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ORIGINAL PAPER

The influence of evolution and plasticity on the behavior of an invasive crayfish

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Abstract Invasion success can be enhanced by evolution and behavioral plasticity, but the importance of these processes for most invasions is not well understood. Previous research suggests there is a genetic basis for differences in growth rate between native and invaded range rusty crayfish (*Orconectes rusticus*). We hypothesized that invaded range *O. rusticus* achieve faster growth by allocating more time to foraging and less to defense. We conducted a laboratory experiment to test the effects of range (native or invaded) and plasticity (as induced by exposure to predators) on crayfish behavior. We collected *O. rusticus* adults and eggs from both ranges, hatched eggs in the lab, and reared juveniles in common conditions either with or without predatory fish. We then quantified adult and juvenile crayfish activity in an experiment with and without predatory fish. In support of our hypothesis, invaded range adults displayed reduced antipredator behavior compared to native range adults. Further, invaded range juveniles were more active than native range juveniles without predators, but all juveniles were inactive with predators. In addition, invaded range juveniles had greater plasticity in behavior than native range juveniles. These results suggest that activity level in the absence of predators has diverged in the invaded range. Because active crayfish consume more prey, this change in behavior may be responsible for rapid growth in the invaded range of *O. rusticus*, a trait that contributes to the strong ecological impacts of this invasive crayfish.

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Introduction

Evolution can alter the success and impacts of invasive species by allowing them to adapt to novel environments (Cox 2004; Huey et al. 2005; Colautti and Barrett 2013) and conditions that arise during the invasion process (Phillips et al. 2010). However, evolution during invasions has been understudied compared to ecological processes (Cox 2004; Colautti and Lau 2015). Therefore, to what extent invasiveness is typically caused by release of species from fitness constraints or to rapid, adaptive evolution is not well understood (Ellstrand and Schierenbeck 2000; Colautti and Lau 2015). Evolution during invasions can occur as a result of stochastic changes, such as founder effects or genetic drift, or as a result of adaptive evolution.

Species may also adapt to novel environments through phenotypic plasticity. The capacity for phenotypic plasticity typically evolves as a result of past selection due to environmental fluctuations (Hendry 2016). When organisms are introduced to a new environment, phenotypic plasticity may reduce the cost of directional selection, allowing a population to persist, so a greater capacity for behavioral plasticity may enhance invasiveness (Sol and Lefebvre 2000; Wright et al. 2010). Further, plasticity may facilitate adaptive evolution if the phenotypes produced are close to optimal but incomplete and selection can act on extreme phenotypes (Price et al. 2003; Ghalambor et al. 2007). In addition, the capacity for phenotypic plasticity may evolve during invasions (Crispo 2010).

Only a small fraction of species that become established in new locations become invasive (spread and cause ecological and/or economic harm), and those species that have strong impacts often have *r*-selected life history traits such as rapid growth and high reproductive rate (Sakai et al. 2001; van Kleunen et al. 2010; Lamarque et al. 2011), traits that are often subject to strong selection. In addition to traits of introduced species, characteristics of the environment and biotic community within the introduced range are often important for invasion success (Catford et al. 2009).

Some species may already possess *r*-selected traits upon introduction, but in other species, these traits may evolve during the invasion process. For example, in the early stages of an invasion, conspecific densities are low and the population is unlikely to be density regulated, and theory indicates that higher fitness is associated with high reproductive rate in non-density-regulated populations (Roughgarden 1971; Burton et al. 2010). Thus, higher reproductive rates may be selected for in invasive populations. Some previous studies have found evidence for evolution of rapid growth or increased investment in reproduction in invasive populations or during range expansions (Burton et al. 2010; Phillips et al. 2010; Flory et al. 2011); however, other studies have found no support for the evolution of these traits in other species (e.g. Bossdorf et al. 2004; Cripps et al. 2009). It has also been hypothesized that the conditions in the anthropogenic vectors that move species, e.g., the live fish bait trade in the case of crayfish, could select for aggressive individuals with associated rapid growth rates (Pintor and Sih 2009). More evidence is needed to determine in what taxa, how often, and in which conditions traits that promote invasion success evolve.

Sargent and Lodge (2014) found that growth rates of rusty crayfish (*Orconectes rusticus*) from invaded range populations were higher than those from native populations when raised in common conditions, suggesting that growth rates have evolved since *O. rusticus* were introduced to the invaded range. The mechanism by which *O. rusticus* achieves rapid growth is currently unknown, but we hypothesize that it is due to higher foraging rates. Pintor and Sih (2009) found that in some conditions *O. rusticus* from invasive populations displayed greater foraging activity and recruitment to bait than native *O. rusticus*. However, it is unclear whether these behavioral differences were genetically based or due to behavioral plasticity.

Regardless of the origins of rapid growth of *O. rusticus* in the invaded range, it may help to explain the crayfish's success following introduction. *O. rusticus* are native to the Ohio River Drainage and have been introduced widely, especially in the Midwest and northeastern United States (United States Geological Survey 2015). In northern Wisconsin, where invasive populations of *O. rusticus* have been well-studied, they have strong ecological impacts. *O. rusticus* has greater impacts on freshwater communities than resident crayfish, *Orconectes virilis* and *Orconectes propinquus* (Wilson et al. 2004). When replacing these congeners, *O. rusticus* often causes dramatic declines in the abundance and richness of macrophytes and other macroinvertebrates, as well as declines in the abundance of some species of fish (Wilson et al. 2004). The ability of *O. rusticus* to replace *O. propinquus* has been attributed in part to its faster growth rate and ability to outcompete smaller individuals for shelter (Hill et al. 1993; Garvey et al. 1994; Hill and Lodge 1994). In addition, larger crayfish produce more eggs (Savolainen et al. 1997; Skurdal et al. 2011), so rapid growth among individuals may promote high *O. rusticus* population growth.

In addition to promoting growth, allocating time to foraging is likely to increase susceptibility to predation. There is a tradeoff between foraging and defense in crayfish: crayfish that spend more time moving or exposed are more vulnerable to fish predators than those that are stationary or within shelter (Garvey et al. 1994). Invasive species may leave behind their natural enemies when they are introduced, and the evolution of increased competitive ability (EICA) hypothesis posits that this process often allows invasive species to invest less in defense and more in growth and competition (Crawley 1987; Blossey and Notzold 1995). However, for *O. rusticus*, predators and pathogens in the invaded range share a long coevolutionary history with other orconectid crayfish and readily infect or consume *O. rusticus* (Peters 2010; Sargent et al. 2014). Further, predatory fish are important in controlling *O. rusticus* abundance in the invaded range (Roth et al. 2007). Therefore, we expect predator avoidance to remain an important strategy for this species, and we were interested in how activity and foraging behavior would differ between native and invasive populations of *O. rusticus* when faced with the threat of predation.

