Canadian Journal of
Fisheries and
Aquatic Sciences

Research Article

Influence of warming on the functional responses of invasive omnivores, *Procambarus* crayfishes

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Abstract

The red swamp crayfish (*Procambarus clarkii*) and the marbled crayfish (*Procambarus virginalis*) are congeneric invasive species whose potential impacts in the Great Lakes basin have generated concern. In laboratory experiments, we tested the functional responses of these omnivores to two common food resources, insect larvae (*Chironomus* bloodworms) and aquatic macrophytes (Eurasian milfoil *Myriophyllum spicatum*), to gain predictive information on their per *capita* effects under present (18 °C) and projected future (26 °C) climate scenarios for the basin. The maximum feeding rate of *Procambarus virginalis* was higher at 18 °C than at 26 °C when presented with bloodworms but did not differ between temperatures when presented with macrophytes. By contrast, the feeding rate of *Procambarus clarkii* did not change with temperature for either food resource. Due to their larger mean size, *Procambarus clarkii* exhibited higher rates of resource (bloodworm and macrophyte) consumption than *Procambarus virginalis* at both temperatures. These results suggest that trophic impacts of *Procambarus virginalis* will dampen with increased warming, whereas *Procambarus clarkii* will sustain larger impacts irrespective of temperature within the range tested.

Key words: biological invasion, crustaceans, ecological impact, feeding behaviour, invasive species, thermal ecology

Introduction

A key trait associated with ecologically disruptive invasive species is a high resource consumption efficiency (Morrison and Hay 2011; Ricciardi et al. 2013), which mediates their interspecific competitive interactions, alters their trophic linkages, and allows them to rapidly attain large population sizes. Resource consumption and other per *capita* effects of invading species vary with local biotic and abiotic conditions (Ricciardi et al. 2013; Dalal et al. 2021; Dickey et al. 2021). As environmental conditions approach the physiological optimum of an invader, its impacts on communities and food webs are predicted to be greater (the Environmental Matching Hypothesis; Ricciardi et al. 2013; Iacarella et al. 2015). This prediction is supported by a growing literature on the temperature dependence of feeding behaviour, which finds the relationships between temperature and functional response parameters (attack rates and handling times) to be unimodal in general (Englund et al. 2011). Temperature shifts linked to climate warming could thus dramatically change the impacts of invasive species.

Invasive omnivores including crayfish can alter ecosystems through their consumptive effects on the population size, biomass, and taxonomic composition of benthic invertebrates, macrophytes, periphyton, and detritus (Olsen et al. 1991; Correia 2002; Carreira et al. 2014; Jackson et al. 2017). Crayfish adapt quickly to novel prey (Tricarico and Aquiloni 2016) and, through direct consumption, can significantly reduce invertebrate, amphibian, and fish populations in their invaded ranges (Dorn and Wojdak 2004; Tricarico and Aquiloni 2016). They can also act as shredders (sensu Cummins et al. 1989) by feeding on coarse particulate organic matter and expediting its microbial breakdown (Correia 2002; Alcorlo et al. 2004; Lipták et al. 2019; Linzmaier et al. 2020). Such activities directly affect the composition and abundance of aquatic macrophytes (Smart et al. 2002; Carreira et al. 2014). For example, the disappearance of native floating-leaved and submerged plants in Lake Naivasha, Kenya, is attributed to a red swamp crayfish *Procambarus clarkii* invasion (Smart et al. 2002).

Procambarus crayfishes as model invasive omnivores

The red swamp crayfish (*Procambarus clarkii*) and the marbled crayfish *Procambarus virginalis* are warm-adapted omnivores that pose ongoing invasion risks to the Great Lakes basin (Hamr 2021). Native to the southern United States, *Procambarus clarkii* began invading the lower Great Lakes by the late 1960s (Peters et al. 2014). Elsewhere, it has established non-native populations on all continents except Antarctica and Australia (Oficialdegui et al. 2020). Owing to its recent population expansions and widespread use as live bait, there is a burgeoning risk of *Procambarus clarkii* invasion in eastern North America (Egly et al. 2019). The recorded impacts of *Procambarus clarkii* are numerous and transmit beyond freshwater environments (Gherardi 2006). In addition to its

burrowing behaviour, which can re-engineer physical habitat (Correia and Ferreira 1995; Souty-Grosset et al. 2016), the generalist feeding activities of *Procambarus clarkii* can cause rapid declines in abundance of macroinvertebrates, macrophytes, amphibians, and waterfowl (Correia 2002; Rodríguez et al. 2005; Carreira et al. 2014).

