

INFLUENCE OF SURFACE AND NEAR-SURFACE GEOLOGY  
ON FISH ASSEMBLAGES IN THE COLORADO RIVER  
BASIN OF TEXAS

by

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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 2019

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## ACKNOWLEDGEMENTS

I would first like to thank my advisor, Dr. Timothy Bonner, for his constant support, encouragement, and availability. This project developed through our conversations and sharing of thoughts on fish distributions and geology of Texas. I arrived at Texas State University with an interest in aquatic systems, but this interest evolved into a passion because of the instruction and knowledge that Dr. Bonner shared with me. I thank Dr. Alan Groeger for both serving on my committee and teaching me so much about limnology and the abiotic factors of the Colorado River. I thank Dr. Ben Schwartz for both serving on my committee and sharing his knowledge about the geology of Texas and how it affects our surface waters.

I would also like to thank Dr. Donna Janes and Dr. Laurence Meissner for continuing to mentor and support me from my time as an undergraduate through to my return to school as a graduate student despite my long detour overseas.

I am also very thankful for all my fellow graduate students and labmates in the Bonner lab, both grad and undergrad: Jeremy Maikoetter, Nicky Hahn-Faucheux, Marisa Quevedo, Ryne Lehman, Jacob Ketchum, Lucas Pustka, Elizabeth Rosas, Audrey Fry, and numerous others. Whether it was working together on a project or just enjoying a conversation, they made my time in the lab brighter. I would like to especially thank Cody Craig, David Ruppel, and Alex Sotola for each supporting and mentoring me through these past two years. They each taught me so much about the world of fish ecology and statistical analyses.

Finally, I would like to thank my family for their constant love and support throughout the years. And to my wife, Ryoko: you, more than anyone, sacrificed so much so that I could return to America to pursue my dreams and follow my passion for biology.

本当にどうもありがとう。

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## ABSTRACT

Fish communities are distributed heterogeneously within river basins. Heterogeneity is attributed to a number of physical, chemical, and biological processes. Among river basins that traverse a diversity of surficial geologies, physical and chemical properties of surficial geologies influence stream characteristics and regional aquatic communities. Likewise, stream characteristics and aquatic communities of distinct surficial geologies (i.e., georegions) can respond differently to anthropogenic stressors. Purposes of this study were to assess the influence of surficial geologies (i.e., georegions) on stream characteristics and fish communities in the Colorado River basin of Texas, a representative western gulf slope basin of southcentral USA, and determine if anthropogenic stressors differentially affect fish communities by georegion. Using measures of discrete (i.e., georegions, stream type) and continuous (e.g., stream order, distance from river mouth) community variation (i.e., spatial delineations), I found that georegion, stream type, stream order, and distance from mouth distinguished stream characteristic types within the basin, but only georegion explained a significant portion (41%) of the fish community variation. Using fish community changes between time periods (1933 to 1980; 1981 to 2018), which generally corresponds with pre- and post-dam constructions within the basin, I found that anthropogenic flow alterations had more of an effect on fish communities in some georegions than others. My findings support the concept of georegions having a hierarchical influence on stream characteristics and aquatic community heterogeneity within a basin, and that anthropogenic modifications

can differentially affect aquatic communities, depending on factors associated with georegions and stream characteristics. Potential benefits of this work include understanding factors influencing the heterogeneity in aquatic communities and the role of anthropogenic stressors across georegions (e.g., prairie streams, karst terrains, lowland coastal rivers) within and outside the western gulf slope basins.

# **I. INFLUENCE OF SURFACE AND NEAR-SURFACE GEOLOGY ON FISH ASSEMBLAGES IN THE COLORADO RIVER BASIN OF TEXAS**

## **INTRODUCTION**

The conceptual framework of community ecology includes the processes of selection, drift, speciation, and dispersal in order to explain how and why communities are not homogeneously distributed across an environment (Vellend 2010). The combination of these processes through the ‘black box’ of community ecology can help to explain species and community distribution patterns. In stream ecology, aquatic communities (e.g., species richness, abundances, and densities in time and space) are heterogeneously distributed within riverine ecosystems. Two of the well-known concepts that address heterogeneous distributions are continuous variation (Gorman and Karr 1978; Vannote et al. 1980; Rahel and Hubert 1991) and discrete variation (Huet 1959; Rahel and Hubert 1991; Mcgarvey 2011).

Continuous variation, which is an integral part of the river continuum concept, is indicated by increases in species richness and accumulation of species longitudinally along a headwaters to river mouth gradient (Vannote et al. 1980). Increases in species richness and accumulation of species are attributed to increases in habitat diversity and greater allochthonous inputs in downstream areas. Additionally, lower order streams (e.g., headwaters reaches) tend to have less water permanency and are more prone to drying events such that they would only be able to harbor and sustain highly mobile or physically tolerant species (Rahel and Hubert 1991). Thus, spatial delineations of a river basin, such as stream order or distance from headwaters or river mouth, are used as

predictors of species richness and community structure. In contrast to continuous variation, discrete variation is indicated by heterogeneity in aquatic communities by basin or geographic area with abrupt differences in species richness, abundances, and densities of species between two communities (Huet 1959; Rahel and Hubert 1991). These abrupt changes in species composition are attributed to various abiotic factors, such as water temperature, elevation, and stream gradient (Rahel and Hubert 1991; Mcgarvey 2011). Both types of variation are observed among aquatic communities and might not be mutually exclusive. For example, coldwater and warmwater fish communities in Rocky Mountain-Great Plains streams displayed discrete variation on a broad spatial scale (i.e., zonation), whereas continuous variation was detected within the warmwater fish community (Rahel and Hubert 1991).

Support for discrete variation is observed in the distributional limits of many species of fishes corresponding with ecoregions (Blair 1950; Hubbs 1957; Griffith et al. 2004). Ecoregions, while created to assess terrestrial taxa, have some correspondence with aquatic systems as they are synthesized from geologic, topographic, and climatic variables. The processes occurring at ecoregion scale influence local habitats in aquatic systems; local habitat factors influence the aquatic communities (Poff et al. 1997; Allan 2004). Previous studies identified several abiotic variables, such as baseflow, discharge patterns, and water chemistry, as selection pressures in shaping freshwater fish communities (Mcgarvey 2011; Perkin and Bonner 2011; Cheek and Taylor 2016). Heterogeneity among abiotic factors within and across basins are attributed to geomorphology (Knisel 1963; Hack 1973; Stallard 1985; Nelson et al. 1992). For example, patterns of discrete variation are observed in unionid communities, which vary

with regional geology in a Michigan stream (Strayer 1983; McRae et al. 2004; Chambers and Woolnough 2018). Links between fish communities and geomorphology has yet to be fully explored among freshwater fish communities in western gulf slope drainages of southwest USA, which traverse distinct geologies from upstream to downstream.

Understanding distributional patterns and how they change over time benefit conservation and management of riverine habitats and biota. Furthermore, an understanding of both distributional patterns of aquatic communities and the underlying mechanisms driving distributional patterns can provide an appropriate scale to assess differential effects anthropogenic modifications have on local environments (Nilsson and Berggren 2000), to implement regionalization of conservation strategies, and to quantify ecological services of instream flows. The purposes of this study were to detect discrete or continuous variation among fish communities within a geologically diverse western gulf slope drainage river basin (i.e., Colorado River of Texas), relate distributional patterns of aquatic habitats and fish communities to geology and other factors influencing species distributions (e.g., stream order; Whiteside and McNatt 1972), and assess if discrete or continuous variation in habitat and fish communities are differentially affected by anthropogenic alterations.

The objective of this study were to 1) delineate the Colorado River and major tributaries into sub-basins, assess each sub-basin based on continuous and discrete spatial delineations: geology, stream type (i.e., mainstem reach or tributary reach), stream order, river km, and sub-basin size, and assess water quality, water quantity, and stream gradient within each sub-basin, 2) assess the contemporary fish communities by each sub-basin and determine which spatial delineations were associated with fish community

structure, 3) assess the contemporary fish community through the scope of significant spatial delineations and find associations between fish communities and abiotic variables, and 4) assess historical and contemporary fish communities through the scope of significant spatial delineations, find associations between changes in flow parameter and shifts in fish community structure, and determine if there are differential effects on fish community structure in different spatial delineations. I predicted that geology will explain more of the variation in fish community structure than other spatial delineations, and that regions of distinct geology would have distinct habitats and fish communities (Strayer 1983; Chambers and Woolnough 2018). Additionally, I predicted that temporal changes in fish communities will not correlate with the level of anthropogenic changes observed in significant spatial delineations (Nilsson and Berggren 2000), because of the differential effect anthropogenic changes have on areas with varying geomorphology.

## **METHODS**

### **Study Area**

The study area is the Colorado River basin, which has a total drainage area of 103,300 km<sup>2</sup>. The basin has two main headwaters areas: the upper Colorado River with perennial flows originating on the eastern edge of the Llano Estacado, and upper reaches of major tributaries (i.e., Concho River, San Saba River, Llano River, Pedernales River) with perennial flows arising from springs on the Edwards Plateau. The study area was delineated among five spatial scales: surficial geology, stream type (i.e., mainstem or tributary), stream order, distance from mouth, and length of river segment.

Surficial geology of the Colorado River basin has five major georegions (Pearson

2013; Figure 1). The Paleozoic Georegion consists of the low-gradient prairie stream region where bedrock is primarily composed of Carboniferous and Permian (with some Triassic) layers of clay, sand, shale, sandstone, siltstone, mudstone, limestone, dolomite, gypsum, and colluvium. This area includes the Colorado River upstream of Colorado Bend State Park, San Saba County (Latitude: 31.090572, Longitude: -98.463806) and the Concho River downstream from OC Fisher Lake and Lake Nasworthy in San Angelo. Aquifers in this region include the Ogallala, Dockum, and Lipan alluvium aquifers (George et al. 2011). The Edwards Georegion consists of the higher gradient, predominately spring-fed streams of the Edwards Plateau. The bedrock in this area is primarily composed of Cretaceous limestone. The rivers in this area include tributaries of the Concho River (North Concho River, Middle Concho River, Spring Creek, Dove Creek, and South Concho River), San Saba River upstream of the Ranch Branch confluence (Latitude: 30.943912, Longitude: -99.384776), Llano River upstream of the Big Bluff Creek confluence (Latitude: 30.691342, Longitude: -99.381314), and the Pedernales River upstream of the North Grape Creek confluence (Latitude: 30.320670, Longitude: -98.492259). The main aquifer in this region is the Edwards-Trinity karst aquifer (George et al. 2011). The Llano Uplift Georegion consists of moderate-gradient streams running over the Llano Uplift, a Pre-Cambrian and Cambrian geologic dome composed of granite, gneiss, schist, limestone, colluvium, and dolomite. This area includes the portions of the San Saba and Llano Rivers downstream from Edwards Georegion, the Pedernales River downstream from Edwards Georegion until its confluence with Miller Creek (Latitude: 30.302674, Longitude: -98.300351), and the mainstem Colorado River downstream from Paleozoic Georegion until its confluence

with Double Horn Creek (Latitude: 30.539430, Longitude: -98.187730) in Lake Travis. Aquifers in this region include Marble Falls and Ellenburger-San Saba karst aquifers (George et al. 2011). The Balcones Georegion includes moderate gradient streams of the Balcones fault zone and escarpment. The geology in this area is Cretaceous limestone and dolomite transitioning into chalk, marl, mudstone, clay, and alluvial shale at lower elevations. This area includes the Pedernales Rivers downstream from Llano Uplift Georegion, the entirety of Barton and Onion Creeks, and the mainstem Colorado River downstream of Llano Uplift Georegion until the confluence with Dry Creek (Latitude: 30.183267, Longitude: -97.472882). The main aquifer in this region is the Edwards-Trinity karst aquifer (George et al. 2011). The Cenozoic Georegion is a low-gradient lowland river that moves through Tertiary sedimentary deposits. This area includes the mainstem Colorado river and all tributaries downstream of Balcones Georegion to the Gulf of Mexico. Aquifers in this region include the Carrizo-Wilcox and Gulf Coast alluvium aquifers (George et al. 2011).

To quantify habitat and fish community variability within georegions, HUC 8 (8-digit Hydrological Unit Codes) sub-basins were identified within each georegion. Twenty-six HUC 8 sub-basins were identified. Six HUC 8 sub-basins, primarily in the ephemeral reaches of the Paleozoic Georegion, lack water quality and fish community data, and were dropped from further analyses. Among the remaining 20 HUC 8 sub-basins, nine were contained within one of the five georegions. The other 11 HUC 8 sub-basins were split smaller sub-basins according to their surficial geology or if areas within the sub-basins had fish community, water quality, and USGS flow station. For example, the HUC 8 that contains the mainstem of the Llano River (12090204) was divided into

the lower Llano River sub-basin in Llano Uplift Georegion and the upper Llano River section in Edwards Georegion. Lentic areas including the Highland Lakes and other reservoirs were excluded from further analysis. A total of 37 sub-basins were identified among the five georegions (Table 1; Figure 2). Stream type (i.e., mainstem or tributary) were determined based on river or tributary name. Stream order, average distance from mouth, and length of river segment were determined within each sub-basin using USGS National Hydrography Dataset in QGIS (USGS 2016a; QGIS Development Team 2018).

### **Data Collection**

Historical (period I) and contemporary (period II) fish collection data by sub-basin were obtained from the Fishes of Texas database (Hendrickson and Cohen 2015), and other published and unpublished data sets (Shattuck 2010; Curtis 2012; B. Littrell, Biowest, unpublished data; V.E. Dautreuil, Texas State University, unpublished data). Two species of *Macrhybopsis* are present in the Colorado River and were diagnosed in 2004 (Eisenhauer 2004). Due to unclarity of identification with historical data, these species were combined under *Macrhybopsis* in this study as they share similar niche characteristics. Additional contemporary collections were made at various sites throughout the Colorado River basin to fill in gaps in the existing database (Table 2). Community sampling was conducted once per site. Sampling methods included common seine (3.0 by 1.8 m; 3.2 mm mesh), bag seine (4.3 x 1.8 x 1.8 m; 3.2 mm mesh), and backpack electroshocking. At each site, all available habitats were exhaustively sampled. Fishes were identified to species level and enumerated in field. Fishes retained for vouchers or lab identification and enumeration were euthanized using tricaine-

methanesulfonate (MS-222) and fixed with 10% formalin following standard procedure (Use of Fishes in Research Committee 2004). After fixation, fish were transferred to 70% ethanol for long-term storage.

Average daily stream flow data were acquired from the USGS (USGS 2016b) for each sub-basin from the beginning of record through 2018. For period I (historical), flow data from beginning of record through 1980 were used. For contemporary analysis, flow data from 1981 through 2018 were used. The years of 1980 and 1981 separate Periods I and II, which roughly follows pre dam to post dam periods (dams were continuously added from 1930 through 1991). Additionally, 1981 begins a period of high-resolution water quality monitoring to be used for robust contemporary analyses and splits the available fish data to maintain a robust sample size for each period (Period I:  $N_{\text{individuals}} = 31,300$ ; Period II:  $N_{\text{individuals}} = 347,194$ ). Flow data were analyzed with IHA (Indicators of Hydrologic Alteration) v.7.1 software along the following parameters (Richter et al. 1996); flow magnitude (cm/s), coefficient of variation (a measure of flow variability), zero flow percentage (a measure of period with no flow magnitude), and base flow index (a measure of intermittency; Poff and Ward 1989).

Water quality was obtained from the Lower Colorado River Authority, (LCRA) water quality database [<https://hydromet.lcra.org/>] from 1981 to 2018 for contemporary (period II) analysis. Due to sparse water quality data in each sub-basin prior to 1981, these data were not used in historical (period I) analysis. Water quality data were taken from the same site as the corresponding sub-basin USGS streamflow gage or the next closest sampling site within the region (Table 3) and included the following parameters; dissolved oxygen (mg/L), pH, conductivity ( $\mu\text{S}/\text{cm}$ ), temperature ( $^{\circ}\text{C}$ ), and turbidity (N).

Stream gradient data were acquired by creating shapefiles of the sub-basins using the most recent satellite imagery from Google Earth. Waypoints were placed every 100 m at mid-channel. Elevation data were then obtained for each waypoint from the USGS National Elevation Dataset. Elevations for each waypoint were then averaged by river km from the mouth of the Colorado River. Linear regression was performed between river kilometer and average elevation of each kilometer section to find average stream gradient within each sub-basin.

### **Data Analysis**

Period I data were only used to assess and associate changes in fish communities through time with changes in flow parameters. Period II data were used to describe the interrelationships among fish community data, spatial delineations, and stream characteristics. Interrelationships within Period II are described and reported first, to assess and understand the appropriate scale (i.e., spatial delineation) to perform temporal assessment.

