



Vegetation associations of the endangered fountain darter *Etheostoma fonticola*

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ABSTRACT: Aquatic vegetation provides many services for aquatic habitats and fish communities. The federally listed fountain darter *Etheostoma fonticola*, found only in spring systems of the San Marcos and Comal rivers in central Texas, is reported to associate with vegetation for feeding, reproduction, and refuge. Descriptions of associations with vegetation range from preferred to exclusive, whereas other studies describe fountain darters found outside of vegetation. The purposes of this study were to quantify fountain darter occurrences and abundances among vegetated habitats using the concept of obligate and facultative habitat use. Wadeable and non-wadeable habitats among multiple reaches of the San Marcos and Comal rivers were sampled with seines and SCUBA diving methods in the spring and fall from 2014 to 2019. Fountain darters were often associated with aquatic vegetation but demonstrated both obligate and facultative tendencies. Fountain darters occurred in vegetation more than expected among wadeable and non-wadeable habitats in the majority of reaches within the San Marcos and Comal rivers. Among vegetation taxa, they were positively associated with bryophytes and negatively associated with Texas wild rice, but associations with other vegetation taxa varied by river and were possibly influenced by other variables. Current vegetation management in both rivers includes the removal of non-native species and restoration of native vegetation, so understanding the patterns of fountain darter associations with vegetation can guide future management and restoration efforts of these spring systems.

KEY WORDS: Endangered fishes · Edwards Plateau springs · Obligate species · Facultative species

1. INTRODUCTION

Aquatic vegetation provides a variety of ecosystem services for fishes. Several lineages of fishes are preferential and opportunistic consumers of aquatic vegetation (Goldstein & Simon 1999) and rely on vegetation for egg deposition (Simon 1999). Aquatic vegetation is positively related to macroinvertebrate diversity, a major food item for fishes (Grenouillet et al. 2002, Yofukuji et al. 2021), and it creates structural complexity (Montoya-Ospina et al. 2020), providing refuge for small fishes (Brusven et al. 1990) and cover for large predatory fishes (Casselman & Lewis 1996). Therefore, in some aquatic systems, the type and amount of aquatic vegetation are strong predictors of fish occur-

rences, more so than other traditional predictors like water quality (Cvetkovic et al. 2010), and are considered primary structuring mechanisms of fish densities, species richness, and recruitment (Willis et al. 2005, Snickars et al. 2009, Ismail et al. 2018). Identifying the direct and indirect mechanisms of fish and aquatic vegetation relationships is necessary to understand aspects of fitness, such as reproductive output or survival, that are associated with individual use of aquatic vegetation.

The subgenus *Microperca* (Percidae) consists of 3 species: least darter *Etheostoma microperca*, cypress darter *E. proeliare*, and fountain darter *E. fonticola* (Near et al. 2011, Echelle et al. 2015), with a collectively broad distribution throughout the Great Lakes

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drainages, Mississippi River drainage, and eastern and western gulf slope drainages of North America (Burr & Page 1978, 1979). Species of *Microperca* are among the smallest species in *Etheostoma*, sharing similar habitat affinities and reproductive strategy. Reported preferred habitats are small to large streams and margins of lakes, specifically slack-water habitats with vegetation and detritus (Schenck & Whiteside 1976, Burr & Page 1978, 1979). Eggs are deposited on vegetation, detritus, and rocks with no parental care (Strawn 1956, Burr & Page 1978, 1979).

The fountain darter has the most limited distribution among *Microperca*, found only in the upper reaches of 2 rivers, San Marcos River and Comal River, supported by spring outflows of the Edwards Aquifer in central Texas. Listed by the US Fish and Wildlife Service (USFWS) as endangered in 1970 (USFWS 1970a), legislative and judicial battles over the 'little fish that roared' (Votteler 1998) led to the creation of the Edwards Aquifer Authority (EAA), and regulation of groundwater withdrawals in contributing zones of the 2 spring systems: San Marcos springs and Comal springs. Persistence of the fountain darter is linked to continuous flows of the spring systems (Schenck & Whiteside 1977, Simon et al. 1995, Votteler 1998, Mora et al. 2013). Continuous spring flows provide the necessary water quality (i.e. stenothermal conditions, high water clarity) for fountain darter and other spring-associated fishes, linked to survival (Brandt et al. 1993, Swanbrow Becker et al. 2016), reproduction (Brandt et al. 1993, Bonner et al. 1998), and performance (Craig et al. 2019). Likewise, the fountain darter associates with aquatic vegetation potentially for feeding, reproduction, and refuge (Alexander & Phillips 2012); however, direct quantification of the association is lacking. The species' association with vegetation is reported as exclusive (Schenck & Whiteside 1976) or preferred (USFWS 1996), but it is also found in areas without vegetation (Linam et al. 1993). Among vegetation types, fountain darter densities tend to be greater in short vegetation than in tall vegetation (Schenck & Whiteside 1976, Linam et al. 1993, Crowe & Sharp 1997) and in dense, ornate vegetation (Alexander & Phillips 2012). Short vegetation might provide optimum conditions for feeding and reproduction (Linam et al. 1993), although the fountain darter spawns on short and tall vegetation as well as other substrates (Brandt et al. 1993). Mechanisms driving fountain darter distributions among vegetation are poorly understood, thus identifying clear patterns in fountain darter association with vegetation is needed.

