Influence of climate warming on the ecological impacts of an invasive crayfish

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Abstract

Climate warming can mediate the ecological impact of invasive species by altering their *per capita* effects, thereby potentially causing shifts in predator-prey dynamics and competitive dominance over native species. Furthermore, invasive populations of a species can exhibit substantial intraspecific trait variability that causes spatial variation in their impacts, even within the same climatic region. Therefore, empirical approaches that account for environmental context-dependencies and interpopulation trait variation are needed to improve impact risk assessment. Several recent studies have demonstrated that the functional response of a species (its predation rate in relation to prey density) is an important indicator of its impact potential when introduced outside its natural range. Using laboratory experiments, I examined the effect of temperature on the functional response of rusty crayfish (*Faxonius rusticus*) from six independent populations distributed across a latitudinal gradient in their invaded range. I tested the prediction that, under elevated temperatures, individuals from southern populations will exhibit higher maximum feeding rates than those from northern populations. Contrary to prediction, individuals from northern and southern populations varied in their response to elevated temperature such that there was no correlation with their latitude of provenance, suggesting that environmental variables other than temperature are driving the observed responses. Nonetheless, while handling times showed no consistent pattern across populations and treatments, the attack rates of individuals from northern populations at both temperatures were consistently higher than those from southern populations. My findings also suggest that there are optimal temperatures at which foraging rates are maximized, but that these optima vary across the populations tested. This study highlights the potential for misleading conclusions to arise from risk assessments whose information is derived from a single population.

Résumé

Le réchauffement climatique peut atténuer l’impact écologique des espèces envahissantes en modifiant leurs effets *per capita*, ce qui pourrait entraîner des changements dans les dynamiques prédateur-proie et dans les conséquences de la concurrence avec les espèces indigènes. De plus, les populations envahissantes d’une espèce peuvent présenter une importante variabilité intraspécifique, ce qui entraîne une variation spatiale de leurs impacts même au sein d’une seule région climatique. Des approches empiriques qui tiennent compte des dépendances du contexte environnemental et de la variation des traits entre les populations sont ainsi nécessaires pour améliorer l’évaluation des risques d’impact. Plusieurs études récentes ont démontré que la réponse fonctionnelle d’une espèce, soitson taux de prédation par rapport à la densité des proies, est un indice utile de son potentiel d’impact dans les cas d’introductions en dehors de son aire de répartition naturelle. À l’aide d’expériences en laboratoire, j’ai testé l’effet de la température sur la réponse fonctionnelle des écrevisses rouilleuses (*Faxonius rusticus*) provenant de six populations indépendantes, réparties à travers un gradient latitudinal dans leur aire de répartition envahie. J’ai testé l’hypothèse qu’à des températures levées, les individus des populations du sud présentent des taux maximaux de consommation plus élevés que ceux des populations du nord. Contrairement aux prévisions, les individus des populations du nord et du sud ont réagi de manière différente aux températures élevées, de sorte qu’il n’y a pas eu de corrélation avec leur latitude de provenance, ce qui suggère que des variables environnementales autres que la température sont à l’origine des réponses observées. Néanmoins, alors que les temps de manipulation n’ont pas varié de façon cohérente entre les populations et les traitements, les taux d’attaque des individus des populations du nord aux deux températures étaient systématiquement plus élevés que ceux des populations du sud. Les résultats suggèrent également qu’il existe des températures optimales pour maximiser les taux de recherche de nourriture, mais que ces optima varient selon les populations testées. Cette étude souligne le risque de conclusions trompeuses découlant d’évaluations des risques qui se basent sur une seule population.

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Author Contributions

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, were led by me, while Prof. Ricciardi provided instrumental feedback and editing of my manuscript. This being the case, and reflecting the intention to submit for publication, plural pronouns are used throughout Chapter 1.

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General Introduction

Invasions as a form of global change

Throughout the history of life, species have spread into regions where they have no evolutionary history – a process typically referred to as *biological invasion*. Under human influence, modern biological invasions are occurring at unprecedented rapid rates, differing in several ways from prehistoric invasions and thus constituting a form of anthropogenic global change (Ricciardi 2007). When outside their natural range, species are described as *non-native*. Non-native species introduced by human activities are among the most important stressors to ecosystems on a global scale (Simberloff et al. 2013; Chapman et al. 2019; Pyšek et al. 2020), largely due to their propensity to undergo damaging outbreaks in the absence of co-evolved natural enemies and because of a lack of evolutionary experience in resident species, which among other things can contribute to heightened prey naiveté (Anton et al. 2020). Invasions can cause a wide range of impacts including species extinctions, disease transmission, physical habitat modification, and alteration of food webs and ecosystem function (Mack et al. 2000; Simberloff et al. 2013; Ricciardi et al. 2013; Bellard et al. 2016; Mollot et al. 2017).

In particular, insular systems such as lakes and river basins are more sensitive to the effects of invasions than mainland terrestrial and marine ecosystems (Sala et al. 2000; Ricciardi & MacIsaac 2011). In the previous century (1900-1999), over 120 freshwater animal species were recorded as extinct in North America, and hundreds of other fishes, mollusks, crayfishes, and amphibians were considered threatened or endangered; rates of extinction are 3 to 5 times greater in freshwater systems than in terrestrial and coastal marine systems in continental North America (Ricciardi & Rasmussen 1999). Invasive species are a major contributing cause of freshwater fish extinction in North America, second only to habitat degradation (Williams et al.

1989; Jelks et al 2008). Large aquatic ecosystems are among those experiencing the highest rates of invasion and have been widely altered by non-native species (Ricciardi 2006; Strayer & Dudgeon 2010; Ricciardi & MacIsaac 2011; MacIsaac et al. 2015). For example, the world's largest freshwater system, the Laurentian Great Lakes basin, has been invaded by >180 non-native species, a fraction of which have caused massive ecological changes (Ricciardi 2006; Pagnucco et al. 2015). The consequences of the vast majority of invasions remain unknown, and impact studies have been subject to taxonomic biases, focusing more often on fishes than invertebrates (Parker et al. 1999; MacIsaac et al. 2011).

In temperate regions, climate change is expected to facilitate invasions of warm-adapted species by removing thermal barriers and increasing seasonal stress for cold-adapted competitors (Sharma et al. 2007; Rahel & Olden 2008; Osmond et al. 2017). It may also mediate the ecological impacts of invaders by altering pathways of introduction (Hellman et al. 2008), by affecting species' *per capita* effects, abundance, and range size (Iacarella et al. 2015a), and by causing shifts in competitive dominance (Rahel & Olden 2008). Given that aquatic habitats are mainly comprised of ectotherms, whose metabolic rates and behavioral traits are highly temperature dependent (Castañeda et al. 2004), shifting thermal regimes have the potential to change consumer-resource interactions (Rall et al. 2012; Gilbert et al. 2014; Sentis et al. 2017; Archer et al. 2018).

Impact risk assessment: prediction and context-dependencies

Predictive approaches that incorporate temperature and other context-dependencies are needed to improve our understanding of the impacts of biological invasion and their interactions with climate warming (Ricciardi et al. 2013). Previous studies have revealed relationships between predator-prey interactions and local environmental conditions such as water chemistry (e.g. oxygen, conductivity), temperature, and habitat complexity (Laverty et al. 2014; Iacarella & Ricciardi 2015; Iacarella et al. 2015a,b; Barrios-O'Neill et al. 2016; Wasserman et al. 2016; South et al. 2017; Cuthbert et al. 2019). Studies have also examined how invader impacts are mediated by biotic interactions and the composition of the invaded community (Barrios-O'Neill et al. 2014; Grimm et al. 2020). Variation in aggression, predation rate, and other *per capita* effects can reflect behavioural and personality traits that differ across conspecific invasive populations owing to post-introduction evolutionary changes, founder effects (William et al 2007; Lee & Gelembiuk 2008; Chapple et al. 2012), and time since invasion (Strayer et al. 2006; Iacarella et al. 2015b,c; Evangelista et al. 2019).

Natural environmental gradients can promote differential behaviors and thermal performances across conspecific populations (Colautti & Barrett 2013; Hodgson & Schwanz 2019; Hargreaves et al. 2020). According to Hodgson and Schwanz (2019), conspecific populations can vary in their response to thermally distinct environments through either plasticity or local adaptation, which can generate one of two different patterns: a co-gradient response (in which cold-adapted individuals show a greater performance at lower temperatures compared to warm-adapted individuals) or a counter-gradient response (cold-adapted individuals exhibit greater performance at higher temperatures). A possible explanation for the counter-gradient response is that populations from northern latitudes have compensated for a short growth season by evolving faster growth rates and associated behavioural traits (Conover & Present 1990). Relatively few studies have investigated local adaptation as a potential driver in non-native species spread and its influence on impact across a latitudinal gradient (Colautti & Barrett 2013; Hargreaves et al. 2020). Collectively, the aforementioned research suggests that context-dependencies and interpopulation trait variation pose a major challenge in generating accurate forecasts for high-risk invaders, particularly for predicting the magnitude and direction of their impacts (Ricciardi et al. 2013; Novoa et al. 2019).

A predictive tool for quantitative assessments: Comparative functional responses

The overall ecological impact of a non-native species can be considered to be a function of their abundance and *per capita* effects (Parker et al. 1999; Ricciardi et al. 2013). An example of a *per capita* effect is resource consumption rate, which tends to be higher in successful and damaging invasive species (Rehage et al. 2005; Morrison & Hay 2011; Chapple et al. 2012; Ricciardi et al. 2013; DeRoy et al. 2020). However, it would be more appropriate to compare *populations* and hypothesize that the most damaging invasive populations contain individuals whose mean consumption rates are higher than individuals in other populations. Furthermore, the magnitude of an invader's *per capita* effect is predicted to be inversely proportional to the difference between local abiotic conditions in the invaded habitat and the physiological optimum of the invader (Iacarella et al. 2015a). Resource consumption efficiency, for example, is expected to be maximized as ambient temperature approaches a thermal optimum (Huey & Stevenson 1979; Iacarella et al. 2015a; Uiterwaal & DeLong 2020).