Principal Component Analysis (PCA; CANOCO 4.5, Microcomputer Power 2002) was used to assess relationships between spatial delineations and stream characteristics (i.e., flow and water quality parameters). Principal component scores were grouped by spatial delineations and difference in stream characteristics among spatial delineations were tested with ANOVA for PC I and II axes. To assess fish communities by sub-basin relationships with spatial delineations, Bray-Curtis dissimilarity matrix was prepared using fourth root transformed data in program R using the vegan package (Bray and Curtis 1957; Greenacre and Primicerio 2014; Oksanen et al. 2015; R Core Team

2017). Permutational Analysis of Variance (PERMANOVA) was performed in program R using the *vegan* package to assess variation in fish community by spatial delineations (Anderson and Walsh 2013; Oksanen et al. 2015; R Core Team 2017). General similarities among sub-basins were visualized with a dendrogram produced in program R. To assess relationships among significant spatial delineations (as identified with PERMANOVA), stream characteristics, and fish community by sub-basin, Canonical Correspondence Analysis (CCA; CANOCO 4.5, Microcomputer Power 2002) was used.

Changes between period I and period II flow parameters were assessed using percent change. Changes between period I and period II fish communities were assessed with taxa richness (S), Shannon-Wiener index (H), Shannon-Weiner evenness (EH), nonmetric multidimension scaling (nMDS) distance between time periods, and Bray-Curtis dissimilarity between time periods. nMDS was calculated using the *vegan* package in program R (Oksanen et al. 2015). In order to assess the relative impact of individual species on the Bray-Curtis dissimilarity between time periods, a similarity percentage (SIMPER) analysis was performed using the *simper* function from *vegan* package in program R (Oksanen et al. 2015).

## RESULTS

### **Spatial delineations and stream characteristics**

The 37 sub-basins within the Colorado River basin were categorized or quantified per each of the five spatial delineations. Sub-basins were grouped among five georegions. Eleven sub-basins were classified as mainstem streams and 26 sub-basins were classified as tributary streams. Stream order ranged from 1 to 4 with the mid-point of the farthest

upstream sub-basin located 1,251 km from river mouth. Mean ( $\pm 1$  SD) length of river segments was 71 (34.5) km and ranged in length from 11 to 167 km.

Estimates of stream characteristics by sub-basin are provided in appendices 1.1 and 1.2. Principal components (PC) axes I and II explained 51% of the stream characteristics (Figure 3). Principal components axis I explained 33% of the variation and described a climate, water permanency, and discharge gradient (Table 4). Stream characteristics with strong loadings on PC axis I were flow coefficient of variation (-0.798), zero flow percentage (-0.635), discharge (0.737), water temperature (0.75) and precipitation (0.759). Principal components axis II explained 19% of the variation and described a stream gradient and conductivity gradient. Strong loadings on PC axis II were stream gradient (-0.652), dissolved oxygen (0.578), turbidity (0.579), and conductivity (0.738).

Four of the five spatial delineations differed among PC axes gradients. Georegions differed along PC axis 1 ( $F_{4,32} = 7.65$ ,  $P < 0.01$ ) and PC axis 2 ( $F_{4,32} = 17.41$ ,  $P < 0.01$ ). Cenozoic Georegion differed ( $P < 0.05$ ) among all other georegions along PC axis 1 (i.e., lower flow coefficient of variation, greater precipitation and discharge, warmer temperature), and Paleozoic Georegion differed ( $P < 0.05$ ) among all other georegions along PC axis 2 (i.e., greater conductivity, lower stream gradient). Stream type differed along PC axis 1 ( $F_{1,48} = 4.48$ ,  $P = 0.04$ ) and PC axis 2 ( $F_{1,48} = 16.65$ ,  $P < 0.01$ ). Mainstem sub-basins had lower flow coefficient of variation, greater precipitation and discharge than tributary sub-basins on PC axis 1 and lower stream gradient and greater conductivity on PC axis 2. Stream order differed along PC axis 1 ( $F_{3,33} = 10.5$ ,  $P < 0.01$ ) and PC axis 2 ( $F_{3,33} = 3.31$ ,  $P = 0.03$ ). Stream order four sub-basins

differed among other stream orders along PC axis 1 (i.e., lower flow coefficient of variation, greater precipitation and discharge, warmer temperature). Stream order one sub-basins differed among other stream orders along PC axis 2 (i.e., greater stream gradient and lower conductivity). Distance from mouth was categorized into three groups: > 1,000 km from mouth, > 500 km from mouth (but < 1,000 km), and < 500 km from mouth. Distance from mouth differed along PC axis 1 ( $F_{2,34} = 15.2$ ,  $P < 0.01$ ) but not for PC axis 2 ( $F_{2,34} = 3.38$ ,  $P = 0.05$ ). Sub-basins <500 km from mouth differed from other distances from mouth by having lower flow coefficient of variation, greater precipitation and discharge. Stream length was also categorized into three groups: > 100 km in length, > 50 km in length (but not < 100 km), and < 50 km in length. Stream length did not differ along PC axis 1 ( $F_{2,34} = 0.75$ ,  $P = 0.48$ ) or along PC axis 2 ( $F_{2,34} = 1.90$ ,  $P = 0.16$ ).

### **Fish community by spatial delineations**

Quantification of contemporary fish community (1981 – 2018) within the Colorado River basin was estimated from a total of 347,194 individuals, 77 species, and 18 families (Table 5). Most abundant family was Cyprinidae (66% relative abundance), followed by Poeciliidae (17%), and Centrarchidae (7.5%). Most abundant species was *Cyprinella lutrensis* (33%), followed by *Gambusia affinis* (16%), *Cyprinella venusta* (14%), and *Pimephales vigilax* (7.9%). Species of greatest conservation need (SGCN) comprised 5.6% of the fish community. Most abundant SGCN species was *Notropis amabilis* (4.1%), followed by *Dionda nigrotaeniata* (0.6%) and *Cyprinodon rubrofluviatilis* (0.5%). Non-native species comprised 3.9% of the fish community. Most

abundant non-native species was *Lepomis auritus* (1.3%), followed by *Gambusia geiseri* (1.2%) and *Astyanax mexicanus* (0.5%).

Contemporary fish communities of sub-basins differed among georegions ( $P < 0.01$ ), accounting for 41% of the variation in sub-basin fish communities (Table 6). Differences among sub-basin fish communities were not detected ( $P > 0.05$ ) for stream type, stream order, distance from mouth, or length of river segment; therefore, fish communities were not assessed by these spatial delineations.

Among georegions, Paleozoic contemporary fish community consisted of 99% native species (species richness [S] = 42) and 0.7% non-native species (S = 7). Most abundant fishes were *Cyprinella lutrensis* (54% in relative abundance), *Gambusia affinis* (14%), and *Pimephales vigilax* (12%; Table 7). Unique forms were *Cyprinodon rubrofluviatilis*, *Fundulus grandis*, and *Cyprinodon variegatus*. Edwards Georegion contemporary fish community consisted of 91% native species (S = 42) and 9% non-native species (S = 8). Most abundant fishes were *Cyprinella venusta* (26%), *Gambusia affinis* (19%), and *Notropis amabilis* (17%). Unique forms were *Gambusia geiseri*, *Lucania parva*, and a disjunct population of *Minytrema melanops*. Llano Uplift Georegion contemporary fish community consisted of 92% native species (S = 35) and 7.9% non-native species (S = 6). Most abundant fishes were *Cyprinella venusta* (55%), *Gambusia affinis* (7.2%), and *Lepomis auritus* (6.5%). Unique form was *Oreochromis aureus*. Balcones Georegion contemporary fish community consisted of 91% native species (S = 38) and 9.4% non-native species (S = 7). Most abundant fishes were *Cyprinella venusta* (32%), *Gambusia affinis* (24%), and *Campostoma anomalum* (13%). An unique form was *Xiphophorus variatus*. Cenozoic Georegion contemporary fish

community consisted of 97% native species (S = 54) and 2.8% non-native species (S = 8). Most abundant fishes were *Cyprinella lutrensis* (18%), *Cyprinella venusta* (14%), *Pimephales vigilax* (12%), and *Gambusia affinis* (11%). Unique forms included *Hybopsis amnis*, *Notropis shumardi*, *Cycleptus elongatus*, *Etheostoma gracile*, and *Etheostoma parvipinne*.

Majority of sub-basin fish communities (N = 29; appendices 2.1 – 2.4) were clustered under two nodes (A and B) based on cluster analysis using Bray-Curtis dissimilarity matrix (Figure 4). Node A consisted of sub-basins within Edwards (N = 8, 80% of all sub-basins within the Edwards Georegion), Balcones (4, 80%), Llano Uplift (3, 60%), and Paleozoic (1, 8%) Georegions, attributed to a higher abundance of *C. venusta*, *N. amabilis*, and *C. anomalum* and a lower abundance of *C. lutrensis* and *P. vigilax*. Node B consisted of sub-basins within Cenozoic (5, 100%), Paleozoic (6, 50%), Edwards (1, 10%), and Balcones (1, 2%) Georegions, attributed to high abundances of *C. lutrensis*, *P. vigilax*, and *M. audens*. Among the remaining eight sub-basins, Node C consisted of sub-basins within Llano Uplift (1, 20%), Edwards (1, 10%), and Paleozoic (1, 8%) Georegions, attributed to high abundances of *L. cyanellus* and *M. salmoides*, Node D were sub-basins within Paleozoic Georegion (4, 33%), attributed to high abundances of *C. rubrofluvialilis* and *F. grandis*, and Node E was one sub-basin (20%) within the Paleozoic Georegion, attributed to high abundances of *F. zebrinus* and *C. anomalum*.

### **Relationships among georegion, stream characteristics, and fish community**

Georegion and stream characteristics of sub-basins explained 59% (F = 2.1; P

<0.01) of the variation in the contemporary fish community. Strong loadings on CCA axis I were Edwards Georegion (-0.577), base flow index (-0.518), turbidity (-0.595), conductivity (0.737), and Paleozoic Georegion (0.808) (Table 8; Figure 5). Strong loadings on CCA axis II were coefficient of variation (-0.536), temperature (0.624), precipitation (0.881), discharge (0.891), and Cenozoic Georegion (0.916). *Cyprinodon rubrofluviatilis*, *Cyprinodon variegatus*, and *Fundulus grandis* were associated with high conductivity. *Dionda nigrotaeniata*, *Gambusia geiseri*, and *Notropis amabilis* were associated with high gradient and baseflow. *Notropis shumardi*, *Opsopoeodus emiliae*, and *Percina sciera* were associated with high discharge.

### **Historical Comparison**

Seventy-two species from 18 families and 31,300 individuals were collected in the Colorado River basin between 1933 and 1979. Most abundant family was Cyprinidae (54.9% relative abundance), followed by Poeciliidae (15.1%), and Centrarchidae (13.4%). Most abundant species was *Cyprinella venusta* (18.1%), followed by *Gambusia affinis* (10.3%), *Cyprinella lutrensis* (9.9%), and *Notropis amabilis* (7.5%). Species of greatest conservation need comprised 5.6% of the fish community. Most abundant SGCN was *Notropis amabilis* (7.5%), followed by *Dionda nigrotaeniata* (2.0%) and *Micropterus treculii* (1.4%). Non-native species comprised 8.5% of the fish community. Most abundant non-native species was *Gambusia geiseri* (4.7%), followed by *Lepomis auritus* (2.6%) and *Astyanax mexicanus* (0.45%).

Differences in species richness and relative abundances were observed between historical fish community (1933 – 1979; Period I) and contemporary fish community

(1980 – 2018; Period II). Seventy-two species were reported in Period I compared to 77 species in period II. Seven species reported in Period I and not detected in Period II were marine species (i.e., *Anchoa mitchilli*, *Mugil cephalus*, and *Membras martinica*), freshwater species (i.e., *Hybognathus placitus*), and introduced species (i.e., *Notropis buccula*, *Notropis oxyrhynchus*, and *Piaractus brachypomus*). Twelve species reported in Period II and not detected in Period I were 7 introduced species (i.e., *Carassius auratus*, *Ctenopharyngodon idella*, *Cyprinus carpio*, *Lucania parva*, *Xiphophorus variatus*, *Cyprinodon variegatus*, and *Oreochromis aureus*) and 5 native species (i.e., *Moxostoma congestum*, *Ictalurus furcatus*, *Aphredoderus sayanus*, *Agonostomus monticola*, and *Etheostoma parvipinne*). Between Period I and Period II, relative abundances increased for Cyprinidae (55% to 66%), Poeciliidae (15% to 18%), and Atherinopsidae (<0.1% to 3.2%) and decreased for Centrarchidae (13% to 7.5%) and Percidae (11% to 1.6%).

Differences in species richness, evenness, relative abundances, and community similarities were observed between periods I and II among georegions. Species richness increased from 3 to 15 species in four of the georegions and decreased by 10 species in Balcones Georegion (Table 9). Shannon-Weiner diversity index decreased in four of the georegions, and Shannon-Weiner evenness index decreased in all georegions. Bray-Curtis dissimilarity between periods I and II ranged from 18% in Edwards Georegion to 31% in Paleozoic Georegion (Table 10). Greatest differences in community structure based on nMDS analysis were in the Paleozoic Georegion followed by Cenozoic and Balcones Georegions (Figure 6). Among species contributing to >50% of the dissimilarity (Table 11), decreases relative abundances were observed for one species (*Macrhybopsis*) at four georegions, one species (*Fundulus zebrinus*) at three georegions,

and six species (*Dionda nigrotaeniata*, *Gambusia geiseri*, *Notropis amabilis*, *Notropis buchanani*, *Notropis shumardi*, and *Opsopoeodus emiliae*) at two georegions. Increases in relative abundances were observed for one species (*Menidia audens*) at four georegions and seven species (*Cyprinus carpio*, *Dorosoma cepedianum*, *D. petenense*, *Gambusia affinis*, *Ictiobus bubalus*, *Lepisosteus osseus*, and *Notropis volucellus*) at two georegions.

Mean annual discharge decreased between time periods for all georegions and ranged between -74% in Paleozoic Georegion to -8% in Edwards Georegion. Base flow index increased for four of five georegions between time periods and ranged between -1% in Cenozoic Georegion to 702% in Paleozoic Georegion. Zero flow percentage decreased for three of five georegions and ranged from -100% in Balcones Georegion to 5% in Edwards Georegion. Coefficient of variation decreased for four of five georegions between time periods and ranged between -36% in Balcones Georegion and 11% in Paleozoic Georegion. Relationships among discharge, base flow index, zero flow percentage, and coefficient of variation and Shannon Index, Shannon Evenness, nMDS distances, and Bray-Curtis similarities were not detected except for a positive relationship between base flow index and nMDS distances between time periods ( $P = 0.02$ ) and negative relationship between zero flow percentage and Shannon Index ( $P = 0.045$ ; Figure 7).

## DISCUSSION

The results support the prediction that geology would explain more variation in fish community structure than other spatial variables. Georegion was the only spatial

variable associated with fish community structure and stream characteristics. Correspondingly, three discrete fish communities were observed in the Paleozoic Georegion, Edwards Georegion, and Cenozoic Georegion. The prediction that anthropogenic changes would correlate with temporal changes in fish community was partially supported. Across all georegions there was a positive association between change in fish community (i.e., nMDS distance) and BFI (i.e., increases in base flows related to dam operations; Gido et al. 2013; Gao et al. 2016a) and changes in fish community (i.e., decreases in Shannon diversity index) and increases in zero flow percentage (i.e., lentic conditions upstream from impoundments; Nilsson and Berggren 2000; Gao et al. 2016b). However, metrics of fish community change were not associated with decreases in discharge or increases in coefficient of variation. This also corroborates previous work showing that anthropogenic effects can have variable impact on river systems (Allan 2004).

Surficial geology and the georegion scale approach explained more variation in the fish community structure than other spatial scales tested. Three distinct georegions were observed based on fish communities: the Paleozoic Georegion fish community, Cenozoic Georegion fish community, and Edwards, Llano Uplift, and Balcones Georegions fish community. First, the Paleozoic Georegion fish community included fishes commonly associated with prairie stream streams, such as the saline-tolerant species *Cyprinodon rubrofluvialis*, *Fundulus grandis*, and *Cyprinodon variegatus* (Minckley 1980; Conner and Suttkus 1986; Warren et al. 2000). The Paleozoic Georegion fish community closely resembles the communities found in regions of similar geology in the adjacent Brazos and Red rivers (Echelle et al. 1972; Wilde et al. 1996).

The Cenozoic Georegion fish community included species found in no other regions, such as *Hybopsis amnis*, *Notropis shumardi*, *Cycleptus elongatus*, and *Etheostoma gracile*. These species are often categorized as big-river, slack water, or low stream gradient specialists (Braasch and Smith 1967; Cross 1967; Clemmer 1980; Li and Gelwick 2005). The Cenozoic Georegion fish community is similar to the adjacent lower Brazos River fish community (Bonner and Runyan 2007), potentially because of similar geology but also because of connections of the two rivers during the Pleistocene and Holocene (Conner and Suttkus 1986). The Edwards, Llano Uplift, and Balcones Georegions grouped together and had similar fish communities. Even though these were separated into distinct georegions for analysis, close proximity and similar geology (Cretaceous) among the three georegions likely contribute to the similarity of fish communities. The fish community consisted of a large number of spring-associated fishes, such as *Dionda nigrotaeniata*, *Gambusia geiseri* and *Notropis amabilis* (Tilton 1961; Warren et al. 2000; Gilbert 1980), and similar to other nearby fish communities in Guadalupe, Nueces, and Rio Grande rivers with Cretaceous geology (Craig et al. 2016). The novel aspect of this work is not in finding that species were often found in areas they are understood to associate with, but rather that their associations could be explained by geology more than other factors that exert a hierarchical control on communities including distance from mouth or headwaters areas. This finding corroborates previous studies that assessed the influence of geology on aquatic communities (Strayer 1983; Chambers and Woolnough 2018).

