. Model explanatory variables were also inspected to ensure normality. Mass was log transformed twice to meet underlying assumptions of the models.

Welch's *t*-tests were used to investigate whether there were differences in initial body mass, length, and condition across control and CT_{max} fish. ANOVAs were also used to evaluate whether body metrics and CDM differed across final status (resident, migrant, unknown fate, predated). These analyses were also performed with raw temperature values at which LOE occurred for further validation of the observed trends with CDM. A Pearson's χ^2 analysis was used to determine whether the proportion of fish with different final status differed between the control and CT_{max} trials.

CDM was used as a proxy for CT_{max}, which adjusted upper thermal tolerance indexes to include effects of different acclimation temperatures and rates of thermal ramping across trials. Linear regression models were used to evaluate whether body metrics (mass and condition factor) affected CT_{max}. The final model included both mass and initial condition factor as explanatory variables.

Generalized linear models (GLMs) were used to investigate potential relationships between CDM and life-history choices (reside or migrate and the corresponding timing of migration). We followed a step-by-step approach of model simplification from a full model that included all explanatory variables (CDM, mass, and condition) and all two-way interactions using Akaike's information criterion (AIC). We also ensured models were distinguishable from one another by comparing Δ AICs, where a difference <2 was considered to be more or less equivalent (Bolker 2008). We then proceeded to check for overdispersion based on the χ^2 approximation of residual deviance and continued with model validation to ensure that all assumptions were met.

The decision to migrate was modeled as a binomial response, where migrants were classified as successes (1) and residents as failures (0), with CDM, mass, and condition as explanatory variables. A sample size of 151 fish was used in this analysis (i.e., only CT_{max} fish with known fates). The final model included only mass as explanatory variable with log-log link function. Similarly, a GLM was used to explore whether CDM, mass, or condition affected the timing of migration. Using a Poisson distribution resulted in an overdispersion leading to the use of a negative binomial distribution with log link function in the analysis. The final model included mass and initial condition factor as explanatory variables. A bimodal distribution of out-migration timing led us to group migrants into two groups: early (0–30 d after sampling) and late (\geq 31 d after sampling). A nonparametric *t*-test was used to compare differences in initial mass of early and late migrants, which further validated the use of mass as a predictor variable in the best model. A *t*-test was used to explore differences in CT_{max} between early and late migrants.

GLMs were also used to explore whether CT_{max} was related to growth in residents (as only residents were recaptured). CT_{max} estimates and SGRs (percentage of growth per day since sampling) were available for only eight resident fish, so only one explanatory variable could be examined per model. A series of GLMs was conducted with mass, initial condition, and CDM as explanatory variables to investigate relationships with SGR. When comparing AIC values with the null model, the model including mass provided the best fit.

Finally, a series of GLMs with binomial distribution and logit link function was used to investigate whether predation by cormorants was affected by CDM, mass, and condition. Models included only one explanatory variable at a time because of low sample size ($N = 26$). The best model was the null model, suggesting that none of the included explanatory variables had an effect on predation. All statistical analyses were performed with R version 3.6.1 (R Development Core Team 2016) using lattice (Sarkar 2008), ggplot2 (Wickham 2016), and MASS (Venables and Ripley 2002) R packages.

Results

A total of 614 juvenile brown trout were initially captured, tagged, and sampled. Of those fish, 320 were exposed to control conditions, while 294 were exposed to acute thermal ramping at a rate of $0.32^\circ \pm 0.02^\circ\text{C min}^{-1}$. Upon resampling, a total of 22 brown trout ranging from 13.2 to 24.7 cm were recaptured. Given that the peak of the typical migration season occurs in the spring, we assume that these fish have assumed residency in their natal stream. PIT data confirmed a total of 288 migrants, while 304 fish were neither detected nor recaptured and were consequently labeled as unknown strategy. It is possible that fish of unknown strategy may not have been recaptured during resampling, although electrofishing in this stream is typically high (>90%; see Midwood et al. 2015; Birnie-Gauvin 2017). These fish are likely dead as a result of predation by cormorants, otters, or seals or other natural causes, such as competition or disease. High rates of mortality during the winter could also account for a large proportion of fish of unknown strategy (Midwood et al. 2015). Among the 614 fish that were tagged, 68 (11.07%) were detected in nearby cormorant colonies, of which 26 had CT_{max} measurements and 42 were control fish. Note that these 68 predated fish included fish classified as migrants, residents, and fish of unknown strategy.

Acute Thermal Shock

To assess whether migratory strategy and final fate were influenced by acute thermal stress induced by the experimental approach used to measure CT_{max} , we used a control group in which fish were exposed to similar handling conditions but lacked acute thermal ramping. A total of 145 of 288 (45%) migratory fish and 14 of 22 (64%) residents were from control treatments. The experimental approach did not affect the fate or migratory strategy of fish ($\chi^2 = 0.445$, $P > 0.05$; table 1).

Initial condition was found to be marginally higher in the CT_{max} group ($t = -2.18$, $P = 0.030$). The slightly lower

condition factor observed among fish in the control group could indicate preparation for a parr-smolt transformation in several control fish (see Boel et al. 2014), leading to higher migration propensity within the control group. However, this marginal difference in condition factor does not appear to have affected fish final status, as evidenced by similar proportions of migrants, residents, and fish of unknown strategy in both CT_{max} and control groups (table 1).