We designed two experiments to compare behavior between native and invaded range *O. rusticus*. First, we conducted a behavioral experiment to test whether there are differences in native and invaded range *O. rusticus* activity and feeding behavior and how these behaviors are altered by the presence of a predator. For this experiment, we used adult *O. rusticus* collected from the native and invaded range. We hypothesized that *O. rusticus* from invasive populations allocate more time to foraging and less time to defense. Second, we conducted a behavioral experiment to test whether differences in activity and feeding behavior between native and invaded range crayfish are due genetic differences or to plasticity. For this experiment, we collected *O. rusticus* as eggs from the native and invaded range and raised them in common conditions either with or without exposure to predators. We then conducted an experiment similar to that for adult crayfish to quantify crayfish activity and feeding behavior as influenced by the presence of a fish predator. Because parents were exposed to different environmental conditions, it is possible that our results could be influenced by maternal and epigenetic effects as well as genetic differences. This approach also enabled us to compare the capacity for behavioral plasticity between native and invaded range *O. rusticus*.

Methods

Adult behavioral experiment

In order to test whether behavioral differences exist between *O. rusticus* from native and invaded range populations, we collected adult crayfish from the native and invaded range in fall 2010 and examined their behavior in the presence and absence of a predatory fish. We collected crayfish from three locations within each range, and conducted a total of ten behavioral trials with crayfish from each location. Native range *O. rusticus* were hand-collected in September 2010 from a location within the Great Miami (39°56′N, 83°44′W), Ohio Brush Creek (38°54′N, 83°34′W), and Scioto (40°00′N, 83°23′W) river drainages in Ohio, USA. Invaded range *O. rusticus* were hand-collected in August 2010 from a location within High Lake (46°08′N, 89°32′W), Big Lake (46°11′N, 89°26′W), and Lake Ottawa (46°04′N, 88°45′W) in northern Wisconsin and Michigan, USA. Until the behavioral trials began, crayfish were housed with other individuals collected from the same site in tanks with constantly flowing, aerated well-water and shelters constructed from polyvinyl chloride (PVC) pipe. Crayfish were fed shrimp pellets ad libitum and were exposed to a 12:12 h light dark cycle. Behavioral trials were conducted between February and April 2011. We tested the behavior of 17 males and 13 females from each range (10 crayfish from each collection location), and crayfish had a mean carapace

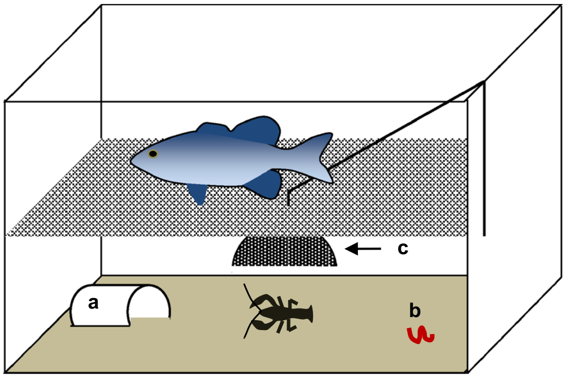

Fig. 1 Setup for behavioral experiment. Experimental aquaria contained (*a*) a shelter constructed from PVC pipe and (*b*) a worm or a section of worm as a food source. The predator-present trials contained a smallmouth bass in the upper section of the tank. A screen divided the *upper* and *lower* sections of the tank so that crayfish could receive visual and chemical cues from fish but could not be closely approached or consumed by the fish. Crayfish were placed under (*c*) a weighted mesh acclimation dome before the start of the trial, and the acclimation dome was lifted via an attached string before crayfish behavior was recorded

length (±SE) of 20.0 ± 0.3 mm from the native range and 20.3 ± 0.4 mm from the invaded range.

Behavioral trials were conducted between 9:00 and 18:00 in 76 L aquaria filled with aerated well-water. Each aquarium contained a PVC pipe shelter on one end and a worm (*Eisenia foetida*) as a food source at the other end. A thin layer of sand covered the bottom of the aquaria, and a screen placed 10 cm from the base divided each aquarium into a top and bottom section (Fig. 1). Water was constantly aerated to maintain high levels of dissolved oxygen. In half of the trials, a smallmouth bass (*Micropterus dolomieu*) between 20 and 26 cm total length (TL) was placed in the top section of the aquarium. This setup allowed the crayfish to receive visual and chemical cues from the bass, but did not allow the bass to closely approach or consume the crayfish. Smallmouth bass are voracious predators of crayfish and are common in both the native and invaded ranges of *O. rusticus* (Boschung et al. 1983; Peters 2010). We conducted a total of 60 trials (2 crayfish ranges × 2 fish treatments × 15 replicates). Males and females were evenly divided between treatment combinations (6–7 females and 8–9 males per treatment combination).

At the start of the trial, we placed a crayfish in the center of the aquarium under a mesh acclimation dome and secured the screen divider in the tank. If the trial was a predator-present trial, we immediately added the smallmouth bass to the top section of the aquarium. In all trials, we allowed the crayfish to acclimate under the mesh dome for 15 min. After the acclimation period, we lifted the dome using an attached string, and recorded the behavior of the crayfish on video for 15 min.

Videos were later scored and the duration of different crayfish behaviors was recorded. Behaviors included time spent active (walking or feeding) and time spent inactive (standing, crouched, or under the PVC shelter). Here, we assumed that both feeding and walking represent allocation of time towards growth and not towards predator avoidance. Previous research indicates that crayfish that are more active consume more prey than inactive crayfish (Pintor et al. 2008). In addition, crayfish that spend more time moving or exposed are more vulnerable to fish predators than those that are stationary or within shelter (Garvey et al. 1994). Therefore, combining these behaviors in the analysis allowed us to determine if crayfish were allocating time towards growth (i.e., active feeding and walking) or predator avoidance (i.e., being inactive). Only behaviors that occurred for 5 s or more were recorded, and no behaviors other than active (walking or feeding) or inactive (standing, crouched, or under the shelter) occurred for 5 s or more. Each crayfish was only used once, and aquaria were drained and refilled after each trial. All predator-absent trials were conducted first so that fish chemical cue would not be present from previous fish in the aquaria.

Juvenile behavioral experiment

In order to test whether differences in behavior between native and invaded range crayfish were due to genetic differences or were due to plasticity, we collected crayfish from both ranges as eggs and raised them in common conditions in mesocosms with predatory fish either present or absent. We then conducted a similar experiment to the one described above to quantify the foraging behavior of these crayfish, as influenced by the presence of a fish predator.