While not directly assessing the individual water quality or quantity parameters that can act as a mechanism shaping species distributions, some inferences can be made

about these mechanisms based on association with georegion stream characteristics. The Paleozoic Georegion consisted of lower gradient streams with higher levels of salinity, influenced by the local geology (Nance 2006). Species in the Paleozoic Georegion, such as *F. grandis*, *Cyprinodon rubrofluvialis*, and *Cyprinodon variegatus*, are often associated with streams of greater conductivity (Cheek and Taylor 2016). The Edwards, Llano Uplift, and Balcones Georegions consisted of streams with low turbidity, steeper stream gradients, and perennially flowing springs from karst aquifers. Species prevalent in the Edwards, Llano Uplift, and Balcones Georegions, such as *N. amabilis* and *E. lepidum*, associate with stenothermic waters (Hubbs 1985; Edwards 1997; Craig et al. 2017) and areas of lower turbidity (Platania 1980). Within the contemporary community, a picture starts to emerge that describes how geology hierarchically influences the various abiotic factors, which are influential in shaping fish communities.

Temporal analysis demonstrates the differential effects that anthropogenic modifications can have on aquatic systems (Allan 2004). The Colorado River and its tributaries contains 16 major in-channel impoundments, and numerous off channel impoundments, diversions, and small weirs. One of the impacts that impoundments have on an aquatic system is an increase in base flow index (Gido et al. 2013). Base flow index was designed to quantify the amount of water that is moving through a system at base flow conditions (Poff et al. 1997). The results corroborate previous studies which found that changes in fish community, especially increased abundances of non-native species and lentic species, were correlated with increases in base flow index (Gao et al. 2010; Gido et al. 2013). Two non-native species, *C. carpio* and *F. grandis*, were detected in period II in the Paleozoic Georegion, but not in period I. Increases in relative abundance

of lentic forms, such as *Menidia audens* and both *Dorosoma* species (Gilbert and Lee 1980; Megrey 1980), were detected in period II. Conversely, in the Paleozoic Georegion, two species (i.e., *H. placitus* and *Macrhybopsis*) were not detected in period II. Similar declines are reported for *Macrhybopsis* and prairie stream fishes, such as *H. placitus*, in general. Declines in occurrences and abundances are related to river fragmentations due to dam placement (Luttrell et al. 1999; Perkin and Gido 2011). Estimates for minimum river lengths required to support *H. placitus* and *Macrhybopsis* are 120 km and 110 km respectively (Perkin and Gido 2011). Current river lengths between impoundments in the Paleozoic Georegion range from 170 km (O.H. Ivie Reservoir to E.V. Spence Reservoir) to 300 km (Lake Buchanan to O.H. Ivie Reservoir) Since river lengths are greater than minimum estimates of river lengths necessary to support *H. placitus* and *Macrhybopsis*, other factors might be responsible for reduction in occurrences and abundances than fragmentation alone.

Geology acts as a hierarchical control on stream characteristics. Hierarchical control might explain the differential effects that anthropogenic modifications have in aquatic systems. For example, the Paleozoic Georegion had the lowest historical sustained base flows among other georegions and the highest magnitude of change to the fish community between time periods. Historically, the Paleozoic Georegion had a community that contained many prairie stream forms, which have adaptations to live in areas of intermittent flow and persisted by movement or persisting in pools during dry times (Ostrand and Wilde 2005). In the contemporary period when the flow dynamic changed and sustained base flows increased, these species were not detected or declined in relative abundance. Alternatively, the Edwards Georegion had a high historical BFI

and showed relatively little change in fish community structure between time periods. This region also had an increase in BFI, but the magnitude of change in fish community was not proportionally as high as in the Paleozoic Georegion. One possible reason for this is that the communities in these areas are thought to be adapted to areas with stable water temperatures (Craig et al. 2019) provided by high base flow conditions. Therefore, the effects of impoundments in this area were not as impactful to the community as areas where communities have adapted to intermittent conditions.

Limitations of this study include a restriction in evaluating only between two time periods, being subject to use of museum collections for historical fish community data, not accounting for all spatial factors commonly used in ecological studies, and having low power in detecting associations between flow changes and fish community structure. This study was restricted to two periods. Previous studies looking at changes in fish community due to anthropogenic effects assess the effect of a single impoundment (Bonner and Wilde 2000; Perkin and Bonner 2011). This allows for splitting of data to coincide with the construction of a dam. This study, however, assessed a river basin with dams installed at different times ranging from 1930 (Lake Nasworthy on the South Concho River) to 1991 (OH Ivie on the mainstem Colorado River). Additionally, there are concerns that fish data collected in Period I were not an accurate reflection of the fish community because of low sample size compared to Period II. Low sample sizes in Period I, alone, could be responsible for the report of increased species richness in some georegions through time. Previous studies assessing anthropogenic effects on water quality or fish communities in river basins have found variables, such as land cover and vegetation, to be influential for explaining some of the variation in water quality and fish

communities (Nilsson and Berggren 2000; Williams et al. 2013). These variables, therefore, cannot be excluded as factors which possibly contribute to the dissimilarity detected between periods. However, previous studies looking at the effects of geology on aquatic systems have found that changes in land cover did not significantly change mussel communities while the influence of geology was still readily observed (Strayer 1983; Chambers and Woolnough 2018). This study assessed a single river basin and created a model with an effective N of 1. In order to show replicability of the findings and gain power in predicting the influence of anthropogenic effects on aquatic systems, further assessment will need to be conducted on other river systems that travel through multiple georegions. Testing for replicability will allow for determination of the level to which surface geology influences fish community structure and how different geological areas respond to anthropogenic influences.

The benefits of using the georegion approach compared to other statistical models include the relative simplicity and accessibility of the assessment. Geological data are easily acquired and interpreted. More complex models that use geology as a single component also require extensive in-field measurements and specialized analysis software (Williams et al. 2013). The future development of a model using surface-geology would easily allow river managers to predict what type of fish community will be in a given area and have some inference as to how that community would change due to anthropogenic impacts.

As demonstrated herein, discreteness of fish communities and their relationship with the underlying geology provides an opportunity to assess fish communities at an appropriate scale. Scale is important when considering changes through time and

remedial conservation efforts (Richards et al. 1996; Allan 2004). By using georegions while accounting for the uniqueness of the fishes (physiological tolerances, etc.), we have a more meaningful approach to quantifying changes in fish communities through time and the differential effects of anthropogenic modifications. Expanding this approach to other river basins (for replication) and identification of additional georegions can benefit natural resources managers in applying anthropogenic effects and threats known in one basin of a georegion to other basins within the same georegion. For example, threats to the prairie streams of SGCN listed species, *Notropis buccula* and *Notropis oxyrhynchus*, in the Brazos River (Paleozoic Georegion), such as impoundments, climate change, land cover, and groundwater withdrawals, could be applied to other basins within the Paleozoic Georegions (i.e., Brazos River, Red River, and many other prairie streams; USFWS 2014). Insights could lead to a more holistic management approach by georegion.

**Table 1.** Sub-basin, map code, and spatial delineations (i.e., georegion, stream type, stream order, distance from mouth, and length of river segment) within the Colorado River basin. Sub-basins are arranged in order of map code (See Figure 1). Abbreviation for georegions: Paleozoic Georegion (PGR), Edwards Georegion (EGR), Llano Uplift Georegion (LGR), Balcones Georegion (BGR), and Cenozoic Georegion (CGR).

Sub-basin	Map code	Georegion	Stream type	Stream order	Distance from mouth (km)	Length of river segment (km)
Beals	1	PGR	Tributary	1	1251	93
Colorado City	2	PGR	Mainstem	1	1267	126
Upper Spence	3	PGR	Mainstem	2	1177	53
Lower Spence	4	PGR	Mainstem	2	1105	53
Elm	5	PGR	Tributary	2	1061	45
Upper Ivie	6	PGR	Mainstem	3	1036	84
Lower Concho	7	PGR	Tributary	3	1020	39
Upper Concho	8	PGR	Tributary	3	1069	58
Lower Ivie	9	PGR	Mainstem	4	885	167
Pecan	10	PGR	Tributary	3	844	85
Lower San Saba	11	PGR	Tributary	2	773	53
Upper Buchanan	12	PGR	Mainstem	4	736	132
South Concho	13	EGR	Tributary	1	1119	31
Dove	14	EGR	Tributary	1	1132	34
Spring	15	EGR	Tributary	1	1136	48
Middle Concho	16	EGR	Tributary	1	1137	50
North Concho	17	EGR	Tributary	1	1123	39
Upper San Saba	18	EGR	Tributary	1	910	89
North Llano	19	EGR	Tributary	1	830	52
South Llano	20	EGR	Tributary	1	830	50
Upper Llano	21	EGR	Tributary	2	773	63
Upper Pedernales	22	EGR	Tributary	2	675	66
Brady	23	LGR	Tributary	1	871	113
Middle San Saba	24	LGR	Tributary	2	833	66
Lower Llano	25	LGR	Tributary	2	683	118
Sandy	26	LGR	Tributary	2	653	82
Middle Pedernales	27	LGR	Tributary	2	626	32
Lower Pedernales	28	BGR	Tributary	2	582	56
Barton	29	BGR	Tributary	2	504	74
Onion	30	BGR	Tributary	2	450	31
Waller	31	BGR	Tributary	1	469	11
Austin	32	BGR	Mainstem	4	443	48
Cummins	33	CGR	Tributary	1	249	81
Bastrop	34	CGR	Mainstem	4	375	87
Smithville	35	CGR	Mainstem	4	270	122
Columbus	36	CGR	Mainstem	4	154	111
Wharton	37	CGR	Mainstem	4	49	98

**Table 2.** Fish community sampling sites used to supplement gaps in existing contemporary collection data. Sites were sampled between June 2017 and July 2018.

<b>System</b>	<b>Site</b>	<b>Latitude</b>	<b>Longitude</b>
Cummins Creek	1291	30.126177	-96.792522
Cummins Creek	237	30.059039	-96.700522
Buckners Creek	609	29.866058	-96.933018
Cummins Creek	Venghaus George Road	29.825153	-96.580461
Skull Creek	CR16	29.53565	-96.4375
San Saba	Toe Nail Trail	30.833358	-100.112768
Middle Colorado	283	31.439373	-99.375271
Middle Colorado	45	31.458621	-98.942771
Middle Colorado	377	31.467868	-99.162178
Middle Colorado	503	31.49361	-99.573608
Concho	381	31.519976	-100.093708
San Saba	2092	30.883666	-99.630342
Middle Colorado	83	31.73012	-99.941609
Middle Colorado	277	31.847792	-100.292091
San Saba	1311	30.912754	-99.492807
Upper Colorado	2059	32.019726	-100.736186
South Concho	277	31.187217	-100.4997
Dove Creek	113	31.20086	-100.713302
South Concho	2335	31.234809	-100.499996
Spring Creek	101	31.2551	-100.814278
Dove Creek	2335	31.273687	-100.630544
Spring Creek	211	31.327365	-100.745492
Upper Colorado	163/167	32.441946	-100.948719
West Rocky Creek	853	31.443611	-100.756668
North Concho	West Carlsbad	31.592931	-100.637428
North Concho	2034	31.661156	-100.741409
Sandy Creek	Crabapple	30.441344	-98.838154
Sandy Creek	71	30.558	-98.472401
Cherokee Creek	442	31.100334	-98.505788
Cherokee Creek	501	31.032466	-98.57784
Cherokee Creek	16	30.99722	-98.708757
South Concho	Anson Spring	31.136534	-100.494357

**Table 3.** Locations of water quality and water quantity stations for each sub-basin.

Map Code	Water Quantity Sites		Water Quality Sites	
	Latitude	Longitude	Latitude	Longitude
1	32.19929	-101.01400	32.19930	-101.01408
2	32.39262	-100.87872	32.38509	-100.86534
3	32.05374	-100.76205	32.01975	-100.73614
4	31.88542	-100.48065	31.88551	-100.48068
5	31.74932	-99.94786	31.74927	-99.94751
6	31.71543	-100.02648	31.73012	-99.94160
7	31.51599	-99.91952	31.51569	-99.91980
8	31.45461	-100.41065	31.45303	-100.41254
9	31.49377	-99.57395	31.49358	-99.57358
10	31.51739	-98.74060	31.51757	-98.74066
11	31.21322	-98.71949	31.21315	-98.71988
12	31.21795	-98.56448	31.21839	-98.56454
13	31.18711	-100.50204	31.18726	-100.49966
14	31.27405	-100.63093	31.27372	-100.63055
15	31.33016	-100.64038	31.33001	-100.64008
16	31.42738	-100.71121	31.44368	-100.75669
17	31.59265	-100.63704	31.59295	-100.63743
18	30.91906	-99.78563	30.91906	-99.78563
19	30.51741	-99.80618	30.50297	-99.77929
20	30.47901	-99.77804	30.44939	-99.81210
21	30.50435	-99.73451	30.58884	-99.59806
22	30.22048	-98.86976	30.22020	-98.87004
23	31.13822	-99.33506	31.13750	-99.33298
24	31.00406	-99.26943	31.00406	-99.26943
25	30.75129	-98.66976	30.75145	-98.66946
26	30.55769	-98.47225	30.55792	-98.47276
27	30.29187	-98.39947	30.27208	-98.54555
28	30.33944	-98.13906	30.33944	-98.13906
29	30.24465	-97.80223	30.24479	-97.80250
30	30.17799	-97.68861	30.17786	-97.68894
31	30.32269	-97.72302	30.30702	-97.72642
32	30.24614	-97.68006	30.24544	-97.69118
33	29.74706	-96.55122	29.74706	-96.55122
34	30.10466	-97.31944	30.10983	-97.32274
35	30.01272	-97.16193	30.01350	-97.15567
36	29.70635	-96.53692	29.71293	-96.54741
37	29.30914	-96.10385	29.30811	-96.10005

**Table 4.** Percent variance explained and variable loadings of PC axes I through IV for stream characteristics in period II (1981-2018).

<b>Variable</b>	<b>Axis I</b>	<b>Axis II</b>	<b>Axis III</b>	<b>Axis IV</b>
Percent Variance Explained	32.7%	18.6%	14.2%	12.1%
Discharge	0.7366	0.0683	0.4451	-0.2359
Coefficient of Variation	-0.798	-0.0753	0.2387	-0.2539
Zero Flow Percentage	-0.6354	-0.2874	0.1243	-0.5037
Base Flow Index	0.4289	-0.1205	0.1948	0.7569
Dissolved Oxygen	0.2709	0.5781	-0.6566	-0.1051
pH	0.4904	0.2264	-0.6125	-0.2534
Conductivity	-0.4744	0.7377	0.0196	0.0224
Temperature	0.75	-0.4475	-0.0109	-0.1676
Turbidity	0.287	0.5794	0.438	-0.3076
Gradient	-0.2566	-0.6519	-0.4906	-0.0936
Precipitation	0.7592	-0.2068	0.1347	-0.4219

**Table 5.** Relative abundance of fishes (listed in family order) detected in the Colorado River in Period II (1981 – 2018). Dagger (†) indicates non-native species.