Given that resource consumption plays a major role in many kinds of impacts (e.g. predator-prey dynamics, competition, nutrient cycling, changes to community composition; Ricciardi et al. 2013), a quantitative, standardized measurement of consumption efficiency would be a valuable tool for invader risk assessment. One such tool is the *functional response* of a species – the relationship between its resource uptake (e.g. predation) and resource (prey) density (Holling 1959). The functional response curve (Figure I.1), characterized as Type I, II or Type

III, indicates whether the predator-prey dynamic is likely to be destabilizing (Type II) or stabilizing (Type II) in nature (Alexander et al. 2014, Dick et al. 2013). It has been shown that high-impact invaders often have higher functional responses than low-impact invaders and functionally-similar native species (Dick et al. 2017). Furthermore, functional response experiments can be designed to incorporate context dependencies (Table I.1), demonstrating their value as a tool for impact risk assessment under environmental stressors (Rall et al. 2012; Dick et al. 2014, 2017; South et al. 2017). However, very few such studies have used this design to compare variation across populations or across their latitudinal range (Table I.1).

Crayfish as a model organism for invasion

Crayfish are considered as ecosystem engineers and, in some cases, keystone species, in nearshore freshwater food webs (Peters et al. 2014; Tricarico & Aquiloni 2016). The importance of these omnivores in aquatic food webs is indicated by studies of their invasion impacts in North American temperate freshwater ecosystems (Hill & Lodge 1999; Willis et al. 2004; Peters et al. 2008; Lodge et al. 2012; Peters et al. 2014). Crayfish have proven to be among the most disruptive invasive freshwater animals globally (Larson & Olden 2016; Madzivanzira et al. 2020), largely due to their broad environmental tolerance, aggressive behaviour, habitat engineering activities, transmission of a fungal pathogen (crayfish plague), and voracious consumption of invertebrates and macrophytes (Lodge et al. 2012; Tricarico & Aquiloni 2016). The genus *Faxonius* includes taxa with extensive invasion histories as well as taxa that are imperilled. Among the former is the rusty crayfish, *Faxonius* (formerly *Orconectes*) *rusticus*, a North American species native to the Ohio River valley but with a history of invasion in the Great Lakes basin (Hamr 2010; Reid & Nocera 2015; Peters et al. 2014). In places where the rusty crayfish has been introduced through human-mediated translocations, it has caused drastic changes local aquatic ecosystems and has replaced in dominance the native northern clearwater crayfish (*F. propinquus*) and virile crayfish (*F. virilis*) (Olden et al. 2006; Reid & Nocera 2015).

Research objectives

The overall goal of my research is to understand how different context dependencies, specifically temperature and geography, interact with each other and ultimately explain variation in invasion impacts across conspecific populations. For this purpose, I examine differences in the *per capita* effects of rusty crayfish (*F. rusticus*) populations distributed along a south-to-north axis, using a comparative functional response approach. My objectives are to determine 1) the effect of temperature increase on prey consumption efficiency across non-native conspecific populations of rusty crayfish; and 2) whether differences in *per capita* effects (i.e. maximum feeding rates) of individuals from these non-native conspecific populations can be predicted by their latitude of provenance. Thus, I also evaluate the prediction that functional responses are maximized as ambient temperature approaches the physiological optimum for each population (in accordance with the Environmental Matching Hypothesis; Ricciardi et al. 2013)

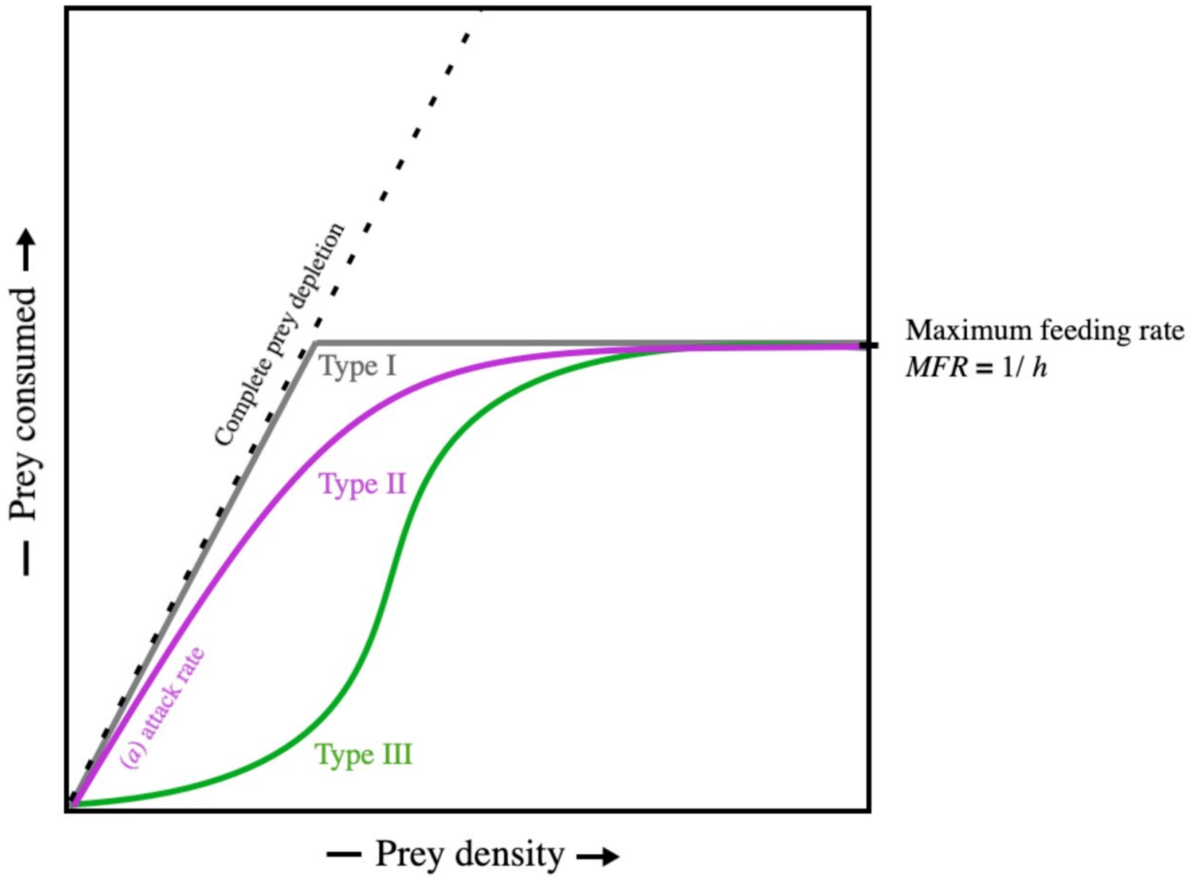
Table I.1 – Summary of studies relating invasive alien species impacts to environmental context.

Reference	Context-dependency	Predator species	Prey species	Results
Grimm et al. 2020	- Geographically disparate native & invasive populations	- *Faxonius limosus*	- *Daphnia magna*	Maximum feeding rates and functional response type varied across conspecific populations; these differences did not correlate with biogeographic origin of the population nor time since invasion.
Haubrock et al. 2020	- Temperature gradient - Life stage	Invasive: - *Lepidodactylus lugubris*	- *Acanthoscelides obtectus*	Life stage temperature dependence, where juvenile geckos showed increased functional response with increasing temperature, but no significant relationship was found for adults.
Archer et al. 2019	- Natural temperature gradient - Laboratory temperature gradient - Population abundance	- *Limnophora riparia* - *Potamophylax cingulatus*	- *Simuliidae*	Temperature had no effect on handling times for both species. However, attack rates showed a significant dependence on temperature but the response varied across species traits.
Cuthbert et al. 2019	- Habitat complexity	- *A. debilis*	- *C. pipiens*	Habitat complexity had no significant effect on handling times. However, attack rates showed a significantly increase in low-complexity habitats.
Paton et al. 2019	- Predator population density - Time since invasion	Invasive: - *Neogobius melanostomus*	- *Hyalella azteca*	Attack rates were influenced by predator population density, where high-density sites exhibited higher rates than low-density sites. However, non significant differences in functional response was between individuals living at the invasion front from those living in established areas.

Vesely et al. 2019	- Temperature gradient - Trophic interactions	- *Aeshna cyanea* - *Procambarus virginalis*	- *Cyprinus carpio*	Functional response parameters *a* and *h* differed in their response to temperature. Attack rates increased significantly at elevated temperatures, but no differential effect was observed in handling times. Differential functional responses were observed in intra- and inter-specific predator interactions depending on species identity, revealing that food web dynamics between true predators and omnivores can be altered by changing environmental variables.
Gebauer et al. 2018	- Temperature	Invasive: - *Neogobius melanostomus* - *Proterorhinus semilunaris*	- *Cyprinus carpio*	No significant temperature dependency was observed on attack rates and handling times in either species. However, inter-specific comparisons revealed slightly higher attack rates for *P. semilunaris* at 20 °C.
South et al. 2017	- Temperature - Habitat complexity - Light regime	Invasive: - *Pterois volitans*	- *Paleomonetes varians*	Functional responses were significantly higher at the high temperature treatment when comparing model fits. There were non-significant effects of habitat complexity on functional responses. The light regime had a significantly higher prey consumption than red (i.e. dark) light regime.
Wasserman et al. 2016	- Habitat complexity - Temperature	Invasive: - *Enithares sobria*	- *Daphnia longispina*	Observed effects of temperature and habitat complexity in functional response parameters.
Wasserman et al. 2016	- Multiple predator effects	Invasive: - *Epomis macrochirus* - *Pseudocrenilabrus philander* - *Tilapia sparrmanii*	- *Oreochromis mossambicus*	Differential functional responses were observed in intra- and inter-specific predator interactions depending on species identity.

Iacarella et al. 2015a	Temperature gradient	Invasive: - *Hemimysis anomala* - *Mysis diluviana*	- *D. pulex*	Exhibited distinct peak performances near their respective thermal optima.
Barrios O'Neill et al. 2014	- Diel vertical migrations	Invasive: - *Hemimysis anomala* Native: - *Mysis salemaai*	- *Daphnia magna*	Invasive *H. anomala* had higher functional responses than native *Mysis salemaai* in all locations during nighttime. However, non-significant difference was observed during the day.
Barrios O'Neill et al. 2014	Predator-free space	Native: - *G. pulex* - *G. d. celticus*	Invasive: - *C. curvispinum*	Increased handling times (*h*) and reduced attack rates (*a*) with increasing predator-free space.
Laverty et al. 2014	- Dissolve oxygen	Invasive: - *G. pulex* Native: - *G. duebeni celticus*	- *Baetis rhodani* - *Simuliidae*	*G. pulex* had higher functional responses than native *G. d. celticus.* Low oxygen concetrations reduced the attack rates for both species, but a differential effect was observed depending of prey type.
Dick et al. 2013	- Geographically disparate invasive populations	- *Hemimysis anomala*	- *Daphnia pulex*	*H. anomala* functional responses varied significantly in the two different invaded ranges, but were higher than functionally-similar natives in both ranges.
Sentis et al. 2012	- Temperature gradient	- *Coleomegilla maculata*	- *Myzus persicae*	Temperature influenced the functional response of *C. maculate* and an optimal performance peak was observed at intermediate temperatures.