Because temperatures are warmer in the native range than in the invaded range, *O. rusticus* reproduce earlier in the native range. Therefore, juveniles from the native range were raised earlier than those from the invaded range, but important variables such as temperature, food quality and quantity, and predator presence were held constant. We hand-collected berried females (those with eggs attached to their abdomen) in early April 2012 from one location within the Ohio Brush Creek (38°54′N, 83°34′W [7 females]), Little Miami River (39°47′N, 83°51′W [2 females]), and Scioto River (40°00′N, 83°23′W [10 females]) drainages in Ohio, USA. In early May 2012, we hand-collected berried females from High Lake (46°08′N, 89°32′W [9 females]), Big Lake (46°11′N, 89°26′W [9 females]), and Papoose Lake (46°10′N, 89°48′W [5 females]) in Wisconsin, USA. Females had a mean carapace length (±SE) of 29.2 ± 1.0 mm from the native range and 26 ± 0.5 mm from the invaded range. Maternal carapace length did not significantly affect juvenile growth rate (Sargent and Lodge 2014). We placed each female in an individual container (18 cm× 18 cm) in the laboratory with constantly-aerated well water, a PVC shelter, and gravel substrate. Eggs hatched, and young became independent from females 3 to 4 weeks after collection. Young of year (YOY) were fed shrimp pellets ad libitum while in the laboratory. A total of 89 juveniles from 42 broods were used in the behavioral experiment.

YOY from the native range were placed in experimental mesocosms in late May, and YOY from the invaded range were placed in mesocosms in late June. We replaced mortalities that occurred within the first two weeks of the experiment with crayfish from the same range and, when possible, the same clutch. Replacement crayfish were housed in the laboratory with the same husbandry and conditions as provided after hatching.

Mesocosms consisted of 416 L plastic tanks with flow-through, aerated well-water, which were located on the shore of Trout Lake (Wisconsin, USA). Temperature was maintained throughout the summer in each mesocosm by a 300 W heater. More details about mesocosms and rearing conditions can be found in Sargent and Lodge (2014). There were 12 mesocosms in total, with 20 YOY *O. rusticus* (10 invaded and 10 native range) in individual containers (described below) reared in each mesocosm. Half of the mesocosms contained three bluegill (9.5–13 cm TL) and three smallmouth bass (10.5–14.5 cm TL). Fish were fed *O. rusticus* once per week and earthworms (*Lumbricus terrestris*) twice per week for the duration of the experiment. Fish readily consumed both food types. Like smallmouth bass, bluegill are common in both the native and invaded range of *O. rusticus* (Boschung et al. 1983) and are major predators of juvenile crayfish (Roth et al. 2007).

Within mesocosms, crayfish were each housed in an individual clear plastic container (18 cm × 18 cm × 12.7 cm) with rectangular holes (14 cm × 8 cm) cut into each side and replaced with window screen. The screened containers prevented direct interaction among crayfish or with predators, but allowed crayfish to receive visual and chemical cues from predators. Two stones were glued to one side of the bottom of the container to provide shelter. On the opposite side, a small nylon nut and bolt held disks of prepared food.

Food consisted of macrophytes, earthworms, and bluegill fillets mixed with sodium alginate and water. All food was prepared at the beginning of the summer and frozen. Crayfish from native and invaded range populations were fed from the same batch of food during the same week of growth. To examine how food quality affects crayfish growth, which is described in Sargent and Lodge (2014), we made both a high quality food (40% macrophytes and 60% animal matter) and a low quality food (80% macrophytes and 20% animal matter). Half of the crayfish in each mesocosm were randomly assigned to one of these food types.

Crayfish were removed from the experiment and tested for their behavioral response to fish after they were reared in experimental mesocosms for 7–8 weeks (or 5–6 weeks if they were replacements). Because they grew more slowly in mesocosms, native range juveniles were smaller during behavioral experiments (16.7 ± 0.4 mm TL ± SE) than invaded range juveniles (19.0 ± 0.4 mm TL ± SE). It is possible that this size difference could contribute behavioral differences, but both size classes would be extremely vulnerable to predatory fish (Stein 1977). Between 48 and 72 h prior to the behavioral trial, crayfish were removed from outdoor tanks and placed in the laboratory. Crayfish were kept in their original individual containers, which were placed in a bucket with aerated well-water, and fed until the start of the trial.

We conducted a total of 89 trials with 2 crayfish range treatments (native or invaded), 2 fish treatments during rearing (crayfish experienced or inexperienced with predators), and 2 fish treatments during the trial (predator present and absent). We did not have an equal number of crayfish within each group because fewer native range crayfish survived in the mesocosms especially when reared with fish. Replicates of each unique treatment combination ranged from 7 to 15. Sex of each crayfish was identified under a dissecting microscope at the end of the experiment. Fifty-eight percent of native range juveniles and 53% of invaded range juveniles were females.

Behavioral trials were identical to those used to test adult crayfish except for the following differences. Tanks were smaller (38 L) to accommodate the smaller crayfish and time spent in the mesh acclimation dome was longer (25–30 min). Smallmouth bass ranged from 10 to 15 cm TL. Instead of using an entire worm as the food source during the trial, we used a 1 cm section of earthworm. Tanks were used for up to two trials before well-water was changed. Predator-present trials were always conducted in the same aquaria so that fish chemical cue was not present in predator-absent trials. In addition to the behaviors recorded for adult crayfish, we recorded the number of tail flips (fast retreat backwards by contraction of the abdomen) each crayfish displayed. Tail flips are an escape behavior (Bruski and Dunham 1987). This behavior was extremely rare in the adult trials, so we only examined it in juvenile trials.

Statistical analyses

To test whether adult crayfish from the native and invaded range of *O. rusticus* responded differently to predators, we used a mixed effects model to examine the effects of range (native or invaded), fish (predator present or absent), and their interaction on the duration of active time (a combination of time spent walking and feeding). Collection location was included as a random effect in the model. We also examined possible influences of sex and carapace length by adding them to the model. To test whether the observed behavioral differences were consistent between different collection locations in each range, we used separate two-way ANOVAs for each range that included the effects of collection location and predator presence (and the interaction between the two) on the duration of active time. Finally, we used generalized linear models with a binomial distribution to determine whether there were differences in the occurrence of feeding or utilizing the shelter during the trial.

To compare adult and juvenile crayfish, we used a mixed effects model to test how age (juvenile or adult), range, fish, and all interactions among these variables influenced crayfish activity level. Collection location was included as a random effect. For this analysis, we used only the juveniles that were exposed to predators during rearing because we expected that all adult crayfish had previous exposure to smallmouth bass.

