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

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Abstract

Climate change mediates the survival, performance, and ecological effects of invasive species and co-occurring native species. Data on the responses of these species to changing thermal conditions are needed for assessing which habitats are most vulnerable to invasion and which species are most likely to be disruptive. Spatiotemporal variation in performance is considered in the Environmental Matching Hypothesis, which predicts that the *per capita* effect of an invader is inversely related to the distance of abiotic habitat conditions from the invader's physiological optimum. A systematic literature review of field and laboratory studies of invasive aquatic animals found broad support for the hypothesis and highlights the value of this predictive framework for guiding risk assessment.

Currently, the most invasive freshwater fish in the Great Lakes-St. Lawrence River basin is the round goby (*Neogobius melanostomus*), a Ponto-Caspian species that has had strong impacts on native benthic invertebrates and fish assemblages in the basin. To understand the resource consumption dynamics and thermal tolerances of ecologically similar native and invasive species under climate warming, I measured the functional responses and critical thermal maxima of juvenile and adult round gobies and a trophically analogous native fish, logperch (*Percina caprodes*), when acclimated to current and projected surface water temperatures in the Great Lakes region. I tested the predictions that 1) round gobies would possess superior foraging abilities and broader thermal tolerance than their native counterpart, 2) resource consumption efficiency and critical thermal maximum tolerance (CT_{max}) of both species to increase with acclimation to elevated temperature, and 3) species perform better at a temperature that closely matches its reported physiological optimum. As predicted, resource consumption and CT_{max} for both species increased with acclimation and at temperatures closer to their physiological optima. Contrary to predictions, logperch consumed more prey and exhibited a greater thermal capacity than round gobies, suggesting that the outcome of competitive interactions may change in the near future—but with the caveat that the outcome will also depend on relative differences in reproduction and resource availability, among other environmental factors.

Résumé

Le changement climatique influence la survie, la performance et les effets écologiques des espèces envahissantes ainsi que des espèces indigènes. Des données sur les réponses de ces espèces aux conditions thermiques changeantes sont nécessaires pour évaluer quels habitats sont les plus vulnérables à l'invasion et quelles espèces sont les plus probables d'être perturbatrices. La variation spatiotemporelle des performances est prise en compte dans l'Hypothèse de Correspondance Environnementale, qui prédit que l'effet *per capita* d'une espèce envahissante est inversement corrélé à la distance entre les conditions abiotiques de l'environnement et l'optimum physiologique de celle-ci. Une revue systématique des études de terrain et de laboratoire des animaux aquatiques envahissants a permis de soutenir largement cette hypothèse et souligner la valeur de ce cadre prédictif pour guider l'évaluation des risques.

Actuellement, le poisson d'eau douce le plus envahissant dans le bassin des Grands Lacs-Fleuve Saint-Laurent est le gobie à taches noires (*Neogobius melanostomus*), une espèce ponto-caspienne qui a eu de fortes impacts sur les invertébrés benthiques indigènes et les assemblages de poissons du bassin. Pour comprendre la dynamique de consommation de ressources et les tolérances thermiques d'espèces indigènes et envahissantes écologiquement similaires sous l'effet du réchauffement climatique, j'ai mesuré les réponses fonctionnelles et les maxima thermiques critiques des gobies à taches noires juvéniles et adultes, ainsi qu'un poisson indigène trophiquement analogue, le logperch (*Percina caprodes*), lorsqu'ils ont été acclimatés aux températures actuelles et projetées de l'eau de surface dans la région des Grands Lacs. J'ai testé les prédictions suivantes : 1) les gobies à taches noires possèderaient des capacités de fouille supérieures et une plus grande tolérance thermique que leur homologue indigène, 2) l'efficacité de la consommation de ressources et le maxima thermique critique (CT_{max}) des deux espèces augmenteraient avec l'acclimatation à une température élevée, et 3) les espèces auraient de meilleures performances à une température qui correspondrait étroitement à leur optimum physiologique. Comme prédit, la consommation de ressources et la CT_{max} des deux espèces ont augmenté avec l'acclimatation et à des températures plus proches de leurs optima physiologiques. Contrairement aux attentes, le logperch a consommé plus de proies et a montré une plus grande capacité thermique que le gobie à taches noires, suggérant que le résultat des interactions compétitives pourrait changer dans un avenir proche - mais avec la mise en garde que le résultat

dépendra également des différences relatives dans la reproduction et la disponibilité des ressources, parmi d'autres facteurs environnementaux.

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Contribution of Authors

This thesis was completed under the supervision of Prof. Anthony Ricciardi at McGill University, who will be a co-author on the submitted manuscript. All experiments, statistical analysis, and literature reviews were led by me, while Prof. Ricciardi contributed research ideas, assisted in developing research protocols, and edited drafts of this manuscript. Dr. Jaclyn Hill, who provided funding and advice on experimental protocols and research ideas, will also serve as a co-author. I planned and conducted field sampling and laboratory experiments in 2022&2023 with the advice and assistance of Matthew Windle, who will be the last co-author on the submitted manuscript.

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General Introduction and Literature Review

i. Biological Invasions and Context-Dependence of Invasive Species Impacts

For the purposes of this thesis, an invasive species is defined as a species that successfully establishes a self-sustaining population in an ecosystem where they lack previous evolutionary history (Ricciardi, 2007; Ricciardi et al., 2013). Anthropogenic activities and disturbances are largely responsible for the deliberate and unintentional dispersal of invasive species into new regions (e.g., Ricciardi, 2006), by facilitating an increase in propagule pressure, accessing new species pools, and providing opportunities for introduction to a broad range of environments (Clavero et al., 2013; Seebens et al., 2018). This has accelerated rates of invasion by several orders of magnitude since prehistoric times (Ricciardi, 2007), and modern rates show no signs of saturation (Seebens et al., 2017). The spread of invasive species triggered a wide variety of negative impacts including biodiversity loss, ecosystem degradation, habitat homogenization, loss of ecosystem services, and economic harm on a global scale (Pyšek et al., 2020).

Impacts generated by invasions are not fixed and can vary as a direct or indirect result of different environmental or biological contexts (Fig. 0.1) (Ricciardi et al., 2013). Context dependencies surrounding environmental heterogeneity and disturbances, natural and anthropogenic, can mediate an invader's impact. Spatial and temporal variation in habitat conditions can either permit/promote or exclude/repress invaders in a particular area, as determined by the invader's environmental tolerance, and thereby govern the outcome of species interactions and ecological impacts (Levine & Rees, 2004; Melbourne et al., 2007; Ricciardi et al., 2013). Similarly, disturbances can facilitate invader impacts to the detriment of native species by generating substantial ecosystem changes that favour particular invaders depending on their tolerance levels (MacDougall & Turkington, 2005; Ricciardi et al., 2013). Invader impacts have further been proven to vary spatially and temporally depending on the fit between abiotic contexts and species-specific physiological tolerances (Iacarella et al., 2015a; Ricciardi et al., 2013). Sub-optimal environmental conditions can directly inhibit the performance and population growth of an invasive species (Ricciardi et al., 2013). Given these environmental contexts and tolerances, interactions with native species in the invaded environment (i.e., competition, predation, parasitic) can directly limit the magnitude and scope of invader impacts

(Kestrup & Ricciardi, 2009b; Ricciardi et al., 2013). For example, invaders that are phylogenetically similar to species in the resident community may encounter resident enemies capable of constraining their population growth and render them less likely to displace natives; conversely, phylogenetically distinct invaders are more likely to encounter naïve enemies and prey, and thus can exert greater impacts (Ricciardi & Atkinson, 2004). Context dependencies limit our predictive understanding of impacts and create challenges for risk assessment of existing, emerging, and future invasive species.

ii. The Influence of Climate Warming

Anthropogenic climate change has implications for the success and performance of both invasive and native species across ecosystems and biomes (Christensen et al., 2020). In freshwater ecosystems, increasing water temperatures, altered stream flow patterns, and shorter durations of ice cover have been observed over the past few decades (e.g., Poff et al., 2002). In the lower Great Lakes basin, mean maximum surface water temperatures are predicted to rise from the current value to >25°C over the next few decades (Trumpickas et al., 2009, 2015), reflecting the limited thermal buffering capacity of nearshore freshwater habitats (O'Reilly et al., 2015).

Native species in the basin may be exposed to a greater risk of extirpation due to these heightened abiotic stressors (Rahel & Olden, 2008). In contrast, increasing water temperatures driven by climate change may create additional opportunities for aquatic invasive species (AIS) to expand their range (Sunday et al., 2012) and enhance their competitive and predatory effects if environmental conditions resemble those to which they are adapted (Rahel & Olden, 2008). Given that the thermal environment of freshwater fish and other ectotherms affects their behaviour, physiology, and life-history (Beitinger et al., 2000; Christensen et al., 2020), water temperatures rising to levels that match the physiological optima of invasive species could intensify the severity of their ecological impacts in invaded environments (Iacarella et al., 2015a). Conducting experiments that examine environmental-mediated variation in invader performance and impacts in a near future climate is crucial for informing risk assessment.

iii. Understanding Invader Impacts Using the Environmental Matching Hypothesis

The Environmental Matching Hypothesis (EMH) predicts that an invader's *per capita* effects will be greater as environmental conditions approach its physiological optimum (Iacarella et al., 2015a; Ricciardi et al., 2013). It is therefore expected that *per capita* effects will follow a modal curvilinear relationship analogous to an invader's performance curve (Angilletta, 2009). Noting that impact is a function of both the invader's *per capita* effect and abundance (Parker et al., 1999), the EMH could guide research and facilitate predictive risk assessment for invasive species management. To assess overall support for this hypothesis, I reviewed the literature using the following combination of search terms in Web of Science: [*environmental matching hypothesis* OR *environmental matching*] AND [*invasive species** OR *invader** OR *non-native** OR *exotic** OR *alien**] AND *impact**. I also searched articles citing Iacarella et al. (2015a). These combined searches yielded a total of 337 relevant articles. Based on my evaluations, I enumerated all studies with results supporting, partially supporting, or rejecting the hypothesis that AIS impacts (*per capita* effects) vary in space or time according to the difference between ambient and optimal (or adapted) physico-chemical conditions (Table 0.1).

Higher impacts under AIS optimal or adapted conditions were detected in 78% of studies reviewed. Case studies examined a variety of physico-chemical predictor variables that followed the relationship expected by the EMH, including conductivity (Dick & Platvoet, 1996; Kestrup & Ricciardi, 2009a), dissolved oxygen concentration (Laverty et al., 2015; MacNeil et al., 2004; Reid et al., 2013), calcium concentration (Iacarella et al., 2015b; Jokela & Ricciardi, 2008), salinity (Alcaraz et al., 2008), hydrology (Boddy et al., 2020; Costanzo et al., 2005) and temperature (Carmona-Catot et al., 2013; Khosa et al., 2020; Madzivanzira et al., 2021; Mofu et al., 2019; Priddis et al., 2009; Rincon et al., 2002; Rowe et al., 2007; Ruokonen & Karjalainen, 2022). Temperature was evidently the most studied variable, being the focus of 58% of articles matching the inclusion criteria in this review. From that subset, 42% of studies supported the hypothesis that AIS impacts increased in conditions approaching their thermal optimum. This result is further corroborated by a meta-analysis published in 2015, which evaluated 29 studies of the trophic impacts of various invasive freshwater fishes and crustaceans and found a significant relationship between impact and the invader's optimal temperature for growth (Iacarella et al., 2015a).

Dissolved oxygen was the second most-tested variable, accounting for ~10% of studies, and all of these studies supported the EMH. Optimal dissolved oxygen concentrations were observed to enhance AIS resource consumption (Laverty et al., 2015; Reid et al., 2013) and dominance in instances of interspecific competition (MacNeil et al., 2004). Among two studies examining salinity as a predictor variable, only one supported the EMH by observing increased predation and aggression by invasive mosquitofish in adapted conditions (Alcaraz et al., 2008). Conductivity, calcium concentration, and hydrologic regime as predictor variables each comprised ~7% of examined studies and exhibited trends supporting EMH. Invasive amphipods were found to be more effective predators in environments with conductivity levels matching their optima (Dick & Platvoet, 1996; Kestrup & Ricciardi, 2009a). In one case, the dominant intraguild predator in a pair of competing native and invasive amphipods switched across sites along a natural conductivity gradient in a fluvial lake, as local conditions shifted between their respective optima (Kestrup & Ricciardi, 2009a). Invasive animals from the Ponto-Caspian region (e.g., dreissenid mussels, gammarid amphipods, gobiid fishes) are adapted to ion-rich waters (Reid & Orlova, 2002). As predicted by the EMH, these species have exhibited increased competitive abilities such as fouling intensity (Jokela & Ricciardi, 2008) and feeding efficiency (Kestrup & Ricciardi, 2009a; Iacarella & Ricciardi, 2015b) in high-calcium or high-conductivity environments. In other studies, adapted stream flow conditions and moisture levels were observed to improve resource consumption (Boddy et al., 2020) and competitive dominance (Costanzo et al., 2005), respectively, by AIS. These studies illustrate that AIS *per capita* effects are sensitive to abiotic environmental context-dependencies, accounting for at least some of the spatial variation in observed field impacts. The EMH could therefore offer a framework for predictive modelling of impact across invaded ranges (e.g., Ricciardi, 2003; Jokela & Ricciardi, 2008) and the resultant predictions could be used to guide pre-emptive allocation of resources toward the most vulnerable ecosystems.

The analogous curvilinear relationship between invader impacts and their performance profile is not always observed and should depend on the traits of the invasive species and environmental context. The EMH was contradicted or partially supported by ~10% and 13% of studies examined in this review, respectively. When examining the effects of substrate type on the prey consumption and growth of individuals from an invasive population of tench (*Tinca tinca*), Avlijaš et al. (2022) found that tench *per capita* effects did not differ between putative optimal and suboptimal substrate for foraging. In this case, assumptions surrounding optimal sediment foraging conditions may have been incorrect, leading to discrepancies with the EMH. These findings suggest that substrate heterogeneity is a less effective variable for predicting the ecological impacts of tench. However, the role of substrate as a moderating variable for the field impacts of this species, and for invasive aquatic animals in general, has not been evaluated.

Abiotic variables have been shown to affect invasive species' performance to differing degrees. For an invasive gammarid amphipod, it was shown that temperature, but not salinity, affected feeding efficiency—consistent with the amphipod's broad salinity tolerance (Cuthbert & Briski, 2021). The respective mediating effect of various abiotic variables on an invader's performance can differ greatly according to the invader's specific tolerances and life history. Temperature is a commonly studied variable in tests of the EMH, as optimal temperatures are typically associated with enhanced resource consumption and growth rates (e.g., Oyugi et al., 2012; Iacarella et al., 2009a). Conversely, other studies contradicted this trend by observing the maintenance of high growth rates (Budy et al., 2013) and consumption levels (Budy et al., 2013; Sheppard et al., 2023) of AIS in putatively sub-optimal water temperatures. This demonstrates inconsistencies with the effect of presumed optimal thermal conditions on the performance of invasive species. Populations of the same invasive species at different latitudes have been found to exert varying levels of resource consumption when exposed to the same thermal gradients, implying that thermal optima differ between populations owing to selection for, or adaptation to, local environmental conditions (Reid & Ricciardi, 2022). Studies contradicting the EMH should be re-examined for evidence of local environmental adaptation.

