

ARTICLE

# Density-Dependent Effects of Invasive Red Swamp Crayfish *Procambarus clarkii* on Experimental Populations of the Amargosa Pupfish

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## Abstract

The adverse effects of invasive species are expected to be proportional to their relative densities. However, interference competition among conspecifics when invasive species are at high densities could limit such effects. These alternative hypotheses inspired us to test the density-specific effects of red swamp crayfish *Procambarus clarkii* on experimental populations of the Amargosa Pupfish *Cyprinodon nevadensis amargosae*. The presence of crayfish had a significant influence on the survival of adult pupfish. In allopatry, adult pupfish survival was nearly 100%. However, the presence of crayfish resulted in significantly lower survival rates for adult pupfish, 84% and 69% survival for the low- and high-density crayfish treatments, respectively. Crayfish also significantly affected the production of juvenile pupfish, with high juvenile production in the allopatric (705 juveniles/mesocosm) and low-density crayfish treatments (705 juveniles/mesocosm). Juvenile production in both of these groups was significantly higher than that in the groups sympatric with high-density crayfish (271 juveniles/mesocosm). The same pattern was observed when we evaluated the number of juvenile pupfish that were produced per adult female. We tested the hypothesis that interference competition among the crayfish would decrease predator efficacy by comparing the high-density crayfish treatment with a fourth high-density crayfish treatment wherein the crayfish were tethered. There was no significant difference in the rate of adult survivorship of the Amargosa Pupfish in the tethered and untethered high-density treatment groups (70% and 69%, respectively). However, tethering resulted in a significant increase in juvenile production in the high-density crayfish treatments (493 and 271 juveniles per mesocosm were produced in the tethered and untethered groups, respectively). The same patterns were observed when we examined the number of juvenile pupfish that was produced per adult female. These findings are inconsistent with the interference competition hypothesis, while supporting the hypothesis of density-dependent effects of crayfish on Amargosa Pupfish populations. These findings suggest that reducing crayfish density will be a beneficial management tool for reducing the effects of crayfish on benthic fish populations.

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The introduction of invasive species is a major driver for the current extinction crisis, with global-level adverse effects on aquatic ecosystems at nearly all macro and microscopic scales (Clavero and García-Berthou 2005; Ilhéu et al. 2007; Villéger et al. 2011; Gallardo et al. 2016). In North America alone, aquatic ecosystems have been severely affected as

reflected by the extinctions of 3 genera, 27 species, and 13 subspecies (Miller et al. 1989). Specifically, 68% of the fish extinctions have been at least partially attributed to introductions of invasive species (Miller et al. 1989).

The adverse effects of invasive species may be particularly problematic for rare endemic species that have

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Received July 8, 2019; accepted November 5, 2019

evolved in simple ecosystems, presumably due to evolutionary naïveté (Miller 1961; Minckley and Deacon 1968; Courtenay and Deacon 1983; Cox and Lima 2006). Examples of such effects are reflected by the widespread declines of native fishes in the North American Southwest that are associated with invasions by nonnative species. Today, many of these taxa are extinct (Miller et al. 1989) or of serious conservation concern (Pister 1974; Miller et al. 1989), often due to the introduction of nonnative species (Minckley and Deacon 1968; Soltz and Naiman 1978; Pool and Olden 2012). For example, the Ash Meadows Killifish *Empetrichthys merriami*, the Raycraft Ranch Poolfish *E. latos concavus*, the Pahrnagat Spinedace *Lepidomeda altivelis*, and the Monkey Spring Pupfish *Cyprinodon* sp. went extinct following the establishment of nonnative species (Miller et al. 1989).

The adverse effects of invasive species on native species often occur only after a nonnative species has become established, suggesting that their effects may be proportional to their densities (Ricciardi 2003). For example, species such as the Yaqui Topminnow *Poeciliopsis sonoriensis* rapidly declined coinciding with the establishment of nonnative Western Mosquitofish *Gambusia affinis* (Minckley and Deacon 1968; Meffe 1984). Yaqui Topminnow abundance was inversely correlated with Western Mosquitofish abundance, with periodic flash floods reducing mosquitofish abundance followed by increases in topminnow populations (Meffe 1984). In another example, the decline and eventual extirpation of the Lake Michigan population of Mottled Sculpin *Cottus bairdii* was directly correlated with the increasing density of the invasive Round Goby *Neogobius melanostomus* (Janssen and Jude 2001). Similarly, crayfish have been shown to have adverse effects on fish populations that are associated with increasing densities, as the rate of egg depredation was density dependent (Fitzsimons et al. 2002; Peay et al. 2009). However, the adverse effects that are caused by invasive species can be acute even when invasive species are at relatively lower densities (Benkwitt 2013). For instance, the increasing density of Red Lionfish was shown to have only a small additive effect on the endemic species, whereas a solitary lionfish had the largest effect on the richness of local species (Benkwitt 2013).

