

EFFECTS OF EXTREME FLOW EVENTS ON COMMUNITY COMPOSITION AND
HABITAT COMPLEXITY IN GROUNDWATER DOMINATED SYSTEMS

by

Joshua D. Tivin, B.S.

A thesis submitted to the Graduate Council of
Texas State University in partial fulfillment
of the requirements for the degree of
Master of Science
with a Major in Aquatic Resources
May 2023

Committee Members:

Timothy Bonner, Chair

Floyd Weckerly

Al Groeger

COPYRIGHT

by

Joshua Tivin

2023

ACKNOWLEDGMENTS

I would first like to thank my major advisor Dr. Timothy Bonner. His knowledge, passion and experience in the classroom and field has been truly inspirational and integral in my success as a student and a professional. I would also like to thank my committee members Dr. Butch Weckerly and Dr. Al Groeger for their contributions to the completion of this manuscript and their guidance to my success.

I want to give a big thank you to my fellow lab members, whom I have had the opportunity to work with and who have pushed me to reach academic and professional success, for their continued help in the field collecting data for this research. Specifically, I would like to thank Steven Lopez for his valued conversations, humor and friendship throughout his time- along with the many taco truck runs that kept us sane during the school year. I would also like to thank Lauren Chappell, Eli Leal and Daisy Blake for the many adventures we were able to be a part of in and out of the field. I will always cherish the close friendships and memories I have made throughout every corner of Texas.

Lastly, I would like to thank my family for their continued support of me moving across the country to pursue my passions and interests. A special thanks to my mom, who has always pushed me towards being my best self and has taught me to be dedicated to everything I do; as well as to my dad, who inspired me to become a biologist and be passionate about nature through the many fishing, hiking and outdoors adventures on which he has taken me ever since I can remember.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	vii
ABSTRACT.....	viii
CHAPTER	
I. INTRODUCTION	1
II. METHODS	5
III. RESULTS	11
IV. DISCUSSION	19
APPENDIX SECTION.....	37
LITERATURE CITED	39

LIST OF TABLES

Table	Page
1. Mean (\pm SE) physical habitat parameters across wadeable and non-wadeable reaches for all sample types in the San Marcos and Comal rivers from May 2014 - November 2022.....	34
2. Mean (\pm SE) percent coverage of vegetation type between high, moderate, and low complexity reaches from May 2014 – November 2022.....	35
3. Mean (\pm SE) percent coverage of vegetation types that had detectable change between stasis, flood and drought periods among complexity reaches from May 2014 - November 2022	36
4. Mean (\pm SE) species richness (R), Shannon-Weiner diversity (H') and evenness (EH) along the complexity gradient from May 2014 – November 2022.....	37
5. Mean (\pm SE) species richness (R), Shannon-Weiner diversity (H') and evenness (EH) among flow periods within each complexity reach from May 2014 – November 2022.....	38

LIST OF FIGURES

Figure	Page
1. The five reaches sampled within the San Marcos River and the four reaches sampled in the Comal River from May 2014 - November 2022.....	39
2. Plot of principal component axes I and II for (Bottom) all sites in the San Marcos and Comal rivers (1:Landa Lake, 2: Spring Lake, 3: New Channel _{non-wadeable} , 4: Old Channel _{non-wadeable} , 5: Upstream _{non-wadeable} , 6: Downstream _{non-wadeable} , 7: Upstream _{wadeable} , 8: Upper Spring Run _{non-wadeable} , 9: New Channel _{wadeable} , 10) Downstream _{wadeable} , 11) Old Channel _{wadeable} , 12) Upper Spring Run _{wadeable}) and (top) mean (\pm SE) PC value for 1) high complexity, 2) moderate wadeable complexity, 3) moderate non-wadeable complexity and 4) low complexity reaches from May 2014 – November 2022	40
3. (Top) Mean (\pm SE) percent vegetation coverage along the complexity gradient and (Bottom) mean (\pm SE) percent vegetation coverage between flow periods (stasis, flood, drought) within each complexity reach from May 2014 – November 2022	41
4. Mean (\pm SE) substrate composition among high, moderate, and low complexity reaches and between flow periods (stasis, flood, drought) from May 2014 – November 2022.....	42
5. Log-transformed density and 1 SE (whiskers) of surface fishes along the complexity gradient and between flow periods from May 2014 - November 2022	43
6. Log-transformed density and 1 SE (whiskers) of pelagic generalist fishes along the complexity gradient and between flow periods from May 2014 through November 2022.....	44
7. Log-transformed density and 1 SE (whiskers) of pelagic fluvialist fishes along the complexity gradient and between flow periods from May 2014 - November 2022.....	45
8. Log-transformed density and 1 SE (whiskers) of benthic fishes along the complexity gradient and between flow periods from May 2014 - November 2022	46

ABSTRACT

Extreme flow events in the form of major floods and droughts are primary drivers in structuring aquatic habitats and communities. While floods and droughts can directly alter aquatic biota by displacement or by increased mortalities, extreme flow events can have an indirect and prolonged effect on biota by altering habitat complexity, which in turn delays the recovery of the aquatic biota. Interrelationships among extreme flow events, habitat complexity, and fish communities are established in hydrologically variable rivers (run-off dominated). Less known are the interrelationships among stream flow extremes, habitat complexity, and fish communities in hydrologically stable rivers (groundwater dominated). The purpose of this study was to assess how extreme flow events effect habitat complexity and the fish community within two hydrologically stable rivers in Texas (San Marcos and Comal rivers) using a 9-year dataset. Habitats (N = 4,863) within 12 reaches of the rivers were categorized as high, moderate, or low complexity along a depth, vegetation, substrate, and current velocity gradient. Following or during extreme flow events, shifts in habitat complexity were not evident except in low complexity habitats that shifted towards greater complexity during drought. Among a total of 43 fish species and 135,199 individuals observed, densities of surface water fishes (*Gambusia*), pelagic generalist fishes (*Lepomis*, *Micropterus*, *Herichthys*), pelagic fluvial fishes (*Dionda*, *Notropis*, and *Astyanax*), and benthic fishes (*Etheostoma*) generally were greater in high and moderate habitat complexity reaches than in lower habitat complexity reaches and generally unaffected by extreme flow events with few

exceptions. These results indicated that habitat complexity in hydrologically stable rivers support greater densities and diversity of fishes similar to hydrologically variable rivers, but habitat complexity and fish community were more resistant and resilient to extreme flow events in hydrologically stable rivers than in hydrologically variable rivers.

I. INTRODUCTION

Extreme flow events in the form of major floods and severe droughts are primary drivers in structuring aquatic habitats and communities (Pearson et al. 1992). Major floods, defined as any high flow event that affects aquatic biota (Matthews 1986), erode stream channels, alter substrate composition, remove aquatic vegetation, and displace aquatic organisms (Harrell 1978, Matthews 1986, Hastie et al. 2001, Sotola et al. 2021). Droughts, defined as periods of unpredictable low flow events that affect aquatic biota (Humphries and Baldwin 2003), degrade water quality, increase algal blooms, and increase aquatic fauna mortalities (Dahm et al. 2003, Rolls et al. 2012). Also, during droughts, predator-prey interactions and abiotic stressors (e.g., temperature change, habitat alteration) are intensified and result in community structural change (Franssen et al. 2006). Although extreme flow events directly alter the aquatic biota by displacement or by increased mortalities, floods and droughts have indirect and prolonged effects by altering habitat complexity, which in turn delays the recovery of the aquatic biota (Rolls et al. 2012).

Habitat complexity within lotic systems strongly influences the diversity of aquatic biota (Gorman and Karr 1978, Willis 2004). Habitat complexity includes the abundance and types of available aquatic vegetation and substrates, range in water depths and current velocities, and the occurrence of structure (e.g., large woody debris; Gorman and Karr 1978, Lamberti 1989, Hastie 2001, Shumway 2007, Tokeshi 2011). With greater habitat complexity in three-dimensional space, fish diversity is higher along vertical and longitudinal gradients attributed to habitat support for a diversity of specialized feeding behaviors and water-column niches (Tramer and Rodgers 1973,

Gorman and Karr 1978). Stream flow, including extreme flow events, is a major determinant of habitat complexity and, therefore, a determinant of biotic composition, trophic structure, and carrying capacity within the aquatic community (Bunn and Arthington 2002, Rolls et al. 2012). In one study, habitat complexity (i.e., water depth, current velocity, structural density, rugosity, and substrate diversity) was inversely correlated with flow rate (Willis et al. 2004). At higher flows, structural components, algal growth and fish densities are reduced. Macroinvertebrates and fishes were more concentrated (i.e., species packing) in areas of higher habitat complexity. At lower flows, accumulated woody debris, leaf litter, and stable substrates supported periphyton growth, which supported greater numbers of macroinvertebrates and fishes (Rolls et al. 2012).

Interrelationships among stream flow extremes, habitat complexity, and stream fish communities are established in streams and rivers with waters dominated by run-off (Ross and Baker 1983, Bunn and Arthington 2002, Willis et al. 2004). Less known are the interrelationships among stream flow extremes, habitat complexity, and fish communities in hydrologically stable aquatic systems, such as spring systems with surface flows provided primarily by groundwater discharges. Hydrologically stable aquatic systems are often considered as hydrologic refugia (Keppel et al. 2015) and evolutionary refugia (Davis et al. 2013, Craig et al. 2016), where local aquatic environments are decoupled from surrounding climates (e.g., spring systems in arid regions) and typically support endemic fauna, including several species of conservation concern. Effects of habitat complexity alterations and, by extension, stream flow extremes on existing fish communities are thought to be more pronounced in hydrologically stable aquatic systems, leading historical claims that minor alterations in

habitat (Peden and Hubbs 1969) and extreme flows (Schenk and Whiteside 1976) could lead to extirpation of endemic fishes (e.g., San Marcos Gambusia *Gambusia georgei*).

