Canadian Journal of
Zoology

Research Article

Intraspecific variation in the functional response of an invasive crayfish under different temperatures

Victoria Chicatun[a], Noemie L. M. Sheppard[a,b], and Anthony Ricciardi[a,b]

[a]Department of Biology, McGill University, 1205 Dr. Penfield Ave., Montreal, QC H3A 1B1, Canada; [b]Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, QC, H3A 0C4, Canada

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

Abstract

Non-native species can react to changes to their thermal environment by altering their feeding behaviour, thereby potentially causing shifts in predator–prey dynamics and competitive dominance over native species. In this study, we measured intraspecific variation in the functional response (i.e., predation rate as a function of prey density) of the rusty crayfish *Faxonius rusticus* (Girard, 1852) at two temperatures (18 °C and 26 °C) in the laboratory. We compared six invasive populations spanning a 2° latitudinal gradient in eastern North America to test the prediction that under warmer conditions individuals from more southerly populations exhibit a higher functional response than those from northern populations. Temperature, latitude, and the interaction between these two variables had significant effects on attack rates and handling times of individual crayfish from the tested populations. Contrary to our prediction, the attack rates of individuals from northern populations were consistently higher than those from southern populations at both temperatures. We propose that these interpopulation differences in functional response could arise, at least in part, from countergradient selection. Our results suggest that climate warming promotes spatiotemporal variation in *per capita* effects across latitudinally distributed populations of aquatic invasive species.

Key words: countergradient variation, functional response, invasive species, interpopulation variation, rusty crayfish, *Faxonius rusticus*

Introduction

Shifting thermal regimes driven by climate change are expected to alter the invasion success and impacts of burgeoning numbers of non-native plants and animals (Hellman et al. 2008; Walther et al. 2009; Ricciardi et al. 2021). At mid-to-high latitudes, surface temperatures of freshwater ecosystems are expected to warm rapidly (Sharma et al. 2007), which can cause seasonally stressful conditions for cold-adapted species and more hospitable conditions for warm-adapted non-native species (Rahel and 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), climate warming is predicted to alter consumer–resource interactions in lakes and rivers (Englund et al. 2011; Osmond et al. 2017) and thus contribute to spatiotemporal variation in the impacts of non-native aquatic species.

Understanding and predicting the impacts of invasion across heterogeneous or changing environments is a major challenge for ecology (Ricciardi et al. 2021). A promising approach is to experimentally test hypotheses that explicitly consider the influence of local environmental variables on the invader's ecological interactions and performance. For example, the environmental matching hypothesis (Ricciardi et al. 2013; Iacarella et al. 2015*a*) predicts that an invader's *per capita* effects increase as habitat conditions approach its physiological optimum, owing to enhanced thermal performance (*sensu* Huey and Stevenson 1979). Indeed, evidence from meta-analyses indicates that feeding rates are maximized as temperatures approach thermal conditions optimal for organismal growth (Englund et al. 2011; Iacarella et al. 2015*a*). A shifting thermal regime could thus alter predator–prey dynamics and competition involving native and non-native species (e.g., Gherardi et al. 2013; South et al. 2018; Mofu et al. 2019; Khosa et al. 2020; Madzivanzira et al. 2021).

Furthermore, an invader's colonization success and impact are both related, in part, to how efficiently it uses limiting resources (Rehage et al. 2005; Morrison and Hay 2011; Chapple et al. 2012; DeRoy et al. 2020). Foraging efficiency can be derived experimentally by measuring a consumer's functional response (i.e., its predation rate as a function of 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 hyperbolic response resulting in rapid prey depletion at low densities; and Type III, a positively density-dependent sigmoidal response resulting in a prey refugium at low density (Holling 1959). Associated parameters include: attack rate (*a*), the rate of discovery of prey; handling time (*h*), the time required for the predator to capture, handle, and ingest captured prey; and the maximum feeding rate (1/*h*), which indicates peak 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 Type II responses than functionally similar native taxa and low-impact invaders (e.g., Dick et al. 2012, 2013, 2017; Alexander et al. 2014; DeRoy et al. 2020).

Interpopulational differences in invader impacts

A comparative functional response approach that incorporates context dependencies such as ambient temperature into the experimental design is a valuable tool for invasive species risk assessment under changing environmental conditions (Rall et al. 2012; Dick et al. 2013, 2017; South et al. 2017; Madzivanzira et al. 2021). It is noteworthy that most studies investigating invader functional responses test a single species across a physical habitat gradient (such as habitat complexity, dissolved ions, and temperature; Iacarella and Ricciardi 2015; Barrios-O'Neill et al. 2016; South et al. 2018; Cuthbert et al. 2019) or compare native and non-native species pairs (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. However, a recent experimental study by Grimm et al. (2020) on the American spinycheek crayfish *Faxonius limosus* (Rafinesque, 1817) demonstrated that maximum feeding rate and functional response type can vary substantively across conspecific populations even within the same biogeographic region; these differences did not correlate with biogeographic origin of the population nor with time since invasion, suggesting a predominant influence of local environmental conditions.

Similarly, population-level responses to increased temperatures have been shown to vary counterintuitively across a latitudinal gradient, such that high latitude aquatic animals outperform those from low latitudes at high temperatures, despite low latitude fish experiencing these temperatures more often in nature ("countergradient variation"; Conover and Present 1990). Contrary to the notion that species adapt to local conditions at the expense of their performance in other environments, organisms from northern latitudes may invest greater effort at foraging in peak summer temperatures as an adaptation to the shorter growing season (Conover and Present 1990; Tripp et al. 2022).

The rusty crayfish *Faxonius rusticus* as a model invader

Colonization success of introduced crayfishes has been attributed to their broad environmental tolerance, rapid reproduction, and aggressive behaviour (Lodge et al. 2012; Tricarico and Aquiloni 2016), as well as a history of widespread dispersal by anglers, aquaculture, and the pet industry (DiStefano et al. 2009; Hänfling et al. 2011; Banha and Anastácio 2015; Faulkes 2015). The Great Lakes basin contains several non-native crayfishes, including the rusty crayfish *Faxonius* (formerly *Orconectes*) *rusticus* (Girard, 1852), which is native to the Ohio River valley (Taylor and Redmer 1996; Peters et al. 2014) and is currently the most invasive and widespread non-native crayfish in the basin (Peters et al. 2014). At many sites in the lower Great Lakes, it has replaced the native northern clearwater crayfish *Faxonius propinquus* (Girard, 1852) and virile crayfish *Faxonius virilis* (Hagen, 1870) as the most abundant crayfish (Olden et al. 2006; Reid and Nocera 2015) and has had detrimental impacts on aquatic macrophytes, macroinvertebrates, and fishes (Hansen et al. 2013; Kreps et al. 2016).

Faxonius rusticus is broadly distributed in North America with an invaded range spanning 40°N to 49°N in latitude (EDDMapS 2014), thereby offering an opportunity to investigate the potential effects of latitude and climate warming on an invader's performance. Given that *F. rusticus* was first recorded in Lake Erie over 120 years ago (Peters et al. 2014), it is conceivable that well-established populations in the Great Lakes basin have undergone local selection pressure such that they vary from being warm-adapted in the south to more cold-adapted in the northern areas of the basin.

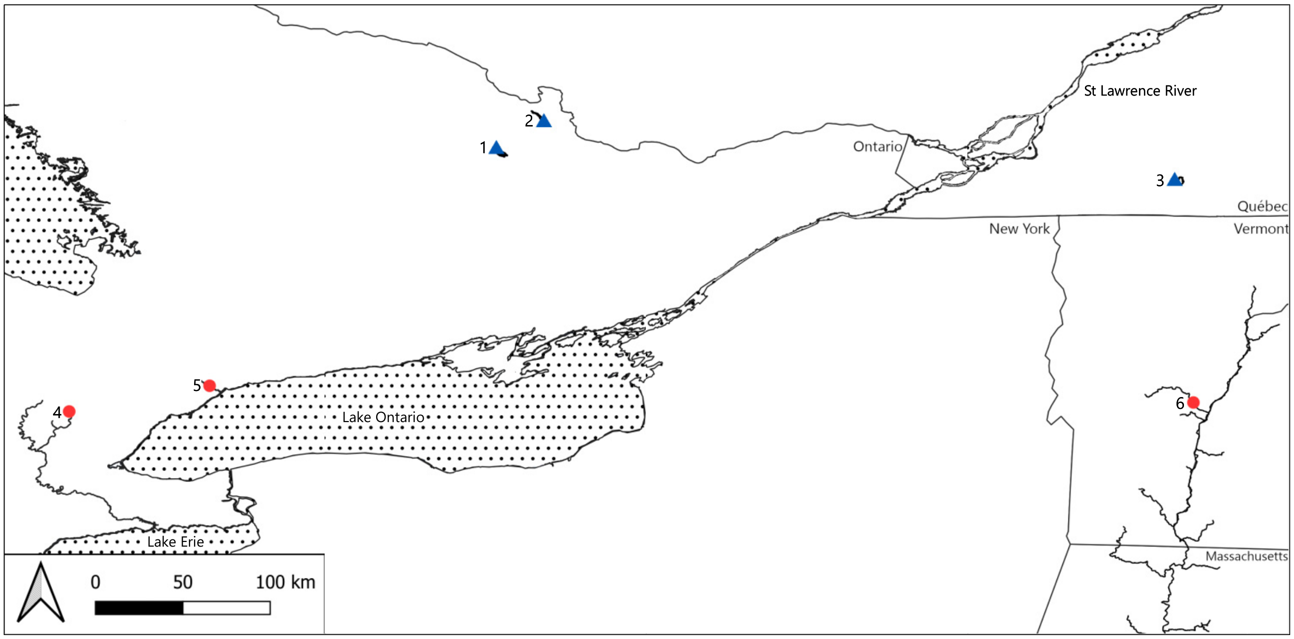
Here, we examined the effects of latitude and temperature on feeding performance of conspecific populations of *F. rusticus* across neighboring regions. We tested the prediction that populations situated further northern (and presumably cold-adapted) would exhibit a higher functional response (high *a*, low *h*) than southern populations at a lower temperature, whereas the opposite would occur at an elevated temperature, following the environmental matching hypothesis (Ricciardi et al. 2013; Iacarella et al. 2015*a*). Alternatively, if this pattern was reversed across latitude, then it would support the countergradient variation hypothesis (Conover and Present 1990).

