

Implications of piscine predator control on the federally listed fountain darter

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Abstract

One strategy for protecting the federally listed fountain darter, *Etheostoma fonticola* (Jordan & Gilbert), during low flow conditions is the removal of piscine carnivores [in this case, largemouth bass, *Micropterus salmoides* (Lacepède)]. However, headwater spring communities of the Comal and San Marcos rivers include another potential predator [red swamp crayfish, *Procambarus clarkii* (Girard)]. Removal of piscine carnivores could produce cascading effects by increasing crayfish consumption of benthic fish. The purpose of this study was to evaluate if piscine carnivore removal will lessen predatory pressure or induce a trophic cascade with crayfish increasing and causing declines in fountain darter. The numbers of fountain darter consumed were quantified among three predator treatments (red swamp crayfish only, largemouth bass only and red swamp crayfish and largemouth bass combined) and vegetation treatments (vegetated and non-vegetated) at three temperature regimes (18, 22, 27°C). Vegetation had no effect on fountain darter predation. Among temperature trials, largemouth bass only and red swamp crayfish and largemouth bass combined consumed similar numbers of fountain darter, and red swamp crayfish only consumed the least numbers of fountain darter, except at 22°C. Largemouth bass did not consume more red swamp crayfish than fountain darter. Therefore, largemouth bass removal appears to be a viable option for reducing fountain darter predation during periods of low flow.

KEYWORDS

Comal river, largemouth bass, red swamp crayfish, San Marcos River, threatened and endangered species, trophic cascade

1 | INTRODUCTION

Freshwater piscine carnivores (e.g. black basses *Micropterus* spp. and *Ambloplites* spp.) consume a variety of food items, including benthic fishes and crayfishes (Magoulick, 2004; Snyder, 2009). To avoid predation, benthic fishes rely on cryptic colouration and reduced movement (Armbruster & Page, 1996; Becker & Gabor, 2012) or seek shelter (Rahel & Stein, 1988). Likewise, crayfish seek shelter in the presence of piscine carnivores (Söderbäck, 1992). Shelter use by benthic fishes and crayfish generates competition for space (Rahel & Stein, 1988) that favours crayfish because they are also predators of benthic fishes (Taylor & Soucek, 2010). As a result, benthic fishes

continue to move, thereby increasing their susceptibility to predation by piscine carnivores (Rahel & Stein, 1988). At times, removal of piscine carnivores is a strategy to lessen mortality on imperilled fishes (Beamesderfer, 2000). However, removal of piscine carnivores in areas with imperilled benthic fishes and crayfishes could have unintended consequences on the trophic dynamics of a system, where removal of the top predator results in an increase of a mid-level consumer and a decrease in the basal consumer (i.e. trophic cascade, Pace, Cole, Carpenter & Kitchell, 1999). Specifically, the release of predation pressure on crayfish (mid-level consumer) by removing piscine carnivores (top predator) could decrease benthic fish (basal consumer) via predation by crayfish.



The endangered fountain darter, *Etheostoma fonticola* (Jordan & Gilbert), inhabits stenothermal reaches (viz. 22–23°C) of the Comal and upper San Marcos rivers of central Texas, USA (Linam, Mayes & Saunders, 1993; Schenck & Whiteside, 1976). This species associates with slack to moderate current velocities in vegetated areas containing silt substrates and open areas containing gravel and cobble substrates (Alexander & Phillips, 2012; Kollaus, Behen, Heard, Hardy & Bonner, 2015; Schenck & Whiteside, 1976). Co-occurring aquatic species include native red swamp crayfish, *Procambarus clarkii* (Girard; Hobbs, 1989; Taylor et al., 1996), native largemouth bass, *Micropterus salmoides* (Lacepède) and several *Lepomis* species. Non-native species include rock bass, *Ambloplites rupestris* (Rafinesque) and redbreast sunfish, *Lepomis auritus* (Linnaeus; Kollaus et al., 2015). Fountain darter populations are considered to be stable in the San Marcos River (Kollaus et al., 2015) and the Comal River (Linam et al., 1993). Currently, fountain darter mortality associated with native or non-native predators is not considered a threat to fountain darter populations in either river system. However, predation of fountain darter by native and non-native predators is a concern under low flow scenarios (Edwards Aquifer Recovery Implementation Plan 2012). Low flows naturally occur among Edwards Aquifer springs (Craig, Kollaus, Behen & Bonner, 2016) but are exacerbated by municipal, agricultural and industrial surface water diversions and groundwater pumping that further reduces river flow, especially during periods of below average precipitation. The Edwards Aquifer Habitat Conservation Plan (Edwards Aquifer Recovery Implementation Plan 2012) suggests removing piscine carnivores during periods of low spring flow to mitigate potential increases of native and non-native predator consumption on fountain darters.

