HYDROLOGY AND GEOLOGY AS STRUCTURING MECHANISMS OF SEMI-ARID FISH COMMUNITIES

by

Lauren E. Chappell, 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 H. Bonner, Chair

Noland H. Martin

Benjamin F. Schwartz

COPYRIGHT

by

Lauren E. Chappell

2023

FAIR USE AND AUTHOR'S PERMISSION STATEMENT

Fair Use

This work is protected by the Copyright Laws of the United States (Public Law 94-553, section 107). Consistent with fair use as defined in the Copyright Laws, brief quotations from this material are allowed with proper acknowledgement. Use of this material for financial gain without the author's express written permission is not allowed.

Duplication Permission

As the copyright holder of this work I, Lauren E. Chappell, authorize duplication of this work, in whole or in part, for educational or scholarly purposes only.

ACKNOWLEDGMENTS

I thank Dr. Tim Bonner for fostering my appreciation and understanding of freshwater ecosystems and allowing me to join in on that first memorable trip up to the Red River as an undergraduate. I would also like to thank my committee members, Dr. Noland Martin and Dr. Benjamin Schwartz. I am grateful for Dr. Martin and his study abroad course which brought me some of my closest friends and most meaningful experiences in nature. I am just as appreciative of Dr. Schwartz and his groundwater resources course for providing me with a depth of knowledge of geology and hydrology, as well as a beautiful trip to the Devil's River with great company.

I have been lucky enough to work alongside and befriend many wonderful people in the Bonner lab, from 2016 to 2023. Anne Beckman, Cody Craig, Nicky Faucheux, Jeremy Maikoetter, Dave Ruppel and Alex Sotola provided me with great opportunities and mentorship as I got my start. Daisy Blake, Brady Boykin, Zach Hutchens, Eli Leal, Steven Lopez, Caite Schoeck, Josh Tivin, Melissa Wolter and Alex Zalmat provided great support as lab mates throughout graduate school. I also thank my family and friends who have stood behind and beside me as I made my way back into academia. Most importantly I would like to thank Cody Craig for allowing me to expand upon his doctoral dataset for my thesis, Josh Tivin for two years of laughs and being a great classmate, Daisy Blake for being the best mentee I could have imagined, Steven Lopez for showing me the ropes my first year, and Dr. Bonner for seeing something in me in 2016 that I now see as well.

TABLE OF CONTENTS

LIST OF TABLES

Table **Page**

LIST OF FIGURES

Figure **Page**

ABSTRACT

In the semi-arid regions of the Edwards Plateau in southwest USA, spring-associated fishes, including several federally and state listed species, are closely associated with spring outflows of karst aquifers. However, not all spring outflows are of sufficient volume to provide surface flows for long distances downstream. Stream disconnectivity can thus occur during dry periods, especially in systems where the surficial geology transitions from water gaining reaches (i.e., spring outflows in Cretaceous Gaining Reach) to water losing reaches (i.e., surface waters lost to recharging another karst aquifer or alluvium in either Cretaceous Losing Reach or Quaternary Losing Reach). The purpose of this study was to describe habitats and fish community distributions, with an emphasis on spring-associated fishes, along a longitudinal gradient consisting of different geologies and gaining/losing reaches between a Wet Hydrological Period (2015 – 2016) and Dry Hydrological Period (2021 – 2022) in three independent river systems. Predictions of the study were that hydrological period would have an effect on the overall fish community along a longitudinal and surficial geological gradient, with a positive relationship between relative abundances of spring-associated fishes and volume of spring outflows (Craig et al. 2016). During five collection events, fish communities consisted of 26 species (6 spring-associated fish species) and 21,297 individuals (10,317 spring associated fishes). Among 366 habitats quantified, reaches consisted primarily of riffles and runs with gravel and cobble substrates, moderately swift current velocities (mean ± 1 SE; 0.33 ± 0.29 cm/s) and shallow depths (0.38 ± 0.27 m) during the Wet Hydrological Period, although two rivers were dry or surface waters were restricted to isolated pools in the Quaternary Losing Reach. During the Dry Hydrological Period, habitats were similar in the Cretaceous Gaining reaches, isolated pools formed in the Cretaceous Losing reaches, and streambeds were completely dry in the Quaternary Losing reaches. Correspondingly, species richness, diversity, and evenness were generally greater in the Cretaceous Gaining and Losing reaches compared to the Quaternary Losing reaches during Wet and Dry Hydrological periods. Surprisingly, spring-associated relative abundances were similar in the Cretaceous Gaining and Losing reaches, despite the formation of isolated habitats in the Cretaceous Losing Reach. In the past, losing reaches of Edwards Plateau streams were interpreted as sinks for spring-associated fishes, yet this study demonstrated that losing reaches can serve as aquatic refugia for sources of spring-associated fish populations even into exceptional drought periods and therefore have conservation value for a number of the Edwards Plateau endemic fauna.

I. HYDROLOGY AND GEOLOGY AS STRUCTURING MECHANISMS OF SEMI-ARID FISH COMMUNITIES

Introduction

Spring systems associated with karst-terrain aquifers often provide unique surface waters (e.g., greater water permanency, thermal consistency) in North America, ranging from the arid southwest to the humid Atlantic coast (Felstead et al. 2015, Work 2021). In arid and semi-arid regions, springs systems with water permanency serve as microrefugia (Rull 2009) or endemic hotspots for aquatic flora and fauna (Davis et al. 2013, Harrison and Noss 2017) and in some instances have served as evolutionary refugia for endemic aquatic flora and fauna through past interglacial cycles (Davis et al. 2013, Cartwright et al. 2020). Water permanency of the spring systems and corresponding aquifers, therefore, is important in arid and semi-arid regions, not only for support of species diversity but also for human uses (Meinzer 1934, Mather and Rose 2012, Davis et al. 2017). As the climate in southwest North America trends towards more arid conditions (MacDonald 2010, Grimm et al. 2013), understanding the linkages between spring systems and their biota is necessary for conservation and management of these unique ecosystems, especially since many spring systems vary widely in terms of geomorphology and private ownership (Keppel et al. 2012, Davis et al. 2017, Stevens et al. 2020).

Spring systems of the karst Edwards Plateau region of Texas support 12 endemic fishes and many other species of flora and fauna that are strongly associated with spring outflows from the Edwards and Edwards-Trinity Aquifer systems (Bowles and Arsuffi 1993). Spring-associated fishes (Hubbs 2001 refers to this community as spring-adapted fishes with their counterparts being riverine-adapted fishes) are more abundant in high-flow (>0.85 m^3/s) vs. low-flow spring systems (<0.85 m^3/s) and are more abundant nearer springs (Craig et al. 2016). In systems with a single headwater spring complex, perennially flowing surface waters support a dominance of spring-associated fishes within the first 4 to 6 km, where community dominance then shifts to riverine-associated fishes (Behen 2013, Scanes 2016). In other spring systems, where spring outflows contribute to baseflows in multiple locations throughout a river's course, spring-associated fishes are more abundant near spring outflows and decrease in abundance in reaches between springs (Kollaus and Bonner 2012).

A third configuration of spring systems exists in the karstic Edwards Plateau. Spring outflows, which along with surface runoff, form perennial surface waters in the headwaters (i.e., gaining reach) and in downstream reaches during wet years with above average precipitation. Under dry years, however, spring discharge is insufficient to compensate for surface water loss to groundwater (i.e., losing reach) in the downstream reaches (> 50 km from headwaters). Losing reaches, therefore, are interpreted as population sinks, which include federally and state-listed spring-associated species. In at least one biological assessment, the loss of surface waters in a losing reach was interpreted as an anthropogenically caused (i.e. over pumping of the groundwater) loss of habitat for a federally-listed species (USFWS 2005). Loss of surface waters to groundwater is common in karst terrains and, with knowledge of the surficial geology, locations of losing reaches are predictable. To date, however, the conservation values of losing reaches for fishes, especially for spring-associated fishes, are unknown during dry periods.

Purposes of this study were to assess interrelationships among surficial geology (i.e., gaining and losing reaches), stream flow, and wet and dry hydrological periods on fish communities, with emphasis on the spring-associated fishes, in three rivers (Nueces River basin) of the Edwards Plateau with reported losing reaches (Banta 2012). Study objectives were to quantify stream flow environments, instream habitats, fish communities (i.e., richness, relative abundances, diversity, evenness), and spring-associated fishes (i.e., richness and relative abundances) across surficial geologies with gaining and losing reaches during wet and dry hydrological periods, including an exceptional drought. Along a longitudinal gradient, I predicted that species richness, species diversity, and evenness would increase from upstream to downstream and spring-associated fish richness and abundance would be greater upstream to downstream during the Wet Hydrological Period. During the Dry Hydrological Period, I predicted that surface waters would be lost in the Cretaceous Losing and Quaternary Losing reaches and, therefore, extirpations of fishes. In contrast, fish communities would persist in the Cretaceous Gaining reaches during the Dry Hydrological periods and will be similar to the fish communities in the Wet Hydrological Period, supporting the concept of the Cretaceous Gaining reaches acting as an evolutionary refugia.