These contrasting findings suggest that density-dependent effects may depend on the context. For instance, the effects of invasive crayfish on experimental populations of the White Sands Pupfish *C. tularosa* were shown to be proportional to crayfish densities (Rogowski and Stockwell 2006), but Thomas and Taylor (2013) reported that the effects of crayfish on small benthic fishes were highest when crayfish were at low densities, possibly due to intraspecific interference competition that occurred when crayfish were at high densities (Thomas and Taylor 2013). In fact, others have reported that conspecific interactions

reduced crayfish predation (Martin and Corkum 1994; Corkum and Cronin 2004).

A critical re-evaluation of the adverse effects of crayfish on endemic species is of particular interest because crayfish threaten the recovery of numerous fish species (Williams and Sada 1985; Guan and Wiles 1997; Carpenter 2005; Rogowski and Stockwell 2006; Peay et al. 2009; Setzer et al. 2011). Therefore, understanding the density-dependent effects of crayfish may be useful for evaluating various management strategies such as the targeted harvest of crayfish. In past efforts, managers have actively reduced crayfish densities to reduce their effects on populations of the endangered Ash Meadows Amargosa Pupfish *Cyprinodon nevadensis mionectes* (Scoppettone et al. 2011; Kilburn 2012).

In the current study, we examined whether the adverse effects of crayfish on experimental populations of the benthic Amargosa Pupfish *Cyprinodon nevadensis amargosae* are correlated with the density of red swamp crayfish *Procambarus clarkii*. We also tested whether limiting intraspecific interactions among crayfish would mitigate the outcomes within high-density treatments. We tested for crayfish effects by evaluating adult survivorship and juvenile production rates for pupfish among (1) allopatric pupfish populations, (2) pupfish populations in the presence of crayfish at low-density, (3) pupfish that were sympatric with crayfish at high densities, and (4) pupfish that were sympatric with tethered high-density crayfish. The fourth treatment allowed us to evaluate whether intraspecific interactions mediate the effects of crayfish on juvenile production and adult survivorship of the Amargosa Pupfish in the high-density crayfish treatments. If interference competition limits the efficacy of crayfish predation, treatments with tethering should result in lower adult survival rates.

## METHODS

Experimental mesocosms were established in circular 1,211-L rigid plastic tanks (1.52 m in diameter and 0.91 m in depth) that were located on North Dakota State University's Agricultural Experiment Station in Fargo. Thirty-two mesocosms were set up with approximately 950 L of dechlorinated water, with water levels maintained through additions of dechlorinated water. Each tank contained 0.03 m<sup>3</sup> of river rock, artificial benthic cover material (five 0.5 m-long clumps of plastic mesh to simulate aquatic plants) that was added uniformly in all tanks to create breeding substrate, and three reclaimed PVC vinyl structures that simulated aquatic vegetation (Fishiding). Each unit had a solid, cemented PVC base with PVC strips with widths of 1.9–2.5 cm and lengths of 20.3–61.0 cm. The strips were hand-molded into various shapes to enhance the structure and simulate aquatic vegetation.

Paulson (2019) reported that adding these elements to mesocosms increased the spatial structure by 30% as measured by using a rugosity index (Risk 1972).

The mesocosms were inoculated with a mixture of plankton from a local semipermanent wetland three weeks prior to adding the fish. All of the tanks were aerated with an air stone to maintain levels of dissolved oxygen at ~8 to 9 mg/L. The water temperatures changed relative to environmental conditions and ranged from 18.8°C to 28.7°C, providing suitable temperatures for successful reproduction by Amargosa Pupfish (24–30°C; Shrode and Gerking 1977). Further, the tanks were checked daily for mortalities and to assure continuous airflow. Regular water quality tests revealed nonstressful conditions for dissolved oxygen, ammonia, and nitrate levels.

Amargosa Pupfish were collected from River Springs in Mono County, California. This population was established in 1940 with Amargosa Pupfish and Salt Creek Pupfish *C. salinarius*, but molecular work suggests that only Amargosa Pupfish persisted (Steve Parmenter, California Department of Fish and Game, personal communication). Crayfish do not occur at River Springs.

