

FACTORS INFLUENCING COMMUNITY STRUCTURE OF RIVERINE
ORGANISMS: IMPLICATIONS FOR IMPERILED
SPECIES MANAGEMENT

by

David S. Ruppel, M.S.

A dissertation submitted to the Graduate Council of
Texas State University in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
with a Major in Aquatic Resources and Integrative Biology
May 2019

Committee Members:

Timothy H. Bonner, Chair

Noland H. Martin

Joseph A. Veech

Kenneth G. Ostrand

James A. Stoeckel

COPYRIGHT

by

David S. Ruppel

2019

FAIR USE AND AUTHOR'S PERMISSION STATEMENT

Fair Use

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

Duplication Permission

As the copyright holder of this work I, David S. Ruppel, authorize duplication of this work, in whole or in part, for educational or scholarly purposes only.

ACKNOWLEDGEMENTS

First, I thank my major advisor, Timothy H. Bonner, who has been a great mentor throughout my time at Texas State University. He has passed along his vast knowledge and has provided exceptional professional guidance and support with will benefit me immensely as I continue to pursue an academic career. I also thank my committee members Dr. Noland H. Martin, Dr. Joseph A. Veech, Dr. Kenneth G. Ostrand, and Dr. James A. Stoeckel who provided great comments on my dissertation and have helped in shaping manuscripts that will be produced in the future from each one of my chapters.

Thank you to all of my past and present lab mates as well as undergraduates who have helped on all of my projects during my time as PhD student: Anne Beckman, Lauren Chappell, Myranda Clark, Cody Craig, Emily Cowells, Nicky Fauchaux, Harlan Nichols, Melody Martinez, Jeremy Miakoetter, Peter Pfaff, Mike Parham, Elizabeth L. Rosas, V. Alex Sotola, Danielle Terrell, and many more. I thank Ashley Seagroves for her love and support while working on the completion of my dissertation proposal and final draft. I thank my parents and grandmother for all their love, support, and encouragement through the whole process.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	viii
ABSTRACT.....	xi
 CHAPTER	
I. APPLICATION OF THE 3R (RESILIENCY, REDUNDANCY, REPRESENTATION) CONCEPT TO A LIFE HISTORY STUDY OF A SPECIES OF GREATEST CONSERVATION NEED, <i>NOTROPIS</i> <i>BAIRDI</i>	
Abstract	1
Introduction.....	2
Methods.....	5
Results.....	10
Discussion.....	15
Literature Cited	28
II. FACTORS ASSOCIATED WITH INSTREAM MOVEMENT OF PRAIRIE STREAM FISHES: A CASE STUDY USING <i>MACRHYBOPSIS</i> <i>AUSTRALIS</i>	
Abstract	33
Introduction.....	34
Methods.....	37
Results.....	44
Discussion	50
Literature Cited	69

III. FISH COMMUNITY STRUCTURE AND HABITAT ASSOCIATIONS OF
THE UPPER RED RIVER OF TEXAS AND OKLAHOMA WITH A
NOTE ON SPECIES OF GREATEST CONSERVATION NEED
POPULATIONS

Abstract77
Introduction.....78
Methods.....80
Results.....83
Discussion89
Literature Cited126

IV. DISTRIBUTION AND HABITAT ASSOCIATIONS OF FRESHWATER
MUSSELS IN THE MAINSTEM COLORADO RIVER, TEXAS

Abstract130
Introduction.....130
Methods.....133
Results.....137
Discussion141
Literature Cited162