The purpose of this study is to assess the effects of a major flood and a severe drought on habitat complexity and fish community within the headwaters of the San Marcos and Comal rivers, the two largest spring systems within the Edwards Plateau, using a 9-year dataset. Objectives of this study are to 1) Identify the levels of complexity within the study basin, 2) quantify the effects of extreme flows on overall habitat complexity and complexity variables (e.g. substrate and vegetation) and 3) identify changes in species composition within and across complexity levels in response to flood and drought events using water-column guilds (e.g., benthic, pelagic, surface) based on habitat use and feeding ecology (Sheldon 1968, Mendelson 1975, Craig et al. 2016). Predictions of habitat responses include: 1) non-wadeable reaches will be affected less by flow extremes than wadeable reaches and contain higher levels of habitat complexity (i.e., high vegetation cover, vegetation diversity, greater depth, lower current velocity, less mobile substrates) than wadeable reaches because the increased hydraulic retention within deeper reaches aids in dissipating high discharge events (Pearsons et al. 1992), 2) aquatic vegetation cover will decrease in low complexity reaches more than in high complexity reaches during extreme flow events because high flows uproot plants and alter substrate composition (Bournette and Puijalon, 2011) and low flows can leave aquatic vegetation dry or shaded by increased algal growth (Bournette and Puijalon, 2011, Rolls 2012, Poole et al. 2022), but effects on diversity will be dependent on plant type, and 3) substrate composition in low complexity reaches will be composed of more mobile substrates (sand, gravel, cobble) and will be more affected by extreme flow events

than high complexity reaches. Predictions for fish responses include: 1) high complexity reaches will have higher overall species densities, richness and diversity than low complexity reaches, because an increase in the number of species will be correlated to increases in niche availability and habitat area (Angermeier and Schlosser 1989, Tokeshi et al. 2011), 2) pelagic generalist species (e.g., Centrarchidae) will have lower resistance and recovery than pelagic fluvialist species (e.g., *Notropis amabilis*) during drought conditions because pelagic generalist species might lack evolutionary characteristics to persist through intense droughts (Lennox et al. 2019) and prefer systems with higher hydrologic stability and retention (Turgeon et al. 2019), along with increased vertical habitat (Tramer and Rodgers 1973, Gorman and Karr 1978), and 3) small-bodied surface fishes will have low resistance during flood events because surface fishes (i. e., *Gambusia sp.*) are more easily displaced during flood events based on their position in the water column (Ross and Baker 1983, Meffe et al. 1984), but will have great recovery because poeciliid species possess high reproductive potential and rapid colonization following extreme flows (Minckley and Meffre 1987) and benthic fishes (*Etheostoma sp.*) will be resistant to flow events based on their ability to use substrates, along with other morphological and behavioral adaptations, to avoid flow extremes (Carlson and Lauder 2011).

II. METHODS

Study Area

The Edwards Plateau is a karst geological feature in central Texas that produces voluminous groundwater discharge to feed the Comal and San Marcos rivers (Kollaus et al. 2015) and is known to be a highly flood prone region (Earl and Vaughn 2015). Five 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, spring, and occasionally summer from May 2014 through November 2022. In the San Marcos River, reaches from upstream to downstream were 1) Spring Lake, 2) Sewell Park, 3) Rio Vista Park, 4) Crooks Park, and 5) Thompson's Island. Reaches 2 and 3 were grouped as upstream San Marcos and reaches 4 and 5 were grouped as downstream San Marcos. In the Comal River, reaches from upstream to downstream were 1) Upper Spring Run, 2) Landa Lake, 3) Old Channel and 4) New Channel (split off from the main channel, equidistant from the headwaters) (Figure 1). During the 9 yr. period, median flow was $4.87 \text{ m}^3/\text{s}$, ranging from $2.19 \text{ m}^3/\text{s}$ to $527^* \text{ m}^3/\text{s}$ in the San Marcos River (USGS Station 08170500, *calculation from D'Ottavio 2020) and $8.50 \text{ m}^3/\text{s}$, ranging from 2.18 to $400 \text{ m}^3/\text{s}$ in the Comal River (USGS Station 08169000). The 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. (Edwards and Bonner 2022).

Field surveys

Fish were quantified in wadeable habitats with standardized seine hauls and non-wadeable habitats using standardized SCUBA techniques (Edwards and Bonner 2022). Wadeable habitats consisted of a 15-m² seine haul 5-m effort with a 3.0 x 1.8 m common seine; mesh size: 3.2 mm) or a 5- m effort of substrate kicking, pending water depth and substrate type. Seine haul transects were spaced cross-sectionally across the width of the reach to provide ample spacing between hauls for minimal disturbance of adjacent areas. After a cross section was completed, another cross section was located 20 m upstream. The goal number of seine hauls per reach was 20. Fishes were identified to the species level, measured, and released after each seine haul. Habitat variables were taken at each seine haul (water depth, current velocity, percent substrate (e.g., clay, silt, sand, gravel, cobble, boulder) woody debris, and percent vegetation, percent detritus coverage, percent on coverage and taxa (e.g., Bryophyte, *Ludwigia*). Algae were differentiated as filamentous (e.g., unattached), epiphytic (e.g., attached to surfaces), and detrital algae (e.g., dead algae). 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) (Edwards and Bonner 2022).

Non-wadeable habitats were sampled at two levels or resolution: mesohabitat to quantify pelagic and topwater species and microhabitat to quantify benthic fishes. For mesohabitats, the areas ranged from 50-1,300 m² were delineated within each reach and sampled across season and years. Four-person dive crews assembled at one end of the transect, spaced out evenly and swam across the transect identifying and counting fishes within the water column. 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 taxonomic resolution possible. Underwater identification of the two *Gambusia* species that are known within the San Marcos River and Comal River (*Gambusia geiseri* and *Gambusia affinis*; Craig and Bonner 2019) were identified as *Gambusia* due to a lack of reliability from underwater identification down to the species level. While adult sunfish (Family Centrarchidae; Genus *Lepomis*) are easy to identify underwater- adult and juvenile sunfishes were classified as *Lepomis* to avoid mistaken identifications. Microhabitats consisted of 10-m² transected marked by plastic tubes. These were established in the benthic region of the water column and spaced equal distances throughout the transect. Each diver completed one microhabitat per transect from downstream to upstream. Fishes were identified and counted along with recording substrate and vegetation. Fishes that were not able to be identified to species for various reasons were listed by their genus (*Etheostoma lepidum* and *Etheostoma fonticola* as *Etheostoma*). Once fish were quantified in the microhabitat, the following habitat variables were quantified for the microhabitat transect: water depth (m), current velocity (benthic and water column in m/s), percent substrate type (e.g., clay, silt, sand, gravel, cobble, and woody debris), percent detritus coverage, percent vegetation coverage and taxa (e.g., Bryophyte, *Hydrilla*). Vegetation was identified to the lowest practical taxonomic level. Algae was differentiated as filamentous (e.g., unattached), epiphytic and detrital algae (e.g., dead algae). The four microhabitats were averaged and used to estimate mean habitat variables for the mesohabitat. Water temperature, pH, dissolved oxygen, and specific conductance of the mesohabitat were measured with a water quality

meter (YSI65 or YSI85) (Edwards and Bonner 2022).

The San Marcos and Comal rivers experience similar levels of perennial flow and disturbance, along with having similar fish communities and habitat complexity so statistical analyses were conducted together. Each species or genus used will be analyzed separately for their occurrence and detectability within wadeable and non-wadable habitats. Fishes were placed into corresponding habitat usage guilds based on water column usage from body type, feeding ecology, and underwater observation (Appendix I). The habitat usage guilds were surface, pelagic generalist, pelagic fluvialist, and benthic etheostomid. Pelagic fishes that were classified as spring-associated by Craig et al. (2016) were placed into the fluvialist guild, while other fishes that were not classified as spring associated were placed into generalist. The most abundant fishes (> 4,500 individuals per species or genus) were selected for their respective guild and used for analysis.

Vegetation was classified based on height and growth type (Schuyler 1984) (Appendix II). Two height categories, tall and short, were derived from Edwards and Bonner (2022). Two growth categories were established, rosette and caulescent, based on the dichotomy of Schuyler (1984) and phylogenetics (De Wilde et al. 2014). The three types of algae were grouped together as “algae” and bryophyte was retained as a single group. The species with percent cover > 5% were included in a category for analysis.

Extreme flow classification

Flow data from USGS and flood peak calculations from D'Ottavio (2020) were used to identify the presence of a flow event at 527 m³/s in October 2015. Based on the classification for overbank flows from Texas Commission of Environmental Quality (2011) this flow reached >1,982 m³/s at San Marcos River at Luling and can be defined as a major flood (1 in 5-year event is defined by a 507 m³/s threshold). A Standard Precipitation Index (SPI) was used to determine periods of severe and extreme drought conditions (McKee et al. 1993) that occurred from June 2022 - November 2022. The average flow during drought conditions in the San Marcos River was 2.6 m³/s (± 0.002), ranging from 2.19 to 6.99 m³/s. In the Comal River the average flow during drought conditions was 3.23 m³/s (± 0.003) ranging from 2.18 to 6.86 m³/s. Sampling periods that did not include an extreme flow event were categorized as “stasis”.

Data analysis

The resistance and recovery of species were assessed for each species using univariate and multivariate statistical analyses. Fishes were transformed into densities to compare wadeable and non-wadeable habitats. Percent frequency of aquatic vegetation and substrate were calculated among wadeable and non-wadable habitats in the San Marcos and Comal rivers. A Principal Component Analysis (PCA) was used to spread out the habitat parameters of each site to identify a complexity gradient of high, moderate, and low complexity reaches. Single factor Univariate Analysis of Variance (ANOVA) were used to detect changes in overall complexity of high, Moderate and low complexity reaches within multivariate space of the PCA between three flow periods (stasis, flood,

drought). Single factor ANOVAs were used to assess differences in diversity indices (i.e., richness, evenness, Shannon-Weiner diversity) and fish habitat usage guild densities between three different complexity levels (high, moderate, low). Single factor ANOVAs were used to detect differences in the three diversity indices between flow periods within each level of complexity. Single factor ANOVAs were conducted in high complexity reaches to detect changes in guild density between flow periods. The estimates and parametric bootstrap 95% confidence intervals were recorded for significant LMER analyses. Two-factor ANOVAs were conducted within the moderate complexity reaches due to the presence of wadeable and non-wadeable sites, when there was a significant interaction term a single factor ANOVA was used for wadeable and non-wadeable separately. Single factor ANOVAs were conducted in the low complexity reaches similar to the analyzation of high complexity reaches. Changes in vegetation percent cover and type were conducted with the same univariate analyses as the fish habitat guilds for each of the corresponding habitat complexity categories. Linear mixed effects models with parametric bootstrapping at 5,000 simulations were used in any complexity reach when the standard error within a flow category could have been due to site level differences. Chi-squared analyses were used to detect differences in the substrate make-up between stasis periods to flood and drought periods for all habitats.