Caveats and limitations

A limitation of the EMH is that it does not account for the interacting effects of abiotic and biotic factors on AIS performance. Invasive species distribution and abundance levels are largely controlled by a combination of interacting abiotic and biotic factors (Lewis et al., 2017). Once established, non-native species abundance and *per capita* effect can be further modified by interactions with the resident community, such that they are limited by biotic resistance, evolutionary naïveté, and enemy release (Ricciardi et al., 2013). These interactions are, in turn, moderated by disturbance and environmental heterogeneity, which can affect types and magnitude of impacts (Ricciardi et al., 2013). Several studies in our review highlight additional abiotic and biotic contexts that contribute to the AIS observed performance. For example, somatic growth rate and body size are performance indicators and indirect predictors of AIS impacts, for various reasons (Oyugi et al., 2011). An invader's body size can determine the outcome of competitive interactions with functionally similar natives (Mills et al., 2004) and set limits on resource consumption that can impact native prey populations (Boddy & McIntosh, 2017). While growth rates of invasive species have been observed to increase in optimal environmental conditions, they are also limited by a suite of biotic factors, including predation pressure (Gestoso et al., 2014), diet and food availability (Budy et al., 2013; Gestoso et al., 2014), and facilitation (Sardiña et al., 2015). Furthermore, invaders that are functionally similar to natives are exposed to similar predation pressure and enemies that can reduce the invader's population abundance and ecosystem impacts (Kestrup & Ricciardi, 2009b). Therefore, although the influences of various biotic and abiotic variables can differ greatly in magnitude, and some can account for disproportionate amounts of observed variation in impact (Ricciardi, 2003), conclusions made using the EMH from only one abiotic variable are potentially misleading.

Additional caveats with the EMH are the degree of certainty of optima estimates and the selection of the proper optimum type. This is because assumptions of optimal conditions may be incorrect in the absence of sufficient data on the physiological ecology of the target species, or the optimum that correlates best with the examined impact may be unrecognized. For example, impacts generated by marine invaders arose largely within their thermal niche following a curvilinear relationship with temperature; however, impact severity peaked in habitats 2.2°C cooler than their thermal optimum (Bennett et al., 2021). A further concern is the measurement of optimal temperatures in a laboratory setting that fails to properly emulate field conditions. Owing to a lack of external stressors, laboratory settings may create an advantageous environment that elicits a less realistic response by the target species, leading to an overestimation in optimal values (Elliott, 1982; Iacarella et al., 2015a). For example, identifying optimal growth temperatures is dependent on the food ration provided (Jobling, 1993), which is controlled in a lab setting. Since food availability is variable in the field, optimal growth temperatures may be an overestimate of the true parameter value we would expect in the wild. Published environmental optimum values may also not account for population-specific adaptations (Jensen et al., 2008). Adaptation to local conditions creating population-specific tolerances may explain why the performance of different populations of the same invader has been seen to vary across the invaded region (Reid & Ricciardi, 2022). This failure to account for differential adaptation may further produce instances that contradict the EMH. Assessments of distribution in relation to temperature have discussed the limitations of the sole use of temperature niches in their study—instead of incorporating physiological temperature ranges which may have produced different trends (D'Amen et al., 2022).

Comparative Environmental Matching

To improve upon impact predictions, researchers should consider applying the concept of Comparative Environmental Matching (CEM). This idea builds upon the EMH by comparing the environmental optima of two or more competing species and predicting their performance and inter-specific success based on the proximity of their specific optima to current environmental contexts (Fig. 0.2). The CEM predicts that the species whose physiological optimum more closely matches ambient conditions will have superior performance and higher *per capita* effects than the other comparator species. In particular, the CEM helps generate performance predictions for species exposed to shifting physico-chemical contexts along spatial or temporal gradients. Environmental heterogeneity can influence the abundance and impacts of native and non-native species by altering habitat conditions and modifying resource acquisition and use (Ricciardi et al., 2013). Even within the same large heterogeneous aquatic system, invader impacts can vary locally. For example, the examination of intraguild predation in experiments involving two freshwater amphipod crustaceans, an invasive Ponto-Caspian species *Echinogammarus ischnus* and a native North American species *Gammarus fasciatus*, revealed that the respective competitive abilities of both species shifted along a conductivity gradient, both in the laboratory and in the field, in a pattern that reflected their respective evolutionary histories (Kestrup & Ricciardi, 2009a). The importance of the proximity of the match of ambient and optimal conditions in explaining differential impacts among species has also been shown in cases examining invader impact severity under the influence of temperature (Khosa et al., 2020) and hydrological regime (Costanzo et al., 2005). CEM can be used in varying abiotic contexts to compare differences in performance between invasive species and their native counterparts, and, different populations of the same invader, ultimately facilitating impact predictions for the species of interest. This concept could streamline the process of risk assessment by allowing performance predictions and impact assessments to be made with the inclusion of a small number of trait-based and environmental metrics.

Risk managers can apply the EMH and CEM as frameworks for developing experimental designs for testing hypotheses that explicitly incorporate different environmental contexts. This will guide impact predictive information on where an invasive species could exert its strongest impacts across a heterogeneous environment, in different areas across an invaded range, and in areas that have not yet been invaded. These concepts are broadly applicable across a range of taxa, environmental variables, and impact types.

iv. The Great Lakes-St. Lawrence River Basin as a Model System

The Laurentian Great Lakes-St. Lawrence River basin is the most invaded freshwater ecosystem worldwide (Pagnucco et al., 2015). Invasive species originating from the Ponto-Caspian region have been particularly successful at establishing populations in the basin, owing in part to similarities in environmental conditions and patterns of transoceanic shipping traffic (Ricciardi & MacIsaac, 2000; Ricciardi, 2006). One such species is a benthivorous fish, the round goby (*Neogobius melanostomus*), which was introduced into the St. Clair River in the 1990s via the release of ballast water from cargo ships (Jude et al., 1992). Within only five years, the round goby had spread throughout much of the Great Lakes basin (Charlebois et al., 2001) and reached the upper St. Lawrence River by 2004 (Hickey & Fowlie, 2005); it thus quickly became the most invasive vertebrate in the basin. Its invasion success can be attributed to opportunistic feeding habits and exploitation of a broad range of habitat types due to their wide thermal, oxygen, and salinity tolerances (Kipp et al., 2012; Kornis et al., 2012; Young et al., 2010). Furthermore, the round goby possesses phenotypic plasticity that buffers against rapid temperature fluctuations and maintains homeostasis, improving their thermal tolerance (Wellband & Heath, 2017). Larger body size and gape size allows the round goby to handle a greater diversity of prey species and thus broaden their dietary niche (Jude 2001). As dietary generalists, they consume a wide variety of benthic invertebrate prey species, including zebra mussels—another Ponto-Caspian invader whose abundant presence may have facilitated a rapid round goby invasion (Barton et al., 2005; Burkett & Jude, 2015; French & Jude, 2001; Kipp et al., 2012).

Round gobies can survive in water temperatures ranging from -1 to 30°C, with a Final Temperature Preferendum (FTP) of 24.6°C (Hatton et al., 2018; Kornis et al., 2012). Their energetic optimum is identified as 25-26°C (Hatton et al., 2018; Kornis et al., 2012) which reflects their current proliferation and establishment throughout the Great Lakes, with their highest and lowest densities occurring in Lake Erie (warmest lake) and Lake Superior (coldest lake), respectively (Kornis et al., 2012). Surface water warming will likely affect the quality and intensity of ecological interactions of invaders in the Great Lakes-St. Lawrence system. The EMH predicts that water temperatures rising to levels matching the thermal optimum of round gobies will intensify the severity of their ecological impacts.

Impacts stemming from the round goby invasion in the Great Lakes basin are widely documented. Round goby predation has been reported to alter the abundance and structure of ecologically naïve native prey communities (Kipp et al., 2012; Krakowiak & Pennuto, 2008), contributing (along with invasive dreissenid mussels) to the shift from a pelagic-based food web to a benthic-based food web in the Great Lakes (Hogan et al., 2007). Native benthic fishes are also significantly affected by the round goby; owing to increased competition for habitat, spawning sites, and prey, some native fishes have been displaced or confined to sub-optimal habitats (French & Jude, 2001; Janssen & Jude, 2001; Kornis et al., 2012). Gobies directly impact the recruitment of native fishes by preying upon their eggs and young-of-year cohort (Jude et al., 1992).

One species negatively impacted by competitive interactions with the round goby is the logperch (*Percina caprodes*), a native darter in the Great Lakes-St. Lawrence River basin (Balshine et al., 2005; French & Jude, 2001; Kornis et al., 2012). Logperch and round gobies occupy the same nearshore habitats and spawning sites composed of sand, gravel, or rocky substrates, creating scenarios of competitive overlap (Greenberg, 1991; Jude et al., 1992; Kornis et al., 2012). Additionally, both species feed preferentially on similar prey (small macroinvertebrates such as amphipods and chironomid larvae) which has contributed to the competitive exclusion of logperch (French & Jude, 2001; Kornis et al., 2012). When in competition scenarios, round gobies dominate over logperch as a result of their heightened aggressive behaviour (Balshine et al., 2005). Given that the competitive ability of ectothermic species is affected by changing water temperatures (Rahel & Olden, 2008), the outcome of competitive interactions between logperch and round gobies can be expected to change in response to climate warming, according to their respective thermal tolerances. Little is known about the thermal ecology of logperch, but metalarva were found to have a final temperature preferendum of 21–25°C (Floyd et al., 1984), suggesting they are a warm-tolerant species—which could facilitate their success against the invasive round goby under future climatic conditions.

v. Research Objectives and Rationale

The goal of this research was to identify how changing environmental contexts affect the ecological and physiological performance of invasive species and co-occurring native species. My specific objectives were to reveal 1) the effect of temperature on resource consumption, and 2) the effect of temperature acclimation on the upper thermal tolerance limits of the round goby and logperch under current and future projected climate conditions. To address the first objective, I used a comparative functional response approach to examine the feeding efficiency of round gobies and logperch at different acclimation temperatures. Measurements of the functional response (FR)—the rate of resource consumption as a function of resource availability—of other invaders and trophically analogous similar native species is a method for predicting the ecological impacts of invasive species created through trophic interactions (e.g., Dick et al., 2014; Iacarella & Ricciardi, 2015b; South & Dick, 2017). Through FR analysis, parameters including attack rate (a), handling time (h), and maximum feeding rates ($1/h$) can be quantified (Dick et al., 2013; Pritchard et al., 2017), and further amalgamated into an informative metric of impact prediction, i.e., the Functional Response Ratio (FRR = a/h) (Cuthbert et al., 2019).

My second objective was evaluated by identifying the critical thermal maximum (CT_{max}) of round gobies and logperch at different acclimation temperatures. CT_{max} is a physiological metric defining the upper lethal thermal limit of a performance window and is the temperature at which a fish fails to maintain equilibrium when exposed to linearly increasing thermal conditions (Becker & Genoway, 1979; Lutterschmidt & Hutchison, 1997). Thermal resilience is indicated if a species possesses a wide thermal performance window and if its CT_{max} increases directly with increasing acclimation temperature (Christensen et al., 2020; Matern, 2001; Vinagre et al., 2016). Both FR and CT_{max} metrics can contribute to a predictive understanding of ecological and physiological responses that are relevant to the risk assessments under changing climatic scenarios.

Table. 0.1. Summary of aquatic invasion studies (n=31) supporting or refuting the Environmental Matching Hypothesis, which predicts that an invader's competitive performance and per capita effects increase in environments that more closely match the conditions in which the invader evolved.

Abiotic Variable	Invasive Species	Measure of Impact or Performance	Result	Support	Reference
Conductivity	*Echinogammarus ischnus* (amphipod)	Intraguild predation	Invader was the dominant predator in ion-rich waters.	Yes	Kestrup & Ricciardi, 2009a
	Gammarus tigrinus (amphipod)	Intraguild predation	Invader was the dominant predator in ion-rich waters.	Yes	Dick & Platvoet, 1996
Dissolved Oxygen Concentration	*Gammarus pulex* (amphipod)	Intraguild predation	Invader was the dominant predator at lower dissolved oxygen concentrations.	Yes	MacNeil et al., 2004
	Gammarus pulex (amphipod)	Resource consumption	Invader displayed increased predation rates in low dissolved oxygen conditions.	Yes	Laverty et al., 2015
	Lates niloticus (fish)	Resource consumption	Invader displayed reduced predation rates in low dissolved oxygen conditions.	Yes	Reid et al., 2013
Calcium Concentration	*Dreissena polymorpha* (mussel)	Fouling of native mussels	Invader’s fouling intensity increased in high-calcium environments.	Yes	Jokela & Ricciardi, 2008
	Neogobius melanostomus (fish)	Resource consumption	Invader increased its prey consumption rate in high-calcium conditions.	Yes	Iacarella & Ricciardi, 2015b
Salinity	*Xenostrobus secures* (mussel)	Growth rate	Invader’s growth rate increased in low salinity conditions, but other environmental factors may have had an influence.	Partial	Gestoso et al., 2014
	Gambusia holbrooki (fish)	Resource consumption & aggression	Invader displayed increased predation and aggression in low-salinity conditions.	Yes	Alcaraz et al., 2008
Substrate Composition	*Tinca tinca* (fish)	Resource consumption & growth rate	Invader’s predation and growth rates did not vary across substrate types.	No	Avlijaš et al., 2022
Temperature & Salinity	*Pontogammarus maeoticus* (amphipod)	Resource consumption & aggression	Invader displayed increased predation and aggression in higher water temperatures. Predation rates were	Yes	Cuthbert & Briski, 2021

			maintained along salinity gradient.		
Temperature	*Membranipora membranacea* (bryozoan)	Growth rate	Invader’s growth rate increased in high water temperatures.	Yes	Denley et al., 2019
	Potamopyrgus antipodarum (snail)	Growth rate	Invader displayed increased growth rates in low water temperatures, but growth rate also depended on species interactions.	Partial	Sardiña et al., 2015
	Cyprinus carpio & Oreochromis niloticus (fishes)	Resource consumption & growth rate	Invaders displayed increased predation and growth rates in adapted thermal conditions.	Yes	Oyugi et al., 2012
	Salmo trutta (fish)	Resource consumption & growth rate	Invader predation and growth rates increased at lower water temperatures.	No	Budy et al., 2013
	Gambusia holbrooki (fish)	Resource consumption & aggression	Invader displayed increased predation and aggression in high water temperatures.	Yes	Rincon et al., 2002
	Gambusia holbrooki (fish)	Resource consumption & aggression	Invader displayed increased predation and aggression in higher water temperatures.	Yes	Carmona-Catot et al., 2013
	Gambusia affinis (fish)	Resource consumption & aggression	Invader displayed increased predation and aggression in higher water temperatures.	Yes	Rowe et al., 2007
	Gambusia affinis (fish)	Resource consumption & aggression	Invader displayed increased predation and aggression in higher water temperatures.	Yes	Priddis et al., 2009
	Cherax quadricarinatus & Procambarus clarkia (crayfishes)	Resource consumption & aggression	Invaders displayed increased predation and aggression in higher water temperatures.	Yes	Madzivanzira et al., 2021
	Pacifastacus leniusculus (crayfish)	Resource consumption & aggression	Invader displayed increased predation and aggression in higher water temperatures.	Yes	Ruokonen & Karjalainen, 2022
	Oreochromis mossambicus & *Gambusia affinis* (fishes)	Resource consumption & aggression	Invaders displayed increased predation and aggression in higher water temperatures.	Yes	Mofu et al., 2019
	Micropterus salmoides & *Micropterus floridanus* (fishes)	Resource consumption & aggression	Invaders displayed increased predation and aggression in adapted thermal conditions.	Yes	Khosa et al., 2020

