ESTABLISHING PATTERNS IN VEGETATION ASSOCIATIONS OF THE FOUNTAIN DARTER *ETHEOSTOMA FONTICOLA* IN THE SAN MARCOS AND COMAL RIVERS OF TEXAS

by

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ABSTRACT

Aquatic vegetation provides many services for aquatic habitats and fish communities. The 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. 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 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 majority of reaches within the San Marcos and Comal rivers, but there were no clear patterns in type of vegetation used. Current vegetation management in both rivers includes the removal of non-native and restoration of native vegetation, so understanding the patterns of Fountain Darter associations with vegetation will guide in future management and restoration efforts of these spring systems.

I. ESTABLISHING PATTERNS IN VEGETATION ASSOCIATIONS OF THE FOUNTAIN DARTER *ETHEOSTOMA FONTICOLA* IN THE SAN MARCOS AND COMAL RIVERS OF TEXAS

Introduction

Aquatic vegetation (e.g., macrophytes, algae) provides a variety of ecosystem services for fishes. Several lineages of fishes are preferential and opportunistic consumers of aquatic vegetation (Goldstein and 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. 2020), 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 and Lewis 1995). Therefore, in some aquatic systems, type and amount of aquatic vegetation are strong predictors of fishes, more so than other traditional predictors of fishes like water quality (Cvetkovic et al. 2010), and are considered primary structuring mechanisms of fish densities, species richness, and recruitment (Willis et al. 1992; Snickars et al. 2009; Ismail et al. 2018). Identifying the mechanisms of fish and aquatic vegetation relationships (i.e., direct, as a food source; indirect, as cover) is necessary to inform species fitness (e.g., reproductive output or survival) associated with fish use of aquatic vegetation.

Subgenus *Microperca* (Percidae, *Etheostoma*) consists of three species (*E. microperca*, *E. proeliare*, and *E. fonticola*) (Near et al. 2015) with a collectively broad distribution throughout the Great Lakes drainages, Mississippi River drainage, and eastern and western gulf slope drainages of North America (Burr and 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 and Whiteside 1976; Burr and Page 1978, 1979). Eggs are deposited on vegetation, detritus, and rocks with no parental care (Strawn 1956; Burr and Page 1978; Burr and Page 1979).

Among the three recognized species of *Microperca* (see Echelle et al. 2015), the Fountain Darter *E. fonticola* has the most limited distribution, found only in two spring systems of central Texas: San Marcos River and Comal River. Listed by US Fish and Wildlife Service 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 two spring systems (Comal springs and San Marcos springs). Persistence of the Fountain Darter is linked to continuous flows of the spring systems (Schenck and Whiteside 1977; Simon et al. 1995; Votteler 1998), specifically flows >2.8 m^3/s in the San Marcos River (Mora et al. 2013). Continuous 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; Becker et al. 2016), reproduction (Brandt et al. 1993; Bonner et al. 1998), and performance (Craig et al. 2019). Likewise, Fountain Darters associate with aquatic vegetation potentially for feeding, reproduction, and refuge (Alexander and Phillips 2012); however, direct quantification of the association is lacking. The Fountain Darter association with vegetation is reported as exclusive (Schenck and Whiteside 1976) or as preferred (USFWS 1996), but Fountain Darters are 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 and Whiteside 1976, Linam et al. 1993) and in dense, ornate vegetation (Alexander and Phillips 2012). Short vegetation might provide optimum conditions for feeding and reproduction (Linam et al. 1993), although Fountain Darters are documented spawning on short and tall vegetation and other substrates (Brandt et al. 1993). Mechanisms driving Fountain Darter distributions among vegetation are poorly understood, thus first identifying clear patterns in Fountain Darter association with vegetation is needed.

Current perspectives of Fountain Darter habitat associations, particularly with aquatic vegetation, are based on short duration studies (i.e., 1 year or less), mainly in wadeable waters, and primarily conducted in the San Marcos River. In 2013, EAA established a biomonitoring program to document bi-annual fish community structure (e.g., species richness and density) and fish-habitat associations among multiple sites in wadeable and non-wadeable habitats within the San Marcos and Comal rivers. Purpose of this study was to assess the relationship between Fountain Darter and aquatic vegetation using a six-year data set taken from multiple sites twice per year, from wadeable and non-wadeable habitats, and within the known range of the Fountain Darter. Currently, Fountain Darter association with vegetation is thought to be obligatory (i.e., “exclusive”, Schenck and Whiteside 1976, or preferred, USFWS 1996). Long term goals of the Edwards Aquifer Habitat Conservation Plan (2012) for Fountain Darters largely include restoration and protection of native vegetation. From 2013 to 2018, vegetation community in the San Marcos and Comal rivers has changed due to non-native vegetation removal in restored reaches. While non-native vegetation has decreased about

30% in experimental reaches, native vegetation, primarily Texas Wild-Rice *Zizania texana*, increased by about 50% (Bio-West 2013-2018). In habitats where Texas Wild-Rice has replaced non-native vegetation, Fountain Darters have decreased (Bio-West, 2019). Therefore, a greater understanding of Fountain Darters association with vegetation is needed to support long term goals and costs associated with vegetation management implemented by the habitat conservation plan, but, perhaps more importantly, to establish patterns in vegetation associations in order to predict and test the mechanisms of Fountain Darter association with aquatic vegetation.