Within juvenile crayfish, we were also interested in whether previous experience with predatory fish altered crayfish activity in the experiment and whether experience had a different effect on native or invaded range crayfish. To examine the effect of experience (and interactions between experience and other variables) on the duration of active time, we used a mixed effects model that included range, predator experience during rearing, predator presence during the trial, and all possible interactions. Food quality during rearing was included as a fixed factor in the model and both collection location and clutch were included as random effects. We also examined the possible influence of sex by adding it to the model. We tested whether behavior was consistent between different collection locations in each range using separate mixed effects models within each range to examine the effects of collection location, predator experience, predator presence, and all interactions on duration of active time. Clutch was included as a random effect in these models. To examine whether differences in juvenile size could influence our results, we added carapace length to the within-range models. We used the same generalized linear models as for adult crayfish to examine differences in the occurrence of feeding or utilizing the shelter during the trial but also included the effect of predator experience. To test whether there were differences in the frequency of tail flips between native range and invaded range juvenile crayfish, we used a generalized linear model with a Poisson distribution. Collection location and clutch were included as random effects. We used likelihood ratio tests to compare Poisson regressions with the effects of range, predator experience, predator presence, and their interactions on tail flip frequency. All analyses were conducted in R, version 2.10.1 (R Foundation for Statistical Computing, Vienna, Austria). We used the lme4 package (Bates et al. 2015) for

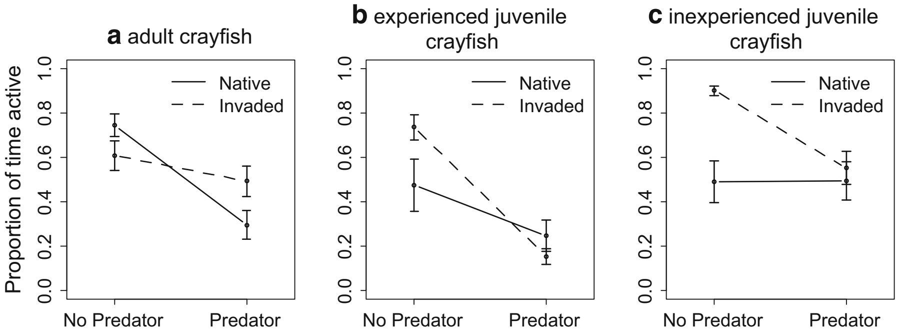

Fig. 2 Interaction plots showing the effect of predatory fish presence on native and invaded range crayfish activity in **a** adult *O. rusticus* (N = 15 for each treatment combination), **b** experienced juvenile *O. rusticus*, (native predator absent N = 7; native predator present N = 8; invasive predator absent N = 12; invasive predator present N = 15) and **c** inexperienced juvenile *O. rusticus* (native predator absent N = 10; native predator present N = 11; invasive predator absent N = 11; invasive predator present N = 15). Experienced crayfish were reared with predatory fish that were fed live *O. rusticus* and inexperienced crayfish were reared without predatory fish present. There was a significant interaction between range and predator presence on activity for both adult and juvenile crayfish. Within juvenile crayfish, there was also a significant effect of experience and a significant interaction between experience and predator presence on activity. Each trial lasted for a total of 900 s (or 15 min). *Error bars* represent standard error

mixed effects models and lmerTest (Kuznetsova et al. 2015) to obtain P values for variables in mixed effects models.

Results

Adult crayfish

A significant interaction existed between range and predator presence ($F_{1,52} = 7.33, P = 0.0091$; Fig. 2a), whereby native range crayfish displayed a greater difference in activity level between predator-present and predator-absent trials than invaded range crayfish. When predators were present, native range crayfish reduced their activity by 61% and invaded range crayfish reduced their activity by 20%. Further, native range adults were actually more active than invaded range adults in the absence of predators. In addition, overall crayfish activity was significantly lower in trials with smallmouth bass present ($F_{1,\ 52} = 20.76$, $P < 0.0001$; Fig. 2a), and there was no significant overall effect of range on activity ($F_{1,\ 4} = 0.17$, $P = 0.7001$). Neither sex nor carapace length influenced activity ($P > 0.2$), so these effects were removed from the model.

Within the native range, there was a significant interaction between collection location and predator presence ($F_{1,30} = 3.87, P = 0.0350$), a significant effect of collection location ($F_{2,24} = 3.91, P = 0.0337$), and a significant effect of predator presence ($F_{1,\ 24} = 42.16$, $P < 0.0001$) on behavior. Great Miami crayfish were more active in the presence of fish than crayfish collected from the other two locations. Within invaded range crayfish, there was no effect of collection location, predator presence, or interaction between collection location and predator presence on activity ($P > 0.2$).

Most of the adult crayfish did not consume the worm or utilize the shelter during the trial (Fig. 3). There was no significant difference in the occurrence of feeding during the trial between native and invaded range adults ($P > 0.1$), but crayfish were less likely to feed when predators were present ($\chi^2 = 4.01$, $P = 0.0454, N = 60$). In addition, native range adults with no predators present tended to feed more frequently than other groups, but the interaction between range and predator presence on feeding was not statistically significant ($\chi^2 = 2.71,\ P = 0.0995$, $N = 60$). There was also a non-significant tendency for invaded range crayfish to use the shelter more often than native range crayfish ($\chi^2 = 5.06,\ P = 0.0797$, $N = 60$). There was no overall effect of fish presence on shelter use ($P > 0.1$). Native range crayfish with fish present also tended to use the shelter less frequently than other groups, but the interaction between range and fish presence on shelter use was non-significant ($\chi^2 = 2.96,\ \ P = 0.0855,\ \ N = 60$). Crayfish that entered the shelter during trials with fish