Methods

Study Area and Geology

The Nueces River basin is on the southwestern edge of the Edwards Plateau of Central Texas (i.e., Edwards and Real counties) and originates from a series of headwater karst springs emerging from the Edwards-Trinity Aquifer (Texas Water Development

Board 1990) where surficial geology is Cretaceous limestone (i.e., Cretaceous Gaining Reach). Three mainstem rivers comprise the upper portion of the basin: the Nueces, Frio and Sabinal rivers. As the rivers flow south, their courses cross Cretaceous limestones until encountering the Balcones Fault Line, ranging from 50 to 100 km downstream from the headwaters, where surface flows are lost in the recharge zone for the karstic Edwards Aquifer system below, or to the alluvium (i.e., Cretaceous Losing Reach) (Sophocleous 2002). Their courses continue farther south, exiting the southern boundary of the Edwards Plateau and encountering Quaternary fluviatile terrace deposits (Pleistocene) and alluvium (Holocene) (USGS Texas Geology Map, https://txpub.usgs.gov/txgeology/), where surface flows are lost to alluvium (i.e., Quaternary Losing Reach) before surface flows reemerge from alluvial groundwater and outflows of the Edwards Aquifer (Banta et al. 2015, Hackett 2019). Farther downstream, the three rivers flow in a southeast direction, encountering Tertiary-age sediments and converge to form the mainstem Nueces River in Three Rivers, Texas. The river ends in Nueces Bay and Corpus Christi Bay, Gulf of Mexico. The study area is limited to the upper reaches of the three rivers including Cretaceous Gaining reaches, Cretaceous Losing reaches, and Quaternary Losing reaches, which generally encompasses the extent of spring-associated fish distributions in the Nueces River basin (Hendrickson and Cohen 2015; Figure 1).

Hydrology

Daily mean flows (period of this study: 2015 – 2022) and median flows (period of record) were obtained from nine USGS gaging stations (Figure 1): Nueces River (N = 4), Frio River (N = 2), and Sabinal River (N = 3). The Nueces River has one station (USGS

0818999010, period of record 2009-2022) in the Cretaceous Gaining Reach, two stations in the Cretaceous Losing Reach (USGS 08189998, period of record 2011-2022 and USGS 08190000, period of record 1923-2022), and one station in the Quaternary Losing Reach (USGS 08192000, period of record 1939-2022). The Frio River lacks a gaging station in the Cretaceous Gaining Reach, has one station in the Cretaceous Losing Reach (USGS 08195000, period of record 1924-2022) and one station in the Quaternary Losing Reach (USGS 08197500, period of record 1953-2022). The Sabinal River has one station in the Cretaceous Gaining Reach, (USGS 08197936, period of record 2013-2022), one station in the Cretaceous Losing Reach (USGS 08198000, period of record 1942-2022) and one station in the Quaternary Losing Reach (USGS 08198500, period of record 1986-2022). Three of the nine USGS stations occasionally lacked daily flow estimates, which were usually days with high flow events because of damage to the USGS stations. To estimate missing daily flows during the sampling period (2015 – 2022), data from a nearby USGS station and linear regression were used. The Nueces River USGS Station 08190000 (located in the Cretaceous Losing Reach) was used to estimate missing daily flows at USGS Station 0818999010 (located in the Cretaceous Gaining Reach; $r^2 = 0.76$) and at USGS Station 08189998 (located in the Cretaceous Losing Reach; $r^2 = 0.62$). The Sabinal River USGS Station 08198000 (located in the Cretaceous Losing Reach) was used to estimate missing daily flows at Sabinal River USGS Station 08197936 (located in the Cretaceous Gaining Reach; $r^2 = 0.83$).

Standardized Precipitation Index (SPI; https://www.drought.gov/) was obtained for the five counties (i.e., Edwards, Real, Bandera, Uvalde and Medina) within the upper reaches of the Nueces River basin between 2015 and 2022. Indices were averaged among counties to generate a composite SPI and overlayed on each of the river's hydrographs. The SPI identifies several levels of conditions for wet and dry periods, ranging from abnormal condition (lightest shade) to exceptional condition (darkest shade) with white representing normal conditions. Hence, SPI provides a systematic and standardized identification of precipitation amounts to assess local trends (McKee 1993), ranging from exceptional wet to exceptional drought, and used to define Wet and Dry Hydrological periods in this study.

Field Surveys

Fish communities and habitats were quantified at 16 sites between 2015 and 2022. Across the three rivers, eight sites were located in the Cretaceous Gaining reaches, five sites were located in the Cretaceous Losing reaches, and three sites were located in the Quaternary Losing reaches (Table 1). Sites were selected based on public access points or by landowner permission. In 2015 and 2016, 14 sites of the 16 sites (excluding two sites in the Nueces River Cretaceous Losing Reach) were sampled as a preliminary investigation to document longitudinal fish community responses to a large flood event (464 m^3/s, USGS Station 08192000; > 1 per 5-year overbank event, Nueces River and Corpus Christi and Baffin Bays BBEST 2011). Sites were again sampled in 2021 and 2022 during increasing drought conditions, ultimately culminating in an exceptional drought condition. The two Nueces River Cretaceous Losing sites were added because the selection of sites in 2015-2016 haphazardly did not include representation of the Nueces River Cretaceous Losing Reach.

Among all sites and years, sampling occurred by using a common-sense seine (3 m x 1.8 m, mesh size = 3.2 mm) or a bag seine (5 m x 1.8 m, mesh size = 3.2 mm) by mesohabitat (i.e., riffle, run, pool, backwater), unless the reach was completely dry. Multiple mesohabitats were sampled in proportion to availability to ensure collections were adequately representative of the site's fish community. Fishes were identified to species and released, except for voucher specimens. Voucher specimens were euthanized with a lethal dose (150 mg/l) of Tricane-S and fixed in 10% formalin, in accordance with protocols stipulated by Texas State University Institute of Animal Care and Use Committee (Protocol 7359) and Texas Parks and Wildlife Department Scientific Permit number SPR-0601-159. After fish quantification, the following instream habitat variables were measured in each mesohabitat: water depth (m), current velocity (cm/s; Marsh-McBirney Model 2000 and Hach Model 950), percent substrate (i.e., gravel, cobble, bedrock; visually estimated), and percent vegetation coverage (visually estimated). At each site, the following water quality variables were taken with a YSI Pro DSS multiprobe: water temperature (°C), dissolved oxygen (mg/l), specific conductance (µS/cm), and pH. Instream habitat measurements were not taken in dry reaches.

Data Analysis

Principal component analysis (PCA; Canoco 4.5, Microcomputer Power 2002) was used to characterize instream habitat among surficial geology and between hydrological period, noting that dry reaches lacked instream habitat measurements and were therefore excluded from the model. Mesohabitat types were coded as dummy variables (0,1). Continuous variables (i.e., depth, current velocity, specific conductance, pH) and percentage data (i.e., substrates and vegetation) were z-transformed before analysis (Krebs, 1999). Water temperature and dissolved oxygen were not included in the PCA model since both might have substantial diel variation dependent on time of day the measurements were taken. Resulting PC scores for axes I and II, using rivers as replicates, were averaged by geology and hydrological period. Canonical Correspondence Analysis (CCA, Canoco 4.5) was used to assess relationships between fishes and the instream habitat variables, surficial geology, and hydrological periods. Surficial geology and hydrological periods were assigned dummy variables and added to the habitat matrix used for PCA. Total variation of the fish community was assessed by using the full model, including all three independent factors (i.e., instream habitat variables, surficial geology, and hydrological periods), and then partitioned by each independent factor (Borcard et al. 1992). Monte Carlo tests (5,000 permutations) were used to assess significance of full model and for each independent factor.

The following community metrics were calculated for each river, surficial geology, and hydrological period: species richness (S), Shannon-Weiner Diversity (H'), and Pileou's Evenness (J'), spring-associated fish richness, and spring-associated fish relative abundances (%). Shannon-Weiner Diversity and Pileous' Evenness could not be calculated for dry river reaches with zero fish recorded. Zeros were used for dry river reaches in the calculation of species richness, spring-associated fish richness, and spring-associated fish relative abundances (i.e., 0% in relative abundance). The six spring-associated fishes were *Cyprinella lepida*, *Dionda serena*, *Notropis amabilis*, *Astyanax mexicanus*, *Ictalurus lupus* and *Etheostoma lepidum* (Craig et al. 2016).

For each metric (i.e., dependent variable), a two-factor ANCOVA model (JMP Pro 15.1; SAS Institute, Inc.) was used to test differences ($\alpha = 0.05$) between surficial geology (Cretaceous Gaining, Cretaceous Losing, Quaternary Losing) and hydrological period (wet, dry) using river as a replicate ($N = 3$). Since richness and abundances of spring-associated fishes are correlated with flow (Craig et al. 2016), daily mean flow on the day of the field survey was added to the model as a covariate, using the representative USGS station per surficial geology (e.g., species richness for the Cretaceous Gaining reach of the Nueces River used USGS 0818999010, located in the Cretaceous Gaining reach). Frio River Cretaceous Gaining Reach lacked a USGS station. Daily flows were estimated from the Frio River Cretaceous Losing Reach, using the intercept ($b_0 = 0.373$) and slope ($b_1 = 0.394$; $F_{1,470} = 4{,}162$, $P < 0.01$, $r^2 = 0.90$) generated from the linear relationship between Nueces River Cretaceous Gaining Reach (y-variable, USGS 0818999010) and Nueces River Cretaceous Losing Reach (x-variable, USGS 08189998). For the initial two factor ANCOVA model, the interaction term between surficial geology and hydrological period was added. If significant, two one-factor ANCOVAs were used, assessing the effect of surficial geology and hydrological period separately. If not significant, the interaction term was dropped from the model. Post-hoc differences were assessed with Fisher's t-test.

Results

Flow quantifications

During the Wet Hydrological Period (June 2015 – April 2016), daily mean flows generally exceeded historical median flows in the Cretaceous Gaining, Cretaceous

Losing, and Quaternary Losing reaches in the Nueces River (Figure 2). In the Frio River, daily mean flows generally exceeded historical median flows in the Cretaceous Losing Reach but rarely exceeded historical median flows in the Quaternary Losing Reach (Figure 3). The Frio River Quaternary Losing Reach lacked surface waters at least during the field surveys. In the Sabinal River, daily mean flows generally exceeded historical median flows in the Cretaceous Gaining and Cretaceous Losing reaches but rarely exceeded historical median flows in the Quaternary Losing Reach (Figure 4). The Sabinal River Quaternary Losing Reach contained isolated pools during field surveys.

