TESTING OF TROPHIC CASCADE WITHIN A HEADWATER SPRING COMMUNITY: IMPLICATIONS FOR WATER QUANTITY MANAGEMENT

by

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ABSTRACT

A management strategy for protecting the federally-listed Fountain Darter *Etheostoma fonticola* during unnatural low flow conditions is the removal of piscine carnivore Largemouth Bass *Micropterus salmoides*. However, headwater spring communities include Red Swamp Crayfish *Procambarus clarkii*, which is prey for Largemouth Bass and a potential predator of the Fountain Darter. Removal of Largemouth Bass could produce an unintentional cascading effect by increasing crayfish consumption of the Fountain Darter. The purpose of this study was to test for cascading effects of benthic fish predation by quantifying the number of Fountain Darters consumed by crayfish only, bass only, and crayfish and bass combined within vegetated and non-vegetated experimental units. Three water temperature trials were conducted to mimic low-flow winter temperatures (18°C), average spring-flow temperatures (22°C) and low-flow summer temperatures (27°C). Among temperature trials, bass only and crayfish and bass combined consumed about equal numbers ($P > 0.05$) of Fountain Darters, whereas crayfish only consumed the fewest number ($P < 0.05$) of Fountain Darters, except at 22°C. Largemouth Bass did not consume more crayfish than darters; therefore, removing Largemouth Bass appears to be a viable option in reducing Fountain Darter predation. However, removal efforts should be monitored to further assess efficacy of the management strategy.

I. TESTING OF TROPHIC CASCADE WITHIN A HEADWATER SPRING COMMUNITY: IMPLICATIONS FOR WATER QUANTITY MANAGEMENT

Introduction

Freshwater piscine carnivores (e.g., basses *Micropterus* and *Ambloplites*) consume a variety of food items, including benthic fishes and crayfishes (Magoulick 2004, Snyder 2009). To avoid predation, benthic fishes rely on cryptic coloration and reduced movement (Armbruster and Page 1996, Becker and Gabor 2012) or seek shelter (Rahel and 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 and Stein 1988) that favors crayfish, since they are also formidable predators of benthic fishes (Taylor and Soucek 2010). As a result, benthic fishes continue to move, thereby increasing their susceptibility to predation by piscine carnivores (Rahel and Stein 1988). Given potential cascading interactions among benthic fishes, crayfish, and piscine carnivores, removal of piscine carnivores as a management strategy to lessen mortality on threatened and endangered benthic fishes could have unintended consequences. Specifically, the release of predation pressure on crayfish by removing piscine carnivores could, in turn, increase benthic fish predation by crayfish.

The federally-listed Fountain Darter *Etheostoma fonticola* inhabits stenothermal reaches of the Comal River and upper San Marcos rivers of central Texas and associates with slack to moderate current velocities in vegetated areas containing silt substrates and open areas containing gravel and cobble substrates (Schenck and Whiteside 1976, Alexander and Philips 2012, Kollaus et al. 2015). Co-occurring aquatic species include native Red Swamp Crayfish *Procambarus clarkii* (Hobbs 1989, Taylor et al. 1996), native Largemouth Bass *Micropterus salmoides* and several *Lepomis* species. Non-native species include Rock Bass *Ambloplites rupestris* and Redbreast Sunfish *Lepomis auritus* (Kollaus et al. 2015). Fountain Darter populations are considered to be stable in the San Marcos River (Kollaus et al. 2015) and likely stable in 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 Darters by native and non-native predators is a concern under low flow scenarios (EARIP 2011). Low flows naturally occur among Edwards Aquifer springs (Craig et al. In Press) but are exacerbated by municipal, agriculture, and industry surface water diversions and groundwater pumping that further reduces river flow. Signatories of the Edwards Aquifer Habitat Conservation Plan (HCP) propose to mitigate potential increases of native and non-native predator consumption of Fountain Darters by removing piscine carnivores during periods of low spring flow (EARIP 2011).

The purpose of this study was to assess if the HCP piscine carnivore removal proposal will lead to lessened or increased predatory pressure on the Fountain Darter. The study objective was to quantify Fountain Darter predation by crayfish only (Red Swamp Crayfish), bass only (Largemouth Bass), and crayfish and 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 account for poikilotherms increased feeding with warmer water temperatures (Kishi et al. 2005). Water temperatures represented ambient cooling (18°C) during the winter and ambient heating (27°C) during the summer of stenothermal conditions (22°C) under low flow scenarios.