	Neogobius melanostomus (fish)	Resource consumption	Invader predation rates varied across temperatures and populations along a latitudinal gradient.	Partial	Reid & Ricciardi, 2022
	Mysis diluviana (mysid shrimp)	Resource consumption	Invader displayed reduced predation rates in higher water temperatures.	Yes	Schoen et al., 2015
	Oncorhynchus mykiss & Salmo trutta (fishes)	Resource consumption	Invaders displayed increased predation rates in lower water temperatures.	Yes	Boddy & McIntosh, 2017
	Procambarus virginalis (crayfish)	Resource consumption	Invader displayed reduced predation rates in higher water temperatures.	No	Sheppard et al., 2023
	Pterois volitans (fish)	Resource consumption	Invader displayed increased predation in higher water temperatures.	Yes	South et al., 2017
	Various marine species	Individual-, community-, and ecosystem-level impacts	Invaders displayed increased impacts in environmental conditions slightly below thermal optima.	Partial	Bennett et al., 2021
Hydrologic Regime	*Aedes albopictus* (mosquito)	Interspecific competition	Invader's competitive ability increased in wet seasonal conditions.	Yes	Costanzo et al., 2005
	Oncorhynchus mykiss & Salmo trutta (fishes)	Resource consumption	Invaders displayed increased predation under more stable stream flows.	Yes	Boddy et al., 2020

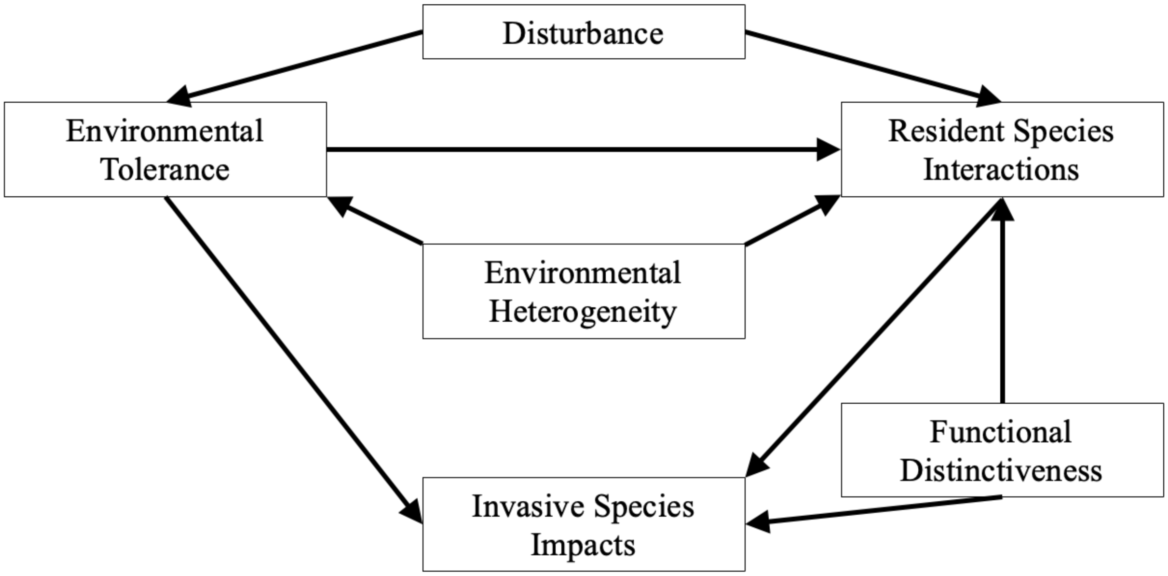

Figure 0.1. Simplified summary of context-dependencies affecting invasive species impacts. Adapted from Ricciardi et al. (2013). Impacts are affected by abiotic and biotic contexts, both indirectly (disturbances, and environmental heterogeneity) and directly (environmental tolerance, resident species interactions, and functional distinctiveness).

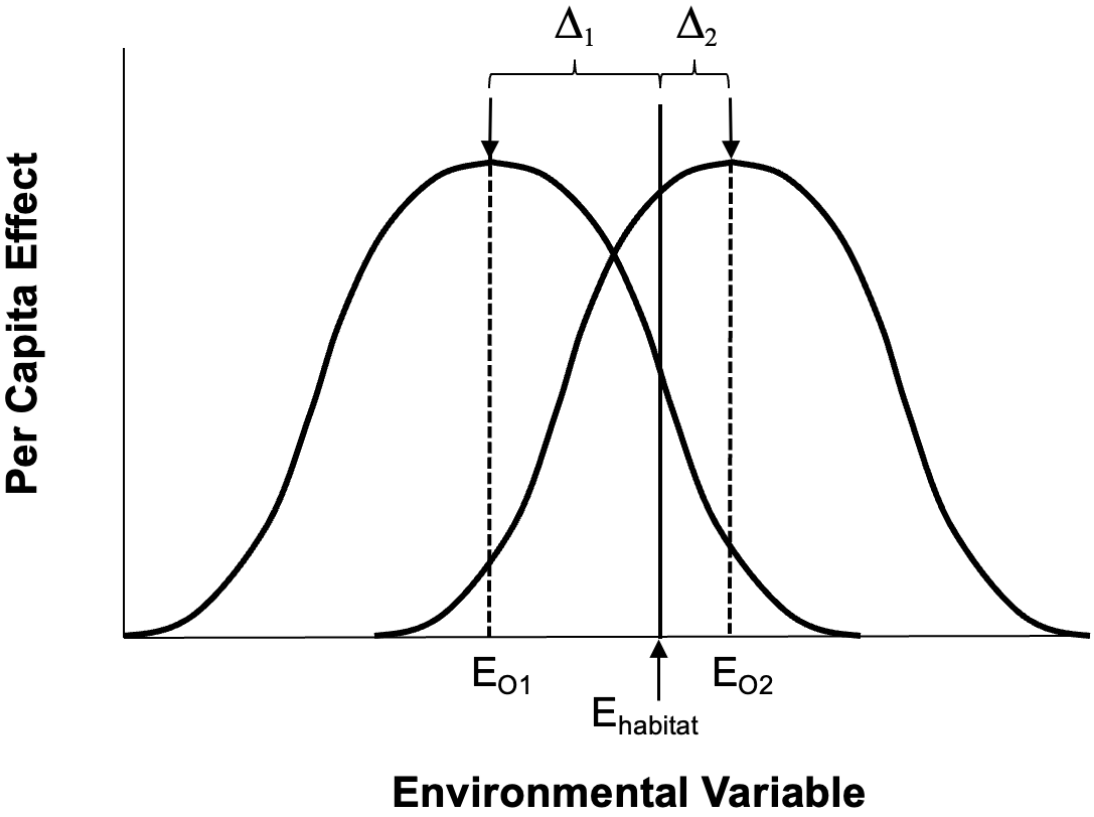

Figure 0.2. A conceptual model of comparative environmental matching (CEM): the comparison of the magnitudes of *per capita* effects between species in relation to an environmental variable. Ecological impact is predicted to be correlated with the distance between the respective environmental optima (E_{01} & E_{02}) of the two species and ambient environmental conditions ($E_{habitat}$). Impact of each species increases as conditions approach the optimum. Species optima in relation to ambient conditions (Δ_1 & Δ_2) can be used to predict which will inflict greater ecosystem impacts, or which will have a competitive advantage over the other (e.g., in the above scenario, species #2 has a greater impact or advantage because $\Delta_2 < \Delta_1$).

Chapter I – Comparative functional responses and thermal tolerance of benthic fishes under current and elevated temperatures

Abstract

The round goby, a Ponto-Caspian freshwater fish, is the most invasive vertebrate species in the Great Lakes-St. Lawrence River basin. Its success and impact have been linked to its broad environmental tolerance, rapid proliferation, and voracious consumption of benthic invertebrates. As thermal conditions in the Great Lakes shift under climate warming, the ecological performance of aquatic animals will be affected, potentially altering their trophic interactions and impacts. We compared the effects of current and projected surface water temperatures in the lower Great Lakes (18°C and 25°C, respectively) on the feeding efficiency and thermal tolerance of juvenile and adult round gobies (*Neogobius melanostomus*) and a trophically analogous native species, logperch (*Percina caprodes*). In one series of experiments, we quantified the functional response—specifically, the ratio of attack rates and handling times (i.e., the functional response ratio, FRR)—of these fishes to compare feeding efficiencies at both acclimation temperatures. At 18°C, logperch consumed more prey and had a higher FRR than juvenile round gobies. When acclimated to 25°C, adult round gobies and logperch were both observed to increase their prey consumption and FRR. In a second series of experiments, critical thermal maxima (CT_{max}) and acclimation response ratios (ARR) were measured to compare the upper thermal tolerance of logperch and both round goby life stages, following a 4- to 6-week acclimation period to different temperatures (18°C and 25°C). CT_{max} was influenced by acclimation temperature and differed between logperch and round gobies at varying life stages. Logperch had a higher ARR, indicating a greater acclimation capacity than round gobies. These results point to the need to consider changing thermal contexts in invasive species risk assessments.

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 outcompetes a trophically analogous native benthic fish, the logperch (*Percina caprodes*). Coinciding with pressures exerted by invasive species, the warming of surface waters through anthropogenic climate change threatens to further alter ecosystem dynamics (Beitinger et al., 2000; Christensen et al., 2020; Trumpickas et al., 2009, 2015) and is expected to alter the distribution, abundance, and impacts of invaders (Rahel & Olden, 2008). We can expect these multiple stressors to interact in ways that have consequences for native species and aquatic food webs.

Changing threats create additional challenges for risk assessment. As a result, there have been efforts to develop predictive metrics that advance the understanding of invader impacts on the broader ecological community (Dick et al., 2014; Dick et al., 2017a; Cuthbert et al., 2019; Dickey at al., 2020). Some of these are experimentally derived from a consumer's functional response (FR)—the relationship between resource consumption and resource availability in their surrounding environment (Dick et al., 2014). FR parameters, including attack rates (a), prey handling times (h), and maximum feeding rates ($1/h$), 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., 2019a) and their FRs have been correlated with their field impacts (Dick et al., 2014, 2017a). A promising metric, the Functional Response Ratio (FRR) (Cuthbert et al. 2019) amalgamates species-specific parameters, attack rate (a) and handling time (h), for a more informative metric: FRR = a/h. A high FRR ratio, resulting from high attack rates and/or low handling times, is associated with invaders that exert strong trophic impacts in the field (Cuthbert et al., 2019) and thus has potential value in risk assessment.

Thermal Tolerance

The thermal tolerance of a species is estimated from experimentally derived critical thermal maxima and minima. An ectotherm's thermal performance window is defined as the range of temperatures suitable to conduct vital functions (Huey & Stevenson, 1979). Critical thermal maximum (CT_{max}) and minimum (CT_{min}) are physiological metrics used to measure the upper and lower lethal thermal limits of a performance window, respectively (Becker & Genoway, 1979; Lutterschmidt & Hutchison, 1997). The CT_{max} is reached when an individual displays a loss of equilibrium caused by physiological disorganization (Becker & Genoway, 1979; Lutterschmidt & Hutchison, 1997), which prevents it from escaping lethal environmental conditions (Cowles & Bogert, 1944). 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 thermal resilience when exposed to fluctuating temperature conditions caused by climate change (Christensen et al., 2020; Matern, 2001). Increasing thermal conditions surpassing the CT_{max} of a given species may impact their abundance levels and range distribution (Sunday et al., 2012, 2014). If 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 as a result of the acclimation temperature (Beitinger et al., 2000); if CT_{max} increases directly with increasing acclimation temperature, it indicates resilience to thermal stress (Christensen et al., 2020; Vinagre et al., 2016). Thus, CT_{max} studies can inform predictive risk assessments by comparing thermal tolerances of native and invasive species populations to ambient and projected temperature regimes (Reid & Ricciardi, 2022). A shift of environmental temperatures closer to an invader's physiological optimum may positively correlate with an increase in its ecological impacts (Iacarella et al., 2015a; Ricciardi et al., 2013), given that a species' thermal window affects their ecological interactions within their environment (Pörtner & Farrell, 2008).

Objectives and Predictions

This research aimed to identify how increased water temperatures created by future climate change conditions affect the resource consumption and thermal tolerance of the round goby (*N. melanostomus*) and the native logperch (*P. caprodes*). Our objectives were to 1) compare the effects of current and projected future summer surface water temperatures for the

Great Lakes-St. Lawrence River system on the prey consumption efficiency of both species; and 2) compare their upper thermal tolerance limits and resilience through long-term temperature acclimation. The first objective was addressed using comparative FR experiments and the derivation of the FRR at acclimation temperatures of 18 and 25°C, representing current and future average summer surface water temperatures of the Great Lakes, respectively (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 Functional Response Ratio (*a/h*) will be higher for *N. melanostomus* than for *P. caprodes* in both temperature scenarios, following the hypothesis that invasive species generally have greater resource use efficiency than native species (Dick et al., 2013; Ricciardi et al., 2013). Following the Environmental Matching Hypothesis, which predicts that the *per capita* effects of a species are maximal under environmental conditions that more closely match its physiologically optimum (Iacarella et al., 2015a), the Functional Response Ratio (*a/h*) for the round goby is expected to be higher at 25°C than at 18°C, because the former matches the growth optimum for the species, i.e., 25-26°C (Hatton et al., 2018; Kornis et al., 2012).
2. The CT_{max} for *N. melanostomus* will be higher than for *P. caprodes* at both acclimation temperatures, following the hypothesis that invasive species generally have broader environmental tolerances than less successful invaders and natives (Vasquez, 2006; Eyster & Wolkovich, 2021). The CT_{max} of both species will be higher at 25°C, and lower at 18°C.

Methods

Fish Collection and Acclimation

All fish were retrieved from sites located on the St. Lawrence River. Juvenile logperch (*Percina caprodes*) were collected in July 2022 in Morrisburg, Ontario (44.873 ºN, 75.240 ºW), while adult and juvenile round gobies (*Neogobius melanostomus*) were collected in June 2023 from Beauharnois, Quebec (44.316 ºN, 73.876 ºW) (Fig. 1.1). 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, at this size, individuals experience an ontogenetic shift in diet from consuming only soft invertebrates to incorporating mollusks (Barton et al., 2005; Dashinov & Uzunova, 2020; French & Jude, 2001; Janssen & Jude, 2001). All fish were captured using a 30-ft bag seine and, within four hours of collection, were transported to McGill University, where they were held in 20-gallon aquaria (51 x 27 x 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. Fish were acclimated to laboratory conditions for 14 days at 18°C. Each aquarium was exposed to a 12:12 day: night cycle photoperiod and was equipped with air stones for oxygenation, PVC shelters, and aquarium gravel to provide environmental enrichment according to animal care protocols (SOP519). Logperch received food pellets (Vibra bites) and round gobies received Hikari chironomid (*Chironomus* sp.) larvae daily until satiated. Initially, both species were fed food pellets; however, in contrast to logperch, which readily consumed the food pellets, round gobies showed less interest in the pellets 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. 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 (Avlijaš et al., 2022; Fitzsimons et al., 2006).

