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ORIGINAL PAPER

When invaders collide: competition, aggression, and predators affect outcomes in overlapping populations of red swamp (*Procambarus clarkii*) and rusty (*Faxonius rusticus*) crayfishes

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Abstract Non-native crayfishes can have large impacts on biodiversity and the provisioning of ecosystem services in freshwaters. In 2015 we discovered an established population of the globally widespread red swamp crayfish (*Procambarus clarkii*) in the North Shore Channel of the Chicago Area Waterway System. This population overlaps with a population of rusty crayfish (*Faxonius rusticus*), a previous invader that is widely distributed and usually the dominant crayfish species across the Great Lakes region. If *P. clarkii* continues to spread in the Great Lakes region it will frequently encounter *F. rusticus*. Factors such as water clarity, competition for food when limited, and susceptibility to predation may alter *P. clarkii*'s ability to become established and spread. We sampled the overlapping populations and found that *P. clarkii* are significantly larger than *F. rusticus*. Next, we conducted lab experiments to examine the outcomes of competition between these species for shelter and food. *F. rusticus* were significantly more likely to seek shelter when threatened, while *P. clarkii* were significantly more likely to respond aggressively. *P. clarkii* won more competitions for food. Finally, we conducted field experiments to investigate rates of predation on each species and found that *P. clarkii* are predated significantly more often. Our results suggest that *P. clarkii* is dominant in interactions with *F. rusticus* but that higher rates of predation, likely occurring because *P. clarkii* is less likely to flee from threats, mitigate these benefits. We suggest that *P. clarkii* will dominate crayfish communities in water with low clarity, but not in clear-water habitats where visual predators are more effective.

Keywords Behavior · Competition · *Faxonius rusticus* · Freshwater · Invasive species · Predation · *Procambarus clarkii* · Species interactions

Introduction

The spread of non-native invasive species is a globally important driver of ecosystem service and biodiversity loss. Freshwater ecosystems are often strongly impacted, with effects including reduced fisheries, reduced water availability for irrigation and municipal use, impeded navigation, and increased habitat for vectors of human disease (Pimental et al. 2005;

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Pejchar and Mooney 2009; Oreska and Aldridge 2011; Keller et al. 2018). Invasive freshwater crayfishes can have particularly large ecological and economic impacts. Crayfishes are the largest invertebrates in many freshwater habitats (Lodge et al. 2000) and often act as ecosystem engineers (Charlebois and Lamberti 1996; Statzner et al. 2000; Creed and Reed 2004). The negative impacts of these species include decreased water quality (Souty-Grosset et al. 2016), altered aquatic macroinvertebrate communities (Wilson et al. 2004), reductions in macrophyte biomass and biodiversity (Lodge et al. 1994; Wilson et al. 2004), and extirpation of native crayfish (Hein et al. 2007; Lodge et al. 2000). Crayfish can also be vectors of disease, including the crayfish plague (*Aphanomyces astaci*), which has been an important agent in the displacement of native European crayfish species by invasive North American species which are immune to the disease (Lodge et al. 2000; Souty-Grosset et al. 2016; Donato et al. 2018).

Much research has been conducted to model the distribution and spatial patterns of non-native freshwater species. This work usually aims to predict future spread of invaders so that such spread can be managed (Clarke Murray et al. 2014). Although models usually predict potential spread as a function of physical factors (e.g., water quality, habitat availability, climate), it is known that interactions between invaders and other species can also be important (Crall et al. 2006; Fletcher 2007; Weis 2010; Behringer and Hart 2017). In particular, previously established species may compete with or predate upon the new arrival, and this can mediate the habitats into which freshwater non-native species can spread (Weis 2010).

The establishment and spread of non-native freshwater crayfishes may be particularly dependent upon their interactions with existing crayfish (Garvey et al. 1994). Crayfish native ranges may not be constrained by just their tolerances of physical factors, but also by their interactions with other species and their ability to access new habitats. When non-native crayfish arrive and spread they often dominate the resulting crayfish community (Garvey et al. 1994). For example, the spread of rusty crayfish (*Faxonius rusticus*; previously *Orconectes rusticus*; Crandall and De Grave 2017) across the U.S. Midwest is associated with massive declines in population sizes of the existing crayfish species, including the native virile crayfish (*Faxonius virilis*), and the northern clear-water crayfish (*Faxonius propinquus*) (Garvey et al. 1994; Olden et al. 2006).

Faxonius rusticus are now widespread and the dominant crayfish across large areas of the Great Lakes region and Midwest (Peters et al. 2014). Likewise, the invasion of Europe by the North American signal crayfish (*Pacifastacus leniusculus*) has caused the widespread decline in native species resulting in communities dominated by the invader (Westman et al. 2002; Dunn et al. 2008). In each of these cases the invader has been shown to be competitively dominant for resources such as food and shelter, and this is presumed to be a main mechanism leading to their success (Gherardi and Daniels 2004).