Three possible outcomes were expected: 1) predation rate by crayfish and bass combined will equal the summation of predation rate by crayfish only and by bass only (i.e., additive mortality model), 2) predation rate by crayfish and bass combined will be greater than the summation of predation rate by crayfish only and by bass only (i.e., synergistic mortality model-competition, where competition for space would be detected in vegetated experimental units with Fountain Darters moving more and therefore susceptible to greater predation by Largemouth Bass; Rahel and Stein 1988), and 3) predation rate by crayfish and bass combined will be less than the summation of predation rate by crayfish only and by bass only (i.e., synergistic mortality model-bass preference for crayfish, where Largemouth Bass prefer to consume crayfish over Fountain Darters most likely because they prefer larger prey items with higher nutrient intake as compared to those that are smaller such as small benthic fishes; Garcia-Berthou 2002, Snyder 2009). Findings of an additive mortality model and synergistic mortality model-competition would support the Edwards Aquifer HCP piscine carnivore removal proposal. Removing Largemouth Bass would feasibly decrease mortalities of Fountain Darters under low flow conditions. However, finding of synergistic mortality model-bass preference for crayfish would not support the Edwards Aquifer HCP piscine carnivore removal proposal. Removing Largemouth Bass could cause a trophic cascading effect, which would feasibly increase mortalities of Fountain Darters, greater than crayfish and bass combined, by unconstrained crayfish predation under low flow conditions.

Methods

Experiments were conducted in the Texas State University (TSU) Freeman Aquatic Biology Building (FAB) outdoor raceways using well water from the same source (i.e., Edwards Aquifer) as spring flows of the Comal and San Marcos rivers and natural photoperiod. For each temperature trial, Fountain Darters (size range: 25-34 mm in total length) were obtained from hatchery stocks, produced by US Fish and Wildlife Service-San Marcos Aquatic Resource Center, or from the wild (Federal Fish and Wildlife Permit TE236730-1, Texas Parks and Wildlife SPR-0601-159, Texas State University IACUC Protocol 0126-0221-03). 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.

Experimental units (N = 24) consisted of four Fountain Darters in a 190-L plastic container (109 x 56 x 45 cm), modified by drilling seep holes to hold 110-L of water, placed six to a row on top of four raceways. For the 18°C trial, well water from the main line flowed into a 0.5-ha pond and allowed to fluctuate with ambient temperatures during January and February 2015. Water from the pond was pumped into each row of experimental units using a 0.25-horsepower utility pump and a single 0.75-in PVC pipe and distributed into each experimental unit by a tee joint fitted with a valve to control exchange rate (0.038 L/s). For the 22°C trial, well water from the main line flowed into each raceway and represented stenothermal conditions. Utility pumps were placed into each raceway and water was distributed in the same manner as the 18°C trial. For the 27°C trial, utility pumps were again placed in the 0.5-ha pond, and allowed to fluctuate with ambient summer temperatures during June and July 2015. Water was distributed among experimental units in the same manner as for the other two trials.

For each temperature trial, experimental units were randomly assigned a vegetation treatment and a predation treatment for a total of three replications for each treatment level. Vegetation treatment consisted of two levels: with and without artificial vegetation. Artificial vegetation was morphologically similar to *Hygrophila*, which is a low growing, frequently occurring vegetation type within the spring systems and is habitat for Fountain Darters (Araujo 2012). Artificial vegetation was secured to the bottom with small weights and covered about 40% of the container bottom, extending < 5 cm into the water column. Predation treatment consisted of four levels: no predator (control), six Red Swamp Crayfish (crayfish only), one Largemouth Bass (bass only), and six Red Swamp Crayfish and one Largemouth Bass combined (crayfish and bass combined). Ratio of Fountain Darters, Red Swamp Crayfish, and Largemouth Bass were determined based on preliminary observations to ensure that Fountain Darters were located and consumed by Red Swamp Crayfish and Largemouth Bass. Ratios are proportionally similar to those observed from field observations (T. Bonner, unpublished data). Sparse amounts of pellet food were provided daily, and water temperature (°C), conductivity (μm/cm^2), pH, dissolved oxygen (DO; mg/L), ammonia (ppm), and nitrate (ppm) were monitored daily to ensure parameters did not exceed stressful or lethal concentrations (DO < 5.0, Edwards Aquifer Authority 2004; 3.8 > water temperatures < 34°C, Brandt et al. 1993, Bonner et al. 1998; Ammonia < 2.79, USEPA 1984; Nitrate < 10ppm, US Environmental Protection Agency 1986, Scott and Crunkilton 2000). Numbers of darters and crayfish per experimental unit were thoroughly searched and counted on days 4, 8 and 11 (Appendix 1). Each trial lasted 11 days. Trial duration was set to allow time for crayfish to find and consume Fountain Darters, based on preliminary observations of crayfish and darter interactions.