Published perspectives of fountain darter habitat associations, particularly with aquatic vegetation,

are based on short-duration studies (i.e. ≤ 1 yr), mainly in wadeable waters, and only within one river at a time. The species' association with vegetation is thought to be obligatory (Schenck & Whiteside 1976, USFWS 1996). In 2013, an additional monitoring component to the larger biomonitoring program through the Edwards Aquifer Habitat Conservation Plan was established to document bi-annual fish community structure (e.g. species richness and density) and fish-habitat associations among multiple reaches in wadeable and non-wadeable habitats within the San Marcos and Comal rivers. The additional monitoring coincided with another long-term goal of the Habitat Conservation Plan: to restore native vegetation within the San Marcos and Comal rivers. From 2013–2018, the aquatic vegetation communities in the San Marcos and Comal rivers changed due to non-native vegetation removal in experimental reaches. While non-native vegetation has decreased about 30% in experimental reaches, native vegetation, primarily the federally listed Texas wild rice *Zizania texana*, has increased by about 50% (BIO-WEST 2013–2018). In habitats where Texas wild rice has replaced non-native vegetation, lower fountain darter numbers have been observed (BIO-WEST 2019). Therefore, a greater understanding of fountain darter association with vegetation is needed to support long-term goals associated with vegetation management implemented by the habitat conservation plan and, perhaps more importantly, to establish patterns in vegetation associations in order to predict and test the mechanisms of fountain darter association with aquatic vegetation.

The purpose of this study was to assess the relationship between the fountain darter and aquatic vegetation using the 6 yr biomonitoring data set, taken from multiple reaches twice per year, from wadeable and non-wadeable habitats, and within the known range of the fountain darter (6.2 river km [rkm] in the San Marcos River and 7.0 rkm in the Comal River). The objectives of this study were to (1) quantify occurrences of vegetation and fountain darters among available habitats from multiple reaches within the San Marcos and Comal rivers, (2) assess the relationship between occurrence and abundance of vegetation and occurrence of fountain darters, and (3) examine the relationship between fountain darter occurrences and type of vegetation among available habitats. If the fountain darter is an obligate plant associate, we predicted that it would occur within vegetation more than expected based on available vegetation and that it will be associated with shorter vegetation (Strawn 1956, Schenck & Whiteside 1977).

Alternatively, if the fountain darter is a facultative plant associate, we predicted that it would occur in vegetation proportionally to the amount of vegetation available.

2. MATERIALS AND METHODS

2.1. Field methods

San Marcos and Comal rivers originate from voluminous groundwater discharges of the Edwards Aquifer on the eastern edge of Edwards Plateau in central Texas (Kollaus et al. 2015). Six reaches in the upper San Marcos River (Hays County, Texas) and 4 reaches in the Comal River (Comal County, Texas) were sampled in the fall and spring seasons from

October 2014 through November 2019 (Fig. 1). At each reach, fishes were quantified in representative wadeable habitats with seines and in representative non-wadeable habitats with visual SCUBA surveys, except in Reach 1 of the San Marcos River and Reach 2 of the Comal River, which lacked wadeable habitats. Wadeable habitats were generally defined as habitats of sufficient depth for effective seining (<1.7 m in depth) and were in mid-channel and edge areas in riffles, runs, and pools. Non-wadeable habitats were generally defined as habitats with depths exceeding effective seining (>1.7 m) and were in mid-channel and edge areas in runs and pools. At times, wadeable habitats were avoided if current velocities rendered seining ineffective, and non-wadeable habitats included depths <1.7 m as observers advanced from deeper water to shallower water during the visual



Fig. 1. Reaches sampled from 2014–2019 within the San Marcos River, Texas, from upstream to downstream: Reach 1 (29.893° N, 97.929° W), Reach 2 (29.889° N, 97.933° W), Reach 3 (29.882° N, 97.934° W), Reach 4 (29.877° N, 97.932° W), Reach 5 (29.869° N, 97.928° W), and Reach 6 (29.859° N, 97.921° W). Reaches sampled from 2014–2019 within the Comal River, from upstream to downstream: Reach 1 (29.720° N, 98.127° W), Reach 2 (29.715° N, 98.132° W), Reach 3 (29.710° N, 98.122° W), and Reach 4 (29.706° N, 98.129° W), with Reaches 3 and 4 occurring in 2 different channels and located about equidistant from the headwaters

SCUBA surveys. Non-wadeable habitats were only sampled during periods of high water clarity (<5 nephelometric turbidity units [NTU]), which is typical water clarity for rivers that originate from groundwater discharges of the Edwards Aquifer (Groeger et al. 1997, Saunders et al. 2001). Periods of higher NTU (>10 NTU), caused by overland surface flow following rainfall events, recreational activities, and research activities, were avoided until high water clarity returned to typical based on visual estimations. As such, non-wadeable habitats were sampled before wadeable habitats, often on different days. Collections were taken according to state permits (SPR-0601-159), federal permits (TE236730), and Texas State University IACUC (1036-1102-32).

Wadeable habitats consisted of a 15 m² downstream seine haul (5 m effort with 3.0 × 1.8 m common sense seines; mesh size: 3.2 mm) or a 5 m effort of substrate kicking, pending water depth and substrate type. Beginning downstream in a reach and working upstream, seine hauls were spaced cross-sectionally across the reach with adequate spacing between hauls to minimize disturbance to adjacent areas. Once a cross-section was completed, another cross-section was located approximately 20 m upstream. The targeted number of seine hauls per reach was 20. After each seine haul, fishes were identified to species, enumerated, and released. The following habitat variables were quantified after each seine haul: water depth, current velocity (benthic and water column), percent substrate type (clay, silt, sand, gravel, cobble, boulder, bedrock), percent detritus coverage, percent woody debris, and percent vegetation coverage and taxa. Vegetation was identified to lowest practical taxonomic level (Table A1 in the Appendix). Algae was differentiated as unattached filamentous algae, epiphytic algae, and detrital algae. Vegetation taxa were categorized as short if typical height was <50% of water depth and tall if typical height was >50% of water depth. Water temperature, pH, dissolved oxygen, and specific conductance in the area of the seine hauls were measured with a water quality meter (YSI-65 or YSI-85).