Procambarus clarkii (red swamp crayfish), native to the southern United States, is a globally widespread invader associated with large ecological and economic impacts (Smart et al. 2002; Yue et al. 2010; Taylor et al. 2015). Non-native populations of this species are established in North America, Africa, Asia, and Europe (Donato et al. 2018; Smith et al. 2018). The invasion of *P. clarkii* in Africa has resulted in the reduction of macrophyte species and damaged shorelines from their burrowing (Smart et al. 2002). In Asia, the species' burrows have led to damaged irrigation systems resulting in poor crop yields and economic losses (Yue et al. 2010). *P. clarkii* can also vector the crayfish plague which is lethal to many other crayfishes and has resulted in biodiversity loss in Europe (Lodge et al. 2000; Donato et al. 2018).

Procambarus clarkii was first recorded in the Great Lakes region in the 1960's in Sandusky Bay in the western portion of Lake Erie (Peters et al. 2014). More recently populations have been found in Michigan and Wisconsin, although the established populations in Wisconsin have likely been eradicated (Wisconsin DNR; Behm 2009; Bunk and Van Egeren 2014). There is concern that this species will continue to spread in the Great Lakes region (Donato et al. 2018), and a recent species distribution model has shown that it has the potential to become established across a far wider area (Egly et al. 2019).

Our work is focused on the Illinois portion of the southern basin of Lake Michigan where *P. clarkii* was first recorded in 2001 (USGS 2019). In 2004 a further record of the species was made in the North Shore Channel of the Chicago Area Waterway system (CAWS; Peters et al. 2014; USGS 2019). Neither of these records was confirmed as being of established populations. In 2015 we confirmed an established population in the North Shore Channel that overlaps with a population of invasive *F. rusticus*, a species that is abundant in the Laurentian Great Lakes region after spreading from the Ohio River drainage (Wilson et al. 2004; Peters and Lodge 2013; Peters et al. 2014). This species has been in the Great Lakes Basin for over 100 years but its spread accelerated in the 1990's (Peters et al. 2014). *F. rusticus* has displaced native crayfish species in multiple waterways throughout the U.S. Midwest (Butler and Stein 1985; Gherardi and Daniels 2004) and has large ecosystem impacts including the alteration of whole lake food-webs (Kreps et al. 2014).

Although sampling data in the region prior to 2015 is limited, the invasion histories of these species make it reasonable to infer that *F. rusticus* was established in the North Shore Channel prior to the arrival of *P. clarkii* (Peters et al. 2014). To the best of our knowledge this is the first example of these two invaders having overlapping populations (Peters et al. 2014). We note that these species may overlap in the Sandusky Bay area of Lake Erie; however, this has not been studied (Peters et al. 2014).

Here, we have made field observations and conducted lab and field experiments to investigate the potential for competition and predation to affect the persistence and spread of *P. clarkii.* We have sampled from the overlapping populations to determine size distributions of each species as this is often an indicator of competitive dominance (Rabeni 1985; Klocker and Strayer 2004). Based on sampling results we designed a series of lab experiments to test for dominance between *P. clarkii* and *F. rusticus* at accessing limited shelter and food. Results suggested that *P. clarkii* are more aggressive and less likely to seek shelter when threatened. We hypothesized that this would expose them to greater predation pressure and tested this in a field experiment that covered different habitats. Our work shows that competitive dominance may be associated with higher risk of predation and indicates that these interactions will likely be important mediators of future spread of these species.

Methods

Trapping

The North Shore Channel of the Chicago Area Waterway System (hereafter: the Channel) is a slow moving canal that was constructed between 1907 and 1910 to connect the North Branch of the Chicago River to Lake Michigan (Fig. 1). Its habitat is homogenous, with a maximum depth of 2.9 m, a consistent width of ∼ 20 m, and almost entirely soft mucky substrate. The Channel connects to Wilmette Harbor in Lake Michigan at its north end, and to the North Branch of the Chicago River at its south end. It was constructed primarily to deliver water from Lake Michigan to the O'Brien Sewage Treatment plant which is located nearby to where the Channel meets the Chicago River. Additionally, during high-flow events the weir at Wilmette Harbor can be opened to allow water to flow into Lake Michigan, reducing flooding throughout the surrounding urban area (Hill 2000).

Crayfish populations in the North Shore Channel, North Branch of the Chicago River, and Wilmette Harbor were surveyed during July and August 2015 at five locations (Fig. 1). Subsequent sampling took place during summers 2016 and 2017. In all cases sampling was conducted using standard minnow traps baited with dry dog food. Traps were modified by increasing the openings to ∼ 5 cm diameter (Capelli and Magnuson 1983). Crayfish are most active at night, and traps were set 1 day and recovered the next. We recorded species, sex, and carapace length (CL; the length from the tip of the rostrum to the posterior end of the carapace) for all crayfish sampled.