Family	Species	Relative Abundance
Lepisosteidae	<i>Lepisosteus oculatus</i>	0.005
	<i>Lepisosteus osseus</i>	0.030
Anguillidae	<i>Anguilla rostrata</i>	0.001
Clupeidae	<i>Dorosoma cepedianum</i>	1.038
	<i>Dorosoma petenense</i>	0.222
	<i>Anchoa mitchilli</i>	0.002
Cyprinidae	<i>Campostoma anomalum</i>	2.329
	† <i>Carassius auratus</i>	0.001
	† <i>Ctenopharyngodon idella</i>	0.000
	<i>Cyprinella lutrensis</i>	31.012
	<i>Cyprinella venusta</i>	13.889
	† <i>Cyprinus carpio</i>	0.226
	<i>Dionda nigrotaeniata</i>	0.724
	<i>Hybognathus placitus</i>	0.049
	<i>Hybopsis amnis</i>	0.043
	<i>Lythrurus fumeus</i>	0.247
	<i>Macrhybopsis</i>	0.310
	† <i>Notemigonus crysoleucas</i>	0.083
	<i>Notropis amabilis</i>	4.363
	† <i>Notropis buccula</i>	0.000
	<i>Notropis buchanani</i>	0.116
	† <i>Notropis oxyrhynchus</i>	0.002
	<i>Notropis shumardi</i>	0.100
	<i>Notropis stramineus</i>	0.599
	<i>Notropis texanus</i>	0.317
	<i>Notropis volucellus</i>	1.304
	<i>Opsopoeodus emiliae</i>	0.080
	<i>Phenacobius mirabilis</i>	0.022
<i>Pimephales promelas</i>	1.854	
<i>Pimephales vigilax</i>	7.493	
Catostomidae	<i>Carpiondes carpio</i>	0.207
	<i>Cycleptus elongatus</i>	0.007
	<i>Ictiobus bubalus</i>	0.030
	<i>Minytrema melanops</i>	0.001
	<i>Moxostoma congestum</i>	0.337
Characidae	† <i>Astyanax mexicanus</i>	0.532
	† <i>Piaractus brachypomus</i>	0.000

Table 5. continued

Family	Species	Relative Abundance
Ictaluridae	<i>Ameiurus melas</i>	0.073
	<i>Ameiurus natalis</i>	0.057
	<i>Ictalurus furcatus</i>	0.000
	<i>Ictalurus punctatus</i>	0.777
	<i>Noturus gyrinus</i>	0.008
	<i>Pylodictis olivaris</i>	0.104
Aphredoderidae	<i>Aphredoderus sayanus</i>	0.001
Mugilidae	<i>Agonostomus monticola</i>	0.000
	<i>Mugil cephalus</i>	0.002
	<i>Membras martinica</i>	0.001
Atherinopsidae	<i>Menidia audens</i>	2.924
Fundulidae	† <i>Fundulus grandis</i>	0.076
	<i>Fundulus notatus</i>	0.102
	<i>Fundulus zebrinus</i>	0.148
	† <i>Lucania parva</i>	0.003
Poeciliidae	<i>Gambusia affinis</i>	15.207
	† <i>Gambusia geiseri</i>	1.449
	† <i>Poecilia latipinna</i>	0.180
	† <i>Xiphophorus variatus</i>	0.074
Cyprinodontidae	<i>Cyprinodon rubrofluviatilis</i>	0.542
	† <i>Cyprinodon variegatus</i>	0.027
Moronidae	<i>Morone chrysops</i>	0.006
Centrarchidae	† <i>Lepomis auritus</i>	1.393
	<i>Lepomis cyanellus</i>	0.942
	<i>Lepomis gulosus</i>	0.099
	<i>Lepomis humilis</i>	0.379
	<i>Lepomis macrochirus</i>	1.876
	<i>Lepomis megalotis</i>	1.770
	<i>Lepomis microlophus</i>	0.114
	<i>Lepomis miniatus</i>	0.062
	† <i>Micropterus dolomieu</i>	0.001
	<i>Micropterus punctulatus</i>	0.047
	<i>Micropterus salmoides</i>	0.815
	<i>Micropterus treculii</i>	0.405
	<i>Pomoxis annularis</i>	0.101
	<i>Pomoxis nigromaculatus</i>	0.004
	Percidae	<i>Etheostoma chlorosoma</i>
<i>Etheostoma gracile</i>		0.026

**Table 5.** continued

<b>Family</b>	<b>Species</b>	<b>Relative Abundance</b>
	<i>Etheostoma lepidum</i>	0.975
	<i>Etheostoma parvipinne</i>	0.003
	<i>Etheostoma spectabile</i>	0.841
	<i>Percina carbonaria</i>	0.373
	<i>Percina macrolepida</i>	0.067
	<i>Percina sciera</i>	0.091
Sciaenidae	<i>Aplodinotus grunniens</i>	0.022
Cichlidae	† <i>Herichthys cyanoguttatus</i>	0.199
	† <i>Oreochromis aureus</i>	0.018

**Table 6.** Degrees of freedom (DF), sum of squares (SS), mean squares (MS), pseudo-F statistic, coefficient of determination (R<sup>2</sup>), and P-value of PERMANOVA analysis of spatial delineations in relation to Colorado River fish communities in period II (1981 – 2018).

	<b>Df</b>	<b>SS</b>	<b>MS</b>	<b>Pseudo-F</b>	<b>R<sup>2</sup></b>	<b>P-value</b>
Georegion	4	2.2977	0.57441	5.767	0.40812	0.0001
Mainstem or Tributary	1	0.0894	0.08943	0.8979	0.01588	0.4812
Stream Order	3	0.4519	0.15064	1.5124	0.08027	0.0883
River km from Mouth	1	0.0831	0.08313	0.8346	0.01477	0.503
Sub-basin Length	1	0.118	0.11805	1.1852	0.02097	0.2866
Residuals	26	2.5897	0.0996		0.45999	
Total	36	5.6298			1	

**Table 7.** Relative abundances (%) of all species (listed in family order) for georegions in time periods I and II. Abbreviation for georegions: Paleozoic Georegion (PGR), Edwards Georegion (EGR), Llano Uplift Georegion (LGR), Balcones Georegion (BGR), and Cenozoic Georegion (CGR). Dagger (†) indicates non-native species.

Family	Species	PGR		EGR		LGR		BGR		CGR	
		Period I	Period II								
Lepisosteidae	<i>Lepisosteus oculatus</i>	-	0.001	-	-	-	-	-	-	0.140	0.056
	<i>Lepisosteus osseus</i>	0.255	0.019	-	0.029	-	0.163	-	-	-	0.056
Anguillidae	<i>Anguilla rostrata</i>	-	-	-	-	-	-	0.039	-	-	0.004
Clupeidae	<i>Dorosoma cepedianum</i>	0.488	1.286	0.058	0.658	-	0.312	1.639	-	0.735	2.602
	<i>Dorosoma petenense</i>	-	0.201	-	0.237	-	-	0.632	0.716	0.245	0.048
Engraulidae	<i>Anchoa mitchilli</i>	-	-	-	-	-	-	-	-	0.315	-
Cyprinidae	<i>Campostoma anomalum</i>	0.212	0.036	1.120	3.060	23.338	3.825	3.337	12.996	0.280	0.416
	† <i>Carassius auratus</i>	-	-	-	-	-	-	-	0.014	-	-
	† <i>Ctenopharyngodon idella</i>	-	-	-	-	-	-	-	-	-	0.004
	<i>Cyprinella lutrensis</i>	52.704	53.989	0.944	4.550	2.570	0.868	1.757	0.940	8.534	18.235
	<i>Cyprinella venusta</i>	3.712	2.328	19.118	26.009	24.309	55.643	30.424	31.922	1.679	13.769
	† <i>Cyprinus carpio</i>	-	0.415	-	0.005	-	0.156	-	-	-	0.071
	<i>Dionda nigrotaeniata</i>	1.230	-	4.479	2.291	0.120	1.472	0.632	-	-	-
	<i>Hybognathus placitus</i>	3.924	-	-	-	-	-	0.020	-	-	-
	<i>Hybopsis amnis</i>	-	-	-	-	-	-	0.474	-	0.315	0.479
	<i>Lythrurus fumeus</i>	-	-	-	-	-	-	0.178	0.074	7.030	2.617
	<i>Macrhybopsis</i>	0.742	-	0.201	-	0.045	0.027	0.217	-	18.328	2.127
	† <i>Notemigonus crysoleucas</i>	0.064	0.046	0.301	0.022	0.015	0.007	0.079	0.082	0.595	0.445
	<i>Notropis amabilis</i>	1.336	0.001	12.442	16.673	2.122	2.116	12.971	0.376	-	0.007
	† <i>Notropis buccula</i>	-	-	-	-	-	-	0.020	-	-	-
	<i>Notropis buchanani</i>	1.166	0.177	-	-	0.209	-	0.533	-	-	-



**Table 7.** continued

Family	Species	PGR		EGR		LGR		BGR		CGR	
		Period I	Period II								
Mugilidae	<i>Agonostomus monticola</i>	-	-	-	-	-	-	-	-	-	0.004
	<i>Mugil cephalus</i>	-	-	-	-	-	-	0.020	-	0.175	-
	<i>Membras martinica</i>	-	-	-	-	-	-	-	-	0.070	-
Atherinopsidae	<i>Menidia audens</i>	-	5.168	-	0.042	-	-	-	3.277	0.035	0.130
Fundulidae	† <i>Fundulus grandis</i>	-	0.148	-	-	-	-	-	-	0.035	-
	<i>Fundulus notatus</i>	0.339	0.033	-	-	-	0.007	1.540	0.128	1.294	0.568
	<i>Fundulus zebrinus</i>	0.233	0.007	0.694	0.012	4.273	0.231	2.428	-	-	-
	† <i>Lucania parva</i>	-	-	-	0.013	-	-	-	-	-	-
Poeciliidae	<i>Gambusia affinis</i>	1.972	14.290	9.083	18.982	17.421	7.176	14.215	23.762	5.841	11.404
	† <i>Gambusia geiseri</i>	0.488	-	12.199	4.853	-	-	-	-	-	-
	† <i>Poecilia latipinna</i>	-	-	-	-	0.015	-	0.079	1.092	-	1.374
	† <i>Xiphophorus variatus</i>	-	-	-	-	-	-	-	0.996	-	-
Cyprinodontidae	<i>Cyprinodon rubrofluviatilis</i>	4.496	0.943	-	-	-	-	-	-	-	-
	† <i>Cyprinodon variegatus</i>	-	0.052	-	-	-	-	-	-	-	-
Moronidae	<i>Morone chrysops</i>	0.042	0.007	-	-	0.030	0.027	-	-	-	0.004
Centrarchidae	† <i>Lepomis auritus</i>	0.064	0.019	1.212	2.243	9.009	6.491	1.402	5.082	-	0.650
	<i>Lepomis cyanellus</i>	7.126	0.554	1.796	0.927	2.391	2.272	3.870	0.936	1.749	0.620
	<i>Lepomis gulosus</i>	0.148	0.067	0.518	0.096	-	0.163	0.257	0.021	0.070	0.189
	<i>Lepomis humilis</i>	2.397	0.459	0.050	0.249	-	0.007	1.224	0.011	0.070	0.549
	<i>Lepomis macrochirus</i>	1.166	1.502	1.186	1.924	0.209	1.994	2.132	3.004	3.498	3.816
	<i>Lepomis megalotis</i>	3.351	1.085	1.270	1.836	0.971	2.699	2.804	2.801	2.064	4.856
	<i>Lepomis microlophus</i>	-	0.053	0.150	0.190	0.060	0.427	0.454	0.135	0.210	0.067
<i>Lepomis miniatus</i>	-	0.001	0.384	0.002	-	-	0.731	0.344	-	0.182	

Table 7. continued

Family	Species	PGR		EGR		LGR		BGR		CGR		
		Period I	Period II									
Percidae	† <i>Micropterus dolomieu</i>	-	-	0.008	0.001	-	-	-	-	-	0.004	
	<i>Micropterus punctulatus</i>	-	0.003	0.025	0.001	0.045	-	0.849	0.248	0.035	0.189	
	<i>Micropterus salmoides</i>	0.933	0.384	2.473	1.273	1.539	0.400	0.849	1.326	0.420	1.318	
	<i>Micropterus treculii</i>	0.021	0.045	0.760	0.365	2.689	0.916	2.962	1.021	0.769	1.028	
	<i>Pomoxis annularis</i>	0.127	0.143	-	0.078	0.030	0.007	0.217	-	0.035	0.074	
	<i>Pomoxis nigromaculatus</i>	-	-	-	0.001	0.015	-	-	-	-	-	0.045
	<i>Etheostoma chlorosoma</i>	-	-	-	-	-	-	0.020	0.209	0.874	0.238	
	<i>Etheostoma gracile</i>	-	-	-	-	-	-	-	-	1.854	0.167	
	<i>Etheostoma lepidum</i>	0.021	0.002	17.463	1.521	0.090	0.203	0.020	1.085	-	-	
	<i>Etheostoma parvipinne</i>	-	-	-	-	-	-	-	-	-	-	0.041
	<i>Etheostoma spectabile</i>	0.976	0.080	5.005	1.730	2.062	3.181	2.034	0.621	-	0.264	
	<i>Percina carbonaria</i>	0.382	0.103	1.613	0.603	0.523	1.858	0.612	0.021	0.665	0.516	
<i>Percina macrolepida</i>	0.212	0.066	0.025	0.059	0.030	-	0.691	0.067	0.280	-		
<i>Percina sciera</i>	-	-	-	0.002	-	-	0.375	0.035	0.385	1.129		
Sciaenidae	<i>Aplodinotus grunniens</i>	0.042	0.031	-	-	0.030	0.095	-	-	-	0.019	
Cichlidae	† <i>Herichthys cyanoguttatus</i>	0.064	0.011	0.618	0.353	0.463	0.522	0.257	0.603	0.070	0.264	
	† <i>Oreochromis aureus</i>	-	-	-	-	-	0.468	-	-	-	-	

**Table 8.** Percent variance explained and variable loadings of CCA axes I through IV for georegions and abiotic variables in period II (1981-2018).

<b>Variable</b>	<b>Axis I</b>	<b>Axis II</b>	<b>Axis III</b>	<b>Axis IV</b>
Percent Variance Explained	0.254	0.179	0.082	0.061
Paleozoid Georegion	0.808	-0.328	-0.030	-0.078
Edwards Georegion	-0.577	-0.425	-0.132	-0.308
Llano Uplift Georegion	-0.240	-0.138	-0.310	0.226
Balcones Georegion	-0.162	0.097	0.684	0.378
Cenozoic Georegion	0.031	0.916	-0.172	-0.029
Discharge	0.026	0.891	-0.284	0.041
Coefficient of Variation	0.299	-0.536	0.078	-0.273
Zero Flow Percentage	0.191	-0.164	0.426	-0.126
Base Flow Index	-0.518	0.149	-0.340	0.055
Dissolved Oxygen	0.315	0.036	-0.106	0.451
pH	-0.034	0.089	-0.452	0.157
Conductivity	0.737	-0.321	-0.103	0.421
Temperature	-0.440	0.624	-0.226	-0.097
Turbidity	0.595	0.247	-0.432	-0.230
Gradient	-0.439	-0.384	0.386	0.201
Precipitation	-0.150	0.881	0.032	0.170

**Table 9.** Species richness, Shannon-Weiner index ( $H$ ), and Shannon-Wiener evenness index ( $E_H$ ) for georegions in time periods I and II. Abbreviation for georegions: Paleozoic Georegion (PGR), Edwards Georegion (EGR), Llano Uplift Georegion (LGR), Balcones Georegion (BGR), and Cenozoic Georegion (CGR).

	PGR		EGR		LGR		BGR		CGR	
	Period I	Period II								
Species Richness	40	49	40	50	38	41	55	45	47	62
$H$	2.07	1.69	2.56	2.46	2.24	1.97	2.69	2.27	2.77	2.83
$E_H$	0.56	0.43	0.69	0.63	0.62	0.53	0.67	0.6	0.72	0.69

**Table 10.** Changes in discharge, base flow index (BFI), zero flow percentage (ZFP), coefficient of variation (CofV), nMDS distance, and Bray-Curtis dissimilarity from period I to period II across georegions. Abbreviation for georegions: Paleozoic Georegion (PGR), Edwards Georegion (EGR), Llano Uplift Georegion (LGR), Balcones Georegion (BGR), and Cenozoic Georegion (CGR).