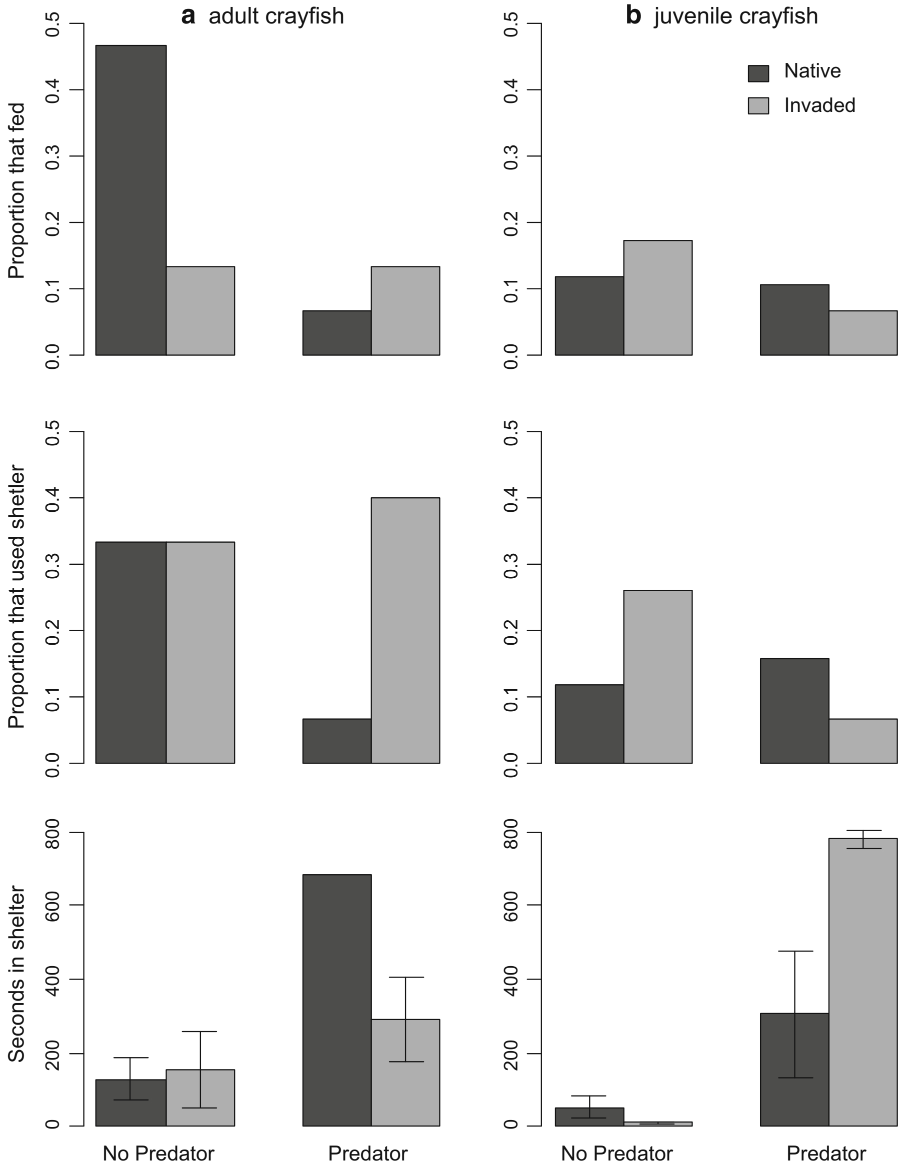

Fig. 3 *Orconectes rusticus* use of food and shelter resources during behavioral trials for **a** adult *O. rusticus* and **b** juvenile *O. rusticus*. Native range crayfish are represented by *dark grey bars* and invaded range crayfish are represented by *light grey bars*. *Top* represent the proportion of trials in which the crayfish fed, *middle* represent the proportion of trials in which the crayfish entered the shelter, and *bottom* represent the duration of shelter use only for those crayfish that entered the shelter during the trial. *Error bars* represent standard error

present tended to spend more time on average in the shelter than crayfish that entered the shelter in trials without fish (Fig. 3).

Adult crayfish versus experienced juveniles

A significant 3-way interaction existed between age (adult or juvenile), range, and predator presence during the trial ($F_{1,\ 91} = 13.44$, $P = 0.0004$; Fig. 2a, b). Whereas native range adults reduced their active time in the presence of predators to a greater extent than invaded range adults, we observed the opposite pattern in juvenile crayfish. Native range juveniles were generally inactive across both predator treatments, but invaded range juveniles were active when predators were absent and inactive when predators were present

(Fig. 2b). In addition, adult crayfish were significantly more active than juvenile crayfish ($F_{1,\ 59} = 7.41$, $P = 0.0085$; Fig. 2a, b), and crayfish were generally less active in the presence of smallmouth bass ($F_{1,\ 90} = 53.36$, $P < 0.0001$; Fig. 2a, b).

Juvenile crayfish

Within juvenile crayfish, a significant interaction existed between range and fish presence during the trial ($F_{1,\ 77} = 13.85$, $P = 0.0004$; Fig. 2b, c), in which invaded range crayfish were more active than native range crayfish in trials without fish, but in trials with fish, crayfish from both ranges were inactive. Overall, fish presence reduced juvenile crayfish activity ($F_{1,\ 77} = 33.18$, $P < 0.0001$), and invaded range juveniles tended to be more active than native range juveniles, but the overall effect of range on activity was not statistically significant ($F_{1,\ 4} = 5.47$, $P = 0.0821$). In addition, experience had a significant effect on activity ($F_{1,\ 77} = 17.22$, $P < 0.0001$; Fig. 2b, c). Crayfish that were reared with fish were generally less active than those that were not. Further, there was a significant interaction between experience and fish presence ($F_{1,\ 77} = 6.08$, $P = 0.0159$; Fig. 2 b, c). Crayfish that were reared with predatory fish were less active during the trials with bass than crayfish that had no prior experience with predators. No other interactions between variables were statistically significant ($P > 0.1$). Crayfish that were provided with high quality food during rearing were more active than those that were provided with low quality food ($F_{1,\ 78} = 4.19$ $P = 0.0440$). There was no significant effect of sex on activity ($P > 0.2$); therefore, it was removed from the model.

Within juvenile crayfish from the native range, there was no effect of collection location, predator presence, predator experience, or interaction between these variables on behavior ($P > 0.1$). Within invaded range juvenile crayfish, there was a significant effect of collection location ($F_{2,\ 32} = 4.157$, $P = 0.0248$), predator presence ($F_{1,\ 32} = 49.88$, $P < 0.0001$), and predator experience ($F_{1,\ 32} = 21.59$, $P < 0.0001$) on activity, but no significant interactions between these variables ($P > 0.1$). Crayfish collected from High Lake were more active than those collected from the other two lakes. However, in predator-absent trials, crayfish from all invaded range locations were more active on average than those from the native range (Fig. 4). There was no effect of carapace length on activity within either range ($P > 0.8$); therefore, it was removed from the models.