Non-wadeable habitats were sampled at 2 levels of resolution: mesohabitat, to quantify pelagic fishes, and microhabitat, to quantify benthic fishes. For mesohabitats, an area ranging in size from 50 to 1300 m² was delineated within each reach and sampled repeatedly across seasons and years. A team of 4 divers assembled on one end of the area boundary, usually the downstream boundary, and swam to the upstream opposite boundary, identifying and enumerating fishes within the mesohabitat. Dive lanes and

field of view were coordinated among divers to avoid double counting of fishes following standardized diving protocols (Brock 1954, Schill & Griffith 1984, Hankin & Reeves 1988). Fishes were identified to the lowest practical taxonomic resolution. Once fish observations were complete for the mesohabitat, 4 microhabitats, consisting of 10 m² transects marked with PVC tubing, were established on the benthos, spaced cross-sectionally and equal distant apart in the mesohabitat. Each diver sampled a transect from downstream to upstream, identifying and enumerating all fishes encountered in the benthos habitat, taking care to detect and identify fishes among vegetation and various substrates such as underneath and around cobbles and boulders. Dive lights were used in low light conditions, common in heavily vegetated areas. Greenthroat darter *E. lepidum* and fountain darter coexist in all reaches of the Comal River (Hubbs et al. 2008). Adults are easily distinguishable to species underwater; however, those darting out of the transect area and juveniles were identified and counted as *Etheostoma* spp. Individuals identified only as *Etheostoma* spp. were excluded from further analysis. Once fishes were identified, measurements of habitat variables within the microhabitat were taken as described above for wadeable habitats. Water temperature, pH, dissolved oxygen, and specific conductance of the mesohabitat were measured with a water quality meter (YSI-65 or YSI-85).

2.2. Statistical methods

The San Marcos and Comal rivers have different plant communities (Edwards Aquifer Authority 2012), so analyses were conducted separately for each river. Wadeable and non-wadeable habitats were also analyzed separately because detectability of fountain darter is greater using methods in non-wadeable habitats than wadeable habitats (Scanes 2016).

Percentages of vegetated habitats and percentages of fountain darters observed in vegetated habitats were calculated for wadeable and non-wadeable habitats by reach in each river. Chi-squared analyses were used to test the relationship between percent vegetated habitats available and percent vegetated habitats observed with fountain darters by reach and in each river. Assumptions of independence and expected cell frequencies were met for the chi-square test. Non-wadeable habitats in Reaches 5 and 6 in the San Marcos River were excluded from chi-squared analyses because of low sample size ($n = 0-1$) of fountain darters observed. Generalized linear models

with Poisson distributions were used in R (Version 3.6.2, R Core Team 2020) to analyze the relationship between fountain darter abundance and percent vegetation coverage, when present. Models analyzed the relationship of combined reaches among wadeable habitats and non-wadeable habitats in each river to increase sample size. Percentages of vegetation taxa and percentages of each vegetation taxon with fountain darters were calculated across reaches for wadeable and non-wadeable habitats in each river. Strauss' linear electivity index (Strauss 1979) was used to analyze the relationship of observed fountain darter occurrence in each vegetation taxon with available occurrence of the vegetation taxon. The index assessed the difference in the observed vegetation taxon observed with fountain darters and in the availability of the taxon across reaches among wadeable habitats and non-wadeable habitats in each river. Positive values indicate an association for the vegetation taxon, and negative values indicate an association away from the vegetation taxon.

3. RESULTS

The numbers of habitats sampled were 1121 wadeable and 518 non-wadeable in the San Marcos River and 816 wadeable and 664 non-wadeable in the Comal River. During the 6 yr period, median flow was $6.0 \text{ m}^3 \text{ s}^{-1}$, ranging from 2.9 to $153 \text{ m}^3 \text{ s}^{-1}$ in the San Marcos River (median daily flow: $5.0 \text{ m}^3 \text{ s}^{-1}$; range: 2.2 – $176 \text{ m}^3 \text{ s}^{-1}$; 1994–2019; USGS Station 08170500) and $8.5 \text{ m}^3 \text{ s}^{-1}$, ranging from 1.8 to $115 \text{ m}^3 \text{ s}^{-1}$ the Comal River (median daily flow: $8.6 \text{ m}^3 \text{ s}^{-1}$; range: 0.16 – $622 \text{ m}^3 \text{ s}^{-1}$; 1927–2019; USGS Station 08169000). Mean (± 1 SE) depths of wadeable habitats were $0.72 \pm 0.01 \text{ m}$ in the San Marcos River and $0.76 \pm 0.01 \text{ m}$ in the Comal River. Mean current velocities of wadeable habitats were $0.34 \pm 0.01 \text{ m s}^{-1}$ in the San Marcos River and $0.22 \pm 0.01 \text{ m s}^{-1}$ in the Comal River. Mean depths of non-wadeable habitats were $1.97 \pm 0.04 \text{ m}$ in the San Marcos River and $1.59 \pm 0.02 \text{ m}$ in the Comal River. Mean current velocities of non-wadeable habitats were $0.17 \pm 0.01 \text{ m s}^{-1}$ in the San Marcos River and $0.08 \pm 0.002 \text{ m s}^{-1}$ in the Comal River. Mean water temperatures were $21.9 \pm 0.01^\circ\text{C}$ in the San Marcos River and $23.1 \pm 0.02^\circ\text{C}$ in the Comal River. The pH ranged from 6.4 to 9.0 in the San Marcos River and from 5.8 to 9.2 in the

Comal River. Specific conductance ranged from 528 to $893 \mu\text{S cm}^{-1}$ in the San Marcos River and from 502 to $592 \mu\text{S cm}^{-1}$ in the Comal River.