Quantifying Habitat Temperatures

Water temperature data were obtained from Melocheville, Quebec (45.319° N, 73.927° W), and Maitland, Ontario (44.635° N, 75.613° W), located on the St. Lawrence River and used as approximations for collection sites in Beauharnois and Morrisburg, respectively. Data from Melocheville was 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-minute intervals. For each location mean daily temperatures were calculated for each 24-hour period from 16 July to 30 September. 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. 1.2). The number of days ≥25°C were 6 in Melocheville and 2 in Maitland.

Comparative Functional Responses

We examined the comparative FR of juvenile logperch, and adult and juvenile round gobies at two acclimation temperatures, 18°C 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 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-hour period, during which they were starved to standardize hunger levels (Mofu et al., 2019a; Reid & Ricciardi, 2022). To prevent external visual stimuli from affecting prey consumption, the sides of the aquaria we covered with an opaque barrier (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) to reduce stress and provide refuge.

For the FR trials, prey items 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 & Jude, 2001; Kornis et al., 2012). Hikari chironomid larvae (previously frozen and thawed for experiments) were distributed in seven densities (2, 4, 8, 16, 32, 64, and 140 larvae for logperch and juvenile round gobies; 2, 4, 8, 16, 32, 64, and 180 larvae for adult round gobies) with four replicates per density. Within each series of 18ºC and 25 ºC temperature experiments, following the 24-hour trial acclimation period, each individual fish was used in one feeding trial, i.e. at one prey density assigned at random, and left to feed for three hours (Mofu et al., 2019a; Mofu et al., 2019b). The use of lower prey densities allows for the distinguishment between Type II and Type III responses (Juliano, 2001). At the end of each FR trial, individuals were removed from their experimental tank, weighed, and measured for total length (TL). The remaining chironomid larvae were collected and counted to identify the number of prey eaten (Mofu et al., 2019a). Control trials with the absence of a fish predator were conducted at each prey density to confirm that the depletion of prey from the experimental tanks was a direct result of predation.

Critical Thermal Maximum

CT_{max} was measured in a 10-gallon aquarium (50 × 19 × 25 cm) at acclimation temperatures of 18°C 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 at 25°C (McDonnell & Chapman, 2015; Reid & Ricciardi, 2022). Size-matching based on total length (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 rearing 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 seven days between experimental trials for recovery (Reid & Ricciardi, 2022). Fish were not reused among CT_{max} experiments.

Prior to the start of each trial, fish were starved for a 24-hour period (McDonnell & 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 two hours while the CT_{max} apparatus circulated water so individuals could recover from handling stress and acclimate to trial conditions (Potts et al., 2021; Reid & 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 & Genoway, 1979) and monitored and recorded for the duration of each trial. Fish were exposed to increasing water temperature until they displayed a loss of equilibrium (LOE) (Becker & Genoway, 1979), at which point the end temperature (CT_{max}) was recorded. LOE for round gobies was determined manually since this species lacks a swim bladder (Kornis & Vander 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 re-orient themselves after five seconds, they were considered to have lost equilibrium (Carline & Machung, 2001). Immediately following the LOE, fish were transferred into a recovery aquarium, containing an aerator, and monitored. Once recovered, the total length (TL) and weight were recorded.

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 seconds, indicating the onset of avoidance behaviour before CT_{max} is reached (McDonnell & Chapman, 2015; Potts et al., 2021). This avoidance behaviour is indicative of the threshold at which fish seek out a cooler environment (McDonnell & 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, L, 1977).

Statistical Analyses

Functional Response

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 (non-asymptotic), 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 (MLE) when the model was chosen and fitted (Pritchard et al., 2017). Rogers' 'random predator equation' for non-replaced 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 time (*h*) were extracted from these models.

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 (CI) for the model fit, and parameter estimates of the FR curve including attack rate and handling time through bootstrapping the model (n = 999) (Grimm et al., 2020; Iacarella et al., 2015a; South et al., 2019). The third method of comparison used the *frair_fit* function to identify individual FR curve parameters and compare their 95% CI (Grimm et al., 2020). Graphed FRs were further compared through visual observation of CI overlap from bootstrapping, where a lack of statistical difference is indicated by the presence of CI overlap (Grimm et al., 2020; South et al., 2019). 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 (GLM) 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 rearing 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 non-parametric 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.

Functional Response Ratio

Functional response parameters were amalgamated into a predictive metric known as the Functional Response Ratio (FRR) (Cuthbert et al., 2019). FRR is calculated as follows:

$$FRR = a/h$$

where a represents the predator's attack rate at low prey densities and h represents the handling time of prey. Identification of FRRs can be used in comparisons between invasive and native species, for insight into an invader's behaviour (Cuthbert et al., 2019; Dick et al., 2017a; Dickey et al., 2020). It can further be used to derive temperature-dependent metrics to predict impacts under future climate change scenarios.

Critical Thermal Maximum

The effect of acclimation temperature on the response variables CT_{max}, T_{ag}, T_{aw}, A_{aw}, and TSM was tested for round goby life stages and logperch using linear regression and linear mixed models. AIC and BIC scores confirmed the selection of fixed and random effects included in the model chosen for each response variable. Based on these criteria, a linear regression including acclimation temperature as a fixed effect was selected for all 5 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% confidence intervals to generate pairwise estimates. Plotting residuals, the Levene's test of equal variance, and the Shapiro-Wilk test for normality were utilized to examine model assumptions.

Results

Functional Response

Mortality occurred during juvenile and adult round goby FR trials when acclimated to the 25°C treatment. During the 24-hour experimental tank acclimation, 42.9% of juveniles and 7.14% of adult round gobies died. The difference in survival outcome between juvenile and adult round gobies when exposed to identical experimental conditions was deemed significant using a Pearson's chi-squared test with Yates continuity correction (χ^2=7.71, df =1, p<0.01). Water temperature and water quality were maintained throughout the acclimation periods and therefore were ruled out as a cause of mortality. Additionally, deceased individuals displayed no external signs of illness or parasites. High mortality rates among juvenile round gobies prevented us from conducting an FR at the 25°C treatment. In contrast, no mortality among logperch was observed during experimental trials.

Functional response curves were consistently Type II for logperch, juvenile round gobies, and adult round gobies across temperature treatments (Fig. 1.3; Table 1.1). For both adult round gobies and logperch, handling times differed between temperatures. At 25°C, both groups exhibited a lower handling time than at 18°C, indicating a higher maximum feeding rate at this temperature (Table 1.2). Juvenile round goby handling times were higher than both logperch and adult round gobies at 18°C, indicating reduced prey consumption (Table 1.2). These results are supported by our generalized linear model, which indicated that handling times were significantly affected by species, temperature, and life stage (Table 1.3a; p<0.001). Our findings further demonstrate that logperch attack rates increase at 25°C, however, adult round goby attack rates remained consistent across both temperature treatments (Table 1.2). Life stage (p<0.01) and temperature (p<0.001) were found to influence attack rates (Table 1.3b). Juvenile round gobies displayed similar attack rates to logperch at 18°C, however, attack rates were lower than adult round gobies at this temperature (Table 1.2).

Calculation of the FRR using derived attack rates and handling times revealed that at both acclimation temperatures, 18°C and 25°C, adult round gobies had the highest FRR among species and life stages (Table 1.1). Both logperch and adult round gobies displayed a higher FRR at 25°C (Table 1.1). The FRR of juvenile round gobies was lower than both logperch and adult round gobies at 18°C therefore possessing the lowest feeding efficiency among species and life stages (Table 1.1).

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) or differ within tested groups of juveniles (p=0.09) and adults (p=0.17) (Fig. 1.4).

Critical Thermal Maximum

The critical thermal maximum was observed to vary in response to acclimation temperature. All species displayed significantly greater CT_{max} when acclimated to 25°C showing improved resilience to thermal stress at higher acclimation temperatures (Fig. 1.5). Mean CT_{max} values were identified as 32.25°C, 32.56°C and 33.01°C for logperch, juvenile round gobies, and adult round gobies, respectively, at 18°C (Table 1.4). These values increased significantly when acclimated to 25°C, up to 35.28°C, 34.61°C, and 34.65°C, respectively. The TSM declined significantly with increasing acclimation temperature for both species and life stages. For logperch, juvenile round gobies, and adult round gobies TSM decreased from 14.25°C, 14.56°C, and 15.01°C, respectively, at 18°C, to 10.27°C, 9.61°C, and 9.65°C, respectively, at 25°C (Table 1.4, Fig. 1.6). CT_{max} and TSM were significantly affected by acclimation temperature and species, but not life stage (Table 1.5). There was also a significant interaction between acclimation temperature and species (Table 1.5), implying that the relationship between CTmax and acclimation temperature, and TSM and acclimation temperature are species-dependent. A post hoc Tukey Kramer test indicated that 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 (Table 1.6, Fig. 1.5). At 25°C, logperch displayed a CT_{max} similar to adult round gobies, but significantly higher than juvenile round gobies (Table 1.6, Fig. 1.5). CT_{max} did not differ between round goby life stages at both acclimation temperatures.

T_{ag} was observed for logperch, but not round gobies. For both the juvenile and adult life stages, round gobies failed to exhibit agitated swimming behaviour for a period longer than 40 seconds at either acclimation temperature, therefore, this metric was not recorded for this species. Instead, round gobies were observed to swim around the breeding box for repeated shorter durations of approximately 5-10 seconds. For logperch, T_{ag} increased from 27.62°C at

18°C to 31.73°C at 25°C (Table 1.4a, Fig. 1.7). 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 1.4a, Fig. 1.8). However, acclimation temperature did not affect T_{aw} ($p>0.05$) (Table 1.4a, Fig. 1.8).

Logperch displayed a higher acclimation capacity than both round goby life stages. The ARR for logperch was 0.431 between 18 and 25°C, followed by juvenile round gobies, then adult round gobies with ARR values of 0.293 and 0.234, respectively.

Discussion

Our experiments suggest that resource consumption and thermal tolerance of invasive round gobies and native 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., 2015a). Logperch feeding efficiency exceeded that of juvenile round gobies at current water temperatures, suggesting that round gobies consume resources less efficiently than natives at sub-optimal temperatures. CT_{max} increased proportionally with rising acclimation temperature but differed between species and life stages, highlighting the influence of past thermal exposure and individual age on thermal tolerance.

Effects of Temperature on Feeding Behaviour

Evidence from our experiments showed increased prey consumption by both adult round gobies and logperch at the elevated temperature. As predicted, adult round gobies showed reduced handling times, higher maximum feeding rates, and a higher FRR at 25°C. In most fish species, warmer temperatures stimulate a spike in metabolic demands requiring an increase in food intake, while sub-optimal temperatures elicit a reduction in feeding (Volkoff & Rønnestad, 2020). Reid and Ricciardi (2022) identified a peak in prey consumption by various adult round goby populations at temperatures 18-24°C. Our findings are consistent with the Environmental Matching Hypothesis (Iacarella et al., 2015a), as we observed increased *per capita* effects in round gobies in conditions matching their thermal optimum of 25-26°C (Hatton et al., 2018; Kornis et al., 2012). This is consistent with the results of a bioenergetics modelling study that found round goby food consumption increased with temperature up to 26°C before sharply declining (Lee & Johnson, 2005). These findings lead us to infer that round gobies will increase their ecological impacts in the Great Lakes and 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 producing a lower handling time, and a higher attack rate, maximum feeding rate, and FRR in projected water temperatures. Logperch metalarva were found to have a final temperature preferendum of 21–25°C (Floyd et al.,1984). This may imply that logperch are approaching their thermal optimum at higher temperatures which would correspond with the observed spike in resource consumption at 25°C. Possessing similar thermal preferences to the invasive round goby may forestall a disadvantage in interspecific competition for resources as habitats occupied by both species continue to warm.

Both the invader and native 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. A meta-analysis found that attack rate and handling time are not maximized at the same temperature (Uiterwaal and DeLong, 2020), which may explain our failure to observe a change in attack rate in adults. Furthermore, our experimental design may have lacked the general complexity required to detect a shift in FR type among species. The incorporation of mobile prey and substrate types can reveal ecologically relevant behaviours (Avlijaš et al., 2022).

Body size is another factor that can affect resource consumption (Avlijaš et al., 2022; Schröder et al., 2016; Toscano & Griffen, 2013). 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), round goby *per capita* effects on prey populations in the field may be mediated by their body size and life stage.

At 18°C, juvenile gobies were less efficient foragers than juvenile logperch, as indicated by a lower FR and FRR. This suggests that the juvenile round goby life stage is less ecologically damaging and may not outcompete logperch of a similar size for prey resources. Typically, invasive species exhibit higher FRs than their native counterparts (Alexander et al., 2014; Dick et al., 2014; Laverty et al., 2017), because they develop increased foraging efficiency resulting from selective pressures during the invasion process (Hudina et al., 2014; Mathakutha et al., 2019; Morrison & Hay, 2011). 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 et al. 2015b). Indeed, a more recently established population of round gobies in the Trent-Severn Waterway exhibited a higher FR than logperch, in contrast with our findings (Paton et al., 2019).

While FRRs serve to identify high-impact predators by identifying their *per capita* effects on prey populations (Cuthbert et al., 2019), Relative Impact Potential (RIP) highlights the importance of including Numerical Response proxies (e.g., predator abundance) when quantifying ecological impacts (Dick et al., 2017b). Though juvenile round gobies were found to have low *per capita* effects on prey populations at 18°C, their high population abundance in invaded regions may contribute to greater ecosystem impacts.

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 changes in feeding behaviour were a direct result of thermal influence.

Effects of Acclimation on Thermal Tolerance

Temperature dictated the thermal performances and tolerances of round gobies and logperch. CT_{max} for both species improved significantly with rising acclimation temperature, increasing from ≥33°C (at 18°C acclimation) to ≤34°C (at 25°C acclimation). A linear relationship between CT_{max} and acclimation temperature, indicating the gain in heat tolerance when fish are acclimated to higher temperatures, was expected (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°C and 26°C, respectively (values extrapolated using PlotDigitizer) and the study suggested that the CT_{max}

peaked at 25°C (Reid & Ricciardi, 2022), which would support our detection of a higher thermal maximum at that corresponding acclimation temperature. Northern populations from two sites on the upper St Lawrence River (Melocheville and Sorel-Tracy) were found to have maximum CT_{max} tolerances of 34.06°C and 33.74°C, respectively, when acclimated to 26°C (Reid & Ricciardi, 2022). These tolerance levels were analogous to those determined in our study, suggesting similar thermal tolerance levels and susceptibility to thermal stress across northern fish populations.