Objectives of this study are to 1) quantify occurrences of vegetation and Fountain Darter among available habitats from multiple reaches within the San Marcos River and Comal River, 2) to assess the relationship between occurrence and abundance of vegetation and occurrence of Fountain Darters, and 3) assess the relationship in Fountain Darter occurrences and type of vegetation among available habitats. If Fountain Darters are an obligate plant associate, I predict they will primarily occur within vegetation and are more abundant in shorter vegetation (Strawn 1956; Schenk and Whiteside 1977). Alternatively, if Fountain Darters are a facultative plant associate, like other species of *Microperca*, I predict they will occur in vegetation similar to its availability and the previously reported association with aquatic vegetation is a consequence of Fountain Darter affinities for slack water habitats (Burr and Page 1978, 1979).

Methods

Field Methods

Six reaches in the upper San Marcos River (Hays County, Texas) and four reaches in the Comal River (Comal County, Texas) were sampled in the Fall and Spring seasons from October 2014 through November 2019. Reaches within the San Marcos River, from upstream to downstream, were Spring Lake, Sewell Park, Rio Vista Park, Crooks Park, Thompson Island, and Smith Property. Reaches within the Comal River, from upstream to downstream, were Upper Spring Run, Landa Lake, and old and new channels (split of the main channel, equidistant from the headwaters) (Figure 1). At each reach, fishes were quantified in non-wadable habitats with SCUBA gear and in wadeable habitats with seines.

Wadeable habitats consisted of a 15-m^2 downstream seine haul (5-m effort with a 3.0 x 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 of adjacent areas. Once a cross section was completed, another cross section was located upstream 20 m. 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 for each seine haul: water depth, current velocity (benthic and water column), percent substrate type (e.g., clay, silt, sand, gravel, cobble), percent detritus coverage, percent woody debris, and percent vegetation coverage and taxa (e.g., Bryophyte, *Hydrilla*). Vegetation was identified to lowest practical taxonomic level (Appendix 1). Algae was differentiated as filamentous (e.g., unattached), epiphytic (e.g., attached to surfaces), and detrital algae (e.g., dead algae). Vegetation taxa was considered short if, in its typical growth form in the San Marcos or Comal rivers, the height was generally < 50% of water depth and tall if the height was generally > 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 two levels of resolution: mesohabitat to quantify pelagic fishes and microhabitat to quantify benthic fishes. For mesohabitats, an area ranging in size from 50 to 1,300 m^2 was delineated within each reach and sampled repeatedly across seasons and years. A team of four 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 similar to standardized diving protocols (Brock 1954; Schill and Griffith 1984; Hankin and Reeves 1988). Fishes were identified to the lowest practical taxonomic resolution. The two *Gambusia* species known to occur throughout the San Marcos River and Comal River (*Gambusia geiseri* and *Gambusia affinis*; Craig and Bonner 2019) were identified as *Gambusia*, since positive identification of either species from underwater observation is unreliable. Although adult sunfishes (Family Centrarchidae; Genus *Lepomis*) are often easily identifiable underwater, adult and juvenile sunfishes were often listed as *Lepomis* to avoid taking the time in species identification. Once fish observations were complete for the mesohabitat, four microhabitats, consisting of 10-m^2 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 various substrates (i.e., underneath and around cobbles and boulders) and vegetation. As with mesohabitats, *Lepomis* and *Gambusia* were often identified to genus level, especially those that darted from substrates and vegetation and out of the transect area during surveys. In addition, Greenthroat Darters *Etheostoma lepidum* and Fountain Darters coexist in all reaches of the Comal River (Hubbs et al. 2008). Adults are easily distinguishable underwater; however, those darting out of the transect area and juveniles were identified and counted as *Etheostoma*. Once fish were quantified in the microhabitat, the following habitat variables were quantified for the microhabitat transect: water depth, current velocity (benthic and water column), percent substrate type (e.g., clay, silt, sand, gravel, cobble), percent detritus coverage, percent woody debris, and percent vegetation coverage and taxa (e.g., Bryophyte, *Hydrilla*). Vegetation was identified to lowest practical taxonomic level (Appendix 1). Algae was differentiated as filamentous (e.g., unattached), epiphytic (e.g., attached to surfaces), and detrital algae (e.g., dead algae). Vegetation taxa was considered short if, in its typical growth form in the San Marcos or Comal rivers, the height was generally < 50% of water depth and tall if the height was generally > 50% of water depth. Mean habitat variables of the four microhabitats were used to estimate habitat variables for the mesohabitat. Water temperature, pH, dissolved oxygen, and specific conductance of the mesohabitat were measured with a water quality meter (YSI-65 or YSI-85).