The majority of the sampled habitats in the San Marcos River and Comal River were vegetated: 57% of wadeable habitats were vegetated in the San Marcos River and 69% were vegetated in the Comal River (Table 1). More vegetated habitats occurred in the upper reaches of the San Marcos River (Reaches 2 and 3: 75–95%) than in the lower reaches (Reaches 4–6: 25–49%). Vegetated habitats ranged between 62 and 73% among Comal River reaches with no distinct upstream to downstream gradient in occurrence. Overall, 63% of non-wadeable habitats were vegetated in the San Marcos River and 95% were vegetated in the Comal River. More vegetated habitats occurred in the upper reaches of the San Marcos River (Reaches 1–3: 73–95%) than in the lower reaches (Reaches 4–6: 10–69%). Vegetated habitats ranged between 91 and 99% among Comal River reaches with no distinct upstream to downstream gradient in occurrence.

There were 501 fountain darters observed in wadeable and 1761 in non-wadeable habitats in the San Marcos River and 669 in wadeable and 5353 in non-wadeable habitats in the Comal River. Among wadeable habitats, 95% of fountain darters occurred in vegetated habitats in the San Marcos River, and 94% occurred in the Comal River (Table 2). Fountain darter occurrences in wadeable vegetated habitats were greater in the upper reaches of the San Marcos River (Reaches 2 and 3: 97–99%) than in lower reaches (Reaches 4–6: 50–86%). Fountain darter occurrences in wadeable vegetated habitats were similar (91–96%) among reaches in the Comal River. Among non-wadeable habitats, 91% of fountain darters occurred in vegetated habitats in the San Marcos River, and 99% of fountain darters occurred

Table 1. Percent vegetation among wadeable and non-wadeable habitats by reach in the San Marcos and Comal rivers, 2014–2019. Wadeable habitats were not sampled in Reach 1 of the San Marcos River or in Reach 2 of the Comal River

Reach	Wadeable % vegetation		Non-wadeable % vegetation	
	San Marcos River	Comal River	San Marcos River	Comal River
1	–	73	95	91
2	75	–	73	99
3	95	62	94	99
4	30	71	69	90
5	49		13	
6	25		10	
Total	57	69	63	95

Table 2. Percent occurrence of fountain darters in transects with vegetation among wadeable and non-wadeable habitats in the San Marcos and Comal rivers, 2014–2019. Wadeable habitats were not sampled in Reach 1 of the San Marcos River or in Reach 2 of the Comal River

Reach	Wadeable % occurrence of fountain darters		Non-wadeable % occurrence of fountain darters	
	San Marcos River	Comal River	San Marcos River	Comal River
1	–	91	90	98
2	97	–	96	100
3	99	95	96	99
4	53	96	92	100
5	50		0	
6	86		0	
Total	95	94	91	99

in the Comal River. Fountain darter occurrences in non-wadeable vegetated habitats were similar among reaches in the San Marcos River (90–96%, excluding Reach 5 and Reach 6 because of low sample size) and in the Comal River (98–100%). Among fountain darters occurring in non-vegetated habitats, mean substrate percentages among wadeable habitats consisted predominantly of gravel (43%), silt (22%), and

sand (14%) in the San Marcos River and gravel (45%), cobble (19%), and silt (14%) in the Comal River. Mean substrate percentages among non-wadeable habitats consisted predominantly of silt (26%), sand (24%), gravel (18%), and cobble (18%) in the San Marcos River and gravel (47%), silt (20%), and bedrock (13%) in the Comal River.

Fountain darters generally had a positive association with vegetated habitats. They occurred more often than expected in wadeable vegetated habitats in both the San Marcos ($\chi^2_4 = 29.4$, $p < 0.01$) and Comal rivers ($\chi^2_2 = 70.8$,

$p < 0.01$; Fig. 2). Fountain darters also occurred more often than expected in non-wadeable vegetated habitats (San Marcos River: $\chi^2_3 = 13.9$, $p < 0.01$; Comal River: $\chi^2_3 = 14.9$, $p < 0.01$). An exception to the positive relationship was observed among non-wadeable habitats in Reach 1 of the San Marcos River, where they occurred in vegetated habitats less often than expected.

