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Brandon L. Paulson and Craig A. Stockwell *

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The Combined Effects of Multiple Invasive Species on Persistence of Experimental Populations of Imperiled Pahrump Poolfish

Brandon L. Paulson [1,2] and Craig A. Stockwell [2,*]

[1] Environmental and Conservation Sciences Program, North Dakota State University, NDSU Box 6050, Fargo, North Dakota, USA 58108

[2] Department of Biological Sciences, North Dakota State University, NDSU Box 6050, Fargo, North Dakota, USA 58108

* Correspondence: Craig.Stockwell@ndsu.edu; Tel.:01-701-429-4748

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Abstract: Many ecosystems have been invaded by more than one non-native species, but research evaluating the combined effects of multiple invasive species has been limited. In the southwest USA, many aquatic systems have been invaded by multiple species such as non-native crayfish and non-native fishes. We used experimental mesocosms to test individual and combined effects of invasive Red Swamp Crayfish, *Procambarus clarkii*, and Western Mosquitofish, *Gambusia affinis*, on endangered Pahrump Poolfish, *Empetrichthys latos*. We found that crayfish alone reduced adult poolfish survival; however, crayfish by themselves had moderate but non-significant impacts on the production of poolfish juveniles. Mosquitofish had no effect on the survival of poolfish adults, but significantly reduced recruitment of juveniles. When both crayfish and mosquitofish were present, both adult survival and juvenile production were significantly decreased. These findings were consistent with the recent decline of a wild poolfish population from over 10,000 fish to less than 1,000 poolfish following the establishment of crayfish and mosquitofish. This study demonstrates that conservation management of the Pahrump Poolfish must have active management and removal of invasive species, otherwise extirpation and eventually extinction will likely occur. This study also provides an example of the compounding effects of multiple invasive species.

Keywords: Empetrichthys; mosquitofish; invasive species; invasional meltdown; crayfish

Key Contribution: Experimental populations of the imperiled Pahrump poolfish were negatively impacted by the presence of crayfish; and mosquitofish which impacted adult survival and juvenile production; respectively

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1. Introduction

The introduction of non-native species has become so widespread that many systems have been invaded by multiple non-native species [1–4]. Once established, invasive species can facilitate the colonization of additional non-native species, an ecological process referred to invasional meltdown [5–7]. Thus, work evaluating the combined effects of multiple species introductions on native species is an important topic of concern for conservation biologists [8,9].

Some studies have shown that multiple invasive species can have substantial impacts on endemic species. The potential for compounded impacts by multiple non-natives is important in many aquatic ecosystems [10]. For example, ballast water exchange introduced Eurasian Zebra Mussel, *Dreissena polymorpha*, and the Round Goby *Neogobius mela nostomus*, resulting in both individual and synergistic impacts on aquatic communities [11,12]. Zebra Mussels altered the

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planktonic community structure that allowed the Round Goby to obtain competitive superiority over endemic species such as the Mottled Sculpin, *Cottus bairdii* [12].

Emergent effects of multiple predators can reduce risk due to interactions among predators or increase risk if prey responses to one predator increases risk to another predator [1]. For example, Palacios et al. [13] discussed the potential implications of introducing novel predators with a piscivorous prey species and found that predator identity determined if there were any positive or negative interactions on the multiple predator effect on prey species persistence. By contrast, Porter-Whitaker et al. [3] reported that prey responses to multiple predators were intermediate to the sole effects of each predator.

A wide variety of invasive species have been directly associated with the decline and extirpation of numerous endemic aquatic species in the southwestern deserts of the United States [14–18]. For example, both Western Mosquitofish, *Gambusia affinis,* and Red Swamp Crayfish, *Procambarus clarkii*, were introduced into the southwest early in the twentieth century [19,20]. The rapid spread of both species was likely facilitated by their rapid population growth rates and broad ecological tolerances [21–23]. Crayfish prey on the adults and larvae of benthic fishes [24,25]., while mosquitofish are voracious predators of fish eggs and larvae [23,26].