The acclimation response ratio (ARR) derived at 18-25°C ranged from 0.234, 0.293, and 0.431 for adult round gobies, juvenile round gobies, and logperch, respectively. Freshwater fish species have been reported to have ARRs ranging from 0.07 to 0.91 (Beitinger et al., 2000; Comte & Olden, 2017). Mid-latitude fishes have been reported to have ARRs spanning this range (McDonnell et al., 2021; Morley et al., 2019). Our reported ARR values for both round goby life stages fall within the range previously measured for northern round goby populations (0.16–0.29; Reid & Ricciardi, 2022), further suggesting that northern fish populations display similar acclimation capabilities to thermal change (Díaz et al., 2002; Reid & Ricciardi, 2022). The ARR value for native logperch determined in this study falls within the range of other freshwater and mid-latitude fishes, and was higher than round gobies, suggesting a superior acclimation capacity. Since all observed CT_{max} values for logperch and round goby were found to exceed projected water temperatures in the Great Lakes region (Trumpickas et al., 2009, 2015), they may prove resilient to the adverse impacts of climate warming, if provided sufficient time for temperature acclimation (Catullo et al., 2015).

Contrary to our hypothesis, round gobies did not continuously demonstrate superior thermal tolerance than logperch. Only when acclimated to current climate conditions did adult round gobies display greater thermal resilience than logperch. Invasive species typically possess a broader niche breadth and generalism which can contribute to an increased thermal tolerance (Vázquez, 2006; Mathakutha et al., 2019), highlighting a potential explanation for observed differences in CT_{max} at this acclimation temperature. In contrast, 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 thermal stress at higher temperatures. Their native counterpart appears to be more thermally resilient during this life stage. It is important to note that the thermal tolerance of juvenile logperch 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 vary significantly between round goby life stages. For many freshwater fishes, upper thermal tolerance was found to be relatively unaffected by size for life stages encompassing fry to adults and subadults (Recsetar et al., 2012). Similarly, variation in size between northern round goby populations yielded comparable acclimation capabilities (Reid & Ricciardi, 2022). Therefore, we suspect that thermal tolerance is fairly consistent across all size ranges 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 suspect that thermal tolerance is population-specific, related to the population's latitudinal position delegating its history and magnitude of thermal exposure, as opposed to being characteristic of a particular species or life stage across its range. Southern round goby populations have been found to display higher ARRs and an improved acclimation response in comparison to their northern equivalents, indicating latitudinal (or climatic) influences (Reid & Ricciardi, 2022). Perhaps both species and life stages examined in this study displayed similar thermal tolerance levels because of their shared latitudinal positions.

The modified thermal safety margin (TSM) was calculated by subtracting the acclimation temperature from CT_{max} (McArley et al., 2017; McDonnell et al., 2021). Logperch and round gobies could withstand changing thermal conditions for a longer period when acclimated to a lower temperature, as indicated by their TSM. In fishes, TSM is generally inversely correlated with acclimation temperature (McDonnell et al., 2021). 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 future temperatures, respectively. Therefore, we infer that logperch are less vulnerable than round gobies of similar sizes to thermal stress when acclimated to warmer conditions.

Thermal agitation temperature (T_{ag}), thermal agitation window (T_{aw}), and acclimation agitation window (A_{aw}) 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 & Chapman, 2015). This agitated response typically overcomes behaviours associated with fitness, including predator avoidance or feeding (McDonnell & Chapman, 2015). For logperch, T_{ag} was significantly lower than CT_{max} at both acclimation temperatures (a pattern observed across fish species; McDonnell & 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 (Christensen et al., 2020). Furthermore, T_{ag} embodied 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 conformed 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 (McDonnell et al., 2019, 2021; Wells et al., 2016). Consistency in the T_{aw} for logperch between current and projected water temperatures eliminates this additional risk. 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 indicates that logperch in high-temperature environments are increasingly sensitive to rising thermal conditions, burdening them with ecological disadvantages as their agitated behaviour can remove them from their refuge and expose them to predators (Kochhann et al., 2021; McDonnell et al., 2021).

Experimental Caveats and Future Directions

While FR experiments provide us with quantitative evidence of the feeding efficiency of consumers, specific experimental designs can create limitations that ultimately affect the predictive and comparative power of FRs. 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 (Avlijaš et al., 2022). Furthermore, to make direct comparisons of derived FR metrics (attack rate, handling time, maximum feeding rate) with published literature there is a need to standardize experimental protocols. The influence of experimental characteristics including prey type and habitat complexity on a predator's feeding behaviour creates different contexts amongst studies and a lack of consistency when deriving FR curves and metrics. Therefore, this creates limitations when comparing the outcome of our FR experiments to those in the literature done on other round goby populations and trophically analogous native species.

Although these results provide relevant 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 in high water temperatures lessens our understanding of the differential feeding responses of invaders in comparison natives when exposed to rising temperatures. 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 demonstrated improved growth rates at lower temperatures (G. D'Avignon et al., unpublished data) suggesting that their feeding may also be improved in these conditions due to the enhancement of food processing for performance benefits (Reid & Ricciardi, 2022). Future research should strive to identify the shape of the FR of juvenile round gobies when exposed to projected warmer temperatures, to confirm the consistency of their feeding response.

Differential mortality rates were observed in juvenile and adult round gobies when subjected to a high thermal environment and handling stress, indicating variation in thermal stress coping abilities between life stages and increased sensitivity to stress in juveniles. However, both life stages produced similar upper thermal tolerance limits during CT_{max} experiments. As fish were re-used 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 for two 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 the nuances of the thermal ecology of trophically analogous native and invasive species, including some results that contradicted predictions. Our results highlight the need for risk assessments to include information on thermal metrics and explicit consideration of the performance and resilience of target species in a rapidly changing climate.

Tables

Table 1.1. Fit coefficients and Functional Response Ratio (FRR) for fitted functional response curves for *P. caprodes,* juvenile *N. melanostomus,* and adult *N. melanostomus.*

Species and Life Stage	Temperature	Type	First-order	*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

Asterisks denote significant *p* values (*** < 0.001)

Table 1.2. Results of a difference test, *frair_compare*, for attack rate (*a*) and handling times (*h*) for *P. caprodes,* juvenile *N. 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***

Asterisks denote significant *p* values (*** < 0.001; * < 0.05)

Table 1.3. 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 *P. caprodes,* juvenile *N. melanostomus* and adult *N. melanostomus* in response to acclimation temperature, using a Type III ANOVA and $\chi 2$ to report the effect size of explanatory variables on the response variable.

a) handling times

Factor	Chisq	*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	0.6283

b) attack rates

Factor	Chisq	*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

Asterisks denote significant *p* values (*** < 0.001; ** < 0.01)

Table 1.4. Linear regression models assessing the effects of acclimation temperature on thermal tolerance metrics of *P. caprodes* (a), juvenile *N. melanostomus* (b), and adult *N. melanostomus* (c).

a) *P. caprodes*

Critical Thermal Maximum (CT_{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 (CT_{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 (CT_{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***

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

Table 1.5. 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 *P. caprodes*, juvenile *N. 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***

Asterisks denote significant *p* values (*** < 0.001; * < 0.05)

Table 1.6. Results of post hoc Tukey-Kramer test with 95% confidence intervals examining the effects of acclimation temperature, species, life stage, and species-temperature interaction on the thermal tolerance metrics for *P. caprodes*, and juvenile and adult *N. melanostomus*.

a) CT_{max}

Comparison	Estimate	SE	df	t ratio	*p* value
P. caprodes 18°C – Juvenile *N. melanostomus* 18°C	-0.404	0.195	62	-2.070	0.4454
P. caprodes 25°C – Juvenile *N. melanostomus* 25°C	0.752	0.195	62	3.855	0.0064**
Adult *N. melanostomus* 18°C - *P. caprodes* 18°C	0.649	0.201	62	3.233	0.0388*
Adult *N. melanostomus* 25°C - *P. caprodes* 25°C	0.245	0.156	62	1.573	0.7639
Adult *N. melanostomus* 18°C - Juvenile *N. melanostomus* 18°C	-0.507	0.204	62	-2.489	0.2195
Adult *N. melanostomus* 25°C - Juvenile *N. melanostomus* 25°C	0.245	0.156	62	1.573	0.7639
P. caprodes 18°C - *P. caprodes* 25°C	-3.025	0.207	62	-14.62	<0.001***
Juvenile *N. melanostomus* 18°C – Juvenile *N. melanostomus* 25°C	-1.869	0.155	62	-12.08	<0.001***
Adult *N. melanostomus* 18°C – 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 – Juvenile *N. melanostomus* 18°C	-0.404	0.195	62	-2.070	0.4454
P. caprodes 25°C – Juvenile *N. melanostomus* 25°C	0.752	0.195	62	3.855	0.0064**
Adult *N. melanostomus* 18°C - *P. caprodes* 18°C	0.649	0.201	62	3.233	0.0388*
Adult *N. melanostomus* 25°C - *P. caprodes* 25°C	-0.507	0.204	62	-2.489	0.2195
Adult *N. melanostomus* 18°C - Juvenile *N. melanostomus* 18°C	0.245	0.156	62	1.573	0.7639
Adult *N. melanostomus* 25°C - Juvenile *N. melanostomus* 25°C	0.245	0.156	62	1.573	0.7639
P. caprodes 18°C - *P. caprodes* 25°C	3.975	0.207	62	19.214	<0.001***

Juvenile *N. melanostomus* 18°C – Juvenile *N. melanostomus* 25°C	5.131	0.155	62	33.179	<0.001***
Adult *N. melanostomus* 18°C – Adult *N. melanostomus* 25°C	5.131	0.155	62	33.179	<0.001***

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

Figures

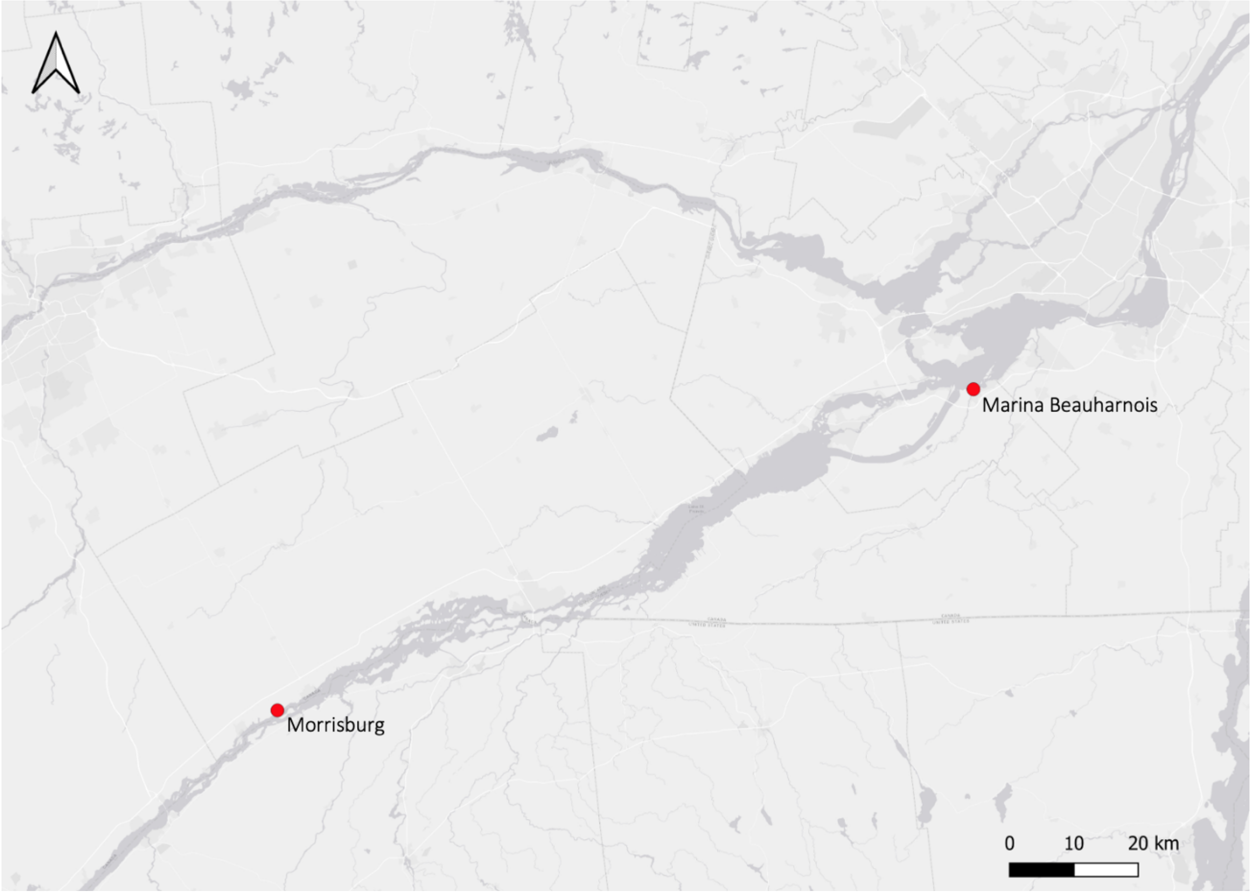

Figure 1.1. Map of sampling sites on the St. Lawrence River. Populations of round gobies (*N. melanostomus*) and logperch (*P. caprodes*) were collected in Beauharnois, Quebec (44.316 ºN, 73.876 ºW) and Morrisburg, Ontario (44.873 ºN, 75.240 ºW), respectively. Figure created using QGIS version 3.32.3.