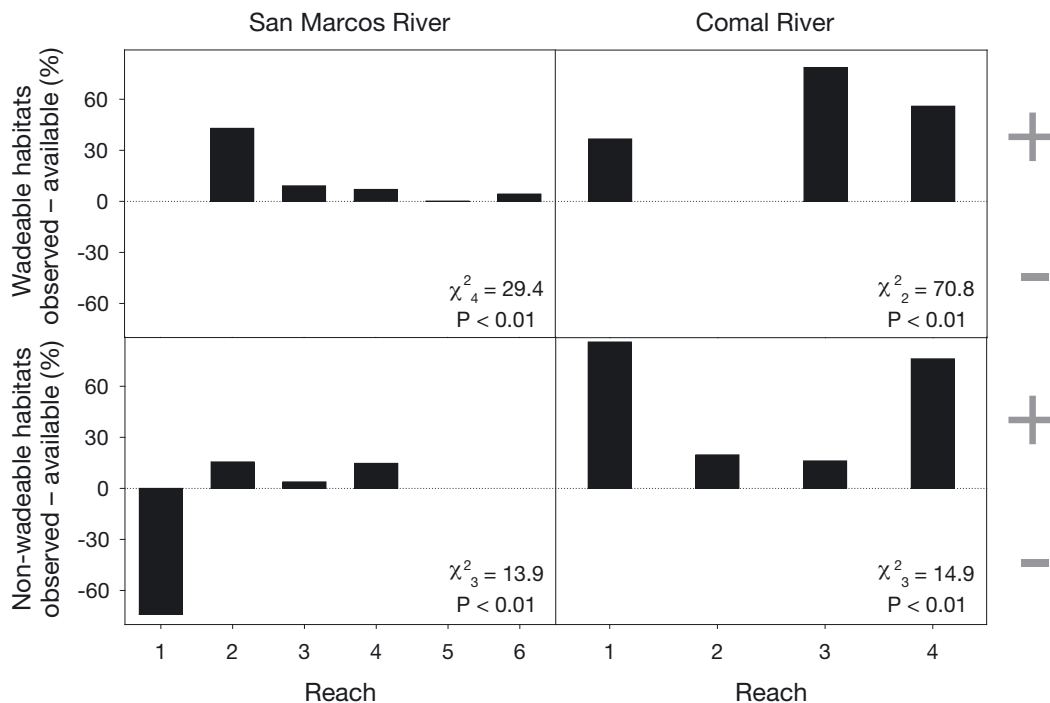


Fig. 2. Differences in the percent (%) of fountain darters across reaches from the San Marcos and Comal rivers observed in vegetated habitats and percent of available vegetated habitats among wadeable and non-wadeable habitats, 2014–2019. Positive symbol represents a positive difference value, indicating that greater percentage of fountain darters were observed in vegetation than the percentage of vegetation available. Negative symbol represents negative difference value, indicating that lesser percentage of fountain darters were observed in vegetation than the percentage of vegetation available. Wadeable habitats were not sampled in Reach 1 of the San Marcos River and Reach 2 of the Comal River. Non-wadeable habitats in Reaches 5 and 6 of the San Marcos River were excluded from analyses because 1 fountain darter was found in Reach 5 and none were found in Reach 6

In vegetated habitats, fountain darter abundance had a positive relationship with the percent vegetation coverage. Among wadeable habitats, the species had a positive linear relationship with percent vegetation coverage in the San Marcos River ($\beta = 0.015$, $p < 0.01$) and Comal River ($\beta = 0.015$, $p < 0.01$) (Table 3). Among non-wadeable habitats, fountain darters had a positive linear relationship with percent vegetation coverage in the San Marcos River ($\beta = 0.004$, $p < 0.01$) and Comal River ($\beta = 0.006$, $p < 0.01$).

Wadeable habitats consisted of 16 plant taxa in the San Marcos and Comal rivers (Table 4). The most abundant vegetation taxon was Texas wild rice (22%),

followed by waterhyme *Hydrilla verticillata* (21%), Indian swampweed *Hygrophila polysperma* (12%), pondweed *Potamogeton* sp. (10%), and filamentous algae (7.6%) in the San Marcos River. The most abundant plant taxon was the bryophyte *Riccia* sp. (29%), followed by Indian swampweed (21%), primrose *Ludwigia repens* (16%), filamentous algae (11%), and fanwort *Cabomba caroliniana* (5.6%) in the Comal River. Electivity indices of fountain darter associations ranged between -5.1 and 2.6 in the San Marcos River, with the strongest negative indices (< -1.0) for Texas wild rice (-5.1), terrestrial vegetation (-1.5), and waterwillow *Justicia americana* (-1.4)

Table 3. General linear regressions of amount of vegetation cover when present and occurrence of fountain darters among wadeable and non-wadeable habitats in the San Marcos and Comal rivers. ** $p \leq 0.01$

	River	No. of fountain darters	<i>b</i>	SE	R ²
Wadeable	San Marcos	474	0.015**	0.0015	0.070
	Comal	1606	0.0150**	0.0013	0.092
Non-wadeable	San Marcos	629	0.0035**	0.0008	0.007
	Comal	5320	0.0059**	0.0005	0.023

and the strongest positive indices (> 1.0) for waterhyme (2.6), coontail/hornwort *Ceratophyllum demersum* (1.9), Indian swampweed (1.6), and eelgrass *Vallisneria* sp. (1.1) (Fig. 3). Electivity indices of fountain darter associations ranged between -2.8 and 6.6 in the Comal River, with the strongest negative indices for filamentous algae (-2.8), eelgrass (-2.4), primrose (-2.1), elephant ear *Colocasia* sp. (-1.9), and pondweed (-1.6) and strongest posi-

Table 4. Percent occurrence of aquatic vegetation taxa and vegetation type among wadeable and non-wadeable habitats in the San Marcos and Comal rivers, 2014–2019

	Wadeable % occurrence of taxa		Non-wadeable % occurrence of taxa	
	San Marcos River	Comal River	San Marcos River	Comal River
Short				
Bryophyte	0.2	29	0.5	37
Detrital algae	0	3.3	4.3	2.6
Epiphytic algae	0	0	5.3	1.0
Filamentous algae	7.6	11	12	9.0
<i>Hygrophila polysperma</i>	12	21	7.1	18
<i>Ludwigia repens</i>	6.3	16	6.6	2.2
<i>Sagittaria platyphylla</i>	2.4	1.6	5.8	5.4
Tall				
<i>Cabomba caroliniana</i>	1.9	5.6	13	12
<i>Ceratophyllum demersum</i>	5.8	0	6.4	0
<i>Chara</i>	0	1.6	0.4	1.6
<i>Colocasia</i>	0	4.1	0.2	0
<i>Hydrilla verticillata</i>	21	0.2	11	0.1
<i>Hydrocotyle verticillata</i>	3.3	0	0.4	0
<i>Justicia americana</i>	1.7	0	0.4	0
<i>Nasturtium</i>	0.2	0	0	0
<i>Nuphar</i>	0	0.4	0	0
<i>Myriophyllum</i>	2.2	0	7.4	1.1
<i>Pistia stratiotes</i>	0	0.2	0	0
<i>Potamogeton</i>	10	2.4	4.3	0
Terrestrial vegetation	1.8	0.1	0	0
<i>Vallisneria</i>	1.9	3.5	2.0	10
<i>Zizania texana</i>	22	0	12	0
Other	0	0.1	0	0