During the Dry Hydrological Period (September 2021 – August 2022), daily mean flows were generally at or below historical median flows in the Cretaceous Gaining, Cretaceous Losing, and Quaternary Losing reaches in the Nueces River. In the Nueces River Cretaceous Losing Reach, habitats were either isolated pools or in a series of run, riffle, and pools with each series connected likely by subsurface flows (Hackett 2019). In the Nueces River Quaternary Losing Reach, habitats were in isolated pools before the reach completely dried by the end of field surveys. In the Frio River, daily mean flows were generally at or below historical median flows in the Cretaceous Losing and Quaternary Losing reaches with isolated pools or a series of run, riffle, and pools in the Cretaceous Losing Reach and completely dry in the Quaternary Losing Reach. In the Sabinal River, daily mean flows were generally at or below historical median flows in the Cretaceous Gaining, Cretaceous Losing, and Quaternary Losing reaches with connected run, riffle, and pools in the Cretaceous Gaining Reach, isolated pools in the Cretaceous Losing Reach, and completely dry in the Quaternary Losing Reach.

Instream habitats

In all, 366 habitats were quantified in the upper Nueces River basin (Table 2). Among the three rivers, habitats consisted primarily of run (43 – 47% of available habitat types) and riffle (30 – 36%) habitats with moderately swift current velocities (range of means: 0.26 – 0.35 m^3/s), shallow depths (0.31 – 0.42 m), moderate amounts of aquatic vegetation (14 - 32%), and gravel (9.6 – 38%), cobble (19 – 40%), bedrock (3.3 – 49%) substrates. Among surficial geologies, Cretaceous Gaining Reach consisted of more riffle habitats (37%) and less backwater habitats (6.8) than Cretaceous Losing Reach and Quaternary Losing Reach (riffle habitats: 13 – 25%; backwater habitats: 16 – 18%), though all had majority run habitats (44 – 47%). Substrates transitioned from bedrock (23 – 28%), cobble (24 – 28%) in the Cretaceous Gaining and Losing reaches to gravel (41%), cobble (39%) in the Quaternary Losing Reach. Between hydrological periods, habitats during the Dry Period had more pools (21% versus 11%), slower mean current velocity (0.18 m/s versus 0.33 m/s), more silt substrates (20% versus 13%), and less gravel substrates (15% versus 27%) than habitats during the Wet Period.

Principal components axis I explained 21% of the variation in habitat variables and described primarily a current velocity and depth gradient with riffle mesohabitats (0.51) and current velocity (0.49) having the strongest positive loadings and silt (-0.37), depth (-0.27), and vegetation (-0.26) having the strongest negative loadings along PC 1 (Figure 5). Principal components axis II explained 13% of the variation in habitat variables and described a substrate gradient with cobble (0.40), gravel (0.34), and vegetation (0.32) having the strongest positive loadings and bedrock (-0.65) having the strongest negative loadings along PC II. Principal component scores were clustered by surficial geology and hydrological period. General patterns among wetted habitats available (i.e., habitats in dry reaches were not quantified) consisted of a greater number of riffle habitats and swifter current velocities during the Wet Hydrological Period. During the Dry Hydrological Period deeper water, slower current velocities, and greater silt and cobble substrates were present in the remaining habitats available in the Quaternary Losing Reach.

Fish communities

Field surveys yielded 21,297 individuals, representing 26 species. Greater numbers of individuals were taken from Nueces River (N = 10,533) among the five collection events (Table 3). Likewise, greater species richness was observed in the Nueces River (S = 24) and the fish community was dominated by spring-associated fishes (74%). However, all three rivers were similar in diversity and evenness metrics. By river, most abundant fishes were *Dionda serena* (55%), *Notropis amabilis* (10%), and *Gambusia affinis* in the Nueces River, *Cyprinella venusta* (39%), *Notropis amabilis* (33%) and *Dionda serena* (7.6%) in the Frio River, and *Gambusia affinis* (40%), *Micropterus salmoides* (33%), and *Cyprinella venusta* (6.4%) in the Sabinal River.

Among the three surficial geologies, greater numbers of individuals (N = 12,299) and greater relative abundances of spring-associated fishes (69%) were taken from the Cretaceous Gaining Reach than in the Cretaceous Losing Reach (N = 4,516; 34% in spring-associated fishes) and Quaternary Losing Reach (4,482; 6.2%). However, Cretaceous Losing Reach had greater species richness (S = 26), greater diversity (2.4) and evenness (0.74) than the other two surficial geologies. By surficial geology, most abundant fishes were *Dionda serena* (44%), *Notropis amabilis* (19%), and *Cyprinella venusta* (10%) in the Cretaceous Gaining Reach, *Cyprinella venusta* (25%), *Dionda serena* (17%), and *Gambusia affinis* (14%) in the Cretaceous Losing Reach, and *Gambusia affinis* (40%), *Micropterus salmoides* (40%), and *Campostoma anomalum* (4%) in the Quaternary Losing Reach.

Between Wet and Dry Hydrological periods, the total number of individuals taken, richness, diversity, evenness, and relative abundance of spring-associated fishes were similar. The most abundant fishes were *Dionda serena* (24%), *Micropterus salmoides* (20%), and *Notropis amabilis* (16%) during the Wet Hydrological Period and *Dionda serena* (33%), *Gambusia affinis* (20%), *Cyprinella venusta* (12%), and *Notropis amabilis* (12%) during the Dry Hydrological Period.

Fish-environmental relationships

Canonical correspondence axes I and II explained 20% (F-ratio: 5.01; $P < 0.01$) of the fish community variation using instream habitat variables, surficial geology, and hydrological period (Figure 6). Among the 20% of variability explained, instream habitat variables accounted for 74%, surficial geology accounted for 15%, and hydrological period accounted for 6.7% of the variation explained. The strongest positive loadings on axis I were bedrock (0.67), current velocity (0.65), riffle (0.43), and Cretaceous Gaining Reach (0.36), whereas strongest negative loadings on axis I were vegetation (-0.56), depth (-0.46), silt (-0.44), and Quaternary Losing Reach (-0.32). The strongest positive loadings on axis II were bedrock (0.53), silt (0.39), and Quaternary Losing Reach (0.38), whereas the strongest negative loadings on axis II were gravel (-0.52), cobble (-0.45), riffle (-0.44) and current velocity (-0.36). Species strongly and positively associated with axis I were *Notropis stramineus*, *Ictalurus lupus*, *Cyprinella venusta*, and *Cyprinella lepida*, whereas species strongly and negatively associated with axis I were *Notropis texanus*, *Lepisosteus oculatus*, and *Lepomis gulosus*. Species strongly and positively associated with axis II were *Lepomis cyanellus*, *Lepomis macrochirus*, and *Notropis stramineus*, whereas species strongly and negatively associated with axis II were *Etheostoma lepidum*, *Pylodictus olivaceous*, *Ameiurus natalis*.

Among univariate relationships, interactive effects between surficial geology and hydrological periods were detected (ANCOVA; $P < 0.01$) for species richness. Richness differed among surficial geology during the Wet Hydrological Period (ANCOVA, $F_{3,20} = 12.9$, $P < 0.01$) with greater richness in Cretaceous Gaining reaches than in Cretaceous Losing reaches and Quaternary Losing reaches (Figure 7a). Richness differed among surficial geology during the Dry Hydrological Period ($F_{3,14} = 25.7$, $P < 0.01$) with greater richness in Cretaceous Gaining and Cretaceous Losing reaches than in Quaternary Losing reaches (Figure 7b). Diversity, with zero fish collections removed from calculations, differed (ANCOVA, $F_{4,30} = 3.62$, $P = 0.02$) only for surficial geology with greater diversity in Cretaceous Gaining and Cretaceous Losing reaches than in Quaternary Losing reaches (Figure 7c). Likewise, evenness differed (ANCOVA, $F_{4,30} = 3.91$, $P = 0.01$) only for surficial geology with greater evenness in Cretaceous Gaining and Cretaceous Losing reaches than in Quaternary Losing reaches (Figure 7d).

Spring-associated fish richness differed only for surficial geology (ANCOVA, $F_{4,37} = 11.7$, $P < 0.01$) with the greatest richness in Cretaceous Gaining reaches, followed by Cretaceous Losing reaches, and least in Quaternary Losing reaches (Figure 7e). Spring-associated fish relative abundances (ANCOVA, $F_{4,37} = 4.1$, $P < 0.01$) differed only for surficial geology with greater relative abundances in Cretaceous Gaining and Cretaceous Losing reaches than in Quaternary Losing reaches (Figure 7f).

Discussion

The initial prediction that species richness, diversity, and evenness would increase from upstream to downstream was not supported, attributed specifically to the absence of surface water in the Quaternary Losing reaches in the Frio River and loss of stream connectivity to upstream reaches in the Sabinal River during the Wet Hydrological Period. Correspondingly, Cretaceous Losing reaches contained isolated surface waters during the Dry Hydrological Period. Collectively, fish communities were similar among all three surficial geologies between wet and dry hydrological periods. The initial prediction that species richness, diversity, evenness, spring-associated fish richness and relative abundances would be similar between wet and dry hydrological periods in the Cretaceous Gaining reaches was supported, providing additional support for Edwards Plateau karstic spring systems acting as evolutionary refugia (Craig et al. 2016).