Effects of vegetation and predator type on Fountain Darters mortality (i.e., missing from each experimental unit) were assessed using a two-factor ANOVA (α = 0.05) among treatments for each temperature trial. Interaction terms (i.e., vegetation * predator) were not significant ($P > 0.05$). Subsequent two-factor ANOVAs were used with the interaction term excluded. Fisher's Least Significance Difference tests were used to assess differences among treatment levels.

Results

Mean ± 1 SD water temperatures were 17.6 ± 1.36 (range: 14.4-21.9) for 18°C trial, 22.3 ± 1.24 (range: 19.9-23.2) for 22°C trial, and 26.5 ± 0.79 (range: 24.9-28.4) for 27°C trial (Table 1). Specific conductance ($\mu m/cm^2$), pH, and dissolved oxygen (mg/l) were similar among trials, although dissolved oxygen was lowest in 27°C trial, and within acceptable concentrations. Likewise, ammonia and nitrate levels were similar among treatments and within acceptable concentrations.

At 18°C, mean mortality (± 1 SE) of Fountain Darters ranged between 0.3 (0.33) in vegetation with crayfish only to 4.0 (0.00) in no vegetation with bass only and in vegetation with crayfish and bass combined. Mortality or loss of fish was not observed in the control. Treatment effects of vegetation and predator on Fountain Darter mortality were detected ($F_{4,\ 19} = 35.49$; $P < 0.01$). Fountain Darter mortality did not differ between levels of vegetation ($P = 0.17$) but differed ($P < 0.01$) among levels of predator. Mean

Fountain Darter mortality was 0.7 (0.33) for crayfish only, 4.0 (0.00) for bass only, and 3.5 (0.50) for crayfish and bass combined (Figure 1). Fountain Darter mortality in bass only and crayfish and bass combined did not differ ($P > 0.05$) from one another but were greater than ($P < 0.05$) Fountain Darter mortality by crayfish only.

At 22°C, mean mortality of Fountain Darters ranged between 0.7 (0.33) in vegetation with crayfish only to 3.0 (1.00) in no vegetation with crayfish and bass combined and in vegetation with bass only. Mortality or loss of fish was not observed in the control. Treatment effects of vegetation and predator on Fountain Darter mortality were detected ($F_{4, 19} = 3.4$; $P = 0.03$). Mortality of Fountain Darters did not differ between levels of vegetation ($P = 0.61$) but differed ($P = 0.02$) among levels of predator. Fountain Darter mortality was 1.2 (0.40) for crayfish only, 1.2 (0.48) for bass only, and 2.5 (0.72) for crayfish and bass combined. Fountain Darter mortality by crayfish and bass combined differed ($P < 0.05$) only from the control.

At 27°C, mean mortality of Fountain Darters ranged between 1.0 (0.00) in no vegetation with crayfish only to 4.0 (0.00) in vegetation with bass only and in no vegetation with crayfish and bass combined. Fountain Darter mortality ($N = 3$) occurred in two control experimental units without vegetation: two by day 8 and one by day 11. Treatment effects of vegetation and predator on Fountain Darter mortality were detected ($F_{4, 19} = 31.79$; $P < 0.01$). Fountain Darter mortality did not differ between levels of vegetation ($P = 0.37$) but differed ($P < 0.01$) among levels of the predator. Fountain Darter mortality was 1.2 (0.40) for crayfish only, 3.8 (0.17) for bass only, and 4.0 (0.00) for crayfish and bass combined. Fountain Darter mortality by bass only and crayfish and bass combined did not differ ($P > 0.05$) from one another but were greater than ($P < 0.05$) Fountain Darter mortality by crayfish only.