Statistical Methods

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

Percent frequency of occurrence of vegetation among wadeable and non-wadeable habitats by reach in the San Marcos River and Comal River was calculated. Fountain Darter frequency of occurrence observed in vegetation was calculated among wadeable and non-wadeable habitats by reach in each river. Chi-square analyses were used to analyze the relationship between observed Fountain Darter occurrence in vegetated habitats and available vegetated habitats across reaches in each river. All Chi-square test assumptions (independence, at least 5 expected) were met. Non-wadeable habitats in reaches 5 and 6 in the San Marcos River were excluded from Chi-square analyses because no Fountain Darters were detected.

Generalized linear models with Poisson distributions were used in R (Version 3.6.2) to analyze a relationship between Fountain Darter abundance and amount of vegetation (percent vegetation cover) when vegetation was present. Models analyzed the relationship of combined reaches among wadeable habitats and among non-wadeable habitats in each river. Reaches were combined to increase sample size.

Percent frequency of occurrence of specific vegetation types was calculated across reaches among wadeable and non-wadeable habitats in the San Marcos River and Comal River. Fountain Darter frequency of occurrence observed in each vegetation type was calculated across reaches among wadeable and non-wadeable habitats in each river. Strauss' linear electivity index was used to analyze relationship of observed Fountain Darter occurrence in vegetation types with available occurrence of vegetation types (Strauss 1979). The index analyzes the difference in the observed vegetation type used by Fountain Darters and overall availability of vegetation type across reaches among wadeable habitats and non-wadeable habitats in each river. Positive values indicate an association for the vegetation type, and negative values indicate an association away from the vegetation type.

Results

A total of 1,937 wadeable habitats and a total of 1,182 non-wadeable habitats were sampled in the San Marcos River (1,121 wadeable and 518 non-wadeable habitats) and Comal River (816 wadeable and 664 non-wadeable habitats) during a six-year period. During the six-year period, median flow was 6.0 m^3/s ranging from 2.9 to 153 m^3/s in the San Marcos River (median daily flow: 5.0 m^3/s; range: 2.2 - 176 m^3/s; 1994 - 2019; USGS Station 08170500) and was 8.5 m^3/s ranging from 1.8 to 115 m^3/s the Comal River (median daily flow: 8.6 m^3/s; range: 0.16 - 622 m^3/s; 1927 - 2019; USGS Station 08169000). One high flow pulse occurred in the San Marcos River in October 2015 with a maximum discharge of 153 m^3/s, and in the Comal River in October 2015 with a maximum discharge of 115 m^3/s. Mean water temperatures (± 1 SE) were 21.9 °C (± 0.01 °C) in the San Marcos River and 23.1 °C (± 0.02 °C) in the Comal River. The pH ranged from 6.4 to 9.0 in the San Marcos River and from 5.75 to 9.24 in the Comal River. Specific conductance ranged from 528 to 893 µS/cm in the San Marcos River and from

502 to 592 µS/cm in the Comal River.

San Marcos River and Comal River were densely vegetated systems. Among wadeable habitats, 57% of the habitats had vegetation in the San Marcos River and 69% of the habitats had vegetation in the Comal River (Table 1). Habitats with vegetation were greater in the upper reaches of the San Marcos River (reaches 2 and 3: 75 to 95%) than in the lower reaches (reaches 4 - 6: 25 to 49%). Habitats with vegetation ranged between 62 and 73% among Comal River reaches with no distinct upstream to downstream gradient. Among non-wadeable habitats, 63% of the habitats had vegetation in the San Marcos River and 95% of the habitats had vegetation in the Comal River. As with wadeable habitats, habitats with vegetation were greater in the upper reaches of the San Marcos River (reaches 1 – 3: 73 to 95%) than in the lower reaches (reaches 4 - 6: 10 to 69%). Habitats with vegetation ranged between 91 to 99% among Comal River reaches with no distinct upstream to downstream gradient.

A total of 1,170 Fountain Darters was observed in wadeable habitats in the San Marcos River (N = 501) and in the Comal River (N = 669), and a total of 7,054 Fountain Darters was observed in non-wadeable habitats in the San Marcos River (N = 1,761) and in the Comal River (N = 5,353). Among wadeable habitats, 95% of the Fountain Darters occurred in habitats with vegetation in the San Marcos River and 94% of the Fountain Darters occurred in habitats with vegetation in the Comal River (Table 2). Fountain Darter occurrences in habitats with vegetation was greater in the upper reaches of the San Marcos River (reaches 2 and 3: 97 to 99%) than in the lower reaches (4 – 6: 50 to 86%). Fountain Darter occurrences in habitats with vegetation were similar (91 to 96%) in the Comal River. Among non-wadeable habitats, 91% of the Fountain Darters occurred in habitats with vegetation in the San Marcos River and 99% of the Fountain Darters occurred in habitats with vegetation in the Comal River. Fountain Darter occurrences were similar among reaches in the San Marcos River (90 to 96%, excluding reach 5 where only one Fountain Darter was found in a habitat without vegetation and reach 6 where no Fountain Darters were found) and in the Comal River (98 to 100%). Among Fountain Darters not occurring in habitats with vegetation, substrates consisted predominantly, on average, of gravel (43%), silt (22%), and sand (14%) among wadeable habitats in the San Marcos River and gravel (45%), cobble (19%), and silt (14%) among wadeable habitats in the Comal River (Table 3). Substrates consisted predominantly, on average, of silt (26%), sand (24%), gravel (18%), and cobble (18%) among non-wadeable habitats in the San Marcos River and gravel (47%), silt (20%), and bedrock (13%) among non-wadeable habitats in the Comal River.