The purpose of this study was to evaluate whether proposed piscine carnivore removal will lessen predatory pressure on the fountain darter as intended or induce a trophic cascade with numbers of crayfish increasing and causing greater declines in the fountain darter. Mesocosm experiments are used to test for trophic cascades in laboratory settings (Grabowski & Kimbro, 2005), but laboratory settings, like mesocosm experiments in field settings, can have limited applicability to a complex trophic system (Schmitz, 2004). Instead of testing directly for trophic cascade in a laboratory setting, a series of experiments were conducted to assess indirectly the potential for trophic cascade. Study objectives were to quantify predation on fountain darter by red swamp crayfish only, largemouth bass only and red swamp crayfish and largemouth bass combined, with or without shelter (i.e. vegetation), at three water temperatures (i.e. 18, 22 and 27°C). Separate tests were conducted within a range of water temperatures to include typical water temperatures that span the range of fountain darter in San Marcos and Comal rivers and account for poikilotherms feeding differently at cooler and warmer water temperatures (Kishi, Murakami, Nakano & Maekawa, 2005).

Three possible outcomes were expected. First, the number of fountain darters consumed by red swamp crayfish only and by largemouth bass only will equal the number of fountain darters consumed by red swamp crayfish and largemouth bass combined. This result, called the additive mortality response, suggests that red swamp crayfish and largemouth bass consume a number of fountain darters, and

the simultaneous presence of red swamp crayfish and largemouth bass does not affect the numbers of fountain darters consumed. Second, the number of fountain darters consumed by red swamp crayfish only and by largemouth bass only will be greater than the number of fountain darters consumed by red swamp crayfish and largemouth bass combined. This result, called the synergistic mortality response, suggests an interaction among largemouth bass, red swamp crayfish and fountain darter. Although the intent of this study is not to identify the mechanisms of observed responses, which are often unclear in trophic cascade studies (Schmitz, Beckerman & O'Brien, 1997), one mechanism could be competition for space between red swamp crayfish and fountain darter in vegetated experimental units that results in the fountain darter moving more to avoid red swamp crayfish and becoming more susceptible to predation by largemouth bass (Rahel & Stein, 1988). Third, the number of fountain darters consumed by red swamp crayfish only and by largemouth bass only will be less than the number of fountain darters consumed by red swamp crayfish and largemouth bass combined. This result, called the antagonistic mortality response, suggests another interaction among largemouth bass, red swamp crayfish and fountain darter. A possible mechanism would be the preference of largemouth bass for larger prey items with greater energy (e.g. crayfish) than smaller prey items, such as small benthic fishes (e.g. fountain darter; García-Berthou, 2002; Snyder, 2009).

Findings consistent with additive mortality and synergistic mortality responses would support the proposed piscine carnivore removal programme under low flow conditions. However, findings consistent with the antagonistic mortality response would not support the proposed piscine carnivore removal programme. With largemouth bass and red swamp crayfish combined and fewer fountain darters consumed, removal of piscine carnivores might induce a trophic cascade where the release of predation pressure on crayfish by removing largemouth bass could increase fountain darter predation by crayfish.

2 | METHODS

Experiments were conducted in the Texas State University Freeman Aquatic Biology Building outdoor raceways using Edwards Aquifer well water. Twenty-four plastic containers (190 L, 109 × 56 × 45 cm) were modified by drilling seep holes to hold 110 L of water and allow flow through. Plastic grates with weights were placed on top of each plastic container to prevent animals escaping or animals entering from the top. Six plastic containers were placed above each of four concrete raceways, which were enclosed in a chain-link fence. For the 18°C (mean = 17.6 ± 1.3 SD; range: 14.4–21.9) and 27°C (mean = 26.5 ± 0.79 SD; range: 24.9–28.4) temperature trials, well water flowed into a 0.5 ha pond and was allowed to fluctuate with the ambient air temperatures during either January and February or June and July, 2015. Water from the pond was then pumped into each plastic container at an exchange rate of 0.038 L/s. For the 22°C (mean = 22.3 ± 1.24 SD; range: 19.9–23.2) temperature trials, conducted during July and August 2014, well water was pumped directly into each raceway and then into each plastic container. Conductivity