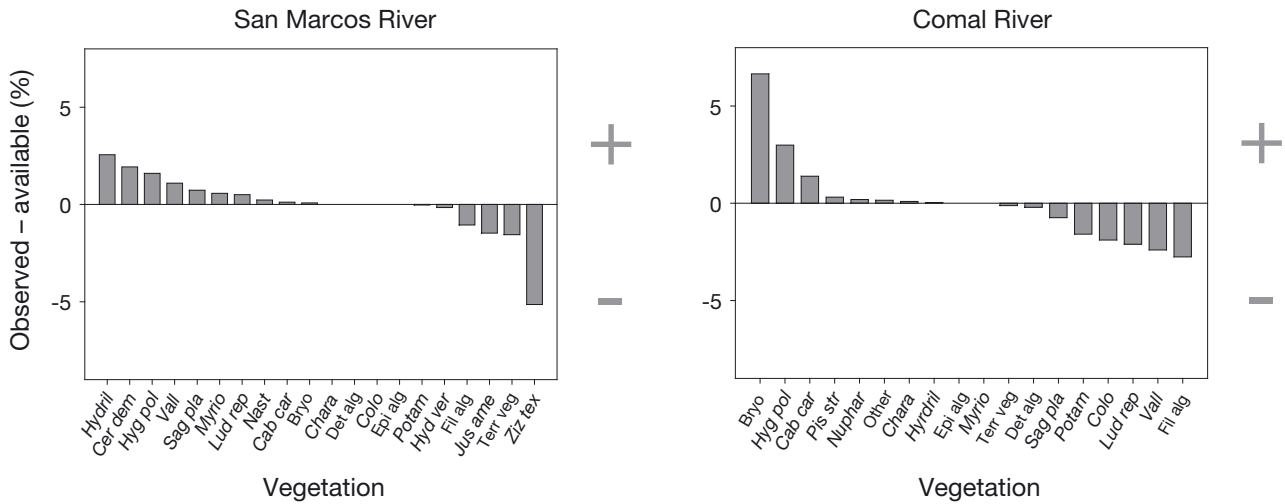


Fig. 3. Electivity index of fountain darters by vegetation taxon among wadeable habitats across reaches of the San Marcos and Comal rivers, 2014–2019. See Table A1 for vegetation taxa abbreviations. Positive and negative symbols defined in Fig. 2

tive indices for bryophyte (6.6), Indian swampweed (3.0), and fanwort (1.4). Among the strong positive indices, 25% were with short and 75% were with tall taxa in the San Marcos River; 66% were with short and 33% were with tall taxa in the Comal River. Among the strong negative indices, 33% were with short and 66% were with tall taxa in the San Marcos River, and 40% were with short and 60% were with tall taxa in the Comal River.

Non-wadeable habitats consisted of 18 plant taxa in the San Marcos River and 12 plant taxa in the Comal River. The most abundant plant taxon was fanwort (13%), followed by filamentous algae (12%), Texas wild rice (12%), waterhyme (11%), parrotfeather/milfoil *Myriophyllum* sp. (7.4%), and Indian swampweed (7.1%) in the San Marcos River. The most abundant plant taxon was bryophyte (37%), fol-

lowed by Indian swampweed (18%), fanwort (12%), eelgrass (10%), and filamentous algae (9%) in the Comal River. Electivity indices of fountain darter associations ranged between -7.8 and 3.5 in the San Marcos River, with the strongest negative indices (<-1.0) for Texas wild rice (-7.8), waterhyme (-2.0), and Indian swampweed (-1.1) and with the strongest positive indices (>1.0) for fanwort (3.5), coontail/hornwort (2.1), parrotfeather/milfoil (2.1), detrital algae (1.7), arrowhead *Sagittaria platyphylla* (1.6), and filamentous algae (1.6) (Fig. 4). Electivity indices of fountain darter associations ranged between -2.3 and 3.1 in the Comal River, with the strongest negative indices for fanwort (-2.3) and the strongest positive indices for bryophyte (3.1). Among the strong positive indices, 50% were with short and 50% were with tall taxa in the San Marcos River and 100%

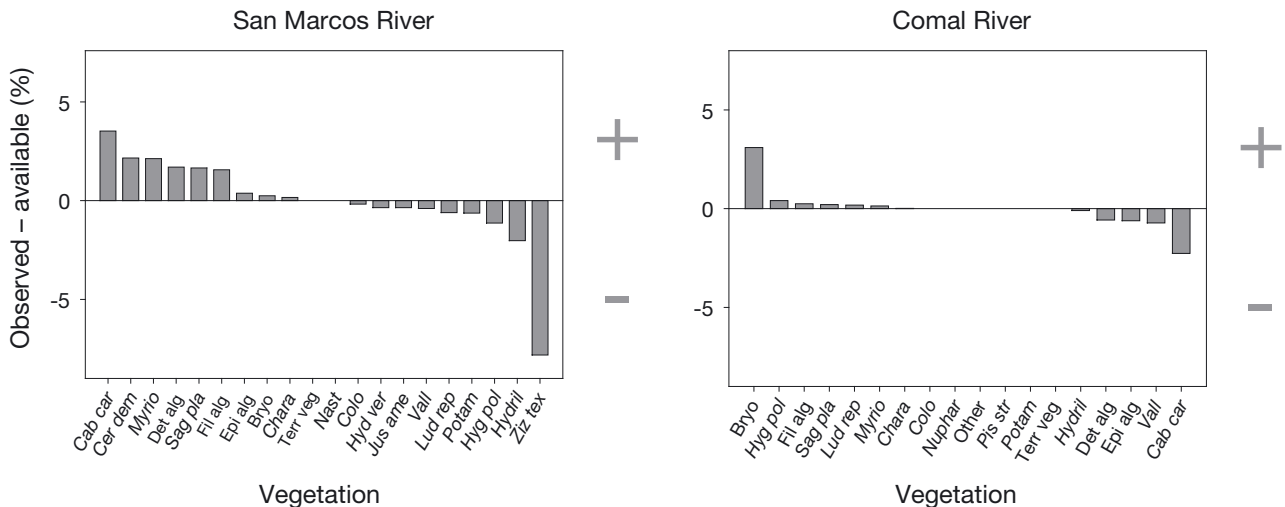


Fig. 4. Same as Fig. 3, but for non-wadeable habitats

were with short in the Comal River. Among the strong negative indices, 33% were with short and 66% were with tall taxa in the San Marcos River and 100% were with tall in the Comal River.