A first observation was that we only found the non-native species *F. rusticus* and *P. clarkii*. Populations of these species overlapped, and multiple size classes of both species were found during all 3 years indicating that they are each well established (see below for full sampling results). These observations motivated the competition and predation experiments described in the following.

Competition experiments

To investigate competition between *F. rusticus* and *P. clarkii* for food and shelter, we conducted lab experiments at Loyola University Chicago during August–

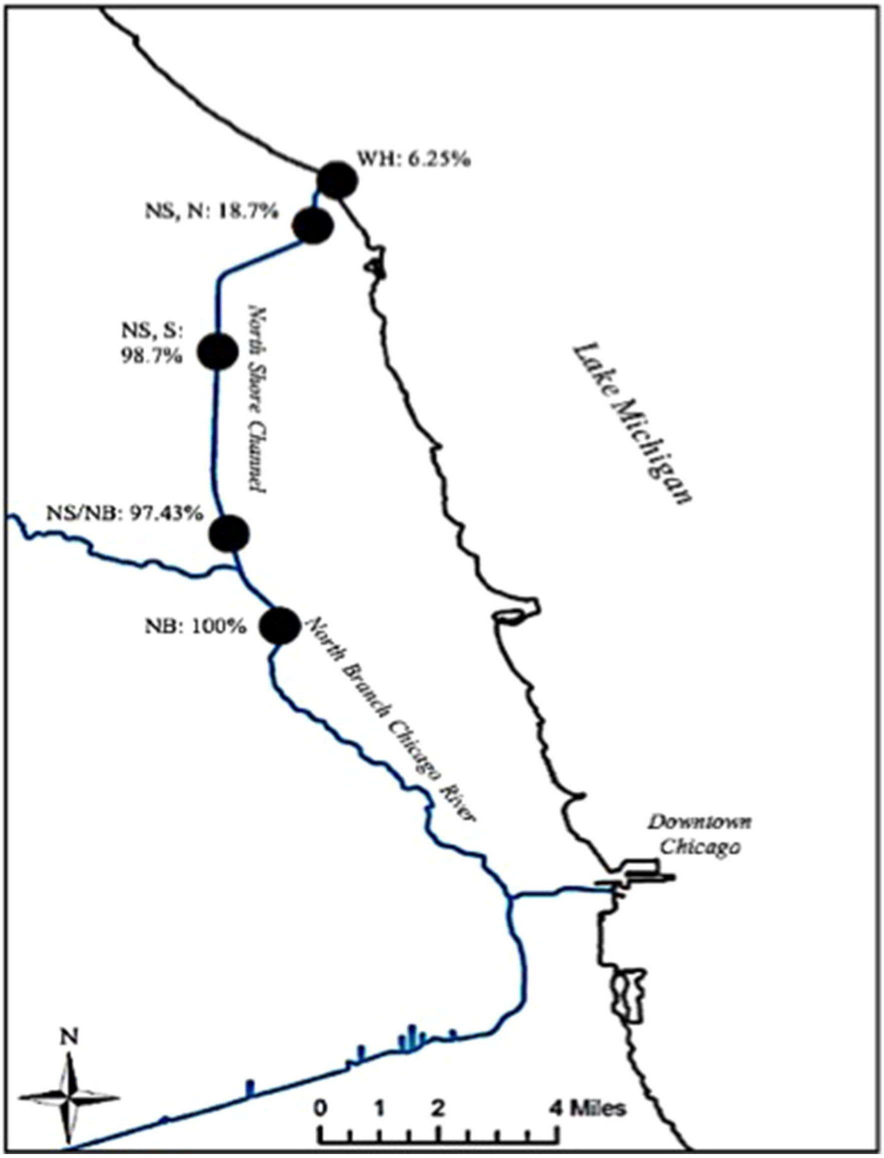

Fig. 1 Map of crayfish sampling locations in the Chicago area waterway system. The percentage of *Procambarus clarkii* found at each site is given; all other crayfish were *Faxonius rusticus*. *WH* Wilmette Harbor; *NS, N* North Shore Channel North; *NS, S* North Shore Channel, South; *NS/NB* North Shore Channel/North Branch, *NB* North Branch of the Chicago River

October 2016. All crayfish used in the experiments were collected during this period from the overlapping populations in the Channel. All collected crayfish were acclimatized to lab conditions for at least 1 week in large cattle tanks prior to being used. Individuals were not re-used for any experiments.

Shelter: two species

Shelter competition experiments were used to test which species is dominant for accessing a single shelter when individuals of both species are threatened. These experiments were conducted in ten-gallon aquaria in a closed lab with no movement (apart from what was necessary to simulate fish attacks, see below) visible to the crayfish. Each aquaria was filled with ~ 8 L of water, giving a depth of 15 cm. Our methods

Table 1 Counts of behaviors shown by each species during shelter trials

Behavior	Level	Description	*Procambarus clarkii*	*Faxonius rusticus*
Submissive	− 2	Fleeing, tail flip, walking away (rapidly)	2	0
	− 1	Avoidance, walking away (slowly)	24	63
		Total submissive	26	63
Neutral	0	Within one body length of other crayfish but no interaction	135	154
Aggressive	1	Approach, turning toward	61	67
	2	Display, claws raised, antenna point	106	62
	3	Physical contact, claw touching, claw tapping (no grasping)	243	227
	4	Physical contact, claw grabbing	80	68
	5	Physical contact, claw ripping	6	2
		Total aggressive	496	426

Behaviors were recorded every 10 s throughout each 20 min trial. No count was made if crayfish were not interacting or nearby to each other. Counts were summed among the 23 test animals of each species

followed Alonso and Martínez (2006), and a total of 23 trials were conducted.