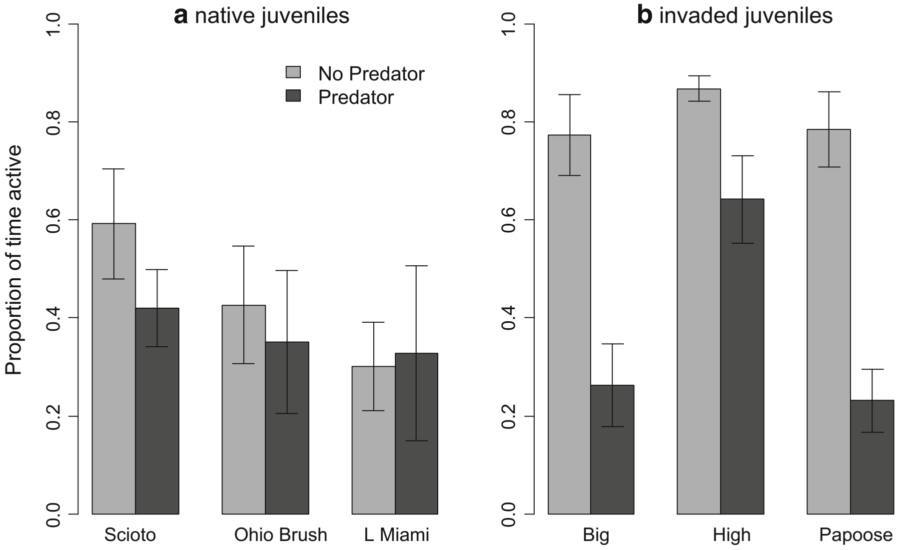

Fig. 4 Differences in activity level of juvenile crayfish collected from different river or lake drainages within each range (Scioto River [N = 19], Ohio Brush Creek [N = 12], Little Miami River [N = 5], Big Lake [N = 19], High Lake [N = 16], Papoose Lake [N = 16]). Trials without predatory fish are represented by *light grey bars* and trials with fish are represented by *dark grey bars*. There was no effect of collection location on activity within native range juveniles. Invaded range juveniles collected from High Lake had greater activity than those from other lakes. *Error bars* represent standard error

Few of the juvenile crayfish consumed the worm or utilized the shelter during the trial (Fig. 3). Overall, crayfish that had experience with predatory fish tended to consume the worm less often than those that were inexperienced, but this result was not statistically significant ($\chi^2 = 3.71$, $P = 0.0542$, $N = 89$). A significant interaction existed between range and experience ($\chi^2 = 6.10$, $P = 0.0135$, $N = 89$). A similar proportion of experienced and inexperienced native range crayfish fed during the trial (Fig. 5). In contrast, invaded range crayfish only fed if they were inexperienced (Fig. 5). A significant interaction also existed between predator presence and experience ($\chi^2 = 6.17$, $P = 0.0130$, $N = 89$). There was little effect of predator presence on feeding among inexperienced crayfish (19% fed in predator-absent trials and 15% fed in predator-present trials). However, for experienced crayfish, 11% fed when predators were absent but none fed when predators were present. No other variable or interaction between variables had a significant effect on the occurrence of feeding ($P > 0.3$). In addition, there were no significant effects of any of these variables on the occurrence of shelter use during the trial ($P > 0.1$). When predators were absent, invaded range crayfish tended to spend very little time within the shelter when they entered it (Fig. 3).

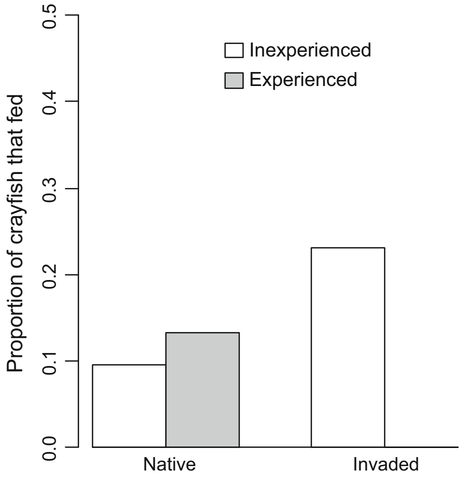

Fig. 5 The effect of experience on the proportion of juvenile crayfish from the native and invaded range that fed during the trial. *White bars* represent inexperienced juveniles (those reared without predatory fish) and *grey bars* represent experienced juveniles (those reared with predatory fish). *Data* represent both trials in which predators were present and those in which predators were absent. There was a significant interaction between range and experience on the occurrence of feeding. No experienced, invaded range juveniles fed during the trial

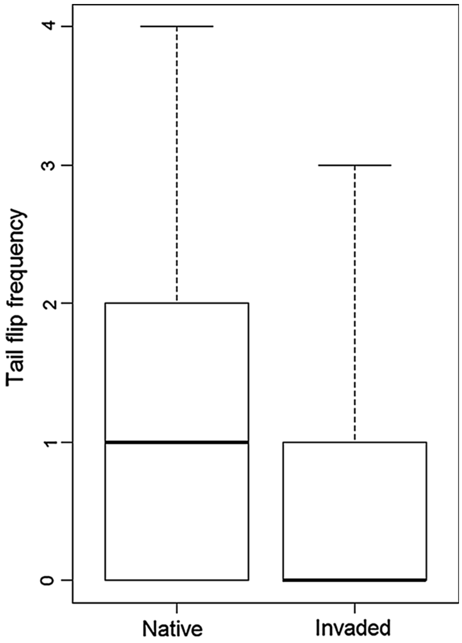

Fig. 6 Differences in the frequency of tail flip behavior between native and invaded range juveniles. There was a significant effect of range on tail flip frequency. *Boxes* represent 1st and 3rd quartiles, *interior lines* represent medians, and *whiskers* represent the range

Native range juveniles exhibited tail flip behavior more frequently than invaded range juveniles ($\chi^2 = 17.17$, $P = 0.0018$, $N = 89$; Fig. 6). No other variable or interaction between variables had a significant effect on tail flip frequency ($P > 0.05$).

Discussion

Adaptive significance of behavioral differences

Our results are consistent with selection for rapid growth and high fecundity within the invaded range. Larger crayfish produce more offspring (Savolainen et al. 1997; Skurdal et al. 2011), and greater growth may be achieved by allocating more time to foraging than to predator avoidance. Juvenile *O. rusticus* from invaded range populations were more active than juveniles from the native range, and previous research indicates that greater crayfish activity is associated with greater prey consumption (Pintor et al. 2008). Therefore, the greater growth of invaded range juveniles observed by Sargent and Lodge (2014) may be due, at least in part, to differences in activity. The proportion of juveniles that actually fed during the trial, however, was similar between native and invaded range crayfish. We also observed greater shifts in activity in invaded range juveniles than native range juveniles, suggesting invaded range crayfish have a greater capacity for plasticity. In addition, in the presence of fish predators, adult invaded range *O. rusticus* reduced their activity to a lesser extent than native range adults, which also suggests they could be investing more in growth and less in predator avoidance than crayfish from the native range. In contrast to our hypothesis, when predators were absent, adult invaded range *O. rusticus* were less active than adult native range *O. rusticus*. However, adults from different ranges may have had different prior experience with predators, which could be an additional influence on their behavior.

