Canadian Journal of
**Fisheries and
Aquatic Sciences**

Research Article

Ecological performance of native and invasive benthic freshwater fishes under elevated temperature

Megan Hutchings[a], **Jaclyn Hill**[b], **Matthew J.S. Windle**[c], **and Anthony Ricciardi**[a]

[a]Department of Biology, McGill University, 1205 Docteur Penfield Ave., Montreal, QC H3A 1B1, Canada; [b]Maurice Lamontagne Institute, Fisheries and Oceans Canada, 850 Rte de la Mer, Mont-Joli, QC G5H 3Z4, Canada; [c]River Institute, 2 St. Lawrence Dr., Cornwall, ON K6H 4Z1, Canada

Corresponding author: **Anthony Ricciardi** (email: tony.ricciardi@mcgill.ca)

Abstract

Climate warming of freshwater ecosystems is altering the performance and trophic interactions of native and non-native species. We compared the feeding efficiency and thermal tolerance of the invasive round goby (*Neogobius melanostomus*) and a trophically analogous native fish, logperch (*Percina caprodes*), under current and projected mean summer surface temperatures for the nearshore lower Great Lakes (18 and 25 °C, respectively). Feeding efficiency at both temperatures was quantified using the functional response ratio (FRR)—the ratio of attack rate and prey handling time. Juvenile logperch had a higher FRR than juvenile gobies at 18 °C; however, adult gobies had a higher FRR than juvenile logperch at both 18 and 25 °C, indicating a greater potential for trophic impacts. At 18 °C, CT_{max} of juvenile logperch was lower than adult gobies but did not differ from juvenile gobies, whereas at 25 °C, logperch CT_{max} was higher than juvenile round gobies. Following acclimation to either 18 or 25 °C, juvenile logperch exhibited a greater thermal acclimation capacity than the round goby. These results underscore the need for risk assessment to account for native and non-native species responses to shifting thermal contexts.

Key words: climate change, critical thermal maximum, functional response, invasive species, temperature tolerance

Introduction

Within the past two centuries, more than 180 non-native plants, phytoplankton, invertebrates, fishes, and microbes have established populations in the Great Lakes–St. Lawrence River basin (Ricciardi 2006; Pagnucco et al. 2015). Among these are some highly invasive species, including the round goby (*Neogobius melanostomus*), a Ponto-Caspian freshwater fish that has become widely distributed in the basin and reportedly competes with a trophically analogous native benthic fish, the logperch (*Percina caprodes*) (Balshine et al. 2005). Coinciding with pressures exerted by invasive species, the warming of surface waters through anthropogenic climate change threatens to further transform ecosystem dynamics (Beitinger et al. 2000; Trumpickas et al. 2009, 2015; Quattrocchi et al. 2023) and alter the distribution, abundance, and impacts of invaders (Rahel and Olden 2008). We can expect the multiple stressors to interact in ways that have consequences for native species and aquatic food webs.

Functional response metrics as a measure of invader performance

Overlapping stressors create challenges for risk assessment. To address these challenges, there have been efforts to develop predictive metrics that advance our understanding of invader impacts under different environmental contexts (Dick et al. 2014, 2017*a*; Cuthbert et al. 2019; Dickey et al. 2020). Some of these metrics are experimentally derived from a consumer's functional response (FR)—the relationship between resource consumption and resource availability—which is classified as one of three distinct types: Type I, a linear increase in feeding rate with no constraint of handling time; Type II, an inverse density-dependent hyperbolic response resulting in rapid prey depletion at low densities, which can destabilize predator-prey population dynamics; and Type III, a positively density-dependent sigmoidal response that results in a prey refugium at low density and therefore can stabilize predator-prey dynamics (Holling 1959; Dick et al. 2014). FR parameters include: attack rate (a), which is the rate at which prey are encountered; handling time (h), the time required for the predator to capture, handle, and ingest captured prey; and the maximum feeding rate ($1/h$), which indicates the maximum rate at which prey are consumed at high prey densities (Holling 1959; Dick et al. 2014). These parameters can be compared between trophically analogous species across different abiotic contexts. High-impact invaders tend to consume resources more efficiently than low-impact invaders or native species (Ricciardi et al. 2013; Dick et al. 2014; Laverty et al. 2017; Mofu et al. 2019*a*), and their FRs have been correlated with their impacts in the field (Dick et al. 2014, 2017*a*; Faria et al. 2023). Furthermore, attack rate (a) and handling time (h)

can be amalgamated into a more informative metric, the functional response ratio (FRR) = a/h. A relatively high FRR ratio, resulting from high attack rates and/or low handling times, is characteristic of invaders that exert strong trophic impacts in the field (Cuthbert et al. 2019; McCard et al. 2021) and thus has predictive value in risk assessment.

Thermal tolerance

The thermal tolerance of a species is estimated from experimentally derived critical thermal maxima (CT_{max}) and minima (CT_{min}), and an ectotherm's thermal performance window is defined as the range of temperatures suitable to conduct vital functions (Huey and Stevenson 1979). CT_{max} and CT_{min} are physiological metrics used to measure the upper and lower lethal thermal limits of a performance window, respectively (Becker and Genoway 1979; Lutterschmidt and Hutchison 1997). The CT_{max} is reached when an individual displays a loss of equilibrium caused by physiological disorganization (Becker and Genoway 1979; Lutterschmidt and Hutchison 1997), which prevents it from escaping lethal environmental conditions. This metric has been identified as a predictor of mortality from thermal stress (Cicchino et al. 2023). A species that possesses a wide thermal performance window has potential resilience when exposed to fluctuating temperature conditions caused by climate change (Matern 2001; Christensen et al. 2021). Increasing thermal conditions to levels that compromise the aerobic scope or approach the CT_{max} of a given species can impact their abundance levels and range distribution (Sunday et al. 2012, 2014; Quattrocchi et al. 2023). Furthermore, if the CT_{max} for a given species exceeds current and future temperatures predicted for their surrounding environment, they are expected to be less vulnerable to warming (Catullo et al. 2015). CT_{max} also varies with acclimation temperature (Beitinger et al. 2000); when CT_{max} increases directly with increasing acclimation temperature, it indicates resilience to thermal stress (Vinagre et al. 2016; Christensen et al. 2021). Thus, CT_{max} experiments can inform predictive risk assessment by comparing thermal tolerances of native and invasive species populations to ambient and projected temperature regimes (Reid and Ricciardi 2022). Furthermore, given that the thermal performance window of a species can mediate its ecological interactions within a given environment (Pörtner and Farrell 2008), a shift of ambient temperatures closer to an invader's physiological optimum positively correlates with an increase in its ecological impacts (Ricciardi et al. 2013; Iacarella et al. 2015*a*).

Objectives and predictions

We aimed to identify how increased water temperatures under a future climate warming scenario would affect feeding efficiency and thermal tolerance of the round goby and the native logperch in the lower Great Lakes–upper St. Lawrence River system. Our objectives were to compare (1) the effects of current and projected future summer surface water temperatures on the prey consumption efficiency of both species; and (2) the upper thermal tolerance limits and resilience of these species through long-term temperature acclimation. The first objective was addressed using FR experiments and the derivation of the FRR at acclimation temperatures of 18 and 25 °C, which represent current and future (projected for 2071) mean summer surface water temperatures, respectively, for nearshore areas of the lower Great Lakes (Trumpickas et al. 2009, 2015). The second objective was addressed using CT_{max} experiments at the same acclimation temperatures. The following predictions were tested:

1. The FRR will be higher for round goby than for logperch in both temperature scenarios, based on the generalization that invasive species have greater resource use efficiency than native species (Dick et al. 2013; Ricciardi et al. 2013). Furthermore, the FRR for the round goby will be higher at 25 °C than at 18 °C, because the former matches its energetic optimum (i.e., 25 °C; Lee and Johnson 2005); this prediction is in accordance with the hypothesis that the per capita effects of an invading species are maximal under abiotic conditions that more closely match its physiologically optimum (environmental matching hypothesis; Iacarella et al. 2015*a*).
2. The thermal performance (e.g., CT_{max}) for round goby will be higher than for logperch at both acclimation temperature, following the hypothesis that invasive species generally have broader environmental tolerances than less successful invaders and native species (Vázquez 2006; Eyster and Wolkovich 2021). The CT_{max} of both species is expected to be higher at an acclimation temperature 25 °C than at 18 °C (cf. Beitinger et al. 2000).