Critical Thermal Maximum

We found that mass was positively correlated to CDM ($t = 4.96$, $P < 0.001$), while initial condition was negatively correlated to CDM ($t = -2.468$, $P = 0.014$). The best model ($F_{2, 291} = 15.73$, $P < 0.0001$, $R^2 = 0.091$) included both mass ($t = 4.96$, $P < 0.001$) and initial condition ($t = -2.47$, $P = 0.014$) as explanatory variables (fig. 2).

Of the 294 fish that experienced thermal ramping, 143 (48.6%) migrated, 8 (5.6%) resided within the stream, and 143 (48.6%) were of unknown strategy. We found that 26 fish had been predated on, representing 8.8% of the treatment group. Mean CDM was similar across all groups (ANOVA, all $P > 0.05$; table 2). These results were further confirmed using raw temperature values where LOE occurred rather than CDM, although CT_{max} was found to be similar across fish with different final statuses.

Migratory Strategy

Mass was not associated with migratory strategy ($Z = -1.588$, $P > 0.05$). CDM was not included as an explanatory variable in the best model, suggesting that CT_{max} does not play a role in the decision to migrate.

Timing of Migration

We observed two peaks in the timing of migration: one occurring 0–30 d after sampling (approximately the end of

Table 1: Summary of tagged fish

Metric	Control	CT_{max}
Sample size	320	294
Mass (g)	31.50 \pm 19.20	32.86 \pm 19.68
Length (cm)	14.1 \pm 2.79	14.3 \pm 2.8
Condition (K)	1.01 \pm .08 ^A	1.02 \pm .08 ^B
Migrants (%)	45.31 (145)	48.64 (143)
Residents (%)	4.38 (14)	2.72 (8)
Unknown (%)	50.31 (161)	48.64 (143)
Predated (%)	13.13 (42)	8.84 (26)

Note. Mean initial length (cm), mass (g), and condition (K) are given for individually tagged *Salmo trutta* for each treatment group (\pm SD). The proportion of fish migrating, residing, or of unknown strategy within each group is shown as a percentage, with the number of individuals in parentheses. Superscript letters indicate significant differences between treatments. Predated fish include residents, migrants, and fish of unknown strategy. CT_{max} = critical thermal maximum.

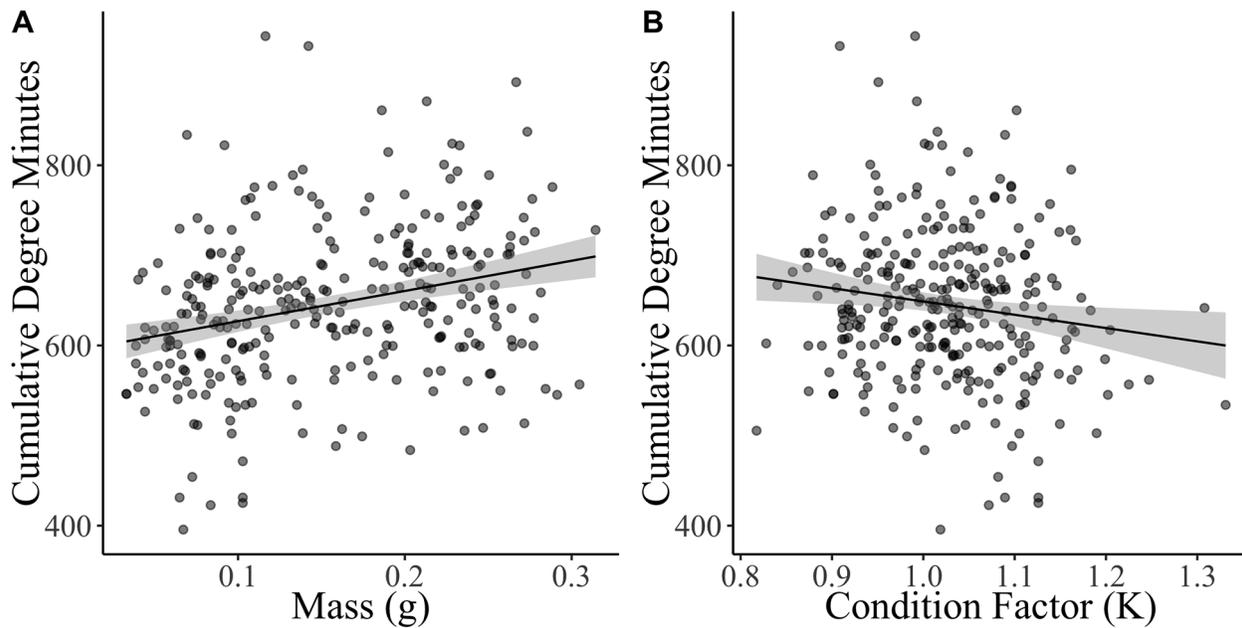


Figure 2. Modeled cumulative degree minutes (CDM) as a function of mass (log-log transformed, with initial condition held at mean values; A) and initial condition factor (K , with mass held at mean values; B) in juvenile *Salmo trutta*. A suggests a positive relationship between mass and CDM, while B suggests a negative relationship between condition factor and CDM. Shaded areas represent 95% confidence intervals.