III. RESULTS

A total of 4,863 habitats (2,745 wadeable, 2,118 non-wadeable) were sampled between May 2014 and November 2022. Among wadeable habitats, current velocities were moderately swift with mean depths ranging from 0.66 to 0.74 m, substrates were predominantly gravel (range of means: 32 to 37%) and silt (29-31%), and with moderate amounts of vegetation cover (37 – 39%) (Table 1). Among non-wadeable habitats, current velocities were moderately slow with mean depths ranging from 1.6 to 1.7 m, substrates were predominantly silt layers (39-64%) and gravel (14-25%), and with high amount of vegetation cover (42-71%) (Table 1). Principal component axes I and II explained 36% of the variation in habitat variables taken among the 4,863 wadeable and non-wadeable habitats (Figure 2). Principal component axis I explained 25% of the habitat variation and described a substrate, depth, and a current velocity gradient. The strongest loadings on PC axis I were silt (-0.94), vegetation cover (-0.89), depth (-0.60), bryophyte (-0.44), sand (0.48), current velocity (0.55), cobble (0.63) and gravel (0.83). Principal component axis II explained 11% of the habitat variation and described a vegetation type, current velocity, and substrate gradient. The strongest loadings on PC axis II were tall rosette plants (-0.71), tall caulescent plants (-0.67), current velocity (-0.45), sand (-0.38), boulder (0.35), bryophyte (0.38), and algae (0.56). Mean (± 1 SE) PC I scores by reach ranged from -1.36 (0.09) in Comal-Old Channel_{non-wadeable} to 1.46 (0.08) in San Marcos-Downstream_{wadeable}, establishing a complexity gradient from high (i.e., negative PC I scores) to low (i.e., positive PC I scores). High complexity habitats (i.e., greater amounts of silt substrates, greater vegetation cover, deeper depths, and slow current velocities) were associated with Comal-Old Channel_{non-wadeable}, Comal- New

Channel_{non-wadeable}, Comal-Landa Lake_{non-wadeable}, and San Marcos-Spring Lake_{non-wadeable}. Moderate complexity habitats (i.e., moderate amounts of silt, gravel, and cobble substrates, moderate amounts of vegetation cover, and moderate depths and current velocities) were associated with Comal-Spring Run_{non-wadeable}, Comal-New Channel_{wadeable}, San Marcos-Downstream_{non-wadeable}, San Marcos-Upstream_{wadeable}, and San Marcos-Upstream_{non-wadeable}. Low complexity habitats (i.e., greater amounts of cobble, gravel, and sand substrates, low amounts of vegetation cover, shallow depths, and swifter current velocities) were associated with San Marcos-Downstream_{wadeable}, Comal-Old Channel_{wadeable}, Comal-Spring Run_{wadeable} (Figure 2). Habitat complexity during extreme flow events (flood and drought) in multivariate space did not differ from habitat complexity observed during stasis in high complexity reaches or in moderate complexity reaches ($P > 0.5$). However, a shift in habitat complexity was detected (ANOVA, $F_{2,62} = 4.799$, $P = 0.01$) during drought among low complexity reaches with habitats shifting to more complexity with greater amounts of silt substrates and vegetation coverage (Figure 2).

Univariate habitat assessments

Percent vegetation coverage differed (ANOVA, $F_{2,332} = 129.2$, $P < 0.01$) along the complexity gradient, with percent vegetation coverage in high complexity reaches (mean ± 1 SE; $76\% \pm 1.5$) greater than percent vegetation coverage in moderate complexity reaches ($44\% \pm 1.8$) and low complexity reaches ($26\% \pm 2.2$) (Figure 3). Among flow periods, percent vegetation coverage differed in high complexity reaches (linear mixed-effects model, Est: -16.9, 95% CI: (-32.0 - -2.19), moderate complexity reaches (ANOVA,

$F_{2,161} = 3.0, P = 0.05$), and low complexity reaches (ANOVA, $F_{2,81} = 12.68, P < 0.01$). Percent vegetation coverage decreased ($P < 0.05$) during floods among all complexity reaches except low complexity reaches and increased during drought in low complexity reaches (Figure 3). Percent vegetation coverages by type were greater ($P < 0.05$) in high complexity reaches than moderate and low complexity reaches for bryophytes, short caulescent, and short rosette vegetation (Table 2). Percent vegetation coverages by type were greater ($P < 0.05$) in high and moderate complexity reaches than in low complexity reaches for tall caulescent and tall rosette vegetation. Only three of the six vegetation types differed ($P < 0.05$) among flow periods with a decrease in coverage of tall caulescent in wadeable moderate complexity reaches and increases in coverage of tall rosette in wadeable moderate complexity reaches and algae in low complexity reaches (Table 3).

The substrate composition of high complexity reaches during stasis conditions consisted of large amounts of silt ($76\% \pm 1.5$), and small amount of gravel (8.4 ± 0.9), and clay ($4.7\% \pm 1.2$). Moderate complexity reaches during stasis conditions consisted of moderate amounts of silt (37.5 ± 2.9), gravel ($29.5\% \pm 1.9$) and small amounts of sand ($14\% \pm 1.5$). Low complexity sites during stasis conditions consisted of large amounts of gravel ($43\% \pm 1.4$), and moderate amounts of silt ($20\% \pm 1.5$) and cobble ($16\% \pm 0.9$). Substrate compositions of stasis differed following floods in high complexity reaches ($X^2 = 103.4, P < 0.01$), non-wadeable moderate complexity reaches ($X^2 = 43.4, P < 0.01$), and in low complexity reaches ($X^2 = 36.8, P < 0.01$) (Figure 4). Within high complexity reaches, the amount of bedrock substrates increased following floods with the scouring of mobile substrates. Within non-wadeable moderate complexity reaches, the amount of

exposed bedrock increased following floods. Within low complexity reaches, the amount of the smallest mobile substrates (i.e., silt and sand) decreased following floods. Substrate compositions of stasis differed during drought in non-wadeable moderate complexity reaches ($X^2= 107.9, P < 0.01$), wadeable moderate complexity reaches ($X^2= 32.2, P < 0.01$) and in low complexity reaches ($X^2= 32.9, P < 0.01$). Within non-wadeable moderate complexity reaches, the amount of cobble and bedrock increased, whereas the amount of gravel, sand and clay decreased. Within wadeable moderate complexity reaches, the amount of sand, gravel, cobble and bedrock increased, whereas the amount of silt decreased. Within low complexity reaches, the amount of gravel decreased, whereas the amount of cobble and bedrock increased (Figure 4).

Fish community

A total of 135,199 individuals and 43 species were recorded from May 2014 to November 2022. Cumulative species richness was 27 in high complexity reaches, 35 in moderate complexity reaches, and 39 in low complexity reaches. Species richness and species evenness did not differ ($P > 0.05$) along the complexity gradient, whereas Shannon-Weiner diversity differed (ANOVA, $F_{2,33} = 4.078, P = 0.027$) with low complexity reaches being more diverse than high complexity reaches (Table 4). Among flow periods, species richness differed in high complexity reaches (ANOVA, $F_{2,9} = 30.36, P < 0.01$) and moderate complexity reaches (ANOVA, $F_{2,12} = 9.345, P < 0.01$) with stasis having greater species richness in comparison to flood and drought conditions (Table 5).

Common taxa (> 4500 individuals) selected for further analyses consisted of 17 species and 123,361 individuals, representing 40% of the species and 91% of the total

individuals recorded in this study. Most abundant taxa were *Gambusia* (24%), *Dionda nigrotaeniata* (19%) and *Astyanx mexicanus* (14%) (Appendix I).

Surface water habitat guild

Consisting of only one group of fishes (*Gambusia*), densities (N of individuals/m²) differed (ANOVA, $F_{2,332} = 9.904$, $P < 0.01$) among low, moderate, and high complexity reaches with greater densities in moderate complexity reaches (mean density ± 1 SE; 0.11 ± 0.01) and high complexity reaches (0.128 ± 0.02) than in low complexity reaches (0.025 ± 0.005). Densities of *Gambusia* in moderate complexity reaches differed (ANOVA, $F_{1,159} = 7.01$, $P < 0.01$) among wadeable and non-wadeable reaches with wadeable reaches being denser (0.16 ± 0.02) than non-wadeable reaches (0.08 ± 0.02). Among flow regimes, densities differed in high complexity reaches (LMER, Est: 0.204, 95% CI= (0.016 - 0.327)) and in moderate complexity non-wadeable reaches (LMER, Est: 0.21, 95% CI= (0.042 - 0.38)) with flood densities being greater than drought densities (Figure 5).

Pelagic generalist habitat guild

Densities of *Lepomis* differed (ANOVA, $F_{2,332} = 12.94$, $P < 0.001$) along the complexity gradient with greater densities in moderate complexity reaches (0.15 ± 0.018) and high complexity reaches (0.17 ± 0.036) than in low complexity reaches (0.009 ± 0.001). Densities of *Lepomis* in moderate complexity reaches differed (ANOVA, $F_{1,159} = 42.1$, $P < 0.01$) among wadeable and non-wadeable reaches with non-wadeable reaches being denser (0.24 ± 0.03) than wadeable reaches (0.018 ± 0.002). Among flow periods,

densities differed only among moderate complexity reaches (ANOVA, $F_{2,159} = 2.94$, $P = 0.05$) with densities of *Lepomis* decreasing during drought.

Densities of *Micropterus* differed (ANOVA, $F_{2,332} = 11.95$, $P < 0.01$) along the complexity gradient with greater densities in high complexity reaches (0.07 ± 0.02) than in moderate complexity reaches (0.04 ± 0.005) and lower densities in low complexity reaches (0.02 ± 0.002). *Micropterus* in moderate complexity reaches differed (ANOVA, $F_{1,159} = 28.4$, $P < 0.01$) among wadeable and non-wadeable reaches with non-wadeable reaches being denser (0.06 ± 0.008) than wadeable reaches (0.006 ± 0.001). Among flow periods, densities of *Micropterus* did not differ within complexity levels.

Densities of *Herichthys cyanoguttatus* differed (ANOVA, $F_{2,332} = 5.022$, $P < 0.01$) along the complexity gradient with greater densities in high complexity reaches (0.013 ± 0.004) and moderate complexity reaches (0.014 ± 0.003) than in low complexity reaches (0.0007 ± 0.0002). Densities of *Herichthys cyanoguttatus* in moderate complexity reaches differed (ANOVA, $F_{1,159} = 12.903$, $P < 0.01$) among wadeable and non-wadeable reaches with non-wadeable reaches being denser (0.021 ± 0.004) than wadeable reaches (0.002 ± 0.0003). Among flow periods, densities did not differ within complexity levels (Figure 6).

Pelagic fluvial habitat guild

Densities of *Dionda nigrotaeniata* differed (ANOVA $F_{2,332} = 22.5$, $P < 0.01$) along the complexity gradient with greater densities in high complexity reaches (0.24 ± 0.05) in comparison to moderate complexity reaches (0.04 ± 0.003) and low complexity reaches (0.002 ± 0.0002). Densities differed (ANOVA, $F_{1,159} = 10.76$, $P < 0.01$) in

moderate complexity reaches among wadeable and non-wadeable reaches with greater densities in non-wadeable reaches (0.066 ± 0.015) than in wadeable reaches (0.002 ± 0.0007). Densities of *Dionda nigrotaeniata* did not differ among flow periods for high and moderate complexity reaches. In low complexity reaches, densities differed (ANOVA, $F_{2,81} = 4.16$, $P < 0.05$) among flow periods with increased densities during drought (0.008 ± 0.005) in comparison to stasis (0.0015 ± 0.0007). *Dionda nigrotaeniata* individuals were not observed during flood conditions in low complexity reaches.

Densities of *Astyanx mexicanus* differed (ANOVA, $F_{2,332} = 23.27$, $P < 0.01$) along the complexity gradient with greater densities in high complexity reaches (0.45 ± 0.05) than in moderate complexity reaches (0.025 ± 0.002) and low complexity reaches (0.005 ± 0.0005). Densities of *Astyanx mexicanus* did not differ among flow periods at any complexity level.