Methods

Sampling sites

Sampling sites were selected based on (1) latitude, (2) a minimum field density of crayfish, and, most importantly, (3) proximity to the laboratory—to reduce transportation stress on individuals. Under scientific permit (SEG-2019-07-10-007-00-S-P; SR-2018-19), a total of 144 *F. rusticus* adults were collected from six populations ($n = 24$ per population; see Fig. 1). In the northern region (hereafter coded *N*), crayfish were collected from Muskrat Lake, Ontario (45°38′22.9″N and 76°53′30.0″W), Lake Clear, Ontario (45°27′49.2″N and 77°13′14.7″W), and Lac-Brome, Quebec (45°15′00.9″N and 72°32′50.1″W). In the southern region (coded *S*), crayfish were collected from the White River, Vermont (43°43′15.4″N and 72°25′13.2″W), Little Rouge River, Ontario (43°50′08.9″N and 79°11′37.3″W), and Eramosa River, Ontario (43°39′31.1″N and 80°09′21.4″W). Collections were conducted using hand-held nets and modified minnow traps (adapted to have wider entrances), 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*). At each site, individuals were collected at nearshore, shallow (<1 m) depths in calm water. The live individuals were transported back to McGill University in aerated coolers within 24 h of collection.

Fig. 1. Locations of the three northern populations of rusty crayfish (*Faxonius rusticus*) (blue triangles), Lake Clear (1), Muskrat Lake (2), and Lac Brome (3), and the three southern populations (red circles) Eramosa River (4), Little Rouge River (5), and White River (6). Map elements and data from Statistics Canada (2011; 2021), United States Census Bureau (2019), and U.S. Geological Survey, National Geospatial Program (2022). Map projection: WGS 84.



As air temperature has been shown to be related to water temperature in lakes and streams in the region (McCombie 1959; Chu et al. 2010), minimum and maximum daily air temperatures were derived from weather stations located within a 50 km radius of each site from 2018 to 2020 (Supplementary Data, Fig. S1). Maximum daily air temperatures were on average 1.8 °C higher in the southern sites (linear mixed model (LMM): $F_{[1095,1]} = 14.17$, $p = 0.02$, see Supplementary Material for methods), whereas there was no significant difference in minimum daily temperatures between northern and southern groups (LMM: $F_{[1095,1]} = 3.52$, $p = 0.13$). Southern sites had fewer days when maximum temperatures were equal to or below 0 °C, which we used as a proxy for the length of the winter season (LMM: $F_{[4,1]} = 25.77$, $p = 0.0071$), but no difference was found in the number of days when maximum temperatures were above 18 °C, a proxy for the length of the summer season ($F_{[4,1]} = 3.90$, $p = 0.12$). No significant difference was observed in the number of days when minimum daily temperatures were either above 18 °C or below or equal to 0 °C (LMM: $F_{[4,1]} = 0.16$, $p = 0.71$ and $F_{[4,1]} = 2.18$, $p = 0.21$, respectively). Thus, daily air temperatures varied between southern and northern latitude groups, with higher maximum temperatures and a shorter winter season in the south.

In general, crayfish prefer shallower (nearshore) waters (Larson and Olden 2016), whose surface temperatures tend to be more variable and respond more quickly to changes in air temperature (Jansen et al. 2009). Nearshore temperatures can be influenced by short-term factors such as solar radiation and wind, but air temperature is the principal variable explaining surface water temperatures in lakes (Piccolroaz et al. 2013).

Experimental treatments

Once crayfish were brought to the laboratory, they were sexed, weighed (in grams), and measured for carapace length (in mm). Crayfish sizes differed between some populations (Supplementary Data, Figs. S2 and S3). Individual crayfish were held in separate 5.6 L plastic containers with air bubblers at 18 °C in a control growth chamber for at least 2 weeks to allow for laboratory acclimation. As *F. rusticus* is a typically nocturnal species, experimental animals were exposed to a reversal of their usual 12:12 h light:dark regime, so that their feeding behaviour could be tested under nocturnal conditions when they are more actively feeding (Lorman 1975). To maintain water quality, 75% of the water volume was replaced weekly and tested biweekly for ammonia, nitrates, and nitrites. Crayfish were fed a standardized diet of two Wardley Shrimp Pellets every 2 days. Individual crayfish were randomly assigned an identification number and a temperature treatment (low: 18 °C, or high: 26 °C; $n = 10$ per treatment). Treatment temperatures were chosen based on current and projected mean summer surface temperatures in nearshore areas of the lower Great Lakes (Trumpickas et al. 2009, 2015). 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 (Whitledge and Rabeni 2002).

Functional response experiments

Functional response experiments were conducted in 20 L aquarium tanks (one crayfish per tank). Crayfish were starved for 24 h to standardize hunger levels before each experimental trial. Each crayfish was acclimatized in the experimental tank for 1 h 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 (15, 25, 50, 100, 140, 160, and 180) of larval *Chironomus* sp. (Diptera: Chironomidae), hereafter referred to as “bloodworms,” which are common prey for *F. rusticus* in the wild (Olsson and Nyström 2009; Kreps et al. 2016). Frozen bloodworms were thawed before being presented to the crayfish. Prey consumption was determined by counting the number of intact prey items remaining after the 3 h trial. Crayfish were then given a recovery time of 4 days until they were next starved for 24 h, following the results of pilot studies (see Supplementary Material). Thus, each crayfish was exposed to each density in a random order. The seven crayfish that molted during the study were set aside and given an extra week of recovery at the treatment temperature before being tested again to avoid consumption bias. Crayfish were euthanized at the end of experimental trials, as per government regulations for invasive species.

Functional response statistical analysis

Functional response curves for each of the 12 trials (six populations at each of two temperature treatments) were derived 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). First, we fitted a polynomial logistic function to proportional consumption data (using *frair_test*) to determine functional response type of our population curves at both temperatures (Guo et al. 2017). Following these results, data were modeled using the Rogers random predator equation for a Type II response (Rogers 1972), which accounts for non-replacement of prey as they are consumed:

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

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 capture, handle, and ingest captured prey, and T is time (Rogers 1972). From each functional response curve, the parameters a (attack rate) and h (handling time) were extracted. It has been demonstrated that without prey replacement the attack rate may be underestimated, but handling times, maximum feeding rates, and functional response curve types remain unaffected (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 using maximum likelihood estimations (Juliano 2001). We used Holm’s method to control the familywise error rate in our hypothesis testing, because it provides higher statistical power and is less conservative than other multiple comparison corrections. 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 (CIs) using the desired quantile predictions: 0.025 and 0.975 for 95% CIs. Variances in functional response parameters a and h were also visually analyzed by comparing histograms of the bootstrapped coefficients.

We then tested the effects of experimental temperature and latitude on functional response using a generalized linear model (GLM). We bootstrapped functional responses (n = 30) following South et al. (2019), extracted attack rates and handling times, and then modelled these parameters as a function of experimental temperature, latitude, and the interaction between them. We ran a Type III Analysis of variance (ANOVA) and Wald’s χ^2 using the car package (Fox and Weisberg 2019) to report the effect size of our explanatory variables on our response variables.

Lastly, we tested the effects of individual crayfish (carapace length and weight) on functional response with a generalized linear model that modelled proportion of prey killed as a function of (1) initial prey density, (2) carapace length, (3) weight, (4) the interaction between carapace length and weight, (5) latitude, (6) temperature, and (7) the interaction between latitude and temperature. This model was tested using a Type III ANOVA and Wald’s χ^2.

Results

Type II responses were found across all temperature treatments and sites, as indicated by each curve having significant negative first-order terms for their polynomial logistic functions (Table 1). Crayfish weight and the interaction term between weight and carapace length were significant predictors of the proportion of prey killed (GLM: weight $\chi^2_{[1]} = 16.78$; $p < 0.001$ and interaction $\chi^2_{[1]} = 17.32$; $p < 0.001$) only within the low temperature treatment (ANOVA: weight $F_{[11,108]} = 2.28$, $p = 0.015$ and carapace length $F_{[11,108]} = 2.11$, $p = 0.025$; see Supplementary Data, Figs. S2 and S3). We attribute this result to differences between the Lake Clear and Lac Brome individuals (TukeyHSD, weight $p = 0.0491$, and carapace length adjusted $p = 0.0036$).