The impacts of non-native species on desert aquatic ecosystems have been attributed to predator naiveté of endemic fishes, which evolved in depauperate communities. Specifically, endemic fishes are hypothesized to have lost anti-predator traits as they evolved in simple systems with limited predation and interspecific competition, thus making them vulnerable to invasive predators [14–16,27,28].

The direct effects of both Red Swamp Crayfish and Western Mosquitofish have been independently evaluated amongst numerous experimental studies [24–26,29–31]. Rogowski and Stockwell [30] showed that experimental populations of the White Sands Pupfish, *Cyprinodon tularosa*, declined when sympatric with Virile Crayfish, *Orconectes virilis*, at high densities or when sympatric with mosquitofish; however, the combined effects of crayfish and mosquitofish have not yet been studied empirically.

Understanding the possible interactions of both Western Mosquitofish and Red Swamp Crayfish is critical for resource management because both of these non-native species a are listed as the greatest threat to the various endemic fishes in the Southwestern US [32]. The co-invasion of Red Swamp Crayfish and Western Mosquitofish have been associated with the decline of two refuge populations of the Endangered Pahrump Poolfish, *Empetrichthys Latos*. The largest refuge population of Pahrump Poolfish, at Lake Harriet rapidly declined following the colonization of the lake by Red Swamp crayfish, in 2012, followed by the discovery of Western Mosquitofish in 2015 [33,34]. The poolfish population was estimated at 12,285 poolfish (10,791 – 13,988, 95% Confidence Interval) in 2015, but within one year declined to 362 poolfish (194-741, 9% Confidence Interval). Over the following year, 688 poolfish were captured and relocated to a fish hatchery (644 fish) and Corn Creek (44 fish)[33,34].

This decline of the poolfish population at Lake Harriet inspired us to take an experimental approach to evaluating the combined effects of crayfish and mosquitofish on experimental poolfish populations. Specifically, this paper focuses on ecological relationships among poolfish, crayfish and mosquitofish to replicate the co-invasion of Lake Harriet by these two species. This study tests the synergistic effects of dual species invasion on Pahrump Poolfish.

2. Materials and Methods

Western Mosquitofish were obtained from Sutter-Yuba Mosquito and Vector Control district in Yuba City, CA. Poolfish used in this experiment included a mixture of wild poolfish and lab-reared poolfish. The wild poolfish were collected from on 13 June 2017 from Shoshone Stock Pond (White Pine County, NV) while the lab-reared poolfish were descendants from poolfish originally collected in 2014 from Spring Mountain Ranch State Park, Clark County [31]. Red Swamp Crayfish were sourced from Carolina Biological suppliers Burlington, NC.

Three fish communities were used in this experiment forming a single block within a randomized block design. Each of seven blocks contained a total of three mesocosms including the following treatments: I.) allopatric poolfish, II.) poolfish sympatric with crayfish, and III.) poolfish sympatric with both mosquitofish and crayfish. We did not include a poolfish + mosquitofish treatment because of the limited number of poolfish available for this experiment. Further, three previous experiments consistently showed that mosquitofish effectively eliminated the production of juvenile poolfish [31,35].

Each block of three tanks was replicated seven times for a total of 21 experimental tanks, arranged in a linear sequence. All 21 tanks received seven adult poolfish of indeterminate sex and of indeterminate population of origin (Shoshone Stock Pond 2017 or Spring Mountain Ranch 2014). Four individual crayfish were introduced into two randomly selected mesocosms per block. One of the two crayfish mesocosms within each block was randomly selected to receive mosquitofish, including five gravid females and two males. Crayfish density was maintained by replacing any crayfish that died.

All mesocosms were provided with reclaimed PVC vinyl Fishiding® structures to simulate aquatic plants and to provide spatial structure along with ~57 L of river rock. Supplemental food was provided every day to each tank at rates of ~2-3% of total fish biomass, while crayfish were fed twice weekly. Food consisted of Tetra tropical flake, and Aquatic Arts (Fish, Inverts, and Aquatic Plant) sinking pellets. Water quality was assessed weekly for ammonia and nitrates. All tanks were checked daily for mortalities, and to ensure air flow was constant from air stones. After ten-weeks, the tanks were drained, and juveniles and adults were counted.