Methods

Fish collection and acclimation

All fish were collected from sites located on the upper St. Lawrence River west of Montreal. Juvenile logperch (*P. caprodes*) were collected in July 2022 at Morrisburg, Ontario (44.873°N, 75.240°W), while adult and juvenile round gobies (*N. melanostomus*) were collected in June 2023 at Beauharnois, Quebec (44.316°N, 73.876°W) (Fig. 1). Logperch and juvenile round gobies were size-matched for total length (TL) to control for size-related differences from affecting prey consumption within and between species (Rall et al. 2012). Adult round gobies were classified as individuals larger than 60 mm, because individuals at this size experience an ontogenetic shift in diet from consuming only soft invertebrates to incorporating mollusks (French and Jude 2001; Janssen and Jude 2001; Barton et al. 2005; Dashinov and Uzunova 2020). All fish were captured using a 30 ft bag seine and within 4 h of collection they were transported to McGill University, where they were held in 20-gallon aquaria (51 × 27 × 31 cm) in a climate-controlled chamber. Each aquarium housed six juvenile round gobies or logperch, while adult round gobies were kept as four individuals per aquarium. Upon arrival from the field, fish were acclimated to laboratory conditions for 14 days at 18 °C; previous studies in our lab indicated the need for an acclimation period of 1–2 weeks to maximize survival (Reid and Ricciardi 2022; M.H., pers. obs.). Each aquarium was exposed to a 12:12 day:night cycle photoperiod and was equipped with air stones for oxygenation, PVC shelters, and

Fig. 1. Map of sampling sites on the upper St. Lawrence River. Populations of the round goby (*Neogobius melanostomus*) and logperch (*Percina caprodes*) were sampled at Beauharnois, Quebec (44.316°N, 73.876°W) and Morrisburg, Ontario (44.873°N, 75.240°W), respectively. Figure was created using QGIS version 3.32.3 (QGIS Development Team 2023). Light Gray Canvas base map from Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community.

aquarium gravel to provide environmental enrichment according to animal care protocols (SOP519). Logperch received protein food pellets (Hikari Vibra bites^{TM}) and round gobies received Hikari chironomid (*Chironomus* sp.) larvae daily until satiated. Initially during acclimation, both species were fed the same food pellets; however, in contrast to logperch, which readily consumed the pellets, round gobies showed less interest, and therefore were switched to chironomid larvae. Aquaria water quality (pH, ammonia, nitrate, nitrite) was monitored weekly using API Freshwater Master test kit and maintained by conducting biweekly 30% water changes done manually. For high-temperature treatments, the chamber temperature was raised by 1 °C per day to reach 25 °C (Stitt et al. 2014). Fish were left to acclimate at 25 °C for 14 days before starting experiments. Individuals were not reused within temperature treatments, but were reused between randomized temperature treatments to prevent bias due to fish size (Fitzsimons et al. 2006; Avlijaš et al. 2022).

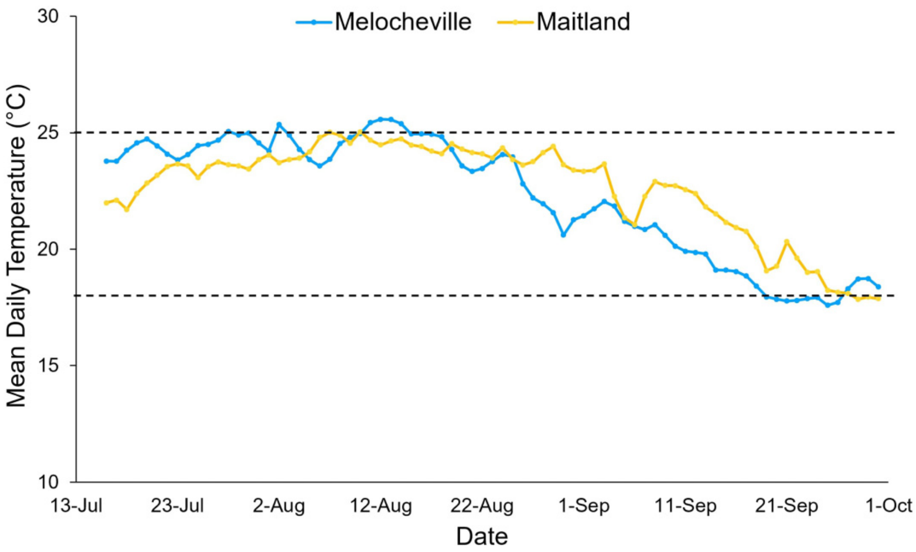
Quantifying habitat temperatures

Water temperature data for the upper St. Lawrence River were obtained from Melocheville, Quebec (45.319°N, 73.927°W), and Maitland, Ontario (44.635°N, 75.613°W), and used as approximations for collection sites at Beauharnois and Morrisburg, respectively. Data from Melocheville were obtained in the summer of 2020 from Reid and Ricciardi (2022) using a temperature logger that recorded water temperatures once per hour. Water temperature data from Maitland was retrieved during the summer of 2022 from the St. Lawrence River Institute using a temperature logger that recorded water temperatures at 15 min intervals. For each location, mean daily temperatures were calculated for each 24 h period from 16 July to 30 September 2022. The mean daily temperatures of Melocheville and Maitland were 22.3 ± 0.30 °C (17.2–34.0 °C, min–max) and 22.6 ± 0.23 °C (16.0–27.3 °C, min–max), respectively (Fig. 2). The total number of days in which temperatures reached ≥25 °C was 6 for Melocheville and 2 for Maitland.

Comparative functional responses

We examined the comparative FR of juvenile logperch and both adult and juvenile round gobies at two acclimation temperatures, 18 and 25 °C, which were selected to represent mean maximum nearshore surface water temperatures at present and in the latter half of this century, respectively, for nearshore lakes Erie and Ontario (Trumpickas et al. 2009, 2015). Both species and life stages were provided with a 2-week temperature acclimation before FR trials began, with

Fig. 2. Mean daily temperatures (°C) for both sampling sites in the St. Lawrence River from 16 July to 27 September 2020 (Melocheville) and 2022 (Maitland). The dashed line shows the projected mean summer maximum and minimum temperatures used in our experiments. Temperatures collected at Maitland (Ontario) and Melocheville (Quebec) represent proxies for fish collection sites at Morrisburg (Ontario) and Beauharnois (Quebec), respectively.



the exception of logperch acclimated to 18 °C. Logperch were provided with an additional 14 days of acclimation at 18 °C to stabilize water quality (Saeed et al. 2022; Yao et al. 2020). At the start of FR trials, individuals were isolated in a 10-gallon aquarium (50 × 19 × 25 cm) and left to acclimate for a 24-h period, during which they were starved to standardize hunger levels (Mofu et al. 2019*a*; Reid and Ricciardi 2022). The sides of aquaria were covered with an opaque barrier to prevent external visual stimuli from affecting prey consumption (Murray et al. 2013). Each experimental aquarium was maintained at the corresponding acclimation temperature (±0.5 °C). Aquaria also contained an air stone for oxygenation and a shelter (PVC pipe) as refuge to reduce stress. Mean lengths and masses of fishes used in the experiment are listed in Table S1.

Prey items used in the FR trials were chironomid (*Chironomus* sp.) larvae, which are typically found in habitats occupied by logperch and round gobies and are a common component of their diets (French and Jude 2001; Kornis et al. 2012). Hikari chironomid larvae (previously frozen and subsequently thawed for experiments) were distributed in seven densities ($n = 2$, 4, 8, 16, 32, 64, and 140 larvae for logperch and juvenile round gobies; $n = 2$, 4, 8, 16, 32, 64, 180 larvae for adult round gobies) with four replicates per density. Within each series of 18 and 25 °C temperature experiments, following the 24-h trial acclimation period, each individual fish was used in one feeding trial (i.e., at one prey density assigned at random) and allowed to feed for 3 h (Mofu et al. 2019*a*, 2019*b*). The use of lower prey densities enables us to distinguish between Type II and Type III FRs (Juliano 2001). At the end of each FR trial, individuals were removed from their experimental tank, weighed, and measured for TL. The remaining chironomid larvae were collected and counted to identify the number of prey eaten (Mofu et al. 2019*a*). Control trials without fish were conducted at each prey density to confirm that the observed depletion of prey from the experimental tanks was a direct result of predation.

Critical thermal maximum

CT_{max} was measured in a 38 L aquarium (50 × 19 × 25 cm) at acclimation temperatures of 18 and 25 °C. Individuals were acclimated to each temperature treatment for 4–6 weeks prior to trials. A total of 12 logperch and 12 juvenile round gobies were tested per acclimation temperature, while 10 adult round gobies were tested at 18 °C and 9 individuals were tested at 25 °C (McDonnell and Chapman 2015; Reid and Ricciardi 2022). Size-matching based on TL was conducted within all groups and between logperch and juvenile round gobies. The experimental aquarium was equipped with an aerator for oxygenation, and an isolating breeding box containing gravel and a PVC shelter to decrease stress and offer refugia. For logperch and juvenile round gobies, two individuals from the same holding tank were placed in separate chambers of the breeding box (25 × 14 × 15 cm) divided using an opaque barrier. Adult round gobies were tested in their own individual breeding box (26 × 15 × 16 cm). Logperch used in CT_{max} trials were the same individuals used for FR trials. CT_{max} trials were conducted after completing FR experiments and each fish was given a minimum of 7 days between experimental trials for recovery (Reid and Ricciardi 2022). Fish were not reused among CT_{max} experiments.