Procambarus virginalis is a much more recent invader in North America (Hamr 2023), yet its invaded range already includes Asia (Kawai and Takahata 2010), Africa (Jones et al. 2009), and Europe—where it has recently undergone a dramatic expansion (Ercoli et al. 2019; Grandjean et al. 2021; Sanna et al. 2021; Scheers et al. 2021). It was first discovered in the German aquarium trade as a parthenogenetic lineage of the American Slough crayfish *Procambarus fallax* (Scholtz et al. 2003) and its self-cloning ability arose following a mutation that rendered it triploid. To date, it has few documented impacts in its invaded range. Some analyses suggest that *Procambarus virginalis* is a generalist feeder like *Procambarus clarkii* (Lipták et al. 2019; Linzmaier et al. 2020; Muuga 2021). In some areas of Europe, it has been shown to rely heavily on arthropod prey (Linzmaier et al. 2020), whereas elsewhere it feeds primarily on algae and detritus (Lipták et al. 2019). The diet of an emerging invader is highly relevant to risk assessment because invasive generalist consumers can create significant trophic disruptions in the absence of sufficient biotic and abiotic constraints (Ricciardi et al. 2013).

Recognizing that crayfish are good model organisms for studying the impacts of invasive omnivores on freshwater ecosystems (e.g., Granados et al. 2019), we conducted a series of feeding experiments that tested the relative abilities of marbled and red swamp crayfishes to exploit insect larvae (bloodworms) and aquatic macrophytes at current and future mean surface water temperatures. We use this information to inform how these species' per *capita* effects could change with increasing temperatures in nearshore areas of the lower Great Lakes. Specifically, we tested the prediction that *Procambarus clarkii* and *Procambarus virginalis*, both presumably warm-adapted invaders, will have higher maximum feeding rates at higher temperatures for both resources.

Methods

Animal and macrophyte collection and care

Crayfish were sourced from local pet breeders, with 24 and 30 adult individuals acquired for *Procambarus clarkii* and *Procambarus virginalis*, respectively. Thus, the individuals were not adapted to wild conditions and species were not sized-matched, owing to stock availabilities (Table S1). However, as these species would most likely be introduced into the wild through pet release (Chucholl and Wendler 2017), the sizes used here are representative of potentially released individuals.

For the duration of the trials, the animals were held in a climate-controlled chamber. Recognizing that crayfish are habitually nocturnal (Larson and Olden 2016), their chambers were kept on a reversal of their usual 12:12 day:night cycle, with light provided during the night from 20:00 to 08:00, to ensure peak activity during experiments. Furthermore, as they are territorial and aggressive (Tricarico and Aquiloni 2016), individuals were kept in separate holding tanks provided with a shelter (a PVC cylinder) to reduce stress. Tanks were aerated using aquarium pumps and air stones. Each crayfish was fed two sinking shrimp pellets (Wardley, USA) every 2 days. To maintain water quality, 75% water changes were done weekly (Linzmaier and Jeschke 2020). Crayfish were initially kept at 18 °C for 2 weeks while they acclimated to the laboratory environment (Whitledge and Rabeni 2002). For the warm temperature treatment, temperature was increased by 1 °C per day until it reached 26 °C. Crayfish were left to acclimate to this new temperature for 1 month and kept at this temperature for the entirety of the experiment.

Macrophytes used in these experiments were Eurasian watermilfoil (*Myriophyllum spicatum*) collected from established non-native populations in a lake (Lac Hertel, Mont St-Hilaire QC; 45°32′39.8″N 73°08′47.8″W) and an artificial boating canal (Parc Jean-Drapeau, Montreal; 45°30′28.3″N 73°31′36.1″W). After being brought into the lab, the macrophytes were stripped of their leaves, blotted dry, cut into individual segments of 5 cm, and then immediately frozen for future use. A pilot study indicated that both crayfishes fed upon both thawed leaf-less and fresh macrophyte segments with leaves at similar rates.