Data were analyzed using JMP Pro 17® software. We tested for treatment effects on adult survival, juvenile production and the number of juveniles produced per surviving adult poolfish. We used ANOVA followed by Tukey HSD while maintaining experimental-wise alpha at 0.05. For each test, block was not significant and was eliminated from the final model. Non-parametric analyses produced the same significance levels among treatments for all tests, but here we report the parametric ANOVA results.

Data Availability: Data are available via Dryad. Paulson, Brandon; Stockwell, Craig (Forthcoming 2024). Crayfish & Mosquitofish impacts on Experimental Poolfish Populations [Dataset]. Dryad. https://doi.org/10.5061/dryad.gqnk98sz3

Ethics Approval: This work has been conducted under Fish and Wildlife Service permit TE126141-4, Nevada scientific collecting permit S-34628, and North Dakota State University (NDSU) Institutional Animal Care and Use Committee protocol #A18054.

3. Results

Adult survival (percentage) significantly differed among the three treatments ($F = 16.65$, $P < 0.001$; Figure 1). In allopatry, adult poolfish survival rates were near 100% (95.9± 2.6%; mean ± one standard error of the mean) and significantly higher compared to adult poolfish survival when sympatric with crayfish (53.1 ± 6.0%; $P < 0.001$) and when poolfish were sympatric with both crayfish and mosquitofish (55.1± 7.9%; $P < 0.001$; Figure 1). The latter two treatments did not significantly differ from each other ($P = 0.969$).

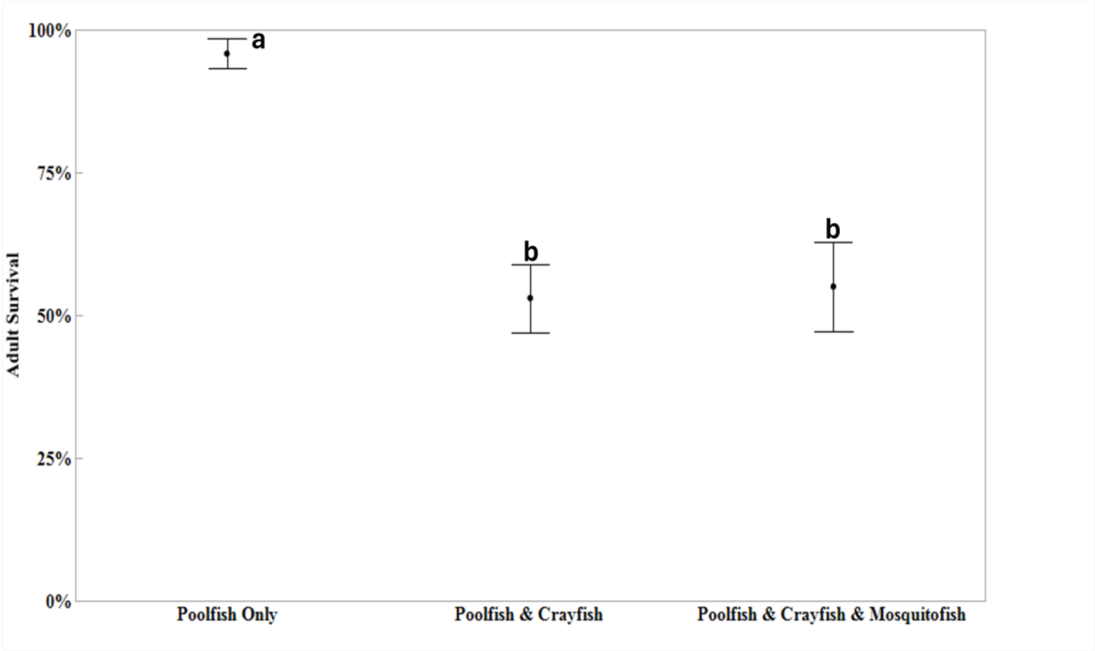

Figure 1. Average adult poolfish survival (+ 95% Confidence Intervals) are shown for populations in mesocosms where poolfish were: I) allopatric poolfish; II) sympatric with crayfish or III) sympatric with both crayfish and mosquitofish. Treatments sharing at least one letter were not significantly different ($p > 0.05$).