The difference in activity between native and invaded range juveniles that we observed when predatory fish were absent could be consistent with the EICA hypothesis (Blossey and Notzold 1995) or with an adaptation for rapid dispersal (Shine et al. 2011). If increased activity makes juvenile crayfish more vulnerable to enemies in the native range than in the invaded range, then the increased activity in invaded range juveniles may be an adaptive response to enemy release. It is possible that increased activity would make crayfish vulnerable to parasites or to predators other than fish, such as terrestrial predators. However, we do not know whether predator or parasite abundance differs between the two ranges. Further, because there are native congers present in northern Wisconsin and Michigan, organisms that infect or consume those species may be able to switch to *O. rusticus*; therefore, there may be no enemy release in this invasion. In addition, because dispersal at the edge of a species' range reduces interspecific competition, traits that enhance dispersal rate may be adaptive for organisms at the range edge (Shine et al. 2011). Evolution of dispersal could occur after *O. rusticus* are introduced to a lake, when the crayfish spread around the littoral zone. Therefore, it is possible that the increased activity in invaded range juveniles was produced by selection for dispersal ability.

The differences in behavior observed between adult and juvenile crayfish are likely due to differences in predation risk. The threat of predation is lower for adult crayfish than juveniles (Stein and Magnuson 1976). This is because many fish are gape limited (especially *Lepomis* spp.) and fish tend to selectively consume smaller crayfish (Stein 1977). Therefore, for adult crayfish, there should be less risk than for juvenile crayfish in allocating time towards foraging when predators are present. Consistent with this, adult crayfish (especially those from the invaded range) were more active in the presence of predatory fish than were juvenile crayfish. The inactivity of both native and invaded range juveniles during trials with fish present may be an adaptation to avoid the high risk of predation. Native range juveniles were generally inactive across all conditions, though, perhaps because the benefit of avoiding predation outweighs the benefit of growing rapidly even when these crayfish do not detect predators. In contrast, invaded range juveniles were active for most of the trial when predators were absent, allowing them to spend more time foraging.

The growth and mortality of juvenile crayfish while they were raised in mesocosms suggest that native range juveniles had a greater behavioral response to predatory fish than we were able to detect in behavioral trials. During behavioral trials, native range juveniles did not have reduced activity in the presence of predatory fish; however, fish presence reduced crayfish growth rate in mesocosms (Sargent and Lodge 2014). In addition, native range juveniles had higher mortality in mesocosms with fish present than mesocosms without fish (Sargent and Lodge 2014). Because there was high (80%) mortality of native range crayfish in mesocosms with predatory fish present, it is likely that those individuals that had the greatest response to the fish (that were most inactive and ate the least) were those that did not survive, and therefore they were not included in this behavioral study. However, this does not explain the low activity of inexperienced native juveniles in both trials with predators present and absent. There was 34% mortality of invaded range crayfish in mesocosms with fish present, so results from the behavioral study better represent the variation in invaded range genotypes. In combination, these data suggest that both native and invaded range crayfish respond to predatory fish presence by reducing their activity level. If there had not been mortalities, we may have found that experienced native range crayfish had an equal or greater reduction in activity in the presence of predatory fish than invaded range crayfish, similar to what we observed in adult crayfish.

In addition to the differences we observed in activity between native and invaded range juvenile crayfish, we observed differences in escape behaviors. Crayfish collected as eggs from the native range typically exhibited tail flip behavior at least once during the trial, but invaded range crayfish often did not. This may be an adaptation to flow conditions. In the native range, *O. rusticus* inhabit lotic waters, so juveniles may be able to effectively escape predation by propelling themselves into the current. Drift is a common mechanism by which invertebrates escape predation in lotic systems (Wooster and Sih 1995). However, in lentic waters, which *O. rusticus* inhabit in the invaded range, predators may be able to more easily capture juvenile crayfish in the water column, so tail flip behavior may not be advantageous. Previous research on crayfish in the invaded range of *O. rusticus* indicates that in the absence of flow swimming by crayfish increases their vulnerability to predation (Garvey et al. 1994).

Mechanisms responsible for behavioral differences

Behavior of juvenile *O. rusticus* in the absence of predators mainly differed between the native and invaded range instead of within each range, possibly because of genetic differences between crayfish from each range. Our experimental design does not allow us to rule out the influence of maternal or epigenetic effects on behavior. However, we collected crayfish from diverse habitats within each range, including a range of stream sizes in the native range and lakes with different densities of rusty crayfish (and therefore different littoral communities, resource availability, and predation regimes; Wilson et al. 2004) in the invaded range. If the influence of the environment on parents was important for juvenile crayfish behavior, it is likely that we would have observed differences in behavior between crayfish collected as eggs from different locations within each range. There was no effect of collection location within the native range on the behavior of juvenile *O. rusticus*. In addition, within predator-absent trials, we consistently observed higher average crayfish activity in juveniles from the invaded range than those from the native range, but invaded range juveniles from High Lake had higher activity than those from Big or Papoose Lakes. Interestingly, High Lake had the lowest abundance of *O. rusticus* (4 per trap) compared to other invaded range lakes (19 and 35 per trap; Sargent and Lodge 2014), and it is possible the low density within this lake could select for individuals with high activity levels. Overall, activity levels were consistently different between the two ranges, suggesting that behavior has diverged between the ranges, and that the divergence we observed is not dependent on the site where crayfish were collected.

Within the native range, we sampled three different tributaries to the Ohio River, and each sampling location was 50–100 km apart. The source location of native range crayfish introduced to the invaded range is unknown; thus, it is possible that the introduction came from a different drainage than we sampled. *O. rusticus* are native to the Ohio River drainage and populations were likely originally restricted to the Ohio River and tributaries including: the Great Miami and Scioto River drainages in southwestern Ohio, the Whitewater River drainage in southeastern Indiana, and the Licking, Salt, and Green River drainages in northern Kentucky (Hay 1896; Taylor 2000; Thoma and Jezerinac 2000). Additional populations have been recorded from additional streams in central and northern Ohio and Indiana (Taylor 2000), but these populations may be from early introductions (Thoma and Jezerinac 2000). Our sampling locations were within or between the Great Miami and Scioto River drainages in southwestern Ohio. We cannot rule out the possibility that there is more variation in *O. rusticus* behavior within the native range than we observed from the sites that we sampled. However, because the behavior we observed was consistent among juveniles from all native range collection locations, it is likely that the differences between ranges represent divergence that occurred during or after the introduction.