Comparative functional response experiments

Functional response experiments were conducted at two different temperatures: 18 °C, which is within the range of current mean maximum nearshore surface water temperatures in the lower Great Lakes, and 26 °C, within the range of mean maximum surface water temperatures projected for nearshore areas of lakes Erie and Ontario in the coming decades (Trumpickas et al. 2009, 2015).

Crayfish were randomly chosen from those that had neither molted nor were gravid for a minimum of 1 week prior, owing to severely reduced feeding rates of gravid females (Little 1976; Mathews 2011; Sheppard et al. 2023) and of individuals during ecdysis (Linzmaier and Jeschke 2020). Crayfish were size-matched between temperatures, but not between trials as no comparison can be made between feeding rates of different food resources (Table S1). Experiments were run on days the crayfish were supposed to be fed instead of usual feeding protocols, to standardize hunger levels in individuals (Grimm et al. 2020; Chicatun et al. 2024). Experimental tanks (24 H × 37 W × 60 L cm) were filled with 20 L of water until the water line went just above the shelters. The chosen crayfish were then moved from their holding tanks to experimental tanks 1hr prior to experiments (Grimm et al. 2020).

In the first set of trials, crayfish were offered varying densities of bloodworms—i.e., *Chironomus* sp. (Chironomidae) larvae (Hikari, Japan). Bloodworms were stored in a freezer and were thawed prior to being introduced to experimental tanks. Using previously frozen bloodworms allows for large numbers of promptly available food items that are readily consumed by crayfish (Carreira et al. 2017; Guo et al. 2017; Laverty et al. 2017). Densities of 5, 15, 25, 50, 100, 140, 160, 180, and 300 bloodworms were selected for use in these

trials, based on pilot studies and previous work (Chicatun et al. 2024). The maximum density (300) was provided only to *Procambarus clarkii*, as our pilot studies showed that they would consume significantly more than *Procambarus virginalis*. Experimental crayfish were allowed to feed for 3 h in the dark, after which they were removed from the tank and the remaining bloodworms were counted (South et al. 2019; Linzmaier and Jeschke 2020; Madzivanzira et al. 2021). Although resource replenishment might have been ideal, allowing for resource depletion is a common practice in functional response experiments (Juliano 2001; Médoc et al. 2018; Grimm et al. 2020; Linzmaier and Jeschke 2020; Dickey et al. 2021; Madzivanzira et al. 2021) as it reduces predator disturbance and can be accounted for later in the analysis with more complex model equations (Juliano 2001). This procedure was replicated eight times for each density. Trials were completed in a randomised order; animals were used more than once, but always at different densities. Re-used experimental crayfish were given 5 days of recovery prior to their use in a new trial (Rosewarne et al. 2016; South et al. 2019; Chicatun et al. 2024).

After our first set of trials, the same crayfish were provided with macrophyte segments following a similar protocol to Mu et al. (2019), which were defrosted, blotted dry, and weighed, prior to being introduced to the experimental tanks. During this second set of trials, experiments were run identically to bloodworm experiments with respect to design, temperature treatments, and replicate numbers. Crayfish were offered macrophyte segments of varying densities (5.49 ± 0.56, 9.84 ± 0.20, 14.91 ± 0.21, 19.23 ± 0.23, 24.26 ± 0.10, 29.64 ± 0.38, 39.84 ± 0.27, and 48.84 ± 0.40 mg) as a food resource. Crayfish were allowed to consume the macrophyte segments for 3 h, after which all remaining fragments were removed, measured, blotted dry, and weighed again. Macrophyte weight data were converted to milligrams to ensure we had whole numbers for the analysis.

Statistical analysis of functional responses

Statistical analyses were conducted using R (version 4.1.2) and the FRAIR package (Pritchard et al. 2017*a*, 2017*b*). To select the best model type, we used Juliano's method (*frair_test*) as outlined by Pritchard et al. (2017*b*) and following previous studies that similarly favoured it (e.g., Guo et al. 2017; Chucholl and Chucholl 2021; Dalal et al. 2021). Juliano's method fits a polynomial logistic function to proportional consumption data to determine functional response type (Table S2): if the first order term is negative, it indicates a Type II response (Pritchard et al. 2017*b*). Data were then fit with Rogers' Type II random predator equation or Hassell's Type III, which account for resource depletion (Juliano 2001; Pritchard et al. 2017*b*). From this fitted equation, we can extract attack rates (a), handling times (h), and maximum feeding rates ($1/h$). Our shorter trial times may have caused our attack rates and maximum feeding rates to be overestimated; however, curve types remained unaffected (Alexander et al. 2012). From the estimated parameters we can then compare each curve using (1) *frair_compare* which applies a difference test using maximum likelihood estimations, and (2) bootstrapping the fits using *frair_boot* ($n = 999$) which uses a non-parametric bootstrapping to generate 95% confidence intervals (CIs) of each functional response.