For each trial, one crayfish of each species was selected while ensuring that the carapace lengths of the two crayfish differed by no more than 10%. The largest difference between carapace length was 4 mm. Because *F. rusticus* are smaller we generally used larger individuals from this species and smaller of *P. clarkii* (but note that a wider range of sizes was used in the field predation experiments, see below). Both chelae of each crayfish were measured prior to each experiment, and only individuals with two functioning chelae were used. We did not match crayfish based upon chelae size or sex. Crayfish were acclimated in the aquaria for 24 h with a divider preventing physical interaction. Each crayfish was provided a length of PVC pipe for shelter.

To begin the experiment the central divider and both shelters were removed from the tank and a single shelter (a 12 cm long, 5.1 cm diameter piece of PVC pipe closed at one end) was added. Trials lasted 20 min, and at 5, 10, and 15 min we used a plastic fish to simulate an attack on the crayfish. Trials were recorded by video to minimize the potential for observers to affect behavior. Videos were later examined to determine the response of each crayfish to the attacks. Additionally, at 10 s intervals, we recorded (a) whether each species was in or out of the shelter; (b) the behavior of each crayfish while out of shelter (active/passive); and (c) the behavior of the crayfish in relation to each other. The behavior of the crayfish in relation to each other was quantified on a scale ranging from − 2 to 5 (Table 1) following Karavanich and Atema (1998). Aggression during the fish attack was shown by raising the chelae and/or grabbing the fish with chelae.

Shelter: single species

Next, we tested the interest of crayfish in shelter when the other species was absent. Identical methods to those just described were followed, with the exception that there was only one crayfish per tank. Twenty-four trials were conducted (i.e., n = 12 trials per species).

Food

To examine competition between the two species for food we conducted 21 feeding trials using similar methods to Hill and Lodge (1999) and Szela and Perry (2013). Crayfish were selected and size matched using the methods described above. No food was available for a minimum of 48 h prior to each trial to encourage crayfish to seek food. To begin the experiment, both crayfish were placed on one side of a divider and a 2 cm piece of earthworm was placed at the opposite end of the tank. The divider was then removed. We recorded the initial winner of the food (i.e., the first individual to access it), the crayfish that ultimately ate the food, and the time elapsed before the food was fully consumed.

Predation

Experiments were conducted in the field to determine relative rates of predation on the two crayfish species in two different habitats. Experiments were conducted in the Channel and in Wilmette Harbor during June and July 2017 (see Fig. 1 for locations) and involved tethering crayfish to weights, leaving them overnight, and checking the next day to see which had been removed. Methods followed those of DiDonato and Lodge (1993) and Childress and Herrnkind (1994). Crayfish were collected from the North Shore Channel and Wilmette Harbor using the sampling methods described above. All individuals used in these experiments were identified to species, measured for carapace length, and sex was determined.

To tether crayfish we cleaned the top of the carapace with 75% alcohol and used superglue to attach a small swivel. This swivel was tied to a 30 cm long piece of four-pound test strength monofilament fishing line, which was in turn tied to a hook in the center of a 15 × 15 cm tile. To ensure that the tethers held, we first tested our methods in the absence of predation in tanks in the lab. Additionally, we included two controls of each species, at each site, each day, where these controls were individuals glued and tethered in the same way but placed inside minnow traps with the openings closed. None of the lab or field crayfish came free of their swivels or line.

Tiles and attached crayfish were placed on the bottom of the habitat at least 5 m apart and left overnight. In Wilmette Harbor the tiles were placed along the edge of the harbor wall, and total of 60 *P. clarkii* and 41 *F. rusticus* trials were conducted. Tiles in the Channel were placed in ~ 1.5 m of water along the bank, alternating species, with a total of 63 *P. clarkii* and 37 *F. rusticus* trials conducted. Each trial was a 24-h period that an individual was tethered. Secchi depth was recorded daily at three points within each site. Tethered crayfish were checked every day for presence/absence and any that were missing were replaced by new crayfish. Missing crayfish were considered to have been predated. This assumption was supported by the controls described above, and by us frequently finding torn pieces of crayfish still attached to swivels.

All statistical analyses were conducted using the statistical software R v 3.4.4 (R Core Development Team 2015).