LIST OF TABLES

Table	Page
1.1. Percent volumes, occurrences, and relative abundances of food items in stomachs of Red River Shiners taken from February 2016 through January 2017.	20
2.1. Percent volumes, occurrences, and relative abundances of food items in stomachs of Prairie Chubs taken from February 2016 through January 2017.....	57
3.1. Common names, scientific names, species codes, and relative abundances for fishes taken among all sites within the upper Red River drainage from September 2015 through September 2016	94
4.1. Surface geology, groundwater sources, stream gradient, and water quality and quantity estimates among georegions of the Colorado River basin.....	147
4.2. Total number, percent, and physical characterizations of habitats sampled within georegions of the Colorado River basin March through October 2017.....	149
4.3. Water quality parameters (mean for temperature, dissolved oxygen, and turbidity, median for pH) for mesohabitats sampled within georegions of the Colorado River basin March through October 2017	151
4.4. Mussel species and relative abundances (% of total N) taken from georegions within the Colorado River basin from March through October 2017.....	152
4.5. Mussel species and occurrences (% of total habitats sampled) taken from georegions within the Colorado River basin from March through October 2017.....	153
4.6. Mesohabitat associations by species using ACFOR scale (Stiers et al. 2011): Abundant (75 – 100% in a species relative abundance), Common (50 – 74%), Frequent (25 – 49%), Occasional (5 – 24%), and Rare (>0 – 4%).....	154
4.7. Species-substrate associations using ACFOR scale (Stiers et al. 2011): Abundant (75 – 100% mean percent substrate), Common (50 – 74%), Frequent (25 – 49%), Occasional (5 – 24%), and Rare (>0 – 4%).....	155
4.8. Differences in mussel community relative abundances before and after Hurricane Harvey and >4,600 cm in Cenozoic Georegion.....	156

LIST OF FIGURES

Figure	Page
1.1. Locations of sites sampled along the upper Red River of Texas and Oklahoma from September 2015 through January 2017	22
1.2. Circles represent each mesohabitat (N = 400) along PC I and PC II gradients (top panel)	23
1.3. Frequency of abundances (top panel) and occurrences (bottom panel) of available habitats (line) and used habitats (bars) by Red River Shiners along current velocity, depth, and specific conductance gradients	24
1.4. Mean $\pm$ 1 SD total lengths (black circles) for Age-0, Age-1, and Age-2 Red River Shiners taken monthly from February 2016 through January 2017.	25
1.5. Mean ($\pm$ 1 SE) monthly gonadosomatic index (GSI) for Red River Shiners taken from February 2016 through January 2017 (top panel)	26
1.6. Frequency of oocyte size distribution in mature ovaries of Red River Shiner taken from May 2016 through September 2016	27
2.1. Site locations (N = 36, black dot) and water bodies (N = 20) for longitudinal surveys within the upper Red River basin of Texas and Oklahoma, September 2015 through September 2016	58
2.2. Circles represent all mesohabitats (N = 400) along PC I and PC II gradients sampled during the longitudinal surveys	59
2.3. Frequency of occurrences and abundances of available habitats (line) and used habitats (bars) by Prairie Chub for current velocity, depth, and specific conductance	60
2.4. Scatter plot of linear genetic differentiation ($GST/(1-GST)$) values among collection sites versus river distance between sites (rkm) not separated by dams (A) and between sites separated and not separated by dams (B)	61

2.5. Mean (± 1 SE) monthly gonadosomatic index (GSI) for Prairie Chubs taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, February 2016 through January 2017, and corresponding ovarian stages (%) by month for immature (white), developing (light gray), and mature (dark gray) females	62
2.6. Frequency of oocyte size distributions in mature ovaries of Prairie Chubs taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, May 2016 through September 2016	63
2.7. Mean ± 1 SD total lengths (black circles) for Age-0, Age-1, and Age-2 Prairie Chubs taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, February 2016 through January 2017	64
2.8. Daily flow (line; USGS Station 07308200) taken near Hwy 283 crossing on the Pease River, and monthly estimates of specific conductance (symbol and line) taken from FM 104 crossing on the Pease River	65
2.9. Daily flow (line; USGS Station 07311700) and monthly estimates of specific conductance (symbol and line) taken near Hwy 6 crossing on the North Wichita River.....	66
3.1. Site locations (N = 36, black dot) and water bodies (N = 20) for longitudinal surveys within the upper Red River basin of Texas and Oklahoma, September 2015 through September 2016.....	96
3.2. Circles represent each mesohabitat (N = 400) along PC I and PC II gradients (top panel).	97
3.3. Fish community similarity groupings among water bodies explained by relative abundance of species in common between each reach	98
3.4. Fish-habitat associations between Canonical Correspondence Analysis (CCA) axis I (x-axis) and CCA axis II (y-axis) for fishes with >1% relative abundance in the upper Red River drainage	99
3.5. Fish-habitat associations between Canonical Correspondence Analysis (CCA) axis I (x-axis) and CCA axis II (y-axis) for fishes with <1% relative abundance in the upper Red River drainage. Genus and species are abbreviated to three characters.....	100