Interpopulation variation in functional responses across latitudes

Our pairwise comparisons showed no consistent latitudinal pattern involving attack rates and handling times (Fig. 2). However, the effects of latitude and the interaction between latitude and temperature were significant for both attack rates (GLM: latitude $\chi^2_{[5]} = 1546.68$; $p < 0.001$ and in-

Table 1. Estimates of attack rate (*a*), handling time (*h*), and maximum feeding rates (1/*h*) of rusty crayfish (*Faxonius rusticus*) from each Type II Functional Response treatment (±standard error) and the first-order term derived with the *frair_fit* function.

			Parameter				
Population	Temperature	1st-order term	*a*	*CI*	*h*	*CI*	1/*h*
a. Northern populations							
Muskrat Lake	26 °C	−0.011*	1.16	(0.69, 1.80)	0.022	(0.014, 0.029)	45.45
Lac Brome	26 °C	−0.019*	1.59	(1.05, 2.35)	0.021	(0.017, 0.024)	47.62
Lake Clear	26 °C	−0.013*	0.89	(0.59, 1.18)	0.029	(0.023, 0.034)	34.48
Muskrat Lake	18 °C	−0.015*	1.12	(0.69, 1.75)	0.021	(0.013, 0.028)	47.62
Lac Brome	18 °C	−0.018*	1.59	(1.14, 2.29)	0.023	(0.018, 0.028)	43.48
Lake Clear	18 °C	−0.014*	0.62	(0.39, 0.94)	0.060	(0.044, 0.078)	16.67
b. Southern populations							
Eramosa River	26 °C	−0.011*	0.96	(0.68, 1.4)	0.017	(0.01, 0.024)	58.82
Little Rouge River	26 °C	−0.013*	0.65	(0.45, 0.88)	0.061	(0.048, 0.073)	16.39
White River	26 °C	−0.007*	0.50	(0.32, 0.70)	0.029	(0.011, 0.042)	34.44
Eramosa River	18 °C	−0.009*	0.77	(0.49, 1.15)	0.023	(0.015, 0.03)	43.49
Little Rouge River	18 °C	−0.008*	0.45	(0.29, 0.68)	0.035	(0.019, 0.048)	28.77
White River	18 °C	−0.008*	0.39	(0.26, 0.55)	0.049	(0.03, 0.064)	20.23

Note: Asterisks denote significant *p* values (<0.001). CI, confidence interval.

Fig. 2. Functional responses of rusty crayfish (*Faxonius rusticus*) using bloodworms as prey. The panels compare the functional responses of southern populations (left panels: red, orange, yellow) and northern populations (right panels: purple, blue, green) at 18 °C (above) and 26 °C (below). Shaded areas represent 95% confidence intervals obtained by bootstrapping ($N = 999$), and the lines represent the fitted models.

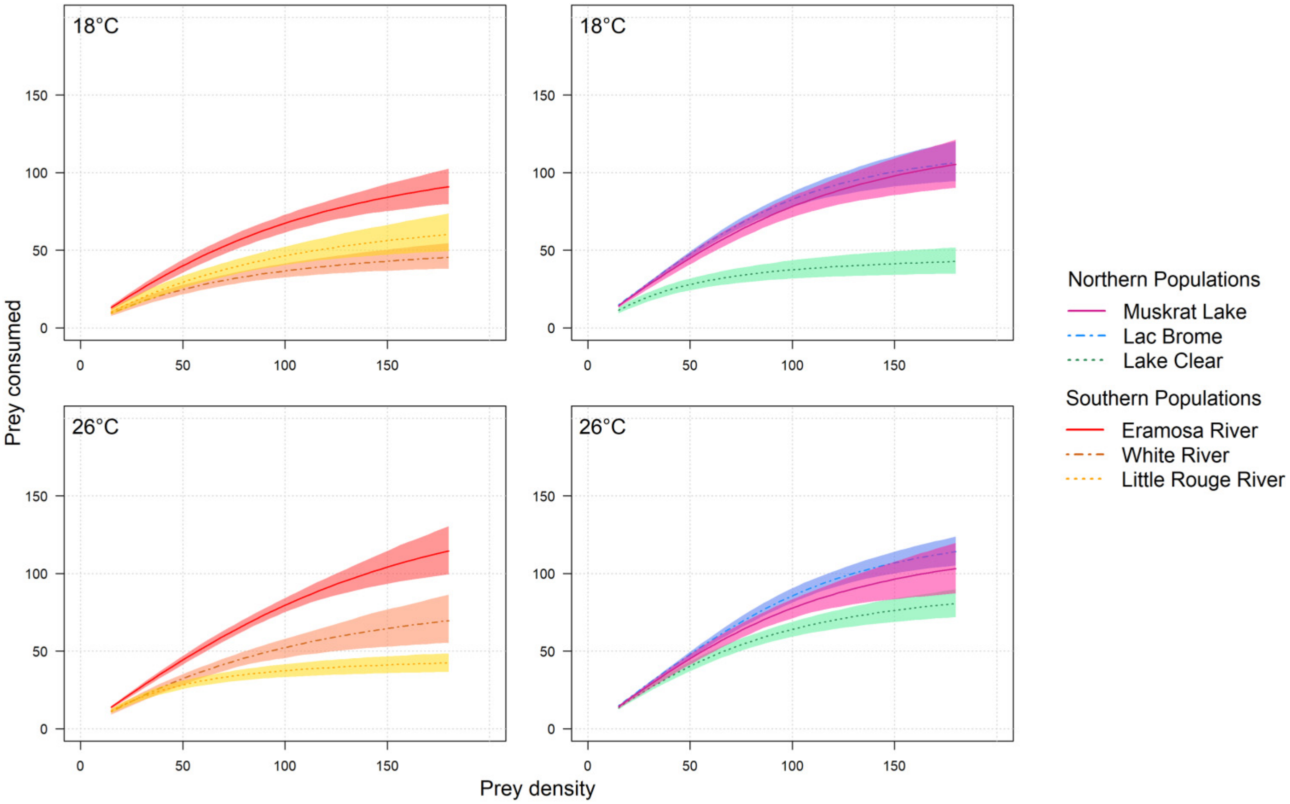


Table 2. Parameter comparisons of attack rates (*a*) and handling times (*h*) of functional response curves between northern and southern latitude populations of rusty crayfish (*Faxonius rusticus*) at 18 °C and 26 °C using *frair_compare* with Holm-adjusted *p* values.

Fit 1	Fit 2	Δ*a*	*a p*-adj.	Δ*h*	*h p*-adj.
a. Northern vs. Southern populations at 18 °C					
Muskrat Lake	Eramosa River	0.344	**<0.0001**	– 0.00203	**0.0130**
Muskrat Lake	Little Rouge River	0.669	**<0.0001**	– 0.01378	**<0.0001**
Muskrat Lake	White River	0.732	**<0.0001**	– 0.02845	**<0.0001**
Lac Brome	Eramosa River	0.818	**<0.0001**	– 0.00012	0.907
Lac Brome	Little Rouge River	1.144	**<0.0001**	– 0.01189	**<0.0001**
Lac Brome	White River	1.207	**<0.0001**	– 0.02654	**<0.0001**
Lake Clear	Eramosa River	– 0.151	**0.008**	0.03711	**<0.0001**
Lake Clear	Little Rouge River	0.174	**<0.001**	0.02535	**<0.0001**
Lake Clear	White River	0.237	**<0.0001**	0.01069	**0.0006**
b. Northern vs. Southern populations at 26 °C					
Muskrat Lake	Eramosa River	0.197	**0.04**	0.00494	**<0.0001**
Muskrat Lake	Little Rouge River	0.508	**<0.0001**	– 0.03909	**<0.0001**
Muskrat Lake	White River	0.658	**<0.0001**	– 0.00711	**<0.0001**
Lac Brome	Eramosa River	0.627	**<0.0001**	0.00375	**<0.0001**
Lac Brome	Little Rouge River	0.939	**<0.0001**	– 0.04027	**<0.0001**
Lac Brome	White River	1.089	**<0.0001**	– 0.00830	**<0.0001**
Lake Clear	Eramosa River	– 0.069	0.289	0.01194	**<0.0001**
Lake Clear	Little Rouge River	0.242	**<0.001**	– 0.03210	**<0.0001**
Lake Clear	White River	0.392	**<0.0001**	– 0.00014	0.9342

Notes: Δ*a* and Δ*h* are differences in attack rate and handling time, respectively. *p* values are bolded if significant.

teraction $\chi^2_{[5]} = 41.35$; $p < 0.001$) and handling times (GLM: latitude $\chi^2_{[5]} = 1326.53$; $p < 0.001$ and interaction $\chi^2_{[5]} = 828.28$; $p < 0.001$). Parameter comparisons between northern and southern populations revealed higher attack rates for all northern populations compared to the southern ones at either temperature (Table 2)—except for Lake Clear (*N*), whose individuals, despite having a larger carapace length and weight, had a lower mean attack rate than those of the Eramosa River (*S*) population.

Comparisons of populations within northern latitudes showed significant differences in model fits and parameter estimates (Tables 1, 3*a*, and 3*b*; Fig. 2). At either temperature, attack rates varied among individuals from the three northern populations as follows: Muskrat Lake > Lac Brome > Lake Clear (Tables 1, 3*a*, and 3*b*). Maximum feeding rates were lower in Lake Clear compared to Muskrat Lake and Lac Brome populations, whereas the latter two populations did not differ (Tables 3*a* and 3*b*).