Results

Trapping

Procambarus clarkii were found at highest catch per unit effort (CPUE; average number of crayfish per trap) compared to *F. rusticus* in the southern site on the North Branch of the Chicago River (CPUE = 0.96 from 2015 to 2017; 100% of 53 crayfish collected were *P. clarkii*). At the junction of the North Branch and North Shore Channel, *P. clarkii* were 97.44% of the 39 crayfish caught (*P. clarkii* CPUE = 0.95, *F. rusticus* CPUE = 0.03), followed by 98.70% of 307 crayfish at the southern site of the Channel (*P. clarkii* CPUE = 0.86, *F. rusticus* CPUE = 0.02). *P. clarkii* were in lowest proportions in the northern most site on the North Shore Channel (18.67% of 332) (*P. clarkii* CPUE = 0.15, *F. rusticus* CPUE = 0.93), and in Wilmette Harbor (6.25% of 32) (*P. clarkii* CPUE = 0.02, *F. rusticus* CPUE = 0.37).

Across all individuals trapped *P. clarkii* were significantly larger (n = 360; average CL = 50.8 mm) than *F. rusticus* (n = 157; 43.0 mm; t test, $p = \ll 0.001$; Fig. 2). Males were captured at higher rates for both *P. clarkii* (65% of all captured) and *F. rusticus* (60%).

Competition experiments

Shelter

Procambarus clarkii responded to fish attacks with aggression at least once during more trials (23/23) than *F. rusticus* (9/23) (X^2 with Yates correction, $p = \ll 0.001$). Fifty-six percent of *F. rusticus* sought shelter during the trial, usually immediately after fish attacks. *F. rusticus* were significantly more likely (X^2 with Yates correction, $p = 0.015$) to spend time in the shelter (n = 13/23) than *P. clarkii* (n = 4/23). However, once inside *P. clarkii* stayed in the shelter longer (t test, $p = 0.017$). The four *P. clarkii* that entered the shelter spent an average of 16.01 min of the 20-min trial inside, while the 13 *F. rusticus* that entered shelter spent an average of 7.67 min inside.