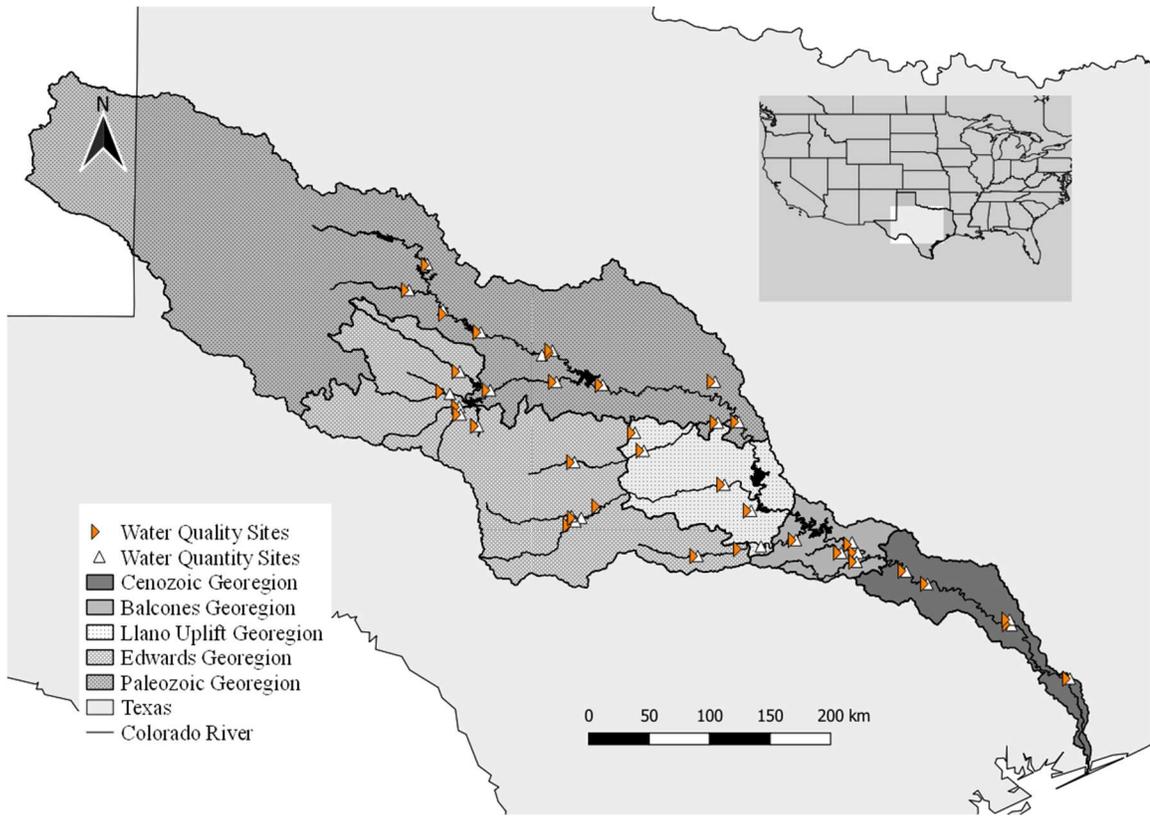
	<b>PGR</b>	<b>EGR</b>	<b>LGR</b>	<b>BGR</b>	<b>CGR</b>
$\Delta$ Discharge	-74%	-8%	-12%	-32%	-12%
$\Delta$ BFI	702%	50%	11%	96%	-1%
$\Delta$ ZFP	-55.36%	4.98%	-16.68%	-100.00%	0.00%
$\Delta$ CofV	11.43%	-27.95%	-5.58%	-36.26%	-35.33%
$\Delta$ nMDS	0.1637	0.0437	0.0333	0.1038	0.1131
Bray-Curtis Dissimilarity	31.22%	18.36%	22.89%	28.71%	27.77%

**Table 11.** SIMPER analysis results for species contributing to 50% dissimilarity between time periods for each georegion. Species are listed in the period in which they had higher abundance. Values indicate percent contribution to total dissimilarity between periods.

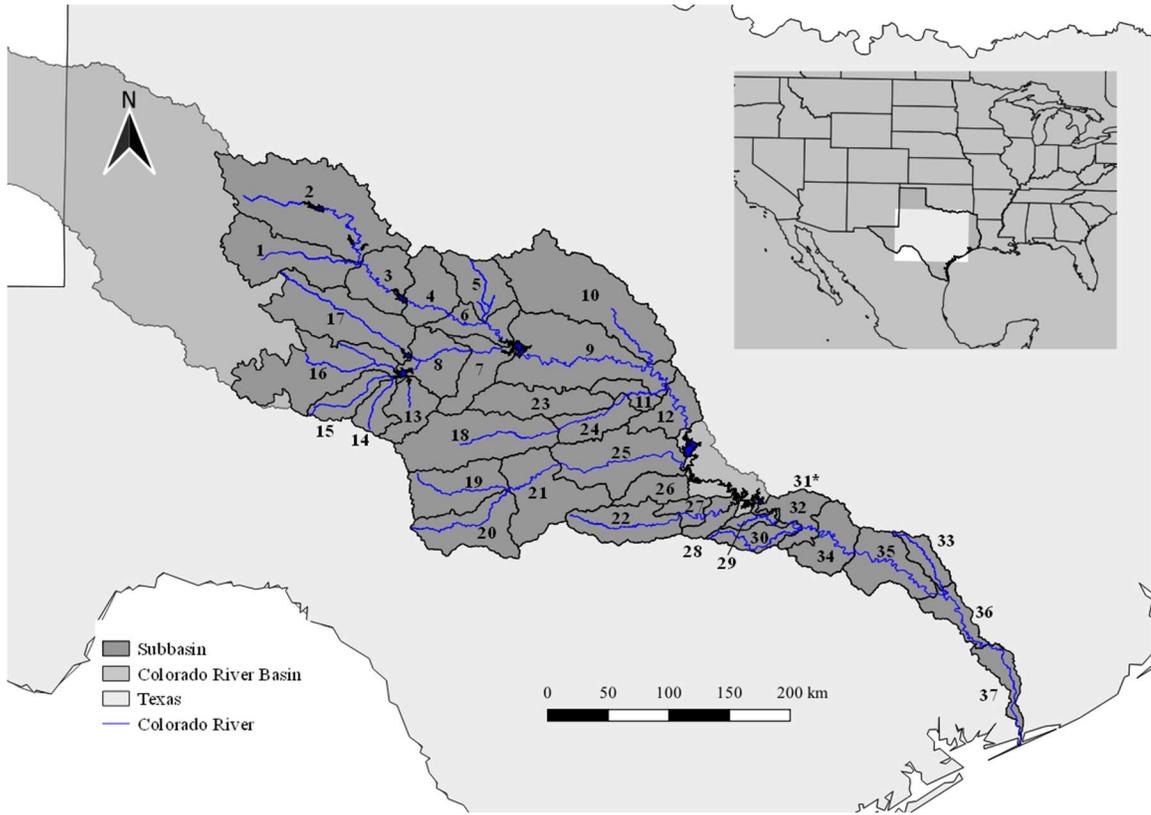
Period I		Period II	
<b>Paleozoic Georegion (31.2%)</b>			
<i>Hybognathus placitus</i>	(6.45)	<i>Menidia audens</i>	(6.91)
<i>Dionda nigrotaeniata</i>	(4.83)	<i>Moxostoma congestum</i>	(3.76)
<i>Macrhybopsis</i>	(4.25)	<i>Cyprinus carpio</i>	(3.68)
<i>Notropis amabilis</i>	(4.24)	<i>Gambusia affinis</i>	(3.48)
<i>Gambusia geiseri</i>	(3.83)	<i>Dorosoma petenense</i>	(3.07)
<i>Lepomis cyanellus</i>	(3.53)	<i>Fundulus grandis</i>	(2.84)
<b>Edwards Georegion (18.4%)</b>			
<i>Etheostoma lepidum</i>	(6.62)	<i>Dorosoma petenense</i>	(4.94)
<i>Macrhybopsis sp.</i>	(4.74)	<i>Pomoxis annularis</i>	(3.74)
<i>Fundulus zebrinus</i>	(4.12)	<i>Notropis volucellus</i>	(3.74)
<i>Lepomis miniatus</i>	(4.01)	<i>Cyprinella lutrensis</i>	(3.36)
<i>Gambusia geiseri</i>	(2.73)	<i>Menidia audens</i>	(3.22)
<i>Notemigonus crysoleucas</i>	(2.52)	<i>Lepisosteus osseus</i>	(2.93)
		<i>Dorosoma cepedianum</i>	(2.90)
		<i>Gambusia affinis</i>	(2.49)
<b>Llano Uplift Georegion (22.9%)</b>			
<i>Campostoma anomalum</i>	(5.05)	<i>Ictiobus bubalus</i>	(5.37)
<i>Fundulus zebrinus</i>	(4.70)	<i>Oreochromis aureus</i>	(5.22)
<i>Notropis buchanani</i>	(4.27)	<i>Dorosoma cepedianum</i>	(4.72)
		<i>Lepisosteus osseus</i>	(4.01)
		<i>Lepomis gulosus</i>	(4.01)
		<i>Cyprinus carpio</i>	(3.97)
		<i>Pylodictis olivaris</i>	(3.50)
		<i>Dionda nigrotaeniata</i>	(3.24)
		<i>Lepomis macrochirus</i>	(3.23)
<b>Balcones Georegion (28.7%)</b>			
<i>Fundulus zebrinus</i>	(5.00)	<i>Menidia audens</i>	(5.39)
<i>Dorosoma cepedianum</i>	(4.53)	<i>Xiphophorus variatus</i>	(4.00)
<i>Notropis amabilis</i>	(4.46)	<i>Etheostoma lepidum</i>	(2.59)
<i>Dionda nigrotaeniata</i>	(3.57)		
<i>Notropis buchanani</i>	(3.42)		
<i>Hybopsis amnis</i>	(3.32)		

**Table 11.** continued

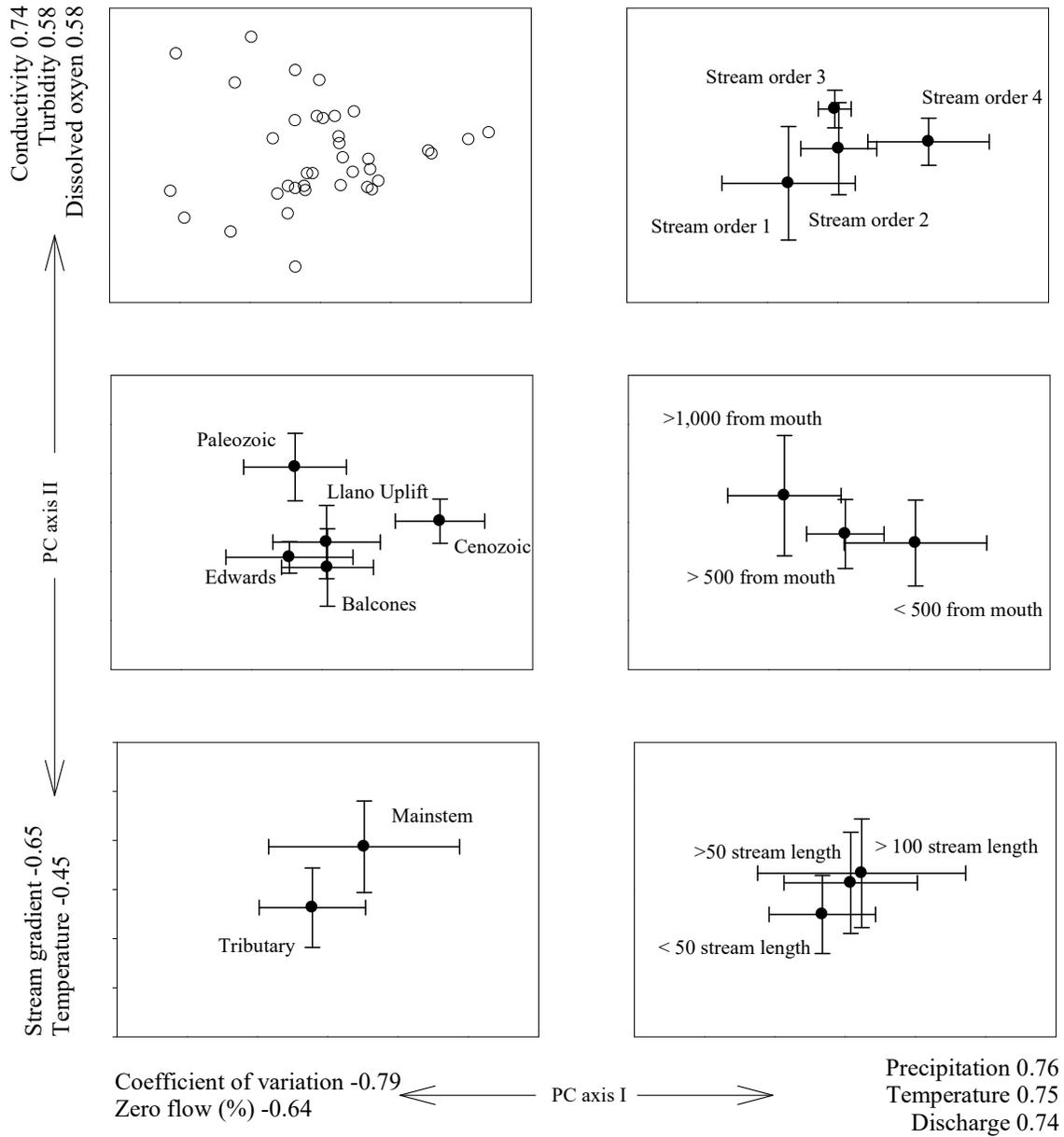
<b>Period I</b>		<b>Period II</b>	
<i>Lepomis humilis</i>	(2.93)		
<i>Macrhybopsis</i>	(2.73)		
<i>Pomoxis annularis</i>	(2.73)		
<i>Opsopoeodus emiliae</i>	(2.68)		
<i>Phenacobius mirabilis</i>	(2.35)		
<i>Notropis shumardi</i>	(2.24)		
 <b>Cenozoic Georegion (27.8%)</b>			
<i>Notropis shumardi</i>	(4.51)	<i>Poecilia latipinnate</i>	(4.15)
<i>Macrhybopsis</i>	(3.30)	<i>Notropis volucellus</i>	(3.81)
<i>Opsopoeodus emiliae</i>	(2.92)	<i>Lepomis auratus</i>	(3.44)
<i>Anchoa mitchilli</i>	(2.87)	<i>Cyprinella venusta</i>	(3.02)
<i>Percina macrolepida</i>	(2.79)	<i>Etheostoma spectabile</i>	(2.75)
<i>Pimephales promelas</i>	(2.70)	<i>Lepomis miniatus</i>	(2.50)
<i>Mugil cephalus</i>	(2.48)	<i>Notropis stramineus</i>	(2.45)
		<i>Ictalurus punctatus</i>	(2.14)
		<i>Cycleptus elongatus</i>	(2.14)
		<i>Ictiobus bubalus</i>	(2.10)



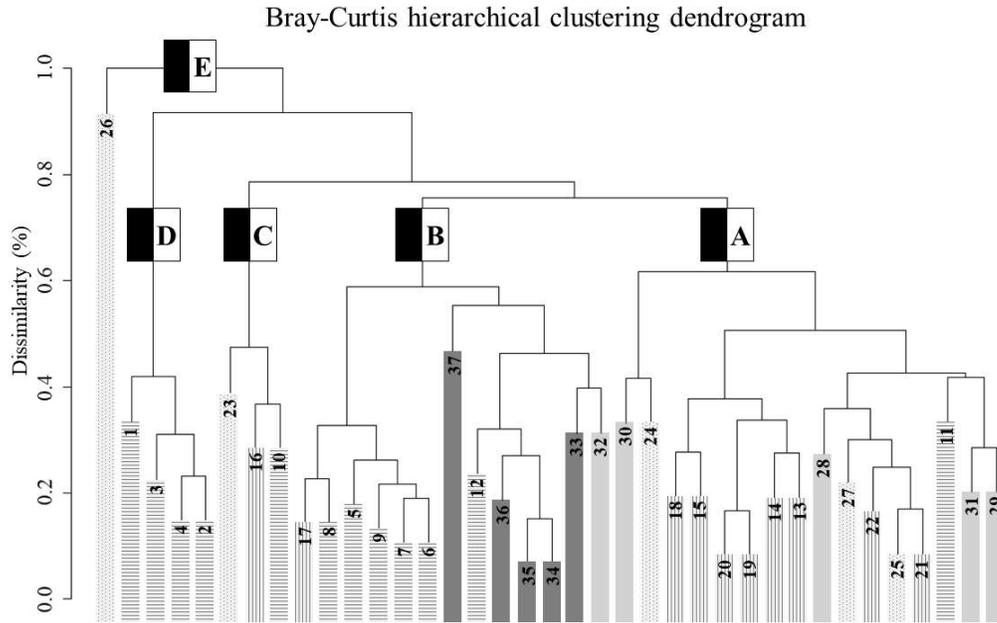
**Figure 1.** Georegions within the Colorado River basin of Texas and New Mexico. Location of water quality sites and water quantity stations are identified by georegion.