When comparing functional responses at 18 °C, maximum feeding rates varied among individuals from the three southern populations as follows: Eramosa River > Little Rouge River > White River (Tables 1 and 3*c*). Contrarily, Eramosa River had the lowest attack rates, whereas Little Rouge River and White River populations did not differ in this parameter (Tables 1, 3*c*, and 3*d*). At 26 °C, Eramosa River crayfish once again had the highest maximum feeding rates (Eramosa River > White River > Little Rouge River) and the highest attack rates (Eramosa River > Little Rouge River > White River) (Tables 1 and 3*d*).

Variation in functional responses across temperatures

Although pairwise comparisons showed no consistent pattern in population response to temperature increase (Fig. 3; Table 4), the generalized linear models indicated that temperature had significant effects on attack rates and handling times (*a*: $\chi^2 = 81.03$, $p < 0.001$ and *h*: $\chi^2 = 78.89$, $p < 0.001$). For northern populations, Muskrat Lake showed a complete overlap in model fits, and response parameters did not differ between temperatures (Fig. 3; Table 4*a*); Lac Brome differed only with higher maximum feeding rates at 26 °C (Table 4*a*); and Lake Clear showed higher attack rates and maximum feeding rates at 26 °C (Fig. 3; Table 4*a*). For southern populations, no consistent pattern was found for handling times. The Eramosa River and White River populations had higher maximum feeding rates at 26 °C, but Little Rouge River experienced the reverse response with a higher maximum feeding rate at 18 °C (Fig. 3; Table 4*b*). However, all three populations experienced higher attack rates at 26 °C (Fig. 3; Table 4*b*).

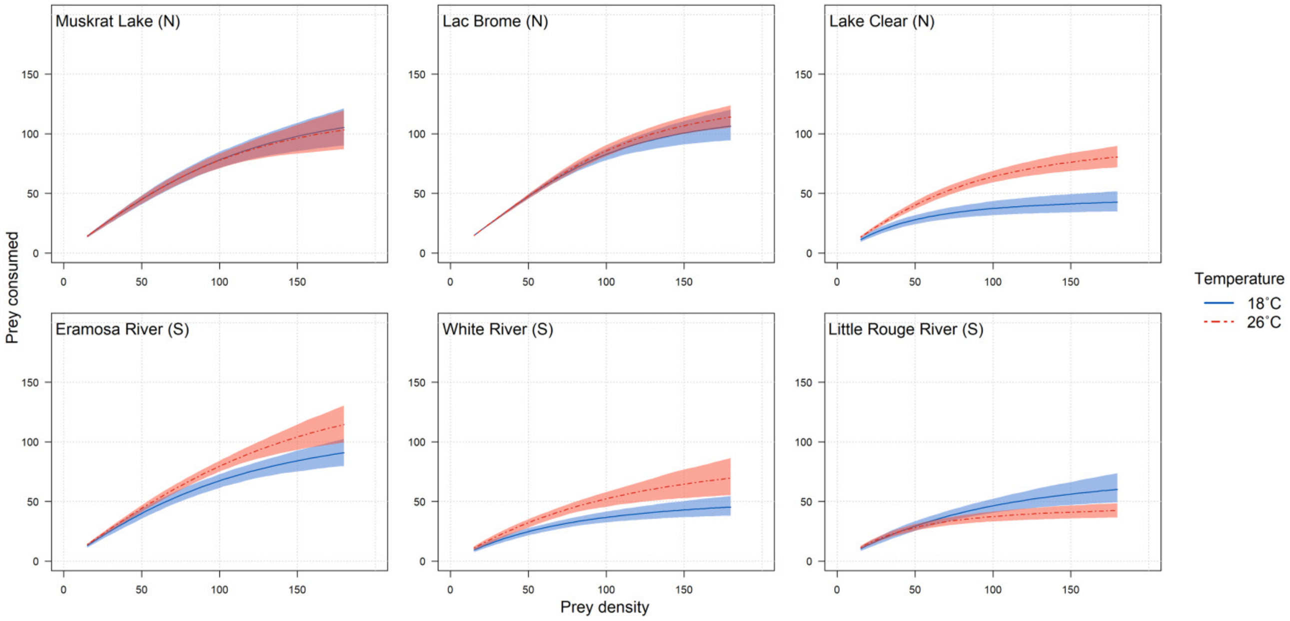
At both experimental temperatures, bootstrapped coefficients of attack rate showed greater variation in northern populations than in southern populations (Fig. 4). Within each population, variation of attack rates seemed largely insensitive to temperature treatment. In contrast, bootstrapped coefficients of handling time 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 (Fig. 4).

Table 3. Parameter comparisons of attack rates (*a*) and handling times (*h*) of functional response curves within northern and southern latitude populations of rusty crayfish (*Faxonius rusticus*) at 18 °C and 26 °C using *frair_compare* with Holm-adjusted *p* values.

Fit 1	Fit 2	Δ*a*	*a p*-adj.	Δ*h*	*h p*-adj.
a. Northern populations at 18 °C					
Muskrat Lake, 18 °C	Lac Brome, 18 °C	– 0.474	**<0.0001**	– 0.00191	0.052
Muskrat Lake, 18 °C	Lake Clear, 18 °C	0.4951	**<0.0001**	– 0.03910	**<0.0001**
Lac Brome, 18 °C	Lake Clear, 18 °C	0.9699	**<0.0001**	– 0.03722	**<0.0001**
b. Northern populations at 26° C					
Muskrat Lake, 26 °C	Lac Brome, 26 °C	– 0.431	**<0.001**	0.00119	0.398
Muskrat Lake, 26 °C	Lake Clear, 26 °C	0.267	**0.003**	– 0.00699	**<0.0001**
Lac Brome, 26 °C	Lake Clear, 26 °C	0.696	**<0.0001**	– 0.00819	**<0.0001**
c. Southern populations at 18 °C					
Eramosa River, 18 °C	Little Rouge River, 18 °C	0.325	**<0.0001**	– 0.01175	**<0.0001**
Eramosa River, 18 °C	White River, 18 °C	0.388	**<0.0001**	– 0.02642	**<0.0001**
Little Rouge River, 18 °C	White River, 18 °C	0.064	0.087	– 0.01465	**<0.0001**
d. Southern populations at 26 °C					
Eramosa River, 26 °C	Little Rouge River, 26 °C	0.312	**<0.0001**	– 0.04403	**<0.0001**
Eramosa River, 26 °C	White River, 26 °C	0.462	**<0.0001**	– 0.01204	**<0.0001**
Little Rouge River, 26 °C	White River, 26 °C	0.149	**0.012**	0.03198	**<0.0001**

Note: Δ*a* and Δ*h* are differences in attack rate and handling time, respectively. *p* values are bolded if significant.

Fig. 3. Functional responses of rusty crayfish (*Faxonius rusticus*) at two temperatures. 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 (*N* = 999), the lines represent the fitted models, and the circles are the experimental observations.



Discussion

Contrary to expectations, individuals from southern populations—which were presumably adapted to warmer temperatures—exhibited lower attack rates than northern populations at both 18 °C and 26 °C, the latter temperature being within the range of the reported growth optimum for *F. rusticus* (Mundahl and Benton 1990). Although individual carapace length and weight can affect feeding rate in *F. rusticus* (Morse et al. 2013; see also Uiterwaal and DeLong 2020), we believe the differences in crayfish carapace length between populations were not large enough to explain the observed patterns.

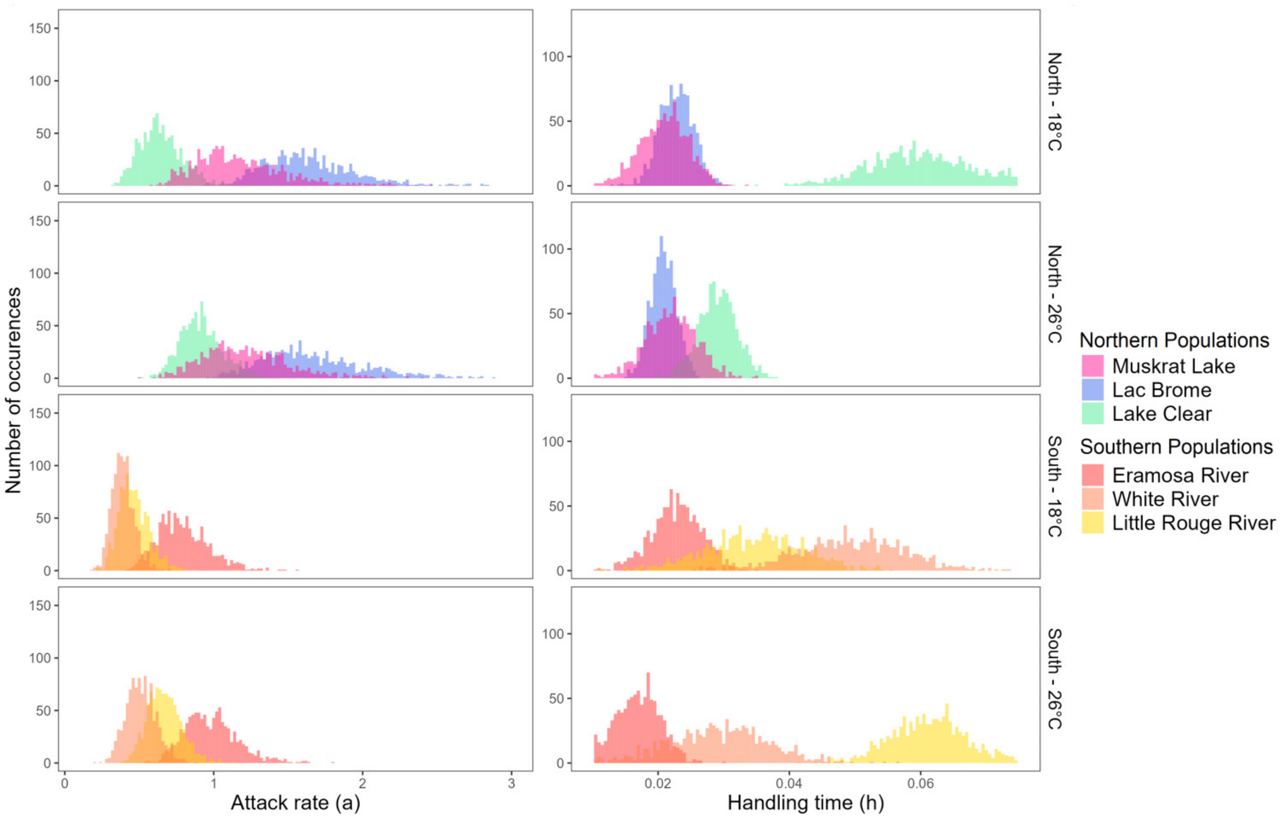
There were no consistent differences in handling times across latitudes, regardless of temperature. This suggests

Table 4. Parameter comparisons of attack rates (*a*) and handling times (*h*) of functional response curves of populations at 18 °C and 26 °C using *frair_compare* with Holm-adjusted *p* values.