3.6. Mean (black circle), 1 SE (whisker), and minimum and maximum (open circle) specific conductance for fishes with >1% relative abundance within the upper Red River drainage (top panel).....	101
3.7. Probability of occurrence (Top) and relative abundance (Bottom) across decades (1950's - 2010's) for four Cyprinidae species that are classified as Species of Greatest Conservation Need in Texas.....	102
3.8. Probability of occurrence (Top) and relative abundance (Bottom) across decades (1950's - 2010's) for four non-Cyprinidae species that are classified as Species of Greatest Conservation Need in Texas.....	103
4.1. Plot of principal components axes I and II for physical characters of mesohabitats taken from Colorado River basins taken from March through October 2017	157
4.2. Plot of conical correspondence axes I and II for mesohabitats and their physical characters taken from the Colorado River basin from March through October 2017 (top panel).....	158
4.3. Weighted mean (black circle) and one SD (whiskers) of current velocities (column, top panel; bottom, bottom panel) for mussels taken from Colorado River from March through October 2017	159
4.4. Weighted mean (black circle) and one SD (whiskers) of FST hemispheres (top panel) and mean sheer stress (bottom panel) for mussels taken from Colorado River from March through October 2017	160
4.5. Weighted mean (black circle) and one SD (whiskers) of depth (top panel) and penetrometer (bottom panel) for mussels taken from Colorado River from March through October 2017	161

ABSTRACT

Riverine environments are dynamic with numerous biophysical components influencing community structure of riverine biota. Common theme among my dissertation chapters is the quantification of community structure related to biophysical components of riverine environments in an effort to identify mechanisms underlying community structure (e.g., species richness, species abundances, life history traits). Communities within two Texas river basins (i.e., Red River drainage, Colorado River drainage) include several species identified as imperiled species, either federally or by states. A goal for each chapter was to integrate patterns and processes of community structure with current efforts to list species under the Endangered Species Act or to mediate negative anthropogenic influences on species and communities. Chapter 1 addressed gaps in life history information, current distribution, and habitat associations for the Red River Shiner, an endemic cyprinid in the Red River basin. Information was used to estimate redundancy, resiliency, and representation of the Red River Shiner, following the framework of U.S. Fish and Wildlife Service in species status assessments and eventually listing decisions. Chapter 2 tested three theories related to largescale migrations of prairie stream fishes, using the federal candidate for listing Prairie Chub as a model organism. Chapter 3 was a fish community assessment of the upper Red River of Texas and Oklahoma and quantified historical to contemporary changes in occurrences and abundances of six species of greatest conservation need. Chapter 4 was a mussel community assessment of the Colorado River basin that identified georegion, along with

associated substrates, stream gradient, and water quality, as more powerful predictor of community structure than smaller scale mesohabitat characteristics. Fish and mussel communities were not homogeneously distributed within a basin, and I successfully quantified the heterogeneity and identify some of the potential mechanisms. However, mechanisms of community structure are still largely elusive and in need of further investigation.

I. APPLICATION OF THE 3R (RESILIENCY, REDUNDANCY, REPRESENTATION) CONCEPT TO A LIFE HISTORY STUDY OF A SPECIES OF GREATEST CONSERVATION NEED, NOTROPIS BAIRDI

Abstract

Red River Shiner *Notropis bairdi* is endemic cyprinid to the Red River basin of Arkansas, Oklahoma, and Texas, and because of this limited distribution, all three states have listed Red River Shiner as a Species of Greatest Conservation Need (SGCN). Benefits to listing species as SGCN include identifying and addressing gaps in species information, mitigating threats, and possibly avoiding listing by USFWS. Concepts of resiliency, redundancy, and representation (3Rs) informs listing recommendation for the USFWS but can be applied to SGCN species. The purpose of this study was to gather life history information for Red River Shiner and apply updated distributions and abundances to the 3Rs concept. Information was gathered over a two-year period in the upper Red River of Texas and Oklahoma. Red River Shiners are early maturing, short-lived species, producing multiple batches of eggs in late spring through the summer and consuming benthic invertebrates and other fishes. Comparing 3R estimates of Red River Shiner to estimates of other imperiled and common species, Red River Shiner was lower than average for redundancy, more resilient, and has greater representation. Basic life history and distribution information provides the foundation of how species interact with the natural environment and enables predictions on how anthropogenic effects can disrupt life cycles and sustainability of populations. Therefore, quantification of a species redundancy, resiliency, and representation can identify those species that are more imperiled and enable prioritization of future conservation efforts.