Prior to the start of each trial, fish were starved for a 24-h period (McDonnell and Chapman 2015; Wells et al. 2016). The experimental aquarium was maintained at the corresponding acclimation temperature (±0.5 °C). Fish were placed in the breeding box and left to acclimate for 2 h, while the CT_{max} apparatus circulated water so individuals could recover from handling stress and acclimate to trial conditions (Potts et al.

2021; Reid and Ricciardi 2022). Water temperature within the experimental aquarium was controlled by a heating immersion circulator (Julabo CORIO^{TM}, Seelbach, Germany). At the start of each trial, the water temperature was increased at a fixed rate of 0.3 °C/min (Becker and Genoway 1979; McDonnell et al. 2019; Potts et al. 2021) and monitored and recorded for the duration of each trial. Fish were exposed to increasing water temperature until they displayed a loss of equilibrium (Becker and Genoway 1979), at which point the end temperature (CT_{max}) was recorded. Loss of equilibrium for round gobies was determined manually since this species lacks a swim bladder (Kornis and Zanden 2010). When individuals began to show signs of increased breathing rates and reduced movement, a probe was used to gently turn the fish over (Matern 2001). If fish were unable to reorient themselves after 5 s, they were considered to have lost equilibrium (Carline and Machung 2001). Immediately following loss of equilibrium, fish were transferred into a recovery aquarium, containing an aerator, and monitored. Once recovered, the TL and weight were recorded, and any mortality was noted.

A time-stamped webcam monitored fish behaviour during trials to reduce disturbance. The footage was reviewed to confirm the onset of behavioural thresholds; CT_{max} and agitation temperature (T_{ag}). T_{ag} was identified as the temperature at which a fish swims agitatedly around the breeding box for a period longer than 40 s, indicating the onset of avoidance behaviour before CT_{max} is reached (McDonnell and Chapman 2015; Potts et al. 2021). This avoidance behaviour is indicative of the threshold at which fish seek out a cooler environment (McDonnell and Chapman 2015; Wells et al. 2016). Additional metrics were derived using CT_{max} and T_{ag} values and compared between acclimation treatments. First, the thermal agitation window (T_{aw}) was calculated by subtracting T_{ag} from CT_{max} (Wells et al. 2016). The acclimation agitation window (A_{aw}) was calculated by subtracting the acclimation temperature from T_{ag} (McDonnell et al. 2021). The modified thermal safety margin (TSM) was calculated by subtracting the acclimation temperature from CT_{max} (McArley et al. 2017; McDonnell et al. 2021). Lastly, the acclimation response ratio (ARR), a metric for quantifying thermal plasticity, was calculated as the change in CT_{max} per degree change in the acclimation temperature (T_{acc}) for both acclimation treatments (Claussen 1977).

Statistical analyses

Comparative functional responses

Statistical analyses were conducted using R (version 4.3.1). For FR analyses, the FRAIR package for fitting and comparing FR curves was used (Pritchard et al. 2017). The first portion of the analysis involved model selection to identify the type of FR curve (Type II or III). It was presumed that no FR curves would be Type I (nonasymptotic), because this is found exclusively with filter feeders (Jeschke et al. 2004). Model selection was accomplished by means of three different methods. The first method tested for the indication of either a Type II or Type III curve utilizing Juliano's method (*frair_test* function of the FRAIR package) to fit logistic functions to proportional consumption data to determine the best curve fit (Pritchard et al. 2017). The second model selection method allowed the variable q, a scaling exponent, to vary while using the *frair_fit* function to fit a generalized FR curve. In Type II curves, q is equal to 0, whereas in Type III curves q is a value greater than 0 (Pritchard et al. 2017). The third model selection method involved a visual review of the proportion of the resource consumed as a function of the initial density of the resource (Alexander et al. 2012). A Type II response was indicated by the weighted regression decreasing, but if the weighted regression increased and then subsequently declined it was considered a Type III response (Pritchard et al. 2017).

When treatment models were chosen, the model was fitted with the *frair_fit* function (Pritchard et al. 2017). The FRAIR package used maximum likelihood estimation when the model was chosen and fitted (Pritchard et al. 2017). Rogers' random predator equation for nonreplaced prey was used to fit the model if the FR was Type II (Alexander et al. 2012). In contrast, a Type III FR was fitted with Hassell's equation (Alexander et al. 2012). Attack rates (a) and handling times (h) were extracted from these models and used to derive the FRR metric (a/h).

Models were compared using three methods once they were fitted (Grimm et al. 2020). If FR treatment curves were of the same type, the *frair_compare* function was selected as the comparison method. The second method of comparison produced 95% confidence intervals (CIs) for the model fit, and parameter estimates of the FR curve including attack rate and handling time through bootstrapping the model ($n = 999$) (Iacarella et al. 2015*a*; South et al. 2019; Grimm et al. 2020). The third method of comparison used the *frair_fit* function to identify individual FR curve parameters a and h, and compare their 95% CI (Grimm et al. 2020). Graphed FRs were further compared through visual inspection of CI overlap from bootstrapping, where a lack of statistical difference is indicated by the presence of CI overlap (South et al. 2019; Grimm et al. 2020). The derivation of FR curves allowed the comparison of resource consumption by round gobies and logperch at different temperature treatments.

To identify the effect of explanatory variables including life stage, temperature, and species on FR parameters, bootstrapped parameter estimates ($n = 30$) were combined into generalized linear models (GLMs) with a quasi-Poisson error distribution (South et al. 2019). Akaike information criterion (AIC) scores confirmed the selection of fixed effect interactions included in the model chosen for the response variable. Based on these criteria, a GLM including life stage and an interaction between species and temperature was selected. A Type III ANOVA and χ^2 reported the effect size of explanatory variables on the response variables' attack rate and handling time (South et al. 2019). Linear models and linear mixed models tested the effect of fish length, acclimation time, and holding tank on the proportion of prey eaten to identify potential confounding variables. These models also included prey density, temperature, species, life stage, and a species–temperature interaction as explanatory variables. AIC and Bayesian information criterion (BIC) scores established the fixed and random effects included in the model. The Kruskal–Wallis nonparametric test was utilized to identify potential significant differences in fish length within juvenile and adult experimental groups. All model assumptions and auto-correlations were examined prior to statistical analyses. Statistical details concerning AIC scores and parameter estimates are shown in Supplementary Tables S2, S3, and S4.

In cases where fish are reused between temperature trials, changes in FR metrics are likely to be a result of broad shifts in temperature rather than individual adaptation to experimental conditions or improved learning. When warming is the only environmental change experienced by fish, Avlijaš et al. (2022) reasoned that the use of prey from a species' natural environment and substantial acclimation to laboratory housing conditions cumulatively prevent the facilitation of improved learning abilities in fish between experiments. All conditions were met in our study, leading us to conclude that observed changes in feeding behaviour were a direct result of thermal influence.

Critical thermal maximum

The effects of acclimation temperature on the response variables CT_{max}, T_{ag}, T_{aw}, A_{aw}, and TSM were tested for round goby life stages and logperch using linear regression and linear mixed models (Table S5). BIC scores were used to confirm the selection of fixed effects (acclimation temperature, acclimation time, TL, length∗temperature interaction) and random effects (holding tank) included in the model chosen for each response variable (Tables S5, S6, and S7). Based on these criteria, a linear regression including acclimation temperature as a fixed effect was selected for all five response variables. Differences in CT_{max} and T_{ag} at both acclimation temperatures were analyzed using a paired t test within species. A Type III ANOVA tested for differences in response variables CT_{max}, T_{ag}, T_{aw}, A_{aw}, and TSM as a result of the explanatory variables species, temperature, and life stage. This was followed by a Tukey Kramer post hoc test with 95% CIs to generate pairwise estimates. Inspection of residual plots, Levene's test of equal variance, and the Shapiro–Wilk test for normality were conducted to examine model assumptions.