Fit 1	Fit 2	Δa	*a p*-adj.	Δh	*h p*-adj.
a. Northern populations					
Muskrat Lake, 26 °C	Muskrat Lake, 18 °C	0.041	1	0.00096	0.395
Lac Brome, 26 °C	Lac Brome, 18 °C	– 0.003	1	– 0.00215	**0.012**
Lake Clear, 26 °C	Lake Clear, 18 °C	0.270	**<0.0001**	– 0.03117	**<0.0001**
b. Southern populations					
Eramosa River, 26 °C	Eramosa River, 18 °C	0.188	**0.012**	– 0.00601	**<0.0001**
Little Rouge River, 26 °C	Little Rouge River, 18 °C	0.205	**<0.0001**	0.02628	**0.0001**
White River, 26 °C	White River, 18 °C	0.115	**0.012**	– 0.02038	**<0.0001**

Note: Δa and Δh are differences in attack rate and handling time, respectively. *p* values are bolded if significant.

Fig. 4. Variation in bootstrapped estimates of attack rates and handling times for functional responses of rusty crayfish (*Faxonius rusticus*) across populations, based on latitude and temperature treatment.



the influence of other environmental factors such as, *inter alia*, time since invasion (Strayer et al. 2006; Iacarella et al. 2015*b*, 2015*c*; Evangelista et al. 2019), abiotic variables unrelated to temperature (Barrios-O'Neill et al. 2015; Wasserman et al. 2016*b*), source community composition (Barrios-O'Neill et al. 2014; Wasserman et al. 2016*a*; Grimm et al. (2020), and phenotypic and genotypic differences—including countergradient variation (Conover and Present 1990; Conover et al. 2009; Hodgson and Schwanz 2019). For example, recent invaders often have different *per capita* effects than individuals from well-established populations (Strayer et al. 2006; Iacarella et al. 2015*b*; Závorka et al. 2017; Evangelista et al. 2019). In our study, however, time since invasion of rusty crayfish at each site cannot be linked to differences in foraging success, as all our populations were well-established; indeed, they were chosen because they were sufficiently abundant to allow for specimen collection.

Interpopulation variation in functional response could arise from differences in composition of the source communities or from hybridization with congeneric species. The presence of a competitor in a community can exert selection pressure for key behaviors such as aggression, voracity, and boldness (Pintor et al. 2008; Hayes et al. 2009). The virile crayfish *F. virilis* was observed at both Clear Lake and Muskrat Lake, whereas the northern clearwater crayfish *F. propinquus* was found at Eramosa River. These congeners were found in none of the other sites and were generally present at low numbers (<5 individuals encountered during a 3 h sampling period), except at Muskrat Lake where up to 10 individual *F. virilis* were encountered during the sample period. A previous study has shown the capacity of *F. rusticus* crayfish to hybridize with *F. propinquus*, with the resulting F1 progeny being extremely aggressive and outcompeting both parental species for food and shelter (Perry et al. 2001). This might explain why individuals from the *F. rusticus* population that co-occurs with *F. propinquus* in the Eramosa River exhibit higher functional responses than those in the Lac Brome (*N*) and Muskrat Lake (*N*) populations. Although care was taken to properly identify and select target species, it is possible that some obscure hybrids were overlooked.

A recent meta-analysis (Uiterwaal and DeLong 2020) of over 2000 functional responses for various consumers, prey types, environmental conditions, and habitats found unimodal relationships between response parameters (attack rates and handling times) and temperature. These responses varied according to the proximity of the ambient temperature relative to the consumer's physiological optimum, as predicted by the environmental matching hypothesis (Ricciardi et al. 2013; Iacarella et al. 2015*a*). Furthermore, Uiterwaal and DeLong (2020) found that the optimal temperature for attack rate is not the same as that for handling time, which perhaps further explains why attack rates of individuals from our northern populations were higher than those from southern populations at either temperature (Table 1). In populations where differences in attack rates were observed between temperatures, attack rates were consistently higher at the warmer temperature; but where differences in handling times were observed, outcomes varied across populations though tended to be reduced at the higher temperature. Our results thus provide additional evidence that attack rates respond more strongly to temperature than handling times.

Countergradient variation in crayfish attack rate

Given that local abiotic conditions can induce interpopulation variation (Barrios-O'Neill et al. 2015; Iacarella et al. 2015*b*; Wasserman et al. 2016*b*; Uiterwaal and DeLong 2020), a possible confounding factor in our study was that southern populations were located in rivers and northern populations were located in lakes. Although all local collection sites were situated in shallow areas with similar low water flows, river and lake ecosystems are generally characterized by contrasting groundwater and flow regimes whose conditions might cause crayfish in these populations to adapt foraging behaviours specific to these different conditions. For the virile crayfish (*F. virilis*), it was found that individuals sourced from rivers and lakes had differing responses to chemical cues under experimental lentic and lotic flow regimes (Hazlett et al. 2006; Moore 2015). Moore (2015) found that lake-collected crayfish crawled at slower speeds in lentic conditions than in lotic conditions and also slower than river-collected crayfish in both lentic and lotic conditions. Both lake and river crayfish, however, had the same rate of success in locating an attractive odour within a timespan of 20 min. If our southern crayfish were adapted to river flows and displayed the same behaviour as documented by Moore (2015), then we would expect them to exhibit higher attack rates in our experiment—contrary to what we observed.

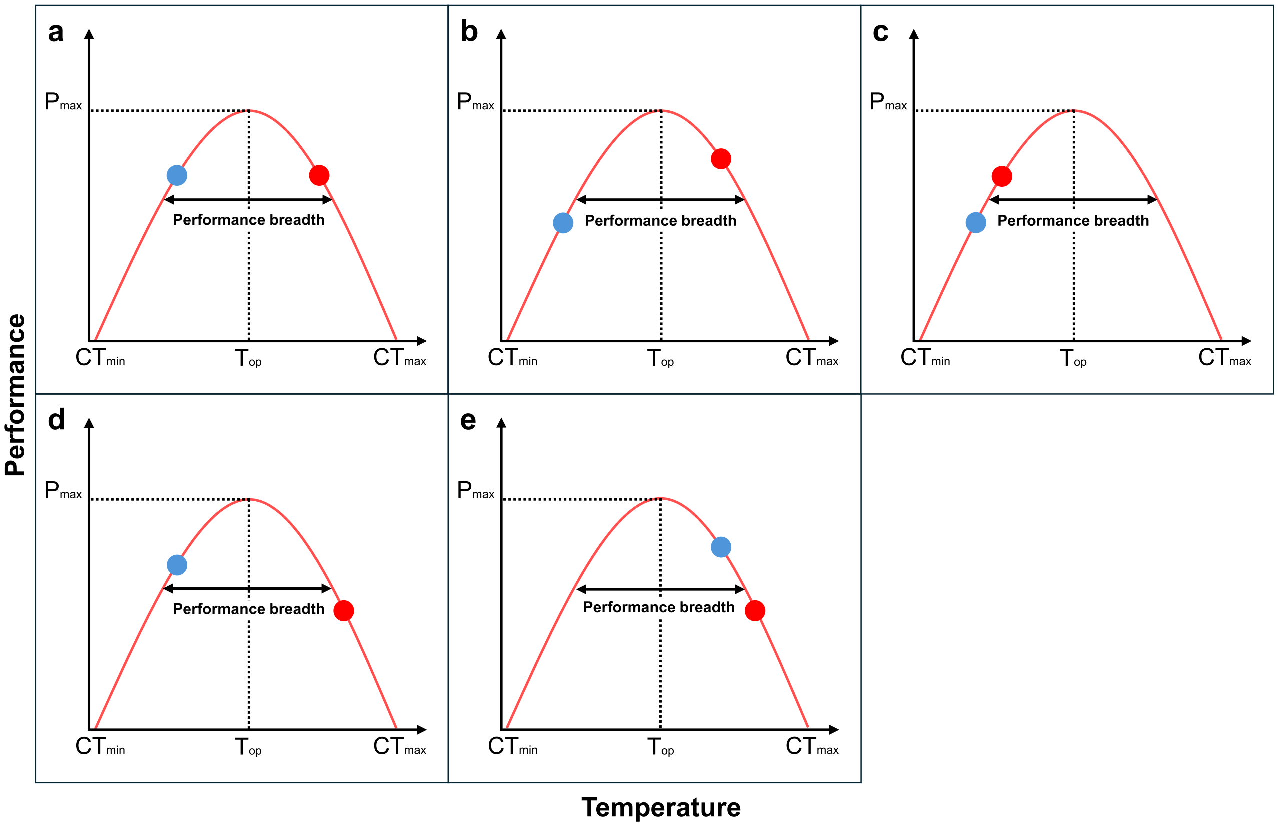
The higher attack rates observed in crayfish from our northern populations could be explained by the countergradient hypothesis that populations living at higher latitudes evolve adaptations to the higher energetic demands of their environment, including increased foraging and growth rates, to compensate for the shorter growing season (Conover 1990; Chavarie et al. 2010; Hodgson and Schwanz 2019). For example, a comparison of growth rates of a marine fish (Atlantic silversides *Menidia menidia* (Linnaeus, 1766)) from different locations along a latitudinal gradient found that high latitude fish outgrew those from lower latitudes when exposed to warm temperatures that the low latitude fish experience more often in the wild (Conover and Present 1990). Similarly, a study of *F. virilis* collected from sites between 39°N and 45°N found that individuals from higher latitudes had increased routine metabolic rates when foraging (Tripp et al. 2022). These studies suggest multiple pathways by which northern populations may be adapted for increased activity during a brief seasonal period of high temperatures.