Geological influences on aquatic biota have been documented for macroinvertebrates (Neff and Jackson 2011), mussels (Strayer 1983), and fishes (Neff and Jackson 2013, Hitt et al. 2022). Geology, amongst other factors, dictates the hydrology, slope, and water quality variables, which, in turn, proximately affects the kinds and numbers of aquatic organisms, based on their life-history traits, associated with particular geologies along longitudinal and geological gradients (Strayer 1983, Neff and Jackson 2011, Neff and Jackson 2013). Specific to karst terrains, voluminous discharges maintain stenoecious water quality of the surface waters (Groeger et al. 1997) with stenothermal conditions likely a major influence on the kinds and numbers of organisms associated with karst terrain (Kollaus et al. 2015, Craig et al. 2019, Ishiyama et al. 2023, Hitt et al. 2023), which tentatively explains the large number of spring-associated fishes persisting in the Cretaceous Gaining reaches of this study.

Failure to detect strong influences of hydrology on the Nueces River basin fish communities was surprising. Other than detecting a hydrological effect on species richness (i.e., a greater number of species observed during Dry Hydrological Period in Cretaceous Losing reaches, likely attributed to not sampling the Nueces River Cretaceous Losing Reach during the Wet Hydrological Period), species diversity, evenness, and abundances of spring-associated fishes among the three geologies were similar between Wet and Dry Hydrological periods. In other studies, fish community differences between seasonal wet and dry periods are attributed to simple mechanistic processes, such as decreases in salinity following high amounts of precipitation and runoff allowing saltwater intolerant species to expand upstream (e.g., in prairie streams where headwater flows are supported by saline groundwater; Ruppel et al. 2020) and downstream into coastal areas (Wang and Raney 1971). Additionally, fish community differences between wet and dry periods are attributed to multiple factors, such as shifts in food web structure between wet and dry periods, providing greater availability of nutritional resources generated during wet periods (Stoner 1986, Castillo-Rivera et al. 2002) and connected habitats, allowing for dispersion to access greater nutritional resources or to select more tolerable abiotic conditions (Gehrke et al. 1995, Barrett and Armstrong 2022).

The lack of hydrological influences, at least in the Cretaceous Gaining reaches, is consistent with, and provides additional support for, the Edwards Plateau serving as an evolutionary refugia for aquatic organisms (Craig et al. 2016). The karst springs in the Edwards Plateau, provided persistent aquatic environments during exceptional drought periods (this study), extreme dry climates during the Holocene (e.g., Altithermal Period; Al-Rabab'Ah and Williams 2004) and over longer geological timescales (e.g., Pleistocene, Toomey et al. 1993) enabling persistence and radiations among many lineages of plants and animals (Russ et al. 2000, Jass et al. 2014, Worsham et al. 2023). Additionally, losing reaches in Cretaceous geology also provided persistent habitats (e.g., isolated pools) for spring-associated fishes during the study period. This study ended just prior to basin-wide rains that produced stream flows in all study reaches of the three, rivers and it is unknown how long the aquatic habitats and spring-associated fishes would have endured without precipitation. Regardless and despite large areas of the reaches being dried out, Cretaceous Losing reaches provided a period of refugia during dry hydrological periods (i.e., conservation value), which subsequently were perhaps source populations once flows returned. Although gaining and losing reaches were somewhat largely resistant to wet and dry cycles, Edwards Plateau springs are suspectable to drying by over pumping of the groundwater for municipal and agriculture purposes (Winemiller and Anderson 1997).

As the regional climate continues to shift towards more arid conditions (Schmidt 1979, Fredrickson et al. 1998, MacDonald 2010), discharge rates and permanency of

Edwards Plateau groundwater are expected to decrease (Pekel et al. 2016). More headwater reaches, which are located in the more arid west, may become disconnected from the lower reaches, which are located in the more humid east. Numerous studies suggest that aquatic refugia, even in their most isolated forms, serve as critical ecological and evolutionary habitats during dry times while supporting a diversity of aquatic species (Magoulick and Kobza 2003, Rull 2009, Keppel et al. 2012, Davis et al. 2013, Pârvaulescu et al. 2013, Murphy et al. 2015, Cartwright et al. 2020). Some level of continuing biomonitoring into the future could be informative for documenting and understanding how aquatic communities actually cope (e.g., restricted to aquatic refugia, move downstream, become extirpated) with drier periods and climates. These studies could help predict effects on aquatic communities as the aridity gradient continues to shift eastward in North America and with increasing groundwater use by municipalities, agriculture, and industry.

Table 1. Sample sites in the Nueces, Frio and Sabinal rivers with corresponding latitudes and longitudes.

Site #	River	Latitude	Longitude
1	Nueces	30.023568	-100.067423
2		29.81025	-100.017415
3		29.667168	-100.028956
4		29.526472	-100.018309
5		29.398221	-100.000744
6		29.206349	-99.903397
7	Frio	29.888226	-99.76679
8		29.800213	-99.691676
9		29.694124	-99.754144
10		29.495313	-99.711625
11		29.446838	-99.664772
12		29.243731	-99.675331
13	Sabinal	29.802779	-99.574889
14		29.744198	-99.553904
15		29.627424	-99.534452
16		29.341323	-99.480097

Table 2. Relative abundance (%) of mesohabitats, means and standard deviations of depth (m), current velocity (cms), specific conductivity (µS/cm), temperature (°C), dissolved oxygen (mg/l), pH, vegetation (%) and substrate (%); grouped by River (Nueces, Frio, Sabinal), Surficial Geology (Cretaceous Gaining, Cretaceous Losing, Quaternary Losing) and Hydrology (Wet, Dry).

	River			Surficial Geology			Hydrological Period	
	Nueces	Frio	Sabinal	Cretaceous Gaining	Cretaceous Losing	Quaternary Losing	Wet	Dry
N of habitats	137	112	117	251	77	38	265	101
Habitat types (%)								
Riffle	30	36	30	37	25	13	34	26
Run	45	47	43	44	47	45	46	43
Pool	13	13	14	12	10	26	11	21
Backwater	12	3.6	14	6.8	18	16	9.8	11
Means (± 1 SD)								
Depth (m)	0.42 (0.28)	0.4 (0.28)	0.31 (0.28)	0.35 (0.27)	0.42 (0.32)	0.50 (0.28)	0.38 (0.27)	0.38 (0.31)
Current velocity (cms)	0.26 (0.24)	0.35 (0.3)	0.26 (0.29)	0.31 (0.27)	0.26 (0.3)	0.21 (0.29)	0.33 (0.29)	0.18 (0.19)
SPC (µS/cm)	415 (23)	399 (50)	453 (101)	413 (47)	466 (74)	392 (119)	424 (69)	418 (67)
Temperature (°C)	24 (2.5)	22 (3.6)	23 (4.2)	22 (3.53)	23 (3.4)	24 (3.6)	22 (3.6)	24 (3.1)
DO (mg/l)	6.2 (3)	5.8 (2.7)	11 (12)	8.3 (8.8)	6.3 (2.6)	4.8 (2.9)	7.4 (8.8)	7.9 (1.6)
pH	8 (.29)	8.3 (0.16)	8.2 (0.25)	8.2 (0.28)	8.2 (0.23)	8 (0.21)	8.1 (0.21)	8.4 (0.21)
Vegetation (%)	32 (33)	15 (27)	14 (25)	20 (29)	20 (29)	32 (31)	20 (29)	24 (32)
Substrate (%)								
Silt	13 (25)	17 (32)	15 (28)	14 (28)	18 (32)	11 (24)	13 (27)	20 (30)
Sand	0.71 (3.5)	0.94 (3.9)	0.43 (2.1)	0.82 (3.7)	0.26 (1.6)	0.7 (2.6)	0.91 (3.8)	0.1 (1)
Gravel	38 (30)	21 (25)	9.6 (17)	22 (28)	21 (24)	41 (25)	27 (29)	15 (23)
Cobble	40 (28)	23 (26)	19 (26)	28 (28)	24 (29)	39 (24)	27 (27)	32 (30)
Boulder	4.7 (11)	14 (25)	7.4 (18)	7.5 (16)	14 (28)	3.1 (6.9)	9.2 (21)	6.7 (12)
Bedrock	3.3 (14)	23 (36)	49 (42)	28 (40)	23 (34)	2.2 (9.1)	23 (37)	26 (38)

Table 3. Relative abundance (%) of fishes collected in the upper Nueces River basin grouped by River (Nueces, Frio, Sabinal), Surficial Geology (Cretaceous Gaining, Cretaceous Losing, Quaternary Losing) and Hydrological Period (Wet, Dry). Asterisk denotes spring-associated species identified by Craig et al. 2016.

	River			Surficial Geology			Hydrological Period	
Scientific Name	Nueces	Frio	Sabinal	Cretaceous Gaining	Cretaceous Losing	Quaternary Losing	Wet	Dry
Lepisosteus oculatus	0.04	-	-	0.01	0.07	-	0.01	0.03
Campostoma anomalum	2.3	1.5	0.32	0.56	2	4	2.3	1.0
*Cyprinella lepida**	1.1	1.4	0.85	1.6	0.8	<0.01	0.51	1.6
Cyprinella venusta	0.33	39	6.4	10.2	25	0.16	11	12
*Dionda serena**	55	7.6	-	44	17	-	24	33
*Notropis amabilis**	10	33	1.4	19	7.7	3.5	16	12
Notropis stramineus	0.04	1.5	2.7	1.4	1.2	-	0.52	1.5
Notropis texanus	2.6	-	-	-	6.2	-	-	2.4
*Astyanax mexicanus**	2.7	1.3	1.7	1.5	5.4	0.31	2.8	1.5
Ameiurus natalis	0.31	0.04	-	0.19	0.27	-	0.07	0.24
*Ictalurus lupus**	-	0.21	-	0.07	0.04	-	0.03	0.07
Ictalurus punctatus	0.54	0.15	0.22	0.42	0.31	0.25	0.17	0.52
Pylodictis olivaris	0.03	0.04	-	0.03	0.02	-	0.03	0.02
Gambusia affinis	10	2.8	40	8.3	14	40	12	20
Lepomis auritus	1.1	5.1	2.3	2.7	3.4	0.4	2.7	2.1
Lepomis cyanellus	-	0.04	1.7	0.03	0.13	2	0.25	0.63
Lepomis gulosus	0.03	-	0.09	0.02	0.13	-	0.03	0.04
Lepomis macrochirus	0.55	1.2	4	0.75	2.2	3.3	1.8	1.5
Lepomis megalotis	3.8	2.1	3	3.3	3.4	2.4	2.6	3.6
Lepomis microlophus	0.11	0.33	0.13	0.2	0.18	0.07	0.24	0.11
Lepomis miniatus	0.24	0.02	0.11	0.04	0.6	-	0.05	0.23
Micropterus salmoides	1.3	2.3	33	1.4	2.6	40	20	1.7
Micropterus treculii	0.56	0.04	0.31	0.5	0.35	-	0.05	0.62
*Etheostoma lepidum**	4.3	0.15	0.85	2.3	2.8	2.4	3	1.9
Oreochromis aureus	0.64	-	-	0.05	1.3	0.02	0.07	0.51
Herichthys cyanoguttatus	1.5	0.33	0.20	0.66	2	0.31	0.16	1.5
Total N	10,533	5,218	5,546	12,299	4,516	4,482	9,475	11,822
Richness (S)	24	22	19	25	26	16	25	26
Diversity (H')	1.7	1.7	1.7	1.9	2.4	1.4	2.1	2.2
Evenness (J')	0.55	0.56	0.57	0.58	0.74	0.52	0.66	0.66
Spring-associated fishes richness*	5	6	4	6	6	4	6	6
% Spring-associated fishes*	74	44	4.8	69	34	6.2	46	50