Juvenile production differed significantly among the three treatments ($F = 12.56$, $P < 0.001$; Figure 2). Juvenile productivity in mesocosms with allopatric poolfish (91.4 ± 12.0; juveniles per tank), was 41% higher than juvenile production for mesocosms hosting poolfish and crayfish (64.9 ± 19.0), but this difference was not significant ($P = 0.339$). However, juvenile production, which plummeted to near zero (1.9 ± 0.5) when poolfish were sympatric with both crayfish and mosquitofish, was significantly different from both allopatric poolfish ($P < 0.001$) and when compared to the poolfish sympatric with only crayfish ($P = 0.008$; Figure 2).

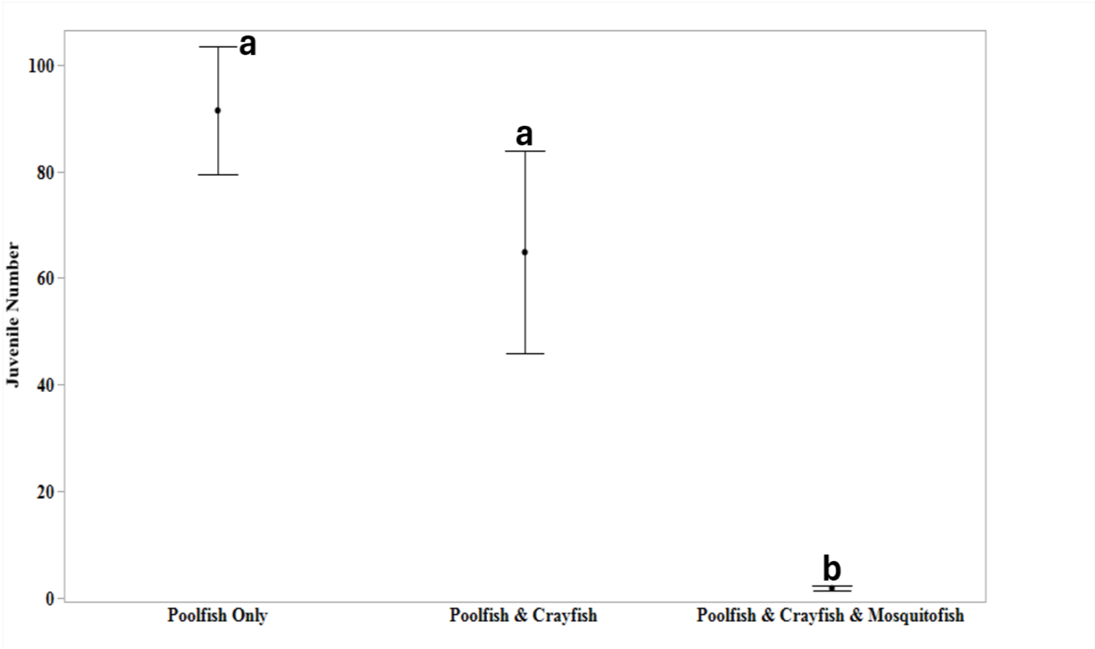

Figure 2. Average juvenile production (+ 95% Confidence Intervals) are shown for populations in mesocosms where poolfish were: I) allopatric; II) sympatric with crayfish or III) sympatric with both crayfish and mosquitofish. Treatments sharing at least one letter were not significantly different ($p > 0.05$).