Conclusions and future directions

Our results suggest there are optimal temperatures at which foraging rates are maximized, but that these optima vary across populations. We hypothesize that the optimal temperature for foraging by crayfish in the Muskrat Lake and Lac Brome populations is between 18 °C and 26 °C, such that the experimental treatment temperatures fall on either side of the peak in their modal thermal performance curve (Fig. 5*a*). Results from Lake Clear (*N*), Eramosa River (*S*), and White River (*S*) populations suggest that the thermal optimum is closer to the high-temperature treatment (26 °C) (Figs. 5*b* and 5*c*), whereas for the Little Rouge River (*S*) population it is closer to the low-temperature treatment (Figs. 5*d* and 5*e*).

Our results have implications for potential future invasion events stemming from poleward range expansions of native and non-native species under climate change. The interpopulation variation in functional response that we observed here warns against risk assessments and models that rely solely on information from a single population. *Per capita* effects are influenced by temperature differently across conspecific populations—even among those occupying the same latitude and having a similar invasion history. This can generate heterogeneity of invader impact across space and time. As surface waters continue to warm, non-native populations within them may dramatically increase their impacts if temperatures shift toward their physiological optima (Iacarella et al. 2015*a*). Furthermore, more recently established non-native populations may have different magnitudes or types of impacts than their source populations within the invaded range (Iacarella et al. 2015*b*; Boets et al. 2019; Grimm et al. (2020), and thus it might be revealing to relate *per capita* effects to ge-

Fig. 5. 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. 2015*a*) 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 and Lac Brome populations of rusty crayfish (*Faxonius rusticus*), where no significant difference was observed in response to temperature increase. Panels (*b*) and (*c*) show the two alternative scenarios for Lake Clear, Eramosa River, and White River, populations for which a significantly higher maximum feeding rate was observed at 26 °C. Panels (*d*) and (*e*) describe the alternative scenarios for Little Rouge River, for which a significantly higher maximum feeding rate was observed at 18 °C.



netic distance between populations. Finally, since prey activity could mediate the outcome of their trophic interactions, future experiments should investigate differences in prey response to temperature using live prey taxa from the same source location as the consumer.

Acknowledgements

We thank Eve-line Bérubé Beaulieu for her assistance. This research was funded by a Strategic Project Grant (NSERC STPGP 506528–17) to AR from the Natural Sciences and Engineering Research Council of Canada.

Article information

History dates

Received: 15 January 2024
Accepted: 15 April 2024
Accepted manuscript online: 17 May 2024
Version of record online: 22 August 2024

Copyright

Data availability

Data are available as supplementary material.

Author information

Author ORCIDs

Noemie L. M. Sheppard https://orcid.org/0000-0001-9081-8022
Anthony Ricciardi https://orcid.org/0000-0003-1492-0054

Author notes

Authors **Victoria Chicatun** and **Noemie L. M. Sheppard** contributed equally to this work.

Author contributions

Conceptualization: VC, AR
Formal analysis: VC, NLMS

Funding acquisition: AR
Investigation: VC
Supervision: AR
Writing – original draft: VC, NLMS, AR

Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2024-0006.

References

Alexander, M., Dick, J., O'Connor, N., Haddaway, N., and Farnsworth, K. 2012. Functional responses of the intertidal amphipod *Echinogammarus marinus*: Effects of prey supply, model selection and habitat complexity. Mar. Ecol.: Prog. Ser. **468**: 191–202. doi:10.3354/meps09978.

Alexander, M.E., Dick, J.T.A., Weyl, O.L.F., Robinson, T.B., and Richardson, D.M. 2014. Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biol. Lett. **10**(2): 20130946. doi:10.1098/rsbl.2013.0946. PMID: 24522629.

Banha, F., and Anastácio, P.M. 2015. Live bait capture and crayfish trapping as potential vectors for freshwater invasive fauna. Limnologica, **51**: 63–69. doi:10.1016/j.limno.2014.12.006.

Barrios-O'Neill, D., Dick, J.T.A., Ricciardi, A., MacIsaac, H.J., and Emmerson, M.C. 2014. Deep impact: in situ functional responses reveal context-dependent interactions between vertically migrating invasive and native mesopredators and shared prey. Freshwater Biol. **59**(10): 2194–2203. doi:10.1111/fwb.12423.

Barrios-O'Neill, D., Dick, J.T.A., Emmerson, M.C., Ricciardi, A., and MacIsaac, H.J. 2015. Predator-free space, functional responses and biological invasions. Funct. Ecol. **29**(3): 377–384. doi:10.1111/1365-2435.12347.

Barrios-O'Neill, D., Kelly, R., Dick, J.T.A., Ricciardi, A., MacIsaac, H.J., and Emmerson, M.C. 2016. On the context-dependent scaling of consumer feeding rates. Ecol. Lett. **19**(6): 668–678. doi:10.1111/ele.12605.

Boets, P., Laverty, C., Fukuda, S., Verreycken, H., Green, K., Britton, R.J., et al. 2019. Intra- and intercontinental variation in the functional responses of a high impact alien invasive fish. Biol. Invasions, **21**(5): 1751–1762. doi:10.1007/s10530-019-01932-y.

Chapple, D.G., Simmonds, S.M., and Wong, B.B. 2012. Can behavioral and personality traits influence the success of unintentional species introductions? Trends Ecol. Evol. **27**(1): 57–64. doi:10.1016/j.tree.2011.09.010.

Chavarie, L., Dempson, J.B., Schwarz, C.J., Reist, J.D., Power, G., and Power, M. 2010. Latitudinal variation in growth among Arctic charr in eastern North America: evidence for countergradient variation? Hydrobiologia, **650**(1): 161–177. doi:10.1007/s10750-009-0043-z.

Chu, C., Jones, N.E., and Allin, L. 2010. Linking the thermal regimes of streams in the Great Lakes Basin, Ontario, to landscape and climate variables. River Res. Appl. **26**(3): 221–241. doi:10.1002/rra.1259.

Conover, D.O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Trans. Am. Fish. Soc. **119**(3): 416–430. doi:10.1577/1548-8659(1990)119⟨0416:trbcfg⟩2.3.co;2.

Conover, D.O., and Present, T.M. 1990. Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia, **83**(3): 316–324. doi:10.1007/bf00317554.

Conover, D.O., Duffy, T.A., and Hice, L.A. 2009. The covariance between genetic and environmental influences across ecological gradients. Ann. N.Y. Acad. Sci. **1168**(1): 100–129. doi:10.1111/j.1749-6632.2009.04575.x.

Cuthbert, R.N., Dalu, T., Wasserman, R.J., Callaghan, A., Weyl, O.L.F., and Dick, J.T.A. 2019. Using functional responses to quantify notonectid predatory impacts across increasingly complex environments. Acta Oecol. **95**: 116–119. doi:10.1016/j.actao.2018.11.004.

DeRoy, E., Scott, R., Hussey, N., and MacIsaac, H. 2020. High predatory efficiency and abundance drive expected ecological impacts of a marine invasive fish. Mar. Ecol.: Progr. Ser. **637**: 195–208. doi:10.3354/meps13251.

Dick, J.T.A., Gallagher, K., Avlijas, S., Clarke, H.C., Lewis, S.E., Leung, S., et al. 2012. Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biol. Invasions, **15**(4): 837–846. doi:10.1007/s10530-012-0332-8.

Dick, J.T.A., Alexander, M.E., Jeschke, J. M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B., et al. 2013. Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biol. Invasions, **16**(4): 735–753. doi:10.1007/s10530-013-0550-8.

Dick, J.T.A., Alexander, M.E., Ricciardi, A., Laverty, C., Downey, P.O., Xu, M., et al. 2017. Functional responses can unify invasion ecology. Biol. Invasions, **19**(5): 1667–1672. doi:10.1007/s10530-016-1355-3.

DiStefano, R.J., Litvan, M.E., and Horner, P.T. 2009. The bait industry as a potential vector for alien crayfish introductions: problem recognition by fisheries agencies and a Missouri evaluation. Fisheries, **34**(12): 586–597. doi:10.1577/1548-8446-34.12.586.