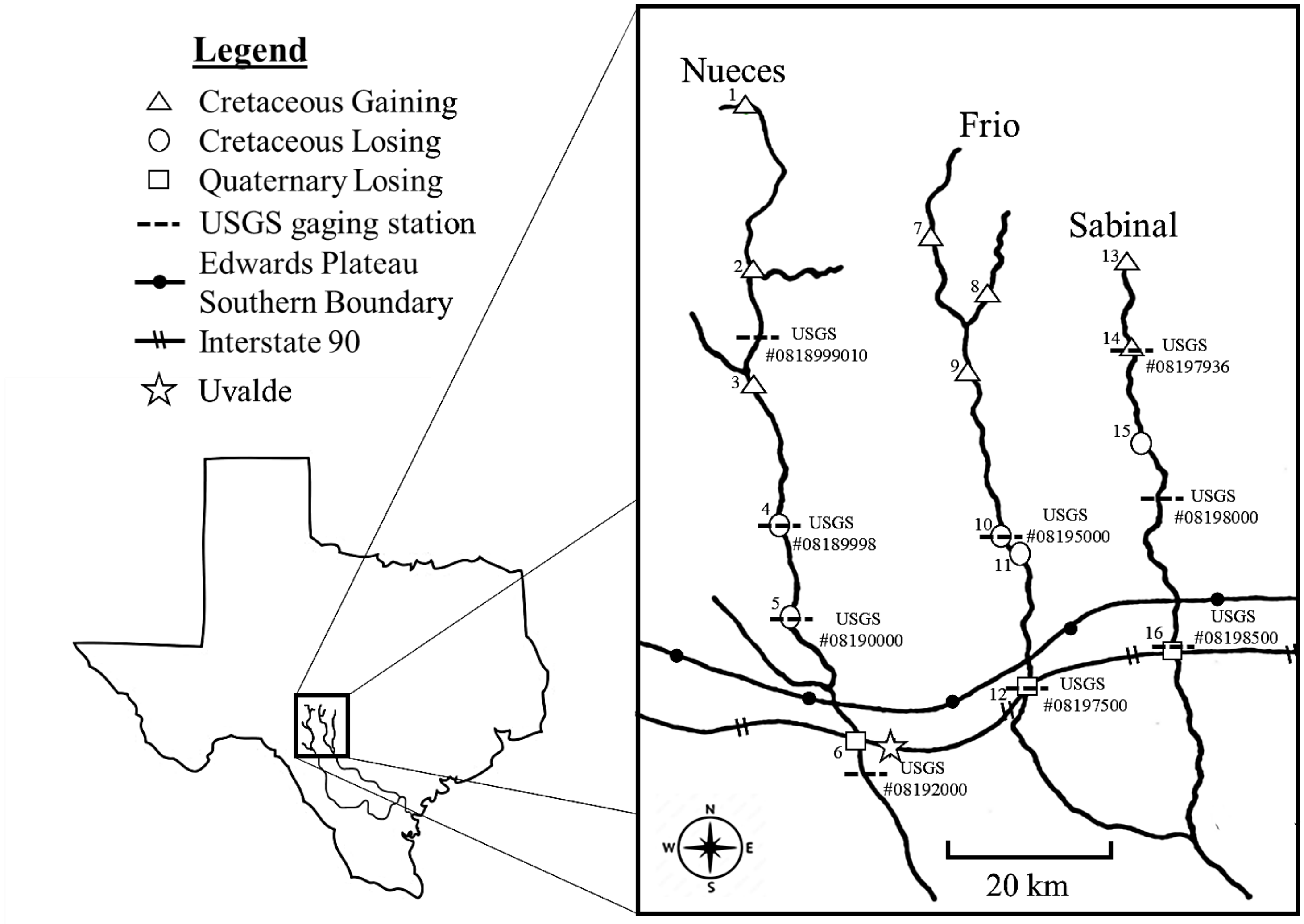

Figure 1. The sixteen sites sampled in the upper Nueces River basin (Nueces, Frio and Sabinal rivers) and USGS gaging stations from which streamflow data was taken between June 2015 and August 2022

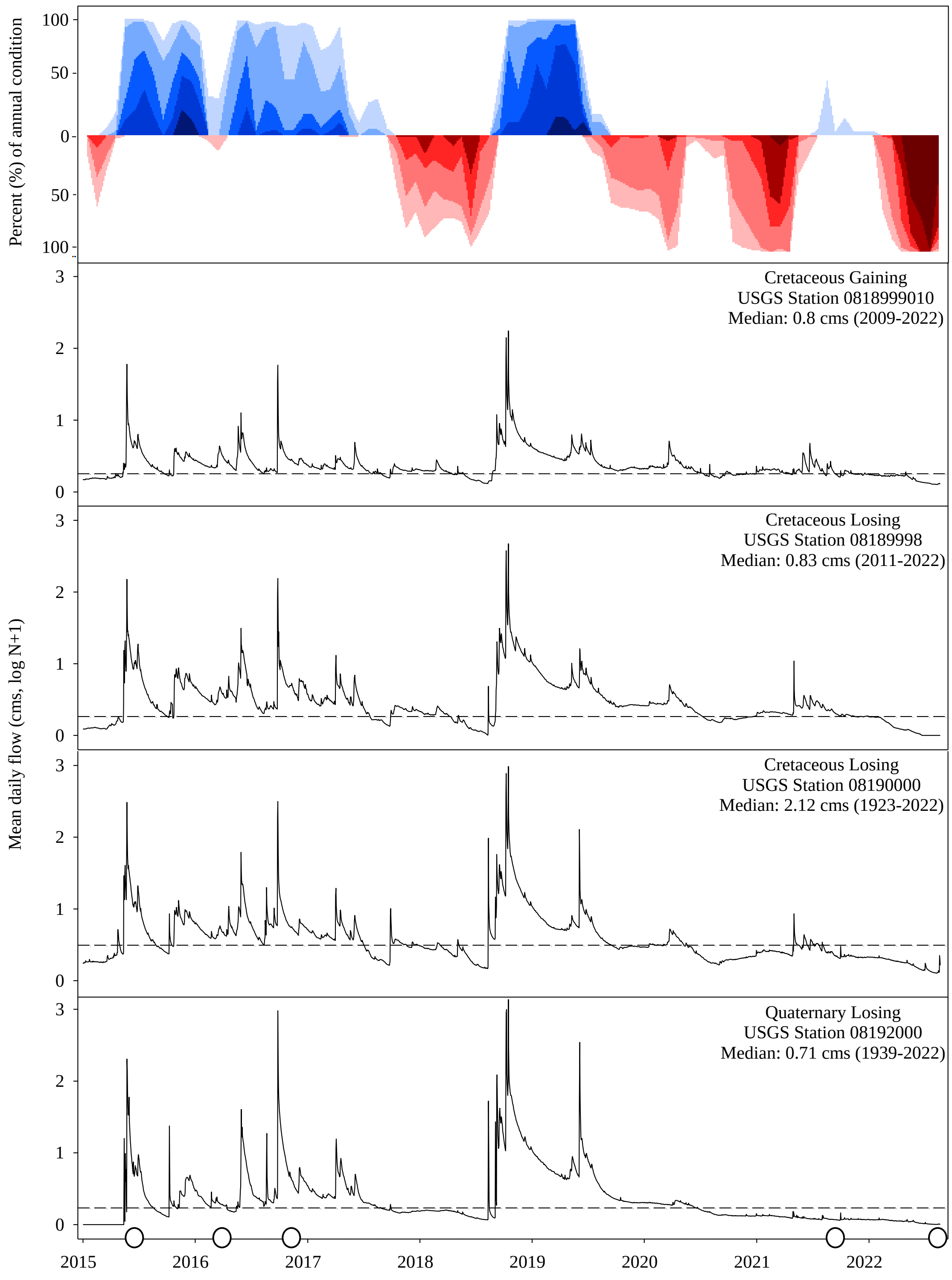

Figure 2. Standardized Precipitation Index (%) of annual conditions for corresponding counties to the survey area and hydrographs of mean daily flow (cms, log N+1) for the five sampling events on the Nueces River between 2015 and 2022 represented by circles on the x axis, with historical median flow plotted along the dotted line.