The red swamp crayfish that were used in this experiment were sourced from Carolina Biological suppliers. We used a randomized block design with eight blocks of the following four treatments: (1) allopatric pupfish, (2) sympatric pupfish with low-density crayfish, (3) sympatric pupfish with high-density crayfish, and (4) sympatric pupfish with high-density tethered crayfish. Allopatric and sympatric refer only to the experimental set-up for the Amargosa Pupfish that were maintained alone or in the presence of crayfish, respectively. All of the tanks were stocked with eight pupfish with a sex ratio of 3:1 (female:male); however, the final sex ratio in a few tanks deviated from this ratio probably due to misidentified sneaker males. Thus, we evaluated juveniles produced per surviving female. The fish were measured prior to introducing them to the mesocosms. The range of standard lengths for the females was 26–49 mm, and that for males was 31–50 mm. We standardized fish biomass across all of the mesocosms.

Low and high crayfish densities were one and four crayfish per tank, respectively, with carapace lengths that were within the range of 44–51 mm. Deceased crayfish were replaced with crayfish of a similar size. This approach was intended to avoid drastic changes in crayfish densities, as even the loss of one crayfish from a high-density tank would decrease crayfish density by 25%, a reduction that would be unlikely to occur under field conditions.

For the tethered-crayfish treatment, the crayfish were tethered by attaching a small loop of fishing line to a 0.1 mm flexible metal wire, with the fishing line glued to the carapace and held in place by a small 2.5- × 2.5-mm

square of Parafilm. The tether lengths were standardized to 0.75 m in length and anchored to the edge of the tank at every 90°, limiting all interactions among the crayfish. The crayfish were checked daily to ensure that the tethers were intact and to retether them as necessary to minimize conspecific interactions.

Supplemental tropical fish food was provided every day within each tank at rates of ~2–3% of the initial fish biomass. We also provided Aquatic Arts sinking pellets as a supplemental food source for the crayfish twice weekly at rates that were ~5% of the initial crayfish biomass.

The experiment was initiated on June 1, 2017 and terminated after 8 weeks when we enumerated the number of adult and juvenile Amargosa Pupfish for each tank. Juvenile fish were not measured to reduce stress because the fish were saved for future experimental work. We used the number of surviving adults to estimate the percentage of adult survival, and we also calculated the number of juveniles that were produced per surviving female.

All of the data that were collected were analyzed by using JMP Pro V14 statistical software. We used parametric ANOVA with the block option to analyze the differences in adult survival rates, juvenile productivity, and number of juveniles produced per adult female for Amargosa Pupfish among three treatments: (1) control, (2) low-density crayfish, and (3) high-density crayfish. These analyses were followed by a post hoc Tukey–Kramer honestly significantly different test for pairwise comparisons. Values were considered significant at  $\alpha < 0.05$ . The high-density tethered crayfish treatment was compared only with the high-density crayfish treatment to determine whether limiting interference competition influenced the adult survival and juvenile production rates of Amargosa Pupfish.

## RESULTS

The mesocosms provided suitable environmental conditions, as mesocosms containing allopatric Amargosa Pupfish had overall high rates of adult survivorship and juvenile production. There was no significant block effect for any of the following tests. The presence of crayfish negatively affected adult pupfish survival ( $F = 7.18$ ;  $df = 2$ ;  $P = 0.001$ ). When allopatric, the percentage of adult survival was  $96.9 \pm 0.61$  (mean percentage of survival  $\pm$  95% confidence interval). In the presence of crayfish, there were significant declines in adult pupfish survival both for the low-density crayfish treatment ( $84.4 \pm 8.96$ ;  $P = 0.04$ ) and the high-density crayfish treatment ( $68.8 \pm 12.25$ ;  $P = 0.0013$ ). The difference in adult pupfish survivorship between the two crayfish treatments approached statistical significance ( $P = 0.063$ ; Figure 1).