Fountain Darters were generally positively associated with vegetated habitats. Among wadeable habitats, Fountain Darters occurred more often in habitats with vegetation than expected in the San Marcos River ($X^2_4 = 29.4$, $P < 0.01$; Figure 2) and in the Comal River ($X^2_2 = 70.8$, $P < 0.01$; Figure 2). Among non-wadeable habitats, Fountain Darters occurred more often in habitats with vegetation than expected in the San Marcos River ($X^2_4 = 13.9$, $P < 0.01$; Figure 3) and in the Comal River ($X^2_3 = 14.9$, $P < 0.01$; Figure 3). An exception to the positive relationship with vegetated habitats was observed among non-wadeable habitats in San Marcos River reach 1, where Fountain Darters occurred less than expected in habitats with vegetation.

When vegetation was present, Fountain Darters had a positive relationship with the amount of vegetation cover. Among wadeable habitats, Fountain Darters had a positive linear relationship with the amount of vegetation cover in the San Marcos River ($\beta = 0.015$, $P < 0.01$) and in the Comal River ($\beta = 0.015$, $P < 0.01$) (Table 4). Among non-wadeable habitats, Fountain Darters had a positive linear relationship with the amount of vegetation cover in the San Marcos River ($\beta = 0.004$, $P < 0.01$) and in the Comal River ($\beta = 0.006$, $P < 0.01$).

Vegetation among wadeable habitats consisted of 16 plant taxa in the San Marcos River and Comal River (Table 5). The most abundant plant taxon was Texas Wild-Rice *Zizania texana* (22%), followed by *Hydrilla verticillata* (21%), *Hygrophila polysperma* (12%), *Potamogeton* (10%), and filamentous algae (7.6%; e.g., *Spirogrya, Cladophora*) in the San Marcos River. The most abundant plant taxon was Bryophyte (29%), followed by *H. polysperma* (21%), *Ludwigia repens* (16%), filamentous algae (11%), and *Cabomba caroliniana* (5.6%) in the Comal River. Electivity indices of Fountain Darter associations in wadeable habitats ranged between -5.1 to 2.6 in the San Marcos River with the strongest negative indices (i.e., < -1.0) for *Z. texana* (-5.1), terrestrial vegetation (-1.5), and *Justicia americana* (-1.4) and with strongest positive indices (i.e., > 1.0) for *Hydrilla verticillata* (2.6), *Ceratophylum demersum* (1.9), *H. polysperma* (1.6), and *Vallisneria* (1.1) (Figure 4). Electivity indices of Fountain Darter associations in wadeable habitats ranged between -2.8 and 6.6 in the Comal River with the strongest negative indices (i.e., < -1.0) for filamentous algae (-2.8), *Vallisneria* (-2.4), *L. repens* (-2.1), *Colocasia* (-1.9), and *Potamogeton* (-1.6) and with strongest positive indices (i.e., > 1.0) for Bryophyte (6.6), *H. polysperma* (3.0), and *C. caroliniana* (1.4) (Figure 4).

Vegetation among non-wadeable habitats consisted of 18 plant taxa in the San Marcos River and 12 plant taxa in the Comal River (Table 5). The most abundant plant taxon was *C. caroliniana* (13%), followed by filamentous algae (12%), *Z. texana* (12%), *Hydrilla verticillata* (11%), *Myriophylum* (7.4%), and *H. polysperma* (7.1%) in the San Marcos River (Table 5). The most abundant plant taxon was Bryophyte (37%), followed by *H. polysperma* (18%), *C. caroliniana* (12%), *Vallisneria* (10%), and filamentous algae (9%) in the Comal River. Electivity indices of Fountain Darter associations in non-wadeable habitats ranged between -7.8 and 3.5 in the San Marcos River with the strongest negative indices (i.e., < -1.0) for *Z. texana* (-7.8), *Hydrilla verticillata* (-2.0), and *H. polysperma* (-1.1) and with strongest positive indices (i.e., > 1.0) for *C. caroliniana* (3.5), *C. demersum* (2.1), *Myriophylum* (2.1), detrital algae (1.7), *Sagittaria platyphylla* (1.6), and filamentous algae (1.6) (Figure 5). Electivity indices of Fountain Darter associations in non-wadeable habitats ranged between -2.3 and 3.1 in the Comal River with the strongest negative indices (i.e., < -1.0) for *C. caroliniana* (-2.3) and with strongest positive indices (i.e., > 1.0) for Bryophyte (3.1) (Figure 5).