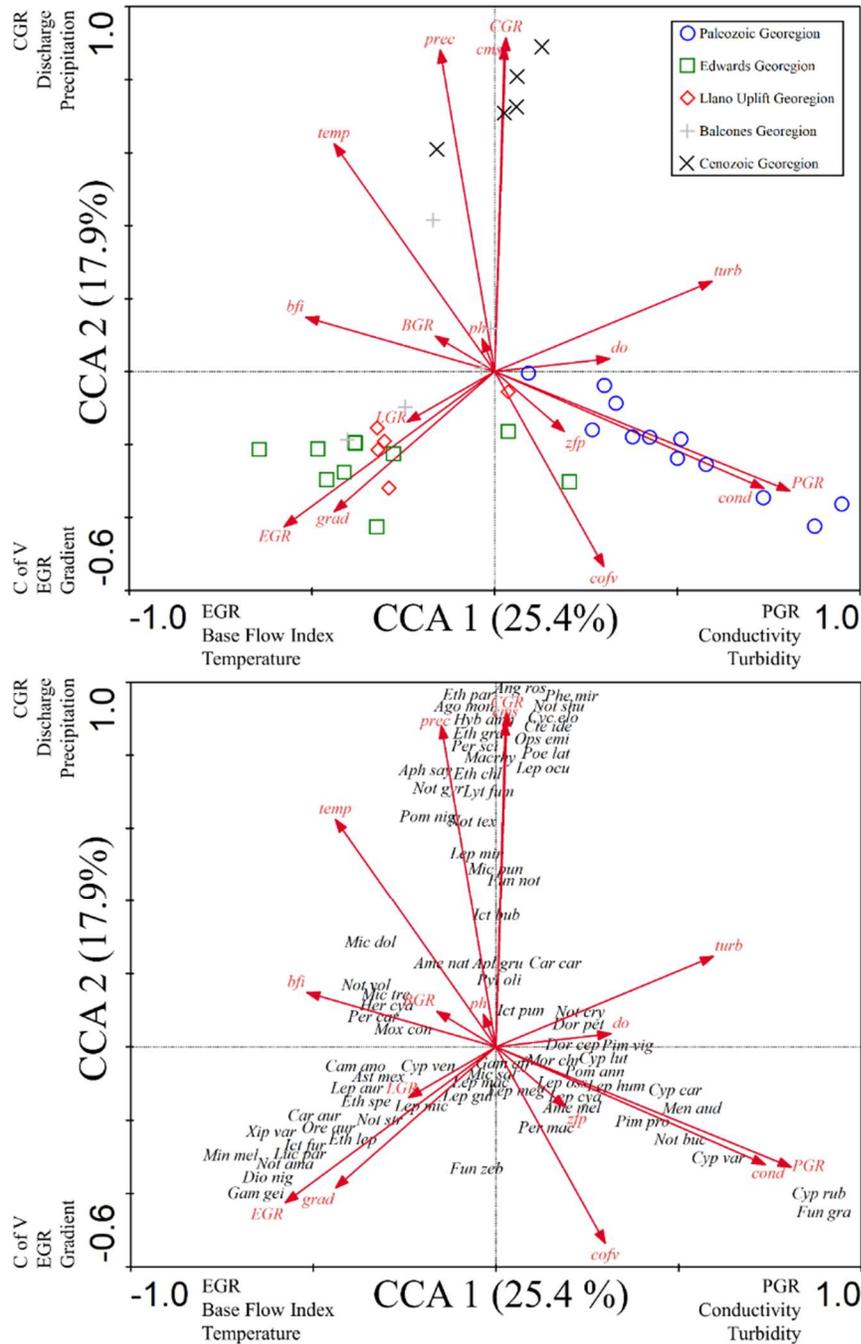
**Figure 2.** Map codes for sub-basins within the Colorado River basin of Texas. Map codes correspond with sub-basins names in Table 1.



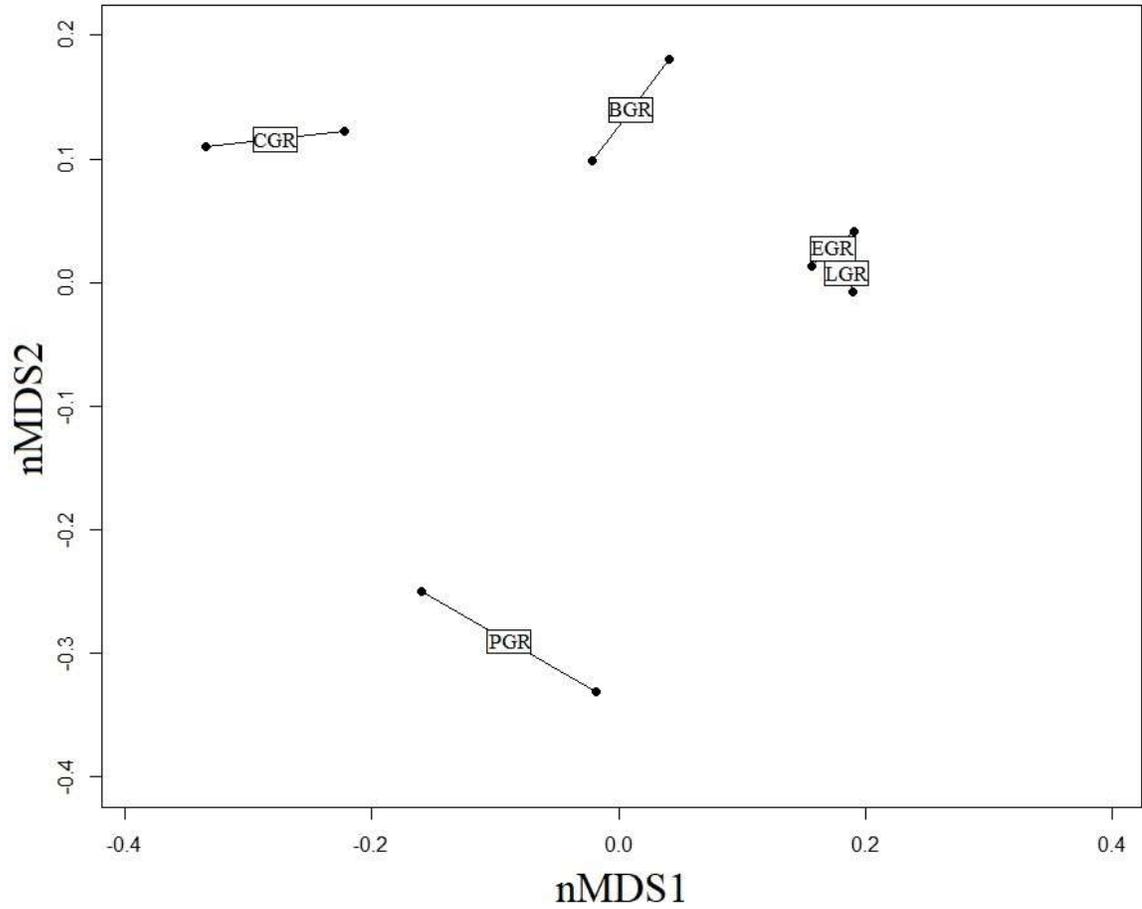
**Figure 3.** PCA plots of abiotic variables arranged by sub-basin (top left), georegion (middle left), stream type (bottom left), stream order (top right), distance from mouth (middle right), and length of river segment (bottom right).



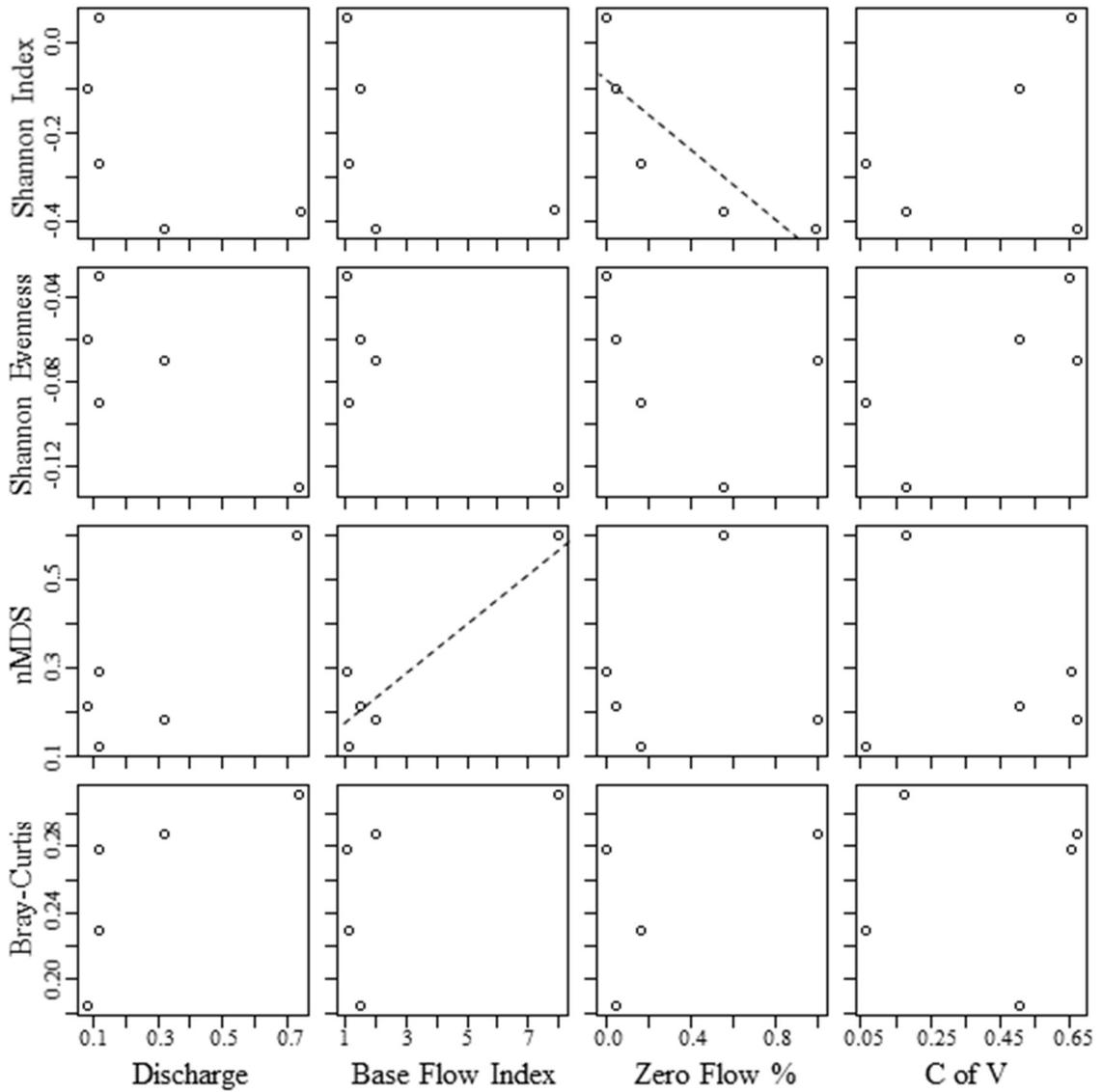
**Figure 4.** Hierarchical clustering dendrogram based on the Bray-Curtis dissimilarity index for fish communities in period II. Colors represent Georegion of each sampling area (dotted pattern – Paleozoic, vertical bars – Edwards, horizontal bars – Llano Uplift, gray – Balcones, black – Cenozoic)



**Figure 5.** CCA plots illustrating site-habitat (top) and species-habitat (bottom) relationships for period II. CCA1 explained 25.4% of variation and CCA2 17.9%. Abiotic variables include discharge (cms), coefficient of variation (cofv), zero flow percentage (zfp), base flow index (bfi), dissolved oxygen (do), pH, conductivity (cond), temperature (temp), turbidity (turb), gradient (grad), and precipitation (prec). Georegions are abbreviated as follows; Paleozoic (PGR), Edwards (EGR), Llano Uplift (LGR), Balcones (BGR), and Cenozoic (CGR) georegions. Species are included as the first three letters of genus and species. Three strongest positive and negative loadings for each axis are listed in respective locations.



**Figure 6.** nMDS plot showing change between time periods I and II for each georegion. Abbreviation for georegions: Paleozoic georegion (PGR), Edwards georegion (EGR), Llano Uplift georegion (LGR), Balcones georegion (BGR), and Cenozoic georegion (CGR).



**Figure 7.** Plots showing relationship between changes in community (Shannon Index, Shannon Evenness, nMDS, and Bray-Curtis dissimilarity) and changes in flow parameter (discharge, base flow index, zero flow percentage (%), and coefficient of variation (C of V)). Dashed line represents significant regression estimates.

## APPENDIX SECTION

**Appendix 1.1** Mean (median for pH) of abiotic variables (discharge, coefficient of variation, zero flow percentage, base flow index, dissolved oxygen, and pH) for each sub-basin. Sub-basins are arranged in order of map code.

Sub-basin	Map Code	Discharge	Coefficient of Variation	Zero Flow Percentage	Base Flow Index	Dissolved Oxygen	pH
Beals	1	21.28	7.59	25.82	0.01	8.70	8.04
Colorado City	2	15.79	10.23	3.85	0.01	8.52	7.53
Upper Spence	3	41.55	6.79	10.57	0.00	9.71	8.00
Lower Spence	4	9.17	5.16	13.06	0.17	10.20	8.00
Elm	5	33.25	8.96	29.21	0.00	8.19	8.19
Upper Ivie	6	36.06	4.88	0.00	0.03	10.13	8.06
Lower Concho	7	46.12	5.82	12.93	0.02	8.52	8.07
Upper Concho	8	15.86	4.53	0.00	0.07	9.81	7.97
Lower Ivie	9	42.58	5.73	1.82	0.17	8.33	8.20
Pecan	10	176.50	5.82	3.27	0.02	8.35	8.00
Lower San Saba	11	141.70	3.64	0.00	0.20	7.91	8.06
Upper Buchanan	12	578.50	3.96	0.00	0.07	8.28	8.10
South Concho	13	17.79	6.43	0.00	0.39	7.92	7.70
Dove	14	13.69	2.51	0.10	0.31	7.92	7.70
Spring	15	11.18	2.38	2.60	0.05	7.87	8.10
Middle Concho	16	5.81	9.43	66.39	0.00	6.80	7.67
North Concho	17	6.71	16.82	49.50	0.01	7.19	7.80
Upper San Saba	18	35.66	6.94	0.00	0.33	7.68	7.60
North Llano	19	35.65	7.51	8.46	0.04	6.98	7.80
South Llano	20	71.17	1.77	0.00	0.55	7.95	8.10
Upper Llano	21	170.50	6.00	0.00	0.49	8.58	8.10

Appendix 1.1 continued

Sub-basin	Map Code	Discharge	Coefficient of Variation	Zero Flow Percentage	Base Flow Index	Dissolved Oxygen	pH
Upper Pedernales	22	125.50	4.72	2.47	0.06	7.93	8.03
Brady	23	1.76	12.80	43.12	0.00	6.00	7.53
Middle San Saba	24	33.86	2.11	0.02	0.12	8.88	8.17
Lower Llano	25	359.90	5.26	0.00	0.14	9.44	8.40
Sandy	26	61.38	5.87	11.88	0.01	9.57	8.40
Middle Pedernales	27	215.20	6.16	4.29	0.02	9.62	8.40
Lower Pedernales	28	51.59	1.37	0.15	0.01	8.89	8.30
Barton	29	49.43	4.92	60.17	0.00	9.38	8.10
Onion	30	93.78	8.32	18.59	0.00	9.13	7.90
Waller	31	0.92	5.26	12.69	0.02	8.18	7.90
Austin	32	1585.00	2.19	0.00	0.15	8.07	7.76
Cummins	33	18.49	2.07	0.00	0.05	8.12	7.70
Bastrop	34	2097.00	2.01	0.00	0.23	8.93	8.10
Smithville	35	1889.00	2.07	0.00	0.24	8.55	8.09
Columbus	36	2411.00	2.26	0.00	0.26	8.28	8.10
Wharton	37	2792.00	2.18	0.00	0.17	8.36	8.10

**Appendix 1.2** Mean of abiotic variables (conductivity, temperature, turbidity, gradient, and precipitation) for each sub-basin.

<b>Sub-basin</b>	<b>Map Code</b>	<b>Conductivity</b>	<b>Temperature</b>	<b>Turbidity</b>	<b>Gradient</b>	<b>Precipitation</b>
Beals	1	5009.44	18.46	39.47	0.98	20
Colorado City	2	10044.13	17.64	16.50	0.51	20
Upper Spence	3	8276.02	19.02	39.47	0.64	21
Lower Spence	4	4662.37	19.61	39.47	0.67	22
Elm	5	2298.83	20.24	39.47	1.47	24
Upper Ivie	6	3304.55	20.22	39.47	0.63	24
Lower Concho	7	2087.67	19.83	39.47	0.97	24
Upper Concho	8	1513.39	21.32	39.47	0.93	22
Lower Ivie	9	1864.26	19.84	37.24	0.48	26
Pecan	10	790.93	19.45	51.34	0.55	29
Lower San Saba	11	539.39	19.90	34.31	0.59	28
Upper Buchanan	12	888.70	20.05	57.94	0.43	29
South Concho	13	651.12	20.06	13.31	2.11	22
Dove	14	651.12	20.06	13.31	2.66	21
Spring	15	1034.36	20.23	13.31	2.46	21
Middle Concho	16	602.91	19.10	13.31	2.32	20
North Concho	17	1626.07	19.17	13.31	1.60	21
Upper San Saba	18	408.30	19.77	13.31	1.43	24
North Llano	19	494.56	21.46	13.00	2.01	24
South Llano	20	405.00	21.10	13.67	1.63	24
Upper Llano	21	424.97	21.04	14.93	1.14	25
Upper Pedernales	22	666.90	19.74	11.63	1.76	30
Brady	23	621.79	21.53	37.57	1.97	26
Middle San Saba	24	462.27	19.75	31.49	1.74	26

Appendix 1.2 continued

<b>Sub-basin</b>	<b>Map Code</b>	<b>Conductivity</b>	<b>Temperature</b>	<b>Turbidity</b>	<b>Gradient</b>	<b>Precipitation</b>
Lower Llano	25	385.11	21.55	10.95	1.53	28
Sandy	26	411.11	21.70	8.62	3.37	29
Middle Pedernales	27	647.35	20.55	13.19	2.62	32
Lower Pedernales	28	544.14	21.37	8.16	1.66	32
Barton	29	489.26	19.74	1.44	2.67	33
Onion	30	538.74	20.83	12.79	2.32	34
Waller	31	717.40	21.12	8.15	7.97	33
Austin	32	537.16	20.93	3.84	0.43	34
Cummins	33	610.80	21.58	17.74	0.86	43
Bastrop	34	602.30	21.43	20.51	0.33	35
Smithville	35	599.60	21.62	28.98	0.30	37
Columbus	36	587.82	21.91	59.50	0.28	43
Wharton	37	573.33	22.36	71.59	0.26	46

**Appendix 2.1** Relative abundances (%) of all species (listed in family order) in each sub-basin (labeled with map code) in period II. Map code one through 10 are displayed in this table. Dagger (†) indicated non-native species.