Analysis of macrophyte feeding propensity

For each trial between 20% and 50% of macrophyte feeding trials resulted in no consumption of macrophyte segments (zero counts) and these were dropped from our functional response analyses to avoid an underestimation of the maximum feeding rate. A logit model was then used to compare the binomial measure of untouched or consumed macrophytes. Consumption was modelled in relation to fixed effects of initial macrophyte density, species, temperature, and the interaction between these last two treatments, as well as the random effect of crayfish individual to compensate for the difference between individual crayfish.

Results

All functional responses fitted from the trials were Type II, as clearly indicated by the negative first order term (Figs. 1 and 2; Tables 1 and 3).

Bloodworm trials

Our results suggest that an elevated temperature had a greater effect on *Procambarus virginalis*, which exhibited higher handling times and attack rates at 26 °C than at 18 °C (Fig. 1). By contrast, *Procambarus clarkii* showed no difference in handling times at both temperatures; only its attack rates were higher at 18 °C (Fig. 1; Tables 1 and 2). As expected, *Procambarus clarkii* had lower handling times (and thus a higher maximum feeding rate) than *Procambarus virginalis* at both temperatures (Tables 1 and 2). However, attack rates for *Procambarus clarkii* were higher than *Procambarus virginalis* at 18 °C, whereas the converse was true at 26 °C.

Macrophyte trials

Temperature had no apparent effect on *Procambarus virginalis* attack rates or handling times when consuming macrophyte detritus (Tables 3 and 4). However, the propensity to consume macrophytes was higher at 26 °C than at 18 °C for *Procambarus virginalis* (logit model, $p = 0.016$), whereas it remained the same at both temperatures for *Procambarus clarkii* (logit model, $p = 0.28$). Handling times of *Procambarus clarkii* did not differ between the two temperatures, but its attack rates were higher at 18 °C (Tables 3 and 4). Owing to its lower handling times, *Procambarus clarkii* consumed macrophytes at a greater rate than *Procambarus virginalis* at 18 °C.

Discussion

Temperature influenced the functional responses of crayfishes differently between consumer species and between animal and plant resources. Given that *Procambarus* species are presumably adapted to warmer temperatures—as indicated by a reported growth optimum in the range of 20–30 °C; Ackefors 1999; Seitz et al. 2005), we expected their

Fig. 1. Functional responses with bootstrapped 95% confidence intervals (shaded regions) for *Procambarus virginalis* crayfish and *Procambarus clarkii* at 18 °C (green) and 26 °C (purple) when presented with bloodworms. Lines represent the best fit model (Type II) for each population.