EDDMapS. 2014. Early detection and distribution mapping system for Ontario. University of Georgia. The Center for Invasive Species and Ecosystem Health. Available from http:/www.eddmaps.org/Ontario [accessed March 2021].

Englund, G., Öhlund, G., Hein, C.L., and Diehl, S. 2011. Temperature dependence of the functional response. Ecol. Lett. **14**(9): 914–921. doi:10.1111/j.1461-0248.2011.01661.x.

Evangelista, C., Cucherousset, J., and Lecerf, A. 2019. Contrasting ecological impacts of geographically close invasive populations. Oecologia, **189**(2): 529–536. doi:10.1007/s00442-018-04333-5.

Faulkes, Z. 2015. The global trade in crayfish as pets. Crustac. Res. **44**(0): 75–92. doi:10.18353/crustacea.44.0_75.

Fox, J., and Weisberg, S. 2019. An R companion to applied regression. Sage publications, Thousand Oaks, CA.

Gherardi, F., Coignet, A., Souty-Grosset, C., Spigoli, D., and Aquiloni, L. 2013. Climate warming and the agonistic behaviour of invasive crayfishes in Europe. NeoBiota, **54**(9): 1958–1967. doi:10.1111/fwb.12183.

Grimm, J., Dick, J.T.A., Verreycken, H., Jeschke, J.M., Linzmaier, S., and Ricciardi, A. 2020. Context-dependent differences in the functional responses of conspecific native and non-native crayfishes. NeoBiota, **54**: 71–88. doi:10.3897/neobiota.54.38668.

Guo, Z., Sheath, D., Trigo, F.A., and Britton, J.R. 2017. Comparative functional responses of native and high-impacting invasive fishes: impact predictions for native prey populations. Ecol. Freshw. Fish, **26**(4): 533–540. doi:10.1111/eff.12297.

Hänfling, B., Edwards, F., and Gherardi, F. 2011. Invasive alien *Crustacea*: dispersal, establishment, impact and control. BioControl, **56**(4): 573–595. doi:10.1007/s10526-011-9380-8.

Hansen, G.J., Hein, C.L., Roth, B.M., Vander Zanden, M.J., Gaeta, J.W., Latzka, A.W., and Carpenter, S.R. 2013. Food web consequences of long-term invasive crayfish control. Can. J. Fish. Aquat.Sci. **70**(7): 1109–1122. doi:10.1139/cjfas-2012-0460.

Hayes, N.M., Butkas, K.J., Olden, J.D., and Vander Zanden, M.J. 2009. Behavioural and growth differences between experienced and naive populations of a native crayfish in the presence of invasive rusty crayfish. Freshw. Biol. **54**(9): 1876–1887. doi:10.1111/j.1365-2427.2009.02237.x.

Hazlett, B.A., Acquistapace, P., and Gherardi, F. 2006. Responses of the crayfish *Orconectes virilis* to chemical cues depend upon flow conditions. J. Crustacean Biol. **26**(1): 94–98. doi:10.1651/C-2595.1.

Hellman, J.J., Byers, J.E., Bierwagen, B.G., and Dukes, J.S. 2008. Five potential consequences of climate change for invasive species. Conserv. Biol. **22**(3): 534–543. doi:10.1111/j.1523-1739.2008.00951.x.

Hodgson, M.J., and Schwanz, L.E. 2019. Drop it like it's hot: Interpopulation variation in thermal phenotypes shows counter-gradient pattern. J. Therm. Biol **83**: 178–186. doi:10.1016/j.jtherbio.2019.05.016.

Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. **91**(5): 293–320. doi:10.4039/ent91293-5.

Huey, R.B., and Stevenson, R. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zool. **19**(1): 357–366. doi:10.1093/icb/19.1.357.

Iacarella, J.C., Dick, J.T.A., Alexander, M.E., and Ricciardi, A. 2015a. Ecological impacts of invasive alien species along temperature gradients: testing the role of environmental matching. Ecol. Appl. **25**(3): 706–716. doi:10.1890/14-0545.1.

Iacarella, J.C., Dick, J.T.A., and Ricciardi, A. 2015*b*. A spatio-temporal contrast of the predatory impact of an invasive freshwater crustacean. Divers. Distrib. **21**(7): 803–812. doi:10.1111/ddi.12318.

Iacarella, J.C., Mankiewicz, P.S., and Ricciardi, A. 2015c. Negative competitive effects of invasive plants change with time since invasion. Ecosphere, **6**(7): art123. doi:10.1890/es15-00147.1.

Iacarella, J.C., and Ricciardi, A. 2015. Dissolved ions mediate body mass gain and predatory response of an invasive fish. Biol. Invasions, **17**(11): 3237–3246. doi:10.1007/s10530-015-0949-5.

Jansen, W., Geard, N., Mosindy, T., Olson, G., and Turner, M. 2009. Relative abundance and habitat association of three crayfish (*Orconectes virilis*, *O. rusticus*, and *O. immunis*) near an invasion front of *O. rusticus*, and long-term changes in their distribution in Lake of the Woods, Canada. Aquat. Invasions, **4**(4): 627–649. doi:10.3391/ai.2009.4.4.9.

Juliano, S.A. 2001. Nonlinear curve fitting. *In* Design and analysis of ecological experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Oxford University Press, Oxford. pp. 178–196.

Khosa, D., South, J., Cuthbert, R.N., Wasserman, R.J., and Weyl, O.L.F. 2020. Temperature regime drives differential predatory performance in Largemouth bass and Florida bass. Environ. Biol. Fishes, **103**(1): 67–76. doi:10.1007/s10641-019-00933-z.

Kreps, T.A., Larson, E.R., and Lodge, D.M. 2016. Do invasive rusty crayfish (*Orconectes rusticus*) decouple littoral and pelagic energy flows in lake food webs? Freshw. Sci. **35**(1): 103–113. doi:10.1086/683358.

Larson, E., and Olden, J. 2016. Field sampling techniques for crayfish. *In* Biology and ecology of crayfish. *Edited by* M. Longshaw and P. Stebbing. CRC Press, Boca Raton, FL. pp. 287–324. doi:10.1201/b20073-9.

Laverty, C., Dick, J.T.A., Alexander, M.E., and Lucy, F.E. 2014. Differential ecological impacts of invader and native predatory freshwater amphipods under environmental change are revealed by comparative functional responses. Biol. Invasions, **17**(6): 1761–1770. doi:10.1007/s10530-014-0832-9.

Lodge, D.M., Deines, A., Gherardi, F., Yeo, D.C., Arcella, T., Baldridge, A.K., et al. 2012. Global introductions of crayfishes: Evaluating the impact of species invasions on ecosystem services. Annu. Rev. Ecol. Evol. Syst. **43**(1): 449–472. doi:10.1146/annurev-ecolsys-111511-103919.

Lorman, J.G. 1975. Feeding and activity of the crayfish Orconectes rusticus in a northern Wisconsin lake. Masters thesis, University of Wisconsin-Madison, Madison, WI. 56p.

Madzivanzira, T.C., South, J., and Weyl, O.L.F. 2021. Invasive crayfish outperform Potamonautid crabs at higher temperatures. Freshw. Biol. **66**: 978–991. doi:10.1111/fwb.13691.

McCombie, A.M. 1959. Some relations between air temperatures and the surface water temperatures of lakes. Limnol. Oceanogr. **4**(3): 252–258. doi:10.4319/lo.1959.4.3.0252.

Mofu, L., Cuthbert, R.N., Dalu, T., Woodford, D.J., Wasserman, R.J., Dick, J.T.A., and Weyl, O.L.F. 2019. Impacts of non-native fishes under a seasonal temperature gradient are forecasted using functional responses and abundances. NeoBiota, **49**: 57–75. doi:10.3897/neobiota.49.34986.

Moore, P.A. 2015. Chemical orientation strategies of the crayfish are influenced by the hydrodynamics of their native environment. Am. Midl. Nat. **173**(1): 17–29. doi:10.1674/0003-0031-173.1.17.

Morrison, W.E., and Hay, M.E. 2011. Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: invasives eat more and grow more. Biol. Invasions, **13**(4): 945–955. doi:10.1007/s10530-010-9881-x.

Morse, J., Baldridge, A., and Sargent, L. 2013. Invasive crayfish *Orconectes rusticus* (Decapoda, Cambaridae) is a more effective predator of substrate nesting fish eggs than native crayfish (*O. virilis*). Crustaceana, **86**(4): 387–402. doi:10.1163/15685403-00003187.

Mundahl, N.D., and Benton, M.J. 1990. Aspects of the thermal ecology of the rusty crayfish *Orconectes rusticus* (Girard). Oecologia, **82**(2): 210–216. doi:10.1007/bf00323537.

Olden, J.D., McCarthy, J.M., Maxted, J.T., Fetzer, W.W., and Vander Zanden, M.J. 2006. The rapid spread of rusty crayfish (*Orconectes rusticus*) with observations on native crayfish declines in Wisconsin (U.S.A.) over the past 130 years. Biol. Invasions, **8**(8): 1621–1628. doi:10.1007/s10530-005-7854-2.

Olsson, K., and Nyström, P. 2009. Non-interactive effects of habitat complexity and adult crayfish on survival and growth of juvenile crayfish (*Pacifastacus leniusculus*). Freshw. Biol. **54**(1): 35–46. doi:10.1111/j.1365-2427.2008.02089.x.