Discussion

Fountain Darters were found in vegetated habitats more than expected, supporting an obligatory relationship with aquatic vegetation. Fountain Darters were positively associated with vegetated habitats more than expected in wadeable and non-wadeable reaches of the San Marcos River and Comal River with few exceptions. Exceptions were among non-wadeable habitats in the San Marcos River in which Fountain Darters were negatively associated with vegetated habitats more than expected in reach 1, only 1 Fountain Darter was found outside of vegetation in reach 5, and no Fountain Darters were found among habitats in reach 6. This association is generally consistent with past collections of Fountain Darters (Schenck and Whiteside 1976; Alexander and Phillips 2012) and other obligate vegetation associated fish (Simon 1999). However, Fountain Darters were negatively associated with vegetated non-wadeable habitats in reach 1 of the San Marcos River, a reach of the river with the highest densities of Fountain Darters (Behen 2013). Fountain Darters negative association with aquatic vegetation in Reach 1 of the San Marcos River is inconsistent with the exclusive association of vegetation as reported by others (Schenck and Whiteside 1976; Alexander and Phillips 2012) and suggests a facultative relationship with aquatic vegetation. Results supporting both obligate and facultative tendencies suggest Fountain Darter association with vegetation could be reach dependent, although possible dependencies are unclear at this time.

Obligate associations with aquatic vegetation are demonstrated for other fishes and for multiple fitness aspects, primarily for feeding and reproduction. Several species are considered obligate associates because they predominantly consume aquatic vegetation such as algae (e.g., Roundnose Minnow *Dionda episcopa* and Central Stoneroller *Campostoma anomalum*, Wayne 1979; Fowler and 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 and Smith 1967; Walsh and Burr 1984). Few species (e.g., Rainwater Killifish *Lucania parva* and this report of the Fountain Darter, Jordan 2002) are reported 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 that we use herein.

Facultative use of vegetation is more reasonable given many other fishes, including those within the *Microperca* group demonstrate facultative associations with vegetation (McCormick and Aspinwall 1982). Least Darter *Etheostoma microperca* was previously reported as an obligate plant spawner (Simon 1999), but habitat information provided later suggest Least Darter is phytolithophilic and its association with vegetation is facultative throughout the year (Hargrave and Johnson 2003). Similarly, Cypress Darter *Etheostoma proeliare* associates primarily with detritus and secondarily with vegetation (Burr and Page 1978). Other darters such as the Watercress Darter *Etheostoma nuchale*, a federally endangered spring-associated darter with a restricted range (USFWS 1970b), associate strongly with vegetated habitats but are sometimes found in structurally complex non-vegetated habitats (Duncan et al. 2010). Although distributions can be informative to estimate associations with vegetation, it is possible that Fountain Darters found in habitats lacking vegetation could move to nearby habitats with vegetation (Dammeyer et al. 2013), obscuring an obligate association.

The prediction that the number of Fountain Darters would have a positive relationship with the amount of vegetation cover was supported. Across all habitats in the San Marcos River and Comal River, Fountain Darters had positive relationships with the amount of vegetation, although the increase in darters (e.g., 0.27 in wadeable habitats of the San Marcos River) when vegetation cover increased from 1 to 100% is likely meaningless for Fountain Darter ecology or population dynamics. Small (e.g., Least Darter and Pugnose Shiner *Opsopoeodus emiliae*, Walsh and Burr 1984; Cudmore-Vokey and Minns 2002) and large species (e.g., Largemouth Bass *Micropterus salmoides* and Bowfin *Amia calva*, Durocher et al. 1984; Midwood et al. 2016) demonstrate positive relationships with amount of vegetation; however, some species (e.g., Red Shiner *Cyprinella lutrensis* and Spotted Gar *Lepisosteus oculatus* are not associated with changes in the amount of vegetation (Bettoli et al. 1993; Ostrand et al. 2004). Species associations with amount of vegetation vary depending on species life history requirements, interspecific competition, or predator-prey interactions (Bettoli et al. 1993; Ostrand et al. 2004). Furthermore, aspects of fish population dynamics (larval development, juvenile recruitment, and fish growth) vary depending on the amount of vegetation and are reduced by excessive amounts of vegetation (> 75%; Ismail et al. 2018) or minimal amounts of vegetation (< 20%; Casselman and Lewis 1995; Durocher et al. 1984; Miranda and Pugh 1997). Understanding the effects of the amount of vegetation on fish can thus provide insight to 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 positively associated primarily with short vegetation in the Comal River. Associations with dense or short vegetation are often reported for small (e.g., Arkansas Darter *Etheostoma cragini*, Smith and Fausch 1997) and large species (e.g., Bowfin *A. calva*, Midwood and Chow-fraser 2011), where they can 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 Fountain Darters had positive associations with tall vegetation, including several non-native taxa. Associations with taller growing vegetation is 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 and Farrell 2006; Troutman et al. 2007), where it is reported that spawning locations and water quality, plant complexity, and niche space are optimized (Grenouillet et al. 2002; Troutman et al. 2007). Structural complexity of vegetation in combination with amount of vegetation cover is important for many benthic fishes like the Fountain Darter (Duncan et al. 2010; Pratt and Lauer 2013). Structurally complex vegetation can decrease feeding efficiency of piscivores (Savino and 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. 2020). Thus, structurally complex vegetated habitats can benefit small benthic fishes by reducing predatory pressures and increasing foraging efficiency (Rozas and Odum 1988). Fountain Darters were associated with short and tall growing vegetation types suggesting a facultative use of multiple vegetation types depending on their needs (e.g., 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). Early planting of Texas Wild-Rice beginning in 1996, continued grooming, and removal of non-native vegetation have facilitated Texas Wild-Rice growth and cover 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 or considering other co-variables. For example, among the sampled reaches, Texas Wild-Rice occurred in swifter currents, whereas Fountain Darters are thought to have slackwater affinities (Alexander and Phillips 2012). Understanding this apparent inverse relationship is needed, given that Texas Wild-Rice coverage is expanding while other non-native plants are being removed. Fountain Darters demonstrated use of non-native vegetation, primarily *Hydrilla* and *H. polysperma*. Native fishes have been reported to have higher densities and abundances in non-native vegetation (Duffy and Baltz 2002). Current vegetation management includes repeated harvesting efforts of both non-native taxa (Edwards Aquifer Habitat Conservation Plan 2012). Removal of non-native vegetation can be important in maintaining endangered fish species (Kennedy et al. 2005). However, mechanical removal of non-native vegetation like *Hydrilla* or *Myriophyllum* can cause minor, short-term changes in pelagic and benthic species composition, richness, and density (Mikol 1985; Maceina et al. 2011; Serafy et al. 1994). Continued monitoring of species like Fountain Darter will shed light on effects of vegetation management on threatened or endangered species.