Discussion

Among the three temperature trials, Fountain Darter mortality did not differ between bass only and crayfish and bass combined. These results are consistent with the additive mortality model and synergistic mortality-competition model, where predation by crayfish and bass combined will be equal to or greater than summation of predation by crayfish only and bass only. Synergistic mortality-competition model was supported in six of the nine experimental units of crayfish and bass combined with vegetation. Fountain Darter mortality was quicker (i.e., more Fountain Darters consumed by day 11) in crayfish and bass combined with vegetation than in bass only with vegetation. However, testing of the synergistic mortality-competition model was incomplete because of limitations with the study design. A greater number of Fountain Darters should have been provided in the crayfish and bass combined treatment in order to assess if consumption was greater than consumption in crayfish only and bass only. Regardless, results consistent with either model would support the removal of Largemouth Bass during low flow periods; therefore, it is not necessary to determine if either model is more appropriate than the other. Study results were least consistent with synergistic mortality model-bass preference for crayfish (i.e., predation rate by crayfish and bass combined will be less than the summation of predation rate by crayfish only and by bass only if Largemouth Bass preferentially feed upon the Red Swamp Crayfish). With and without vegetation, Fountain Darters were consumed prior to crayfish in 14 of the 18 experimental units with crayfish and bass combined.

Evidence supporting trophic cascading effects were not conclusive in this study. Crayfish might have altered the activity of Fountain Darters, leading to quicker consumption of Fountain Darters by Largemouth Bass, but Fountain Darters were more often consumed than crayfish regardless if vegetation (i.e., shelter) was present or not. Rahel and Stein (1988) reported that the Johnny Darter *Etheostoma nigrum* was displaced from shelter by Rusty Crayfish *Orconectes rusticus* but displacement did not result in greater consumption of the darter by Smallmouth Bass *M. dolomieu*. Similar results were reported by Snyder (2009), who found that Rusty Crayfish displaced Tessellated Darter *E, olmstedi*, but displacement did not increase Tessellated Darter consumption by Largemouth Bass. As such, altered behaviors of benthic fishes by crayfish might be inconsequential in affecting consumption by piscine carnivores. In a northern lake, piscine carnivore Walleye *Sander vitreus* consumed benthic darters before consuming more mobile cyprinids and at times yellow perch (Lyons and Magnuson, 1987). Therefore, and as suggested by the results of this study, Largemouth Bass will consume Fountain Darters regardless if another larger prey item, like crayfish, are available.

Failure to detect vegetation effects was unexpected in this study. Predator success decreases with vegetation complexity by obscuring predator vision (Savino and Stein 1982, Angermeier 1992). For Largemouth Bass specifically, prey consumption is inversely related to vegetation density (Bettoli et al. 1992). Ecological value of vegetation for Fountain Darters includes shelter from predation and habitat for prey items (Linam et al. 1993, Phillips et al. 2011). Vegetation type and density used in this study were selected only to test synergistic mortality model-competition and not to assess ecological values of vegetation on Fountain Darter predator avoidance. Furthermore, 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 and Greenberg 1996, Magoulick 2004, Sullivan et al. 2012) and predators (Sih et al. 1998, Thomas 2011), also could provide greater insights into potential cascading effects. Perhaps a range of vegetation types, densities in larger-scale experiments, and more complex interactions could generate a more accurate understanding of cascading effects and threats of multiple predators on the Fountain Darter. However, questions addressed in this study were sufficient to inform management decisions in the San Marcos and Comal rivers and consistent with Snyder's (2009) findings (i.e., crayfish displace darters but did not affect Largemouth Bass consumption rates of darters), who used larger (606 L) mesocosms.

From a management perspective, the intended purpose of the HCP piscine carnivore removal proposal can be achieved based on the results of this study. Removal of top predators for the purpose of decreasing predation on targeted prey species is successful in small (Lepak et al. 2006) to large (Daskalov 2002, Myers et al. 2007) aquatic systems. However, other cascading effects might 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). Within the San Marcos River, black basses (*Micropterus*) compose 2% of the fish community, based on historical averages (Kollaus et al. 2015). Additional predators of benthic fishes include ictalurids (1% in relative abundance), *Ambloplites* (1%), and several *Lepomis* (*L. auritus*, *L. cyanellus, L. gulosus*; collectively 3%). Given the complexity of trophic cascade (Dahl and Greenberg 1996, Sih et al. 1998), piscine carnivore removal program should be monitored *in situ* in the San Marcos and Comal rivers to further validate the effectiveness in reducing mortality of the Fountain Darter during anthropogenically-induced low flow periods.