The presence of crayfish had a significant effect on the number of juvenile Amargosa Pupfish that were produced

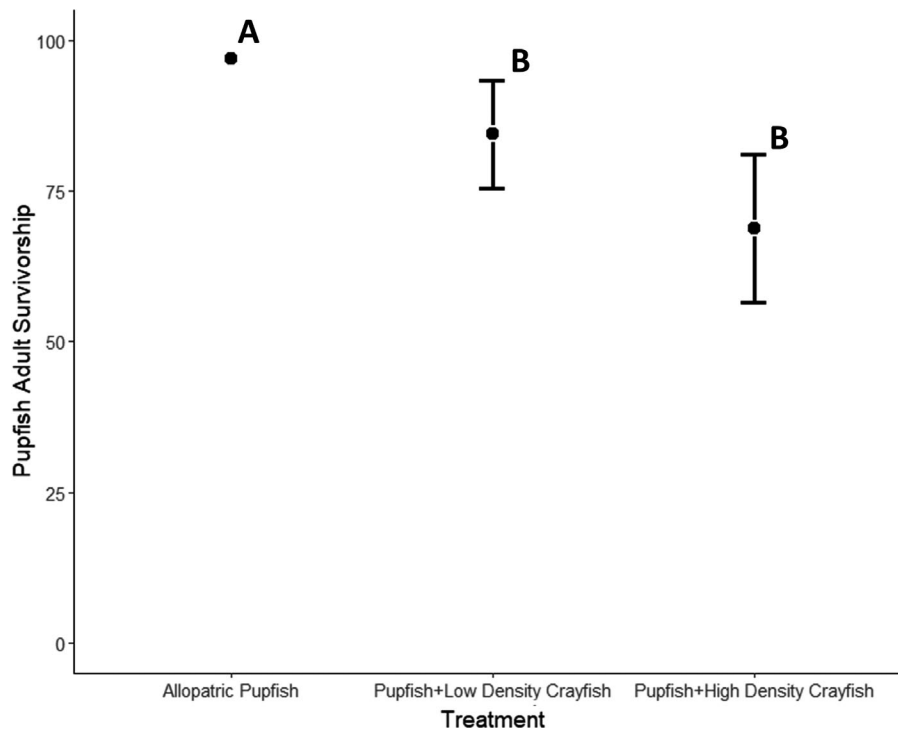


FIGURE 1. Average percentage of survivorship of adult Amargosa Pupfish populations in allopatry, in sympatry with low-density crayfish, and in sympatry with high-density crayfish. The bars indicate  $\pm 95\%$  confidence intervals. The treatments that share a letter were not significantly different.

( $F=9.98$ ;  $df=2$ ;  $P=0.0001$ ). Juvenile production did not differ between the allopatric ( $705 \pm 65.32$  juveniles per mesocosm [mean  $\pm 95\%$  CI]) and the low-density crayfish ( $705 \pm 151.2$ ) treatments ( $P=0.98$ ). However, the fish in both the allopatric and low-density treatments had significantly higher rates of juvenile production than the fish in the high-density crayfish treatments did ( $271 \pm 70.26$ ;  $P < 0.0001$  and  $P=0.0002$ , respectively; Figure 2).

The presence crayfish in the high-density treatment had a significant effect on the number of juvenile Amargosa Pupfish that were produced per surviving female ( $F=9.73$ ;  $P=0.001$ ). Juvenile production per surviving female did not differ between fish in the allopatric ( $132.41 \pm 26.81$  [mean  $\pm 95\%$  CI]) and low-density crayfish treatments ( $163.4 \pm 141.12$ ;  $P=0.34$ ), but the fish in both of these treatments produced significantly more juveniles than those in the high-density treatment did ( $69.8 \pm 19.86$ ;  $P=0.022$ ;  $P=0.0008$ , respectively; Figure 3).

Tethering the crayfish had no significant effect on adult survivorship among Amargosa Pupfish ( $F=0.037$ ,  $df=1$ ;  $P=0.85$ ). Adult survival was  $68.8 \pm 12.25\%$  and  $70.3 \pm 10.29\%$  in the presence of high-density free-ranging crayfish and high-density tethered crayfish, respectively (Figure 4). For the two high-density crayfish treatments, juvenile production was significantly higher for the fish in the tethered crayfish treatment ( $493 \pm 184.11$  [mean  $\pm 95\%$  CI]) than for those in the free-ranging crayfish treatment

( $271 \pm 70.26$ ;  $F=4.9$ ;  $df=1$ ;  $P=0.044$ ; Figure 5). However, the number of juveniles that were produced per surviving female was not significantly different between fish that were in the high-density untethered ( $69.8 \pm 19.86$ ) and tethered crayfish treatments ( $114.94 \pm 43.63$ ;  $F=3.55$ ;  $P=0.081$ ; Figure 6).