Densities of *Notropis amabilis* differed (ANOVA $F_{2,332} = 3.237$, $P < 0.05$) along the complexity gradient with greater densities in high complexity reaches (0.014 ± 0.002) than in moderate complexity reaches (0.003 ± 0.0002); however, high and moderate complexity densities were similar to densities low complexity reaches (0.010 ± 0.001). Densities differed (ANOVA, $F_{1,159} = 5.636$, $P < 0.05$) in moderate complexity reaches among wadeable and non-wadeable reaches, with greater densities in wadeable reaches (0.006 ± 0.003) than in non-wadeable reaches (0.001 ± 0.0005). Densities of *Notropis amabilis* did not differ among flow periods at any complexity level; however, individuals were not observed during flood conditions at any complexity level (Figure 7).

Benthic habitat guild

Densities of *Etheostoma fonticola* differed (ANOVA, $F_{2,332} = 104.6$, $P < 0.01$) along the complexity gradient with greater densities in high complexity reaches (0.12 ± 0.013) than in moderate complexity reaches (0.04 ± 0.003) and lowest densities in low complexity reaches (0.006 ± 0.0007). Densities differed in moderate complexity reaches (ANOVA, $F_{1,159} = 16.6$ $P < 0.01$) among wadeable and non-wadeable reaches with greater densities in non-wadeable reaches (0.048 ± 0.005) than wadeable reaches (0.022 ± 0.003). *Etheostoma fonticola* densities did not differ among flow periods at any complexity level (Figure 8).

IV. DISCUSSION

Results from this study supported several initial predictions on how habitat complexity including vegetation cover, vegetation type and substrate composition were affected by extreme flow events, but not the prediction on non-wadeable reaches with greater levels of habitat complexity being less affected by the extreme flow events. These findings in hydrologically stable systems are similar to hydrologically variable systems. In hydrologically variable systems, greater depths are associated with greater complexity along with greater vegetation cover, less mobile substrates (Shumway et al. 2007), and lower current velocities (Tramer and Rodgers 1973, Tokeshi and Arakaki 2011). Likewise, greater habitat complexity is more resistant to extreme flow events. Habitat resistance to extreme flood events is related to hydraulic retention, which dissipates the energy generated during flood events more in high complexity reaches than in low complexity reaches (Pearsons et al. 1992, Turgeon et al. 2019). However, hydrologically stable systems differed markedly from hydrologically variable systems during periods of low flow. In hydrologically variable systems, drought conditions and low flows lead to decreases in the three axes of hydrological connectivity (i.e., vertical, lateral, and longitudinal; Pringle 2001). Vertical and lateral habitats decrease with decreasing water levels and longitudinal connections are fragmented leading to disconnected stream reaches (Larned et al. 2010) with intermittent flows (Magoulick et al. 2021). In this study, flows were not intermittent nor were reaches fragmented even during extreme drought conditions, attributed to persistent base flow from groundwater (Saunders et al. 2001). As such, even low complexity reaches were resistant to habitat changes during low flow periods with low complexity reaches becoming more complex.

Among habitat variables, vegetation cover and smaller substrates (i.e., silt, sand, gravels) decreased during floods among all habitat complexity levels and vegetation cover increased during drought in low complexity reaches. Decreases in vegetation types were more notably in tall caulescent plants, especially in wadeable habitats. Decreases in vegetation and smaller substrates during floods are commonly reported in hydrologically variable systems (Reice et al 1990, Henry et al. 1996, Crouzy et al. 2013). Likewise, increases in vegetation during low flow periods are often associated with algal blooms (Bournette and Puijalón, 2011, Rolls et al. 2012). In low complexity reaches of the lower San Marcos River and Comal River, increases in algae occurred during low flows, but also increases in tall rosette growth forms, such as Texas wild rice *Zizania texana* in moderate complexity reaches in the upper San Marcos River. Also, during low flows, substrate composition shifted unexpectedly from low percent cover of sand, cobble and bedrock to increased coverage of all substrate types in wadeable and non-wadeable moderate complexity reaches. Moderate and low complexity reaches of the San Marcos and Comal rivers are areas of intense recreational activities (Owens et al. 2001), which feasibly might explain observed changes in substrate composition. Recreational activities alter substrate compositions in marine (Meyer et al. 2008) and freshwater habitats (Agare 2016) by increasing turbidity due to movement and the suspension of fine sediments in the water column.

Among the initial predictions on fish community responses to flow extremes, only one was supported by the study results. High complexity reaches had the greatest densities of fishes among fish habitat guilds although not all species within a guild (e.g., *Notropis amabilis*, pelagic fluvial habitat guild) were most abundant in high complexity

reaches. Greater densities of stream fishes are positively related to habitat availability (Gorman and Karr 1978, Schlosser 1982), therefore suggesting a mechanistic relationship between fish densities and high complexity reaches with more habitat available for the various habitat guilds. However, the majority of the initial predictions were not supported by study results.

Surprisingly, the hydrologically stable system fish community demonstrated remarkable resistance or recovery during and after extreme flow events across the habitat complexity gradient, species richness and evenness were independent of levels in habitat complexity, and diversity was greatest in low complexity reaches. In hydrologically variable systems, floods typically have greater effect on fish communities in low complexity reaches than in high complexity reaches (Pearsons et al. 1992) and high complexity reaches serve as a refugia for fishes during flow extremes (Tschaplinski and Hartman 1983, Minckley 1987, Lamberti et al. 1991, Magoulick and Kobza 2003). Yet in this study, fish habitat guilds were largely unaffected by flow extremes, including members (*Gambusia*) of the surface habitat guild that are usually displaced downstream by high flow events (Meffe 1984, Chapman and Warburton 2006) and the benthic habitat guild that are susceptible to increased mortality via crushing by mobile substrates (Reice et al. 1990).

Resistance and recovery of the hydrologically stable system fish community to flow extremes could be attributed to evolutionary adaptations, especially since a majority of the fish communities (e.g., *Dionda nigrotaeniata*, *Notropis amabilis*, *Gambusia geiseri*, *Etheostoma fonticola*, comprising 41% of the total fish community) originated on the Edwards Plateau during the Pleistocene or earlier (Craig and Bonner 2021). In part,

evolutionary adaptations likely explain patterns in species diversity observed in this study with greater diversity in low complexity reaches (i.e., downstream from spring headwaters). In hydrologically stable systems of the Edwards Plateau, spring-associated fishes are more abundant near the head springs (Craig et al. 2016), associated with stenothermal waters and perhaps temperature mediates competition (Craig et al. 2019), whereas riverine-associated fishes are less abundant near the head springs and more abundant in eurythermal waters in downstream reaches. Hence in this study, greater diversity in the low complexity habitats were in downstream reaches and consisted primarily of riverine-associated fishes. Alternatively, fish community resistance and recovery during and after flow extremes could be related to instream habitat modifications within the two rivers. Both rivers consist of several low head dams (Kollaus et al. 2015, Thiels et al. 2022). Slackwater habitats with greater depths and greater amounts of vegetation (i.e., high habitat complexity) in most reaches of both rivers are influenced by a low head dam. Low head dams increase water depth and hydraulic retention (Pringle et al. 2001, Turgeon et al. 2019). Therefore, resistance and recovery in high complexity reaches could be artificially inflated by the low head dams, but low head dam effects do not clearly explain the resistance and recovery of the fish community in the moderate and low complexity reaches.

Past approaches into understanding hydrologically stable systems have focused primarily on threatened and endangered species (Schenk and Whiteside 1976; 1977, Bonner et al. 1998, Dwyer et al. 2005, Edwards and Bonner 2022, Poole et al. 2022). By assessing a greater number of species that encompass multiple habitat usage guilds, this study provided a more holistic perspective and framework for understanding how

groundwater dominated fish communities change under flow extremes. Historically, these hydrologically stable systems have been thought to be sensitive to environmental changes in the form of habitat alteration (Hubbs and Peden 1969) and extreme flow events (Schenk and Whiteside 1976). Based on the results of this study, these hydrologically stable systems offer greater resistance to flow extremes than previously thought, despite flow extreme levels in this study being less than those reported in the past (max flood levels near 2265 m³/s, min flow levels reaching 0.16 m³/s). While extreme flow events are an integral mechanism in the organization of aquatic habitat complexity and for maintaining prominent levels of biodiversity (Pearsons et al. 1992, Lake 2000), the effects are different for hydrologically variable and stable systems. While previously thought to be sensitive to minor alterations (Peden and Hubbs 1969, Schenk and Whiteside 1976), hydrologically stable systems offer high complexity habitats that are important for maintaining high taxa densities that are highly resistant, within both the habitat and community, to alterations from extreme flow events.

Table 1. Mean (\pm SE) physical habitat parameters across wadeable and non-wadeable reaches for all sample types in the San Marcos and Comal rivers from May 2014- November 2022.

Reach	Wadeable		Non-wadeable	
River	<u>San Marcos</u>	<u>Comal</u>	<u>San Marcos</u>	<u>Comal</u>
<u>Total observations (N)</u>	1452	1296	807	1311
<u>Habitat Parameters</u>				
Current Velocity (m/s)	0.37 (0.02)	0.22 (0.15)	0.2 (0.02)	0.1 (0.01)
Depth (m)	0.66 (0.02)	0.74 (0.18)	1.7 (0.18)	1.6 (0.02)
<u>Substrate (%)</u>				
Silt	31.2 (2.7)	28.9 (2.2)	33.8 (3.4)	63.6 (2.5)
Sand	15.1 (1.3)	10.2 (0.9)	19.1 (1.9)	2.6 (0.5)
Gravel	32.3 (1.8)	37.1 (1.6)	24.9 (2.5)	14.0 (1.6)
Cobble	13.6 (1.0)	13.2 (0.9)	10.2 (1.0)	4.1 (0.6)
Clay	2.3 (0.5)	0.3 (0.1)	10.1 (0.7)	2.7 (0.6)
Boulder	1.5 (0.2)	5.6 (0.8)	2.5 (0.2)	1.3 (0.3)
Bedrock	1.2 (0.4)	0.6 (0.2)	1.9 (0.2)	4.0 (1.0)
<u>Vegetation Cover (%)</u>				
Algae	36.8 (2.8)	38.7 (2.5)	41.6 (4.1)	71.3 (1.9)
Bryophyte	1.5 (0.3)	10.3 (2.3)	7.4 (0.7)	12.3 (2.0)
Short Caulescent	0.2 (0.1)	7.8 (1.3)	0.3 (0.03)	19.7 (1.8)
Tall Caulescent	4.5 (0.5)	12.1 (1.3)	5.3 (0.5)	16.6 (2.1)
Short Rosette	13.4 (1.8)	3.5 (0.6)	18.9 (1.9)	7.3 (1.5)
Tall Rosette	0.2 (0.1)	0.7 (0.2)	1.7 (0.2)	4.5 (1.0)
Tall Rosette	15.9 (1.7)	3.1 (0.9)	7.4 (0.7)	9.8 (1.8)

Table 2. Mean (\pm SE) percent coverage of vegetation type between high, moderate, and low complexity reaches from May 2014 - November 2022.