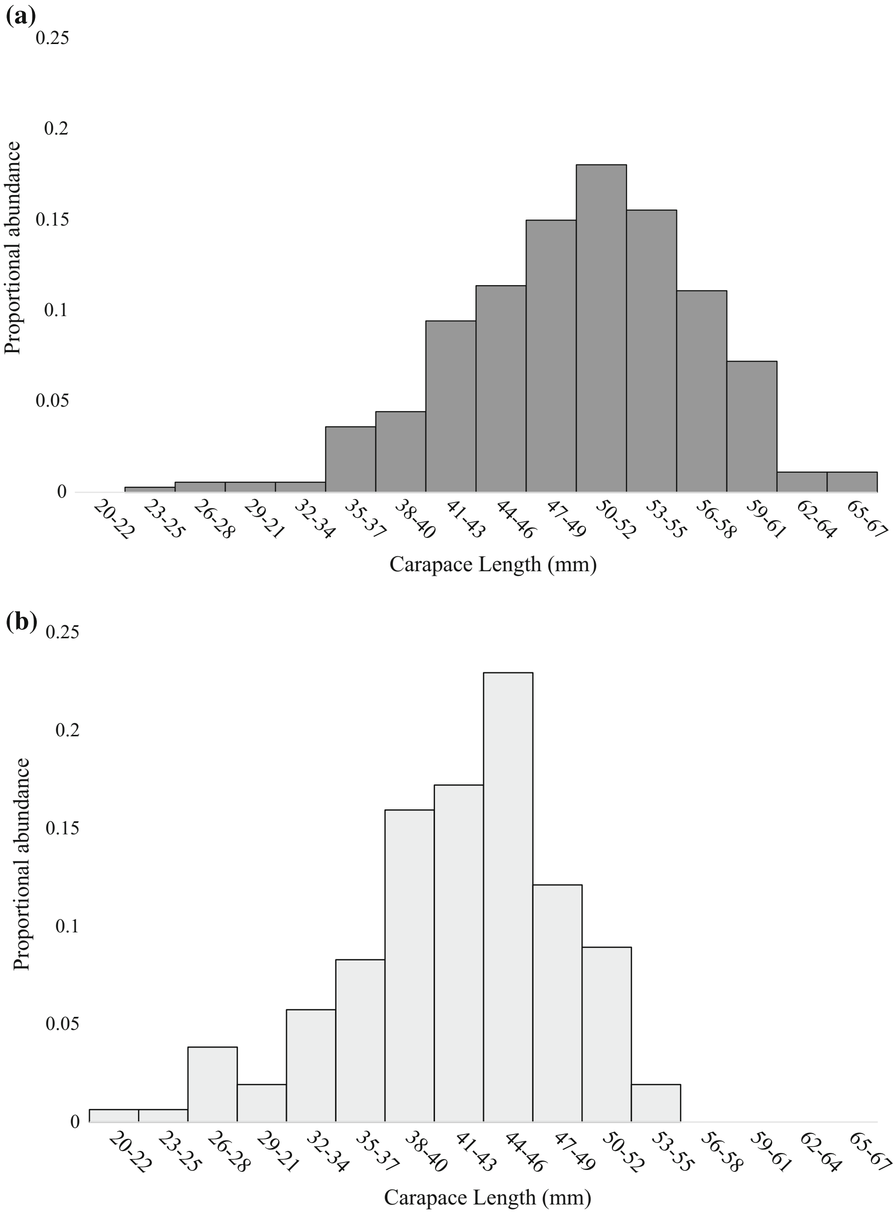

Fig. 2 Distribution of carapace length of **a** *Procambarus clarkii* and **b** *Faxonius rusticus* in the North Shore Channel, North Branch, and Wilmette Harbor

Interaction between *P. clarkii* and *F. rusticus* was recorded every 10 s during the entire trial (Table 1). *P. clarkii* displayed aggressive behaviors [1–5; Table 1] significantly more often than *F. rusticus* (Wilcoxon signed rank test with paired data, $p = 0.042$). *F. rusticus* displayed submissive behaviors [− 1, − 2; Table 1] significantly more often than *P. clarkii* ($p = 0.049$). When competition was eliminated and trials with one crayfish per tank were conducted, *F. rusticus* entered the shelter in 41% of the trials and *P. clarkii* in 25%.

Food

Procambarus clarkii ate the food in two-thirds of the food competition trials (n = 14/21), though this result is only marginally significant (X^2 with Yates correction, $p = 0.064$, see supplementary tables). When *P. clarkii* ate the food, they did so more quickly than *F. rusticus* (average time to consumption of 58.2 min for *P. clarkii* vs. 81.4 min for *F. rusticus*; Mann–Whitney U, $W = 35$, $p = 0.322$), though this result is not significant. There was no significant difference in the gender of the crayfish that won the food when trials were mixed sex (4/7 mixed sex trials were won by females; X^2, $p = 0.593$; see supplementary data). In all trials examining food competition the two crayfish showed aggressive behavior toward each other, indicating that competition was taking place.

Predation experiment

We report predation rates as the percent of 24-h trials after which we found crayfish had been removed from their tethers. *P. clarkii* were predated at a significantly higher rate (32%) than *F. rusticus* in (17%; X^2 with Yates correction, $p = 0.049$) when both habitats were combined (Fig. 3). This trend was also significant in the North Shore Channel, where 29% of *P. clarkii* were predated versus 8% of *F. rusticus* (X^2 with Yates correction, $p = 0.030$). Differences in predation rate were not significant when only Wilmette Harbor was considered (35% of *P. clarkii* predated vs. 24% *F. rusticus*; X^2 with Yates correction, $p = 0.360$). Although not significant, *F. rusticus* were predated at higher rates in Wilmette Harbor than the Channel, and no significant difference was seen between the two sites for *P. clarkii* (X^2 with Yates correction, *F. rusticus:* $p = 0.105$; *P. clarkii:* $p = 0.567$).

There was no effect of gender on predation rate for either species (X^2, *P. clarkii* $p = 0.734$; *F. rusticus* $p = 0.309$). Water clarity in Wilmette Harbor was higher (average 207 cm Secchi depth) than in the North Shore Channel (81 cm Secchi depth). In three of our 18 Secchi measurements at Wilmette Harbor the bottom could be seen. For these measurements, the water depth was used as a proxy for Secchi depth, although we acknowledge this was a low estimate.

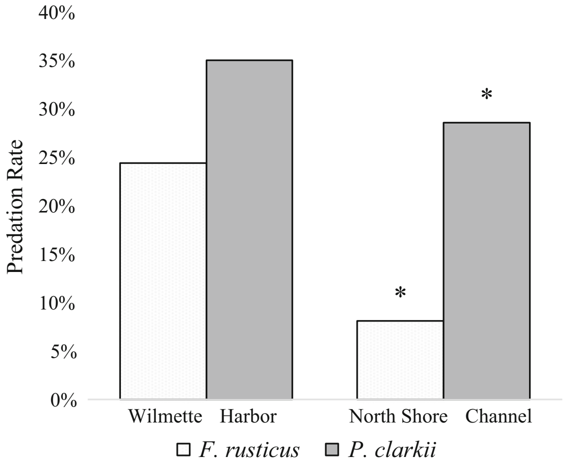

Fig. 3 Predation rates on *F. rusticus* and *P. clarkii* in the North Shore Channel and Wilmette Harbor. *Significantly different, $p = 0.030$. See text for details

Crayfish sizes for experiments

Crayfish size is known to affect competitive interactions (Issa et al. 1999; see supplementary material for sizes of all crayfish used in all experiments). There was no significant difference in the carapace length of the crayfish used in the shelter trials and the food trials (t test, $p = 0.528$). Additionally, there was no significant difference in the carapace size of *P. clarkii* used among competition experiments and the predation experiment (ANOVA, $p = 0.416$). There was no significant difference in *F. rusticus* used in the shelter and food trials (t test, $p = 0.721$), but the *F. rusticus* used in the predation trials were significantly smaller (ANOVA, $p = 0.001$) that those used in the competition experiments. This difference arose because we used a full range of *F. rusticus* sizes in the predation experiments, whereas our size matching meant that we could only use larger individuals for competition experiments.