Introduction

United States Fish and Wildlife Service (USFWS) listing process has historically focused on threats subjectively without any analysis of species responses, which provided low repeatability and transparency (Andelman et al. 2004). In an attempt to improve consistency and transparency the USFWS listing process now involves a Species Status Assessments (SSA; USFWS 2016, Smith et al. 2018). The SSA reviews all information known about a species to address three primary questions: what the species life history and ecology, current condition, and future threats. Measuring species life history and ecology includes quantification of trophic niche, reproductive strategies, biologic interactions, and habitat requirements, current condition of a species incorporates concepts of resiliency, redundancy, and representation (3Rs; Shaffer and Stein 2000, Smith et al. 2018). Measurement of the ecology, current conditions, and future conditions ultimately informs listing recommendation but determining future conditions can be complicated by the uncertainty of future events and the response of the species to future scenarios is imperfect (Smith et al. 2018). However, gathering information that is necessary for determining a species ecology and current conditions are more straight forward and quantifiable. Resiliency is ability of species to withstand stochastic disturbances, redundancy is a species ability to survive catastrophic events, and representation is a species ability to endure natural variability (Shaffer and Stein 2000). Quantifying the 3Rs is a challenge because each is measured indirectly with surrogates or indicators, which are often limited from available information available (Sheffer et al. 2015). Measures for resiliency include species persisting at a location (Shaffer and Stein 2000) or by its population size (Smith et al. 2018). Measures for redundancy include

number of locations where a species persists. Measures for representation include breadth of genetic diversity, using either genetics or relative abundance given that genetic variation is positively related to population size (Frankham 1996), and environmental diversity (Smith et al. 2018). Recently, Faucheux et al. (2019) used observations commonly available in the fish literature (e.g., occurrence, abundance) to rapidly assess 3Rs for majority of fishes in three ecoregions of Texas. In doing so, the authors were able to rank species along a low 3R gradient to a high 3R gradient. Quantifying life history and ecology components, in combination with using Faucheux et al. (2019) approach, provides updated information on species distributions using the 3Rs, which uses the same language and approach as the USFWS process.

One species that would benefit from a 3R assessment is the Red River Shiner (*Notropis bairdi*, Hubbs and Ortenburger 1929). The Red River Shiner is endemic to the upper Red River basin of the Mississippi River drainage (Robison and Buchanan 1988; Miller and Robison 2004; Thomas et al. 2007) and is listed as a Species of Greatest Conservation Need (SGCN) in Arkansas, Oklahoma, and Texas (ODWC 2005; TPWD 2012; AGFC 2015). Introduced populations exist in the Cimarron River basin and Arkansas River basin of Oklahoma and Kansas (Marshall 1978; Cross et al. 1983; Luttrell et al. 1995). The Red River Shiner is a small bodied (Hubbs & Ortenburger 1929), short lived, obligate riverine insectivore (Cross et al. 1983), tolerant to a wide range of environmental conditions (Hubbs & Ortenburger 1929; Luttrell et al. 1995; Winston et al. 1991; Hargrave and Taylor 2010). Similar life history traits are noted for other closely related species in the subgenus *Alburnops* (Mayden 1989), such as the Smalleye Shiner *N. buccula* (Marks 1999) and Chub Shiner *N. potteri* (Perkin et al.

2009). Collectively, species of the subgenus *Alburnops*, which inhabit semi-arid prairie streams of central USA, are of increasing conservation concern. Recently, the Smalleye Shiner, the sister species of Red River Shiner and having similar range distribution as the Red River Shiner but in adjacent Brazos River drainage, was listed as an endangered species by USFWS in 2014 because of two primary threats: river fragmentation and instream flow alterations (USFWS 2014). Filling in gaps of Red River Shiner's life history, ecology, and current condition would inform the SSA process by USFWS standards (Association of Fish and Wildlife Agencies 2012).

