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

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The combined effects of multiple invasive species on the persistence of experimental populations of imperiled Pahrump Poolfish

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Authors' contributions: BLP and CAS conceived the idea and designed the mesocosm experiment; BLP conducted the experiment; BLP and CAS analyzed the data; BLP wrote the initial draft; BLP and CAS revised the manuscript

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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 did not limit production of poolfish juveniles. By contrast, mosquitofish had no effect on 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 and provides an example for the compounding effects of multiple invasive species for other study systems.
Introduction:

The introduction of non-native species has become so widespread that many systems have been invaded by multiple non-native species (García-Berthou et al. 2005; Gallardo et al. 2016). Once established, an invasive species can facilitate the colonization of additional non-native species, an ecological process referred to invasional meltdown (Simberloff and Von Holle 1999; Simberloff 2006; Braga et al. 2018). Thus, work evaluating the combined effects of multiple species introductions on native species is an important topic of concern for conservation biologists (Pyšek & Richardson 2010; Ricciardi et al. 2013).

Some studies have shown that multiple invasive species can have substantial impacts on endemic species. For example, Dénes et al. (2018) demonstrated the additive impacts of invasive mammals directly lowered seed abundance of the endangered Paraná pine, *Araucaria angustifolia*. This impact effectively lowered food availability for ~70 endemic species, and ultimately lowered successful recruitment of Paraná pine saplings (Dénes et al. 2018). Similarly, avian malaria spread to Hawaiian avifauna due to the co-introduction of *Plasmodium relictum*, and its associated vector the southern house mosquito, *Culex quinquefasciatus*. Avian malaria became widespread as the southern house mosquito’s breeding habitat expanded due to the foraging behavior of yet another invasive species, the feral pig, *Sus scrofa* (LaPointe et al. 2012).

The potential for compounded impacts by multiple non-natives is likely important in many aquatic ecosystems (Cariton and Geller 1993). For example, ballast water exchange introduced Eurasian zebra mussel, *Dreissena polymorpha*, and the Round goby *Neogobius melanostomus*, resulting in both individual and synergistic impacts on aquatic communities (Jude et al. 1992; Janssen and Jude 2001). Zebra mussels altered the planktonic community structure
that allowed the round goby to obtain competitive superiority over endemic species such as the Mottled sculpin, *Cottus bairdii* (Janssen and Jude 2001).

Invasive species are a major concern in desert springs in the southwestern United States, where invasive species have been directly associated with the decline and extirpation of numerous endemic aquatic species (Minckley and Deacon 1968; Soltz and Naiman 1978; Cucherousset and Olden 2011). In several cases, multiple non-native species have co-invaded habitats within the desert southwest. For example, numerous poeciliid species invaded springs in southern Nevada (La Rivers 1962; Deacon et al. 1964). Furthermore, non-native macroinvertebrates such as Red Swamp Crayfish were introduced into the southwest through means of commercial production, and likely dispersed from an aquaculture facility in the 1930’s (Hobbs 1948; Deacon et al. 1964; Hobbs et al. 1989; Miller et al. 1989; Deacon and Williams 1991; Paulson and Martin 2014). These introductions were often associated with the decline of native fishes (Deacon et al. 1964).

The impacts of non-native species on desert ecosystems have been attributed to predator naïveté of endemic fishes, which evolved in depauperate communities. Specifically, endemic fishes are hypothesized to have lost anti-predator traits as they evolved in allopatric systems with limited predation and interspecific competition, thus making them vulnerable to invasive predators (Miller 1961; Minckley and Deacon 1968; Courtenay and Deacon 1983; Cox and Lima 2006), such as the Western Mosquitofish, *Gambusia affinis*, and Red Swamp Crayfish, *Procambarus clarkii*.

Western Mosquitofish were introduced to California in 1922 and subsequently to Nevada in 1934 (La Rivers 1962; Stockwell et al. 1996), while Red Swamp Crayfish were used commonly in aquaculture in the 1930’s and first documented in southern Nevada in the early
1940’s (Hobbs 1948; Deacon et al. 1964; Hobbs et al. 1989; Miller et al. 1989; Paulson and Martin 2014). Both species can have rapid population growth rates and broad ecological tolerances (Krumholz 1948; Huner and Lindqvist 1995; Pyke 2008; Paulson and Martin 2014), resulting in the ability to have substantial impacts on native fishes (Miller et al. 1989; Meffe et al. 1985). Mosquitofish are voracious predators of fish eggs and larvae (Pyke 2008), while crayfish prey on the adults and larvae of benthic fishes (Thomas and Taylor 2013; Paulson and Stockwell 2020). For example, the decline of the Gila topminnow, *Poeciliopsis occidentalis*, corresponded with the invasion of Western Mosquitofish and habitat degradation (Miller 1961; Minckley and Deacon 1968; Meffe et al. 1985). Similarly, Red Swamp Crayfish presumably contributed to the extinction of the Ash Meadows killifish, *Empetrichthys merriami* (Miller et al. 1989).

The direct effects of both Red Swamp Crayfish and Western Mosquitofish have been independently evaluated amongst numerous experimental studies (Mills et al. 2004; Rogowski and Stockwell 2006; Thomas and Taylor 2013; Henkanaththegedara and Stockwell 2014; Goodchild and Stockwell 2016; Paulson and Stockwell 2020). Rogowski and Stockwell (2006) 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 species are capable of rapidly spreading and are listed as the greatest threat to the various endemic fishes in the Southwestern US (Sada 1990). 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. The largest refuge population of the endangered Pahrump Poolfish, *Empetrichthys latos*, 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 the lake in 2015. The poolfish population was estimated at 12,285 poolfish (10,791 < 12,285 < 13,988), but within one year declined to an estimated poolfish population size of 362 poolfish (194 ≤ 362 ≤ 741; estimate and 95% Confidence Interval) (Burg and Guadalupe NDOW Report, 2015; Guadalupe NDOW Report 2016, 2020). Over the next year, 688 poolfish were salvaged and relocated to a fish hatchery (644 fish) and to another refuge population at Corn Creek (44 fish) (Guadalupe 2020).