## DISCUSSION

Our results demonstrated that the presence of crayfish had significant effects on adult survivorship of Amargosa Pupfish. Compared with pupfish in the allopatric treatments, adult survival was statistically lower when the fish were sympatric with crayfish, with a trend toward lower survival when crayfish were at higher densities. This suggests that the mere presence of crayfish may have adverse effects on the overall annual survivorship of Amargosa Pupfish and that effects are proportional to crayfish density. Similarly, Guan and Wiles (1997) reported that increasing crayfish densities had significant negative relationships for both the Stone Loach *Noemacheilus barbatulus* and the European Bullhead *Cottus gobio* within a British lowland river.

A reduction of juvenile production was also associated with increasing crayfish density for Amargosa Pupfish within our mesocosm experiment. The presence of crayfish in the low-density treatment had no effect on the

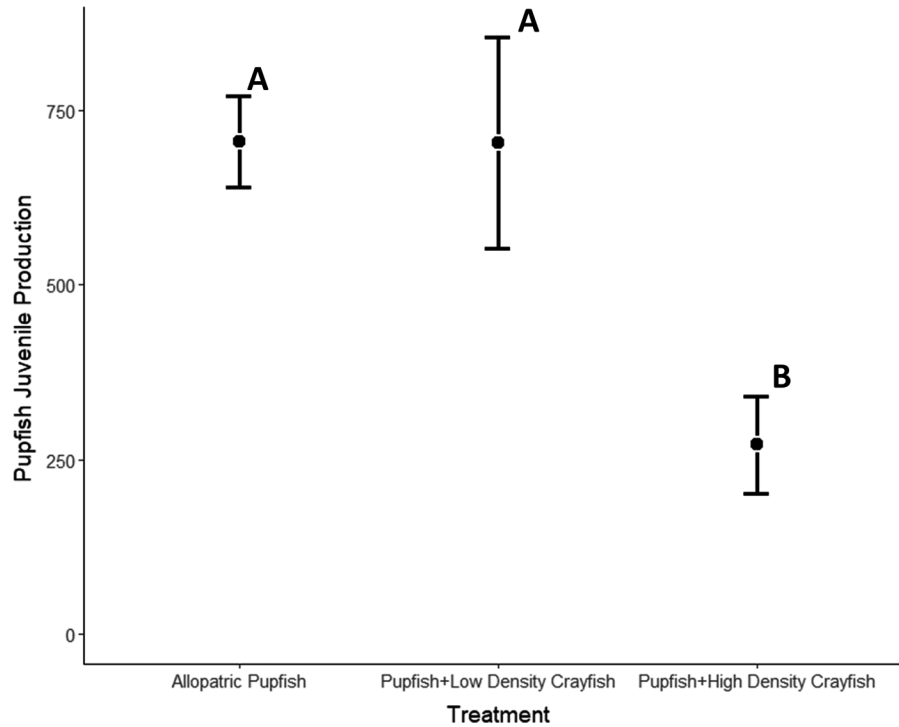


FIGURE 2. Average number of juveniles that were produced ( $\pm 95\%$  confidence intervals) for Amargosa Pupfish populations in allopatry, in sympatry with low-density crayfish, and in sympatry with high-density crayfish. The treatments that share a letter were not significantly different.