February) and the other occurring ≥ 31 d after sampling (April–May). We did not find any indication that CT_{\max} differed among early or late migrants ($t = 1.500$, $P = 0.137$). We found that the number of days spent in the river before migration was negatively related to mass ($Z = -2.685$, $P = 0.007$; fig. 3A) but not to condition ($Z = 1.689$, $P = 0.091$), suggesting that larger fish migrated earlier. This is further supported by a direct comparison of mass between early (≤ 30 d after sampling; $N = 54$; mean = 36.8; SD = 19.6) and late (≥ 31 d after sampling; $N = 88$; mean = 27.4; SD = 19.6) migratory groups, where we found early migrants to have significantly greater mass on average than late migrants ($P = 0.008$; fig. 3B).

Growth

Of the fish that were exposed to acute thermal stress and later recaptured in the stream (i.e., residents; $N = 8$), mass was

positively correlated to SGR ($t = 5.443$, $P = 0.002$) such that residents that were larger at the time of tagging grew faster. Similar trends were observed among control fish that assumed residency ($N = 14$; $t = 11.05$, $P < 0.001$), suggesting that acute thermal stress did not influence growth rates. We found no difference ($t = -0.36$, $P = 0.723$) in SGR between control fish ($x = 405.18$; $N = 14$) and CT_{\max} fish ($x = 412.48$; $N = 8$), indicating that acute thermal shock did not affect growth rates in resident fish. Since these models are limited by a low sample size, caution should be taken when interpreting this result.

Predation

We found no significant differences in rate of predation ($\chi^2 = 2.43$, $P = 0.119$) in fish from different groups (i.e., control or CT_{\max}). Thus, acute thermal shock did not increase the probability of being predated. Mean CDM for predated fish was

Table 2: Total number (N); mean, minimum, and maximum cumulative temperature; and temperature at loss of equilibrium for individually tagged *Salmo trutta* exposed to thermal ramping

Final status (N)	Cumulative temperature (CDM)			Temperature ($^{\circ}\text{C}$)		
	Mean \pm SD	Min	Max	Mean \pm SD	Min	Max
Total (294)	645.25 \pm 85.88	395.65	943.33	25.63 \pm 1.49	21.68	30.08
Migrants (143)	646.12 \pm 78.37	422.78	932.36	25.65 \pm 1.48	21.73	30.08
Residents (8)	685.47 \pm 85.67	617.1	870.98	26.52 \pm 1.15	25.51	28.7
Unknown (143)	642.12 \pm 92.80	395.65	943.33	25.56 \pm 1.51	21.68	29.52
Predated (26)	645.25 \pm 85.88	395.66	943.33	25.63 \pm 1.49	21.68	30.08

Note. Data are based on statuses as of June 8, 2020. Predated fish include residents, migrants, and fish of unknown strategy. CDM = cumulative degree minutes.

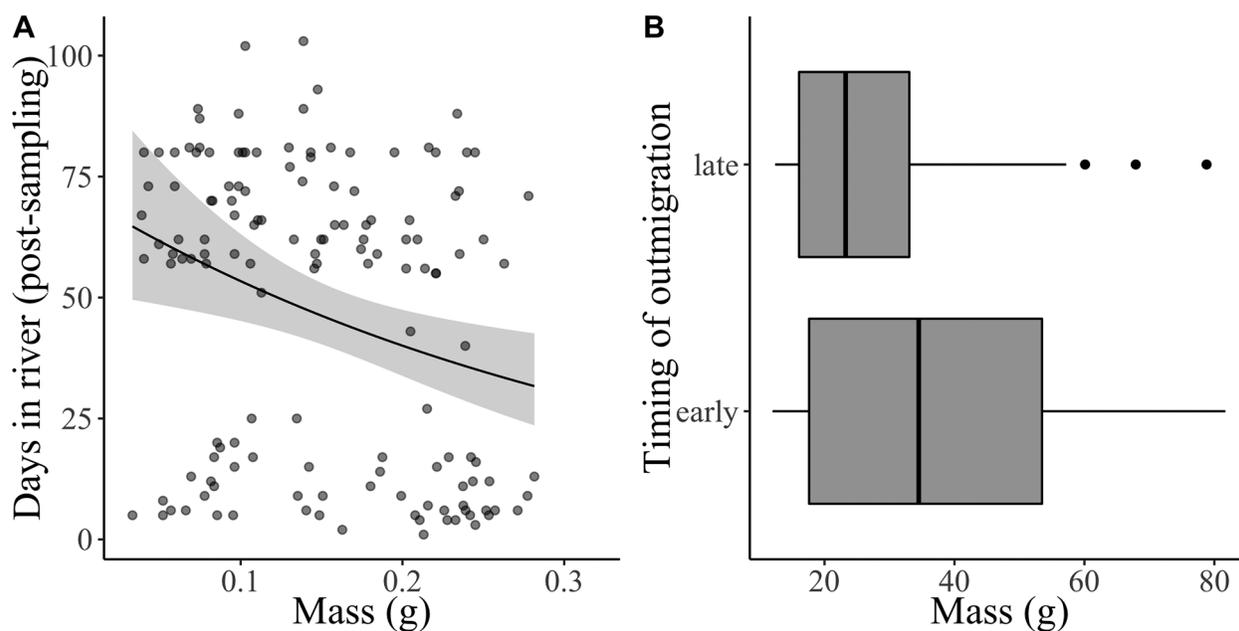


Figure 3. *A*, Modeled probability of timing of migration (days spent in river after sampling) as a function of mass (log-log transformed, with initial condition held at mean values) in juvenile *Salmo trutta*, illustrating a significant negative relationship between mass and migration timing ($Z = -2.685$, $P = 0.007$). Shaded areas represent 95% confidence intervals. *B*, Distribution of initial mass (g) demonstrating significantly greater mass ($P = 0.008$) of early migrants (0–30 d after sampling; $N = 54$) compared with late migrants (≥ 31 d after sampling; $N = 88$).

found to be 637.5 and did not differ from the mean CDM of fish that were not predated (average = 646; $t = 0.55$, $df = 32$, $P = 0.587$). Likelihood of predation by cormorants was not predicted by mass, condition, or CDM (GLMs, all $P > 0.05$; table 3).