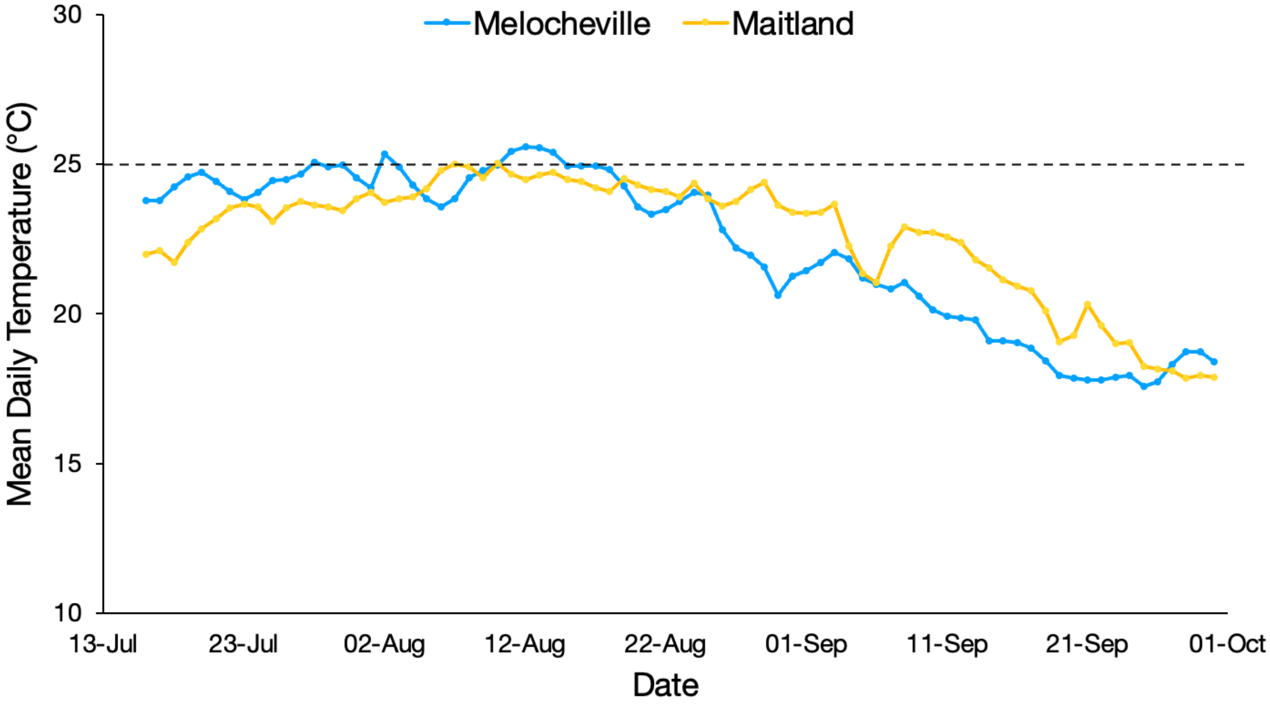

Figure 1.2. Mean daily temperatures (ºC) for both study sites in the St. Lawrence River from 16 July to 27 September 2020 (Melocheville) and 2022 (Maitland). The dashed line represents 25ºC. Temperatures collected in Maitland, Ontario, and Melocheville, Quebec, represent a proxy for fish collected in Morrisburg, Ontario, and Beauharnois, Quebec, respectively.

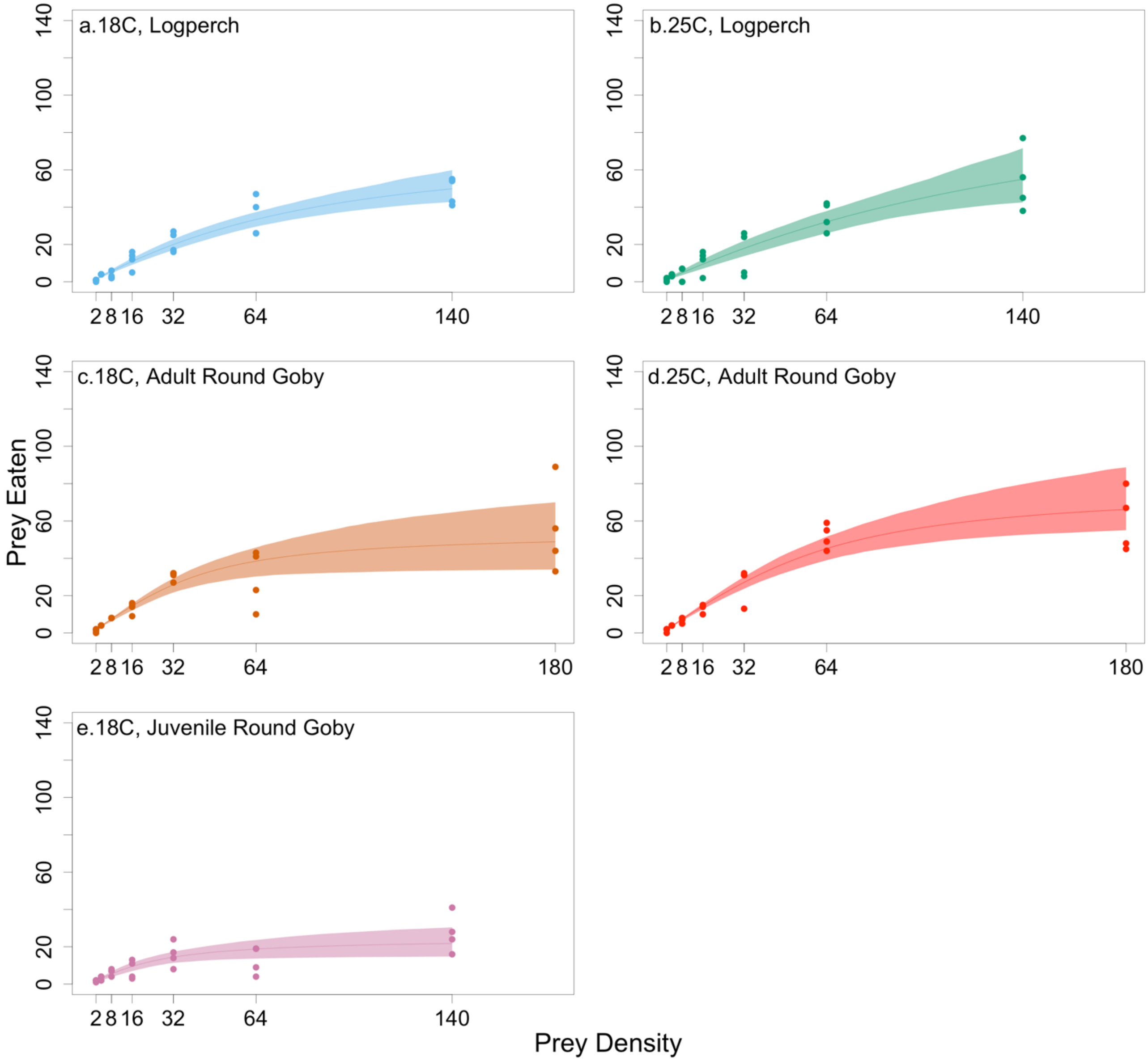

Figure 1.3. Type II functional response curves for a) logperch (*Percina caprodes*) at 18°C (blue), b) logperch (*Percina caprodes*) at 25°C (green), c) adult round gobies (*Neogobious melanostomus*) at 18°C (orange), d) adult round gobies (*Neogobious melanostomus*) at 25°C (red) and e) juvenile round gobies (*Neogobious melanostomus*) at 18°C (pink). Shading represents bootstrapped 95% confidence intervals at both temperature treatments. n=3-4 for each treatment.

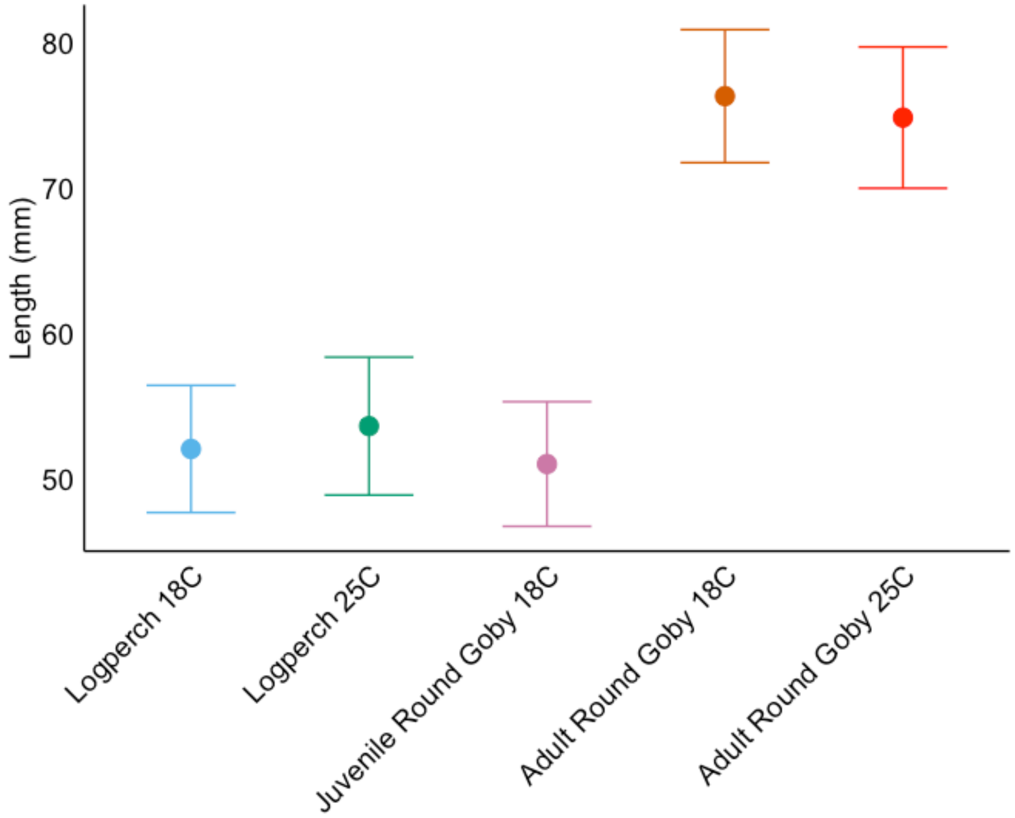

Figure 1.4. Fish total length across experimental groups. Kruskal-Wallis non-parametric tests indicated there was no significant difference between juvenile (p=0.09) and adult groups (p=0.17). Circles indicate the mean total lengths while bars represent standard error.

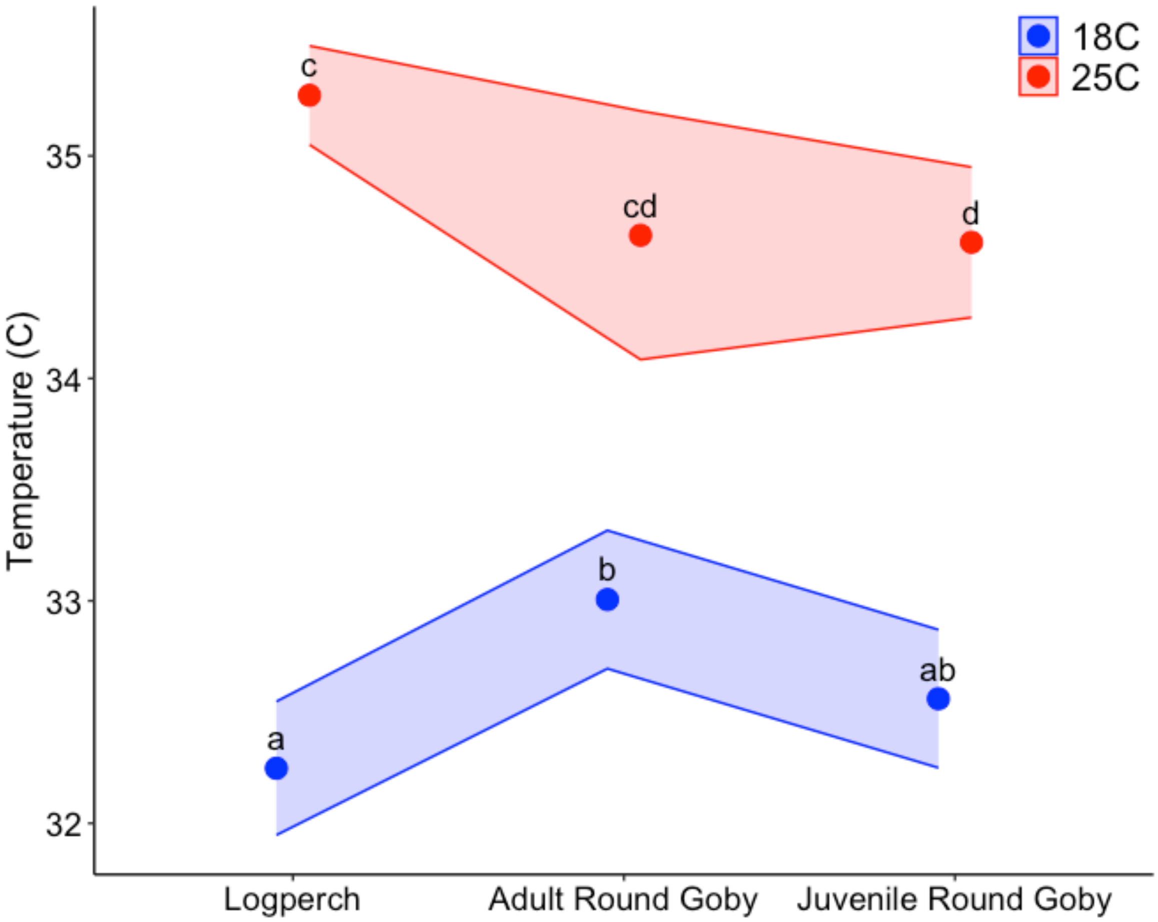

Figure 1.5. Mean values of critical thermal maximum (CT_{max}; ±95%CI) of logperch (*Percina caprodes*), adult and juvenile round gobies (*Neogobius melanostomus*) at two acclimation temperatures. Acclimation periods to trial temperatures continued for 4-6 weeks. Different letters represent significant differences between groups ($p<0.05$) derived from a post hoc Tukey Kramer test with 95% confidence intervals.

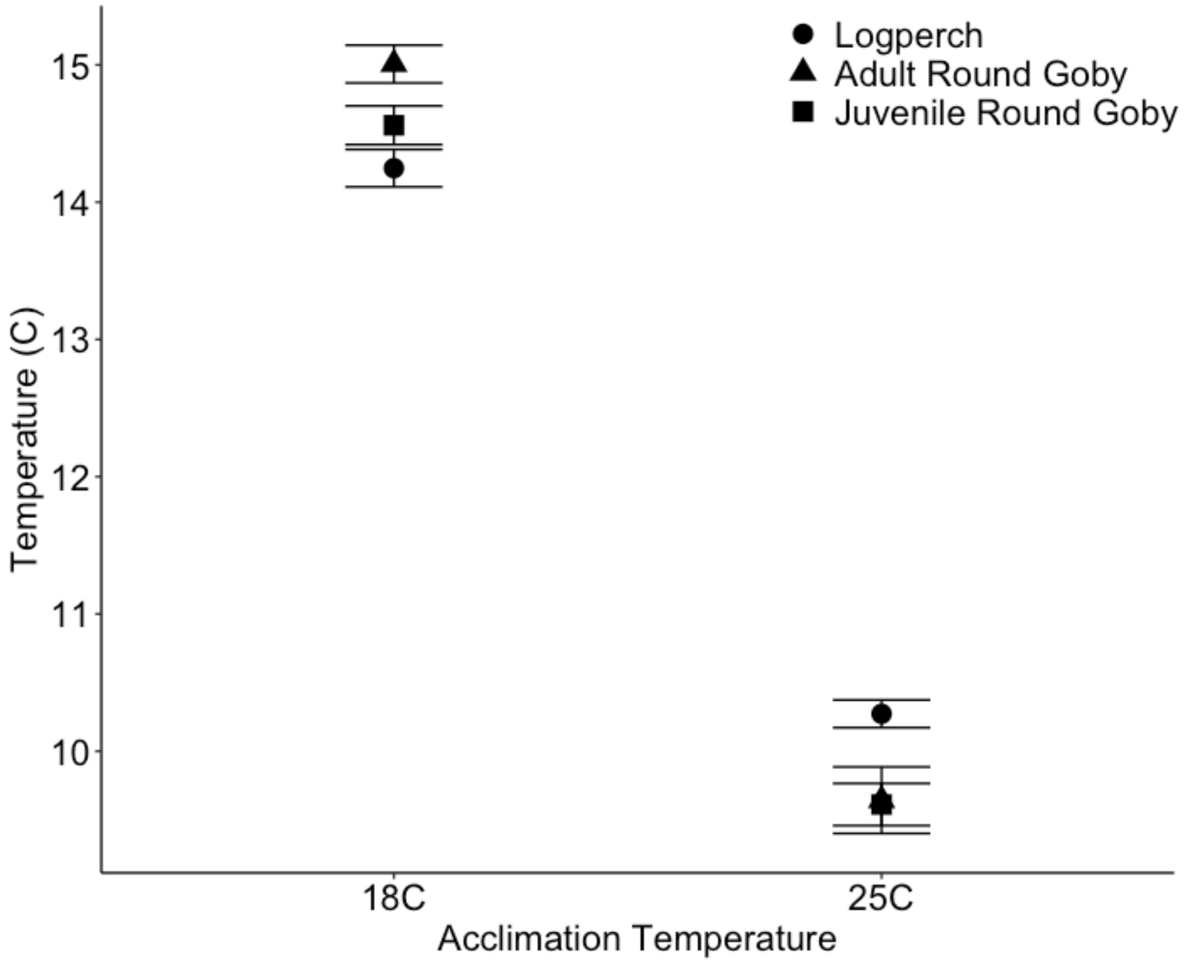

Figure 1.6. Effects of acclimation temperature on mean thermal safety margin (TSM; ±SE) of logperch (*Percina caprodes*) and adult and juvenile round gobies (*Neogobius melanostomus*) at two acclimation temperatures. Fish were exposed to the corresponding acclimation temperature 4-6 weeks prior to trials.