Existing gaps in information for the Red River Shiner include updated information on distribution and abundances, habitat associations, reproductive biology, and food habits. Red River Shiner has not been reported in Arkansas since the 1950s, but it is unknown if an established population existed or that the few collections represented transient individuals from upstream reaches (Robison and Buchanan 1988). A population in the North Fork of the Red River of Oklahoma was possibly extirpated (Winston et al. 1991). However, Red River Shiner was considered stable in 2000 (Warren et al. 2000) and not identified as an imperiled freshwater fish by the 2008 American Fisheries Society Endangered Species Committee (Jelks et al. 2008), likely due to their reported high abundances within streams of their native (Gilbert 1980) and non-native (Cross et al. 1983; Luttrell et al. 1995) ranges. Descriptions of habitat associations include turbid waters of shallow sand-bed streams (Gilbert 1980) with fluctuating flows (Cross et al. 1983) and salinities (0.4 – 21.7 ppt; Echelle et al. 1972). Red River Shiners are thought to spawn during the summer (Hubbs and Ortenburger 1929) at a minimum length of 39 mm (Cross et al. 1983). Gut contents consisted primarily of terrestrial insects (assessed

in five individuals; Cross et al. 1983) and aquatic insects (assessed in three individuals; Echelle et al. 1972).

Purpose of this study was to gather distribution, habitat association, and life history information for Red River Shiner in order to fill in existing knowledge gaps using an approach that informs future USFWS listing process. Objectives of this study were to provide information on the current distribution, ecology, life history attributes, and population age structure of Red River Shiner in the Red River mainstem of Texas and Oklahoma and tributaries of Texas. Assessment of occurrence and abundance were done at the water body scale (i.e. semi-independent drainages). This will enable estimates of redundancy (e.g., number of occupied semi-independent drainages), representation (e.g., percent abundance within semi-independent drainages), and resiliency (e.g., percent of semi-independent drainages with an absence) in Texas drainages and the Red River of Oklahoma. In addition, we compared the 3R estimates for the Red River Shiner directly to estimates provided by Faucheux et al. (2019) in order to provide a context among other fishes that are federally listed, SGCN listed, or of no conservation concern.

Methods

Longitudinal surveys were conducted among 20 named rivers or tributaries (i.e., water body) and 36 sites within the upper Red River drainage between September 2015 and September 2016 (Figure 1.1). Sites were sampled twice, once during the cool season (September through March) and again during the warm season (April through August), unless the stream was dry. At each site, available mesohabitats (i.e., riffle, run, pool, backwater, and eddy) were delineated and sampled in proportion to their availability.

Fishes taken from each mesohabitat were identified to species, and the first 30 individuals of a species were measured (i.e., total length, nearest mm). Length and width of area sampled (e.g., long seine hauls) or length and width of mesohabitats were measured. Substrate (i.e., clay, silt, sand, gravel, cobble, boulder, and bedrock), vegetation, and woody debris were visually or tactilely estimated and represented as a percent coverage of the total mesohabitat area. Water depth (m) and current velocities (m/s) were estimated from three to five-point estimates within a representative cross section of the mesohabitat and water quality: Dissolved oxygen (mg/l), pH, specific conductance ($\mu\text{S}/\text{cm}$), and temperature ($^{\circ}\text{C}$).

Red River Shiners were collected monthly between February 2016 and January 2017 from three sites on the Pease River (i.e., FM 104, Hwy 6, Hwy 283) and two sites on the North Wichita – Wichita River (i.e., Hwy 6 and FM 1919). At each site and date, multiple seine hauls were made to capture up to 10 mature Red River Shiners (> 24 mm in total length; Hubbs and Ortenburger 1929). Fishes were anesthetized with a lethal dose of tricane methanesulfonate and fixed in 10% formalin. When available, total length of additional Red River Shiners were measured, and the fish released.

In the laboratory, up to five females were selected, measured to the nearest mm, and weighed to the nearest mg for each site and month. Incision was made from the urogenital opening to isthmus. The esophagus was severed, and the stomach, intestine, and ovaries were removed. With the use of a dissecting scope, the stomach was severed from the intestine at the pyloric sphincter muscle, and ovaries were removed. The stomach wall was cut longitudinally from the sphincter muscle to the esophagus, carefully exposing the gut contents. Stomach fullness (i.e., proportion of stomach filled

by contents) was determined by two independent observers, assigning a number from 0 (empty) to 100 (full) in increments of 10. Stomach contents were sorted and identified. Percent volume was defined as the volume of algae, invertebrate and vertebrate material, substrate, and plastics comprising the total volume of stomach fullness. Percent occurrence was defined as the number of fish with a food item identified to the lowest practical taxonomic level. Invertebrate and vertebrate material was identified lowest practical taxonomic level and counted in order to calculate relative abundance of each item.