Results

Comparative functional responses

Mortality of juvenile and adult round gobies occurred during the 24-h experimental tank acclimation at 25 °C, during which 42.9% of juveniles and 7.1% of adult round gobies died. The difference in survival between juvenile and adult round gobies when exposed to identical experimental conditions was significant (Pearson's χ^2 test with Yates continuity correction, $\chi^2 = 7.71$, df = 1, $p < 0.01$). Water temperature and water quality were stable (nitrite, nitrate and ammonia levels remained negligible) throughout the acclimation periods and therefore were ruled out as causes of mortality (e.g., Table S10). Deceased individuals displayed no visible signs of illness (scale loss, fin damage, wounds) or parasites (e.g., water mould; *Ichthyophthirius multifiliis*). These high mortality rates prevented us from conducting FR trials for juvenile round gobies at the 25 °C treatment. In contrast, no mortality among logperch was observed during experimental trials.

FR curves were consistently Type II for both species across temperature treatments (Fig. 3; Table 1). The controls indicated that no prey were lost due to tank conditions. Adult gobies and logperch exhibited a lower handling time (and thus a higher maximum feeding rate) at 25 °C than at 18 °C, and juvenile round goby handling times were higher (and maximum feeding rate was lower) than both logperch and adult round gobies at 18 °C (Table 2). These results are supported by our GLM, which indicated that handling times were significantly affected by species, temperature, and life stage (Table 3*a*; $p < 0.001$; Tables S8 and S9). Our findings further demonstrate that logperch attack rates increase at 25 °C, whereas adult round goby attack rates remained consistent across both temperature treatments (Table 2). Attack rates were influenced significantly by life stage ($p < 0.01$) and temperature ($p < 0.001$) (Table 3*b*). Juvenile round gobies displayed attack rates similar to those of logperch at 18 °C; however, attack rates were lower than those of adult gobies at this temperature.

The FRR of adult round gobies was higher than logperch at 18 and 25 °C, supporting our prediction, and higher than juvenile gobies at 18 °C (Table 1). Both logperch and adult round gobies displayed a higher FRR at 25 °C than at 18 °C, whereas juvenile round gobies at 18 °C had the lowest feeding efficiency among all groups (Table 1). Variation in acclimation time had no significant effect on the proportion of prey eaten among species and life stages (range of p values: 0.225–0.895). Additionally, fish length did not significantly affect the proportion of prey eaten (range of p values: 0.405–0.639) and did not differ within tested groups of juveniles ($p = 0.09$) and adults ($p = 0.17$) (Fig. S1).

Critical thermal maximum

The CT_{max} varied in response to acclimation temperature. As predicted, both species displayed significantly greater CT_{max} when acclimated to 25 °C, showing improved resilience to thermal stress at higher acclimation temperatures (Fig. 4). Mean CT_{max} values were identified as 32.25, 32.56, and 33.01 °C for logperch, juvenile round gobies, and adult round gobies, respectively, at 18 °C (Table 4). When acclimated to 25 °C, these values increased significantly to 35.28, 34.61, and 34.65 °C, respectively. The TSM declined with increasing acclimation temperature for both species and life stages. For logperch, juvenile round gobies, and adult round gobies, TSM decreased from 14.25, 14.56, and 15.01 °C, respectively, at 18 °C, to 10.27, 9.61, and 9.65 °C, respectively, at 25 °C (Table 4; Fig. 5). Both CT_{max} and TSM were significantly affected by acclimation temperature and species, but not life stage (Table 5). There was also a significant interaction between acclimation temperature and species (Table 5), implying that the relationships between CT_{max} and acclimation temperature and TSM and acclimation temperature are species dependent. Juvenile logperch CT_{max} and TSM were significantly lower than adult round gobies at 18 °C but did not differ from juvenile round gobies at this temperature (Tukey–Kramer post hoc test;

Fig. 3. Type II functional response curves for (*a*) logperch (*Percina caprodes*) at 18 °C (blue), (*b*) logperch (*P. caprodes*) at 25 °C (green), (*c*) adult round goby (*Neogobious melanostomus*) at 18 °C (orange), (*d*) adult round goby (*N. melanostomus*) at 25 °C (red), and (*e*) juvenile round goby (*N. melanostomus*) at 18 °C (pink). Shading represents bootstrapped 95% confidence intervals at both temperature treatments. $n = 3$–4 fish per treatment.

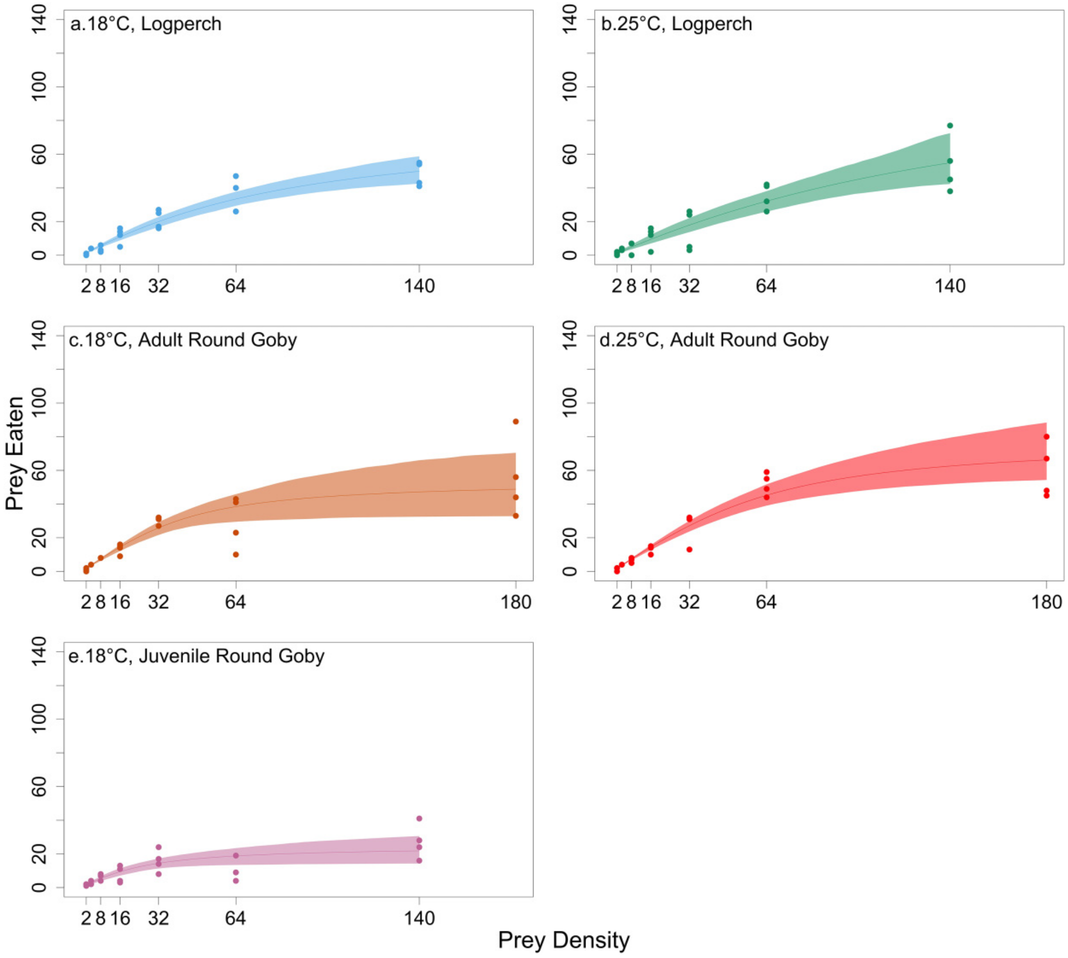


Table 1. Fit coefficients and functional response ratio (FRR) for fitted functional response curves for *Percina caprodes*, juvenile *Neogobius melanostomus*, and adult *N. melanostomus.*

Species	Temperature	Type	Estimate	a	h	$1/h$	FRR (a/h)
P. caprodes	18 °C	II	-0.011^{***}	0.447^{***}	0.040^{***}	25	11.18
P. caprodes	25 °C	II	-0.006^{***}	0.326^{***}	0.027^{***}	37.04	12.07
Juvenile *N. melanostomus*	18 °C	II	-0.012^{***}	0.483^{***}	0.122^{***}	8.197	3.975
Adult *N. melanostomus*	18 °C	II	-0.013^{***}	1.056^{***}	0.056^{***}	17.86	18.86
Adult *N. melanostomus*	25 °C	II	-0.016^{***}	0.961^{***}	0.038^{***}	26.34	25.29

Note: Asterisks denote significant p values ($^{***} < 0.001$). "Estimate" = first-order probability estimate for change in prey consumption, as measured in the logistic regression; a = attack rate; h = handling time; $1/h$ = maximum feeding rate.

Table 6; Fig. 4). At 25 °C, logperch displayed a CT_{max} similar to adult round gobies, but significantly higher than juvenile round gobies (Table 6; Fig. 4). CT_{max} did not differ between round goby life stages at both acclimation temperatures.