Osmond, M.M., Barbour, M.A., Bernhardt, J.R., Pennell, M.W., Sunday, J.M., and O'Connor, M.I. 2017. Warming-induced changes to body size stabilize consumer-resource dynamics. Am. Nat. **189**(6): 718–725. doi:10.1086/691387.

Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford, S., Murdock, C.C., and Thomas, M. B. 2013. Temperature variation makes ectotherms more sensitive to climate change. Global Change Biol. **19**(8): 2373–2380. doi:10.1111/gcb.12240.

Perry, W.L., Feder, J.L., Dwyer, G., and Lodge, D.M. 2001. Hybrid zone dynamics and species replacement between *Orconectes* crayfishes in a northern Wisconsin lake. Evolution. **55**(6): 1153. doi:10.1554/0014-3820(2001)055[1153:hzdasr]2.0.co;2.

Peters, J. A., Cooper, M.J., Creque, S.M., Kornis, M.S., Maxted, J.T., Perry, W.L., et al. 2014. Historical changes and current status of crayfish diversity and distribution in the Laurentian Great Lakes. J. Great Lakes Res. **40**(1): 35–46. doi:10.1016/j.jglr.2014.01.003.

Piccolroaz, S., Toffolon, M., and Majone, B. 2013. A simple lumped model to convert air temperature into surface water temperature in lakes. Hydrol. Earth Syst. Sci. **17**(8): 3323–3338. doi:10.5194/hess-17-3323-2013.

Pintor, L.M., Sih, A., and Bauer, M.L. 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. Oikos, **117**: 1629–1636. doi:10.1111/j.0030-1299.2008.16578.x.

Pritchard, D.W., Paterson, R.A., Bovy, H.C., and Barrios-O'Neill, D. 2017. Frair: an R package for fitting and comparing consumer functional responses. Methods Ecol. Evol. **8**(11): 1528–1534. doi:10.1111/2041-210x.12784.

Rahel, F.J., and Olden, J.D. 2008. Assessing the effects of climate change on aquatic invasive species. Conserv. Biol. **22**(3): 521–533. doi:10.1111/j.1523-1739.2008.00950.x.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., and Petchey, O. L. 2012. Universal temperature and body-mass scaling of feeding rates. Philos. Trans. R. Soc., B. **367**(1605): 2923–2934. doi:10.1098/rstb.2012.0242.

Rehage, J.S., Barnett, B.K., and Sih, A. 2005. Foraging behaviour and invasiveness: Do invasive *Gambusia* exhibit higher feeding rates and broader diets than their noninvasive relatives? Ecol. Freshw. Fish, **14**(4): 352–360. doi:10.1111/j.1600-0633.2005.00109.x.

Reid, S., and Nocera, J. 2015. Composition of native crayfish assemblages in southern Ontario rivers affected by rusty crayfish (*Orconectes rusticus* Girard, 1852) invasions—implications for endangered queensnake recovery. Aquat. Invasions, **10**(2): 189–198. doi:10.3391/ai.2015.10.2.07.

Ricciardi, A., Hoopes, M.F., Marchetti, M.P., and Lockwood, J.L. 2013. Progress toward understanding the ecological impacts of nonnative species. Ecol. Monogr. **83**(3): 263–282. doi:10.1890/13-0183.1.

Ricciardi, A., Iacarella, J.C., Aldridge, D.C., Blackburn, T.M., Carlton, J.T., Catford, J.A., et al. 2021. Four priority areas to advance invasion science in the face of rapid environmental change. Environ. Rev. **29**: 119–141. doi:10.1139/er-2020-0088.

Rogers, D. 1972. Random search and insect population models. J. Anim. Ecol. **41**(2): 369. doi:10.2307/3474.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Sharma, S., Jackson, D.A., Minns, C.K., and Shuter, B.J. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biol. **13**(10): 2052–2064. doi:10.1111/j.1365-2486.2007.01426.x.

South, J., Dick, J.T.A., McCard, M., Barrios-O'Neill, D., and Anton, A. 2017. Predicting predatory impact of juvenile invasive lionfish (*Pterois volitans*) on a crustacean prey using functional response analysis: effects of temperature, habitat complexity and light regimes. Environ. Biol. Fishes, **100**(10): 1155–1165. doi:10.1007/s10641-017-0633-y.

South, J., Welsh, D., Anton, A., Sigwart, J.D., and Dick, J.T.A. 2018. Increasing temperature decreases the predatory effect of the intertidal shanny *Lipophrys pholison* on an amphipod prey. J. Fish Biol. **92**(1): 150–164. doi:10.1111/jfb.13500.

South, J., McCard, M., Khosa, D., Mofu, L., Madzivanzira, T.C., Dick, J.T.A., and Weyl, O.L.F. 2019. The effect of prey identity and substrate type on the functional response of a globally invasive crayfish. NeoBiota, **52**: 9–24. doi:10.3897/neobiota.52.39245.

Statistics Canada. 2011. Water File—Lakes and Rivers (polygons) - 2011 Census [dataset]. Open Government Canada. ef70dc3b-1069-4037-9bce-61f47e628a1d. Available from https://open.canada.ca/data/en/dataset/ef70dc3b-1069-4037-9bce-61f47e628a1d [accessed March 2023].

Statistics Canada. 2021. 2021 Census—Boundary files [dataset]. Open Government Canada. 448ec403-6635-456b-8ced-d3ac24143add. Available from https://open.canada.ca/data/en/dataset/448ec403-6635-456b-8ced-d3ac24143add [accessed March 2023].

Strayer, D.L., Eviner, V.T., Jeschke, J.M., and Pace, M.L. 2006. Understanding the long-term effects of species invasions. Trends Ecol. Evol. **21**(11): 645–651. doi:10.1016/j.tree.2006.07.007.

Taylor, C.A., and Redmer, M. 1996. Dispersal of the crayfish *Orconectes rusticus* in Illinois, with notes on species displacement and habitat preference. J. Crustac. Biol. **16**(3): 547. doi:10.2307/1548745.

Tricarico, E., and Aquiloni, L. 2016. How behaviour has helped invasive crayfish to conquer freshwater ecosystems. *In* Biological invasions and animal behaviour. *Edited by* J. Weis and D. Sol. Cambridge University Press, Cambridge. pp. 291–308. doi:10.1017/CBO9781139939492.017.

Tripp, N.K., Kabalan, B.A., Stoeckel, J., and Reisinger, L.S. 2022. Metabolic rates of a widely distributed crayfish shift along a latitudinal gradient. Hydrobiologia, **849**(16): 3565–3579. doi:10.1007/s10750-022-04961-2.

Trumpickas, J., Shuter, B.J., and Minns, C.K. 2009. Forecasting impacts of climate change on Great Lakes surface water temperatures. J. Great Lakes Res. **35**(3): 454–463. doi:10.1016/j.jglr.2009.04.005.

Trumpickas, J., Shuter, B.J., Minns, C.K., and Cyr, H. 2015. Characterizing patterns of nearshore water temperature variation in the North American Great Lakes and assessing sensitivities to climate change. J. Great Lakes Res. **41**: 53–64. doi:10.1016/j.jglr.2014.11.024.

Uiterwaal, S.F., and DeLong, J.P. 2020. Functional responses are maximized at intermediate temperatures. Ecology, **101**(4): e02975. doi:10.1002/ecy.2975.

United States Census Bureau. 2019. Cartographic Boundary Files—States [dataset]. Available from https://www.census.gov/geographies/mapping-files/time-series/geo/cartographic-boundary.2019.html#list-tab-1883739534 [accessed March 2023].

U.S. Geological Survey. 2022. USGS National Hydrography Dataset Plus High Resolution (NHDPlus HR) for Hydrological Unit (HU) 4 - 0108 (published 20220324) FileGDB. ScienceBase. Available from https://www.sciencebase.gov/catalog/item/5d30c266e4b01d82ce84a919 [accessed March 2023].

Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., et al. 2009. Alien species in a warmer world: risks and opportunities. Trends Ecol. Evol. **24**: 686–693. doi:10.1016/j.tree.2009.06.008.

Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H., and Weyl, O.L.F. 2016a. Using functional responses to quantify interaction effects among predators. Funct. Ecol., **30**(12): 1988–1998. doi:10.1111/1365-2435.12682.

Wasserman, R.J., Alexander, M.E., Weyl, O.L.F., Barrios-O'Neill, D., Froneman, P. W., and Dalu, T. 2016b. Emergent effects of structural complexity and temperature on predator–prey interactions. Ecosphere, **7**(2): e01239. doi:10.1002/ecs2.1239.

Whitledge, G.W., and Rabeni, C.F. 2002. Maximum daily consumption and respiration rates at four temperatures for five species of crayfish from Missouri, U.S.A. (Decapoda, Orconectes spp.). Crustaceana, **75**(9): 1119–1132. doi:10.1163/156854002763270518.

Woodward, G., Perkins, D.M., and Brown, L.E. 2010. Climate change and freshwater ecosystems: Impacts across multiple levels of organization. Philos. Trans. R. Soc., B. **365**(1549): 2093–2106. doi:10.1098/rstb.2010.0055.

Závorka, L., Koeck, B., Cucherousset, J., Brijs, J., Näslund, J., Aldvén, D., et al. 2017. Co-existence with non-native brook trout breaks down the integration of phenotypic traits in brown trout parr. Funct. Ecol. **31**(8): 1582–1591. doi:10.1111/1365-2435.12862.