Figure 1.1 – Types of functional response curve



Chapter 1- Intraspecific variation in functional response of an invasive crayfish to climate warming

Abstract

Studies suggest that climate warming can facilitate warm-adapted species invading temperate regions through the removal of thermal barriers and increased seasonal stress for cold-adapted competitors. Elevated temperatures could also mediate the ecological impacts of an invader by altering its *per capita* effects, such as its functional response, potentially causing shifts in predator-prey dynamics and competitive dominance over native species. Here, in laboratory experiments we examine the effect of temperature on the functional response of rusty crayfish (*Faxonius rusticus*) from six populations spanning a latitudinal gradient in their invaded range. We tested the prediction that individuals from southern populations would exhibit higher maximum feeding rates than those from northern populations, under an elevated temperature. Contrary to our hypothesis, individuals from northern and southern populations varied in their response to elevated temperature such that there was no correlation to their latitude of provenance, suggesting that variables other than temperature are more important drivers of the observed patterns. However, while handling times showed no consistent pattern across populations and treatments, the attack rates of individuals from northern populations at both temperatures were consistently higher than those from southern populations. We propose that these interpopulation differences in functional response could arise from 1) founder effects of genetically distinct propagules that establish populations at each site, 2) phenotypic plasticity (the counter-gradient hypothesis), and 3) differences in the composition of the source community (such as presence of congeners) which could influence selection of feeding behaviors.

Introduction

Species invasions interact with climate warming

Climate change significantly impacts native and non-native species by altering organismal phenology, species ranges, and ecosystem processes (Walther et al. 2002; Cahill et al. 2013; Khosa et al. 2020). Most studies exploring the effects of climate change on biodiversity focus on changes to the distribution and abundance of native taxa of conservation concern, or economically important pest species (Hellman et al 2008), but climate change is also expected to influence the invasion success and impact of a potentially enormous number of non-native species (Dukes & Mooney 1999; Ward & Masters 2007; Englund et al. 2011; Mofu et al. 2019).

Freshwater biodiversity is already being rapidly transformed across spatial scales. Large lakes and rivers are among the most invaded systems on the planet (Ricciardi 2006) and freshwater taxa are among the most imperiled (Ricciardi and Rasmussen 1999; Strayer and Dudgeon 2010). Mid-to-high latitude aquatic systems are particularly sensitive to climate warming, which can cause seasonally stressful conditions for cold-adapted species and more hospitable conditions for non-native warm-adapted species (Sharma et al 2007; Rahel & Olden 2008). Given that freshwater assemblages mainly comprise ectotherms whose foraging and metabolic rates are constrained by ambient temperatures (Woodward et al. 2010; Paaijmans et al. 2013), consumer-resource interactions and their consequences will be affected by shifting temperature regimes (Osmond et al. 2017). Thus, climate warming can contribute to context-dependent variation in the distribution, abundance, and impact of invading non-native species (Walther et al. 2009; South et al. 2018; Khosa et al. 2020).

Empirical approaches to understanding and predicting invasion

Context dependencies pose a major challenge to invader risk assessment, particular for impact prediction, and hypotheses must therefore consider the influence of local environmental variables (Ricciardi et al. 2013). The Environmental Matching Hypothesis (Ricciardi et al. 2013; Iacarella et al. 2015a) predicts that the *per capita* effect of an invader increases as habitat conditions approach its physiological optimum owing to enhanced performance. Thus, feeding rates and other *per capita* effects that mediate consumptive impacts and competition are maximized as temperatures approach thermal conditions optimal for organismal growth (Huey & Stevenson 1979; Iacarella et al. 2015a), as demonstrated by independent meta-analyses of consumptive impacts of invasive aquatic animals (Englund et al. 2011; Iacarella et al. 2015a).

Empirical evidence suggests that an invader's success and impact are related, in part, to how efficiently it uses limiting resources (Rehage et al. 2005; Morrison & Hay 2011; Chapple et al. 2012; DeRoy et al. 2020). Foraging efficiency can be derived experimentally by measuring a consumer's functional response – its rate of prey consumption in relation to prey density, which can be categorized as three distinct types: Type I – a linear increase in feeding rate with no constraint of handling time; Type II – an inversely density-dependent (destabilizing) response resulting in rapid resource depletion at low densities; and Type III – a positively density-dependent sigmoidal (stabilizing) response resulting in a resource refugium at low density (Holling 1959). Associated parameters include: attack rate (a) – the instantaneous rate of successful search and detection of resources, which reflects foraging efficiency at low prey densities; handling time (h) – the time required for the predator to handle, consume, and digest captured prey; and the maximum feeding rate ($1/h$), which reflects foraging efficiency at high prey densities (Holling 1959; Alexander et al. 2012). High-impact invaders generally exhibit a higher maximum feeding rate and more destabilizing responses than functionally similar native taxa and low-impact invaders (Alexander et al. 2014; Dick et al. 2013, 2017; DeRoy et al. 2020).

A shifting thermal regime is expected to transform the impacts of non-native species through changes to their *per capita* effects, abundance, and area occupied (Walther et al. 2009; Iacarella et al. 2015a), resulting in altered predator-prey dynamics and competitive interactions with native species (Rahel & Olden 2008; Gherardi et al. 2013; South et al. 2018; Khosa et al. 2020). For example, Khosa et al. (2020) measured the functional responses of young-of-year congeneric species largemouth bass *Micropterus salmoides* and Florida bass *M. floridanus* at different temperatures and found that Florida bass, the warm-water adapted species, exerted greater predation pressure than largemouth bass at high temperatures, whereas the opposite pattern was observed at lower temperatures.

A comparative functional response approach that incorporates abiotic context dependencies into the experimental design is a valuable tool for risk assessment of invader impacts under changing environmental conditions (Rall et al. 2012; Dick et al. 2014, 2017; South et al. 2017). It is noteworthy that most studies investigating invader functional rsponses tested a single species across different habitat gradients (such as habitat complexity, dissolved ions, temperature; Iacarella & Ricciardi 2015; Barrios-O'Neill et al. 2016; South et al. 2018; Cuthbert et al. 2019) or were comparative studies between native and non-native species (Dick et al. 2013; Alexander et al. 2014; Laverty et al. 2014), with the general assumption that under the same conditions population-level functional responses are conserved, on average. However, a recent experimental study by Grimm et al. (2020) on the American spinycheek crayfish *Faxonius limosus* demonstrated that maximum feeding rate and functional response type can vary across conspecific populations; these differences did not correlate with biogeographic origin of the population nor time since invasion, suggesting a predominant influence of local environmental conditions.

The Rusty Crayfish as a model invader

Broadly distributed invasive species like the rusty crayfish (Peters et al. 2014; Larson & Olden 2016) offer opportunities to investigate the potential effects of climate warming on invader impact, by allowing us to examine predator-prey dynamics across the species' invaded range. Crayfish are ecosystem engineers and keystone species in nearshore freshwater food webs (Peters et al. 2014; Tricarico & Aquiloni 2016). Nearly half of the described species in North America are considered imperiled or vulnerable (Taylor et al. 2007; Crandall and Buhay 2008). Conversely, crayfishes are among the world's most invasive freshwater animals (Larson & Olden 2016); their colonization success is attributable to their broad environmental tolerance, rapid reproduction, and aggressive behaviour (Lodge et al. 2012; Tricarico & Aquiloni 2016), as well as a history of dispersal by anglers and the pet industry (DiStefano et al. 2009; Banha & Anastacio 2015; Faulkes 2015). The Great Lakes basin contains at least five non-native crayfishes (Peters et al. 2014), including the rusty crayfish *Faxonius* (formerly *Orconectes*) *rusticus*, native to the Ohio River valley (Taylor & Redmer 1996; Peters et al. 2014; Tricarico & Aquiloni 2016). *Faxonius rusticus* is presently the most widespread invasive crayfish in the basin (Peters et al. 2014) and has replaced the northern clearwater crayfish (*F. propinquus*) and virile crayfish (*F. virilis*) in dominance at many sites (Olden et al. 2006). In addition, it has been shown to have detrimental impacts on aquatic macrophytes, slow-moving macroinvertebrates, and fishes (Hansen et al 2013; Kreps et al. 2016)

Based on experimentally-determined responses, Mundahl and Benton (1990) reported that *F. rusticus* in its native range has a preference for temperatures of 20–22°C and exhibits maximal growth rates at temperatures of 26–28°C; the difference in these ranges could be due to post-molting problems at high temperatures (Mundahl and Benton 1990). Given that *F. rusticus* was first recorded in Lake Erie in 1897 (Peters et al. 2014), populations in the Great Lakes could conceivably be locally adapted such that they vary from being more warm-adapted in the south to more cold-adapted in the north.

Collectively, the aforementioned studies suggest the importance for risk assessment to account for population-level differences in *per capita* effects. We examined the effects of latitude and temperature on functional responses of conspecific populations of *F. rusticus*. Based on the premise that functional response types and associated parameters (a, h) would be maximized as temperature approached the physiological optimum for each population (Environmental Matching Hypothesis; Ricciardi et al. 2013), we predicted that at low temperatures northern (presumably cold-adapted) populations would exhibit higher functional responses than (presumably warm-adapted) southern populations, whereas at high temperatures the pattern would be reversed.

Methods

Study system

Sites within the Great Lakes basin were selected based on latitude, accessibility, and a minimum field density of crayfish to avoid bias introduced by density effects. In total, 144 adult individuals were collected from six populations. From the northern region (hereafter coded *N*), crayfish were collected from Muskrat Lake, Ontario (45°38'22.9"N, 76°53'30.0"W), Lake Clear, Ontario (45°27'49.2"N 77°13'14.7"W), and Lac-Brome, Quebec (45°15'00.9"N 72°32'50.1"W). From the southern region (*S*), crayfish were collected from the White River, Vermont (43°43'15.4"N 72°25'13.2"W), Little Rouge River, Ontario (43°50'08.9"N 79°11'37.3"W), and Eramosa River, Ontario (43°39'31.1"N 80°09'21.4"W). Collections were conducted using hand-held nets and adapted minnow traps, between May and August 2018 for Lake Clear (*N*), White River (*S*), and Little Rouge River (*S*), and between May and August 2019 for Lac-Brome (*N*), Muskrat Lake (*N*), and Eramosa River (*S*). These crayfish were transported back to McGill University in coolers with air bubblers.