In 88% of the competition trials the *P. clarkii* individual was larger (but never by more than 10%) and in 73% of the trials the *F. rusticus* had larger chelae (see supplementary data). The difference in chelae length varied from 1 to 20 mm with an average of 8.8 mm. Although the *F. rusticus* were often smaller (by CL) than *P. clarkii* they had significantly larger chelae in the shelter and food competition experiments (t test, $p = 0.002$).

Discussion

Procambarus clarkii is an internationally well-known invader of freshwaters, with populations established in Africa, Asia, Europe, and elsewhere in North America (Yue et al. 2010; Smith et al. 2018). It has been shown to outcompete native species in many regions (Yue et al. 2010; Smith et al. 2018). There is much concern about the continued spread of this species in the Great Lakes region, and if this occurs it will likely frequently come into contact with established populations of *F. rusticus* (Egly et al. 2019; Smith et al. 2018). Our results from the Channel demonstrate that *P. clarkii* are larger than *F. rusticus* and are more often behave aggressively when threatened. We followed our field observations of crayfish size with lab experiments to test competition between these species for two resources that have been found by other studies to be important predictors of dominance and survival (Figler et al. 1999; Gherardi and Daniels 2004).

Although the food competition results were only marginally significant, *P. clarkii* ate the food in two-thirds of all trials when individuals were size-matched. Our size matching likely gave an advantage to the smaller species (*F. rusticus*) relative to what would be experienced in the field because we chose larger *F. rusticus* and smaller *P. clarkii*. Our results are consistent with previous work showing that body size is a determinant of dominance in crayfish (Pavey and Fielder 1996; Issa et al. 1999), with larger individuals most often winning competitive interactions for resources (Butler and Stein 1985; Mazlum 2007).

Our field observations of crayfish size combine with our competition experiments to indicate that *P. clarkii* is likely able to outcompete *F. rusticus* for food. We note, however, that it is unknown whether food is limiting for these populations, and that the omnivorous behavior of crayfish (Lodge et al. 1994) may make it unlikely. Multi-week lab studies have shown that there may be an effect on long term growth and survival when crayfish are stocked with and without other invasive crayfish, even in a system with ample food (Hill and Lodge 1999). The behavior of crayfishes in our system may be altered based on the presence of an invasive crayfish species, and this may include feeding behaviors. Thus, although food as a resource may not be limited the aggressive behavior of *P. clarkii* may lead to worse growth outcomes for *F. rusticus*. *P. clarkii* showed significantly greater aggression in direct response to *F. rusticus*, and in response to our simulated fish attack.

During our shelter experiments we found that once inside a shelter *P. clarkii* stayed there for a significantly longer time than *F. rusticus*. We do not have a good explanation for this but suggest that it may be an underlying behavioral trait of unknown importance to competition. *P. clarkii* are a burrowing crayfish species (Correia and Ferreira 1995) and remaining in the shelter may have been akin to remaining in a burrow once one is found.

Based on our field sampling and results of the competition trials we hypothesized that the higher levels of aggression shown by *P. clarkii* may come at the cost of higher predation. Specifically, responding aggressively may be useful when interacting with another crayfish, especially one from a species that is generally smaller. In contrast, this behavior may be detrimental when the threat is a much larger predator such as largemouth bass (Garvey et al. 1994). Further, we hypothesized that the detrimental effects of aggression would be greater in clearer water where visual predators—such as fishes—are more effective (Crowl 1987). Although fish tend to predate large crayfish less often, we believed that the aggression of *P. clarkii* would increase the rates at which they were predated (Stein 1977, Garvey et al. 1994, Kershner and Lodge 1995).

To test this we looked at differential predation on *P. clarkii* and *F. rusticus* in two habitats, one of which (Wilmette Harbor) has significantly greater water clarity. Our results support our hypotheses. Specifically, *P. clarkii* were predated at significantly higher rates across both habitats, and this was also true in just the Channel habitat. Both species were predated more often in Wilmette Harbor than the Channel but this trend was not significant. Although the 30-cm tether line would have limited the ability to flee from a threat, the experiments were conducted during late summer when macrophyte cover was plentiful in both habitats. Thus, we believe it likely that predation rates may have been somewhat inflated over what would occur without tethering, but that the difference between the species is indicative of true susceptibility to predation. Previous studies in habitats with high macrophyte cover have found that crayfish with smaller carapace lengths are predated at significantly higher rates compared to larger crayfish (Garvey et al. 1994). Given that *F. rusticus* are smaller in general, and that the individuals used in our tethering were smaller, this provides further support for our contention that the behavior of *P. clarkii* exposes it to greater risk.