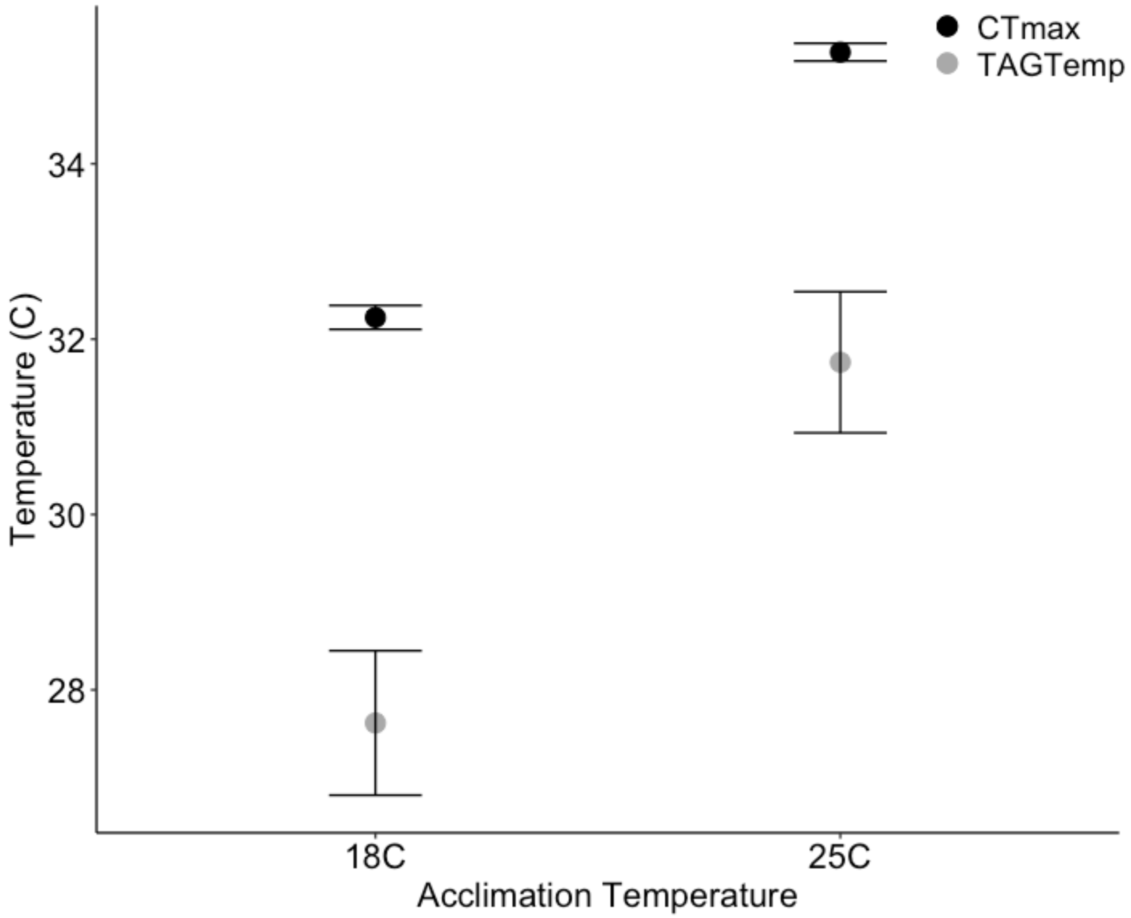

Figure 1.7. Mean values of critical thermal maximum (CT_{max}; ±SE) and thermal agitation temperature (T_{ag}; ±SE) of logperch (*Percina caprodes*) at two acclimation temperatures. Acclimation periods to trial temperatures continued for 4-6 weeks.

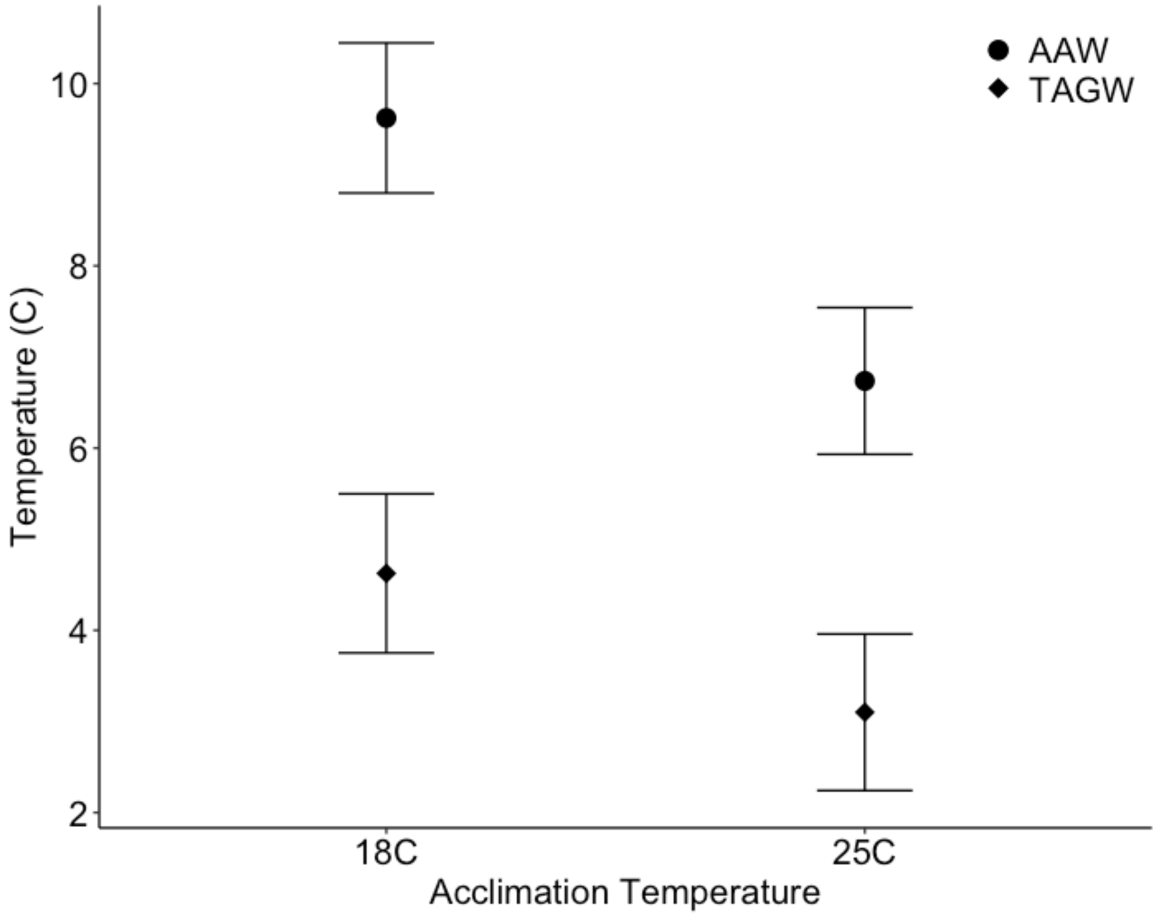

Figure 1.8. Effects of acclimation temperature on mean thermal agitation window (T_{aw}; ±SE) and acclimation-agitation window (A_{aw}; ±SE) of logperch (*Percina caprodes*). Fish were exposed to the corresponding acclimation temperature 4-6 weeks prior to trials.

General Conclusions

This study and the others that have explored the EMH have revealed its value for informing context dependencies and risk assessment, particularly in terms of identifying habitat conditions in which invader impacts are maximal. I conclude that the ecological performance of invasive and native fishes is highly dependent on environmental heterogeneity in space and time, and are expected to alter current food webs and community interactions under climate change. Rising water temperatures in the Great Lakes-St. Lawrence River region (Trumpickas et al., 2009, 2015) are predicted to stimulate an increase in the negative impacts generated by certain invasive species as environmental conditions approach their thermal optima. This provides competitive advantages for invasive species, such as the round goby, that possess a broad thermal tolerance range and thermal optimum value matching projected temperature conditions in invaded regions. However, the application of this framework is limited by knowledge of environmental optima, especially for emerging or poorly studied invasive (and native) species.

As predicted, temperature affected the resource consumption of the invasive round goby and native logperch by stimulating an increase in prey consumption in warmer temperatures. I expect that in future climate change conditions, the demand for resources will be greater for both species leading to higher instances of inter-specific competition among benthic fishes especially if conditions rise to match the thermal optimum of competing species. The demand for resources is greater in adult life stages owing to their larger body size and reproductive needs. This leads to adult life stages of invasive species exerting greater *per capita* effects on native prey communities. Contrary to my prediction, juvenile round gobies consumed fewer resources than juvenile logperch at current water temperatures. Therefore, in areas where the invader and native populations presently overlap, logperch may be less vulnerable to the negative impacts of inter-specific competition for resources due to their improved foraging ability. However, high round goby population densities may overwhelm the native competitor.

Acclimation to higher temperatures improved the thermal tolerance of round gobies and logperch. Both species and life stages displayed CT_{max} values surpassing projected water temperatures in the Great Lakes region, therefore we expect they will be able to withstand future water temperature conditions. Thermal tolerance remained consistent between life stages but differed between species. These results imply that thermal tolerance predictions can applied to multiple life stages within a population, enhancing our understanding of population responses to temperature shifts. Logperch displayed superior resilience to future climatic conditions, indicating they may possess a broader thermal tolerance range or higher thermal optima than invasive round gobies. We conclude that there are species- and population-level differences in thermal performance depending on local adaptation to the climate conditions. These implications impose limitations on the broadscale application of concepts in invasion ecology, such as the EMH. It will require risk managers to assess impacts at a smaller scale to understand how these performance metrics vary amid populations situated in differing geographical regions.

Impacts of the invasive round goby will likely be enhanced by climate warming in the Great Lakes-St. Lawrence River regions. We expect that round gobies will increase their *per capita* impacts on native prey populations in future water temperature scenarios, as well as tolerate these thermal shifts. However, native logperch populations may be able to compete with round gobies for food resources and display greater thermal resilience to climate change. My findings emphasize the management importance of evaluating context-dependencies of existing and emerging invasive species' impacts when testing hypotheses or making predictions for risk assessment.

Future Directions – Comparative Functional Responses

The lack of a complete functional response (FR) curve for juvenile round gobies at high temperatures impedes the direct comparison of feeding behaviour to logperch in future climate conditions. Since the feeding efficiency of juvenile logperch and adult round gobies improved in warmer temperatures, size-matched comparisons between these species should be conducted in future water temperature conditions to make direct resource consumption comparisons. This will indicate whether native benthic fishes will sustain their competitive ability against the invasive round goby.

The FR curves were observed to differ between round goby life stages and size ranges. I would suggest that researchers derive FR curves across all age ranges and size structures for invasive species in heterogeneous environmental conditions to determine if trends in resource consumption remain consistent. This will provide crucial information about the food demand (i.e., *per capita* effects) of an invasive population.

Future Directions – Environmental Matching Hypothesis

The thermal optimum of logperch has not been identified, preventing us from determining whether the observed ecological and physiological responses coincide with the EMH framework. Identification of optimal performance metrics for native species across populations and geographical regions would facilitate performance predictions, such as CME, between competing invaders and natives in situations of environmental heterogeneity.

Due to the observed mortality of round gobies in FR experiments when exposed to thermal and handling stress, it may be crucial to examine the combined effects of multiple stressors on performance and incorporate these into the EMH framework. Aquatic ecosystems are constantly subjected to a diverse range of overlapping chemical, physical, and biological stressors that fluctuate spatially and temporally (Dafforn et al., 2016). Particular species and life stages could be more equipped to handle combined stressors, rendering them more resilient to large ecosystem shifts. Although one stressor may have overwhelming influence on an environment at a given place and time, making predictions about invasive species performance under a single stressor could produce misleading results in over a range of ecosystems. Nevertheless, the application and enhancement of predictive frameworks like the EMH and CEM are necessary for achieving some useful measure of accuracy in risk assessment of invasive species (as well as native species-at-risk) in rapidly changing environments.

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Supplementary Material

Table S.1. Mean total length (TL) and weight (W) of *P. caprodes,* juvenile *N. melanostomus,* and adult *N. melanostomus* used in feeding experiments at two acclimation temperatures. Data are presented as mean ± standard error.

Species and Life Stage	Temperature (°C)	*n*	TL (mm)	W (g)
P. caprodes	18	28	52.07±0.83	1.13±0.08
	25	28	53.64±0.90	1.11±0.06
Juvenile *N. melanostomus*	18	28	51.04±0.69	1.19±0.07
Adult *N. melanostomus*	18	28	76.32±0.86	4.74±0.20
	25	26	74.85±0.95	4.20±0.18

Table S.2. Akaike Information Criterion (AIC) scores comparing the best model fit for functional response curves. The lowest AIC scores are bolded.

Model	*P. caprodes* - 18	*P. caprodes* - 25	Juvenile *N. melanostomus* -18	Adult *N. melanostomus* -18	Adult *N. melanostomus* -25
Flex (III)	**181.21**	275.32	**187.37**	253.72	**191.15**
Type III	181.98	275.84	194.46	**250.67**	196.28
Type II	182.58	**272.92**	191.95	252.21	199.18

Table S.3. *Frair_fit* estimated values.