Despite the variety of thoughts regarding the Fountain Darter's relationship with vegetation, a positive association exists that is likely facultative but could be obligatory depending on site or habitat characteristics. However, more work will be needed (e.g., manipulative studies) to understand mechanisms underlying the Fountain Darter relationship with vegetation. Clearer understanding of this relationship will provide insight into the role of aquatic vegetation and benefit current management of native and non-native vegetation removal and future management of San Marcos and Comal rivers, including how floods, which do periodically happen and are listed as a possible reason for the extirpation of Fountain Darters in the Comal River (Schenck and Whiteside 1976) can affect Fountain Darter occurrences and abundances. Scouring due to floods or high flows can also allow non-native vegetation to persist, so monitoring of vegetation after high flow events is necessary to maintain native biotic communities (Edwards Aquifer Habitat Conservation Plan 2012). Habitat degradation of structurally complex vegetated habitats that provide ecological services (Montoya-Ospina et al. 2020) and reduction in spring flow can alter fish communities (Craig and Bonner 2020). Restoring degraded habitats and maintaining natural fish communities thus requires first determining fish-habitat associations, including the direct and indirect influences of vegetation and the mechanisms by which fish use vegetation (Bond and Lake 2003).

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

	Wadeable % vegetation		Non-wadeable % vegetation	
Reach	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 River and Comal River, 2014 - 2019. Wadeable habitats were not sampled in Reach 1 of the San Marcos River or in Reach 2 of the Comal River.

	Wadeable % occurrence of Fountain Darters		Non-wadeable % occurrence of Fountain Darters	
Reach	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		0.0	
6	86		0.0	
Total	95	94	91	99

Table 3. Substrate composition of habitats when Fountain Darters were found in transects with no vegetation in the San Marcos River and Comal River, 2014-2019.

Substrate (%)	Wadeable San Marcos River	Wadeable Comal River	Non-wadeable San Marcos River	Non-wadeable Comal River
Clay	3.0	0.7	2.0	
Silt	22	14	26	20
Sand	14	9.5	24	
Gravel	43	45	18	47
Cobble	7.8	19	18	10
Bedrock	2.5	0.5		13
Boulder	0.5	7.0	9.0	0.1
Taylor Marl		0.4	4.3	

Table 4. 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 River and Comal River. Symbol “**” denotes significance at the 1% level.

	Reach	N Fountain Darters	b	SE	R^2
Wadeable					
	San Marcos River	474	0.015**	0.0015	0.070
	Comal River	1,606	0.0150**	0.0013	0.092
Non-wadeable					
	San Marcos River	629	0.0035**	0.0008	0.007
	Comal River	5,320	0.0059**	0.0005	0.023

Table 5. Percent (%) occurrence of aquatic vegetation taxa in transects with vegetation among wadeable and non-wadeable habitats in the San Marcos River and Comal River, 2014 - 2019.