Due to the high variation in adult survival among treatments, we also examined the number of juveniles per surviving adult. After adjusting for the number of surviving adults, relative juvenile production was significantly different among the three treatments (F = 11.94 ; P < 0.001; Figure 3). Relative juvenile production for mesocosms with allopatric poolfish (13.6 ± 1.7 juveniles/surviving adult) did not differ from mesocosms with poolfish sympatric with crayfish (17.5 ± 4.1 juveniles/surviving adult; P = 0.545). However, relative juvenile production was significantly higher for both of these treatments compared to Poolfish sympatric with both crayfish and mosquitofish (0.5 ± 0.1 juvenile/surviving adult; P < 0.01 and P < 0.001, respectively).

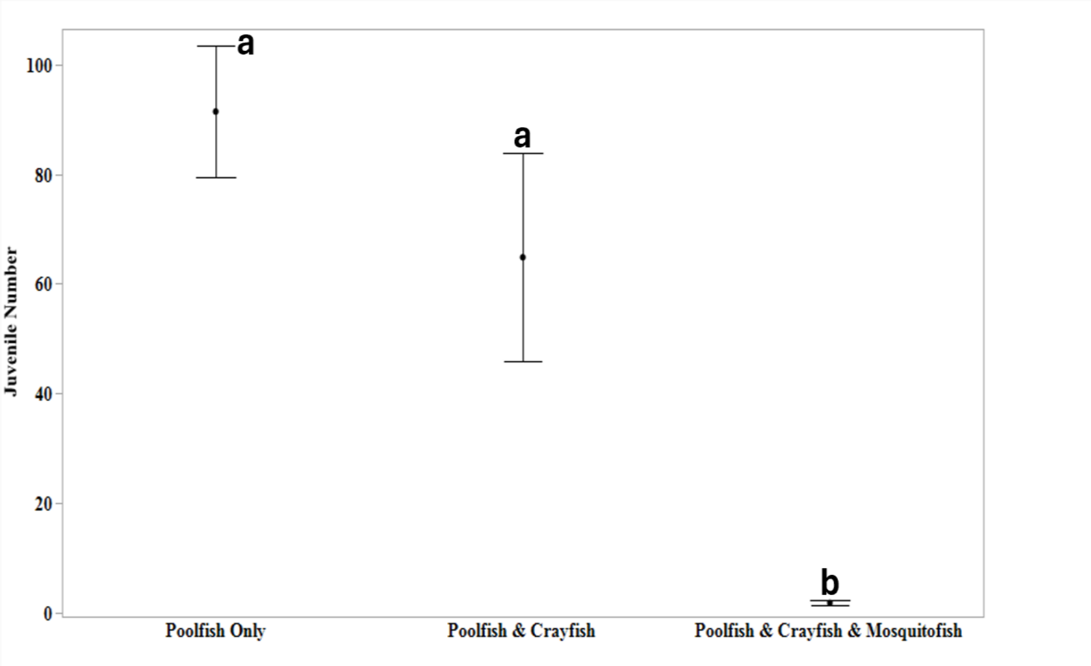

Figure 3. Average relative recruitment defined as number of juveniles produced per surviving adult poolfish (+ 95% Confidence Intervals) are shown for populations in mesocosms where poolfish were: I) allopatric; II) sympatric with crayfish or III) sympatric with both crayfish and mosquitofish. Treatments sharing at least one letter were not significantly different (p > 0.05).

4. Discussion

In our study, crayfish caused an approximately 40% increase in adult poolfish mortality, but the addition of mosquitofish did not have any additional effects on poolfish adult mortality. Such impacts on adult survival would be expected to decrease juvenile productivity. In fact, there was a notable, but non-significant, reduction in poolfish juvenile production for the poolfish & crayfish mesocosms. It is notable, however, that relative juvenile production (juveniles / surviving adult poolfish) was not significantly impacted by the sole presence of crayfish.

The combined effects of both crayfish and mosquitofish effectively eliminated the production of poolfish juveniles. It is noteworthy, that similar work has shown mosquitofish to virtually eliminate poolfish juvenile production [25,35]. Our findings suggest a lack of emergent effects of multiple predators [sensu 1] on poolfish.