Family	Species	Map Code									
		1	2	3	4	5	6	7	8	9	10
Lepisosteidae	<i>Lepisosteus oculatus</i>	-	-	-	-	-	-	-	-	0.00	-
	<i>Lepisosteus osseus</i>	-	-	-	0.01	0.04	0.01	0.04	0.01	0.03	-
Anguillidae	<i>Anguilla rostrata</i>	-	-	-	-	-	-	-	-	-	-
Clupeidae	<i>Dorosoma cepedianum</i>	0.19	0.06	1.04	0.56	0.99	0.75	5.45	0.96	0.15	-
	<i>Dorosoma petenense</i>	-	0.03	-	-	-	-	0.01	2.50	0.21	0.05
Cyprinidae	<i>Campostoma anomalum</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Carassius auratus</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Ctenopharyngodon idella</i>	-	-	-	-	-	-	-	-	-	-
	<i>Cyprinella lutrensis</i>	60.07	57.67	84.89	58.98	55.15	77.61	61.72	30.41	59.52	24.39
	<i>Cyprinella venusta</i>	-	0.24	-	0.15	0.64	-	1.38	18.23	0.91	3.09
	† <i>Cyprinus carpio</i>	-	5.86	0.02	0.07	0.01	-	0.00	-	-	0.07
	<i>Dionda nigrotaeniata</i>	-	-	-	-	-	-	-	-	-	-
	<i>Hybopsis amnis</i>	-	-	-	-	-	-	-	-	-	-
	<i>Lythrurus fumeus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Macrhybopsis</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Notemigonus crysoleucas</i>	-	0.02	-	0.01	0.02	0.00	0.03	0.15	0.00	1.31
	<i>Notropis amabilis</i>	-	-	-	-	0.01	-	-	-	-	-
	<i>Notropis buchanani</i>	-	-	-	0.01	0.34	0.53	0.00	-	0.46	-
	<i>Notropis shumardi</i>	-	-	-	-	-	-	-	-	-	-
	<i>Notropis stramineus</i>	-	0.02	-	-	-	-	-	-	0.38	-
	<i>Notropis texanus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Notropis volucellus</i>	-	-	-	-	-	-	-	-	0.10	-
	<i>Opsopoeodus emiliae</i>	-	-	-	-	-	-	-	-	-	-
	<i>Phenacobius mirabilis</i>	-	-	-	-	-	-	-	-	-	-
	<i>Pimephales promelas</i>	0.07	4.03	0.76	1.64	-	0.82	1.25	0.74	1.02	0.67
<i>Pimephales vigilax</i>	0.41	3.07	4.84	2.45	10.18	7.76	16.33	17.83	13.40	21.32	
Catostomidae	<i>Carpiodes carpio</i>	0.04	0.02	-	0.09	0.18	0.03	0.05	-	0.03	0.07

Appendix 2.1 continued

	Family	Species	Map Code									
			1	2	3	4	5	6	7	8	9	10
		<i>Cycleptus elongatus</i>	-	-	-	-	-	-	-	-	-	-
		<i>Ictiobus bubalus</i>	-	-	-	-	-	-	0.02	-	0.00	-
		<i>Minytrema melanops</i>	-	-	-	-	-	-	-	-	-	-
		<i>Moxostoma congestum</i>	-	-	-	-	-	-	0.06	0.02	0.00	-
	Characidae	† <i>Astyanax mexicanus</i>	-	-	-	-	-	-	0.03	-	-	-
	Ictaluridae	<i>Ameiurus melas</i>	-	0.09	-	0.00	0.06	0.00	-	-	0.01	0.69
		<i>Ameiurus natalis</i>	-	-	-	-	-	-	-	-	-	0.12
		<i>Ictalurus furcatus</i>	-	-	-	-	-	-	-	-	-	-
		<i>Ictalurus punctatus</i>	-	0.07	0.09	0.15	0.23	0.14	0.65	0.18	0.28	0.07
		<i>Noturus gyrinus</i>	-	-	-	-	-	-	-	-	-	-
		<i>Pylodictis olivaris</i>	-	-	-	0.01	-	0.09	0.02	-	0.14	-
	Aphredoderidae	<i>Aphredoderus sayanus</i>	-	-	-	-	-	-	-	-	-	-
	Mugilidae	<i>Agonostomus monticola</i>	-	-	-	-	-	-	-	-	-	-
	Atherinopsidae	<i>Menidia audens</i>	3.33	3.32	0.16	14.12	3.85	1.95	1.45	8.74	2.64	-
	Fundulidae	† <i>Fundulus grandis</i>	10.22	0.01	0.19	-	-	-	-	-	-	-
		<i>Fundulus notatus</i>	-	-	-	-	-	-	-	-	0.02	1.21
		<i>Fundulus zebrinus</i>	0.26	-	0.12	-	-	-	-	-	-	-
		† <i>Lucania parva</i>	-	-	-	-	-	-	-	-	-	-
	Poeciliidae	<i>Gambusia affinis</i>	5.56	16.21	6.56	20.96	18.25	7.81	6.93	11.60	15.47	10.52
		† <i>Gambusia geiseri</i>	-	-	-	-	-	-	-	-	-	-
		† <i>Poecilia latipinna</i>	-	-	-	-	-	-	-	-	-	-
		† <i>Xiphophorus variatus</i>	-	-	-	-	-	-	-	-	-	-
	Cyprinodontidae	<i>Cyprinodon rubrofluviatilis</i>	19.85	7.43	0.40	0.40	-	0.02	-	-	0.65	-
		† <i>Cyprinodon variegatus</i>	-	-	-	-	0.76	-	-	-	0.01	-
	Moronidae	<i>Morone chrysops</i>	-	-	-	0.00	-	-	-	-	-	0.02
	Centrarchidae	† <i>Lepomis auritus</i>	-	0.02	-	-	-	-	-	0.25	0.00	-
		<i>Lepomis cyanellus</i>	-	0.41	0.47	0.11	0.89	0.14	0.40	0.14	0.39	12.18
		<i>Lepomis gulosus</i>	-	-	-	-	0.17	0.29	0.06	0.04	0.01	0.07

Appendix 2.1 continued

Family	Species	Map Code									
		1	2	3	4	5	6	7	8	9	10
Percidae	<i>Lepomis humilis</i>	-	0.06	-	0.03	0.41	0.25	0.54	0.43	1.41	1.49
	<i>Lepomis macrochirus</i>	-	0.62	-	0.00	4.09	0.78	2.19	5.16	0.79	9.98
	<i>Lepomis megalotis</i>	-	0.72	0.43	0.18	1.76	0.79	1.00	1.27	1.20	0.99
	<i>Lepomis microlophus</i>	-	-	-	-	-	-	-	0.01	0.01	2.40
	<i>Lepomis miniatus</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Micropterus dolomieu</i>	-	-	-	-	-	-	-	-	-	-
	<i>Micropterus punctulatus</i>	-	-	-	-	0.04	-	-	-	-	-
	<i>Micropterus salmoides</i>	-	0.02	0.03	0.05	0.85	0.07	0.27	0.92	0.10	8.81
	<i>Micropterus treculii</i>	-	0.01	-	-	-	-	-	-	0.01	-
	<i>Pomoxis annularis</i>	-	-	-	0.00	0.06	0.14	0.08	0.15	0.54	0.17
	<i>Pomoxis nigromaculatus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma chlorosoma</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma gracile</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma lepidum</i>	-	-	-	-	-	-	0.00	-	-	-
	<i>Etheostoma parvipinne</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma spectabile</i>	-	-	-	-	0.66	-	-	-	-	-
	<i>Percina carbonaria</i>	-	-	-	-	-	-	-	-	-	0.07
	<i>Percina macrolepida</i>	-	-	-	0.00	0.37	0.02	0.03	0.10	0.14	0.20
	<i>Percina sciera</i>	-	-	-	-	-	-	-	-	-	-
	Sciaenidae	<i>Aplodinotus grunniens</i>	-	-	-	-	-	-	-	-	-
Cichlidae	† <i>Herichthys cyanoguttatus</i>	-	-	-	-	-	-	-	0.17	-	
	† <i>Oreochromis aureus</i>	-	-	-	-	-	-	-	-	-	

**Appendix 2.2** Relative abundances (%) of all species (listed in family order) in each sub-basin (labeled with map code) in period II. Map code 11 through 20 are displayed in this table. Dagger (†) indicated non-native species.

Family	Species	Map Code									
		11	12	13	14	15	16	17	18	19	20
Lepisosteidae	<i>Lepisosteus oculatus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Lepisosteus osseus</i>	-	0.04	-	-	-	0.45	0.02	0.02	0.04	-
Anguillidae	<i>Anguilla rostrata</i>	-	-	-	-	-	-	-	-	-	-
Clupeidae	<i>Dorosoma cepedianum</i>	-	1.08	0.48	0.11	-	6.13	3.97	0.02	0.17	-
	<i>Dorosoma petenense</i>	-	-	-	-	-	0.87	2.85	0.02	-	-
Cyprinidae	<i>Campostoma anomalum</i>	2.30	0.87	1.20	2.76	0.97	2.47	-	1.59	0.55	0.85
	† <i>Carassius auratus</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Ctenopharyngodon idella</i>	-	-	-	-	-	-	-	-	-	-
	<i>Cyprinella lutrensis</i>	21.97	40.13	-	0.20	-	3.40	21.19	-	-	-
	<i>Cyprinella venusta</i>	23.06	17.51	8.22	29.35	15.30	9.17	-	12.73	40.09	33.58
	† <i>Cyprinus carpio</i>	-	0.61	0.01	-	-	0.06	0.02	-	-	-
	<i>Dionda nigrotaeniata</i>	-	-	2.20	0.09	2.33	-	-	20.40	1.01	1.88
	<i>Hybopsis amnis</i>	-	-	-	-	-	-	-	-	-	-
	<i>Lythrurus fumeus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Macrhybopsis</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Notemigonus crysoleucas</i>	-	-	-	0.09	0.08	0.08	0.02	0.02	-	-
	<i>Notropis amabilis</i>	-	-	29.01	41.33	25.87	-	-	0.90	35.86	14.80
	<i>Notropis buchanani</i>	1.09	-	-	-	-	-	-	-	-	-
	<i>Notropis shumardi</i>	-	-	-	-	-	-	-	-	-	-
	<i>Notropis stramineus</i>	1.31	-	0.02	0.09	1.28	-	-	1.05	0.04	-
	<i>Notropis texanus</i>	-	-	0.02	-	-	-	-	-	-	-
<i>Notropis volucellus</i>	6.23	0.37	2.35	2.75	-	-	-	4.81	9.47	14.51	
<i>Opsopoeodus emiliae</i>	-	-	-	-	-	-	-	-	-	-	
<i>Phenacobius mirabilis</i>	-	-	-	-	-	-	-	-	-	-	
<i>Pimephales promelas</i>	-	-	-	-	0.02	-	-	-	-	-	
<i>Pimephales vigilax</i>	2.51	10.01	-	0.02	0.30	2.81	10.75	0.94	-	-	
Catostomidae	<i>Carpionodes carpio</i>	-	0.36	-	0.01	-	0.53	-	-	-	

Appendix 2.2 continued

Family	Species	Map Code									
		11	12	13	14	15	16	17	18	19	20
	<i>Cycleptus elongatus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Ictiobus bubalus</i>	-	0.06	-	-	-	-	-	-	-	-
	<i>Minytrema melanops</i>	-	-	-	-	-	-	-	-	-	0.02
	<i>Moxostoma congestum</i>	0.33	1.50	0.03	0.09	0.18	0.51	0.31	0.02	0.61	0.32
Characidae	† <i>Astyanax mexicanus</i>	10.93	-	10.13	-	-	-	-	-	-	-
Ictaluridae	<i>Ameiurus melas</i>	-	-	0.01	-	0.02	4.36	0.02	-	-	-
	<i>Ameiurus natalis</i>	-	0.04	0.25	-	-	-	-	0.04	-	-
	<i>Ictalurus furcatus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Ictalurus punctatus</i>	1.42	2.28	0.03	0.06	0.14	0.08	0.21	0.10	0.04	1.06
	<i>Noturus gyrinus</i>	-	-	0.01	-	-	-	-	-	-	-
	<i>Pylodictis olivaris</i>	1.09	1.53	-	0.01	0.04	-	-	0.02	-	0.23
Aphredoderidae	<i>Aphredoderus sayanus</i>	-	-	-	-	-	-	-	-	-	-
Mugilidae	<i>Agonostomus monticola</i>	-	-	-	-	-	-	-	-	-	-
Atherinopsidae	<i>Menidia audens</i>	-	0.42	0.06	-	-	0.48	0.16	-	-	-
Fundulidae	† <i>Fundulus grandis</i>	-	-	-	-	-	-	-	-	-	-
	<i>Fundulus notatus</i>	-	0.16	-	-	-	-	-	-	-	-
	<i>Fundulus zebrinus</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Lucania parva</i>	-	-	-	-	-	-	-	0.21	-	-
Poeciliidae	<i>Gambusia affinis</i>	17.38	4.09	5.28	8.09	31.98	32.84	40.73	46.59	1.07	9.24
	† <i>Gambusia geiseri</i>	-	-	32.96	5.17	-	0.65	-	-	-	-
	† <i>Poecilia latipinna</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Xiphophorus variatus</i>	-	-	-	-	-	-	-	-	-	-
Cyprinodontidae	<i>Cyprinodon rubrofluviatilis</i>	-	-	-	-	-	-	-	-	-	-
	† <i>Cyprinodon variegatus</i>	-	-	-	-	-	-	-	-	-	-
Moronidae	<i>Morone chrysops</i>	-	0.18	-	-	-	-	-	-	-	-
Centrarchidae	† <i>Lepomis auritus</i>	-	0.40	0.73	1.43	3.13	0.06	0.03	1.02	2.31	5.04
	<i>Lepomis cyanellus</i>	1.20	0.82	0.46	0.13	0.06	15.41	0.05	0.02	0.02	0.07
	<i>Lepomis gulosus</i>	-	0.04	0.04	0.13	0.32	0.11	0.16	0.04	0.08	0.16

Appendix 2.2 continued

Family	Species	Map Code									
		11	12	13	14	15	16	17	18	19	20
	<i>Lepomis humilis</i>	-	0.12	-	-	0.34	0.06	1.92	0.13	-	-
	<i>Lepomis macrochirus</i>	1.42	1.74	0.53	0.58	4.71	7.98	7.67	1.11	0.23	0.18
	<i>Lepomis megalotis</i>	2.62	9.40	0.66	4.03	2.29	2.33	3.86	0.65	0.99	1.65
	<i>Lepomis microlophus</i>	0.11	0.04	0.03	0.05	2.56	0.03	0.07	0.04	0.02	0.02
	<i>Lepomis miniatus</i>	0.11	0.01	0.02	-	-	-	-	-	-	-
	† <i>Micropterus dolomieu</i>	-	-	-	0.01	-	-	-	-	-	-
	<i>Micropterus punctulatus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Micropterus salmoides</i>	-	0.55	0.68	0.63	5.50	5.17	5.35	0.42	0.40	0.12
	<i>Micropterus treculii</i>	1.75	1.02	0.18	0.24	-	-	-	0.31	0.55	1.47
	<i>Pomoxis annularis</i>	-	0.04	0.02	-	0.02	1.29	0.21	0.04	-	-
	<i>Pomoxis nigromaculatus</i>	-	-	-	-	-	-	-	-	-	-
Percidae	<i>Etheostoma chlorosoma</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma gracile</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma lepidum</i>	-	0.04	2.43	2.46	2.46	2.05	-	2.91	1.54	0.35
	<i>Etheostoma parvipinne</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma spectabile</i>	1.53	0.84	1.69	-	0.04	0.62	-	2.57	4.15	9.35
	<i>Percina carbonaria</i>	1.64	2.74	0.12	-	-	-	-	1.15	0.61	3.78
	<i>Percina macrolepida</i>	-	-	0.05	0.12	-	-	0.42	0.10	-	-
	<i>Percina sciera</i>	-	-	-	-	-	-	-	-	-	-
Sciaenidae	<i>Aplodinotus grunniens</i>	-	0.91	-	-	-	-	-	-	-	-
Cichlidae	† <i>Herichthys cyanoguttatus</i>	-	-	0.14	-	0.04	-	-	0.02	0.15	1.31
	† <i>Oreochromis aureus</i>	-	-	-	-	-	-	-	-	-	-

**Appendix 2.3** Relative abundances (%) of all species (listed in family order) in each sub-basin (labeled with map code) in period II. Map code 21 through 30 are displayed in this table. Dagger (†) indicated non-native species.