Vegetation Type	High (n=87)	Moderate (164)	Low (84)	F_{2,332}	P-value
Algae	8.7 (1.2)	7.3 (1.2)	8.4 (1.9)	0.25	0.78
Bryophyte	16.5 (1.7) a	3.3 (0.7) b	3.8 (1.0) b	42.93	<0.01***
Short Caulescent	18.7 (2.1) a	6.5 (0.7) b	5.6 (0.7) b	34.86	<0.01***
Tall Caulescent	12.9 (1.8) a	13.5 (1.6) a	4.3 (0.8) b	10.13	<0.01***
Short Rosette	6.2 (1.1) a	0.2 (0.1) b	0.5 (0.2) b	42.65	<0.01***
Tall Rosette	10.1 (1.8) a	12.1 (1.2) a	2.5 (0.7) b	10.97	<0.01***

Table 3. Mean (\pm SE) percent coverage of vegetation types that had detectable change between stasis, flood and drought periods among complexity reaches from May 2014 - November 2022.

Reach	Stasis	Flood	Drought	Test	Value	P-value/CI
<u>High</u>	-	-	-	-	-	NS
<u>Moderate</u>						
Tall						
Caulescent						
Wadeable	16.6 (2.3) a	14.2 (8.2) a	4.0 (1.8) b	LMER	11.64	(2.1 - 21.3)
Tall Rosette						
Wadeable	19.7 (2.0) a	4.4 (2.5) ab	30.0 (4.3) b	ANOVA	3.79	< 0.05*
<u>Low</u>						
Algae	6.4 (0.8) a	0 (0) a	24.9 (7.9) b	ANOVA	5.99	<0.01**

Table 4. Mean (\pm SE) species richness (R), Shannon-Weiner diversity (H') and evenness (EH) along the complexity gradient from May 2014 - November 2022.

Index	High (12)	Moderate (15)	Low (9)	F_{2,33}	P
R	14.8 (1.7)	18.5 (2.3)	18.8 (0.89)	1.70	0.2
H'	1.7 (0.11) b	1.9 (0.07) ab	2.1 (0.04) a	4.08	0.027*
EH	0.66 (0.03)	0.70 (0.03)	0.75 (0.01)	2.18	0.131

Table 5. Mean (\pm SE) species richness (R), Shannon-Weiner diversity (H') and evenness (EH) among flow periods within each complexity reach from May 2014 - November 2022.

Index	Stasis	Flood	Drought	F	P
<u>High (12)</u>					
R	21.5 (1.0) a	8.75 (1.6) b	14.25 (0.63) c	30.36	<0.01***
H'	1.99 (0.15)	1.42 (0.13)	1.76 (0.20)	3.13	0.09
EH	0.65 (0.04)	0.68 (0.06)	0.66 (0.07)	0.07	0.93
<u>Moderate (15)</u>					
R	26.75 (2.8) a	11.5 (2.5) b	17.25 (2.2) b	9.35	<0.01**
H'	1.99 (0.14)	1.76 (0.07)	2.04 (0.14)	1.52	0.27
EH	0.61 (0.04)	0.76 (0.06)	0.72 (0.04)	2.96	0.10
<u>Low (9)</u>					
R	26.3 (4.1)	12 (2.5)	18.3 (3.2)	4.52	0.06
H'	2.32 (0.01)	1.79 (0.11)	2.29 (0.21)	4.74	0.06
EH	0.72 (0.03)	0.75 (0.07)	0.79 (0.03)	0.64	0.56

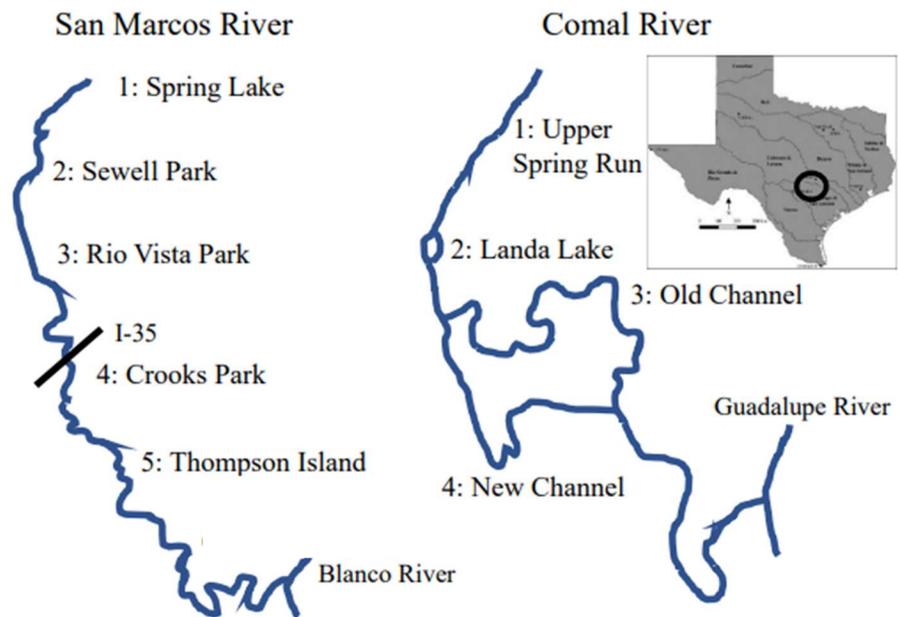


Figure 1. The five reaches sampled within the San Marcos River and the four reaches sampled in the Comal River from May 2014 - November 2022.

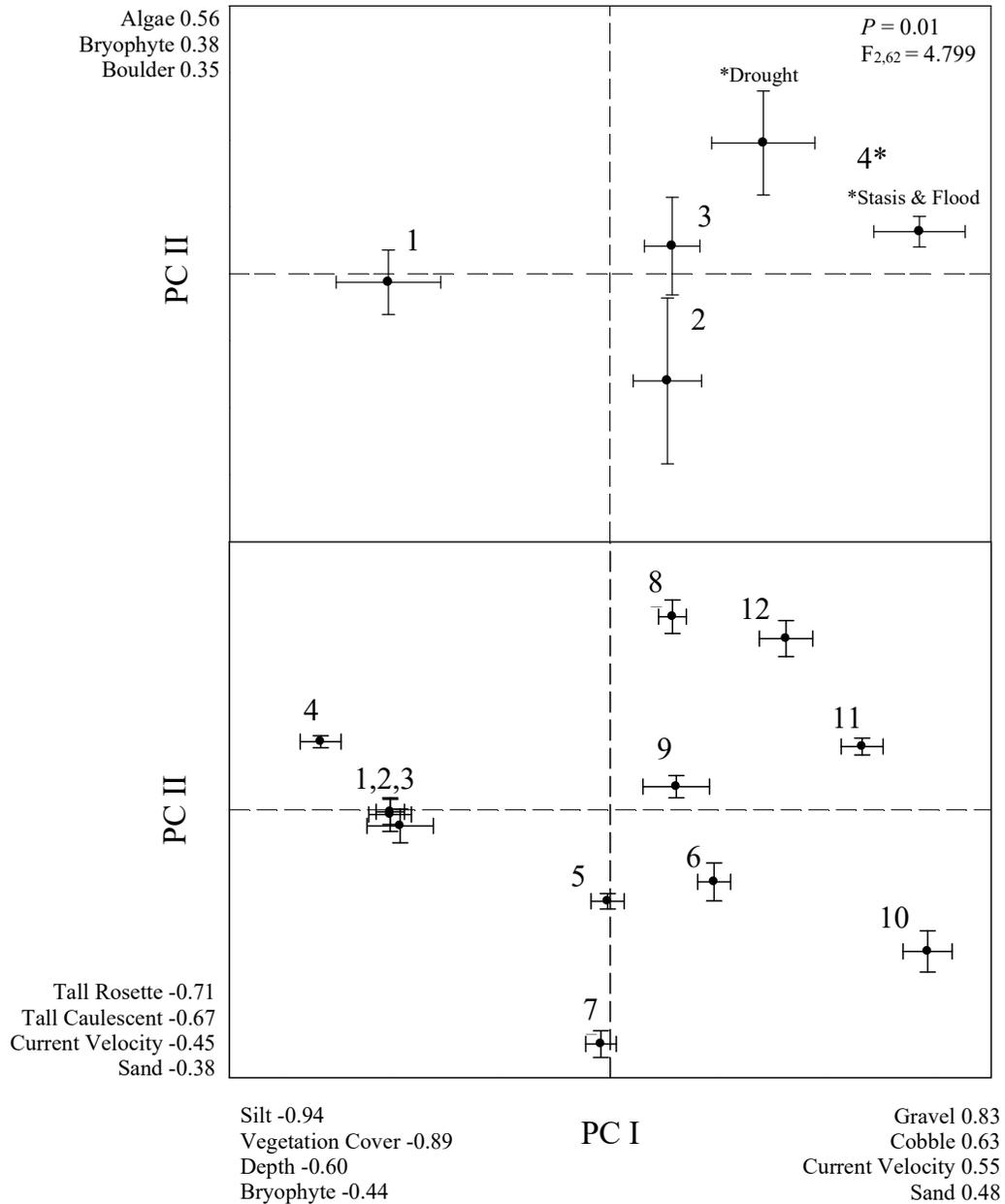


Figure 2. Plot of principal component axes I and II for (Bottom) all sites in the San Marcos and Comal rivers (1:Landa Lake, 2: Spring Lake, 3: New Channel_{non-wadeable}, 4: Old Channel_{non-wadeable}, 5: Upstream_{non-wadeable}, 6: Downstream_{non-wadeable}, 7: Upstream_{wadeable}, 8: Upper Spring Run_{non-wadeable}, 9: New Channel_{wadeable}, 10) Downstream_{wadeable}, 11) Old Channel_{wadeable}, 12) Upper Spring Run_{wadeable}) and (top) mean (\pm SE) PC value for 1) high complexity, 2) moderate wadeable complexity, 3) moderate non-wadeable complexity and 4) low complexity reaches. Only habitat variables with the strongest loadings on PC axes I and II are provided. Black circle represents mean PC scores among sites (bottom) and reaches (top). Error bars denote 1 SE.