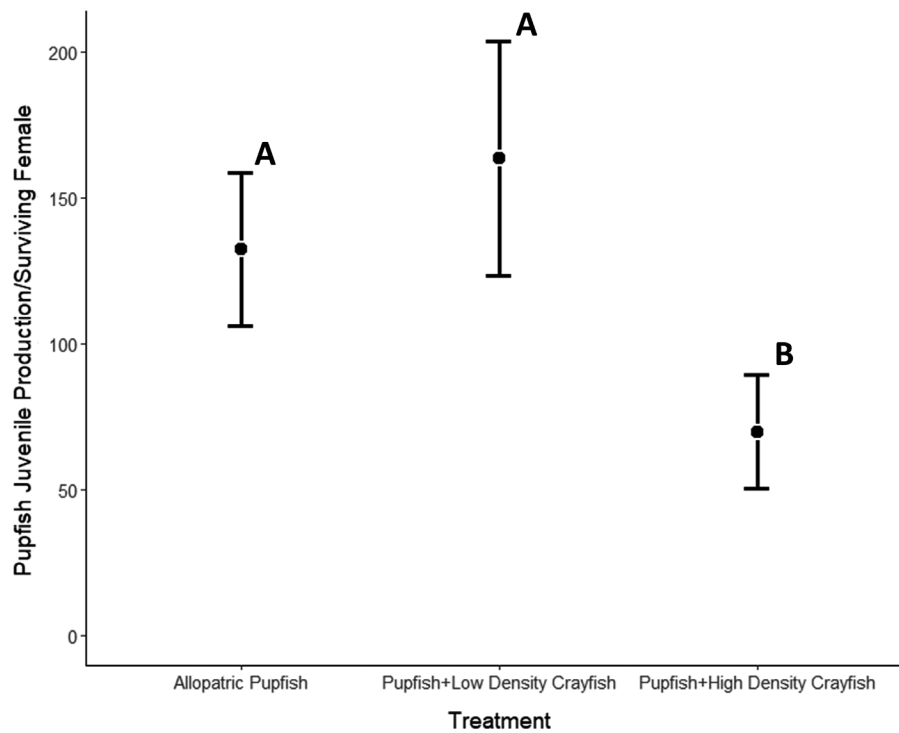


FIGURE 3. Average number of juveniles that were produced per surviving female ( $\pm 95\%$  confidence intervals) for Amargosa Pupfish populations in the three primary treatment conditions. The treatments that share a letter were not significantly different.

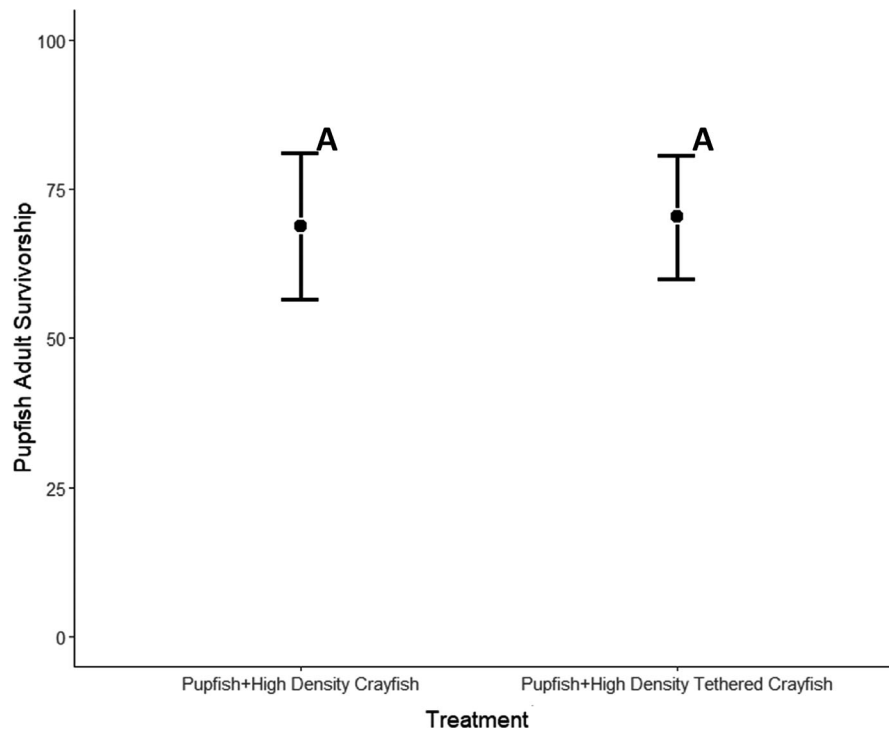


FIGURE 4. Adult percentage of survivorship ( $\pm 95\%$  confidence intervals) for Amargosa Pupfish populations in sympatry with high-density crayfish and in sympatry with high-density tethered crayfish. The treatments that share a letter were not significantly different.