Family	Species	Map Code									
		21	22	23	24	25	26	27	28	29	30
Lepisosteidae	<i>Lepisosteus oculatus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Lepisosteus osseus</i>	0.02	0.01	-	-	0.18	-	-	-	-	-
Anguillidae	<i>Anguilla rostrata</i>	-	-	-	-	-	-	-	-	-	-
Clupeidae	<i>Dorosoma cepedianum</i>	0.02	0.14	-	-	0.31	-	-	-	-	-
	<i>Dorosoma petenense</i>	-	-	-	-	-	-	-	-	-	-
Cyprinidae	<i>Campostoma anomalum</i>	4.58	3.98	-	2.33	3.94	11.18	15.41	18.82	15.52	9.15
	† <i>Carassius auratus</i>	-	-	-	-	-	-	-	0.11	-	-
	† <i>Ctenopharyngodon idella</i>	-	-	-	-	-	-	-	-	-	-
	<i>Cyprinella lutrensis</i>	0.02	18.77	-	-	1.79	1.16	1.44	8.52	0.03	0.09
	<i>Cyprinella venusta</i>	47.44	28.10	-	46.51	58.05	2.44	36.58	34.23	37.11	62.77
	† <i>Cyprinus carpio</i>	-	-	-	-	0.16	-	0.07	-	-	-
	<i>Dionda nigrotaeniata</i>	1.01	1.12	-	-	0.08	-	6.50	-	-	-
	<i>Hybopsis amnis</i>	-	-	-	-	-	-	-	-	-	-
	<i>Lythrurus fumeus</i>	-	-	-	-	-	-	-	-	-	1.90
	<i>Macrhybopsis</i>	0.02	-	-	-	0.01	-	-	-	-	-
	† <i>Notemigonus crysoleucas</i>	-	-	2.04	-	-	-	-	0.06	0.04	0.09
	<i>Notropis amabilis</i>	16.67	3.66	-	-	1.37	-	1.07	5.94	-	-
	<i>Notropis buchanani</i>	-	-	-	-	-	-	-	-	-	-
	<i>Notropis shumardi</i>	-	-	-	-	-	-	-	-	-	-
	<i>Notropis stramineus</i>	4.43	0.22	-	-	4.76	-	-	-	0.01	5.89
	<i>Notropis texanus</i>	-	-	-	-	-	-	-	-	1.06	-
<i>Notropis volucellus</i>	4.82	0.97	-	-	2.11	-	-	-	0.82	-	
<i>Opsopoeodus emiliae</i>	-	-	-	-	-	-	-	-	-	-	
<i>Phenacobius mirabilis</i>	-	-	-	-	-	-	-	-	-	-	
<i>Pimephales promelas</i>	-	-	-	-	-	-	-	-	1.67	-	
<i>Pimephales vigilax</i>	0.02	2.47	-	-	0.89	-	-	6.11	-	-	
Catostomidae	<i>Carpionodes carpio</i>	0.14	0.02	-	-	0.77	-	-	0.06	-	-

Appendix 2.3 continued

	Family	Species	Map Code										
			21	22	23	24	25	26	27	28	29	30	
69	Characidae	<i>Cycleptus elongatus</i>	-	-	-	-	-	-	-	-	-	-	
		<i>Ictiobus bubalus</i>	-	-	-	-	0.71	-	-	-	-	-	
		<i>Minytrema melanops</i>	0.01	-	-	-	-	-	-	-	-	-	
		<i>Moxostoma congestum</i>	0.36	0.10	-	-	0.16	-	0.13	0.11	0.18	-	
		† <i>Astyanax mexicanus</i>	0.01	-	-	-	-	-	1.24	-	1.90	-	
		Ictaluridae	<i>Ameiurus melas</i>	-	0.09	4.08	-	-	-	-	-	0.01	-
			<i>Ameiurus natalis</i>	0.00	0.02	-	-	-	-	-	0.67	0.03	-
			<i>Ictalurus furcatus</i>	-	0.01	-	-	-	-	-	-	-	-
			<i>Ictalurus punctatus</i>	0.26	4.28	-	-	0.27	-	0.57	0.39	0.26	0.18
		Aphredoderidae	<i>Noturus gyrinus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Pylodictis olivaris</i>		0.04	0.13	-	1.16	0.06	-	-	-	0.01	-	
	Mugilidae	<i>Aphredoderus sayanus</i>	-	-	-	-	-	-	-	-	-	-	
	Atherinopsidae	<i>Agonostomus monticola</i>	-	-	-	-	-	-	-	-	-	-	
	Fundulidae	<i>Menidia audens</i>	-	0.01	-	-	-	-	-	0.45	0.11	-	
		† <i>Fundulus grandis</i>	-	-	-	-	-	-	-	-	-	-	
		<i>Fundulus notatus</i>	-	-	2.04	-	-	-	-	-	0.06	-	
	Poeciliidae	<i>Fundulus zebrinus</i>	0.02	0.02	-	-	0.04	3.34	0.30	-	-	-	
		† <i>Lucania parva</i>	-	-	-	-	-	-	-	-	-	-	
		<i>Gambusia affinis</i>	6.92	23.07	38.78	5.81	8.51	72.43	11.56	2.46	20.83	4.98	
		† <i>Gambusia geiseri</i>	-	-	-	-	-	-	-	-	-	-	
† <i>Poecilia latipinna</i>		-	-	-	-	-	-	-	-	-	-		
Cyprinodontidae	† <i>Xiphophorus variatus</i>	-	-	-	-	-	-	-	-	-	-		
	<i>Cyprinodon rubrofluviatilis</i>	-	-	-	-	-	-	-	-	-	-		
Moronidae	† <i>Cyprinodon variegatus</i>	-	-	-	-	-	-	-	-	-	-		
	<i>Morone chrysops</i>	-	-	-	-	0.02	-	-	-	-	-		
Centrarchidae	† <i>Lepomis auritus</i>	3.28	3.64	-	2.33	6.61	3.02	3.42	1.29	7.40	2.17		
	<i>Lepomis cyanellus</i>	0.05	0.91	6.12	-	0.35	-	9.45	3.36	0.79	0.36		
	<i>Lepomis gulosus</i>	0.08	0.07	8.16	-	0.12	-	0.03	0.17	0.01	-		

Appendix 2.3 continued

Family	Species	Map Code									
		21	22	23	24	25	26	27	28	29	30
Percidae	<i>Lepomis humilis</i>	-	0.54	-	-	-	-	0.03	-	-	-
	<i>Lepomis macrochirus</i>	0.81	2.07	18.37	1.16	1.18	0.90	3.25	1.46	4.27	0.82
	<i>Lepomis megalotis</i>	1.06	2.43	12.24	9.30	1.29	0.45	4.19	9.86	1.95	5.80
	<i>Lepomis microlophus</i>	0.03	0.07	-	-	0.06	0.13	1.71	-	0.18	-
	<i>Lepomis miniatus</i>	-	-	-	-	-	-	-	-	0.51	-
	† <i>Micropterus dolomieu</i>	-	-	-	-	-	-	-	-	-	-
	<i>Micropterus punctulatus</i>	-	0.01	-	-	-	-	-	-	0.29	-
	<i>Micropterus salmoides</i>	0.17	0.51	6.12	-	0.22	2.06	0.60	0.50	1.49	4.71
	<i>Micropterus treculii</i>	0.77	0.38	-	6.98	0.70	-	0.77	4.03	1.11	-
	<i>Pomoxis annularis</i>	-	-	2.04	-	-	-	-	-	-	-
	<i>Pomoxis nigromaculatus</i>	-	0.01	-	-	-	-	-	-	-	-
	<i>Etheostoma chlorosoma</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma gracile</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma lepidum</i>	0.76	1.10	-	-	0.14	-	0.37	0.11	1.60	0.91
	<i>Etheostoma parvipinne</i>	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma spectabile</i>	3.73	0.16	-	-	3.04	2.89	0.40	1.23	-	-
	<i>Percina carbonaria</i>	1.37	0.76	-	24.42	1.15	-	0.40	-	0.01	0.09
	<i>Percina macrolepida</i>	-	0.02	-	-	-	-	-	-	-	0.09
	<i>Percina sciera</i>	-	0.02	-	-	-	-	-	-	-	-
	Sciaenidae	<i>Aplodinotus grunniens</i>	-	-	-	-	0.09	-	-	-	-
Cichlidae	† <i>Herichthys cyanoguttatus</i>	1.08	0.12	-	-	0.65	-	0.50	0.06	0.74	
	† <i>Oreochromis aureus</i>	-	-	-	-	0.21	-	-	-	-	

**Appendix 2.4** Relative abundances (%) of all species (listed in family order) in each sub-basin (labeled with map code) in period II. Map code 31 through 37 are displayed in this table. Dagger (†) indicated non-native species.

Family	Species	Map Code						
		31	32	33	34	35	36	37
Lepisosteidae	<i>Lepisosteus oculatus</i>	-	-	-	0.07	0.07	0.04	0.03
	<i>Lepisosteus osseus</i>	-	-	-	0.07	0.10	-	-
Anguillidae	<i>Anguilla rostrata</i>	-	-	-	-	-	0.04	-
Clupeidae	<i>Dorosoma cepedianum</i>	-	-	4.17	3.81	1.30	2.17	0.65
	<i>Dorosoma petenense</i>	-	4.01	0.32	0.03	-	-	0.06
Cyprinidae	<i>Campostoma anomalum</i>	10.91	4.21	0.28	0.56	0.58	0.07	-
	† <i>Carassius auratus</i>	0.07	-	-	-	-	-	-
	† <i>Ctenopharyngodon idella</i>	-	-	-	0.01	-	-	-
	<i>Cyprinella lutrensis</i>	1.77	1.13	4.78	12.81	12.70	22.64	52.37
	<i>Cyprinella venusta</i>	21.30	12.32	16.37	17.23	15.67	9.67	0.54
	† <i>Cyprinus carpio</i>	-	-	-	0.09	0.13	-	-
	<i>Dionda nigrotaeniata</i>	-	-	-	-	-	-	-
	<i>Hybopsis amnis</i>	-	-	-	1.17	-	-	-
	<i>Lythrurus fumeus</i>	-	-	3.81	3.17	3.64	0.07	-
	<i>Macrhybopsis</i>	-	-	-	2.03	0.74	3.02	6.02
	† <i>Notemigonus crysoleucas</i>	-	0.28	-	0.05	1.63	-	-
	<i>Notropis amabilis</i>	-	-	-	0.02	-	-	-
	<i>Notropis buchanani</i>	-	-	-	-	-	-	-
	<i>Notropis shumardi</i>	-	-	-	0.40	-	-	0.17
	<i>Notropis stramineus</i>	-	-	-	0.41	-	-	-
	<i>Notropis texanus</i>	-	1.89	2.09	2.64	5.59	0.04	-
	<i>Notropis volucellus</i>	-	1.41	2.69	8.73	6.90	2.99	0.09
<i>Opsopoeodus emiliae</i>	-	0.10	-	0.24	0.18	1.67	-	
<i>Phenacobius mirabilis</i>	-	-	-	0.07	0.09	1.64	0.26	
<i>Pimephales promelas</i>	0.11	0.97	0.04	-	-	0.04	0.03	
<i>Pimephales vigilax</i>	-	2.48	1.16	14.66	9.15	12.30	12.87	
Catostomidae	<i>Carpionodes carpio</i>	-	-	0.04	0.97	0.75	3.63	4.17

Appendix 2.4 continued

	Family	Species	Map Code							
			31	32	33	34	35	36	37	
63	Characidae	<i>Cycleptus elongatus</i>	-	-	-	0.14	0.14	-	-	
		<i>Ictiobus bubalus</i>	-	0.02	-	0.05	0.13	0.21	0.09	
		<i>Minytrema melanops</i>	-	-	-	-	-	-	-	
		<i>Moxostoma congestum</i>	0.32	0.06	0.12	0.67	0.78	0.39	-	
		† <i>Astyanax mexicanus</i>	2.41	0.40	-	0.03	-	-	-	
		Ictaluridae	<i>Ameiurus melas</i>	0.11	-	-	0.05	0.01	-	-
			<i>Ameiurus natalis</i>	0.35	-	0.16	0.19	0.31	0.07	-
			<i>Ictalurus furcatus</i>	-	-	-	-	-	-	-
			<i>Ictalurus punctatus</i>	0.07	0.08	0.04	1.28	5.10	12.87	14.77
		Aphredoderidae	<i>Noturus gyrinus</i>	-	-	0.56	0.02	0.01	-	0.06
	<i>Pylodictis olivaris</i>		-	0.02	0.08	0.52	0.91	0.53	0.23	
	<i>Aphredoderus sayanus</i>		-	-	0.12	-	-	-	-	
	Mugilidae		<i>Agonostomus monticola</i>	-	-	-	0.01	-	-	-
	Atherinopsidae	<i>Menidia audens</i>	-	17.80	-	0.32	-	-	-	
Fundulidae	† <i>Fundulus grandis</i>	-	-	-	-	-	-	-		
	<i>Fundulus notatus</i>	0.11	0.44	2.41	0.45	0.37	0.60	-		
	<i>Fundulus zebrinus</i>	-	-	-	-	-	-	-		
Poeciliidae	† <i>Lucania parva</i>	-	-	-	-	-	-	-		
	<i>Gambusia affinis</i>	32.28	40.80	18.26	12.52	15.72	1.85	2.04		
	† <i>Gambusia geiseri</i>	-	-	-	-	-	-	-		
	† <i>Poecilia latipinna</i>	-	6.11	-	2.10	0.31	0.50	2.90		
Cyprinodontidae	† <i>Xiphophorus variatus</i>	9.96	-	-	-	-	-	-		
	<i>Cyprinodon rubrofluviatilis</i>	-	-	-	-	-	-	-		
	† <i>Cyprinodon variegatus</i>	-	-	-	-	-	-	-		
Moronidae	<i>Morone chrysops</i>	-	-	-	0.01	-	-	-		
Centrarchidae	† <i>Lepomis auritus</i>	2.91	0.26	3.57	0.29	0.67	0.25	-		
	<i>Lepomis cyanellus</i>	2.20	-	0.16	0.62	1.15	0.46	-		
	<i>Lepomis gulosus</i>	-	0.02	0.64	0.18	0.16	-	0.11		

Appendix 2.4 continued

Family	Species	Map Code						
		31	32	33	34	35	36	37
	<i>Lepomis humilis</i>	-	0.06	-	1.31	0.04	-	-
	<i>Lepomis macrochirus</i>	1.70	0.38	14.53	2.58	2.76	6.29	0.26
	<i>Lepomis megalotis</i>	7.12	0.18	15.13	2.50	4.55	10.74	0.88
	<i>Lepomis microlophus</i>	0.25	-	-	0.07	0.13	0.04	-
	<i>Lepomis miniatus</i>	-	0.16	1.04	0.12	0.07	0.18	-
	† <i>Micropterus dolomieu</i>	-	-	-	-	0.01	-	-
	<i>Micropterus punctulatus</i>	0.04	0.38	0.20	0.38	-	0.04	0.09
	<i>Micropterus salmoides</i>	0.21	0.93	2.85	0.80	2.35	1.03	0.03
	<i>Micropterus treculii</i>	0.32	0.28	1.85	0.79	1.47	1.32	0.09
	<i>Pomoxis annularis</i>	-	-	0.24	0.08	0.03	0.04	0.06
	<i>Pomoxis nigromaculatus</i>	-	-	0.44	-	-	0.04	-
Percidae	<i>Etheostoma chlorosoma</i>	-	1.17	0.32	0.14	0.58	-	-
	<i>Etheostoma gracile</i>	-	-	0.16	0.14	0.31	0.11	-
	<i>Etheostoma lepidum</i>	0.14	0.22	-	-	-	-	-
	<i>Etheostoma parvipinne</i>	-	-	-	0.10	-	-	-
	<i>Etheostoma spectabile</i>	4.78	0.36	-	0.51	0.21	-	-
	<i>Percina carbonaria</i>	-	0.08	0.08	0.58	0.78	0.57	0.06
	<i>Percina macrolepida</i>	0.04	0.34	-	-	-	-	-
	<i>Percina sciera</i>	-	0.20	1.16	1.13	1.08	1.24	1.11
Sciaenidae	<i>Aplodinotus grunniens</i>	-	-	-	0.01	0.04	0.04	-
Cichlidae	† <i>Herichthys cyanoguttatus</i>	0.53	0.48	0.12	0.10	0.57	0.60	-
	† <i>Oreochromis aureus</i>	-	-	-	-	-	-	-

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