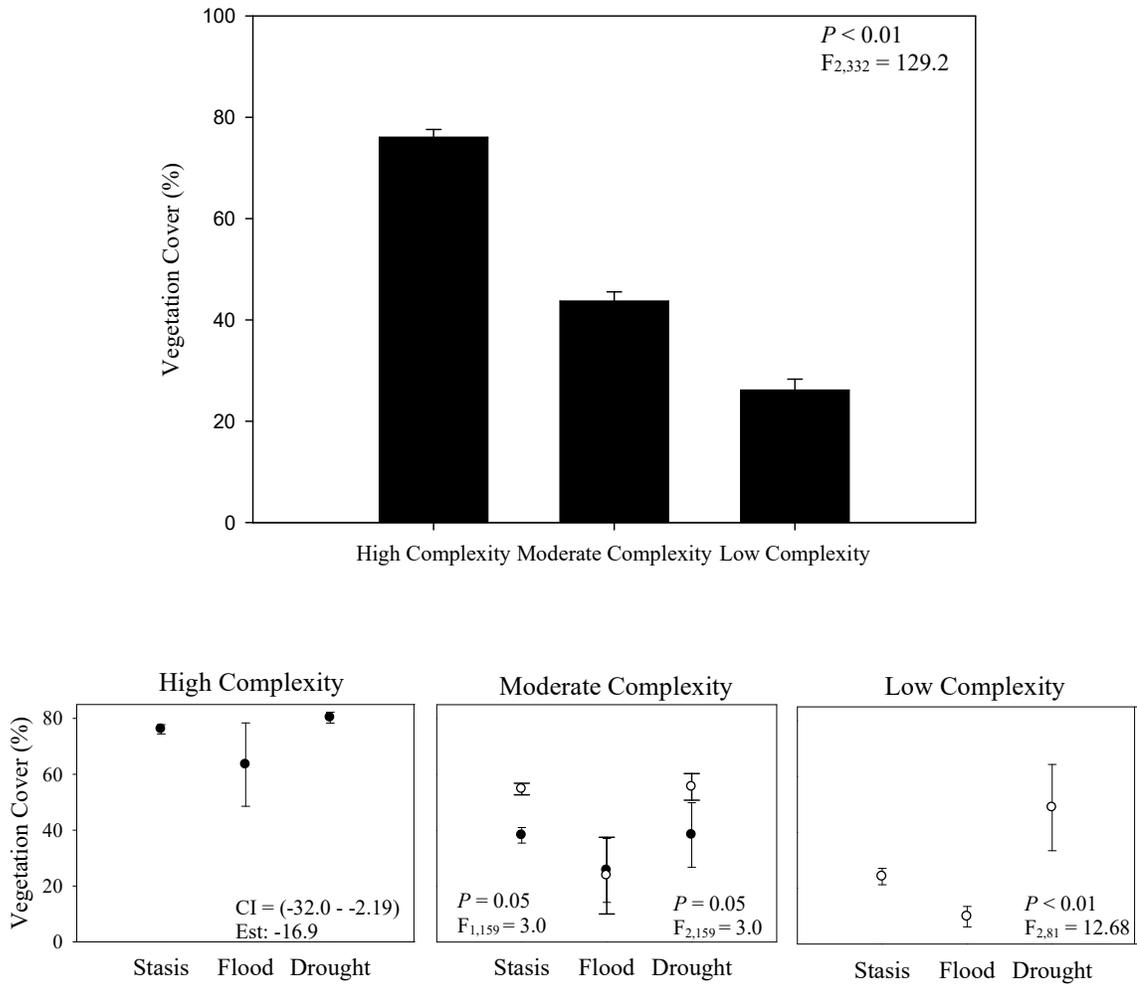


Figure 3. (Top) Mean (\pm SE) percent vegetation coverage along the complexity gradient and (Bottom) mean (\pm SE) percent vegetation coverage between flow periods (stasis, flood, drought) within each complexity reach from May 2014 - November 2022. The black circle represents mean vegetation coverage in non-wadeable reaches and the white circle represents mean vegetation coverage in wadeable reaches. Error bars denote 1 SE.

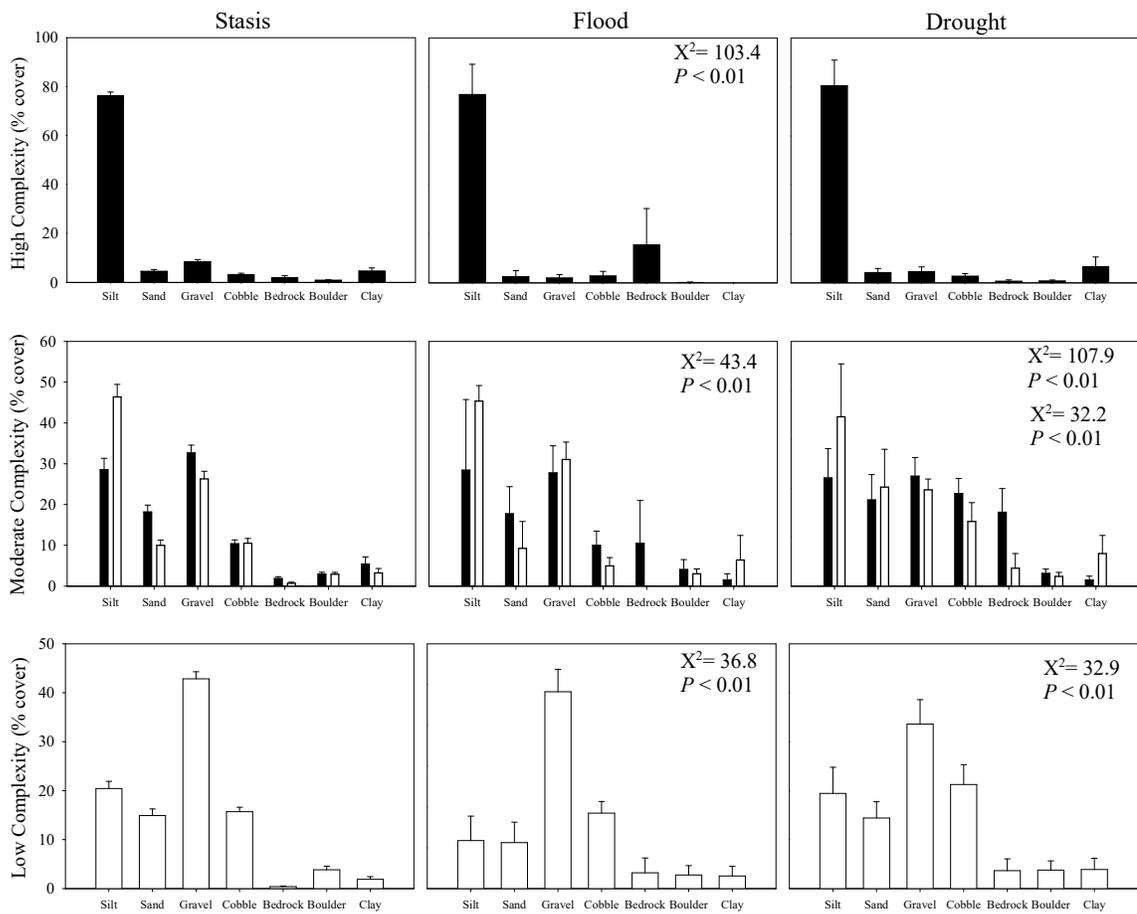


Figure 4. Mean (\pm SE) substrate composition among high, moderate, and low complexity reaches and between flow periods (stasis, flood, drought) from May 2014 - November 2022. Black bars represent mean coverage in non-wadeable reaches and white bars represent mean coverage in wadeable reaches. Error bars denote 1 SE.

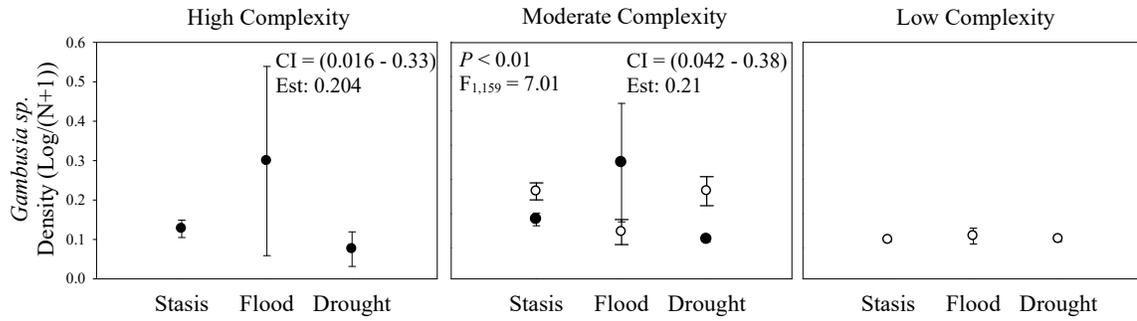


Figure 5. Log-transformed density and 1 SE (whiskers) of surface fishes along the complexity gradient and between flow periods from May 2014 - November 2022. The black circle represents mean log transformed density in non-wadeable reaches and the white circle represents mean log transformed density in wadeable reaches. Error bars denote 1 SE.

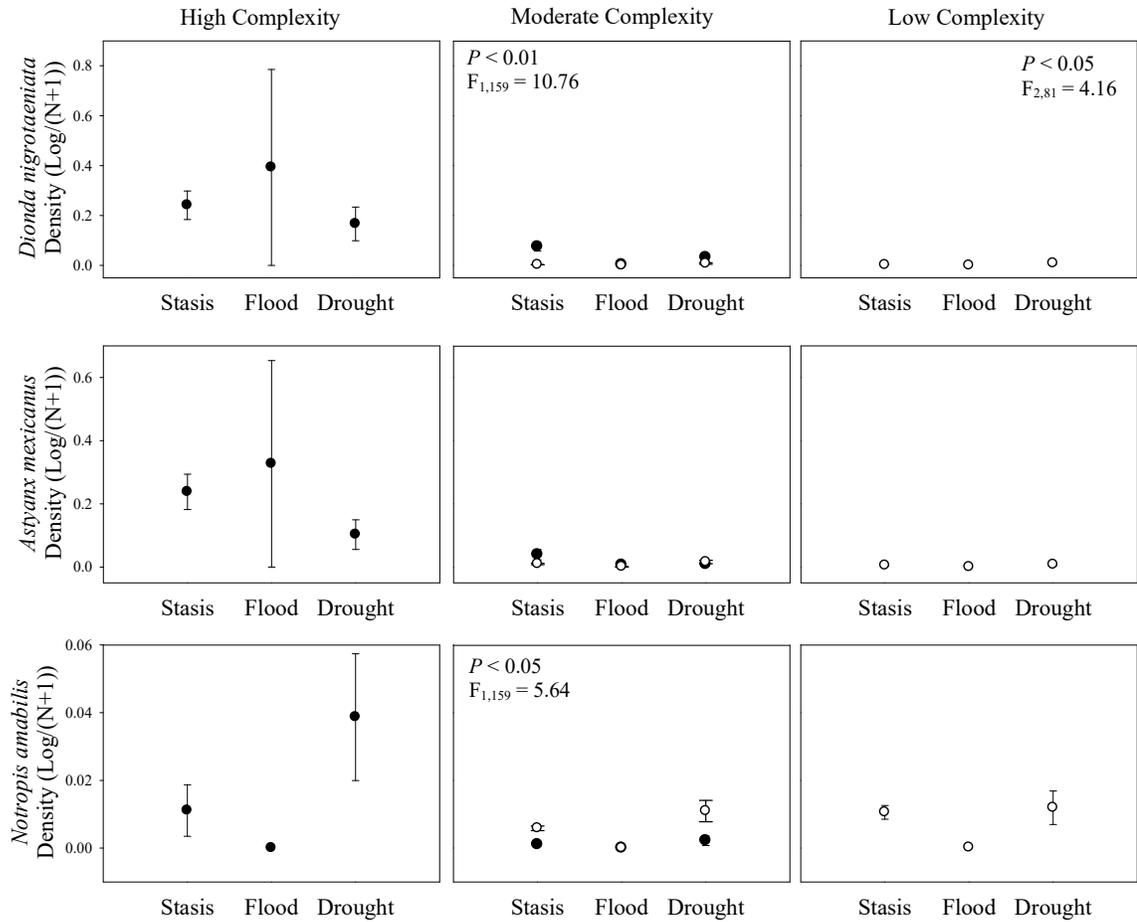


Figure 6. Log-transformed density and 1 SE (whiskers) of pelagic generalist fishes along the complexity gradient and between flow periods from May 2014 - November 2022. The black circle represents mean log transformed density in non-wadeable reaches and the white circle represents mean log transformed density in wadeable reaches. Error bars denote 1 SE.