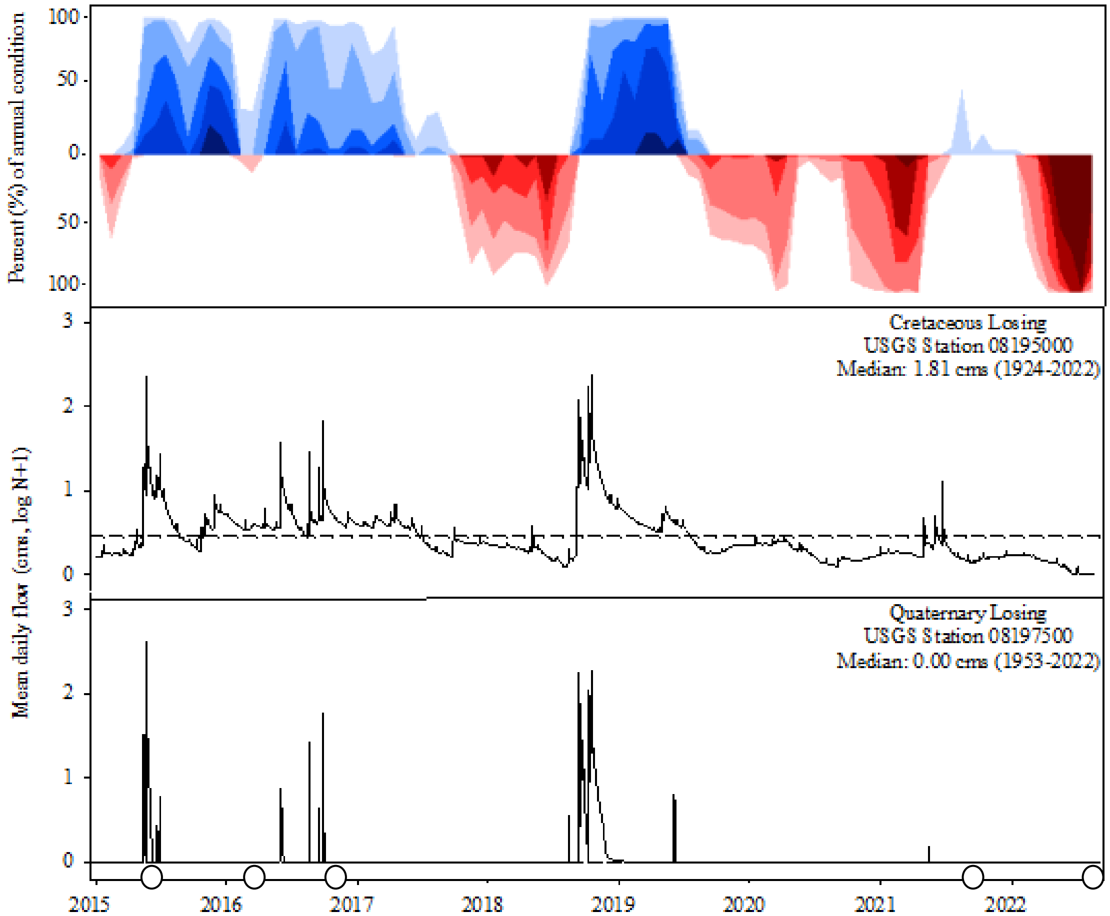

Figure 3. Standardized Precipitation Index (%) of annual conditions for corresponding counties to the survey area and hydrographs of mean daily flow (cms, log N+1) for the five sampling events on the Frio River between 2015 and 2022 represented by circles on the x axis, with historical median flow plotted along the dotted line.

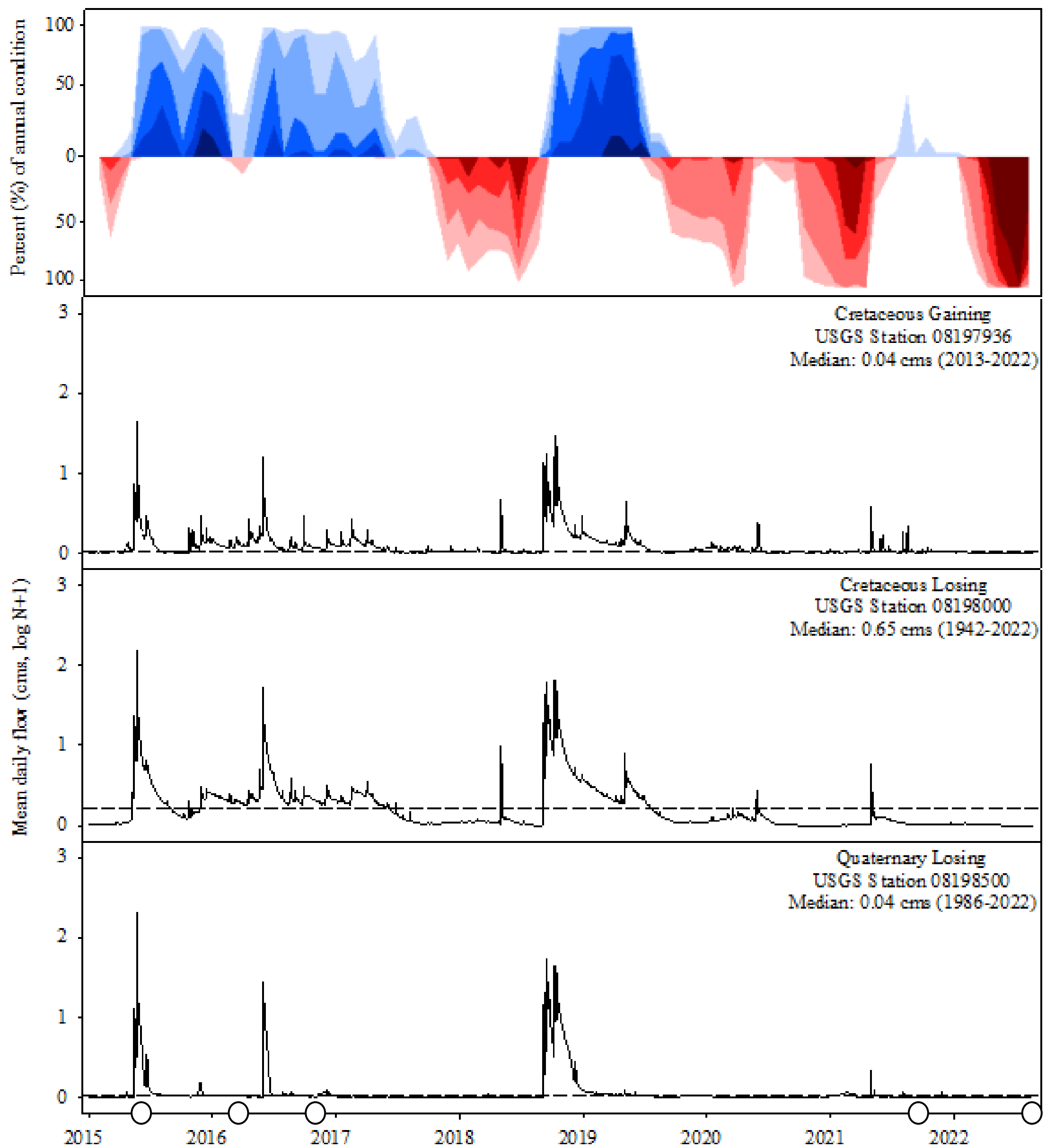

Figure 4. Standardized Precipitation Index (%) of annual conditions for corresponding counties to the survey area and hydrographs of mean daily flow (cms, log N+1) for the five sampling events on the Sabinal River between 2015 and 2022 represented by circles on the x axis, with historical median flow plotted along the dotted line.

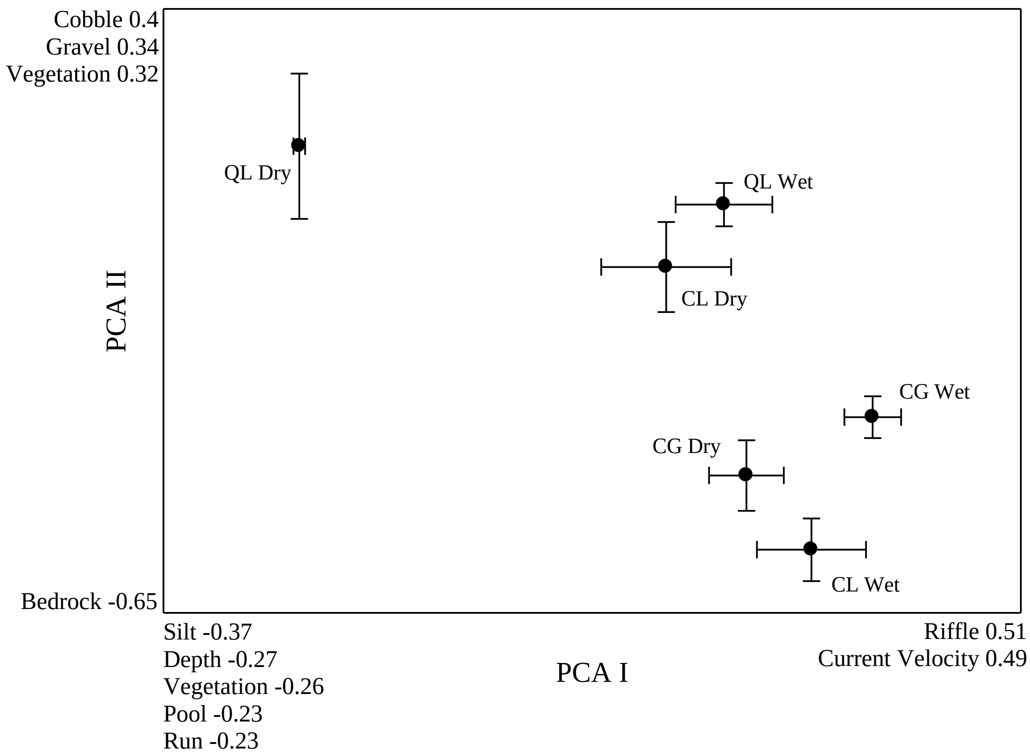

Figure 5. Mean ± SE of habitat variables quantified by surface geology (CG: Cretaceous Gaining, CL: Cretaceous Losing, QL: Quaternary Losing) and Wet and Dry hydrology within the upper Nueces River basin along PC axis I (21% variation explained) and PC axis II (13%).