Table 1. Mean and standard deviation for water quality parameters including water temperature (°C), conductivity (µm/cm²), pH, dissolved oxygen (mg/L), ammonia (ppm), and nitrate (ppm) for 18°C, 22°C and 27°C trials taken from experimental units on a daily basis.

	18°C Trial		22°C Trial		27°C Trial	
Parameters	Mean	SD	Mean	SD	Mean	SD
Water Temperature (°C)	17.6	1.36	22.3	0.04	26.5	0.79
Cond (µm/cm²)	614.5	0.18	631.1	0.39	549.1	36.37
pH	7.3	0.01	7.9	0.03	8.0	0.04
Dissolved Oxygen (mg/L)	8.1	0.02	8.1	0.13	6.9	0.32
Ammonia (ppm)	0.1	0.00	0.0	0.03	0.0	0.04
Nitrate (ppm)	5.0	0.00	8.4	0.21	5.0	0.00

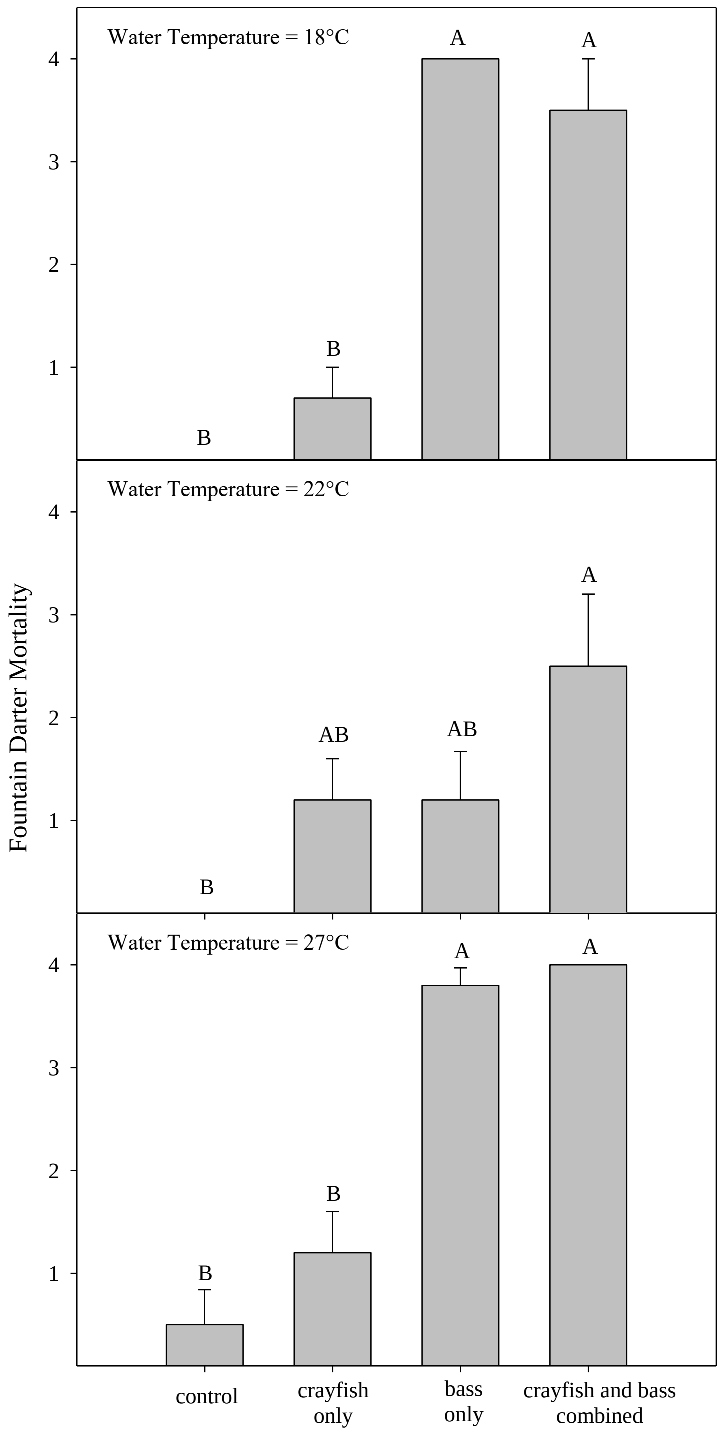

Figure 1. Fountain Darter mortality at four treatment levels (no predator: control, crayfish only, bass only and crayfish and bass combined) using 18°C, 22°C and 27°C water temperature conditions. Same letters represent no significant difference ($P > 0.05$).