Our findings suggest that the sole introduction of crayfish may have notable impacts on the survival of poolfish adults, and these in turn reduce the number of juveniles produced. However, poolfish populations grew by nearly 10-fold when in the presence of crayfish. Thus, crayfish are unlikely to have immediate acute impacts. Indeed, the Corn Creek refuge population of poolfish co-persisted with Red Swamp Crayfish for 5 years. However, this population collapsed shortly after non-native fish were detected (Kevin Guadalupe Nevada Department of Wildlife, personal communication). Furthermore, following the discovery of Red Swamp Crayfish, the Lake Harriet Poolfish population displayed an initial decline in abundance, but fluctuated around 10,000

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individuals for the next three years [33,34]. Nevertheless, this poolfish population declined to less than 1,000 poolfish one year after the detection of Western Mosquitofish [34]. These findings are consistent with earlier work showing severe impacts of mosquitofish on recruitment of poolfish juveniles [31,36].

Numerous mesocosm and observational studies have focused on the effects of individual non-native species. For instance, many studies have shown that mosquitofish have significant impacts on production of juveniles of native fishes [25,26,29–31,35,36]. However, there have been limited efforts to evaluate the combined effects of multiple invasive species such as the combination of Western Mosquitofish and Red Swamp Crayfish. Other studies have considered the synergistic interactions among invasive species on facilitating the invasion of additional invasive species, referred to as invasional meltdown [5–7]. However, the impacts of multiple invasive species have not received as much attention.

Our work has relevance for understanding historic impacts of non-native species on several endemic species within Ash Meadows. For example, Miller et al. [17] attributed extinction of the Ash Meadows Killifish to crayfish, while Minckley and Deacon [16] inferred that the extinction of the Ash Meadows Killifish occurred following the *co-invasion* of both crayfish and mosquitofish. However, it is notable that the Ash Meadows Amargosa Pupfish, *C. nevadensis mionectes*, persisted with both non-natives at various springs in Ash Meadows. Scoppettone et al. [37] hypothesized that spatial variability in temperature may have facilitated co-persistence as native pupfish utilized warmer waters limiting interspecific interactions of pupfish with crayfish and mosquitofish [37]. Collectively, these observations combined with our experimental data suggest that the extinction of *E. merriami* within Ash Meadows may have been due to more than the solitary impacts of Red Swamp Crayfish.

Overall, this study, combined with previous mesocosm experiments [25,35], demonstrates that Pahrump Poolfish are severely impacted by the presence of non-native species. The vulnerability of Pahrump Poolfish to non-native predators is consistent with the predator naiveté hypothesis [28]. In contrast to other desert fishes, poolfish do not respond to conspecific alarm cues, suggesting limited anti-predator competence [28,38,39]. Thus, the current approach of managing Pahrump Poolfish in single species refugia is clearly warranted. Poolfish may be able to co-persist with invasive crayfish, but immediate intervention should be taken if Western Mosquitofish invade any of the poolfish refuge habitats. Our study shows the value of evaluating the effects of multiple invasive species on native species, but additional work should be undertaken to evaluate other combinations of invasive species.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Figure S1: title; Table S1: title; Video S1: title.

Author Contributions: For research articles with several authors, a short paragraph specifying their individual contributions must be provided. The following statements should be used "Conceptualization, B.P and C.S.; methodology, B.P. and C.S.; formal analysis, B.P. and C.S.; investigation, B.P.; resources, C.S.; data curation, C.S.; writing—B.P.; writing—review and editing, B.P. and C.S.; supervision, C.S.; project administration, C.S.; funding acquisition, B.P. and C.S. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: The study was conducted in accordance with the North Dakota State University's Institutional Animal Care & Use Committee, protocol #A18054.

Data Availability Statement: Data are available via Dryad. Paulson, Brandon; Stockwell, Craig (Forthcoming 2024). Crayfish & Mosquitofish impacts on Experimental Poolfish Populations [Dataset]. Dryad. https://doi.org/10.5061/dryad.gqnk98sz3

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