Ovaries were weighed, and gonadosomatic index (GSI; $[\text{mass of ovaries} / \text{mass of fish}] \times 100$) was calculated for each fish. Ovaries were macroscopically categorized as 1) immature or resting ovaries with small, translucent oocytes; 2) developing ovaries with small (< 0.2 mm in diameter), translucent oocytes and small (< 0.5 mm) opaque oocytes indicating early stages of yolk deposition; 3) mature ovaries with small translucent oocytes, small opaque oocytes, and large (> 0.5 mm in diameter) vitellogenic oocytes; and 4) spent ovaries with small translucent oocytes and a few large vitellogenic oocytes (Williams and Bonner 2006). The left ovary of up to three females with mature ovaries were selected, and individually oocytes were removed by teasing oocyte mass apart and redistributing them on a petri dish with a gentle swirling. Oocyte diameters were measured for oocytes > 0.2 mm to the nearest 0.01 mm for the first 100 oocytes in the field of view with dissection microscope fitted with an ocular micrometer. Oocyte diameters were plotted by percent frequency of occurrence to estimate number of modality of clutch production (i.e., single spawning or multiple batch spawning), maximum oocyte diameter size, and range of oocyte diameters for the final batch of

oocytes. Minimum oocyte diameters for the final batch were 0.6 mm for Red River Shiner. Minimum oocyte diameter was used in all other mature females (left side only and doubled) to estimate batch fecundity. Only range of batch fecundity was reported to indicate reproductive potential of Red River Shiner. Batch fecundity estimates of multiple spawning fishes are underestimations of spawning season fecundity.

Habitat associations were assessed from Principal Component Analysis (PCA) model developed for the longitudinal survey of the fish communities and mesohabitats. Mesohabitat PC axes I and II scores and Red River Shiner occurrences were compared to mesohabitat PC scores without Red River Shiner occurrences, with t-tests. Association between numbers and Red River Shiners with $\log_{10}(N+1)$ transformation (i.e., dependent variable) and mesohabitat PC axes I and II scores (i.e., independent variables) were assessed with linear regression. Mesohabitat type, water depth, current velocity, and specific conductance were identified as indicators of fish community segregation with Canonical Correspondence Analysis (CCA). As such, occurrences and abundances of Red River Shiners were assessed among mesohabitat types with Chi-square test and among depth, current velocity, and specific conductance gradients with a Kolmogorov-Smirnov (KS) tests. Significance was set at $\alpha = 0.05$ for each test.

Length frequency histograms were constructed from monthly collections of Red River Shiner using 2-mm bin increments combined across sites to assess number of age groups within each population and life span. Modal progression analysis (Bhattacharya's Method; Fish Stock Assessment Tools II; FiSAT II) was used to estimate the number of age groups and their sizes monthly between February 2016 and January 2017. Analysis of growth increments (Appeldoorn's Method; FiSAT II) was used to estimate growth

rates of Red River Shiner. Asymptotic length (L_{∞}) maximum were set larger than reported maximum length in this study to account for larger fish within the population.

Estimates for the 3Rs were calculated following Faucheux et al. (In press) from information gathered during the longitudinal survey. Redundancy was determined from number by the rivers and named tributaries that Red River Shiner was observed during this study. For representation, relative abundance of Red River Shiner was calculated among all semi-independent drainages and were categorized using the ACFOR scale (Stiers et al. 2011): Abundant (75 – 100%), Common (50 – 74%), Frequent (25 – 49%), Occasional (5 – 24%), and Rare (>0 – 4%). Estimates for representation were determined by the number of semi-independent drainages where Red River Shiners were considered rare. Percent rare was calculated by the number of semi-independent drainages where Red River Shiners were rare divided by the number of semi-independent drainages where Red River Shiner were present multiplied by 100. For resiliency, historical records were gathered from Wilde et al. 1996 and Fishes of Texas (Hendrix et al. 2017) among all sampled semi-independent drainages to determine if a population of Red River Shiner was present. Semi-independent drainages where Red River Shiners were not observed during the longitudinal survey compared to historical locations were classified as absent. Percent absent was calculated by the number of semi-independent drainages where Red River Shiners were absent divided by the number of semi-independent drainages where Red River Shiner was historically present multiplied by 100. Percent abundance within semi-independent drainages), and resiliency (e.g., percent of semi-independent drainages with an absence)