In addition to divergence in behavior between the native and invaded range, our experiment demonstrated a strong effect of experience on crayfish activity in the presence of predators, but not on activity level when predators were absent. Further, the magnitude of behavioral differences was similar when comparing crayfish from different ranges and crayfish raised with and without predators. Behavioral differences between native and invaded range crayfish were most pronounced when predators were absent: in trials without fish, juveniles from the invaded range were 67% more active on average than those from the native range. Behavioral differences between crayfish that were experienced or inexperienced with predators were most pronounced when predators were present: in trials with fish, inexperienced juveniles were 87% more active on average than experienced juveniles. Overall, these data suggest that activity level in the absence of predators has diverged between the two ranges, but that the behavior of crayfish in the presence of a predator is plastic and largely depends on their prior experience.

In other invertebrates, increased plasticity often evolves in response to environmental change such as introduction to a novel environment (Crispo 2010). For example, blue mussels in the Gulf of Main rapidly adapted to the presence of a nonindigenous predatory crab by thickening their shells when its cue was detected (Freeman and Byers 2006), and the non-indigenous green grab introduced to this region demonstrated plasticity in claw morphology in response to thicker shells of their molluscan prey (Baldridge and Smith 2008). Further, in response to the addition of planktivorous fish to a pond, daphnia evolved rapidly, toward more plastic phototactic behavior (Cousyn et al. 2001). Similar to these findings, in this experiment invaded range juveniles displayed greater behavioral plasticity than native range juveniles in response to the presence of a predator. Invaded range juveniles had reduced activity in the presence of the fish, even when they were raised without fish. However, there was no trend indicating a similar response in native range juveniles. Further, the significant interaction between range and experience on the occurrence of feeding during the trial indicates that invaded range crayfish may have a greater capacity for plasticity than native range crayfish. The occurrence of feeding was similar between experienced and inexperienced crayfish from the native range, but within crayfish from the invaded range, inexperienced crayfish were more likely than experienced crayfish to feed during the trial. We did not, however, find an interaction between experience and range on overall activity. If invaded crayfish do have a greater capacity for behavior plasticity, this trait may allow invaded range crayfish to succeed across habitats with diverse predator communities, which is likely to be beneficial during the spread phase of an invasion.

The strong effect of experience on antipredator behavior in juveniles can inform our interpretation of the adult behavioral results because the adult crayfish had experience with predators prior to collection. We did not collect data on predator abundance, but within the native range, it is possible that the reduced behavioral response of Great Miami drainage crayfish to predatory fish could have been due to reduced prior experience of these crayfish with smallmouth bass predators. Alternatively, there may have been greater mortality in this location of juveniles that had a strong behavioral response to fish (Grafen 1988), and those individuals would not be included in the population as adults.

Further, the greater behavioral response of native range adults to fish compared to that of invaded range adults could be due to greater exposure to predatory fish. However, we think this is unlikely because we collected invaded range crayfish from lakes with substantial smallmouth bass populations. Lake Ottawa, in particular, has abundant, large smallmouth bass because regulations require anglers to release this species (Baldridge and Lodge 2013), and thus we believe crayfish from this lake would have had much experience with smallmouth bass consuming conspecifics. Therefore, native range crayfish probably had equal or lesser exposure to predators than invaded range crayfish, which suggests that the greater behavioral response of adult native range crayfish to predators was not due to experience.

Without predators present, mean activity was slightly higher in native range adults than invaded range adults and native range adults tended to consume the worm more frequently. These data do not support our hypothesis that invaded range crayfish have greater foraging rates; however, it is unclear whether these results are due to reduced exposure to predators in the native range, greater loss of inactive juveniles in the native range, or to genetic differences that manifest when crayfish are adults. There was also a tendency of invaded range adults to use the shelter more frequently during the trial, but this may be because active individuals encounter the shelter more often.

While rearing *O. rusticus* from the native and invaded range in common conditions demonstrated divergence in antipredator behavior, it is unclear whether the same behaviors would be observed if crayfish were raised in conditions more representative of the native range. For example, mesocosm conditions such as temperature, water chemistry, and/or flow may have more closely resembled invaded range habitat than native range habitat. Therefore, if crayfish are locally adapted to their environment, native range crayfish may have been in sub-optimal condition after we raised them in mesocosms. However, we observed the most tail flips in trials with native range juveniles, suggesting they are capable of energetically costly behavior, and while they were less active than invaded range juveniles, they spent a mean of 40% the trial walking. Thus, we expect that the differences in behavior are not likely due to negative impacts of the mesocosm conditions on native range juveniles. Conducting a similar experiment where *O. rusticus* from both ranges are raised in conditions that reflect native range habitat would provide additional insight into how local adaptation contributes to behavioral differences between ranges.

Ecological significance

The behaviors we tested are relevant to interpreting *O. rusticus* impacts on freshwater communities. Our behavioral plasticity results highlight the capacity for early exposure to fish predators to induce enhanced anti-predator behaviors among crayfish. In addition to the suppression of activity that resulted when predatory fish were in the immediate vicinity, crayfish that were raised with predatory fish exhibited reduced activity levels in general, and therefore are likely to have lesser impacts. The greater level of activity in invaded range *O. rusticus* compared to native range *O. rusticus* is likely to cause greater impacts on lower trophic levels and increased energy flow to predators in the invaded range because crayfish are investing more time in foraging and less in predator avoidance.

If the behaviors we observed in invaded range crayfish are commonly selected for when crayfish are introduced to new locations, such as when conspecific densities are low or when crayfish are in the bait trade, the introduction process may often enhance the ecological impacts of crayfish. In addition to our results for *O. rusticus*, previous studies have also found greater foraging rates among some invasive populations of signal crayfish (*Pacifastacus leniusculus*) compared to native populations (Pintor et al. 2008). To our knowledge, differences in foraging behavior and growth have not been compared between other native and invaded range populations of crayfish. Nonindigenous crayfish have caused major ecological and economic impacts globally, including extirpation of native crayfishes, harm to fisheries, and altered lake and stream ecosystems (Lodge et al. 2000, 2012). If there are parallel changes in behavior across independent crayfish introductions, these changes may contribute to the strong impacts of invasive crayfish on freshwater communities. Further, our results suggest that invaded range *O. rusticus* have greater behavioral plasticity than those from the native range, which is likely to be beneficial during the spread phase of an invasion. The importance of evolution during invasions is gaining attention (Phillips et al. 2010; Flory et al. 2011; Colautti and Lau 2015), and our results provide support for contemporary evolution enhancing the impacts of invasive species.

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