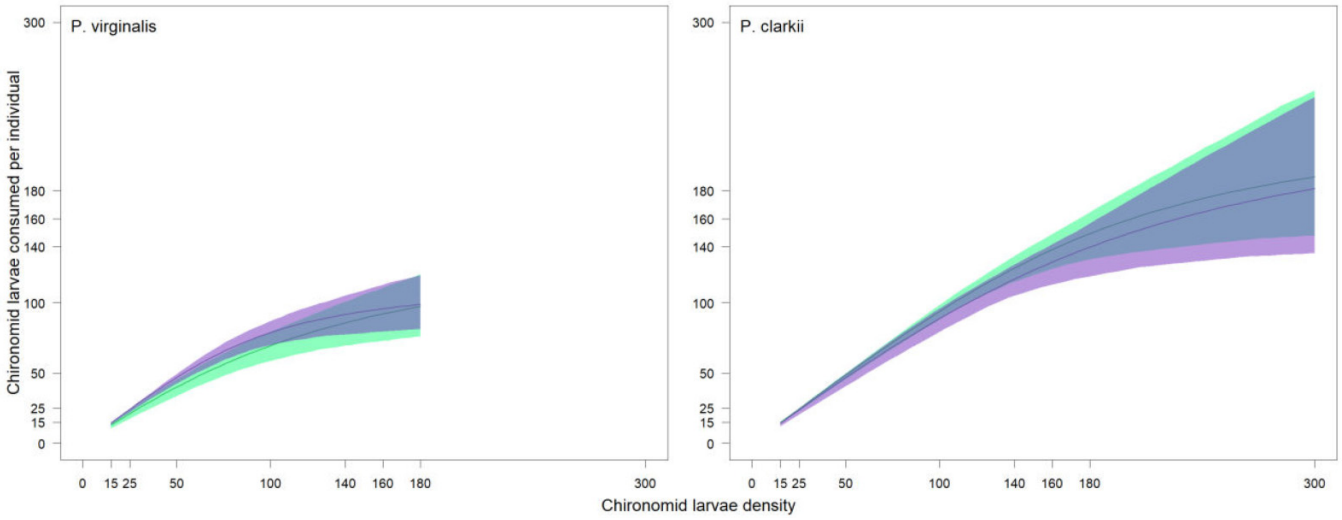

Fig. 2. Functional responses with bootstrapped 95% confidence intervals (shaded regions) for *Procambarus virginalis* crayfish and *Procambarus clarkii* at 18 °C (green) and 26 °C (purple), when presented with macrophytes. Lines represent the best fit model (Type II) for each population.

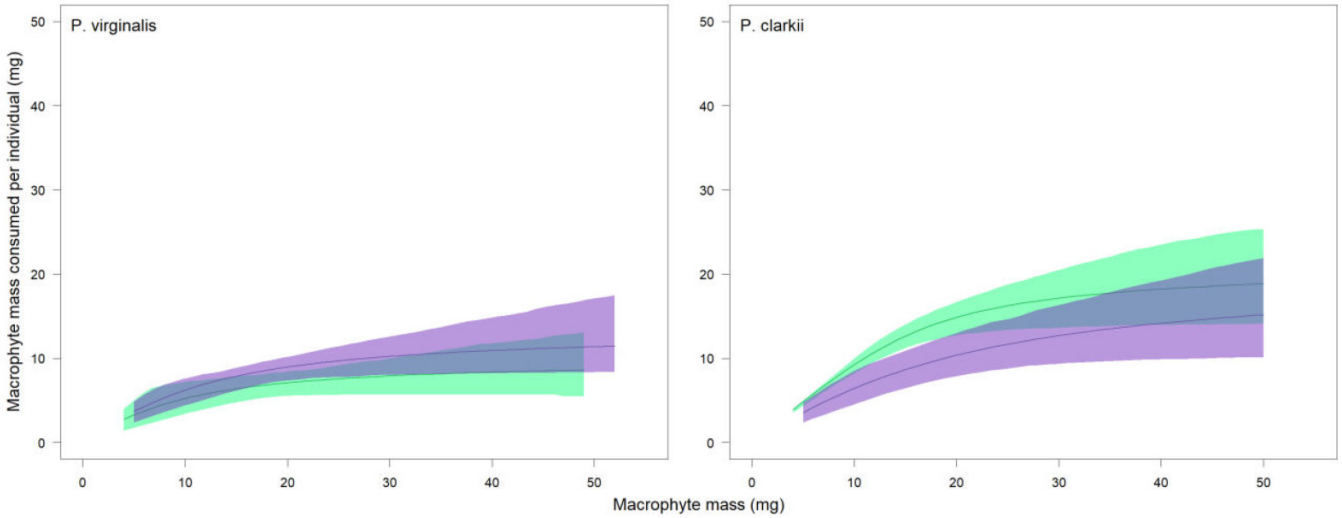

Table 1. Fitted coefficients and curve types for each *Procambarus virginalis* and *Procambarus clarkii* functional responses at both temperatures for bloodworms.