Discussion

The phenotypic differences between migratory and resident brown trout are not well understood. This study found a range of CT_{max} values within a population of semianadromous brown trout (table 2); this variation could be beneficial under different thermal conditions. Given the recent evidence supporting the

ecological relevance of CT_{max} , we investigated whether these differences were related to the decision to migrate and the timing of migration. We speculated that fish with low CT_{max} values may be more likely to migrate, as stream temperatures tend to be warmer than sea temperatures and thus may act as a thermal stressor. We further speculated that differences in CT_{max} values may affect migration timing, survival, and growth given that temperature is viewed as a primary factor affecting metabolism, growth, reproduction, and survival (Fry 1971), but we found no indication that intraspecific variation in CT_{max} predicted migration strategy, timing, growth, or predation vulnerability.

Table 3: Total number (N) and mean \pm SD and range of body metrics obtained during initial sampling of control and CT_{max} *Salmo trutta* in February 2020 according to final statuses

Final status (N)	Length (cm)	Mass (g)	Condition (K)
Total (614)	14.2 \pm 2.7 (11.0–22.7)	32.13 \pm 19.43 (11.0–115.6)	1.017 \pm .084 (.663–1.360)
Migrants (288)	14.1 \pm 2.6 (11.0–21.5)	31.20 \pm 17.8 (12–115.4)	1.012 \pm .082 (.828–1.360)
Residents (22)	15.3 \pm 3.1 (11.0–22.7)	40.28 \pm 25.3 (14.4–115.6)	1.015 \pm .061 (.927–1.113)
Unknown (304)	14.2 \pm 2.8 (11.0–21.7)	32.42 \pm 20.4 (11.0–107.6)	1.021 \pm .087 (.663–1.331)
Predated (68)	14.5 \pm 2.8 (11.0–20.6)	33.97 \pm 19.39 (12.0–87.0)	1.008 \pm .072 (.784–1.229)

Note. Predated fish include residents, migrants, and fish of unknown strategy. CT_{max} = critical thermal maximum.

Regardless, the role of upper thermal tolerance in mediating migration propensity and timing could be further explored by considering alternative indicators of thermal tolerance, such as the expression of heat-shock proteins (Fangue et al. 2006). Similarly, morphological and physiological differences related to oxygen transport among individuals within a population could also provide insight on the role of thermal tolerance in regulating life-history strategies in salmonids (Eliason et al. 2011).

While several studies have found relationships between mass, condition (or both), and the decision to migrate or assume residency, the relationship between condition and mass with thermal tolerance indicated by CT_{max} appears to be rather subtle. We found that CT_{max} correlated positively with mass and negatively with condition. While we failed to detect an effect of CT_{max} on the decision to migrate or the timing of migration, our results suggest that high body mass and low body condition are associated with higher CT_{max} in juvenile brown trout. However, the relationship between body size and condition with CT_{max} has yet to be validated in wild fish populations. Previous studies report positive correlations (e.g., Zhang and Kieffer 2014; Bard and Kieffer 2019), while others report no correlations or negative correlations with mass (e.g., Morgan et al. 2018; O'Donnell et al. 2020). Discrepancies in CT_{max} experimental protocols among studies may mask relationships between fish size and CT_{max}, where rapid heating rates may result in lags between environmental and core body temperatures in larger fish (Becker and Genoway 1979; Lutterschmidt and Hutchison 1997; Zhang and Kieffer 2014).

Compared with residents, migratory individuals have been found to be either smaller (Morinville and Rasmussen 2003; Theriault and Dodson 2003; Peiman et al. 2017; Archer et al. 2020) or larger (Bohlin et al. 1994; Olsson et al. 2006; Acolas et al. 2012) and to have lower body condition (Wysujack et al. 2009; Boel et al. 2014; Peiman et al. 2017; Archer et al. 2020). The present study did not find any significant associations between body metrics and migratory tactics, although relatively few residents were recaptured, and low sample sizes may have hindered our ability to detect patterns.