Treatment	Species	Temp (°C)	Fit	Response	a±SE, p	h±SE, p
LP-18	*P. caprodes*	18	Flex (type III)	"flexpnr"	n/a	0.0404117± 0.0043649, <2.2e-16
LP-18	*P. caprodes*	18	Type III	"hassIIInr"	n/a	0.0452495± 0.0053344, <2e-16
LP-18	*P. caprodes*	18	Type II	"rogersII"	0.4467997± 0.0439888, <2.2e-16	0.0404117± 0.0043649, <2.2e-16
LP-25	*P. caprodes*	25	Flex (type III)	"flexpnr"	n/a	0.0267776± 0.0047071, 1.279e-08
LP-25	*P. caprodes*	25	Type III	"hassIIInr"	n/a	2.4434e-02± 2.9813e-03, 2.486e-16
LP-25	*P. caprodes*	25	Type II	"rogersII"	0.3258559± 0.0317026, <2.2e-16	0.0267776± 0.0047071, 1.279e-08
RGJ-18	Juvenile *N. melanostomus*	18	Flex (type III)	"flexpnr"	n/a	0.121614± 0.012498, <2.2e-16
RGJ-18	Juvenile *N. melanostomus*	18	Type III	"hassIIInr"	n/a	1.2213e-01± 9.3621e-03, <2.2e-16
RGJ-18	Juvenile *N. melanostomus*	18	Type II	"rogersII"	0.483560± 0.081174, <2.567e-16	0.121614± 0.012498, <2.2e-16
RGA-18	Adult *N. melanostomus*	18	Flex (type III)	"flexpnr"	n/a	0.0553221± 0.1259550, <2.2e-16
RGA-18	Adult *N. melanostomus*	18	Type III	"hassIIInr"	n/a	0.0592229± 0.0041519, <2.2e-16
RGA-18	Adult *N. melanostomus*	18	Type II	"rogersII"	1.0560731± 0.1259550, <2.2e-16	0.0553221± 0.0036054, <2.2e-16

RGA-25	Adult *N. melanostomus*	25	Flex (type III)	“flexpnr”	n/a	0.0380987± 0.0022629, <2.2e-16
RGA-25	Adult *N. melanostomus*	25	Type III	“hassIIInr”	n/a	0.0404769± 0.0025766, <2e-16
RGA-25	Adult *N. melanostomus*	25	Type II	“rogersII”	0.9605040± 0.0843744, <2.2e-16	0.0380987± 0.0022629, <2.2e-16

Table S.4. *Frair_boot* estimates for 95% bootstrapped confidence intervals for attack rate and handling time reported as percentile CI. Bca were not recorded as bootstrap estimates were less than 100.

Treatment	a	h	Fit
P. caprodes -18	0.303-0.657	0.028-0.057	Type II
P. caprodes -25	0.183-0.049	0-0.049	Type II
Juvenile *N. melanostomus* -18	0.224-0.852	0.068-0.193	Type II
Adult *N. melanostomus* -18	0.421-1.857	0.026-0.078	Type II
Adult *N. melanostomus* -25	0.571-1.496	0.027-0.05	Type II

Table S.5 AIC and BIC scores of linear regression models and linear mixed model fits for logperch (*P. caprodes*) critical thermal maximum (CT_{max}) (a), agitation temperature (T_{ag}) (b), agitation window (T_{aw}) (c), acclimation agitation window (A_{aw}) (d), and thermal safety margin (TSM) (e).

a) CT_{max}

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	32.24	+					22	29.89	**33.43**
8	29.81	+	+				21	29.66	34.37
11	24.55	+	+		+		20	**29.15**	35.04
14	24.55	+			+		20	**29.15**	35.04
10	32.33	+	+	+			20	29.65	35.55
1	32.24	+				+	7	35.04	39.76
9	34.29	+		+			21	31.07	35.79
12	27.05	+	+	+	+		19	28.86	35.92
2	28.66	+	+			+	16	38.58	44.47
3	33.02	+		+		+	8	40.01	45.91
5	23.52	+	+		+	+	16	40.98	48.05
13	23.52	+	+			+	16	40.98	48.05
4	30.12	+	+	+		+	10	43.19	50.25
6	25.39	+	+	+	+	+	19	45.16	53.41

b) T_{ag}

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	27.62	+					22	121.8	**125.3**
1	27.62	+				+	22	**121.0**	125.7
8	21.10	+	+				21	123.5	128.2
9	27.79	+		+			21	123.8	128.5
3	27.99	+		+		+	6	123.8	128.5
2	21.10	+	+			+	21	124.1	130.0
11	26.68	+	+		+		20	125.4	131.3
14	26.68	+			+		20	125.4	131.3
10	23.25	+	+	+			20	125.4	131.3
5	26.68	+	+		+	+	20	125.4	132.5
13	26.68	+			+	+	20	125.4	132.5
4	23.68	+	+	+		+	8	125.6	132.6
12	28.75	+	+	+		+	19	127.4	134.5
6	28.68	+	+	+	+	+	19	126.9	135.1

c) T_{aw}

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	4.62	+					22	124.7	**128.3**
1	4.63	+				+	7	**123.7**	128.4
3	0.46	+		+		+	7	125.0	130.9
8	12.0	+	+				21	126.4	131.1
9	2.19	+		+			21	126.7	131.4
2	12.3	+	+			+	18	126.5	132.4
11	-2.13	+	+		+		20	128.1	133.9
14	-2.13	+			+		20	128.1	133.9
10	7.64	+	+	+			20	128.3	134.1
5	-1.38	+	+		+	+	19	127.6	134.6
13	-1.38	+			+	+	19	127.6	134.6
4	6.01	+	+	+		+	9	127.6	134.7
6	-6.27	+	+	+	+	+	18	128.7	136.9
12	-6.35	+	+	+	+		19	130.0	137.1

d) A_{aw}

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	9.62	+					22	121.8	**125.3**
1	9.62	+				+	22	**121.0**	125.7
9	28.8	+		+			22	124.3	127.9
8	3.10	+	+				21	123.5	128.2
3	9.99	+		+		+	6	124.3	128.5
2	3.10	+	+			+	21	124.1	130.0
11	8.68	+	+		+		20	125.4	131.3
14	8.68	+			+		20	125.4	131.3
10	5.25	+	+	+			20	125.4	131.3
5	8.68	+	+		+	+	20	125.4	132.5
13	8.68	+			+	+	20	125.4	132.5
4	5.68	+	+	+		+	8	125.6	132.6
12	10.8	+	+	+	+		19	127.4	134.4
6	10.7	+	+	+	+	+	19	45.16	53.41

e) TSM

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	14.2	+					22	29.90	**33.43**
8	11.8	+	+				21	29.66	34.37
11	6.55	+	+		+		20	**29.15**	35.04
14	6.55	+			+		20	**29.15**	35.04
10	14.3	+	+	+			20	29.65	35.54
9	16.3	+		+			21	31.07	35.79
12	9.05	+	+	+	+		19	28.86	35.92
1	14.2	+				+	7	35.05	39.76
2	10.7	+	+			+	21	38.58	44.57
3	15.0	+		+		+	8	40.01	45.91
5	5.52	+	+		+	+	16	40.98	48.05
13	5.52	+			+	+	16	40.98	48.05
4	12.1	+	+	+		+	10	43.19	50.25
6	7.39	+	+	+	+	+	19	45.16	53.41

Note: Acclimation temperature = Temp; total length = Length; acclimation time = Tacc; acclimation temperature and length interaction term = Length*Temp; rearing tank = HT.

Table S.6. AIC and BIC scores of linear regression models and linear mixed model fits for juvenile round gobies (*N. melanostomus*) critical thermal maximum (CT_{max}) (a) and thermal safety margin (TSM) (b).

a) CT_{max}

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	32.56	+					22	39.76	**43.29**
11	27.99	+	+		+		20	**39.34**	45.23
14	27.99	+			+		20	**39.34**	45.23
9	31.34	+		+			21	41.56	46.26
8	32.05	+	+				21	41.61	46.32
12	26.68	+	+	+	+		19	41.02	48.08
10	31.18	+	+	+			20	43.47	49.37
1	27.99	+				+	20	45.82	50.53
3	31.34	+		+		+	21	50.76	56.65
2	32.04	+	+			+	10	53.09	58.98
5	27.99	+	+		+	+	20	55.44	62.51
13	27.99	+			+	+	20	55.44	62.51
4	31.40	+	+	+		+	12	57.99	65.07
6	26.68	+	+	+	+	+	19	60.29	68.54

b) TSM

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	14.56	+					22	39.76	**43.29**
11	9.989	+	+		+		20	**39.34**	45.23
14	9.989	+			+		20	**39.34**	45.23
9	13.34	+		+			21	41.55	46.26
8	14.05	+	+				21	41.61	46.32
12	8.68	+	+	+	+		19	41.02	48.08
10	13.18	+	+	+			20	43.48	49.37
1	14.56	+				+	2	45.82	50.52
3	13.34	+		+		+	21	50.76	56.65
2	14.04	+	+			+	10	53.09	58.98
5	9.989	+	+		+	+	20	55.45	62.52
13	9.989	+			+	+	20	55.45	62.52
4	13.40	+	+	+		+	12	57.99	65.07
6	8.684	+	+	+	+	+	19	60.30	68.54

Note: Acclimation temperature = Temp; total length = Length; acclimation time = Tacc; acclimation temperature and length interaction term = Length*Temp; rearing tank = HT.

Table S.7. AIC and BIC scores of linear regression models and linear mixed model fits for adult round gobies (*N. melanostomus*) critical thermal maximum (CT_{max}) (a) and thermal safety margin (TSM) (b).

a) CT_{max}

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	33.01	+					17	37.78	**40.62**
11	35.35	+	+		+		15	**36.95**	41.67
14	35.35	+			+		15	**36.95**	41.67
12	32.17	+	+	+	+		14	37.16	42.83
9	30.28	+		+			16	39.06	42.83
8	32.28	+	+				16	39.66	43.43
1	32.99	+				+	4	41.50	45.28
10	29.89	+	+	+			8	40.99	45.72
3	28.08	+		+		+	12	44.07	48.79
2	30.89	+	+			+	16	47.78	52.51
4	25.91	+	+	+		+	14	50.32	55.99
5	33.87	+	+		+	+	15	51.05	56.72
13	33.87	+			+	+	15	51.05	56.72
6	27.89	+	+	+	+	+	9	52.59	59.20

b) TSM

Model	(Intercept)	Temp	Length	Tacc	Length*Temp	(1|HT)	df	AIC	BIC
7	15.01	+					17	37.78	**40.62**
11	17.35	+	+		+		15	**36.95**	41.67
14	17.35	+			+		15	**36.95**	41.67
12	14.17	+	+	+	+		14	37.16	42.83
9	12.28	+		+			16	39.06	42.83
8	14.28	+	+				16	39.66	43.43
1	14.99	+				+	4	41.50	45.28
10	11.89	+	+	+			15	40.99	45.72
3	10.08	+		+		+	12	44.07	48.79
2	12.89	+	+			+	16	47.78	52.51
4	7.905	+	+	+		+	14	50.32	55.99
5	15.87	+	+		+	+	15	51.05	56.72
13	15.87	+			+	+	15	51.05	56.72
6	9.887	+	+	+	+	+	9	52.59	59.20

Note: Acclimation temperature = Temp; total length = Length; acclimation time = Tacc; acclimation temperature and length interaction term = Length*Temp; rearing tank = HT.

Table S.8. AIC and BIC scores of linear regression models and linear mixed model fits examining the correlation with the proportion of prey consumed in response to fixed and random effects.

Model	(Intercept)	Density	Temp	Sp	LS	Length	Sp*Temp	Tacc	(1|HT)	df	AIC	BIC
9	0.883	+	+	+	+					133	**40.63**	**58.19**
10	0.576	+	+	+	+	+				132	42.01	62.50
12	0.931	+	+	+	+		+			132	42.49	62.98
16	0.849	+	+	+	+			+		132	42.61	63.10
15	3.526	+	+	+	+		+	+		131	42.94	66.35
11	0.610	+	+	+	+	+	+			131	43.76	67.18
14	0.479	+	+	+	+	+		+		131	43.92	67.34
13	3.021	+	+	+	+	+	+	+		130	44.56	70.91
1	0.899	+	+	+	+				+	131	77.64	98.13
3	0.943	+	+	+	+		+		+	132	86.12	109.5
2	0.630	+	+	+	+	+			+	57	87.89	111.3
8	0.864	+	+	+	+			+	+	129	88.12	111.5
7	3.508	+	+	+	+		+	+	+	112	91.73	118.1
4	0.650	+	+	+	+	+	+		+	63	96.23	122.6
6	0.532	+	+	+	+	+		+	+	68	98.27	124.6
5	3.109	+	+	+	+	+	+	+	+	104	102.1	131.4

Note: Acclimation temperature = Temp; species = Sp; life stage = LS; total length = Length; acclimation temperature and species interaction term = Sp*Temp; acclimation time = Tacc; rearing tank = HT.

Table S.9. AIC and BIC scores of generalized linear model fits examining the correlation with functional response parameters attack rate, handling time, maximum feeding rate, and FRR in response to fixed.

a) Attack Rate

Model	Intercept	Temp	Sp	LS	Sp*Temp	LS*Temp	Sp*Temp*LS	df	AIC
1	0.140	+	+	+				5	NA
2	0.169						+	6	NA
3	0.169			+	+			6	NA
4	0.169		+			+		6	NA

b) Handling Time

Model	Intercept	Temp	Sp	LS	Sp*Temp	LS*Temp	Sp*Temp*LS	df	AIC
1	-3.945	+	+	+				5	NA
2	-3.949						+	6	NA
3	-3.949			+	+			6	NA
4	-3.949		+			+		6	NA

c) Maximum Feeding Rate

Model	Intercept	Temp	Sp	LS	Sp*Temp	LS*Temp	Sp*Temp*LS	df	AIC
1	-4.242	+	+	+				5	NA
2	3.979						+	6	NA
3	3.979			+	+			6	NA
4	3.979		+			+		6	NA

d) Functional Response Ratio

Model	Intercept	Temp	Sp	LS	Sp*Temp	LS*Temp	Sp*Temp*LS	df	AIC
1	-3.029	+	+	+				5	NA
2	4.113						+	6	NA
3	4.113			+	+			6	NA
4	4.113		+			+		6	NA

Note: Acclimation temperature = Temp; species = Sp; life stage = LS; acclimation temperature and species interaction term = Sp*Temp; life stage and acclimation temperature interaction term = LS*Temp; species, life stage and acclimation temperature interaction term = Sp*Temp*LS.

Table S.10. Summary of average temperature during fish-holding period. Temperature measurements were recorded weekly.

Treatment	Temperature (°C)
P. caprodes - Functional Response 18°C	18.30
P. caprodes - Functional Response 25°C	24.66
Juvenile *N. melanostomus* - Functional Response 18°C	18.35
Adult *N. melanostomus* - Functional Response 18°C	18.27
Adult *N. melanostomus* - Functional Response 25°C	24.85
P. caprodes - CT_{max} 18°C	18.05
P. caprodes - CT_{max} 25°C	24.68
Juvenile *N. melanostomus* - CT_{max} 18°C	18.40
Juvenile *N. melanostomus* - CT_{max} 25°C	24.98
Adult *N. melanostomus* - CT_{max} 18°C	18.42
Adult *N. melanostomus* - CT_{max} 25°C	24.96