T_{ag} was observed for logperch, but not for the round goby. For both the juvenile and adult life stages, round gobies failed to exhibit agitated swimming behaviour for a period longer than 40 s at either T_{acc}; therefore, this metric was not recorded for the round goby. Instead, round gobies were observed to swim around the breeding box for repeated shorter durations of approximately 5–10 s. For logperch, T_{ag} increased from 27.62 °C (at 18 °C) to 31.73 °C (at 25 °C) (Table 4*a*; Fig. 6*a*). Using a paired t test, T_{ag} was found to be significantly lower than CT_{max} at both 18 °C ($n = 12$, $t = 5.298$, $p < 0.001$) and 25 °C ($n = 12$, $t = 4.064$, $p < 0.01$). The A_{aw} decreased from 9.62 °C (at 18 °C) to 6.74 °C (at 25 °C) ($p < 0.05$; Table 4*a*; Fig. 6*b*). However, acclimation temperature did not affect T_{aw} ($p > 0.05$; Table 4*a*; Fig. 6*b*).

Logperch displayed a higher acclimation capacity than both round goby life stages. The ARR for logperch was 0.431

Table 2. Results of a difference test, *frair_compare*, for attack rates (*a*) and handling times (*h*) for *Percina caprodes*, juvenile *Neogobius melanostomus*, and adult *N. melanostomus.*

Fit 1	Fit 2	Parameter	Estimate	Std. error	*p* value
P. caprodes 18 °C	*P. caprodes* 25 °C	Δa	0.121	0.054	$<0.05^{*}$
		Δh	0.013	0.006	$<0.05^{*}$
P. caprodes 18 °C	Juvenile *N. melanostomus* 18 °C	Δa	− 0.037	0.092	0.689
		Δh	− 0.081	0.013	$<0.001^{***}$
Adult *N. melanostomus* 18 °C	Juvenile *N. melanostomus* 18 °C	Δa	0.572	0.149	$<0.001^{***}$
		Δh	− 0.066	0.013	$<0.001^{***}$
Adult *N. melanostomus* 18 °C	Adult *N. melanostomus* 25 °C	Δa	0.095	0.152	0.529
		Δh	0.017	0.004	$<0.001^{***}$

Note: Asterisks denote significant *p* values ($^{***} < 0.001$; $^{*} < 0.05$).

Table 3. Results from generalized linear models with a quasi-Poisson error distribution determining differences in bootstrapped ($n = 30$) estimates of handling times and attack rates for *Percina caprodes*, juvenile *Neogobius melanostomus*, and adult *N. melanostomus* in response to acclimation temperature, using a Type III ANOVA and χ^2 test to report the effect size of explanatory variables on the response variable.

(a) Handling times			
Factor	χ^2	df	*p* value
Species	282.8	1	$<0.001^{***}$
Temperature	49.93	1	$<0.001^{***}$
Life stage	136.2	1	$<0.001^{***}$
Species*Temperature	0.234	1	0.628
(b) Attack rates			
Factor	χ^2	df	*p* value
Species	0.027	1	0.828
Temperature	10.41	1	$<0.01^{**}$
Life stage	157.6	1	$<0.001^{***}$
Species*Temperature	4.653	1	0.221

Note: Asterisks denote significant *p* values ($^{***} < 0.001$; $^{**} < 0.01$)

between 18 and 25 °C, followed by juvenile round gobies (0.293) and adult round gobies (0.234).

Discussion

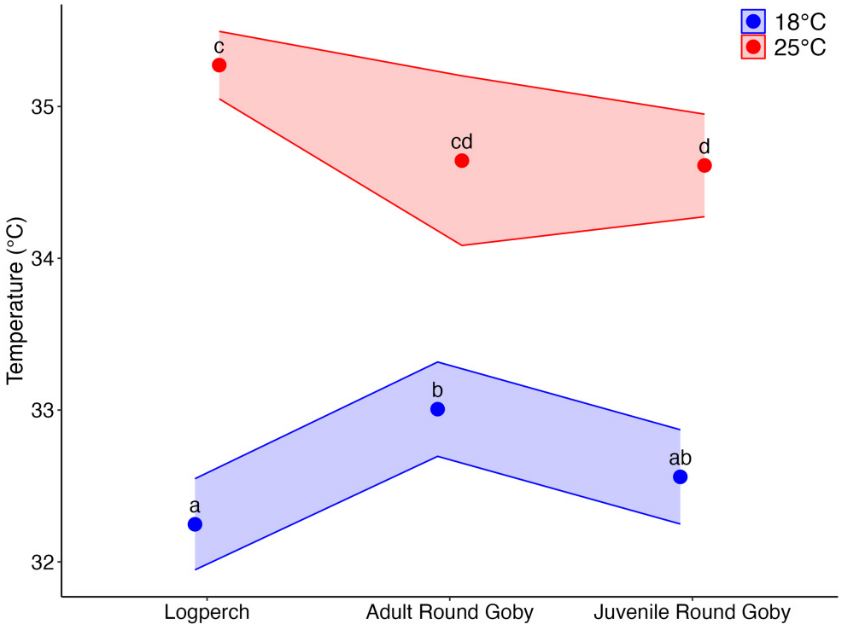
Our results suggest that food resource consumption and thermal tolerance of both round goby and logperch will rise under projected climate warming. The FRR and maximum feeding rate of adult round gobies were greatest at 25 °C, consistent with the predicted amplification of per capita effects at temperatures matching their thermal growth optimum (cf. Iacarella et al. 2015*a*). Logperch feeding efficiency exceeded that of juvenile round gobies at current water temperatures, suggesting that round gobies consume resources less efficiently than some native species in sub-optimal thermal conditions. $\mathrm{CT}_{\mathrm{max}}$ increased proportionally with rising acclimation temperature but differed between species, reflecting the influence of past thermal exposure and species identity on thermal tolerance of functionally similar fishes.

Effects of temperature on feeding behaviour

Our experiments found increased prey consumption by both adult round gobies and juvenile logperch at the elevated temperature. As predicted, adult round gobies exhibited reduced handling times, higher maximum feeding rates, and a higher FRR at 25 °C. For fish in general, warmer temperatures stimulate a spike in metabolic demands that require an increase in food intake, whereas suboptimal temperatures elicit a reduction in feeding (Volkoff and Rønnestad 2020). Reid and Ricciardi (2022) identified a peak in prey consumption by various adult round goby populations at temperatures of 18–24 °C. Our findings support the environmental matching hypothesis (Iacarella et al. 2015*a*), as we observed increased per capita effects in round gobies in conditions matching their reported temperature preferendum of ∼25 °C (Lee and Johnson 2005; Hatton et al. 2018). The findings are also consistent with the results of a bioenergetics modelling study that observed round goby food consumption to increase with temperature up to 26 °C before sharply declining (Lee and Johnson 2005). From these findings we predict that round gobies will increase their ecological impacts in the lower Great Lakes and upper St. Lawrence River as future climatic conditions drive nearshore water temperatures toward their preferred optima (Trumpickas et al. 2009, 2015), although not beyond that point. Logperch demonstrated comparable behaviour by exhibiting a lower handling time and a higher attack rate, maximum feeding rate, and FRR in projected higher water temperatures. Logperch metalarvae are known to have a final temperature preferendum of 21–25 °C (Floyd et al. 1984), which implies that logperch are approaching their thermal optimum at higher temperatures, which would correspond with their observed spike in resource consumption at 25 °C. Logperch possessing similar thermal preferences to the invasive round goby may forestall a disadvantage in interspecific competition for resources as their shared habitats continue to warm.

Both the invader and native species displayed Type II prey population de-stabilizing behaviour in current and projected water temperatures. Additionally, for adult round gobies, temperature elicited significant differences in handling time, but not attack rate. One potential explanation for this result is provided by a meta-analysis that showed that attack rate and handling time are not maximized at the same temper-

Fig. 4. Mean values of critical thermal maximum (CT_{max}; ±95% confidence interval (CI)) of logperch (*Percina caprodes*), adult and juvenile round gobies (*Neogobius melanostomus*) at two acclimation temperatures. Acclimation periods to trial temperatures continued for 4–6 weeks. Different letters represent homogenous groupings ($p < 0.05$) derived from a post hoc Tukey Kramer's test, with shading representing 95% CIs.



ature (Uiterwaal and DeLong 2020). In addition, our experimental design might have lacked the general complexity required to detect a shift in FR type among species; the incorporation of mobile prey and heterogeneous substrate types can reveal ecologically relevant behaviours (Avlijaš et al. 2022).

Resource consumption is also affected by body size (Toscano and Griffen 2013; Schröder et al. 2016; Avlijaš et al. 2022). Adult round gobies were larger in body size and exhibited higher prey consumption than juveniles in current water temperatures. Since FRs can predict field impacts (Dick et al. 2014), we expect round goby per capita effects on prey populations in the field to be mediated by their body size and life stage.