In addition to its correlation to CT_{max}, mass was also correlated to migration timing, a finding that is supported by previous studies (e.g., Metcalfe et al. 1990; Bohlin et al. 1996; Birnie-Gauvin et al. 2017). We found that larger individuals tended to migrate earlier and have higher thermal tolerance. Since mass is known to positively correlate with metabolic rate (Økland et al. 1993; Thorpe et al. 1998), the metabolic demands of larger individuals are likely higher, and thus these individuals require more resources to sustain metabolic demands and high growth rates. By entering the sea earlier, larger individuals gain greater feeding opportunities earlier, thus enabling them to meet their metabolic demands. This idea also supports the size threshold hypothesis that larger individuals migrate earlier (Økland et al. 1993; Bohlin et al. 1996). These results demonstrate that individual variation in migration timing (which is a function of temperature and flow) is a result of phenotypic variation (Bohlin et al. 1996). While we did not find any correlations between variation in CT_{max} and timing of migration, phenotypic variation

in thermal tolerance may still account for variation in the timing of migration, but CT_{max} may not be the most appropriate method for detecting this link. Considering the importance of temperature in triggering migration, future studies should focus on the use of alternative metrics of thermal tolerance, such as measuring maximum metabolic rates and aerobic scope under warm (sub-lethal) temperatures.

The intrinsic correlation between mass and metabolism provides a foundation to speculate about the role of thermal tolerance in mediating migration timing. The idea that larger individuals have higher CT_{max} and migrate earlier as a result of higher metabolic demands could indicate that traits involved in regulating thermal tolerance are likely to be acting on metabolic rates as well. Since metabolism has been hypothesized to influence the timing of migration in brown trout (Økland et al. 1993), it is also conceivable that a link exists between upper thermal tolerance and timing of migration. Predicted temperature fluctuations associated with climate change may simultaneously alter metabolism and thermal tolerance and lead to shifts in migration timing (Whitney et al. 2016). Changes in the timing of migration could have important and wide-ranging effects on ecosystems and result in misalignments between resource availability and arrival of migratory individuals.

Although CT_{max} did not predict the timing of migration in this study, the relationship could be masked by average thermal conditions. Here, maximum stream temperatures (19.5°C) remain approximately 2°C below the minimum CT_{max} measured (21.68°C), suggesting that fish do not currently experience sufficient selective pressure to drive a difference in CT_{max} between residents and migrants. With progressively warmer stream temperatures predicted in the near future (IPCC 2014), thermal conditions might reveal a stronger relationship between CT_{max} and migration strategy and timing. A recent review found that fish perceive sudden exposure to high temperature as a stressor, inducing high levels of cortisol and catecholamines (Alfonso et al. 2020). In turn, high levels of cortisol have been shown to correlate with earlier migration in salmonids (Birnie-Gauvin et al. 2019). Increasingly prevalent extreme weather events, such as heat waves, could promote out-migration of fish with low CT_{max} if warmer stream temperatures induce stress responses. Understanding the role of individual thermal tolerance indicated by CT_{max} in relation to life-history strategies under future climate scenarios is an interesting avenue for future research.

Limitations

It is important to address the limitations associated with the uncertainty regarding the ultimate fate of individuals. Although PIT station detection efficiency was high (91.2%), some individuals may have migrated without detection, just as some individuals that assumed residency may not have been recaptured within the stream during resampling or detected at cormorant colonies. For the purpose of this study, we assumed that fish from both the control and treatment groups had equal chances of being undetected, predated, or recaptured. Moreover, even larger sample sizes would be required in future

studies to facilitate comparisons between migrants and residents in populations where migratory phenotypes typically exceed residents. Low sample sizes of resident trout in this study make it particularly difficult to detect significant interactions, especially those relevant to CT_{max} .

It is also worth noting that CT_{max} measurements were somewhat low compared with other studies on brown trout (e.g., Carline and Machung 2001; Galbreath et al. 2004). This may be due to the effect of photoperiod or seasonal changes on thermal tolerance as well as differences in experimental protocols (e.g., acclimation and rates of thermal ramping). There is an abundance of literature stating that longer days (i.e., during the summer) lead to higher upper thermal tolerance (Lutterschmidt and Hutchison 1997). In this study, wild trout were captured in the winter, thus exposed to short days and low temperatures, and were likely acclimated to cooler temperatures than if they had been captured in the summer. In the wild, fish are exposed to constant fluctuations in air and water temperatures, which may explain differences observed between wild fish and those kept under controlled laboratory conditions before trials. For these reasons, the CT_{max} values obtained here should not be directly compared with other studies assessing thermal tolerance in brown trout unless similar conditions and methodologies were used.

Conclusions

To our knowledge, this is the first study that attempts to link individual variation in CT_{max} to migratory tactics in a partially migrant population of wild fish. After estimating CT_{max} in 294 wild juvenile brown trout, we found no evidence that this metric of upper thermal tolerance affected migratory propensity, although the generality of our result is somewhat hindered by a low sample size of resident fish. We found that larger fish migrated earlier, consistent with previous findings. We also found that larger fish and fish in better condition had higher CT_{max} values, but CT_{max} did not predict probability of migration, growth, or vulnerability to predation. Although CT_{max} did not predict migration strategy, further investigating the relationships between metabolism, mass, and thermal tolerance using maximum metabolic rate and aerobic scope measurements could provide insight into the potential role of upper thermal tolerance in determining life-history strategies. We speculate that CT_{max} may play more important roles in the determination of life-history strategies, growth, or predation in populations that are exposed to more frequent extreme heat events. Future research should focus on understanding how these extreme weather events impact thermal tolerance in wild populations and how these changes subsequently influence migration propensity, timing, growth, and predation. While CT_{max} remains a common tool in the field of thermal biology, its role in mediating life-history strategies remains unclear. Given the urge to manage, conserve, and protect biodiversity in a rapidly warming world, such tools are important to understand how temperature may impact population dynamics in the wild.