APPENDIX SECTION

Appendix I. Number of Fountain Darter mortality in control, crayfish only, bass only and crayfish and bass combined. Number of crayfish mortality in crayfish and bass combined were enumerated in each experimental unit for days 4, 8 and 11 at Low Temperature (17.6°C).

		Vegetation					No Vegetation				
		control	crayfish only	bass only	crayfish and bass combined		control	crayfish only	bass only	crayfish and bass combined	
					Fountain Darter	Crayfish				Fountain Darter	Crayfish
Replication	Day	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*
Low Temperature (17.6°C)											
1	4	0	1	3	4	1	0	1	4	4	2
	8	0	0	1	0	0	0	0	0	0	2
	11	0	0	0	0	0	0	0	0	0	1
	Total	0	1	4	4	1	0	1	4	4	5
2	4	0	0	3	0	3	0	0	4	4	1
	8	0	0	1	1	0	0	0	0	0	1
	11	0	0	0	0	0	0	0	0	0	0
	Total	0	0	4	1	3	0	0	4	4	2
3	4	0	0	4	4	0	0	1	3	4	2
	8	0	0	0	0	0	0	1	1	0	0
	11	0	0	0	0	0	0	0	0	0	0
	Total	0	0	4	4	0	0	2	4	4	2

Appendix II. Number of Fountain Darter mortality in control, crayfish only, bass only and crayfish and bass combined. Number of crayfish mortality in crayfish and bass combined were enumerated in each experimental unit for days 4, 8 and 11 at Average Temperature (22.3°C).

		Vegetation					No Vegetation				
		control	crayfish only	bass only	crayfish and bass combined		control	crayfish only	bass only	crayfish and bass combined	
					Fountain Darter	Crayfish				Fountain Darter	Crayfish
Replication	Day	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*
Average Temperature (22.3°C)											
1	4	0	1	2	1	0	0	0	1	1	0
	8	0	0	1	1	0	0	1	0	0	0
	11	0	0	0	0	0	0	0	0	0	0
	Total	0	1	3	2	0	0	1	1	1	0
2	4	0	0	0	0	0	0	1	0	3	1
	8	0	0	0	0	0	0	2	0	1	2
	11	0	0	0	0	0	0	0	0	0	0
	Total	0	0	0	0	0	0	3	0	4	3
3	4	0	0	0	1	1	0	0	0	4	0
	8	0	0	1	1	1	0	0	0	0	0
	11	0	1	1	2	0	0	1	1	0	0
	Total	0	1	2	4	2	0	1	1	4	0

Appendix III. Number of Fountain Darter mortality in control, crayfish only, bass only and crayfish and bass combined. Number of crayfish mortality in crayfish and bass combined were enumerated in each experimental unit for days 4, 8 and 11 at High Temperature (26.5°C).

		Vegetation					No Vegetation				
		control	crayfish only	bass only	crayfish and bass combined		control	crayfish only	bass only	crayfish and bass combined	
					Fountain Darter	Crayfish				Fountain Darter	Crayfish
Replication	Day	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*	*N*
High Temperature (26.5°C)											
1	4	0	0	0	2	3	0	1	4	2	0
	8	0	0	0	2	2	1	0	0	1	0
	11	0	1	3	0	0	0	0	0	1	0
	Total	0	1	3	4	5	1	1	4	4	0
2	4	0	2	2	3	2	0	1	4	4	1
	8	0	1	1	0	0	1	0	0	0	4
	11	0	0	1	1	0	1	0	0	0	0
	Total	0	3	4	4	2	2	1	4	4	5
3	4	0	0	1	1	3	0	1	3	4	2
	8	0	0	0	0	0	0	0	1	0	0
	11	0	0	3	3	0	0	0	0	0	0
	Total	0	0	4	4	3	0	1	4	4	2

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