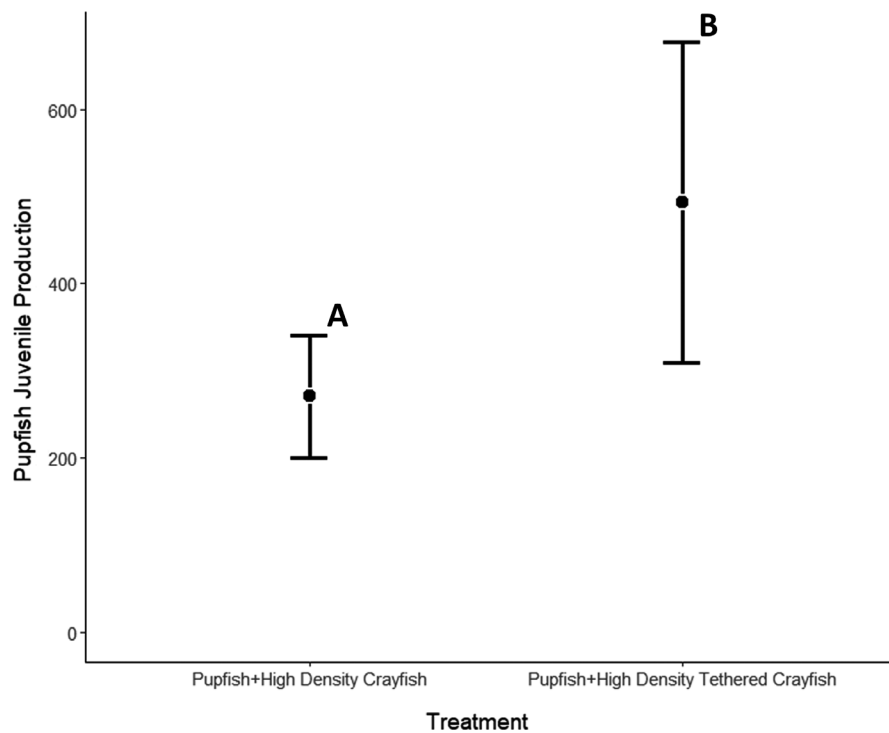


FIGURE 5. Average number of juveniles that were produced ( $\pm 95\%$  confidence intervals) for Amargosa Pupfish populations in sympatry with high-density crayfish and in sympatry with high-density tethered crayfish. The treatments that share the same letter were not significantly different.

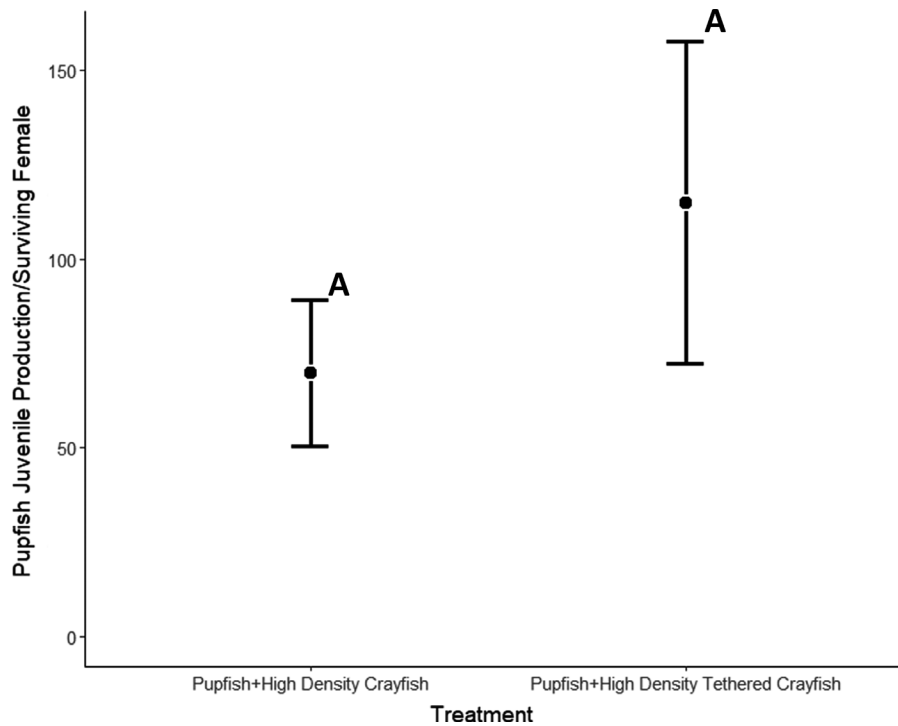


FIGURE 6. Average number of juveniles that were produced per surviving female ( $\pm 95\%$  confidence intervals) for pupfish populations in sympatry with high-density crayfish and in sympatry with high-density tethered crayfish. The treatments that share the same letter were not significantly different.

production of juvenile pupfish; however, juvenile production declined by over 60% in the presence of crayfish at high-density. We observed a similar pattern for the number of juveniles produced per female, with approximately a 50% reduction when the fish were sympatric with crayfish at high densities. This suggests that crayfish either actively preyed upon juveniles or disrupted the breeding habitat (Ilhéu et al. 2007).