($\mu\text{m}/\text{cm}^2$), pH and dissolved oxygen (mg/L) were recorded with a YSI Model 556 multiprobe meter (YSI Incorporated, Yellow Springs, OH), and ammonia (mg/L) and nitrate (mg/L) were recorded with test kits (API, Mars Fishcare, Hackettstown, NJ, USA) from one plastic container within each raceway on days 1, 4, 8 and 11 of each trial. Among trials, mean conductivity ranged between 549 ± 36.3 SD and 631 ± 0.39 SD $\mu\text{m}/\text{cm}^2$, median pH ranged between 7.3 and 8.0 and mean dissolved oxygen ranged between 6.9 ± 0.32 SD and 8.1 ± 0.13 SD mg/L. Ammonia was <0.1 mg/L, and nitrate was <10 mg/L.

A completely randomised design was used to test effects of vegetation and predation (i.e. independent variables) on fountain darter mortality (i.e. dependent variable) in each temperature trial. Each temperature trial was conducted separately because laboratory space was limited. An experimental unit was a plastic container with four fountain darters (size range: 25–34 mm total length) obtained from the wild for the 18 and 27°C temperature trials or obtained from a hatchery stock (San Marcos Aquatic Resources Center, TX, USA) for the 22°C temperature trial. A vegetation treatment (with and without plastic vegetation) and a predation treatment (control, red swamp crayfish only, largemouth bass only and crayfish and bass combined) were randomly assigned three times to experimental units for a total of three replicates per treatment and a total of 24 experimental units per temperature trial. Plastic vegetation was secured to the bottom of experimental units with small weights and covered 40% of the container bottom, extending <5 cm into the water column. Plastic vegetation was morphologically similar to *Hygrophila* spp., which is commonly associated with fountain darter occurrences in the Comal and San Marcos rivers (Araujo, 2012). Fountain Darters also often associate with silt substrates with and without vegetation (Nichols, 2015). The bottom of each plastic container was similar in colour (i.e. grey) and lacked the structural complexity of silt substrates found within the Comal and San Marcos rivers. Silt substrate was initially considered as a bottom cover for experimental units, but silt substrates within the Comal and San Marcos rivers tend to be compacted, whereas silt substrate in experimental units were not compacted and easily suspended into the water column, creating turbid conditions and potentially confounding predator and prey interactions. Therefore, natural substrates were not used. Predation treatment consisted of no predator (control), six red swamp crayfish (hereafter referred to as red swamp crayfish only), one largemouth bass (largemouth bass only) or six red swamp crayfish and one largemouth bass combined (red swamp crayfish and largemouth bass combined). Red swamp crayfish (size range: 35–109 mm carapace length) and largemouth bass (size range: 216–368 mm in total length) were purchased from commercial vendors and occasionally supplemented with wild stocks. The ratio of fountain darter, red swamp crayfish and largemouth bass were determined based on preliminary laboratory observations to ensure that fountain darters were located and consumed by red swamp crayfish and largemouth bass. Ratios are similar to those observed from field observations from Comal and San Marcos rivers, although densities of fountain darter, red swamp crayfish and largemouth bass among mesohabitats and microhabitats were highly variable (Scanes, 2016). Sparse amounts of sinking pellet food were provided as a food source for the fountain darter daily prior to the start of experiments. The numbers of

fountain darter and crayfish per experimental unit were enumerated on days 4, 8 and 11. However, only day 11 counts were used for statistical analyses. Mortality was the number of fountain darter missing. An 11-day trial duration was set to allow time for six red swamp crayfish to find and consume four fountain darters based on preliminary observations.

Effects of vegetation and predator type on fountain darters mortality were assessed using a two-factor ANOVA (SAS Institute, Cary, NC, USA) for each temperature trial. ANOVA was repeated with the interaction term excluded if the interaction term (i.e. vegetation \times predator) was not significant ($p > .05$). Significant ($p < .05$) ANOVAs were followed with Fisher's least significant difference tests to assess differences among treatments.