Results

Red River Shiners ($N = 6,387$) were taken from 185 (46%) of 400 mesohabitats, 21 (58%) of the 36 sites, and 8 (40%) of the 20 water bodies. Relative abundance of Red River Shiner in the upper Red River basin was 18% but ranged between 0.4% and 56% among sites where they were detected. Density of Red River Shiner in the upper Red River basin was 0.11 fish/m² but range between >0.01 and 1.8 fish/m² among sites where they were detected.

Thirty-six sites among 20 water bodies were sampled within the upper Red River drainage. Mesohabitats ($N = 400$) among sites primarily consisted of runs (70%) and pools (12%). Mean (± 1 SE) depths among sites was 0.3 (± 0.3) m and ranged from 0.02 to 1.6 m. Mean current velocity among sites was 0.2 (± 0.2) m/s and ranged from 0 to 0.9 m/s. Specific conductance ranged from 115 to 49,968 $\mu\text{S}/\text{cm}$ with greater specific conductance observed in the western portion of the study area and lower specific conductance observed in the eastern portion of the study area. Dominate substrate comprised of sand (57%), silt (30%), and gravel (9%). Woody debris, detritus, and aquatic vegetation were rare among mesohabitats and sites.

Principal component axes I and II explained 24% of the variation among the 400 habitats. Axis I explained 13% of the variation and represented habitat type (i.e., pool and run) and substrate gradients. Strongest loadings for PC axis I were pool (0.33), silt (0.30), run (-0.46), and sand (-0.45) (Figure 1.2). Axis II explained 11% of the variation and represented a habitat type (i.e., riffle and backwater), substrate, and current velocity gradients. Strongest loadings for PC axis II were riffle (0.42), gravel (0.40), current velocity (0.39), and silt (-0.37). Mean PC I scores, averaged across habitats and sites for

each reach, ranged between -2.30 for North Fork Red River to 3.83 for Pecan Creek, contrasting sand-bed prairie streams with shallow to moderate depths, flowing run and pool habitats with sand and silt substrates (negatively associated with PC I) versus more entrenched channel streams, common to eastern tributaries within the upper Red River drainage, with predominantly run and pool habitats with shallow to deep depths, sluggish current velocities except in riffle habitats, and silt and gravel habitats.

Mesohabitats with Red River Shiner occurrences were negatively associated with PC axis I (t-test, $t_{0.05(2), 398} = 3.11$, $P < 0.01$) but were not associated with PC axis II (t-test, $t_{0.05(2), 398} = 0.09$, $P = 0.93$). Mesohabitats with Red River Shiner abundances were not associated with PC axis I (linear regression; $F_{1,398} = 0.64$, slope = -0.015, $P = 0.42$) or PC axis II ($F_{1,398} = 0.08$, slope = -0.006, $P = 0.78$). Mesohabitat scores among eight water bodies with Red River Shiners differed from mesohabitats among 12 water bodies without Red River Shiners for PC I (t-test, $t_{0.05(2), 398} = -9.80$, $P < 0.01$) but did not differ for PC II (t-test, $t_{0.05(2), 398} = -0.79$, $P = 0.43$). Water bodies with Red River Shiners generally consisted more of swifter waters (i.e., sand-bed prairie streams common in Red River and western tributaries) than water bodies without Red River Shiners, which consisted of more slow-moving pools with silt substrates within the eastern tributaries of the upper Red River drainage. However, Red River Shiners were not taken from several prairie-type streams (i.e., negative reach scores on PC I). Red River Shiners were not detected in North Fork Red River, Adams Creek, or Cottonwood Creek.