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

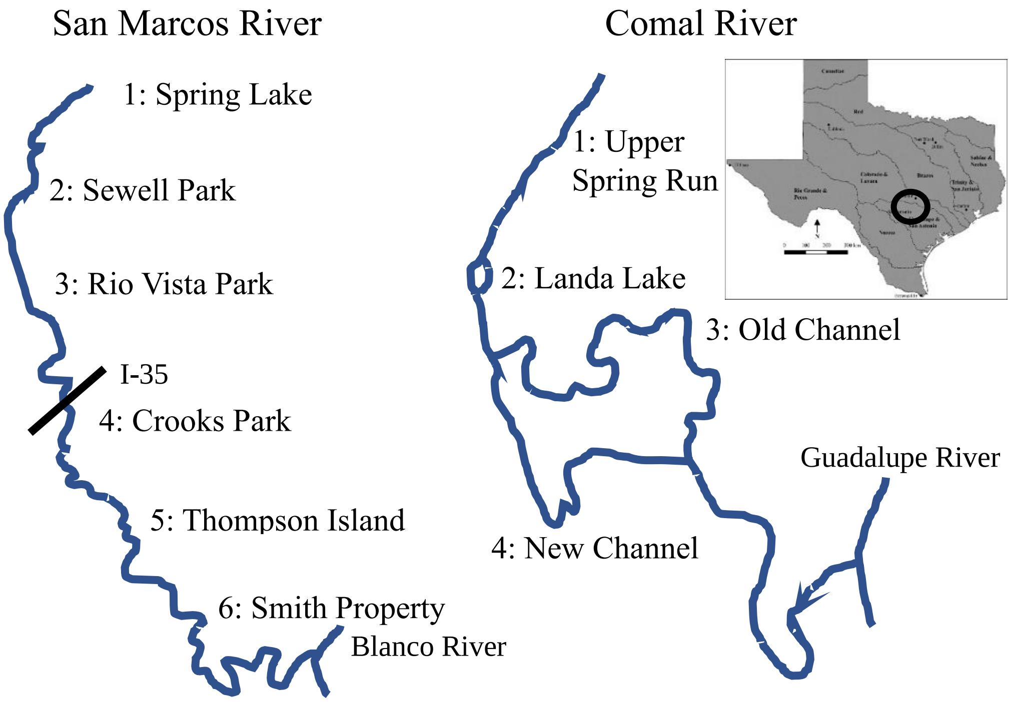

Figure 1. Reach number and site name sampled in San Marcos River and Comal River, 2014 - 2019.

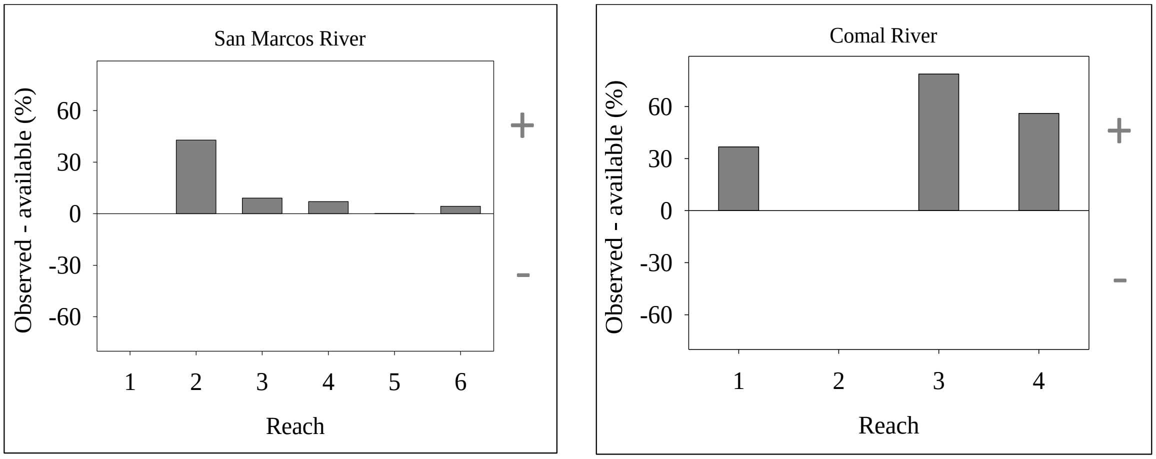

Figure 2. Differences in the percent (%) of Fountain Darters across reaches from the San Marcos River (N = 474) and Comal River (N = 629) observed in vegetated habitats and the percent of available vegetated habitats among wadeable habitats, 2014 – 2019. Positive (+) symbol represents a positive difference 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**.**

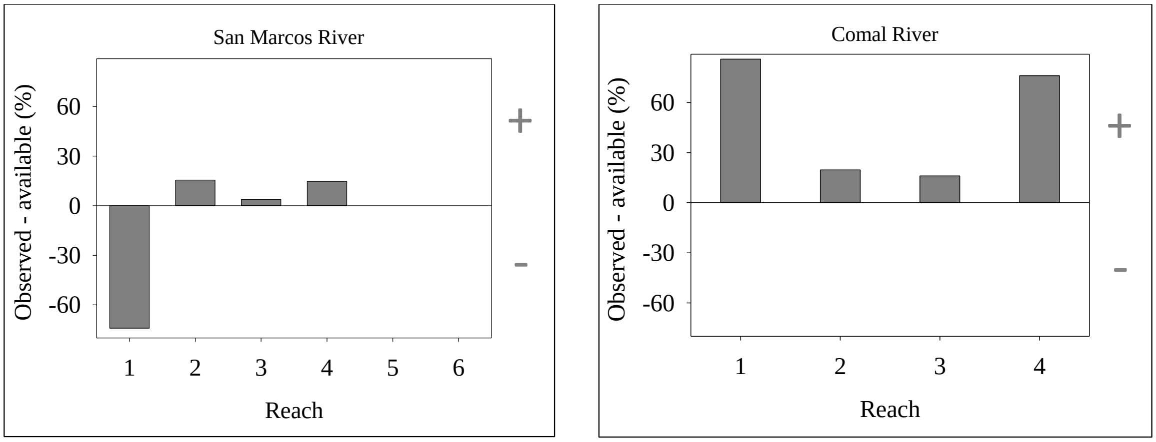

Figure 3. Differences in the percent (%) of Fountain Darters across reaches from the San Marcos River (N = 1,606) and Comal River (N = 5,320) observed in vegetated habitats and the percent of available vegetated habitats among non-wadeable habitats, 2014-2019. Positive (+) symbol represents a positive 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. 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 no Fountain Darters were found in reach 6.