3 | RESULTS

At 18°C, treatment effects of vegetation and predator on fountain darter mortality were detected (ANOVA; $F_{4, 19} = 35.49$; $p < .01$). Fountain darter mortality did not differ between vegetation treatments ($p = .17$) but differed ($p < .01$) among predator treatments. Mortality of fountain darter was not observed in the control, and mean mortality of red swamp crayfish was 36% ($SE = 11.7$) in the red swamp crayfish and largemouth bass combined treatment. Mean mortality ranged between 0.7 ($SE = 0.33$) fountain darter consumed by red swamp crayfish only to 4.0 ($SE = 0.00$) fountain darter consumed by largemouth bass only (Figure 1). Fountain darter mortality in largemouth bass only and red swamp crayfish and largemouth bass combined treatments did not differ ($p > .05$) but were greater than ($p < .05$) fountain darter mortality by red swamp crayfish only.

At 22°C, effects of vegetation and predator on fountain darter mortality were detected (ANOVA; $F_{4, 19} = 3.4$; $p = .03$). Fountain darter mortality did not differ between vegetation treatments ($p = .61$) but differed ($p = .02$) among predator treatments. Mortality of fountain darter was not observed in the control, and mean mortality of red swamp crayfish was 14% ($SE = 9.0$) in the red swamp crayfish and largemouth bass combined treatment. Mean mortality ranged between 1.2 (0.40) fountain darter consumed by red swamp crayfish only to 2.5 (0.72) for red swamp crayfish and largemouth bass combined. Fountain darter mortality by red swamp crayfish and largemouth bass combined differed ($p < .05$) only from the control.

At 27°C, effects of vegetation and predator on fountain darter mortality were detected (ANOVA; $F_{4, 19} = 31.79$; $p < .01$). Fountain darter mortality did not differ between vegetation treatments ($p = .37$) but differed ($p < .01$) among predator treatments. Three fountain darter died in two control experimental units, and mean mortality of red swamp crayfish was 47% ($SE = 13.2$) in the red swamp crayfish and largemouth bass combined treatment. Mean mortality ranged between 1.2 (0.40) fountain darter consumed by red swamp crayfish only to 4.0 (0.00) fountain darter consumed for red swamp crayfish and largemouth bass combined. Fountain darter mortality by largemouth bass only and red swamp crayfish and largemouth bass combined did not differ ($p > .05$) but were greater than ($p < .05$) fountain darter mortality by red swamp crayfish only.

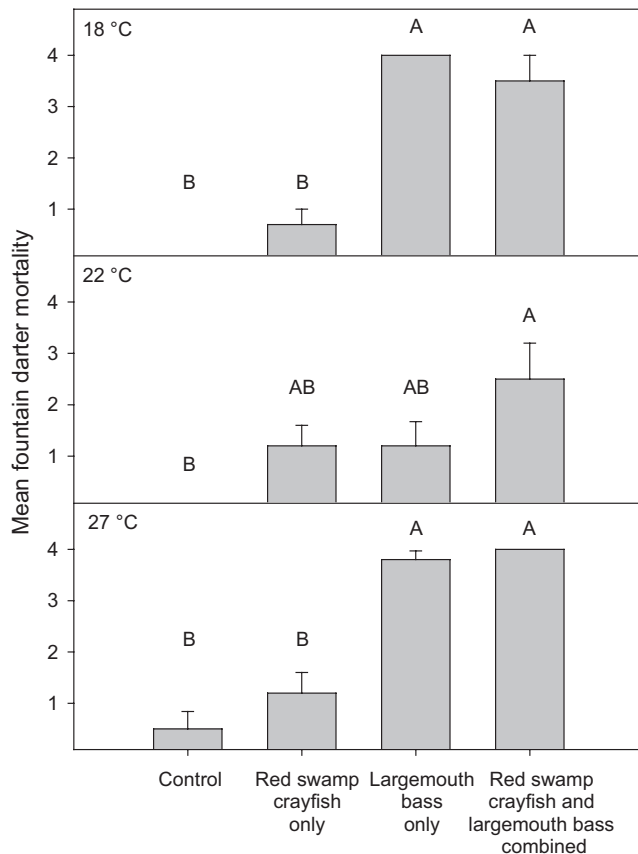


FIGURE 1 Mean (\pm SE) fountain darter mortality when stocked with no predator (control), red swamp crayfish only, largemouth bass only and red swamp crayfish and largemouth bass combined at 18, 22 and 27°C. Fountain darter mortalities were not observed for controls at 18 and 22°C. Means with different letters are significantly different ($p < .05$)