Temperature treatments

Once the crayfish were brought back to the lab, they were sexed, weighed (in grams) and measured for carapace length (in mm). Individual crayfish were held in separate 5.6L plastic tanks with air bubblers at 18°C in a control growth chamber for at least 2 weeks to allow for laboratory acclimation. During this period, experimental animals were exposed to a reversal of their usual 12:12 hour light:dark regime, so that their feeding behaviour could be tested under nocturnal conditions (Alexander et al. 2012). Aquarium maintenance included weekly water changes (75%) and biweekly water quality testing. Individual crayfish were randomly assigned an identification number and a temperature treatment (low: 18°C, or high: 26°C; n=10 per treatment) and size-matched for weight and carapace length. Treatment temperatures were chosen based on current and projected mean summer surface temperatures in nearshore areas of the lower Great Lakes (Trumpickas et al. 2008). For individuals assigned to the 26°C treatment, water temperature was raised at 1°C/per day until the treatment temperature was attained, and then individuals were given two additional weeks for acclimation.

Functional response experiments

Functional response experiments were conducted in 20L aquarium tanks (1 crayfish per tank). Crayfish were fed a standardized diet of Wardley Shrimp Pellets on a strict schedule, and they were starved for 24hr before each experimental trial to standardize hunger levels. Each crayfish was acclimatized in the experimental tank for 1hr prior to the start of the trial. A trial consisted of a temperature treatment (18°C or 26°C) in which individuals were exposed randomly to one of the seven densities (n=15, 25, 50, 100, 140, 160, and 180) of bloodworms *Chironomus* sp. (Diptera: Chironomidae), which are common prey for crayfish in the wild (Olsson & Nydtröm 2009; Kreps et al. 2016). Bloodworms were thawed from the freezer before being presented to the crayfish. Prey consumption was determined by counting the remaining number of intact prey items after the 3hr trial. In order to avoid consumption bias, if a crayfish molted during the set of experimental trials (a total of 7), the individual was set aside and allowed an extra week of recovery before being tested again. From the numbers consumed for each prey density, a functional response curve was constructed: one for each population at each temperature, yielding 6 curves per temperature treatment and 12 curves in total.

The recovery time between experiments was determined for both temperatures in preliminary trials, which showed that an intervening 5-day resting period is sufficient to prevent a previous feeding experiment (e.g. being exposed to a high density) from affecting the outcome of subsequent testing. The individuals (26°C: 13 replicates, 18°C: 9 replicates) used in the recovery time experiments were size matched and kept under the same conditions as the functional response experiments for 2 weeks previous to testing. Subsequently, they were starved for 24hr before being exposed to 180 bloodworms (highest density used in the functional response experiment), and prey consumption was determinated at the end of the 6hr trial.

Afterwards, the indivduals were given 4 days of recovery time during which they returned to their previous scheduled diet. After recovery, they were starved for 24hr and exposed again to 180 bloodworms. A t-test in R v3.6.1 (R Core Team 2019) that compared prey consumption before and after the recovery time showed no significant difference in prey consumption at both temperature treatments (26°C: t=-2.0638, p=0.9693; 18°C: t=-0.60453, p=0.7189).

Statistical analysis

Functional response curves of the 12 *F. rusticus* trials (6 populations and 2 temperature treatments) were constructed in R v3.6.1 (R Core Team 2019) using the Frair package for selecting, fitting, and comparing consumer functional responses (Pritchard et al. 2017). Data were modeled using the Rogers random predator equation for a Type II response (Rogers 1972; Equation 1, below), which accounts for non-replacement of prey as they are consumed. It has been demonstrated that without prey replacement the attack rate may be underestimated, but the type of functional response curve, handling time, and maximum feeding rates remain unaffected (Alexander et al. 2012).

$$N_e = N_0 \left\{1 - \exp\left[a\left(N_e h - T\right)\right]\right\} \qquad (1)$$

In Equation 1, N_e is the number of prey consumed, N_0 is the initial prey density, a is the attack rate (the rate at which the predator encounters the prey), h is the handling time – the time required for the predator to consume captured prey, and T is time (Rogers 1972). From each functional response curve, the parameters a (attack rate) and h (handling time) were extracted (Alexander et al. 2012).

To analyze the response of each population to temperature, functional response parameters were compared using two different methods from the Frair package (Pritchard et al.

2017). Each population pair was examined using the *frair_compare* function, which applies a difference test with the null hypothesis that the fitted parameters *a* and *h* do not differ (Juliano 2001). Secondly, the *frair_boot* function, a more conservative non-parametric method, was used to generate multiple estimates of curves and respective parameters from the raw data and report 95% confidence (Bias-corrected and accelerated, 'BCa') intervals. Once the bootstrap outputs (n=999) were obtained, visual comparisons of entire functional response curves were built using the *drawpoly* function, which plots empirical approximations of the confidence intervals using the desired quantile predictions: 0.025 and 0.975 for 95% CIs. The effects of crayfish size (carapace length and weight) and sex on maximum feeding rate and proportion of prey killed were tested using generalized linear mixed models. Variances in functional response parameters *a* and *h* were analyzed by comparing histograms of the bootstrapped coefficients.

Results

Inter-population functional responses to temperature and latitude of provenance

Contrary to our hypothesis, there was no consistent latitudinal pattern in the functional responses of northern and southern populations at high and low temperatures (Figure 1.1). At 26°C, the bootstrapped 95% confidence intervals indicated a significant overlap in model fits across all prey densities of the Lac Brome (*N*), Muskrat Lake (*N*), and Eramosa River (*S*) populations. The Lake Clear (*N*) population overlapped with the White River (*S*) population at high, but not at low, prey densities. The population from Little Rouge River (*S*) had the lowest maximum feeding rate at 26°C and overlapped with one other population, White River (*S*), but only at low prey densities. However, parameter comparisons using the *frair_compare* function (Table 1.1) indicate significant differences in attack rates and handling times among populations, with two exceptions: attack rates for Lake Clear (*N*) and Eramosa River (*S*), and handling times for the Lake Clear (*N*) and White River (*S*) populations. Where significant differences were detected, attack rate was always higher in northern populations.

At 18°C, the bootstrapped 95% confidence intervals showed overlap in model fits of populations of Lac Brome (*N*), Muskrat Lake (*N*), and Eramosa River (*S*), and these populations exhibited higher functional responses (attack rates and maximum feeding rates) than the others (Figure 1.1). A significant overlap in model fits was also found among the White River (*S*), Little Rouge River (*S*) and the Lake Clear (*N*) populations. Parameter comparisons using the *frair_compare* function indicated higher attack rates for all northern populations compared to the southern ones, except for Lake Clear (*N*) which had a lower attack rate than the Eramosa River (*S*) population. As was observed at 26°C, there was no consistent pattern in handling times (Table 1.1).

There were significant differences in model fits and parameters estimates between some of the northern populations (Table 1.1; Figure 1.1). At 26°C, attack rates varied among individuals from the three populations as follows: Muskrat Lake > Lac Brome > Lake Clear. Handling times were lower in Muskrat Lake and Lac Brome populations compared to Lake Clear, whereas no difference was found between Muskrat Lake and Lac Brome populations. In addition, no overlap in model fits was observed between Lac Brome and Lake Clear, indicating a higher attack rate and lower handling time for the Lac Brome population. At 18°C, a significant overlap in model fits was observed for Muskrat Lake and Lac Brome populations. However, parameter comparisons using the *frair_compare* function indicated higher attack rates and lower handling times for Muskrat Lake compared to the Lac Brome and Lake Clear populations.

When comparing functional responses of the southern populations at 26°C, no overlap in model fits were observed at high prey densities; the Eramosa River population showed a significantly higher functional response compared to the White River and Little Rouge River populations (Figure 1.1, Table 1.1). At low prey densities, there was partial overlap of model fits for the White River and Little Rouge River populations; however, parameter comparisons using the *frair_compare* function indicated significantly higher attack rates and handling times for the Little Rouge River population. Similarly, at 18°C, the Eramosa River population exhibited a significantly higher maximum feeding rate than the other two populations. Conversely, the Little Rouge River population exhibited no significant difference in attack rate but had lower handling times than the White River population.

No consistent pattern was found for northern or southern populations in their response to temperature increase (Figure 1.2, Table 1.1). The northern populations of Muskrat Lake and Lac Brome showed an almost complete overlap in their model fits when comparing temperature treatments. Furthermore, a southern population (Little Rouge River) showed a reverse in their response to temperature where a higher maximum feeding rate was observed at 18°C.

Variation in functional response parameters

At both experimental temperatures, bootstrapped coefficients of attack rate (a) showed greater variation in northern populations than in southern populations (Figure 1.3). Within each population, variation of attack rates seemed largely insensitive to temperature treatment. In contrast, bootstrapped coefficients of handling time (h) at both temperatures showed greater variation for the southern populations compared to northern populations. Handling times for the

Lake Clear population were conspicuously more dispersed at 18°C compared to 26°C (Figure 1.4).

Model biases and prey recovery

Crayfish predation on frozen bloodworms was the major source of prey removal or damage in experimental trials, as indicated by high recovery rates (>99%) of intact prey in control treatments. Type II responses were found across all temperature treatments (Table 1.2). Crayfish mean size between treatments did not differ significantly (linear model: weight, $F_{11,109}$=1.653, p= 0.0942; Figure A.1) although there were significant differences in carapace length (linear models: $F_{11,109}$=1.938, p=0.042; Figure A.2), attributable to differences between the Lake Clear and Eramosa River individuals used at low temperature treatments (TukeyHSD, adjusted p=0.0061). Proportion of prey consumed were not affected by differences in sex (generalized linear mix models; sex: Z= -1.28, p=0.20).