Additional support for our hypotheses comes from our sampling results which show that although *P. clarkii* are found throughout the North Shore Channel they are rarely found in Wilmette Harbor of Lake Michigan. These habitats are separated by a weir, but given the propensity of *P. clarkii* to travel overland (Ramalho and Anastácio 2015; Smith et al. 2018) we doubt that this is a serious barrier to movement, particularly given that the weir is occasionally opened to allow water to flow from the Channel into the Harbor. Our results suggest the possibility that *P. clarkii* have access to Wilmette Harbor, which has a similar substrate to the Channel, but cannot persist there due to higher predation. An alternative explanation for the distribution patterns is that the population of *P. clarkii* is still spreading within the Channel and will eventually move into the Harbor and Lake Michigan. We consider this unlikely because of the high population of *P. clarkii* in much of the Channel and right up to the weir that separates the Channel and Harbor, but further sampling over subsequent years will be needed to determine whether this is the case.

Lower rates of predation on *F. rusticus* are consistent with past studies that have found this species to be superior at avoiding predators compared to native crayfish species (DiDonato and Lodge 1993). *F. rusticus* were found to have lower mortality rates compared to *Faxonius propinquus* and *Faxonius virilis* (Hill and Lodge 1999), both of which are native in our study area (Peters et al. 2014), when in tanks in the presence of a largemouth bass. In our predation experiment the average chelae size of *F. rusticus* was significantly greater than for *P. clarkii* which may have aided in their defense against predation. Chelae size has been found to be positively associated with success in encounters with fish and other crustaceans in both lobsters (Scrivner 1971) and crayfish (Stein 1976). Overall our results indicate that shelter seeking by *F. rusticus*, and potentially their larger chelae, significantly increased their likelihood of survival compared to *P. clarkii*. This occurred despite the *P. clarkii* in the experiment having significantly larger carapace size which in other cases has been associated with lower predation.

Male *P. clarkii* and *F. rusticus* alternate during the year between form I and form II, which are reproductively active and inactive respectively. Form I crayfish are generally more aggressive (Tierney et al. 2008), which may affect competition and predation outcomes. A previous study showed that form I males were less likely to be predated than form II and female crayfish, with the latter two equally likely to be predated (Stein 1977). We used males and females of each species in our experiments but did not record form. To test whether changes in form may have affected our results we compared males to females, the latter of which should have stable behaviors (note that no berried [= with eggs] females were included in our experiments). Although the behaviors of form I males, form II males, and females has been found to be different in the past, we found that males and females of each species did not differ significantly in the rates at which they were predated. Further, the outcomes for males and females of each species in the competition experiments were not different. Thus, we do not see evidence that the form of male crayfish affected our results.

If there is a trade-off between competitive advantage and exposure to predation that explains the distribution patterns observed then we would expect *P. clarkii* to continue their spread into habitats that either have low water clarity, or that are clear but have few predators of crayfish. This would make many rivers and wetlands across the Great Lakes region susceptible. While much of the Great Lakes themselves may be too clear, there are large and productive areas that have secchi depths similar to those observed in the Channel (GLEC 2006; Qualls et al. 2013). These include Lake Michigan's Green Bay (Qualls et al. 2013) and Lake Huron's Saginaw Bay (GLEC 2006). The only known populations of *P. clarkii* that have existed in the Great Lakes region over a long period are in wetlands connected to Sandusky Bay in the western basin of Lake Erie (USGS 2019). *P. clarkii* were first recorded at the Winous Bay Shooting Club there in 1967, and the Resthaven Wildlife Area in 1982 (Nagy et al. 2018). Both populations persist in the wetlands, but in neither case is there evidence that *P. clarkii* have moved into the western areas of Lake Erie, which tend to be clearer (USGS 2019). Based on our results from the predation experiments, this lack of spread could be partially attributed to water clarity and predation, with habitat type perhaps also playing a role.

Procambarus clarkii is a recent and spreading crayfish invader of freshwaters in the Laurentian Great Lakes region (Nagy et al. 2018). There is much concern about its potential impacts and a desire to prevent its further spread. If it does continue to spread it will come into contact and competition with established crayfishes, and often this will be the widely established and currently dominant *F. rusticus* (Peters et al. 2014). A recent study has suggested that the potential range of *P. clarkii* in the Great Lakes is much larger than its current range and includes areas such as Saginaw Bay in Lake Huron, Green Bay in

Lake Michigan, and Henderson Bay in Lake Ontario (Egly et al. 2019). Our work shows that *P. clarkii* are larger and more aggressive than *F. rusticus*, and that when threatened they are less likely to seek shelter. A consequence of this aggression, however, is that *P. clarkii* respond to threats—such as predators—by aggressively displaying their chelae rather than fleeing. Our experiments and observations offer a mechanistic explanation for patterns of distribution of *P. clarkii* and can be used to aid predictions of future spread.

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