4 | DISCUSSION

Fountain darter predation did not differ between largemouth bass only and red swamp crayfish and largemouth bass combined, regardless of water temperature. Red swamp crayfish consumed the fountain darter but at lower numbers than largemouth bass only and red swamp crayfish and largemouth bass combined, except at 22°C. These results were consistent with predicted additive mortality or synergistic mortality response and inconsistent with antagonistic mortality response. With additive mortality or synergistic mortality responses, largemouth bass was predicted to consume the fountain darter regardless whether red swamp crayfish was present or not. With an antagonistic mortality response, largemouth bass was predicted to preferentially consume red swamp crayfish before fountain darter; therefore, fewer fountain darter were consumed. Although red swamp crayfish were consumed by largemouth bass at all three temperatures, greater numbers of fountain darter than crayfish were consumed by largemouth bass. Consequently, intended consequences of lessening fountain darter predatory pressure by removing largemouth bass from Comal and San Marcos rivers during low flow periods is

feasible given that the potential for causing a trophic cascade (e.g. consistent with antagonistic mortality response) is less likely based on the results of this study.

Red swamp crayfish might have altered the activity of the fountain darter, but lack of differences between the number of fountain darter consumed by largemouth bass only and by red swamp crayfish and largemouth bass combined does not support greater largemouth bass predation on fountain darter in the presence of red swamp crayfish after an 11-day period of observation. Rahel and Stein (1988) reported that johnny darter, *Etheostoma nigrum* Rafinesque, increased activity and decreased shelter use in the presence of rusty crayfish, *Orconectes rusticus* (Girard), but displacement did not result in greater consumption of johnny darter by smallmouth bass, *M. dolomieu* Lacepède in a 24-hr laboratory study. Similar results were reported by Snyder (2009), who found rusty crayfish might have displaced tessellated darter, *E. olmstedii* Storer, but displacement did not increase tessellated darter consumption by largemouth bass within a 3-day mesocosm study. As such, altered behaviours of at least some benthic fishes by crayfish might be inconsequential in affecting consumption by black bass.

Failure to detect vegetation effects was unexpected in this study. Predator success decreases with vegetation complexity by obscuring predator vision (Angermeier, 1992; Savino & Stein, 1982). For largemouth bass specifically, prey consumption is inversely related to vegetation density (Bettoli, Maceina, Noble & Betsill, 1992). Ecological value of vegetation for fountain darter includes shelter from predation and habitat for prey items (Linam et al., 1993; Phillips, Alexander & Gonzales, 2011). Vegetation type and density used in this study were selected only to test for a synergistic mortality response and not to assess ecological values of vegetation on fountain darter predator avoidance. Savino and Stein (1982) provided 50% area of vegetated cover but used a greater density (1,000 stem/m²) than this study (8 stem/m²), and Rahel and Stein (1988) provided 53% area of artificial cover using opaque tiles. The lower density cover used in this study (i.e. 40%) could decrease vegetation effects on predator success. However, Pace et al. (1999) suggested that tests of trophic cascades should be assessed at scales larger than mesocosm experiments used in this study. More complex interactions, such as additional prey (Dahl & Greenberg, 1996; Magoulick, 2004; Sullivan, Zhang & Bonner, 2012) and predators (Sih, Englund & Wooster, 1998; Thomas, 2011), also could provide greater insights into potential cascading effects. Perhaps a range of vegetation types and densities in larger-scale experiments and more complex interactions could generate a more complete understanding of cascading effects and threats of multiple predators on the fountain darter. Regardless, questions addressed in this study were sufficient to inform decisions in the San Marcos and Comal rivers, and consistent with Snyder's (2009) findings in larger mesocosms (606 L) that the interactions of largemouth bass and red swamp crayfish do not affect largemouth bass consumption of fountain darter.

Based on the results of this study, the removal of largemouth bass will reduce mortality of the fountain darter. However, other cascading effects might also occur, such as decreases in zooplankton, which is a



food source for fountain darters, with increases in planktivorous fishes (Daskalov, 2002). Also, roles of the top predator can be replaced by other predators (Pinnegar et al., 2000). Black bass composes 2% of the fish community in the San Marcos River based on historical averages (Kollaus et al., 2015). Additional predators of benthic fishes include ictalurids (1% in relative abundance), rock bass (1%) and several *Lepomis* spp. [*L. auritus* (L.), *L. cyanellus* Rafinesque and *L. gulosus* (Cuvier) collectively 3%]. Given the complexity of trophic cascade (Dahl & Greenberg, 1996; Sih et al., 1998), the largemouth bass removal programme should be monitored in situ in the San Marcos and Comal rivers to further validate the effectiveness in reducing mortality of the fountain darter.

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