Our findings are consistent with those in other systems where the adverse effects of an invasive species are proportional to its relative densities (Ricciardi 2003). Previous studies have documented substantial effects of nonnative crayfish on invaded systems (for a review see Ilhéu et al. 2007), and many others have reported density-dependent predation of crayfish on the eggs of various salmonid species (Savino and Miller 1991; Fitzsimons et al. 2002; Peay et al. 2009). These results also demonstrate reproducible effects for a similar system involving crayfish and Amargosa Pupfish. Rogowski and Stockwell (2006) reported significant density-dependent effects of crayfish on experimental populations of the White Sands Pupfish. Therefore, these studies suggest that pupfish populations are likely to decline in response to increasing densities of nonnative crayfish.

Our results were inconsistent with the hypothesis that interference competition among crayfish at high-density would enhance pupfish survival. To test this hypothesis, we

included a treatment with tethered crayfish at high-density and compared the results with those for the high-density treatment with free-ranging crayfish. The interference competition hypothesis predicts that Amargosa Pupfish survival should decrease when crayfish interference is limited. However, we found that tethering had no effect on survivorship among adult fish. These findings suggest that interference competition between crayfish did not constrain the predation effects of the crayfish on the adult pupfish. Contrary to expectations from the interference competition hypothesis, juvenile production increased when conspecific interactions were constrained via tethering. It is worth noting that while tethering limited interference competition, it also limited the movement of the crayfish, which in turn may have limited their effects on juvenile production because a predator-free refuge may have increased juvenile production.

Collectively, our work shows that the presence of crayfish limited adult survival rates among Amargosa Pupfish and the effects were proportional to crayfish densities. However, we recognize some limitations of our experimental design. First, we used commercially available crayfish as opposed to wild-caught red swamp crayfish, which were used in earlier studies (Rogowski and Stockwell 2006; Thomas and Taylor 2013). It has been shown that intraspecific aggression within crayfish may vary between

different species of crayfish, so adverse effects on certain benthic fishes may be species specific with respect to the invasive crayfish (Atkinson 1989; Pintor et al. 2008). Our findings with commercially sourced crayfish were similar to those reported by Rogowski and Stockwell (2006), who used wild-caught virile crayfish *Orconectes virilis*. However, it is possible that the crayfish species that was used by Thomas and Taylor (2013) had much higher intraspecific aggression than the species that was used our work or in the work reported by Rogowski and Stockwell (2006). Second, we did not record the sex of the crayfish that were used in this experiment. We are unaware of work that has evaluated whether predation efficiency on fish differs between male and female crayfish; however, crayfish sex did not affect predation efficiency on zebra mussels (Martin and Corkum 1994; Zu Ermgassen and Aldridge 2011). However, it is important to note that crayfish predation has been shown to be correlated with the body size of crayfish (Bovbjerg 1956), and we used crayfish of similar sizes across the treatments.

Our results suggest that reducing crayfish densities may be an effective management tool for minimizing the adverse effects of crayfish. However, continual harvest is necessary because female crayfish are capable of laying 800 eggs within one spawning event, resulting in population recovery if overharvest does not result in complete removal (Holdich et al. 1999). Such active management has been applied for controlling invasive crayfish in Ash Meadows National Wildlife Refuge (Scoppettone et al. 2011; Kilburn 2012). Annual mechanical removal of crayfish was correlated with apparent increased population sizes for both Ash Meadows Speckled Dace *Rhinichthys osculus nevadensis* and Ash Meadows Amargosa Pupfish (Scoppettone et al. 2011). Our results combined with these observations suggest that a similar approach may be widely profitable for the conservation of other native fishes. For example, mechanical removal of nonnative crayfish may prove to be beneficial to many salmonids, as decreasing crayfish density should increase salmonid egg survival (Peay et al. 2009).

#### ACKNOWLEDGMENTS

We would like to thank M. Snider, B. Gillis, S. Kettelhut, S. Parmenter, S. Goodchild, J. Waraniak, and C. Anderson for their assistance with field work as well as K. Guadalupe (Nevada Department of Wildlife), James Harter (U.S. Fish and Wildlife Service), S. Parmenter (California Department of Fish and Game), and the Poolfish Recovery Implementation Team for providing logistical support. We are grateful to J. Sweetman, M. Harris, J. Waraniak, and three anonymous reviewers for their insightful comments on earlier drafts of this manuscript. We also thank K. Grafton for allowing us to conduct this work in North Dakota State University's Agricultural Experiment

Station. This work was conducted under North Dakota State University Institutional Animal Care and Use Committee Protocol A18054, and the study was supported by the North Dakota State University Environmental and Conservation Sciences Graduate Program and a Desert Fishes Council Conservation Grant. There is no conflict of interest declared in this article.

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