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Literature Cited

- Aarestrup K., C. Nielsen, and A. Koed. 2002. Net ground speed of downstream migrating radio-tagged Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) smolts in relation to environmental factors. *Hydrobiologia* 483:95–102.
- Aarestrup K., C. Nielsen, and S.S. Madsen. 2000. Relationship between gill Na^+ , K^+ -ATPase activity and downstream movement in domesticated and first-generation offspring of wild anadromous brown trout (*Salmo trutta*). *Can J Fish Aquat Sci* 57:2086–2095.
- Acolas M.L., J. Labonne, and J.L. Bagliniere. 2012. The role of body size versus growth on the decision to migrate: a case study with *Salmo trutta*. *Naturwissenschaften* 99:11–21.
- Alfonso S., M. Gesto, and B. Sadoul. 2020. Temperature increase and its effects on fish stress physiology in the context of global warming. *J Fish Biol* 2020:1–13. <https://doi.org/10.1111/jfb.14599>.
- Anttila K., R.S. Dhillon, E.G. Boulding, A.P. Farrell, B.D. Glebe, J.A. Elliott, R.W. Wolters, and P.M. Schulte. 2013. Variation in temperature tolerance among families of Atlantic salmon (*Salmo salar*) is associated with hypoxia tolerance, ventricle size and myoglobin level. *J Exp Biol* 216:1183–1190.
- Archer L.C., S.A. Hutton, L. Harman, S.D. McCormick, M.N. O'Grady, J.P. Kerry, W.R. Poole, P. Gargan, P. McGinnity, and T.E. Reed. 2020. Food and temperature stressors have opposing effects in determine flexible migration decisions in brown trout. *Glob Chang Biol* 26:2878–2896.
- Armstrong J.B., D.E. Schindler, K.L. Omori, C.P. Ruff, and T.P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology* 91:1445–1454.
- Åsheim E., A.H. Andreassen, R. Morgan, and F. Jutfelt. 2020. Rapid-warming tolerance correlates with tolerance to slow warming but not growth at non-optimal temperatures in zebrafish. *J Exp Biol* 223:jeb229195.
- Bard B. and J.D. Kieffer. 2019. The effects of repeat acute thermal stress on the critical thermal maximum (CT_{max}) and physiology of juvenile shortnose sturgeon (*Acipenser brevirostrum*). *Can J Zool* 97:576–572.
- Baroudy E. and J.M. Elliott. 1994. The critical thermal limits for juvenile Arctic charr *Salvelinus alpinus*. *J Fish Biol* 45: 1041–1053.