Discussion

There were fundamental differences in the functional responses of conspecific populations exposed to the same temperature conditions. These differences were observed despite consistent application of a standard experimental protocol by a single handler. It was not possible to explain inter-population differences in attack rates or handling times based on the latitude of provenance. Contrary to expectations, presumably warm-adapted southern populations exhibited lower attack rates than presumably cold-adapted northern populations at a temperature (26°C), which is closer to the reported growth optimum for this species (Mundahl and Benton 1990). Likewise, at the lower temperature (18°C), southern populations exhibited lower attack rates than northern populations. Variation in maximum feeding rate ($1/h$) could not be explained by any of the variables we tested. Individual body size, specifically carapace length, in *F. rusticus* crayfish can affect their feeding rate (Morse et al 2013; see also Uiterwaal & DeLong 2020), creating a potential confounding effect; however, our results found no significant differences in crayfish body size between populations. There were also no sex-related differences in functional response in our study, consistent with observations in one other decapod study (Taylor & Dunn 2018).

Invasive conspecific populations, even those within the same ecoregion, can exhibit potentially substantial intraspecific trait variability (Evangelista et al. 2019). Our northern and southern populations did not differ consistently in their response to temperature, suggesting the influence of other environmental factors – such as 'time since invasion' (Strayer et al. 2006; Iacarella et al. 2015b,c; Evangelista et al. 2019), abiotic variables other than temperature (Barrios-O'Neill et al. 2015; Wasserman et al. 2016b), source community composition (Barrios-O'Neill et al. 2014; Wasserman et al. 2016a; Grimm et al. 2020), and phenotypic plasticity including counter-gradient variation (Conover & Present 1990; Conover & Duffy 2009; Hodgson & Schwanz 2019). For example, recent invaders often have different *per capita* effects and related impacts than individuals from well-established populations (Strayer et al. 2006; Iacarella et al. 2015b; Zavorka et al. 2017; Evangelista et al. 2019). In our study, the best estimates of time since invasion of rusty crayfish at each site (Table 1.3) suggest no relationship to differences in foraging success, likely because our populations were selected for their sufficiently large crayfish density and are therefore well established. The consumer's population density can also influence its functional response, such that attack rates are significantly higher in high-density sites, unrelated to time since invasion (Paton et al. 2019). Our findings provide partial support for this hypothesis; attack rates appear to be higher in medium- to high-density sites (Tables 1.1 & 1.3).

Given that abiotic conditions could induce inter-population variation (Barrios-O'Neill et al.2015; Iacarella et al. 2015b; Wasserman et al. 2016b; Uiterwaal & DeLong 2020), a potential confounding factor in our study was that all southern populations collected in this study were situated in lotic habitats, whereas northern populations were situated in lentic habitats. Lotic populations are exposed to the periodic invertebrate drift which might cause a higher variation in availability of prey, but it is not clear how this would produce adapted differences in attack rates. Furthermore, although crayfish in these populations might have been differentiated by adaptive behaviours in foraging amongst different flow and substrate conditions that characterized our collection sites (Table 1.3), it is unlikely that these behaviours would be expressed in our experimental arenas.

Interpopulation variation in functional response could arise from differences in composition of the source communities. For example, the presence of a competitor can exert selection pressure for key behaviors such as aggression, voracity, and boldness (Hayes et al. 2009; Pintor et al. 2008). At some sites, the presence of a native congener was observed (Table 3), usually in low numbers (< 5 individuals), except for Muskrat Lake where 5–10 individuals were encountered over the 3hr sample period. Differences in foraging rates between populations could also arise from hybridization with congeneric species. Previous studies have shown the capacity of *F. rusticus* crayfish to hybridize with *F. propinquus*, and the resulting F1 progeny were extremely aggressive and out-competed both parental species for food and shelter (Perry et al. 2001). This could potentially explain why the *F. rusticus* population in Eramosa River, where the native *F. propinquus* was observed, exhibits higher functional responses compared to Lac

Brome (*N*) and Muskrat Lake (*N*) populations. Although care was taken to properly identify the specimens, it is possible that some hybrids were overlooked.

A recent meta-analysis (Uiterwaal & DeLong 2020) of over two thousand functional responses for a wide range of consumers, prey types, environmental conditions, and habitats, found unimodal relationships between response parameters (attack rates and handling times) and temperature, and these responses varied according to the location of the consumer's ambient temperature relative to the optimum, as predicted by the Environmental Matching Hypothesis (Ricciardi et al. 2013; Iacarella et al. 2015a). Uiterwaal and DeLong (2020) also found that the optimal temperature for attack rate is not the same as that for handling time, perhaps explaining some differences in patterns involving the two parameters in our study. Whereas, overall, the northern populations' maximum feeding rates (calculated as the inverse of *h*) were not consistently higher than the southern ones, we observed a pattern in which attack rates of northern populations at both temperatures were higher but handling times varied across population and treatments (Table 1.1). Thus, our results provide additional evidence that attack rates (ability to search prey) and handling time (time required to attack, consume, and digest the prey) respond differently to temperature.

A potential explanation for the higher attack rates observed in crayfish from northern populations is the counter-gradient hypothesis, which predicts that populations living under harsh conditions (e.g., a short realized growth season at northern latitudes) have evolved faster growth rates compared to populations living under more benign conditions (Conover 1990; Chavarie et al. 2010; Hodgson & Schwanz 2019). Conover and Present (1990) compared the growth rates of a marine fish, Atlantic silversides *Menidia menidia*, from different locations along a latitudinal gradient and found that high-latitude fish outgrew those from low latitudes, at warm temperatures that the low-latitude fish should experience more often in the wild. Rather than being adapted for growth at the cold temperatures to which they are accustomed, the high-latitude fish were adapted for rapid growth during the brief seasonal period in which high temperatures occur (i.e., counter-gradient variation). Likewise, the phenotypic pattern observed in overall higher attack rates and lower handling times in our northern crayfish at high temperatures could reflect adaptations to suboptimal temperatures and the length of the growing season.

Finally, some of the differences in variance observed among populations' *per capita* effects (*a* and *h*) in this study could conceivably arise from founder effects of genetically distinct propagules at each site (Simberloff 2009; Mueller et al. 2017). In particular, variation in personality traits can affect the intensity and propagation of ecological impacts across different levels of biological organisation (Chapple et al. 2012). According to Dall et al. (2004), variation in genetically determined behavioural traits can arise from frequency-dependent selection, mutation versus weak selection, and spatiotemporal variation in behavioural optima.

Future directions

Although sources of differences between populations remain to be identified, this study revealed unexpected, counter-intuitive variation in functional response that highlights the potential for error in risk assessments derived from a single population. Our results provide tentative support for the Environmental Matching Hypothesis (Ricciardi et al. 2013; Iacarella et al. 2015a) by suggesting that there are optimal temperatures at which foraging rates are maximized, but that these optima vary across populations. The causes of this variation remain to be explored and might provide predictive information for range expansions and future impacts of invasive crayfishes. No one population is likely to be representative of the potential impacts of a species under climate warming, as the *per capita* effects are influenced by temperature differently across populations – even among populations that are occupying the same latitude and with a similar relative density, invasion history, and community structure (presence/absence of congeners). It might be revealing to relate *per capita* effects to genetic distance between populations. Furthermore, since prey activity could mediate the outcome of trophic interactions, future experiments should investigate differences in prey response to temperature using live prey representative of the source location.

Tables

Table 1 – Parameter comparisons between functional response curves using frair_compare with Holm p-adjusted values

Fit 1	**Fit 2**	**Δa (a)**	**a p-adj.**	**Δh (h)**	**h p-adj.**
Northern populations					
Muskrat Lake, 26C	Muskrat Lake, 18C	0.041	1	0.00096	0.395
Lac Brome, 26C	Lac Brome, 18C	-0.003	1	-0.00215	0.012 **
Lake Clear, 26C	Lake Clear, 18C	0.270	5e-05 ***	-0.03117	1.8e-15***
Muskrat Lake, 26C	Lac Brome, 26C	-0.431	4e-04 ***	0.00119	0.398
Muskrat Lake, 26C	Lake Clear, 26C	0.267	0.003 **	-0.00699	1.8e-15***
Lac Brome, 26C	Lake Clear, 26C	0.696	2e-15 ***	-0.00819	1.8e-15 ***
Muskrat Lake, 18C	Lac Brome, 18C	-0.474	2e-15 ***	-0.00191	0.052
Muskrat Lake, 18C	Lake Clear, 18C	0.4951	2e-15 ***	-0.03910	1.8e-15***
Lac Brome, 18C	Lake Clear, 18C	0.9699	2e-15 ***	-0.03722	1.8e-15***
Southern populations					
Eramosa River, 26C	Eramosa River, 18C	0.188	0.012 **	-0.00601	1.8e-15***
Little Rouge River, 26C	Little Rouge River, 18C	0.205	1.8e-15***	0.02628	1e-04 ***
White River, 26C	White River, 18C	0.115	0.012**	-0.02038	1.8e-15***
Eramosa River, 26C	Little Rouge River, 26C	0.312	1.8e-15***	-0.04403	1.8e-15***
Eramosa River, 26C	White River, 26C	0.462	1.8e-15***	-0.01204	1.8e-15***
Little Rouge River, 26C	White River, 26C	0.149	0.012 **	0.03198	1.8e-15***
Eramosa River, 18C	Little Rouge River, 18C	0.325	1.8e-15***	-0.01175	1.8e-15***

Eramosa River, 18C	White River, 18C	0.388	1.8e-15***	-0.02642	1.8e-15***
Little Rouge River, 18C	White River, 18C	0.064	0.087	-0.01465	1.8e-15***
Northern vs. Southern populations at 26C					
Muskrat Lake	Eramosa River	0.197	0.04 *	0.00494	1.8e-15***
Muskrat Lake	Little Rouge River	0.508	1.8e-15***	-0.03909	1.8e-15***
Muskrat Lake	White River	0.658	1.8e-15***	-0.00711	6e-05 ***
Lac Brome	Eramosa River	0.627	1.8e-15***	0.00375	6e-05 ***
Lac Brome	Little Rouge River	0.939	1.8e-15***	-0.04027	1.8e-15***
Lac Brome	White River	1.089	1.8e-15***	-0.00830	1.8e-15***
Lake Clear	Eramosa River	-0.069	0.289	0.01194	1.8e-15***
Lake Clear	Little Rouge River	0.242	0.0003 ***	-0.03210	1.8e-15***
Lake Clear	White River	0.392	1.8e-15***	-0.00014	0.9342
Northern vs. Southern populations at 18C					
Muskrat Lake	Eramosa River	0.344	1.8e-15***	-0.00203	0.0130
Muskrat Lake	Little Rouge River	0.669	1.8e-15***	-0.01378	1.8e-15***
Muskrat Lake	White River	0.732	1.8e-15***	-0.02845	1.8e-15***
Lac Brome	Eramosa River	0.818	1.8e-15***	-0.00012	0.907
Lac Brome	Little Rouge River	1.144	1.8e-15***	-0.01189	1.8e-15***
Lac Brome	White River	1.207	1.8e-15***	-0.02654	1.8e-15***
Lake Clear	Eramosa River	-0.151	0.008 **	0.03711	1.8e-15***
Lake Clear	Little Rouge River	0.174	0.0004 ***	0.02535	1.8e-15***
Lake Clear	White River	0.237	1.8e-15***	0.01069	0.0006 ***

Table 2 – Parameter estimates for each Type II Functional Response treatment (± standard error) derived with the frair_fit function and the first-order term.