Fit	Type	First-order term		*a*		*h*	1/*h*	*a*/*h*
P. virginalis 18 °C	II	−0.011	0.73	(0.39; 1.25)	0.02	(0.005; 0.03)	50	36.7
P. virginalis 26 °C	II	−0.017	1.51	(0.86; 2.69)	0.025	(0.015; 0.032)	40	60.48
P. clarkii 18 °C	II	−0.012	1.53	(0.91; 3.22)	0.012	(0.006; 0.019)	83.33	127.58
P. clarkii 26 °C	II	−0.0073	1.14	(0.57; 2.09)	0.012	(0; 0.02)	83.33	94.67

consumption rates would be higher at 26 °C; but this was not the case for either species. These results appear to contradict the Environmental Matching Hypothesis (Iacarella et al. 2015), which predicts greater consumer performance at temperatures closer to the growth optimum of the species. For *Procambarus virginalis*, only attack rates followed the predicted trend. As observed elsewhere, functional responses can vary across conspecific populations (Grimm et al. 2020), and attack rates can have steeper bell-shaped responses to temperatures than handling times or different optimal temperatures

Table 2. Results from *frair_compare*, a difference test of the attack rates (*a*) and handling time (*h*) between the fitted *Procambarus virginalis* and *Procambarus clarkii* functional responses at both temperatures for bloodworms.

Fit 1	Fit 2	Parameter	Estimate	Std. error	*p*-value	
P. virginalis 18 °C	*P. virginalis* 26 °C	Δa	− 0.78	0.10	<0.001	***
		Δh	− 0.0052	0.0011	<0.001	***
P. clarkii 18 °C	*P. clarkii* 26 °C	Δa	0.39	0.074	<0.001	***
		Δh	0.00033	0.00053	0.54	
P. virginalis 18 °C	*P. clarkii* 18 °C	Δa	− 0.80	0.068	<0.001	***
		Δh	0.0075	0.00096	<0.001	***
P. virginalis 26 °C	*P. clarkii* 26 °C	Δa	0.38	0.11	0.00041	***
		Δh	0.013	0.00078	<0.001	***

Note: Asterisks denote significant *p*-values (*** < 0.001).

Table 3. Fitted coefficients and curve types for each *Procambarus virginalis* and *Procambarus clarkii* functional responses at both temperatures for macrophytes.

Fit	Type	First-order term	*a*		*h*		1/*h*	*a*/*h*
P. virginalis 18 °C	II	− 0.043	0.53	(0.16; 34.59)	0.31	(0.079; 0.50)	3.27	1.73
P. virginalis 26 °C	II	− 0.035	0.62	(0.24; 2.89)	0.23	(0.07; 0.35)	4.4	2.71
P. clarkii 18 °C	II	− 0.07	1.55	(0.73; 4.58)	0.14	(0.081; 0.20)	6.99	10.86
P. clarkii 26 °C	II	− 0.041	0.51	(0.22; 1.46)	0.15	(0.046; 0.27)	6.63	3.37

Table 4. Results from *frair_compare*, a difference test of the attack rates (*a*) and handling time (*h*) between the fitted *Procambarus virginalis* and *Procambarus clarkii* functional responses at both temperatures for macrophytes.

Fit 1	Fit 2	Parameter	Estimate	Std. error	*p*-value	
P. virginalis 18 °C	*P. virginalis* 26 °C	Δa	− 0.087	0.29	0.77	
		Δh	0.079	0.057	0.17	
P. clarkii 18 °C	*P. clarkii* 26 °C	Δa	1.046	0.26	<0.001	***
		Δh	− 0.0079	0.022	0.72	
P. virginalis 18 °C	*P. clarkii* 18 °C	Δa	− 1.025	0.35	0.0034	**
		Δh	0.16	0.053	0.0019	**
P. virginalis 26 °C	*P. clarkii* 26 °C	Δa	0.11	0.18	0.55	
		Δh	0.076	0.031	0.015	*

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

altogether (Englund et al. 2011; Rall et al. 2012; Archer et al. 2019; Uiterwaal and DeLong 2020). Therefore, optimal temperature ranges of growth might not predict higher maximum feeding rates for crayfish, unlike what has been observed in other aquatic ectotherms (Iacarella et al. 2015). It is worth noting, however, that as our study spanned only two temperatures, a wider range of temperatures might have yielded more information on how optimal temperatures affect resource consumption.