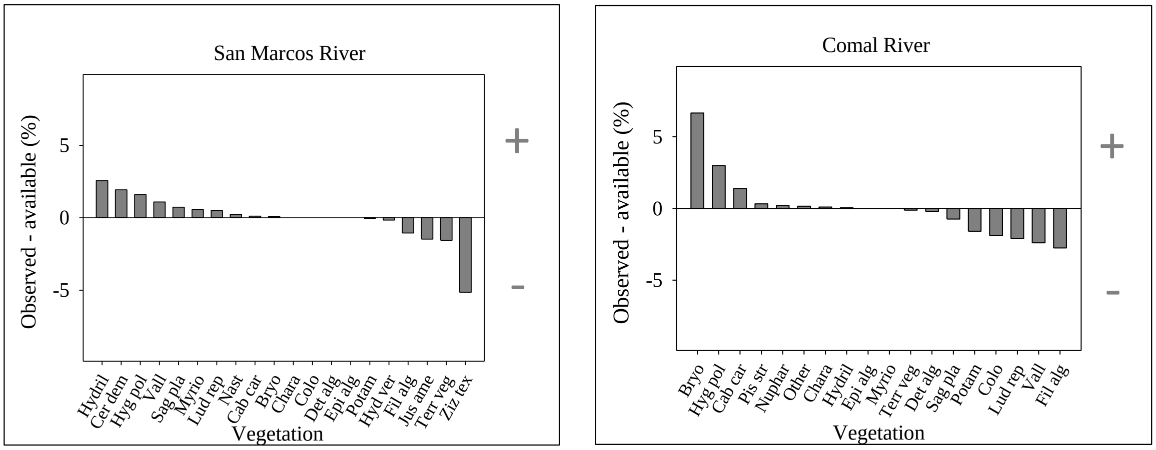

Figure 4. Electivity index of vegetation type of Fountain Darters among wadeable habitats across reaches of the San Marcos River and Comal River, 2014 – 2019. See appendix 1 for vegetation taxa abbreviations. Positive (+) symbol represents a positive difference value, indicating that greater percentage of Fountain Darters were observed in vegetation type than the percentage of vegetation type available. Negative (-) symbol represents negative difference value, indicating that lesser percentage of Fountain Darters were observed in vegetation type than the percentage of vegetation type available.

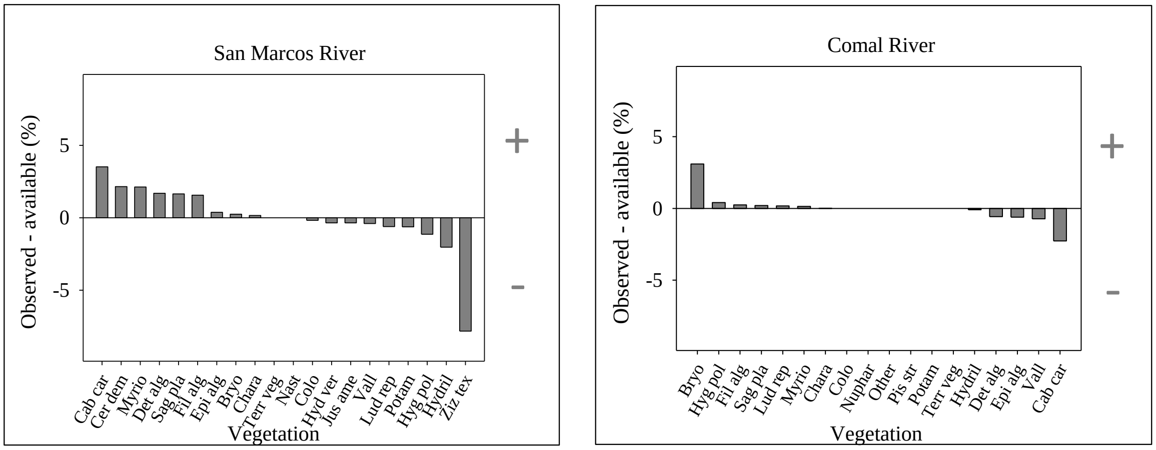

Figure 5. Electivity index of vegetation type of Fountain Darters among non-wadeable habitats across reaches of the San Marcos River and Comal River, 2014 – 2019. See appendix 1 for vegetation taxa abbreviations. Positive (+) symbol represents a positive difference value, indicating that greater percentage of Fountain Darters were observed in vegetation type than the percentage of vegetation type available. Negative (-) symbol represents negative difference value, indicating that lesser percentage of Fountain Darters were observed in vegetation type than the percentage of vegetation type available.

APPENDIX SECTION

Appendix 1. Aquatic vegetation taxa in transects with vegetation among wadeable and non-wadeable habitats in the San Marcos River and Comal River, 2014 - 2019.

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

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