- Bates A.E. and S.A. Morley. 2020. Interpreting empirical estimates of experimentally derived physiological and biological thermal limits in ectotherms. *Can J Zool* 98:237–244.
- Becker C.D. and R.G. Genoway. 1979. Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater fish. *Environ Biol Fish* 4:245–256.
- Birnie-Gauvin K. and K. Aarestrup. 2019. A call for a paradigm shift: assumed-to-be premature migrants actually yield good returns. *Ecol Freshw Fish* 28:62–68.
- Birnie-Gauvin K., H. Flávio, M.L. Kristensen, S. Walton-Rabideau, S.J. Cooke, W.G. Willmore, A. Koed, and K. Aarestrup. 2019. Cortisol predicts migration timing and success in both Atlantic salmon and sea trout kelts. *Sci Rep* 9:1–9.
- Birnie-Gauvin K., K.S. Peiman, M.H. Larsen, H. Baktoft, K. Aarestrup, W.G. Willmore, and S.J. Cooke. 2017. Oxidative stress and partial migration in brown trout (*Salmo trutta*). *Can J Zool* 95:829–835.
- Boel M., K. Aarestrup, H. Baktoft, T. Larsen, S. Madsen, H. Malte, C. Skov, J.C. Svendsen, and A. Koed. 2014. The physiological basis of the migration continuum in brown trout (*Salmo trutta*). *Physiol Biochem Zool* 87:334–345.
- Bohlin T., C. Dellefors, and U. Faremo. 1994. Probability of first sexual maturation of male parr in wild sea-run brown trout (*Salmo trutta*) depends on condition factor 1 yr in advance. *Can J Fish Aquat Sci* 51:1920–1926.
- . 1996. Date of smolt migration depends on body-size but not age in wild sea-run brown trout. *J Fish Biol* 49:157–164.
- Bolker B. 2008. Ecological models and data in R. Princeton University Press, Princeton, NJ.
- Brander K., G. Blom, M.F. Borges, K. Erzini, G. Henderson, B.R. MacKenzie, H. Mendes, J. Ribeiro, A.M.P. Santos, and R. Toresen. 2003. Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature? *ICES Mar Sci Symp* 219:261–270.
- Carline R.F. and J.F. Machung. 2001. Critical thermal maxima of wild and domestic strains of trout. *Trans Am Fish Soc* 130:1211–1216.
- Chapman B.B., C. Bronmark, J.-A. Nilsson, and L.-A. Hansson. 2011a. The ecology and evolution of partial migration. *Oikos* 120:1764–1775.
- Chapman B.B., K. Hulthen, D.R. Blomqvist, L.-A. Hansson, J.-A. Nilsson, J. Broderson, P.A. Nilsson, C. Skov, and C. Bronmark. 2011b. To boldly go: individual difference in boldness influence migratory tendency. *Ecol Lett* 14:871–876.
- Clark T.D., E. Sandblom, G.K. Cox, S.G. Hinch, and A.P. Farrell. 2008. Circulatory limits to oxygen supply during an acute temperature increase in the Chinook salmon (*Oncorhynchus tshawytscha*). *Am J Physiol* 295:R1631–R1639.
- Comte L. and J.D. Olden. 2017. Climatic vulnerability of the world's freshwater and marine fishes. *Nat Clim Change* 7:718–722.
- Cowles R.B. and C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History*, volume 83, article 5. *Q Rev Biol* 20:170.
- Deutsch C.A., J.J. Tewksbury, R.B. Huey, K.S. Sheldon, C.K. Ghalamborm, D.C. Haak, and P.R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105:6668–6672.
- Eliason E.J., T.D. Clark, M.J. Hague, L.M. Hanson, Z.S. Gallagher, K.M. Jeffries, M.K. Gale, D.A. Patterson, S.G. Hinch, and A.P. Farrell. 2011. Differences in thermal tolerance among sockeye salmon populations. *Science* 332:109–112.
- Fangue N.A., M. Hofmeister, and P.M. Schulte. 2006. Intraspecific variation in thermal tolerance and heat shock protein gene expression in common killifish, *Fundulus heteroclitus*. *J Exp Biol* 209:2859–2872.
- Ferguson A., T.E. Reed, T.F. Cross, P. McGinnity, and P.A. Prodöhl. 2019. Anadromy, potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the environment. *J Fish Biol* 95:692–718.
- Ficke A., C.A. Myrick, and L.J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. *Rev Fish Biol Fish* 17:581–613.
- Forseth T., S. Larsson, A.J. Jensen, B. Jonsson, I. Näslund, and I. Berglund. 2009. Thermal performance of juvenile brown trout, *Salmo trutta* L.: no support for thermal adaptation hypotheses. *J Fish Biol* 74:133–149.
- Fry F.E.J. 1971. The effect of environmental factors on the physiology of fish. *Fish Physiol* 1:98.
- Galbreath P.F., N.D. Adams, and T.H. Martin. 2004. Influence on heating rate on measurement of time to thermal maximum in trout. *Aquaculture* 241:587–599.
- Galbreath P.F., N.A. Adams, L.W. Sherrill, and T.H. Martin. 2006. Thermal tolerance of diploid versus triploid rainbow trout and brook trout assessed by time to chronic lethal maximum. *Environ Biol Fish* 75:183–193.
- Gibbons J.W. and K.M. Andrews. 2004. PIT tagging: simple technology at its best. *BioScience* 54:447–454.
- Grayson K.L. and H.M. Wilbur. 2009. Sex- and context-dependent migration in a pong-breeding amphibian. *Ecology* 90:306–311.
- Grinder R.M., R.D. Bassar, and S.K. Auer. 2020. Upper thermal limits are repeatable in Trinidadian guppies. *J Therm Biol* 90:102597.
- Gross M.R. 1987. Evolutionary of diadromy in fishes. *Am Fish Soc Symp* 1:14–25.
- Kilgour M. and R.W. McCauley. 1986. Reconciling the two methods of measuring upper lethal temperatures in fishes. *Environ Biol Fish* 17:281–290.
- Hebblewhite M. and E.H. Merrill. 2009. Trade-offs between predation risk and forage differ between migration strategies in a migratory ungulate. *Ecology* 90:3445–3454.
- IPCC (Intergovernmental Panel on Climate Change). 2014. Climate change 2014: synthesis report—contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva.
- Jonsson B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Trans Am Fish Soc* 114:182–194.