This recent 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 directly tests for synergistic effects of dual species invasion on Pahrump Poolfish.

**Methods:**

Western Mosquitofish were obtained from Sutter-Yuba Mosquito and Vector Control district in Yuba City, CA. Poolfish used in this experiment included wild poolfish collected from Shoshone Stock Pond (White Pine County, NV) on June 13, 2017, and lab-reared poolfish which were descended from poolfish originally collected in 2014 from Spring Mountain Ranch State Park, Clark County (Goodchild and Stockwell 2016). 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 three previous experiments consistently showed that mosquitofish effectively target juvenile poolfish (Goodchild and Stockwell 2016; Paulson 2019).

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 periodically 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 used JMP Pro 15 software. We conducted a non-parametric permutation procedure for analysis of variance followed by a permutation procedure for the HSD
Tukey pairwise comparisons. The p-value was estimated as the number of times the re-sampled difference exceed the original test statistic out of 10,000 times. Our findings replicated the statistical outcomes obtained when using non-parametric Friedman Rank tests with a block option followed by Steel Dwass pairwise comparisons, but we only report the permutation results.

**Results:**

For adult survival there was not a significant block effect ($F = 0.5189, P = 0.1107$), but adult survival significantly differed among the three treatments ($F = 13.9833, P = 0.0008$). In allopatry, adult poolfish survival rates were near 100% (95.9 ± 4.33%; mean ± one standard error of the mean) and significantly higher compared to adult poolfish survival when sympatric with crayfish (53.1 ± 5.3%; $P = 0.0016$) and when poolfish were sympatric with both crayfish and mosquitofish (55.1 ± 6.0, $P = 0.0032$; Figure 1). The latter two treatments did not significantly differ from each other ($P = 0.8837$).

For juvenile production there was not a significant block effect ($F = 0.5782, P = 0.1128$), but juvenile production differed significantly among the three treatments ($F = 10.7926, P = 0.0027$). Juvenile productivity in mesocosms with allopatric poolfish (91.4 ± 11.9; juveniles per tank) did not differ from mesocosms hosting poolfish and crayfish (64.9 ± 14.6; $P = 0.5158$). However, juvenile production plummeted to near zero (1.9 ± 6.2) when poolfish were sympatric with both crayfish and mosquitofish, which was significantly different from allopatric poolfish ($P = 0.0243$), but was not significant when compared to the poolfish sympatric with only crayfish ($P = 0.1261$; Figure 2).
Discussion:

In our study, adult poolfish mortality was significantly higher for treatments including crayfish, but the addition of mosquitofish did not have any additive effects on poolfish adult survival. The presence of crayfish alone resulted in a significant 30% reduction in poolfish juvenile production, but it is worth noting the total poolfish population still grew by a factor of 9. The combined effects of both crayfish and mosquitofish effectively eliminated the production of poolfish juveniles.

Our findings suggest that the sole introduction of crayfish may have notable impacts on the survival of poolfish adults; however, such impacts may be mediated by substantial juvenile production. 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, but then collapsed when 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, to fluctuated around 10,000 individuals for the next three years (Burg and Guadalupe NDOW Report 2015; Guadalupe NDOW Report 2016). Nevertheless, within one year of mosquitofish invasion, this poolfish population declined to less than 1,000 poolfish (Guadalupe NDOW Report 2016). These findings are consistent with earlier work showing severe impacts of mosquitofish on recruitment of poolfish juveniles (Goodchild 2015; Goodchild and Stockwell 2016).

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 (Rogowski and Stockwell 2006; Goodchild
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* (Simberloff and Von Holle 1999; Simberloff 2006; Braga et al. 2018). However, the collective impacts of multiple invasive species have not received as much attention. Johnson et al. (2009) reported that multiple invasive species within experimental mesocosms had minimal impact on the other invasive species, however combined effects ultimately extirpated the native species.

Our work has relevance for understanding historic impacts of non-native species on several endemic species within Ash Meadows. For example, Miller et al. (1989) attributed extinction of the Ash Meadows Killifish, *Empetrichthys merriami*, to crayfish, while Minckley and Deacon (1968) inferred that the extinction of the Ash Meadows Killifish occurred following the co-invasion of both crayfish and mosquitofish. The more recent decline of Warm Springs Pupfish, *C. nevadensis pectoralis*, was similarly attributed to the combination of crayfish and mosquitofish (Sada 1990). However, it is notable that the Ash Meadows Amargosa Pupfish, *C. n. mionectes*, persisted with both non-natives at various springs in Ash Meadows. Scoppettone et al. (2005) 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 (Scoppettone et al. 2005). 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 (Goodchild 2016; Paulson and Stockwell 2020), demonstrates that Pahrump Poolfish are severely impacted by the presence of non-native species. 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 synergistic effects of multiple invasive species on native species, but additional work should be undertaken to evaluate other combinations of invasive species.

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**Figure Captions:**

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).

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).
Figure 1.
Figure 2.
Figure 1

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Supplementary Files

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- PaulsonStockwellPoolfishCrayfishMFdataset21221.csv