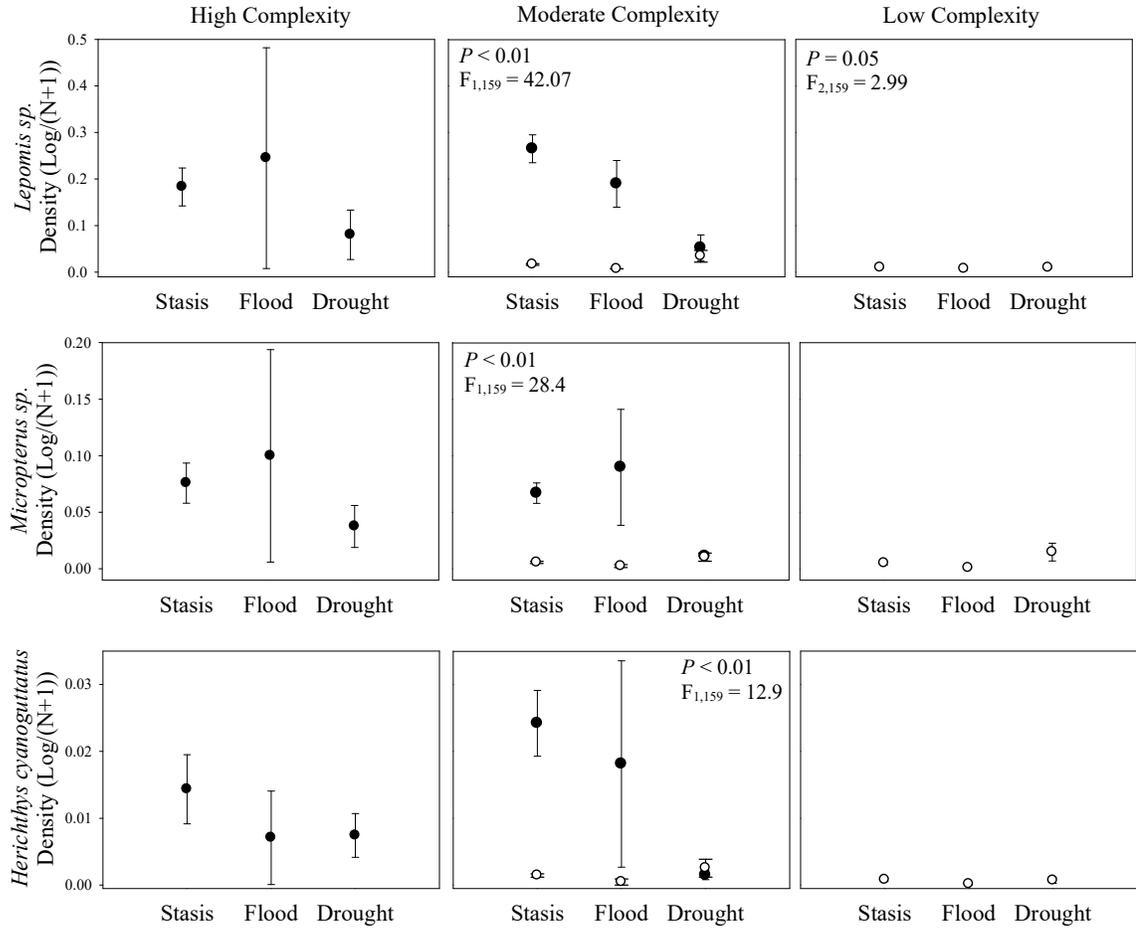


Figure 7. Log-transformed density and 1 SE (whiskers) of pelagic fluvialist fishes along the complexity gradient and between flow periods from May 2014 - November 2022. The black circle represents mean log transformed density in non-wadeable reaches and the white circle represents mean log transformed density in wadeable reaches. Error bars denote 1 SE.

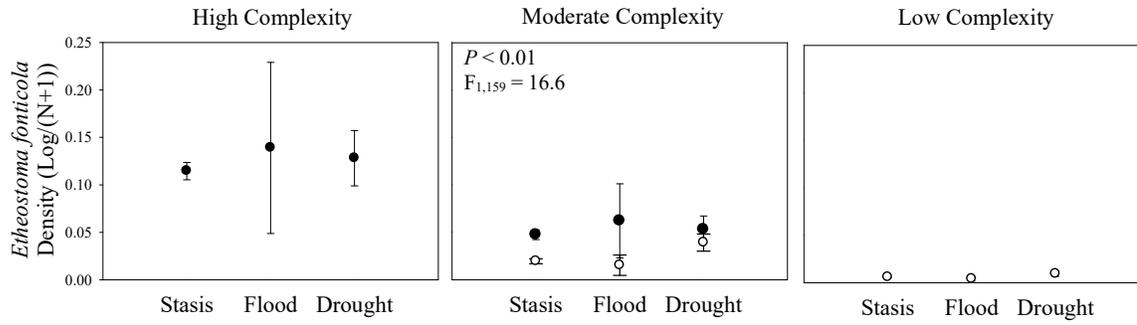


Figure 8. Log-transformed density and 1 SE (whiskers) of benthic fishes along the complexity gradient and between flow periods from May 2014 - November 2022. The black circle represents mean log transformed density in non-wadeable reaches and the white circle represents mean log transformed density in wadeable reaches. Error bars denote 1 SE.

APPENDIX SECTION

Appendix 1. Common taxa (>4500 individuals) placed into habitat usage guilds and relative abundance identified in wadeable and non-wadeable reaches in the San Marcos River and Comal River from May 2014- November 2022.

Species Name	Habitat Guild	Abundance (%)
<i>Gambusia sp.</i>	Surface	24.23
<i>Gambusia geiseri</i>	Surface	9.31
<i>Gambusia affinis</i>	Surface	0.94
<i>Dionda nigrotaeniata</i>	Pelagic Fluvial	19.07
<i>Astyanx mexicanus</i>	Pelagic Fluvial	14.18
<i>Notropis amabilis</i>	Pelagic Fluvial	3.83
<i>Lepomis sp.</i>	Pelagic General	5.03
<i>Micropterus salmoides</i>	Pelagic General	4.84
<i>Lepomis auritus</i>	Pelagic General	3.06
<i>Herichthys cyanoguttatus</i>	Pelagic General	1.65
<i>Lepomis macrochirus</i>	Pelagic General	1.33
<i>Lepomis miniatus</i>	Pelagic General	0.79
<i>Lepomis megalotis</i>	Pelagic General	0.47
<i>Lepomis microlophus</i>	Pelagic General	0.42
<i>Lepomis cyanellus</i>	Pelagic General	0.06
<i>Lepomis gulosus</i>	Pelagic General	0.05
<i>Micropterus punctatus</i>	Pelagic General	0.01
<i>Micropterus sp.</i>	Pelagic General	<0.01
<i>Micropterus dolomieu</i>	Pelagic General	<0.01
<i>Etheostoma fonticola</i>	Benthic	8.71
<i>Etheostoma sp.</i>	Benthic	2.01
	Total N	123361

Appendix 2. Common (> 5% cover) aquatic vegetation taxa identified by height (tall or short) and growth form (Bryophyte, algae, caulescent and rosette) among wadeable and non-wadeable reaches in the San Marcos River and Comal River from May 2014 - November 2022.

Lowest taxonomic level	Common Name	Height	Classification
<i>Bryophyta</i>	Bryophyte	Short	Bryophyte
Detrital Algae	Detrital Algae	Short	Algae
Filamentous Algae	Filamentous Algae	Short	Algae
Epiphytic Algae	Epiphytic Algae	Short	Algae
<i>Hydrilla verticillata</i>	Hydrilla	Tall	Caulescent
<i>Cabomba caroliniana</i>	Cabomba	Tall	Caulescent
<i>Characeae</i>	Chara	Tall	Caulescent
<i>Haloragaceae</i>	Myrio-Millfoil & parrotfeather	Tall	Caulescent
<i>Ceratophyllum demersum</i>	coontail	Tall	Caulescent
<i>Justicia americana</i>	Justicia	Tall	Caulescent
Potamogetonaceae	Potamogeton	Tall	Caulescent
<i>Hygrophila lacustris</i>	Hygrophila	Short	Caulescent
<i>Ludwigia repens</i>	Ludwigia	Short	Caulescent
<i>Hydrocotyle verticillata</i>	Hydrocotyle pennywort	Short	Caulescent
<i>Vallisneria americana</i>	Vallisneria	Tall	Rosette
<i>Zizania texanus</i>	Texas Wild Rice	Tall	Rosette
<i>Sagittaria platyphylla</i>	Sagittaria	Short	Rosette

LITERATURE CITED

- Agare, O. O. (2016). Seasonal and longitudinal investigation on the impacts of recreational activities on the aquatic macroinvertebrate community within the San Marcos River. Unpublished thesis.
- Bbest, R. G. (2011). Environmental flows recommendations report. *Final submission to the Guadalupe, San Antonio, Mission, and Aransas Rivers and Mission, Copano, Aransas, and San Antonio Bays Basin and Bay Area Stakeholder Committee, Environmental Flows Advisory Group, and Texas Commission on Environmental Quality.*
- Behen, K., Bonner, T. H. (2013). Influence of connectivity and habitat heterogeneity on fishes in the upper San Marcos River, Texas. Unpublished thesis.
- Bonner, T. H., Brandt, T. M., Fries, J. N., & Whiteside, B. G. (1998). Effects of temperature on egg production and early life stages of the fountain darter. *Transactions of the American Fisheries Society*, 127(6), 971-978.
- Bornette, G., Puijalon, S. (2011). Response of aquatic plants to abiotic factors: a review. *Aquat Sci* 73, 1–14. <https://doi.org/10.1007/s00027-010-0162-7>
- Brock, V. E. (1954). A Preliminary Report on a Method of Estimating Reef Fish Populations. *The Journal of Wildlife Management*, 18(3), 297–308.
- Bunn, S., Arthington, A.(2002). Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. *Environmental Management* 30, 492–507.
- Chapman, P., & Warburton, K. (2006). Postflood movements and population connectivity in gambusia (*Gambusia holbrooki*). *Ecology of Freshwater Fish*, 15(4), 357-365.
- Craig, C. A. (2014). Relationship between base flow magnitude and spring fish communities (Unpublished thesis). Texas State University, San Marcos, Texas.
- Craig, C.A., K. A. Kollaus, K. P. K. Behen, and T.H. Bonner. 2016. Relationships among spring flow, habitats, and fishes within evolutionary refugia of the Edwards Plateau. *Ecosphere* 7:1-13.
- Craig, C. A., Maikoetter, J. D., & Bonner, T. H. (2019). Temperature-mediated feeding between spring-associated and riverine-associated congeners, with implications for community segregation. *PeerJ*, 6, e6144.
- Craig, C. A., & Bonner, T. H. (2021). Spring flow lost: a historical and contemporary perspective of an urban fish community. *Urban Ecosystems*, 24, 417-427.