Population	**Latitude**	**Temperature**	**First-order term, *p***	**Parameter**				
				a±SE	*p*	*h*±SE	*p*	1/*h*±SE
Muskrat Lake	North	26C	-0.011, <2.2e-16 ***	1.159±0.069	<2.2e-16 ***	0.022±0.0007	<2.2e-16 ***	45.593±1.584
Lac Brome	North	26C	-0.019, <2.2e-16 ***	1.589±0.086	<2.2e-16 ***	0.021±0.0005	<2.2e-16 ***	48.210±1.213
Lake Clear	North	26C	-0.013, <2.2e-16 ***	0.893±0.044	<2.2e-16 ***	0.029±0008	<2.2e-16 ***	34.563±0.977
Muskrat Lake	North	18C	-0.015, <2.2e-16 ***	1.118±0.053	<2.2e-16 ***	0.021±0.0006	<2.2e-16 ***	47.674±1.385
Lac Brome	North	18C	-0.018, <2.2e-16 ***	1.592±0.084	<2.2e-16 ***	0.023±0.0005	<2.2e-16 ***	43.698±0.987

Lake Clear	North	18C	-0.014, <2.2e-16 ***	0.623±0.039	<2.2e-16 ***	0.060±0.001	<2.2e-16 ***	16.636±0.499
Eramosa River	South	26C	-0.011, <2.2e-16 ***	0.963±0.048	<2.2e-16 ***	0.017±0.0007	<2.2e-16 ***	58.820±2.523
Little Rouge River	South	26C	-0.013, <2.2e-16 ***	0.651±0.045	<2.2e-16 ***	0.061±0.002	<2.2e-16 ***	16.386±0.507
White River	South	26C	-0.007, <2.2e-16 ***	0.501±0.029	<2.2e-16 ***	0.029±0.001	<2.2e-16 ***	34.438±1.747
Eramosa River	South	18C	-0.009, <2.2e-16 ***	0.023±0.041	<2.2e-16 ***	0.023±0.0009	<2.2e-16 ***	43.484±1.737
Little Rouge River	South	18C	-0.008, <2.2e-16 ***	0.449±0.026	<2.2e-16 ***	0.035±0.0015	<2.2e-16 ***	28.773±1.309
White River	South	18C	-0.008, <2.2e-16 ***	0.386±0.026	<2.2e-16 ***	0.049±0.0022	<2.2e-16 ***	20.234±0.913

Table 3 – Summary of invasion history for *F. rusticus* populations, field observations of habitat, capture depth, and relative density.

Population	**Latitude**	**Relative density**	**Congener**	**Invasion history, Source**	**Habitat**	**Depth**
Muskrat Lake	North	Medium	*F. virilis*	2001, EDDMapS ID: 2952190	Mostly sand with medium to large cobble	0.5-1m
Lac Brome	North	Medium	NA	2011, Desroches et al. (2014)	Mostly sand with medium to large cobble	0.5-1m
Lake Clear	North	High	*F. virilis*	1988, EDDMapS ID: 2952108	Mostly sand with small to medium stones	0.5m
Eramosa River	South	High	*F. propinquus*	2010, EDDMapS ID: 3125006	Mostly small to medium sized stones, some sand present	0.5m
White River	South	Low	NA	2005, Guarino et al.2012	Mostly sand with medium to large cobble	0.5m
Little Rouge River	South	Low	NA	2002, EDDMapS ID: 2951685	Mostly small to medium sized stones, some sand present	0.5-1m

Figure 1 – Functional response curves of *F. rusticus* populations consuming inactive bloodworms. The left and right panels compare the functional responses of northern populations (green) and southern populations (blue) at 26ºC and 18ºC, respectively. Shaded areas represent 95% confidence intervals obtained by bootstrapping using the frair_boot function (N=999), and the lines represent the fitted models.

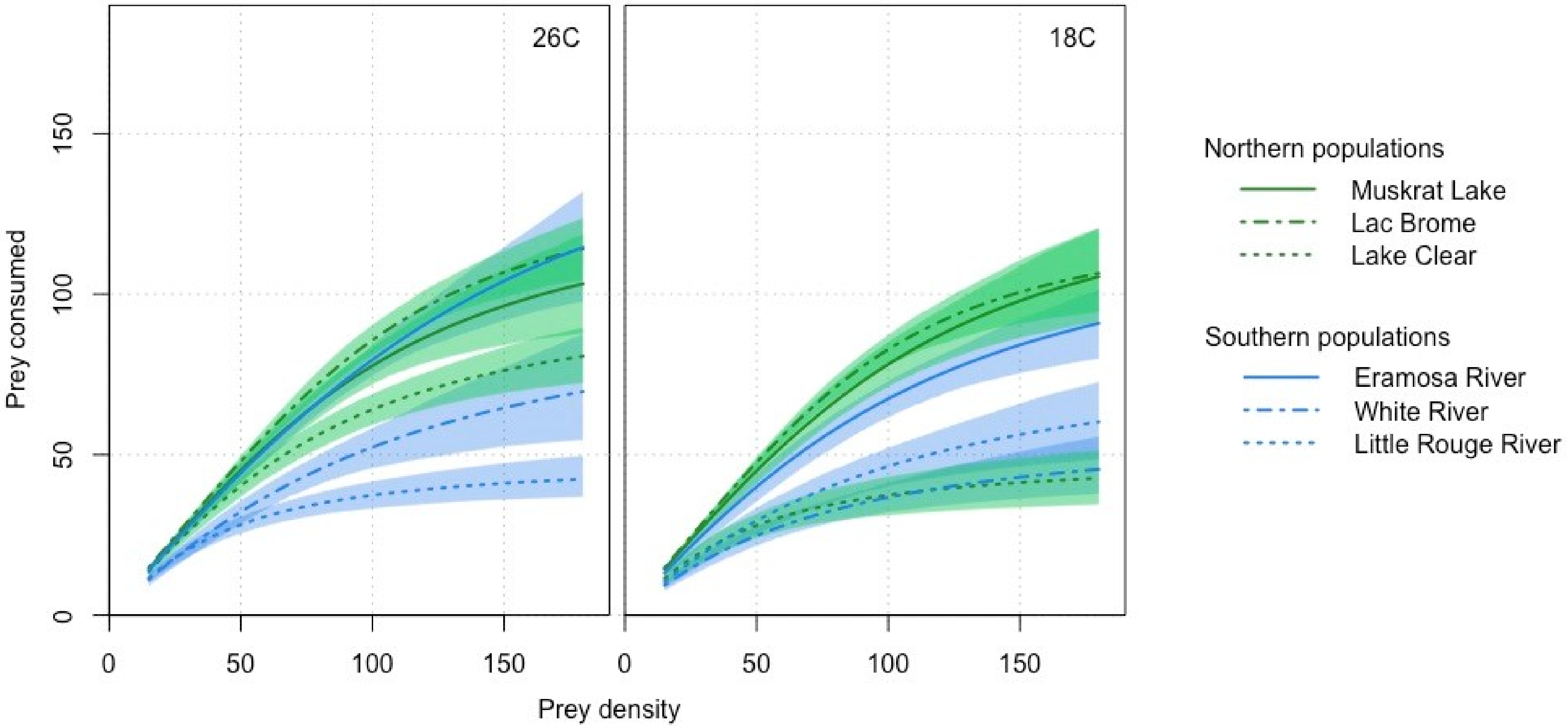


Figure 2 – Functional response curves of *F. rusticus* populations consuming inactive bloodworms in response to temperature increase. Top panels compare the responses of northern (*N*) populations, and the bottom panels compare the responses of southern (*S*) populations. Shaded areas represent 95% confidence intervals obtained by bootstrapping using the frair_boot function (N=999), the lines represent the fitted models, and the circles are the experimental observations.