At 18 °C, the lower FRR for juvenile gobies suggest that they are less efficient foragers than juvenile logperch and are unlikely to outcompete logperch of similar size and abundance for prey resources. Typically, invasive species exhibit higher FRs than their native trophic counterparts (e.g., Alexander et al. 2014; Dick et al. 2014; Laverty et al. 2017), because of an increased foraging efficiency resulting from selective pressures during the invasion process (Morrison and Hay 2011; Hudina et al. 2014; Mathakutha et al. 2019). Selective pressures, including per capita effects, may also change with time-since-invasion such that more recently established populations or individuals at the front of an expanding population, may have higher per capita effects than longer established populations or population cores (e.g., Iacarella and Ricciardi 2015*b*). Indeed, a more recently established population of round gobies in the Trent–Severn Waterway exhibited a higher maximum feeding rate (1/*h*) than resident logperch, in contrast with our findings (Paton et al. 2019). Bolder round gobies, such as those selected at the invasion front, have a higher standard metabolic rate than shy conspecifics (Behrens et al. 2020), and this cause them to have a higher FR.

While FRRs serve to identify high-impact predators by quantifying their per capita effects on prey populations (Cuthbert et al. 2019), relative impact potential accounts for numerical response (using proxies such as predator abundance) when quantifying ecological impacts (Dick et al. 2017*b*). Though juvenile round gobies were found to have relatively low per capita effects on prey populations at 18 °C, their high local abundance in invaded regions may contribute to greater trophic impacts.

Effects of acclimation on thermal tolerance

Temperature acclimation dictated the thermal performances of round gobies and logperch. CT_{max} for both species increased substantially with rising acclimation temperature but to similar limits, increasing to ≥33 °C after 18 °C acclimation and to ≤34.6 °C after 25 °C acclimation. We expected a linear relationship between CT_{max} and acclimation temperature, indicating the gain in heat tolerance when fish are acclimated to higher temperatures (Beitinger et al. 2000). The CT_{max} range for round gobies in our study (32.56–34.65 °C) aligns with findings of another study comparing round goby populations across a latitudinal gradient; round gobies from St. Lawrence River populations had a mean CT_{max} range of 31.72–34.06 °C when acclimated to 18 and 26 °C, respectively (values extrapolated using PlotDigitizer), and the study suggested that the CT_{max} peaked at 25 °C (Reid and Ricciardi 2022), which would support our detection of a higher thermal maximum at that corresponding acclimation temperature. Northern populations from two sites on the up-

Table 4. Linear regression models assessing the effects of acclimation temperature on thermal tolerance metrics of (a) *Percina caprodes*, (b) juvenile *Neogobius melanostomus*, and (c) adult *N. melanostomus*.

(a) *P. caprodes*				
Critical thermal maximum ($\mathrm{CT}_{\mathrm{max}}$)				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	32.25	0.12	268.6	$<0.001^{***}$
Acclimation temperature	3.025	0.16	17.82	$<0.001^{***}$
Agitation temperature (T_{ag})				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	27.62	0.81	33.92	$<0.001^{***}$
Acclimation temperature	4.114	1.15	3.573	$<0.01^{**}$
Agitation window (T_{aw})				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	4.625	0.86	5.341	$<0.001^{***}$
Acclimation temperature	−1.524	1.22	−1.245	0.22
Acclimation agitation window (A_{aw})				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	9.623	0.81	11.82	$<0.001^{***}$
Acclimation temperature	−2.886	1.15	−2.506	$<0.05^{*}$
Thermal safety margin (TSM)				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	14.25	0.12	118.7	$<0.001^{***}$
Acclimation temperature	−3.975	0.17	−23.42	$<0.001^{***}$
(b) Juvenile *N. melanostomus*				
Critical thermal maximum ($\mathrm{CT}_{\mathrm{max}}$)				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	32.56	0.15	220.9	$<0.001^{***}$
Acclimation temperature	2.052	0.21	9.841	$<0.001^{***}$
Thermal safety margin (TSM)				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	14.56	0.15	98.77	$<0.001^{***}$
Acclimation temperature	−4.948	0.21	−23.42	$<0.001^{***}$
(c) Adult *N. melanostomus*				
Critical thermal maximum ($\mathrm{CT}_{\mathrm{max}}$)				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	33.01	0.19	176.8	$<0.001^{***}$
Acclimation temperature	1.637	0.27	6.036	$<0.001^{***}$
Thermal safety margin (TSM)				
Fixed effect	Estimate	SE	*t* value	*p* value
(Intercept)	15.01	0.19	80.37	$<0.001^{***}$
Acclimation temperature	−5.363	0.27	−19.77	$<0.001^{***}$

Note: Asterisks denote significant *p* values (*** < 0.001; ** < 0.01; * < 0.05).

per St. Lawrence River (Melocheville and Sorel-Tracy, Quebec) were found to have maximum $\mathrm{CT}_{\mathrm{max}}$ tolerances of 34.06 and 33.74 °C, respectively, when acclimated to 26 °C (Reid and Ricciardi 2022). These tolerance levels were analogous to those determined in our study, suggesting similar thermal tolerance and susceptibility to thermal stress across these northern fish populations. Similar results were obtained in a study of round gobies collected from the Baltic Sea, which found a $\mathrm{CT}_{\mathrm{max}}$ of 34.0 ± 0.1 °C for fish acclimated at 28 °C (Christensen et al. 2021).

A broad range of ARRs (ARR = 0.07–0.91) have been reported for freshwater fishes, including those with mid-latitude populations (Beitinger et al. 2000; Comte and Olden 2017; Morley et al. 2019; McDonnell et al. 2021). Our measured ARR values for both round goby life stages fall within the range previously measured for round goby populations in the St. Lawrence River (0.16–0.29; Reid and Ricciardi 2022), further suggesting that fish populations at this latitude exhibit similar acclimation capabilities to thermal change (Dı́az et al. 2002; Reid and Ricciardi 2022). The ARR value for native logperch determined in this study falls within the range of other mid-latitude freshwater fishes and was higher than round gobies, suggesting a superior acclimation capacity. Since all observed $\mathrm{CT}_{\mathrm{max}}$ values for juvenile

Fig. 5. Effects of acclimation temperature on mean thermal safety margin (TSM; ±SE) of logperch (*Percina caprodes*) and adult and juvenile round gobies (*Neogobius melanostomus*) at two acclimation temperatures. Fish were exposed to the corresponding acclimation temperature 4–6 weeks prior to trials.

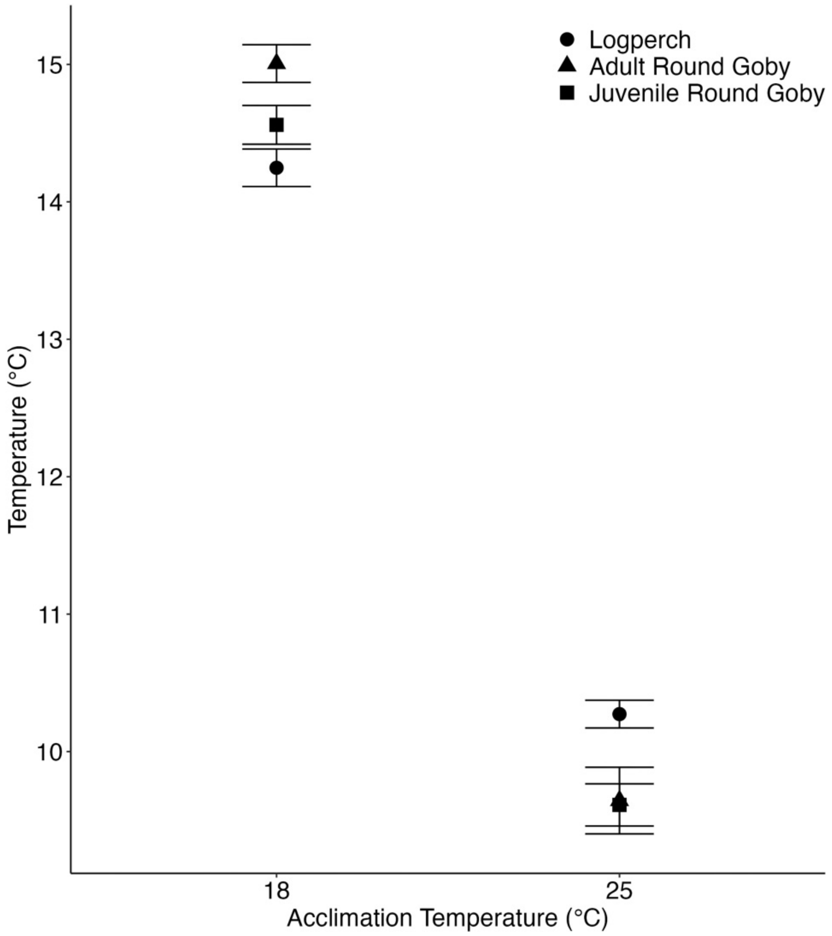


Table 5. Results of a Type III ANOVA examining the effects of acclimation temperature, species, life stage, and species–temperature interaction on the thermal tolerance metrics for *Percina caprodes*, juvenile *Neogobius melanostomus*, and adult *N. melanostomus*.