Effect of temperature on prey-switching

Studying the effect of resource type on the performance of *Procambarus clarkii* during simulated heat waves, Carreira et al. (2017) found that carnivorous diets reduced survival and growth rates of crayfish under higher temperatures. Carreira et al. (2017) observed increased consumption of macrophyte-based diets (either solely macrophytes or macrophytes mixed with bloodworms), and improved adult survival, in spite of higher energetic demands under warmer temperatures. This suggested resource preference could be strongly linked to temperature; however, feeding rates of *Procambarus clarkii* on both bloodworms and macrophytes were unaffected by temperature, in spite of increased energetic demands of warmer temperatures in general and the higher treatment temperature being closer to its reported optimal range for growth (21–27 °C; Ackefors 1999). Although heightened metabolism and energetic demands are provoked by increased temperatures (Hochachka and Somero 2014), metabolic performance is also mediated by acclimation time. Sentis et al. (2022) found that a 24 h acclimation period was sufficient to increase *Procambarus virginalis*' handling times and attack rates when moved from 20 to 16 °C but had the opposite effect when moved from 20 to 24 °C. As such, we used a longer pre-trial acclimation period than Carreira et al. (2017), which might have reduced the difference in feeding between temperatures.

Implications for risk assessment

Maximum feeding rates were higher for *Procambarus clarkii* than for *Procambarus*, at both temperatures and for both resource types, likely owing to *Procambarus clarkii*'s larger mean body size in our trials (Table S1). Nevertheless, our design still allowed for field-relevant comparisons of the foraging efficiencies of each species as these sizes reflect the larger sizes *Procambarus clarkii* attain in the wild (Kouba et al. 2021). This study attempted to compare these species physiologically, recognising that size matching ignores interspecific differences, to better compare per *capita* effects in established populations. Compared with *Procambarus virginalis*, consumption of bloodworms by *Procambarus clarkii* was 1.67 times higher at 18 °C and 2.08 times higher at 26 °C, whereas its consumption of macrophytes was 2.14 times higher at 18 °C and 1.51 times higher at 26 °C. Consumption rates may have been further amplified by the lack of motility of our food sources; however, because live bloodworms are minimally motile, defrosted individuals are arguably a reasonable substitution.

Both *Procambarus clarkii* and *Procambarus virginalis* are very common pet species and, therefore, at high risk of being widely introduced (Chucholl 2013; Faulkes 2015). Owing to its increased popularity in the North American pet trade (Faulkes 2015) and parthenogenetic ability, *Procambarus virginalis* is perhaps subject to more release events, rapid population growth, and higher field densities. This is relevant to their potential field impact, which is a function of their population abundance and per *capita* effect (Parker et al. 1999). Documented information on field abundances is sparser for *Procambarus virginalis* than for *Procambarus clarkii*, whereas fecundity is better studied. Vogt (2021) found that while, on average, *Procambarus virginalis* produces 40% more pleopodal eggs than equal-sized *Procambarus clarkii*, the latter grows faster and attains a larger body size—thus generating larger clutch sizes than *Procambarus virginalis*. However, owing to its self-cloning ability, *Procambarus virginalis* could be gravid far more frequently than *Procambarus clarkii*, as we have observed in a rapid succession of reproductive events during our experiments. Without more available information on abundances of these congeneric species in their invaded ranges, as well as on the abiotic and biotic constraints on their population growth, differences in the potential trophic impacts as inferred from their functional responses remain speculative. Future research might also consider the trade-offs between the thermal ecology of extreme increases in water temperatures, higher predation risks in deeper waters and the temperature-driven food preferences (i.e., potential shifts towards temperature refugia in macrophyte-reduced deeper waters as shallow nearshore waters heat up).

More broadly, plant-based functional responses should be considered when designing experiments to predict the trophic impacts of omnivorous predators. Omitting consideration of omnivory from these types of experiments can limit impact prediction. The effects of temperature acclimation time on metabolic activity and predatory performance in crayfish also requires further investigation. Though heat waves may have strong impacts on food preferences, temperature adaptation may lead to contradictory results. Risk assessments must consider how temperature exposure and acclimation affect resource preference, particularly for emerging invasion threats like *Procambarus virginalis*, whose feeding preferences and trophic ecology remain understudied.

Acknowledgements

The authors thank Jessie Ye and Jennifer Pham for assistance in caring for crayfish used in these experiments.

Article information

History dates

Received: 25 October 2024
Accepted: 28 February 2025
Accepted manuscript online: 13 March 2025
Version of record online: 4 April 2025

Data availability

Available on Dryad (https://doi.org/10.5061/dryad.12jm63z89).

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Competing interests

The authors declare no competing interests.

Funding information

Financial support was provided by Fisheries and Oceans Canada (Grant #007-00397) and the Natural Sciences and Engineering Research Council of Canada (NSERC RGPIN-2022-03235).

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0334.

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