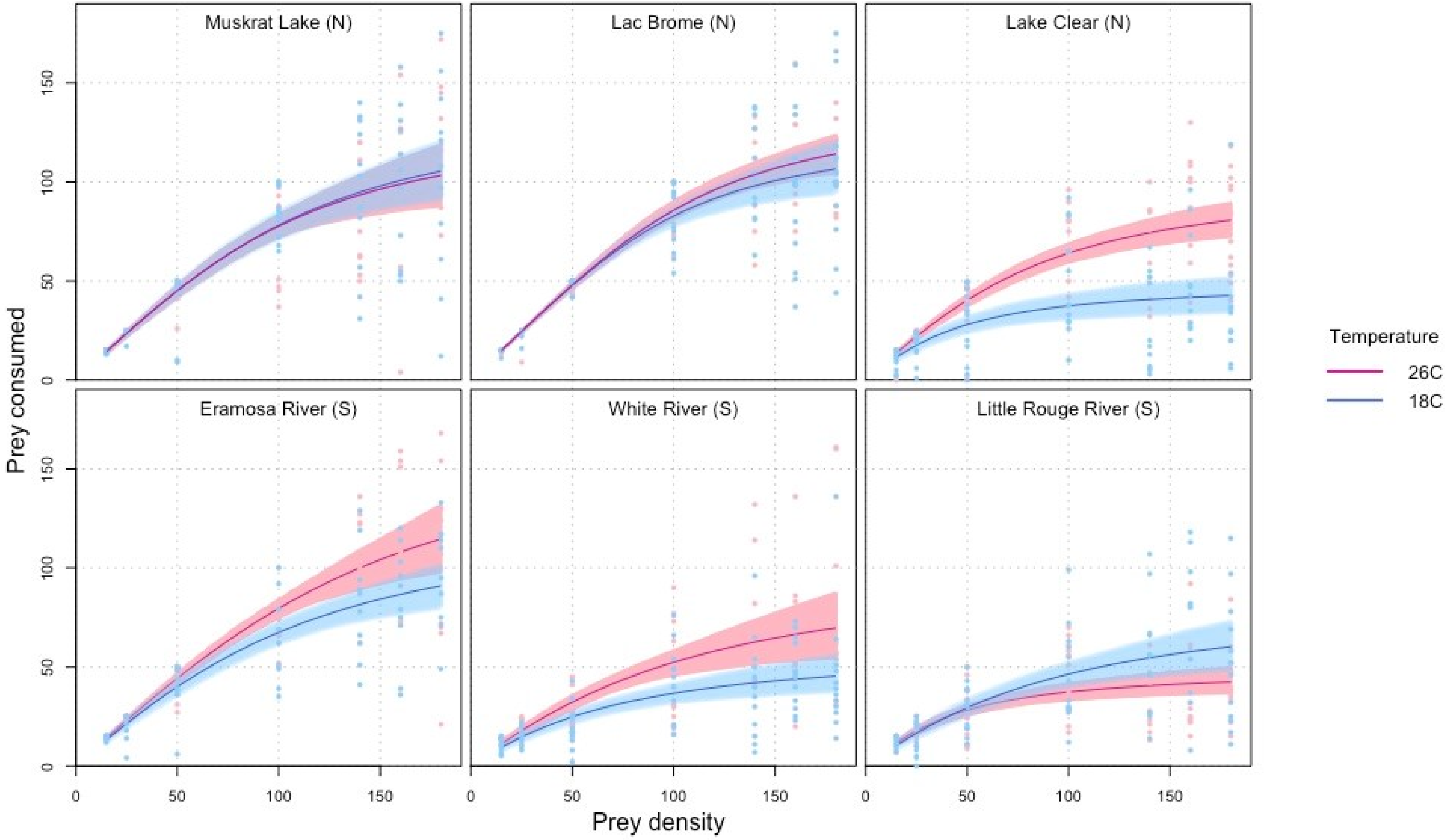


Figure 3 – Variation in bootstrapped estimates of attack rates for functional responses of *F. rusticus* populations based on latitude and temperature treatment.

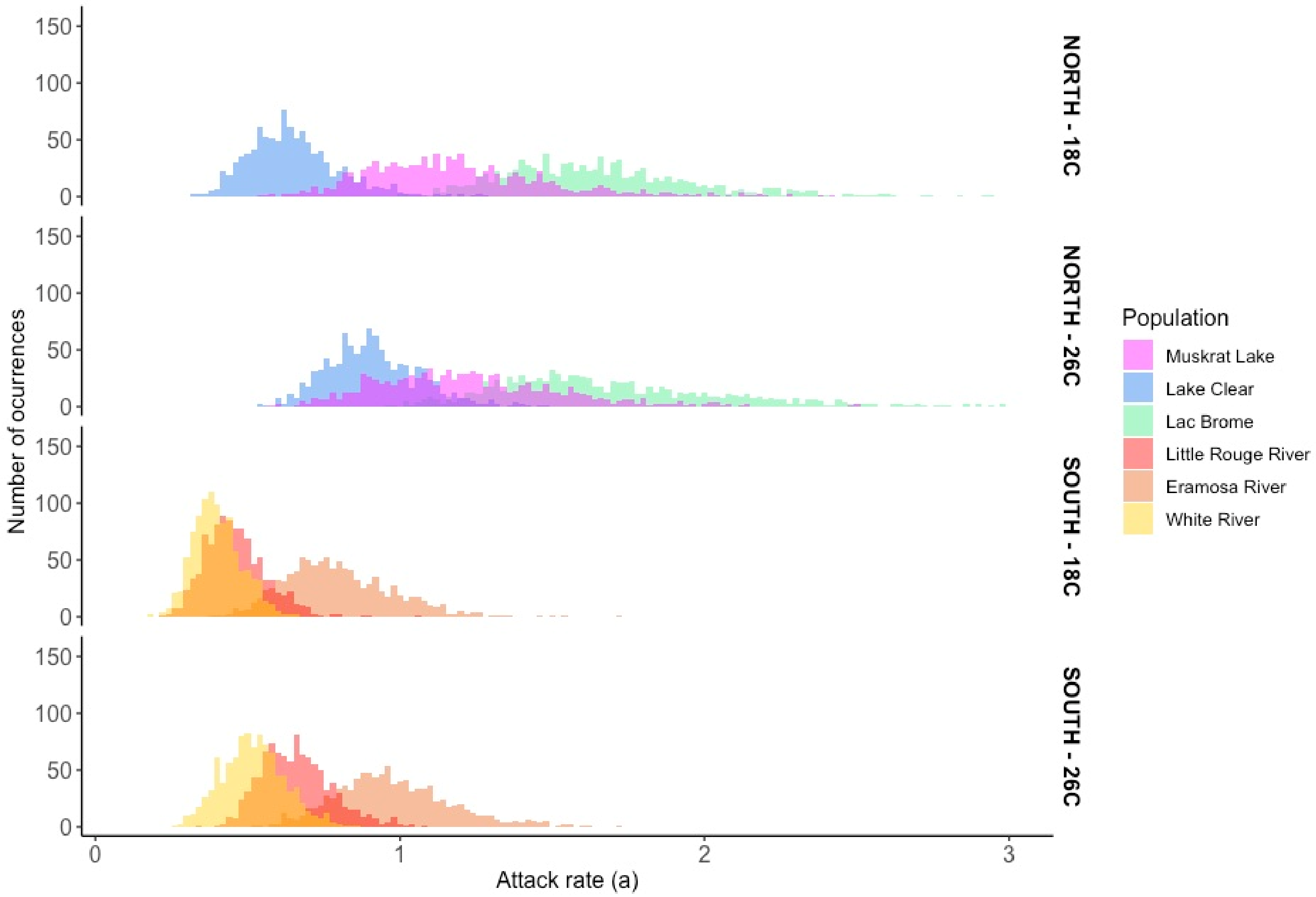
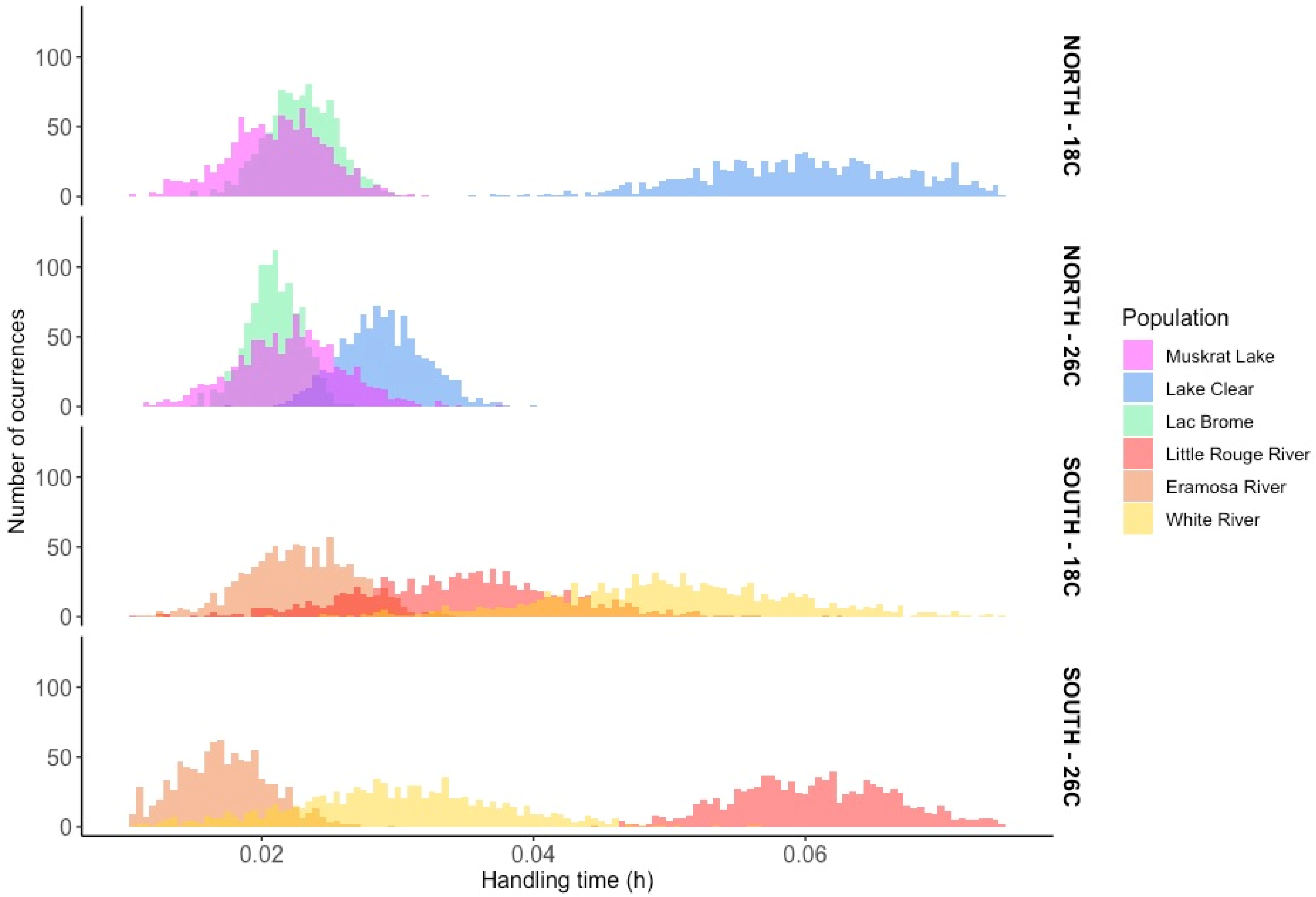


Figure 4 – Variation in bootstrapped estimates of handling times for functional responses of *F. rusticus* populations based on latitude and temperature treatment.



General conclusions

Predictive approaches that incorporate temperature and other context dependencies are needed to improve our understanding of the impacts of biological invasion and their interactions with climate warming (Ricciardi et al 2013). In this study, I applied a simple experimental design to compare the performance of individuals from different populations under the contexts of temperature and geography. Contrary to predictions, inter-population differences in functional response at an elevated temperature were not well explained by the latitudinal distribution of the populations, suggesting that other environmental variables are driving the observed responses. However, while variation in handling time showed no consistent pattern across populations and treatments, the attack rates of individuals from northern populations were consistently higher than those from southern populations at both temperatures. The observed differences could arise from founder effects of genetically distinct propagules that established populations at each site, phenotypic plasticity (the counter-gradient hypothesis), or differences in the composition of the source community (such as the presence of congeners), each of which could influence the selection of feeding behaviors.