4. DISCUSSION

Fountain darters were found in vegetated habitats more than expected in all reaches except one, largely supporting an obligatory relationship with aquatic vegetation. The species was positively associated with vegetation more than expected in wadeable and non-wadeable habitats of the San Marcos and Comal rivers, except in the non-wadeable habitats of San Marcos River Reach 1. This positive association with vegetation is generally consistent with previous reports of the fountain darter (Schenck & Whiteside 1976, Alexander & Phillips 2012) and obligate vegetation-associated fishes (Simon 1999). However, fountain darters were negatively associated with non-wadeable vegetated habitats in Reach 1 of the San Marcos River, a reach of the river with the highest densities of fountain darters (Behen 2013). Therefore, this one observation suggests a facultative relationship with vegetation and is inconsistent with previous reports of exclusive association with vegetation (Schenck & Whiteside 1976, Alexander & Phillips 2012). Results supporting both obligate and facultative tendencies suggest the fountain darter's association with vegetation could be reach-dependent, although possible mechanisms are unclear at this time.

Obligate associations with vegetation are demonstrated for other fishes related to multiple fitness aspects, primarily feeding and reproduction. Several species are considered obligate associates because they predominantly consume vegetation such as algae (e.g. roundnose minnow *Dionda episcopa* and central stoneroller *Campostoma anomalum*; Wayne 1979, Fowler & Taber 1985) and macrophytes (e.g. grass carp *Ctenopharyngodon idella*; Kilambi 1980). Other species are obligate associates because they predominantly spawn on vegetation (e.g. slough darter *Etheostoma gracile* and banded pygmy sunfish *Elassoma zonatum*; Braasch & Smith 1967, Walsh & Burr 1984). Few species (e.g. rainwater killifish *Lucania parva* Jordan 2002, and herein for the fountain darter) are suggested to be obligate associates but exact mechanisms are unclear. Without a known mechanism, it is difficult to positively conclude an obligatory association for the fountain darter, despite the definitions of obligate and facultative used in this study.

Facultative use of vegetation is more reasonable given many other fishes, including those within the *Microperca* group, demonstrate facultative associations with vegetation (McCormick & Aspinwall 1983). The least darter was previously reported as an obligate plant spawner (Simon 1999), but habitat information provided later suggests the least darter is phytolithophilic, and its association with vegetation is facultative throughout the year (Hargrave & Johnson 2003). Similarly, cypress darter associates primarily with detritus and secondarily with vegetation (Burr & Page 1978). Watercress darter *Etheostoma nuchale*, a federally endangered spring-associated darter with a restricted range (USFWS 1970b) similar to that of the fountain darter, associates strongly with vegetated habitats but is sometimes found in structurally complex non-vegetated habitats (Duncan et al. 2010).

Numbers of fountain darters were positively correlated with percent vegetation coverage. Across all habitats in the San Marcos and Comal rivers, fountain darters had positive relationships with percent vegetation coverage, although the model-predicted increase in darters (e.g. 0.27 in wadeable habitats of the San Marcos River) when vegetation coverage increased from 1 to 100% is likely of little value for fountain darter ecology or population dynamics. Small (e.g. least darter and pugnose minnow *Opsopoeodus emiliae*; Walsh & Burr 1984, Cudmore-Vokey & Minns 2002) and large fishes (e.g. largemouth bass *Micropterus salmoides* and bowfin *Amia calva*; Durocher et al. 1984, Midwood et al. 2018) demonstrate positive relationships with percent vegetation coverage; however, some species occurrences (e.g. red shiner *Cyprinella lutrensis* and spotted gar *Lepisosteus oculatus*) are independent of percent vegetation coverage (Bettoli et al. 1993, Ostrand et al. 2004). Species associations with percent vegetation coverage vary depending on life history requirements, interspecific competition, or predator-prey interactions (Bettoli et al. 1993, Ostrand et al. 2004). Furthermore, aspects of fish population dynamics such as larval development, juvenile recruitment, and fish growth vary depending on the amount of vegetation and are reduced by greater amounts of vegetation (>75%; Ismail et al. 2018) or lower amounts of vegetation (<20%; Durocher et al. 1984, Casselman & Lewis 1996, Miranda & Pugh 1997). Understanding the effects of the amount of vegetation on fish can thus provide insight into the mechanism by which fish use vegetation.

Predictions that fountain darters would be positively associated with dense, short vegetation were partially supported. Fountain darters were posi-

tively associated primarily with short vegetation like bryophytes in the Comal River. Associations with dense or short vegetation are often reported for small (e.g. Arkansas darter *Etheostoma cragini*; Smith & Fausch 1997) and large species (e.g. bowfin; Midwood & Chow-Fraser 2012), which allows them to feed on benthic or pelagic food items while being in close proximity to cover protecting prey or concealing ambush predators (Brusven et al. 1990). However, the prediction was not supported in the San Marcos River, where less than half of the positive associations were with short vegetation taxa. Associations with tall vegetation are often reported for small (e.g. taillight shiner *Notropis maculatus* and Devils River minnow *Dionda diaboli*; Robison 1978, Garrett et al. 2004) and large species (e.g. muskellunge *Esox masquinongy* and largemouth bass; Jonckheere 1994, Murry & Farrell 2006, Troutman et al. 2007), where it is suggested that spawning locations and water quality, plant complexity, and niche space are optimized (Grenouillet et al. 2002, Troutman et al. 2007). Vegetation height alone, however, does not best depict structural complexity. Multiple factors such as quantification of submerged branches and roots, plant density, and percent light transmitted are needed to provide a 3-dimensional view of vegetation structure (Grenouillet et al. 2002, Montoya-Ospina et al. 2020). Structural complexity of vegetation in combination with percent vegetation coverage is important for many benthic fishes like the fountain darter (Duncan et al. 2010, Pratt & Lauer 2013). Structurally complex vegetation can decrease feeding efficiency of piscivores (Savino & Stein 1982, Bettoli et al. 1992) and predatory fish movement (Killgore et al. 1989). Increased macrophyte complexity and diversity also increases richness and diversity of invertebrates, providing increased foraging opportunities for small fish (Biles 2017, Yofukuji et al. 2021). Thus, structurally complex vegetated habitats can benefit small benthic fishes by reducing predatory pressures and increasing foraging efficiency (Rozas & Odum 1988). Fountain darters were associated with both short and tall vegetation types, suggesting a facultative use of multiple vegetation types depending on their need for foraging or cover.