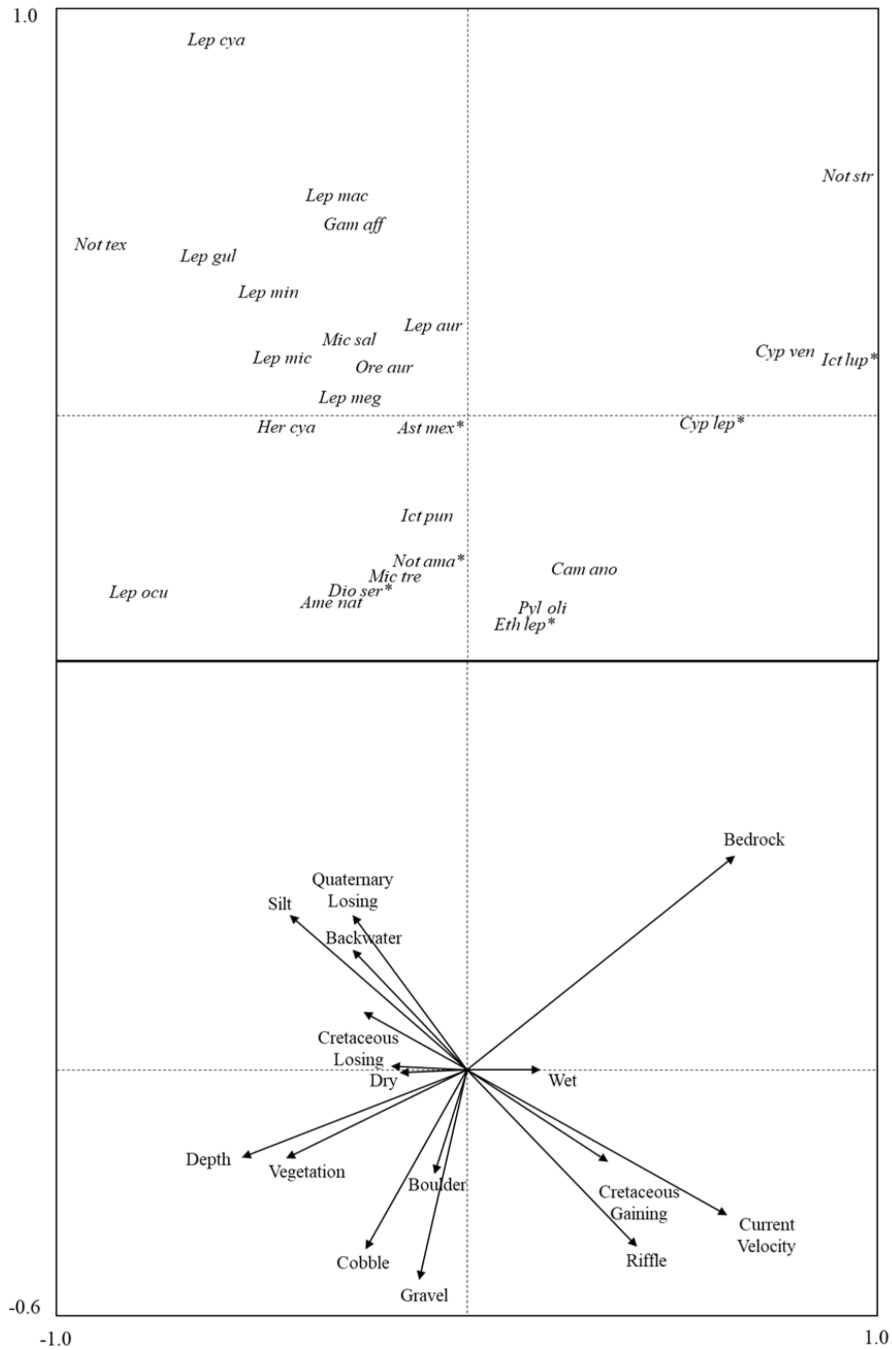

Figure 6. Plot of canonical correspondence axes I and II for habitat parameters (including Surficial Geology and Hydrological Period) and species (spring-associated fishes denoted with asterisk) from the upper Nueces River basin from June 2015 through August 2022.

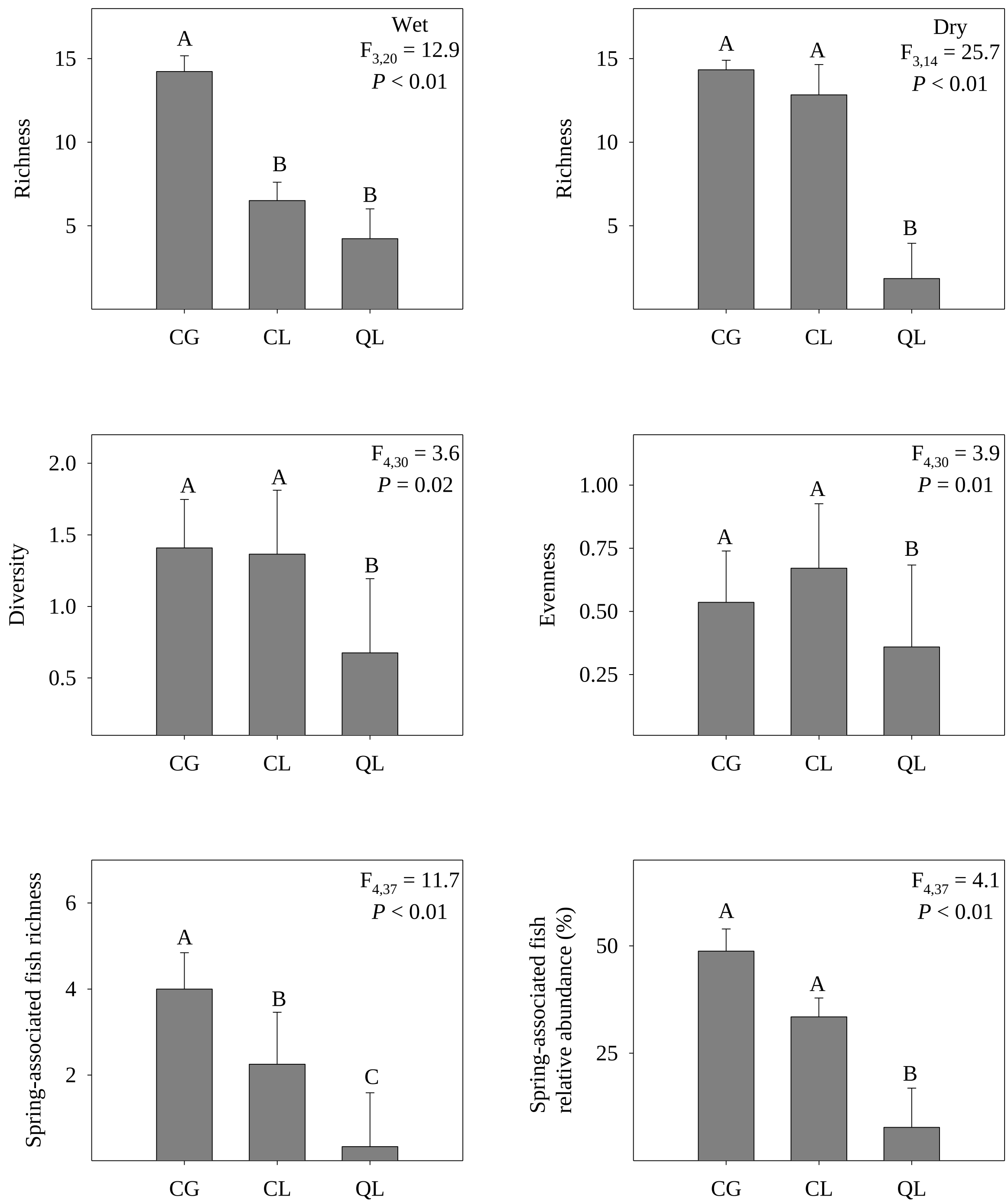

Figure 7. Bar plots (Mean ± SE) for richness (wet and dry hydrological periods), Shannon-Weiner Diversity, Pileou's Evenness, Spring-associated fishes richness and relative abundance (across hydrological periods among the three surface geologies: Cretaceous Gaining (GC), Cretaceous Losing (CL), and Quaternary Losing (QL). Different letters per panel represent differences among surface geologies.

LITERATURE CITED

Al-Rabab'ah, M. A., and C. G. Williams. 2004. An ancient bottleneck in the lost pines of Central Texas. Molecular Ecology 13:1075–1084.

Banta, J. R., R. B. Lambert, R. N. Slattery, and D. J. Ockerman. 2012. Streamflow gain and loss and water quality in the upper Nueces River Basin, south-central Texas, 2008–10: U.S. Geological Survey Scientific Investigations Report 2012–5181, 40 p.

Barrett, H. S., and J. B. Armstrong. 2022. Move, migrate, or tolerate: Quantifying three tactics for cold-water fish coping with warm summers in a large river. Ecosphere 13:e4095.

Behen, K. P. K. 2013. Influence of connectivity and habitat heterogeneity on fishes in the upper San Marcos River, Texas (Unpublished thesis). Texas State University, San Marcos, Texas.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045e1055.