(a) CT_{max}			
Factor	*F*	df	*p* value
Temperature	213.8	1	$<0.001^{***}$
Species	4.284	1	$<0.05^{*}$
Life stage	2.476	1	0.1207
Species: temperature	20.03	1	$<0.001^{***}$
(b) TSM			
Factor	*F*	df	*p* value
Temperature	369.2	1	$<0.001^{***}$
Species	4.284	1	$<0.05^{*}$
Life stage	2.476	1	0.1207
Species: temperature	20.03	1	$<0.001^{***}$

Note: Asterisks denote significant *p* values ($^{***} < 0.001$; $^{*} < 0.05$). CT_{max}, critical thermal maximum; TSM, thermal safety margin.

logperch and round goby were found to exceed projected water temperatures in the Great Lakes region (Trumpickas et al. 2009, 2015), they might prove resilient to the adverse impacts of climate warming in the near future—if given sufficient time for acclimation (Catullo et al. 2015). Based on the aerobic metabolic rates and CT_{max} of a Baltic Sea population, Christensen et al. (2021) similarly concluded that the round goby had a high level of thermal resilience that made the species competitive under continuing climate change.

Contrary to our hypothesis, round gobies did not consistently demonstrate superior thermal tolerance than juvenile logperch. Only when acclimated to current climate conditions did adult round gobies show greater thermal resilience than logperch, reflecting the broad tolerance and niche breadth generally associated with highly successful invasive species (Vázquez 2006; Mathakutha et al. 2019). However, juvenile logperch thermal tolerance was greater than that of juvenile round gobies when acclimated to future climate conditions. In combination with the observed mortality in our feeding experiments, we suspect that the juvenile round goby life stage possesses reduced abilities to cope with

Table 6. Results of post hoc Tukey–Kramer's test with 95% confidence intervals examining the effects of acclimation temperature, species, life stage, and species–temperature interaction on the thermal tolerance metrics for *Percina caprodes*, and juvenile and adult *Neogobius melanostomus*.

(a)CT$_{max}$

Comparison	Estimate	SE	df	*t* ratio	*p* value
P. caprodes 18 °C vs. juvenile *N. melanostomus* 18 °C	– 0.404	0.195	62	– 2.070	0.4454
P. caprodes 25 °C vs. juvenile *N. melanostomus* 25 °C	0.752	0.195	62	3.855	0.0064^{**}
Adult *N. melanostomus* 18 °C vs. *P. caprodes* 18 °C	0.649	0.201	62	3.233	0.0388^{*}
Adult *N. melanostomus* 25 °C vs. *P. caprodes* 25 °C	0.245	0.156	62	1.573	0.7639
Adult *N. melanostomus* 18 °C vs. juvenile *N. melanostomus* 18 °C	– 0.507	0.204	62	– 2.489	0.2195
Adult *N. melanostomus* 25 °C vs. juvenile *N. melanostomus* 25 °C	0.245	0.156	62	1.573	0.7639
P. caprodes 18 °C vs. *P. caprodes* 25 °C	– 3.025	0.207	62	– 14.62	$<0.001^{***}$
Juvenile *N. melanostomus* 18 °C vs. juvenile *N. melanostomus* 25 °C	– 1.869	0.155	62	– 12.08	$<0.001^{***}$
Adult *N. melanostomus* 18 °C vs. adult *N. melanostomus* 25 °C	– 1.869	0.155	62	– 12.08	$<0.001^{***}$

(b) TSM

Comparison	Estimate	SE	df	*t* ratio	*p* value
P. caprodes 18 °C vs. juvenile *N. melanostomus* 18 °C	– 0.404	0.195	62	– 2.070	0.4454
P. caprodes 25 °C vs. juvenile *N. melanostomus* 25 °C	0.752	0.195	62	3.855	0.0064^{**}
Adult *N. melanostomus* 18 °C vs. *P. caprodes* 18 °C	0.649	0.201	62	3.233	0.0388^{*}
Adult *N. melanostomus* 25 °C vs. *P. caprodes* 25 °C	– 0.507	0.204	62	– 2.489	0.2195
Adult *N. melanostomus* 18 °C vs. juvenile *N. melanostomus* 18 °C	0.245	0.156	62	1.573	0.7639
Adult *N. melanostomus* 25 °C vs. juvenile *N. melanostomus* 25 °C	0.245	0.156	62	1.573	0.7639
P. caprodes 18 °C vs. *P. caprodes* 25 °C	3.975	0.207	62	19.214	$<0.001^{***}$
Juvenile *N. melanostomus* 18 °C vs. juvenile *N. melanostomus* 25 °C	5.131	0.155	62	33.179	$<0.001^{***}$
Adult *N. melanostomus* 18 °C vs. adult *N. melanostomus* 25 °C	5.131	0.155	62	33.179	$<0.001^{***}$

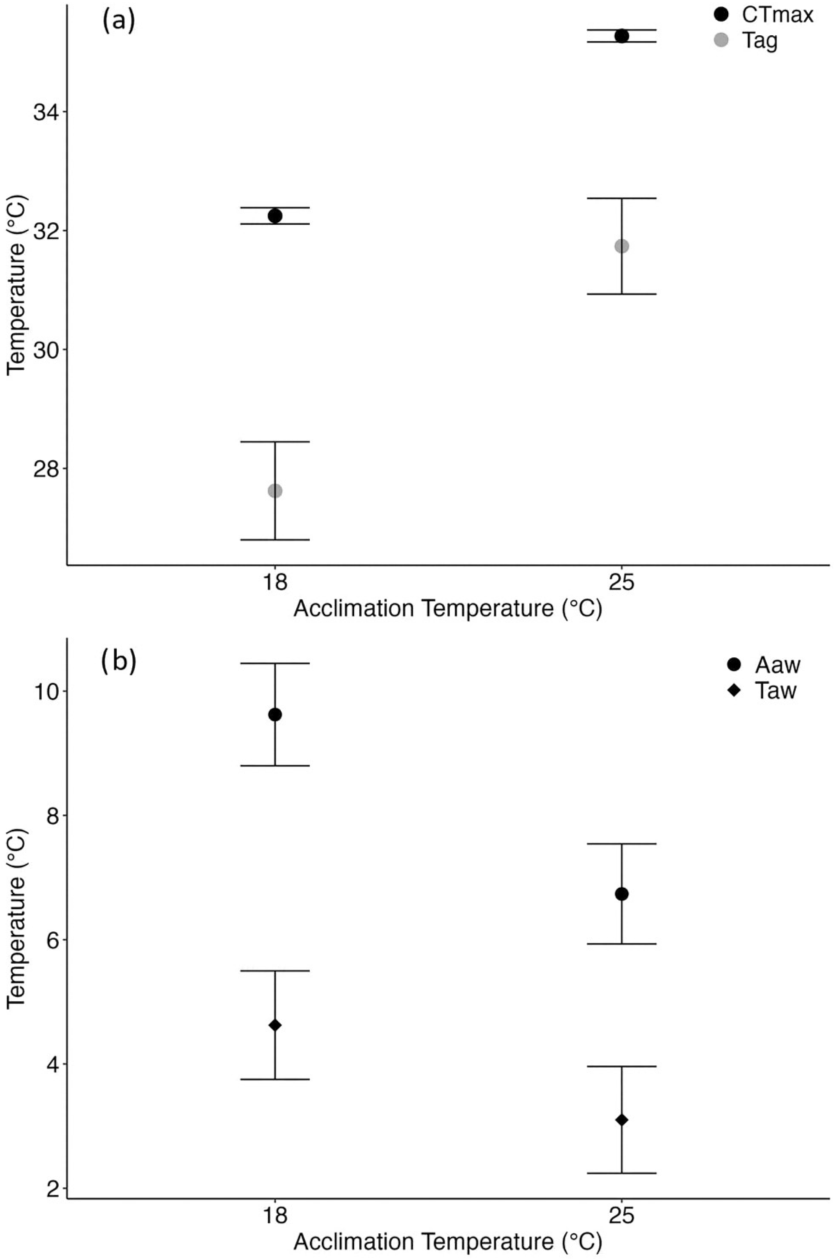
Note: Asterisks denote significant *p* values (*** < 0.001; ** < 0.01; * < 0.05). CT$_{max}$, critical thermal maximum; TSM, thermal safety margin.