One notable exception of fountain darter association with tall vegetation is with Texas wild rice, a federally endangered aquatic macrophyte located only in the upper San Marcos River (Terrell et al. 1978). Planting of Texas wild rice after 2013, continued grooming, and removal of non-native vegetation have facilitated Texas wild rice growth and expansion (BIO-WEST 2019). In this study, we found

that fountain darters were negatively associated with Texas wild rice. This is reasonable considering small benthic darters might not utilize the structure provided by Texas wild rice leaves that float in the water column. Other co-variables include stream flow; for example, among the sampled reaches, Texas wild rice occurs in swifter currents, whereas fountain darters have slack-water affinities (Alexander & Phillips 2012). Given that Texas wild rice coverage is expanding while other non-native plants are being removed, understanding this apparent inverse relationship is important in regard to fountain darter habitat. Fountain darters demonstrated positive associations with non-native vegetation, primarily waterhyme and Indian swampweed, which can be expected given that several native fishes are reported to have higher densities and abundances in non-native vegetation (Duffy & Baltz 1998). Additionally, mechanical removal of non-native vegetation, like waterhyme or parrotfeather/milfoil, can cause minor, short-term changes in pelagic and benthic species composition, richness, and density (Mikol 1985, Maceina et al. 1991, Serafy et al. 1994). Continued monitoring of fish and vegetation community composition will enable the assessment of vegetation management activities on the existing native fish community.

Despite fountain darters being reported as 'exclusive in' or preferring vegetation (especially short vegetation), our multi-year and multi-site study documented that a positive association exists between fountain darters and vegetation but could not conclude with certainty whether this relationship was obligatory or facultative. Manipulative studies (Woodley & Peterson 2003, Griffen & Byers 2006, Swanbrow Becker & Gabor 2012) would be beneficial next steps, providing a mechanistic understanding of the relationship by assessing the survival, behavioral, and physiological responses of fountain darters among various types and amounts of structurally complex vegetation (Montoya-Ospina et al. 2020). Mechanisms could also provide a basis to assess additional threats to the fountain darter, such as high-flow events (Schenck & Whiteside 1976) and reduction in flows (Mora et al. 2013) on vegetation coverage, and to guide ongoing vegetation restoration efforts. Restoration efforts and maintaining viable aquatic communities within critical habitats of endangered fishes requires first determining fish-habitat associations, including the direct and indirect influences of vegetation and the mechanisms by which fish use vegetation (Bond & Lake 2003).

Acknowledgements. Funding was provided by the EAA. We thank Kristy K. Smith (EAA) and Kenny P. K. Behen (Washington Department of Fish and Wildlife) for their assistance in developing sampling protocols of the fish biomonitoring program, and numerous Texas State University graduate and undergraduate students that assisted in field sampling.

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Appendix.

Table A1. Aquatic vegetation taxa in transects with vegetation among wadeable and non-wadeable habitats in the San Marcos and Comal rivers, 2014–2019

Common name	Scientific name	Abbreviation
Arrowhead	<i>Sagittaria platyphylla</i>	<i>Sag pla</i>
Bryophyte	<i>Riccia fluitans</i>	Bryo
Coontail or hornwort	<i>Ceratophyllum demersum</i>	<i>Cer dem</i>
Detrital algae		Det alg
Eelgrass	<i>Vallisneria</i>	<i>Vall</i>
Elephant ear	<i>Colocasia</i>	<i>Colo</i>
Epiphytic algae		Epi alg
Fanwort	<i>Cabomba caroliniana</i>	<i>Cab car</i>
Filamentous algae	<i>Spirogyra, Bulbochaeta, Oscillatoria, Rhizoclonium</i>	Fil alg
Indian Swampweed	<i>Hygrophila polysperma</i>	<i>Hyg pol</i>
Muskgrass, stonewort	<i>Chara</i>	<i>Chara</i>
Parrot feather, milfoil	<i>Myriophyllum</i>	<i>Myrio</i>
Pennywort	<i>Hydrocotyle verticillata</i>	<i>Hyd ver</i>
Pondweed	<i>Potamogeton</i>	<i>Potam</i>
Primrose	<i>Ludwigia repens</i>	<i>Lud rep</i>
Terrestrial vegetation		Terr veg
TX wild rice	<i>Zizania texana</i>	<i>Ziz tex</i>
Water lettuce	<i>Pistia stratiotes</i>	<i>Pis str</i>
Water lily	<i>Nuphar</i>	<i>Nuphar</i>
Watercress	<i>Nasturtium</i>	<i>Nast</i>
Waterthyme	<i>Hydrilla verticillata</i>	<i>Hydril</i>
Waterwillow	<i>Justicia americana</i>	<i>Jus ame</i>

Editorial responsibility: Susana Caballero,
Bogota, Colombia
Reviewed by: S. Ismail and 2 anonymous referees

Submitted: May 31, 2021
Accepted: October 20, 2021
Proofs received from author(s): December 14, 2021