- Jonsson B. and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Rev Fish Biol Fish* 3:348–365.
- . 2009. A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *J Fish Biol* 75:2381–2447.
- Jonsson N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. *Nord J Freshw Res* 66: 20–35.
- Larsen M.H., A.N. Thorn, C. Skov, and K. Aarestrup. 2013. Effects of passive integrated transponder tags on survival and growth of juvenile Atlantic salmon *Salmo salar*. *Anim Biotelemetry* 1:19–25.
- Lemopoulos A., S. Uusi-Heikkilä, P. Hyvärinen, N. Alioravainen, J.M. Prokkola, C.K. Elvidge, A. Vasemägi, and A. Vainikka. 2019. Association mapping based on a common-garden migration experiment reveals candidate genes for migration tendency in brown trout. *G3 Genes Genomes Genet* 9:2887–2896.
- Lutterschmidt W.I. and V.H. Hutchison. 1997. The critical thermal maximum: history and critique. *Can J Zool* 75:1561–1574.
- Metcalfe N.B., F.A. Huntingford, J.E. Thorpe, and C.E. Adams. 1990. The effects of social status on life-history variation in juvenile salmon. *Can J Zool* 68:2630–2636.
- Midwood J.D., M.H. Larsen, M. Boel, K. Aarestrup, and S.J. Cooke. 2015. An experimental field evaluation of winter carryover effects in semi-anadromous brown trout (*Salmo trutta*). *J Exp Zool A* 323:645–654.
- Morgan R., M.H. Finnøen, and F. Jutfelt. 2018. CT_{max} is repeatable and doesn't reduce growth in zebrafish. *Sci Rep* 8:7099.
- Morinville G.R. and J.B. Rasmussen. 2003. Early juvenile bioenergetics differences between anadromous and resident brook trout (*Salvelinus alpinus*) in Norway. *Can J Fish Aquat Sci* 40:1372–1387.
- Muñoz M.M., M.A. Stimola, A.C. Algar, A. Conover, A.J. Rodriguez, M.A. Landestoy, G.S. Bakken, and J.B. Losos. 2014. Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proc R Soc B* 281:20132433.
- Muñoz N.J., A.P. Farrell, J.W. Heath, and B.D. Neff. 2015. Adaptive potential of a Pacific salmon challenged by climate change. *Nat Clim Change* 5:163–166.
- Nielsen C., K. Aarestrup, and S.S. Madsen. 2006. Comparison of physiological smolt status in descending and nondescending wild brown trout (*Salmo trutta*) in a Danish stream. *Ecol Freshw Fish* 15:229–236.
- Nielsen C., K. Aarestrup, U. Nørum, and S.S. Madsen. 2004. Future migratory behaviour predicted from premigratory levels of gill Na^+/K^+ -ATPase activity in individual wild brown trout (*Salmo trutta*). *J Exp Biol* 207:527–533.
- Nilsson A.L.K., T. Alerstam, and J.-A. Nilsson. 2008. Diffuse, short and slow migration among blue tits. *J Ornithol* 149:365–373.
- O'Donnell M.J., A.M. Regish, S.D. McCormick, and B.H. Letcher. 2020. How repeatable is CT_{max} within an individual brook trout over short and long-time intervals? *J Therm Biol* 89:102559.
- Økland F., B. Jonsson, A.J. Jensen, and L.P. Hansen. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? *J Fish Biol* 42:541–550.
- Olsson I.C., L.A. Greenberg, E. Bergman, and K. Wysujack. 2006. Environmentally induced migration: the importance of food. *Ecol Lett* 9:645–651.
- Parmesan C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Peiman K.S., K. Birnie-Gauvin, J.D. Midwood, M.H. Larsen, A.D.M. Wilson, K. Aarestrup, and S.J. Cooke. 2017. If and when: intrinsic differences and environmental stressors influence migration in brown trout (*Salmo trutta*). *Oecologia* 184:375–384.
- Perry A.L., P.J. Low, J.R. Ellies, and J.D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915.
- Perry G.M., C.M. Martyniuk, M.M. Ferguson, and R.G. Danzmann. 2005. Genetic parameters for upper thermal tolerance and growth-related traits in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* 250:120–128.
- Pinsky M.L., A.M. Eikeset, D.J. McCauley, J.L. Payne, and J.M. Sunday. 2019. Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* 569:108–111.
- R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Ricker W.E. 1975. Computation and interpretation of biological statistics of populations. *Bull Fish Res Board Can* 191: 382.
- Sandblom E., T.D. Clark, A. Gräns, A. Ekström, J. Brijs, L.F. Sundström, A. Odelström, A. Adill, T. Aho, and F. Jutfelt. 2016. Physiological constraints to climate warming in fish follow principles of plastic floors and concrete ceilings. *Nat Commun* 7:1–8.
- Sarkar D. 2008. Lattice: multivariate data visualization with R. Springer, New York.
- Sloat M.R. and G.H. Reeves. 2014. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (*Oncorhynchus mykiss*) life histories. *Can J Fish Aquat Sci* 71:491–501.
- Sunday J.M., A.E. Bates, and N.K. Dulvy. 2012. Thermal tolerance and the global redistribution of animals. *Nat Clim Change* 2:686–690.
- Sunday J.M., J.M. Bennett, P. Calosi, S. Clusella-Trullas, S. Gravel, A.L. Hargreaves, F.P. Leiva, W.C.E.P. Verberk, M.Á. Olalla-Tárraga, and I. Morales-Castilla. 2019. Thermal tolerance patterns across latitude and elevation. *Philos Trans R Soc B* 374:20190036.
- Theriault V. and J.J. Dodson. 2003. Body size and the adoption of a migratory tactic in brook charr. *J Fish Biol* 63:1144–1159.
- Thomas C.D., E.J. Bodsworth, R.J. Wilson, A.D. Simmons, Z.G. Davies, M. Musche, and L. Conrads. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–581.

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- Thorpe J.E., M. Mangel, N.B. Metcalfe, and F.A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evol Ecol* 12:581–599.
- Venables W.N. and B.D. Ripley. 2002. *Modern applied statistics with S*. 4th ed. Springer, New York.
- Whitney J.E., R. Al-Chokhachy, D.B. Bunnell, C.A. Caldwell, S.J. Cooke, E.J. Eliason, M. Rogers, A.J. Lynch, and C.P. Paukert. 2016. Physiological basis of climate change impacts on North American inland fishes. *Fisheries* 41:332–345.
- Wickham H. 2016. *ggplot2: elegant graphics for data analysis*. Springer, New York.
- Wysujack K., L.A. Greenberg, E. Bergman, and I.C. Olsson. 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecol Freshw Fish* 18:52–59.
- Zhang Y. and J.D. Kieffer. 2014. Critical thermal maximum (CT_{max}) and hematology of shortnose sturgeons (*Acipenser brevirostrum*) acclimated to three temperatures. *Can J Zool* 92:215–221.
- Zydlewski G.B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. *Fisheries* 31: 492–502.