- Crouzy, B., Edmaier, K., Pasquale, N., & Perona, P. (2013). Impact of floods on the statistical distribution of riverbed vegetation. *Geomorphology*, 202, 51–58.
- Dahm, C.N., M.A. Baker, D.I. Moore, and J.R. Thibault. 2003. Biogeochemistry of surface waters and alluvial ground waters in streams and rivers during drought. *Freshwater Biology* 48:1219-1231.
- Davis J, Pavlova A, Thompson R, and Sunnucks P. 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Glob Change Biol*19: 1970–84
- De Wilde, M., Sebei, N., Puijalón, S., & Bornette, G. (2014). Responses of macrophytes to dewatering: Effects of phylogeny and phenotypic plasticity on species performance. *Evolutionary Ecology*, 28(6), 1155–1167.
- D’Ottavio, R.J., and R.A. Earl. 2020. The “mystery flood” on the upper San Marcos River, Texas, October 2015. Unpublished thesis.
- Dwyer, F. J., Mayer, F. L., Sappington, L. C., Buckler, D. R., Bridges, C. M., Greer, I. E., ... & Neuderfer, G. N. (2005). Assessing contaminant sensitivity of endangered and threatened aquatic species: Part I. Acute toxicity of five chemicals. *Archives of environmental contamination and toxicology*, 48, 143-154.
- Edwards, C.R., and T.H. Bonner. 2022. Vegetation associations of the endangered Fountain Darter *Etheostoma fonticola*. *Endangered Species Research* 47:1-13.
- Earl, R. A., & Vaughan, J. W. (2015). Asymmetrical response to flood hazards in south central Texas. *Papers in Applied Geography*, 1(4), 404-412.
- Franssen, N.R, Gido, K.B, Guy, C.S., Tripe, J.A., Shrank, S.J., Strakosh, T.R., Bertrand, K.N., Franssen, C.M., Pitts, K.L. and Paukert, C.P.(2006), Effects of floods on fish assemblages in an intermittent prairie stream. *Freshwater Biology*, 51: 2072-2086.
- Gorman, O. T., & Karr, J. R. (1978). Habitat structure and stream fish communities. *Ecology*, 59(3), 507–515.
- Hankin, D. G., & Reeves, G. H. (1988). Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Canadian Journal of Fisheries and Aquatic Sciences*, 45(5), 834–844. <https://doi.org/10.1139/f88-101>
- Harrell, H. L. (1978). Response of the Devil’s River (Texas) Fish Community to Flooding. *Copeia*, 1978(1), 60–68. <https://doi.org/10.2307/1443822>
- Hastie, L. C., Boon, P. J., Young, M. R., & Way, S. (2001). The effects of a major flood on an endangered freshwater mussel population. *Biological Conservation*, 98(1), 107–115. [https://doi.org/10.1016/s0006-3207\(00\)00152-x](https://doi.org/10.1016/s0006-3207(00)00152-x)

- Henry, C. P., Amoros, C., & Bornette, G. (1996). Species traits and recolonization processes after flood disturbances in riverine macrophytes. *Vegetatio*, 122(1), 13–27.
- Hitt, N. P., Landsman, A. P., & Raesly, R. L. (2022). Life history strategies of stream fishes linked to predictors of hydrologic stability. *Ecology and Evolution*, 12(5).
- Hubbs, C., & Peden, A. E. (1969). *Gambusia georgei* sp. nov. from San Marcos, Texas. *Copeia*, 1969(2), 357–364.
- Humphries, P., & Baldwin, D. S. (2003). Drought and aquatic ecosystems: An introduction. *Freshwater Biology*, 48(7), 1141–1146.
- Kollaus, K. A., Behen, K. P., Heard, T. C., Hardy, T. B., & Bonner, T. H. (2015). Influence of urbanization on a karst terrain stream and fish community. *Urban ecosystems*, 18, 293–320.
- Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the north american Benthological society*, 19(4), 573–592.
- Lamberti, G. A., Gregory, S.V., Ashkenas, L.R., Wildman, R.C., Steinman, A.G. (1989). Influence of Channel Geomorphology on Retention of Dissolved and Particulate Matter in a Cascade Mountain Stream. In: Abell, Dana L., Technical Coordinator. 1989. Proceedings of the California Riparian Systems Conference: protection, management, and restoration for the 1990s; 1988 September 22–24; Davis, CA. Gen. Tech. Rep. PSW-GTR-110. Berkeley, CA: Pacific Southwest Forest and Range
- Larned, S.T., Datry, T., Arscott, D.B., & Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology*, 55(4), 717–738.
- Lennox, R.J., Crook, D.A., Moyle, P.B. (2019). Toward a better understanding of freshwater fish responses to an increasingly drought-stricken world. *Rev Fish Biol Fisheries* 29, 71–92
- Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: a review and synthesis. *Freshwater biology*, 48(7), 1186–1198.
- Magoulick, D. D., Dekar, M. P., Hodges, S. W., Scott, M. K., Rabalais, M. R., & Bare, C. M. (2021). Hydrologic variation influences stream fish assemblage dynamics through flow regime and drought. *Scientific Reports*, 11(1), 1–15.
- Matthews, W. J. (1986). Fish faunal structure in an Ozark stream: Stability, persistence and a catastrophic flood. *Copeia*, 1986(2), 388.

- McKee, T.B., N. J. Doesken, and Kliest, J. (1993). The relationship of drought frequency and duration to time scales. In *Proceedings of the 8th Conference of Applied Climatology, 17-22 January, Anaheim, CA*. American Meteorological Society, Boston, MA. 179-184.
- Meffe, G.K. (1984). Effects of Abiotic Disturbance on Coexistence of Predator-Prey Fish Species. *Ecology*, 65: 1525-1534.
- Mendelson, J. (1975). Feeding relationships among species of Notropis (Pisces: Cyprinidae) in a Wisconsin Stream. *Ecological Monographs*, 45(3), 199–232.
- Meyer, C. G., & Holland, K. N. (2008). Spatial dynamics and substrate impacts of recreational snorkelers and SCUBA divers in Hawaiian Marine Protected Areas. *Journal of Coastal Conservation*, 12, 209-216.
- Minckley, W.L., and G.K. Meffe. (1987). Differential selection for native fishes by flooding in stream communities of the American southwest. Pages 93-104 in W. J.
- Owens, C. S., Madsen, J. D., Smart, R. M., & Stewart, R. M. (2001). Dispersal of native and nonnative aquatic plant species in the San Marcos River, Texas. *Journal of Aquatic Plant Management*, 39, 75-79.
- Pearsons, T. N., Li, H. W., & Lamberti, G. A. (1992). Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society*, 121(4), 427–436.
- Poole, J., Hutchinson, J. T., Hathcock, C. R., & Han, D. (2022). A thirty-year assessment of the endangered aquatic macrophyte, *Zizania texana*, endemic to the upper reach of the San Marcos River in Central Texas, USA. *Aquatic Botany*, 177, 103482.
- Pringle, C. M. (2001). Hydrologic connectivity and the management of biological reserves: A global perspective. *Ecological Applications*, 11(4), 981–998.
- Reice, S. R., Wissmar, R. C., & Naiman, R. J. (1990). Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental management*, 14, 647-659.
- Riis, T., Suren, A.M., Clausen, B. & Sand-Jensen, K. (2008). Vegetation and flow regime in lowland streams. *Freshwater Biology*, 53: 1531-1543.
- Rolls, R. J., Leigh, C., & Sheldon, F. (2012). Mechanistic effects of low-flow hydrology on riverine ecosystems: Ecological principles and consequences of alteration. *Freshwater Science*, 31(4), 1163–1186. <https://doi.org/10.1899/12-002.1>

- Ross, S. T., & Baker, J. A. (1983). The response of fishes to periodic spring floods in a southeastern stream. *American Midland Naturalist*, 109(1), 1.
- Saunders, K. S., Mayes, K. B., Jurgensen, T. A., Trungale, J. F., Kleinsasser, L. J., Aziz, K., & Moss, R. E. (2001). An evaluation of spring flows to support the upper San Marcos River spring ecosystem, Hays County, Texas. *Texas Parks and Wildlife Department. River Studies Report*, (16).
- Schenck, J. R., & Whiteside, B. G. (1977). Reproduction, fecundity, sexual dimorphism and sex ratio of *Etheostoma fonticola* (Osteichthyes: Percidae). *American Midland Naturalist*, 365-375
- Schenck, J. R., & Whiteside, B. G. (1976). Distribution, habitat preference and population size estimate of *Etheostoma fonticola*. *Copeia*, 697-703.
- Schill, D. J., & Griffith, J. S. (1984). Use of underwater observations to estimate cutthroat trout abundance in the Yellowstone River. *North American Journal of Fisheries Management*, 4(4B), 479–487.
- Schlosser, I. J. (1982). Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* 52:395–414.
- Schuyler, A. E. (1984). Classification of Life Forms and Growth Forms of Aquatic Macrophytes. *Bartonia*, 50, 8–11.
- Sheldon, A. L. (1968). Species Diversity and Longitudinal Succession in Stream Fishes. *Ecology*, 49(2), 193–198.
- Shumway, C. A., Hofmann, H. A. & Dobberfuhl, A. P, (2007). Quantifying habitat complexity in aquatic ecosystems. *Freshwater Biology*, 52(6), 1065–1076.
- Sotola, V. A, K. T. Sullivan, B. M. Littrell, N. H. Martin, D. S. Stich, and T. H. Bonner. 2021. Short-term responses of freshwater mussels to floods in a southwestern U.S.A. river estimated using mark-recapture sampling. *Freshwater Biology* 66:349-361.
- Theils S. and T. H. Bonner. (2021). Reproduction, life history, and diets of the greenthroat darter *Etheostoma lepidum* in low-flow and high-flow environments. Unpublished thesis.
- Tokeshi, M., & Arakaki, S. (2011). Habitat complexity in aquatic systems: Fractals and beyond. *Hydrobiologia*, 685(1), 27–47.
- Tramer, E. J., & Rogers, P. M. (1973). Diversity and longitudinal zonation in fish populations of two streams entering a metropolitan area. *American Midland Naturalist*, 90(2), 366.

- Tschaplinski, P. J., and G. F. Hartman. (1983). Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for over-winter survival. *Canadian Journal of Fisheries and Aquatic Sciences* 40:452-461.
- Turgeon, K., Turpin, C., & Gregory-Eaves, I. (2019). Dams have varying impacts on fish communities across latitudes: A quantitative synthesis. *Ecology Letters*, 22(9), 1501–1516.
- Willis, S. C., Winemiller, K. O., & Lopez-Fernandez, H. (2004). Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical Floodplain River. *Oecologia*, 142(2), 284–295.