Bowles, D. E., and T. L. Arsuffi. 1993. Karst aquatic ecosystems of the Edwards Plateau region of Central Texas, USA: A consideration of their importance, threats to their existence, and efforts for their conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 3:317–329.

Cartwright, J. M., K. A. Dwire, Z. Freed, S. J. Hammer, B. McLaughlin, L. W. Misztal, E. R. Schenk, J. R. Spence, A. E. Springer, and L. E. Stevens. 2020. Oases of the future? Springs as potential hydrologic refugia in drying climates. Frontiers in Ecology and the Environment 18:245–253.

Castillo-Rivera, M., J. A. Zavala-Hurtado and R. Zárate. 2002. Exploration of spatial and temporal patterns of fish diversity and composition in a tropical estuarine system of Mexico. Reviews in Fish Biology and Fisheries 12:167-177.

Craig, C. A., K. A. Kollaus, K. P. Behen, and T. H. Bonner. 2016. Relationships among spring flow, habitats, and fishes within evolutionary refugia of the Edwards Plateau. Ecosphere 7:e01205.

Craig, C. A., J. D. Maikoetter, and T. H. Bonner. 2019. Temperature-mediated feeding between spring-associated and riverine-associated congeners, with implications for community segregation. PeerJ 6:e6144.

Davis, J., A. Pavlova, R. Thompson, and P. Sunnucks. 2013. Evolutionary refugia and ecological refuges: Key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Global Change Biology 19:1970–1984.

Davis, J. A., A. Kerezsy, and S. Nicol. 2017. Springs: Conserving perennial water is critical in arid landscapes. Biological Conservation 211:30–35.

Felstead, N. J., M. J. Leng, S. E. Metcalfe, and S. Gonzalez. 2015. Understanding the hydrogeology and surface flow in the Cuatro Ciénegas Basin (NE Mexico) using stable isotopes. Journal of Arid Environments 121:15–23.

Fredrickson, E., K. M. Havstad, R. Estell, and P. Hyder. 1998. Perspectives on desertification: south-western United States. Journal of Arid Environments 39:191-207.

Gehrke, P. C., P. Brown, C. B. Schiller, D. B. Moffatt, and A. M. Bruce. 1995. River regulation and fish communities in the Murray-Darling river system, Australia. Regulated Rivers: Research & Management 11:363-375.

Grimm, N. B., F. S. Chapin, B. Bierwagen, P. Gonzalez, P. M. Groffman, Y. Luo, F. Melton, K. Nadelhoffer, A. Pairis, P. A. Raymond, J. Schimel, and C. E. Williamson. 2013. The impacts of climate change on ecosystem structure and function. Frontiers in Ecology and the Environment 11:474–482.

Groeger, A., P. Brown, T. Titjen, and T. Kelsey. 1997. Water quality of the San Marcos River. Texas Journal of Science 49:4.

Hackett, C. C. 2019. Storage dynamics of the upper Nueces River alluvial aquifer: Implications for recharge to the Edwards Aquifer, Texas (Unpublished thesis). University of Texas, Austin, Texas

Harrison, S., and R. Noss. 2017. Endemism hotspots are linked to stable climatic refugia. Annals of Botany 119:207–214.

Hendrickson, D.A., and A.E. Cohen. 2015. Fishes of Texas project database (version 2.0). Texas Advanced Computing Center, University of Texas at Austin, Austin, TX. Available online at http://www.fishesoftexas.org/home/.

Hitt, N. P., A. P. Landsman and R. L. Raesly. 2022. Life history strategies of stream fishes linked to predictors of hydrologic stability. Ecology and Evolution 12: e8861.

Hitt, N. P., K. M. Rogers, K. G. Kessler, M. A. Briggs, and J. H. Fair. 2023. Stabilising effects of karstic groundwater on stream fish communities. Ecology of Freshwater Fish 2023;00:1-14.

Hubbs, C. 2001. Environmental correlates to the abundance of spring-adapted versus stream-adapted fishes. The Texas journal of science 53: 299-327.

Ishiyama, N., M. Sueyoshi, J. García Molinos, K. Iwasaki, J. N. Negishi, I. Koizumi, S. Nagayama, A. Nagasaka, Y. Nagasaka, and F. Nakamura. 2023. Underlying geology and climate interactively shape climate change refugia in mountain streams. Ecological Monographs 2023:e1566.

Jass, C. N., M. F. Poteet, and C. J. Bell. 2014. Response of pocket gophers (geomys) to late quaternary environmental change on the Edwards Plateau of Central Texas. Historical Biology 27:192–213.

Keppel, G., K. P. Van Niel, G. W. Wardell-Johnson, C. J. Yates, M. Byrne, L. Mucina, A. G. Schut, S. D. Hopper, and S. E. Franklin. 2012. Refugia: Identifying and understanding safe havens for biodiversity under climate change. Global Ecology and Biogeography 21:393–404.

Kollaus, K. A., and T. H. Bonner. 2012. Habitat associations of a semi-arid fish community in a karst spring-fed stream. Journal of Arid Environments 76:72–79.

Krebs, C.,J., 1999. Ecological Methodology. Addison Wesley Longman, New York, pp.1e496.

MacDonald, G. M. 2010. Water, climate change, and sustainability in the Southwest. Proceedings of the National Academy of Sciences 107:21256–21262.

Magoulick, D.D., and R. M. Kobza. 2003. The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology 48:1186-1198.

Mather, J. D., and E. P. F. Rose. 2012. Military aspects of hydrogeology: an introduction and overview. Geological Society Publications 362:1-18.

McKee, T. B., N. J. Doesken, and J. Kleist. 1993. The Relationship of Drought Frequency and Duration to Time Scales. Paper Presented at 8th Conference on Applied Climatology. American Meteorological Society, Anaheim, CA.

Meinzer, O.E. 1934. The history and development of ground-water hydrology. Journal of the Washington Academy of Sciences 24:6-32.

Murphy, N. P., M. T. Guzik, S. J. Cooper, and A. D. Austin. 2015. Desert spring refugia: museums of diversity or evolutionary cradles?. Zoologica Scripta 44:693-701.

Neff, M. R. and D. A. Jackson. 2011. Effects of broad-scale geological changes on patterns in macroinvertebrate assemblages. Journal of the North American Benthological Society 30: 459-473.

Neff, M. R. and D. A. Jackson. 2013. Regional-scale patterns in community concordance: testing the roles of historical biogeography versus contemporary abiotic controls in determining stream community composition. Canadian Journal of Fisheries and Aquatic Sciences 70:1141-1150

Nueces River and Corpus Christi and Baffin Bays Basin and Bay Expert Science Team. 2011. Environmental Flows Recommendations Report. Final Submission to the Environmental Flows Advisory Group, Nueces River and Corpus Christi and Baffin Bays Basin and Bay Area Stakeholders Committee, and Texas Commission on Environmental Quality.

Pârvulescu, L., C. Zaharia, A. Satmari, and L. Drăguţ. 2013. Is the distribution pattern of the stone crayfish in the Carpathians related to karstic refugia from Pleistocene glaciations?. Freshwater Science 32:1410-1419.

Pekel, J. F., A. Cottam, N. Gorelick, and A. S. Belward. 2016. High-resolution mapping of global surface water and its long-term changes. Nature 540:418-422.

Rull, V. 2009. Microrefugia. Journal of Biogeography 36:481–484.

Ruppel, D. S., V. A. Sotola, C. A. Craig, N. H. Martin, and T. H. Bonner. 2020. Assessing functions of movement in a great plains endemic fish. Environmental Biology of Fishes 103:795–814.

Russ, J., D. H. Loyd, and T. W. Boutton. 2000. A paleoclimate reconstruction for southwestern Texas using oxalate residue from lichen as a paleoclimate proxy. Quaternary International 67:29–36.

Scanes, C. M. 2016. Fish community and habitat assessments within an urbanized spring complex of the Edwards Plateau (Unpublished thesis). Texas State University, San Marcos, Texas.

Schmidt Jr, R. H. 1979. A climatic delineation of the 'real' Chihuahuan Desert. Journal of Arid Environments 2:243-250.

Sophocleous, M. 2002. Interactions between groundwater and surface water: The state of the science. Hydrogeology Journal 10:348–348.

Stevens, L. E., E. R. Schenk, and A. E. Springer. 2020. Springs Ecosystem Classification. Ecological Applications 31:e02218.

Stoner, A. W. 1986. Community structure of the demersal fish species of Laguna Joyuda, Puerto Rico. Estuaries 9:142-152.

Strayer, D. 1983. The effects of surface geology and stream size on freshwater mussel (Bivalvia, Unionidae) distribution in southeastern Michigan, U.S.A. Freshwater Biology 13:253-264.

Texas Water Development Board. 1990. Water for Texas, today and tomorrow: Texas Water Development Board Document No. GP-5-1,186 p.

Toomey, R. S., M. D. Blum, and S. Valastro. 1993. Late quaternary climates and environments of the Edwards Plateau, Texas. Global and Planetary Change 7:299–320.

U.S. Fish and Wildlife Service. 2005. Devils River Minnow (Dionda diaboli) Recovery Plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.

Wang, J. C. and E. C. Raney. 1971. Distribution and fluctuations in the fish fauna of the Charlotte Harbor estuary, Florida (Unpublished report). Mote Marine Laboratory, Sarasota, Florida.

Winemiller, K. O., and A. A. Anderson. 1997. Response of endangered desert fish populations to a constructed refuge. Restoration Ecology 5:204–213.

Work, K. 2021. The role of emergent physical and chemical properties of Florida spring complexes in predicting fish assemblage structure. Freshwater Science 40:478–493.

Worsham, M. L., A. Bond, J. R. Gibson, and D. G. Huffman. 2023. Biogeography of selected spring endemics in Texas interglacial-drought refugia with unexpected insights from a spring-dependent nematode parasite. Hydrobiology 2:97–133.