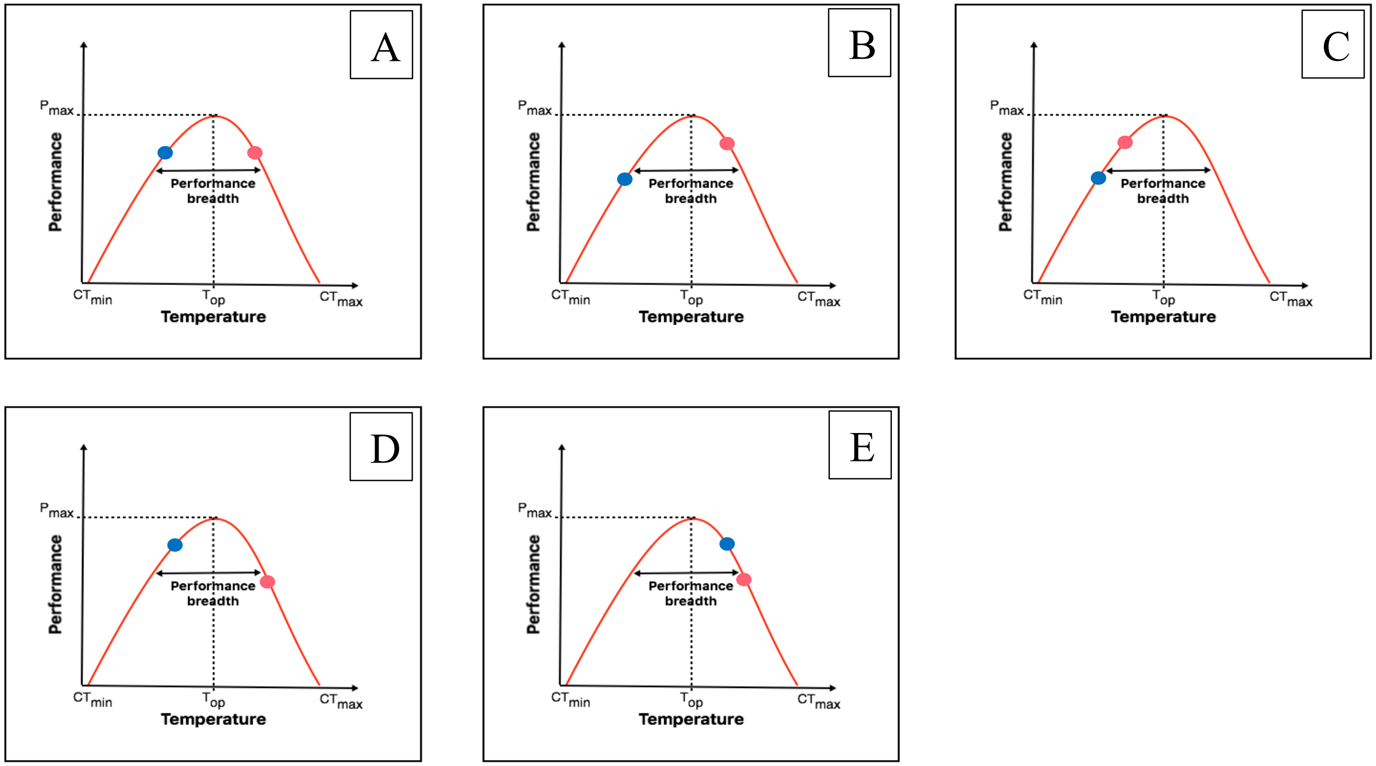
This study offers tentative support for the Environmental Matching Hypothesis (Ricciardi et al. 2013; Iacarella et al. 2015a) by suggesting that there are optimal temperatures at which foraging rates are maximized but that these optima vary across populations. I hypothesize that the optimal temperature for foraging by crayfish in the Muskrat Lake and Lac Brome populations is between 18°C and 26°C, meaning that the experimental treatment temperatures fall on either side of the peak in the thermal performance curve (Figure 5A). Results from Lake Clear (*N*), Eramosa River (*S*) and White River (*S*) populations suggest that the optimal temperature may be closer to the high temperature treatment (26°C) (Figure 5B-C), whereas for the Little Rouge River population it may closer to the low-temperature treatment (Figure 5D-E).

Future directions

This study highlights the potential value of inter-population comparisons for advancing invasion ecology and risk assessment. Research that focuses on variation at the population-level, rather than species-level, should lead to a greater understanding of the role of environmental context in mediating invader impact. Functional response experiments provide important insights, partly because they offer a standardized method of quantifying feeding behaviour that, as shown here, can be used to compare multiple populations. Such experiments are quite flexible in their design and can be expanded to test multiple factors simultaneously. For example, it might be revealing to investigate differences in prey response to temperature, since prey activity could mediate the outcome of trophic interactions (Haddaway et al 2012; Kreps et al. 2016)

Furthermore, recent studies have investigated possible synergistic effects of climate change and invasion on native species which alter the strength and direction of agonistic interactions (Rahel et al 2008; Gherardi et al. 2013). For example, Gherardi et al (2013) found differential agonistic strategies between species and, furthermore, that behavioural responses to high temperatures varied among crayfish species. In accordance with their hypothesis, in agonistic encounters at high temperatures the warm-adapted red swamp crayfish *Procambarus clarkii* dominated two other species, whose performance was likely impaired by their narrower temperature tolerance. However, as observed in this study and by Grimm et al. (2020), no single population is likely to be fully representative of the potential impacts of a species under climate warming. Thus, future research should focus on how these interactions will be affected by stressors such as climate warming and inter-population variation among native and invasive species, by taking into account the different context dependencies of the source population and the recipient community.

Figure G.1 – Hypothetical thermal performance curves (range of maximum feeding rates) for the study populations, based on the Environmental Matching Hypothesis (Ricciardi et al. 2013; Iacarella et al. 2015a) and information from fitted models. Blue dots and red dots represent maximum feeding rates at 18°C and 26°C, respectively, placed relative to an unknown optimum temperature. Panel A represents the hypothetical thermal performance for Muskrat Lake (*N*) and Lac Brome (*N*) populations, where no significant difference was observed in their response to temperature increase. Panels B & C show the two possible scenarios for Lake Clear (*N*), Eramosa River (*S*) and White River (*S*), populations for which a significantly higher maximum feeding rate was observed at 26°C. Panels D and E describe the two possible scenarios for Little Rouge River (*S*), where a significantly higher maximum feeding rate was observed at 18°C.



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Appendix

Figure A1 - Mean crayfish body mass for each population of *F. rusticus* at low and high temperature treatment

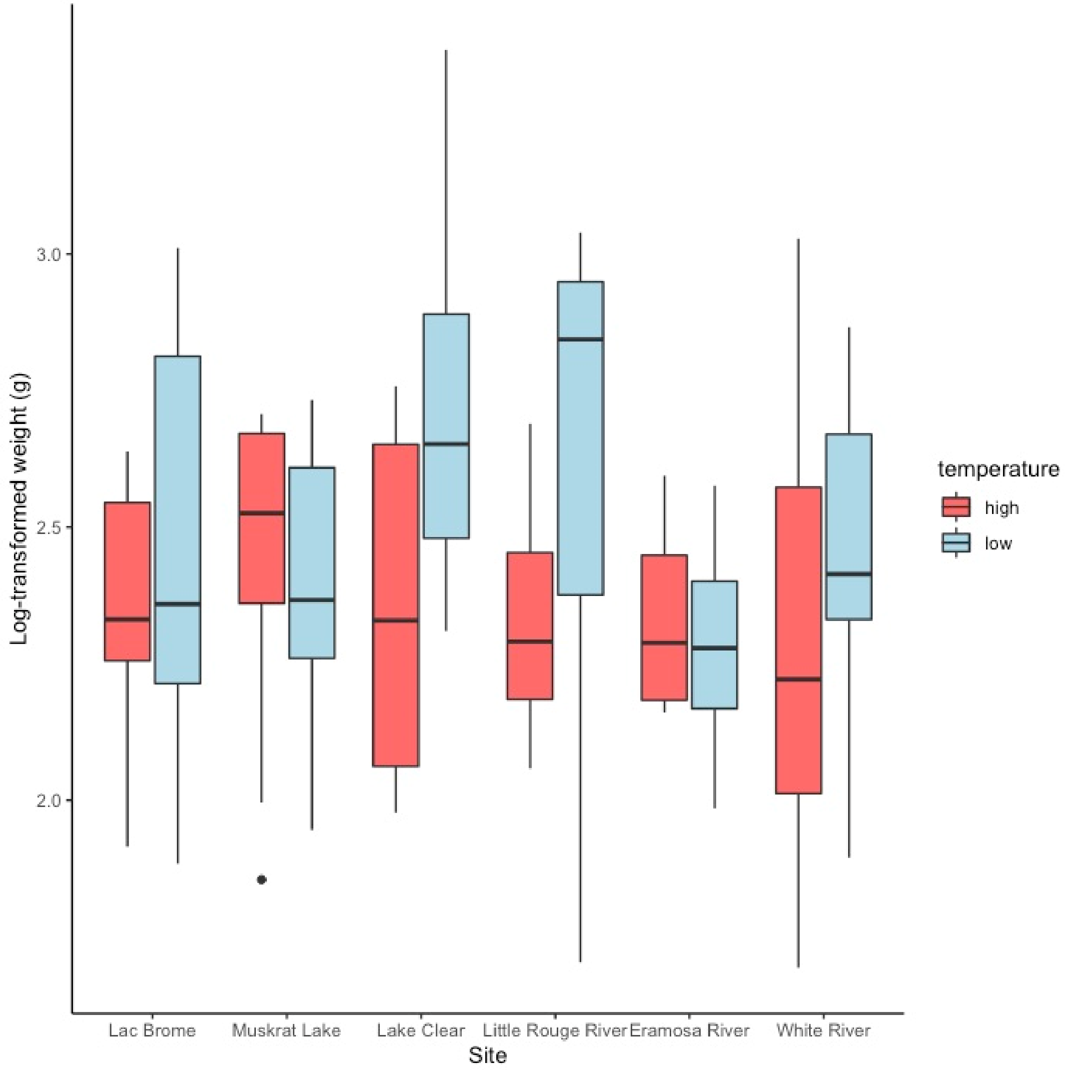

Figure A2 - Mean crayfish carapace length for each population of *F. rusticus* at low and high temperature treatment