thermal stress at higher temperatures compared with logperch. It is important to note that the thermal tolerance of juvenile logperch in our study was similar to that of juvenile round gobies at low temperatures and of adult round gobies at high temperatures. Studies have shown a lack of generality when it comes to defining a relationship between thermal tolerance and life stage (Recsetar et al. 2012; Troia et al. 2015; Turko et al. 2020). In our experiment, CT$_{max}$ did not differ significantly between round goby life stages. For some freshwater fishes, upper thermal tolerance was found to be relatively unaffected by size for life stages encompassing fry to adults and subadults (e.g., Recsetar et al. 2012), whereas other fishes show significant variation across size and life stage (e.g., Zhang and Kieffer 2014; Andrew et al. 2024). Despite differences in body size, round goby populations in the St. Lawrence River yielded comparable acclimation capabilities (Reid and Ricciardi 2022). Therefore, we suspect that thermal tolerance is fairly consistent across sizes of adults within our examined round goby population. Nevertheless, our findings highlight the value of examining the influence of life stages on the thermal resilience of independent fish populations, as there is presently a lack of evidence to make specific generalizations. We further contend that thermal tolerance is population-specific and related to the population's latitudinal position within a region determining its history of thermal exposure, as opposed to being characteristic of a particular species or life stage across its range. Southern round goby populations in the Great Lakes basin have been found to display higher ARRs and an improved acclimation response in comparison to their northern equivalents, indicating latitudinal (or climatic) influences (Reid and Ricciardi 2022). Perhaps both species and life stages examined in this study displayed similar thermal tolerance levels because of their shared latitudinal positions.

Logperch and round gobies could withstand changing thermal conditions for a longer period when acclimated to a lower temperature, as indicated by their TSM. For fishes, TSM is generally inversely correlated with T$_{acc}$ (McDonnell et al. 2021) and a reduced TSM in projected climate conditions insinuates increased susceptibility to temperature-induced stress. Like the pattern observed for CT$_{max}$, logperch displayed a lower TSM than adult round gobies and a higher TSM than juvenile round gobies in current and projected future temperatures, respectively. Therefore, we infer that juvenile logperch are less vulnerable than round gobies of similar sizes to thermal stress when acclimated to warmer conditions.

Thermal agitation temperature, thermal agitation window, and acclimation agitation window metrics were quantified only for logperch, owing to a lack of prolonged agitation behaviour in round gobies. T$_{ag}$ is recognized as a thermal stress indicator of the onset of avoidance behaviour as fish attempt to find thermal refugia (McDonnell and Chapman 2015). This agitated response typically overcomes behaviours associated with fitness, including predator avoidance or feeding (McDonnell and Chapman 2015). For logperch, T$_{ag}$ was significantly lower than CT$_{max}$ at both acclimation tempera-

Fig. 6. Mean values of thermal metrics for logperch (*Percina caprodes*) at two acclimation temperatures: (*a*) critical thermal maximum (CT_{max}; ±SE) and thermal agitation temperature (T_{ag}; ±SE); (*b*) acclimation-agitation window (A_{aw}; ±SE) and thermal agitation window (T_{aw}; ±SE). Acclimation periods to trial temperatures continued for 4–6 weeks.



tures (a pattern observed across fish species; McDonnell and Chapman 2015; Wells et al. 2016), implying that logperch began exhibiting avoidance behaviour and seeking refuge from harsh thermal environments before their CT_{max} was reached (cf. Christensen et al. 2021). Furthermore, T_{ag} demonstrated an identical relationship to CT_{max} by increasing significantly with acclimation temperature. Avoidance behaviour occurring later in logperch acclimated to 25 °C is indicative of a higher temperature threshold when exposed to projected water temperatures. Although there was a delay in the onset of T_{ag} at high temperatures, the duration of agitated behaviour (T_{aw}) remained consistent across acclimation temperatures. A longer T_{aw} is considered unfavourable because individuals will change their behaviour earlier to seek thermal refuge (Wells et al. 2016; McDonnell et al. 2019, 2021). Consistency in the T_{aw} between current and projected water temperatures eliminates this additional risk for logperch. Finally, there was a trend toward a shorter A_{aw} for logperch acclimated to a higher temperature, indicating a hastened onset of avoidance behaviour from thermal stress. This suggests that juvenile logperch in high-temperature environments are increasingly sensitive to rising thermal conditions, burdening them with ecological disadvantages as their agitated behaviour may remove them from their refuge and expose them to predators (Kochhann et al. 2021; McDonnell et al. 2021).

Caveats and future directions

While FR experiments provide us with quantitative evidence of the feeding efficiency of consumers, their predictive and comparative power is ultimately limited by specific experimental designs. As a result of reusing fish, temperature trials were conducted consecutively, beginning at 18 °C and concluding at 25 °C, eliminating randomization—which could present a potential confounding factor when comparing FR results with other studies (Avlijaš et al. 2022). To allow direct comparisons of derived FR metrics with published literature, experimental protocols should be standardized. The influence of experimental design characteristics including prey type and habitat complexity on a predator's feeding behaviour generates heterogeneity among studies that, although expanding our understanding of context dependencies, contributes to a lack of consistency that constrains comparisons of published experimental results.

Although our results offer insight into the trophic dynamics of the Great Lakes benthic fishes in response to climate warming, the absence of a FR curve for juvenile round gobies at projected high-water temperatures is a gap in our understanding of the differential feeding responses of invaders in comparison with natives under climate warming. The increased feeding efficiency of adult round gobies in warmer temperatures could signify the behaviour of this species throughout all life stages. However, juvenile round gobies from the upper St. Lawrence River demonstrate higher growth rates at 18 °C compared to 26 °C (D'Avignon et al. 2023), possibly reflecting a greater ability to assimilate food at the lower temperature (Reid and Ricciardi 2022). Future research should strive to test the FR curve for juvenile round gobies exposed to projected warmer temperatures. In addition, a comparison of adult and juvenile logperch FR under ambient and elevated temperatures would fill gaps in the understanding how logperch life stages impact their feeding efficiency and thermal tolerance.

Differential mortality rates were observed in juvenile and adult round gobies when subjected to high temperatures and handling stress, indicating variation in thermal stress coping abilities between life stages and increased sensitivity in juveniles. However, both life stages exhibited similar upper thermal tolerance limits during CT_{max} experiments—although it is conceivable that more thermally sensitive juveniles were removed through mortality during these experiments. As fish were reused between FR experiments at 18 and 25 °C, individuals were exposed to handling prior to 25 °C trials, whereas CT_{max} fish were left undisturbed for a longer duration. Additionally, it is important to note that CT_{max} individuals were acclimated to the high-temperature treatment 2 weeks longer than individuals in FR trials. Thus, we hypothesize that the juveniles required an extended acclimation time to reduce their sensitivity to external stressors.

In summary, our experiments revealed nuances of the thermal ecology and temperature-mediated FR of trophically analogous native and invasive species. The results highlight a need for invasive species risk assessments to include information on thermal metrics and to explicitly consider the performance and resilience of target species in a rapidly changing climate.

Acknowledgements

We thank Noemie Sheppard and Geneviève D'Avignon for their advice. We also thank Courtney Holden for contributing to the data collection of this project, and Catalina Claus, Brielle Comartin, Kennedy Zwarych, Jennifer Pham, Maya Moghrabi, Audrey Blanchette, Claire Boudard, Angelina Nikolaeva, Layla Razek, Elizabeth Hall, Elizabeth Grohmann, Emma Ehrenfeld, and Bailey Ruest for assistance in the field and laboratory.

Article information

History dates

Received: 3 July 2024
Accepted: 16 January 2025
Accepted manuscript online: 27 February 2025
Version of record online: 26 March 2025

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Data availability

Data, supplementary material, and code are available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.1jwstqk3z.

Author information

Author ORCIDs

Jaclyn Hill https://orcid.org/0000-0003-0703-3772
Matthew J.S. Windle https://orcid.org/0000-0003-1109-9571
Anthony Ricciardi https://orcid.org/0000-0003-1492-0054

Author contributions

Conceptualization: MH, JH, AR
Data curation: MH
Formal analysis: MH
Funding acquisition: AR
Investigation: MH, MJSW
Methodology: MH, JH, MJSW, AR
Supervision: JH, AR
Visualization: MH
Writing – original draft: MH
Writing – review & editing: JH, MJSW, AR

Competing interests

The authors declare no competing interests.

Funding information

This research was supported by a Fisheries and Oceans Canada grant (ITS2021-008) to AR.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0195.

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