Red River Shiners were taken more often in run (74%) and riffle (10%) mesohabitats than available (70% runs, 9% riffles) and less often in pool (7%) mesohabitats than available (12% pools; Chi-square, $\chi^2 = 17.4$, $P < 0.01$). Red River

Shiner occurrence among current velocities ranged between 0.1 and 1.6 m/s with 90% of Red River Shiners captured between 0.1 and 0.7 m/s. Use of slower current velocities did not differ from expected for Red River Shiner occurrence, but differed for abundances ($KS = 0.16, P < 0.01$) (Figure 1.3). Red River Shiner occurrences among water depths ranged between 0.01 and 1.5 m with 96% of Red River Shiners captured between 0 and 0.5 m. Use of shallow water depths did not differ from expected for Red River Shiner occurrence, but differed for abundances ($KS = 0.13, P < 0.01$). Red River Shiner occurrence among specific conductance range between 2,215 and 38,420 $\mu\text{S}/\text{cm}$ with 73% of Red River Shiners captured between 2,500 and 27,500 $\mu\text{S}/\text{cm}$. Use of moderate to moderately high specific conductance differed from expected for Red River Shiner occurrence ($KS = 0.24, P < 0.01$) and abundance ($KS = 0.34, P < 0.01$).

Among monthly collections at three sites on the Pease River and two sites on the Wichita River, 2,342 Red River Shiners were taken between February 2016 and January 2017. During this period, Red River Shiners consisted of three age classes: 0, 1, and 2 (Figure 1.4). Age-2 fish represented 7% of the adult population, observed February through August 2016, and reached a maximum total length of 74 mm. Age-1 fish represented 93% of the adult population and were observed every month except December 2016. Age-0 fish were first observed in July 2016 and reached a mean length of $36 (\pm 7)$ mm TL by December 2016. Growth rate was $k = 0.636 \text{ year}^{-1}$ and $L_{\infty} = 85$ mm.

A total of 260 Red River Shiners were taken for reproductive assessments between February 2016 through January 2017. Red River Shiners invested energy into reproduction (i.e., reproductive season) between the months of March through September

(Figure 1.5). Ovaries from adult fish (N = 101; range in total length [TL]: 35 – 75 mm) were taken between October through February and classified as immature or resting. Developing ovaries were observed in two females (45 – 53 mm in TL) in March and were observed through April. Mature ovaries (N = 94; 35 – 72 mm in TL) in April and were observed through September (i.e., spawning season). Spent ovaries (N = 4; 40 – 54 mm in TL) were observed in September. Mean monthly GSI for Red River Shiner females corresponded with stages of ovarian development. Mean monthly GSIs were greatest (9.6% to 11.4%) May through July (Figure 1.6). Female GSI with immature or resting ovaries range between 0.9% to 3.4%. Female GSI with developing ovaries ranged between 1.0% to 6.5%. Female GSI with mature ovaries ranged between 1.1% to 24%. Size distribution of oocytes taken from one female per month with mature ovary indicated continuous recruitment of oocytes (Figure 6). Maximum size of a vitellogenic oocyte was 1.04 mm, and batch fecundity ranged from 44 to 882 late vitellogenic oocytes (diameter: 0.60 – 1.04 mm) among 19 females with mature ovaries.

A total of 261 Red River Shiners were examined for diet analysis from February 2016 through January 2017. Gut content by volume consist of aquatic invertebrates, terrestrial invertebrates, and vertebrates (79%), clay/silt (13%), filamentous algae (5%), grass seed (2%), sand (0.5%), aquatic plants (0.1%), diatoms (<0.1%) and plastic (<0.1%) (Table 1.1). Mean ($\pm$ 1 SD) monthly gut fullness ranged from 1% ($\pm$ 0.4) in December 2016 to 67% ($\pm$ 28.8) in May 2016. Frequency of empty stomachs was 4.2%. The most frequently occurring gut contents were silt or clay (63% occurrence), filamentous algae (53%), and sand (33%). Silt or clay substrate occurred in Red River Shiners stomachs year-round with monthly occurrences ranging from 14% in May 2016

to 95% in August 2016. Among aquatic invertebrates, terrestrial invertebrates, and vertebrates, Chironomidae was the most abundant food item (17%) followed by unidentifiable aquatic invertebrates (15%) and Coleoptera (1%). Eleven other aquatic invertebrate taxa were consumed but at low (<1%) relative abundance. Likewise, terrestrial invertebrates and vertebrates (e.g., Red River Pupfish *Cyprinodon rubrofluviatilis*) were consumed but at low relative abundance.

Estimates of the 3Rs were calculated from results of this study and from published literature. As a measure of redundancy, Red River Shiner is endemic to one river drainage and occurs in 10 water bodies within the one river drainage. As a measure of resiliency, Red River Shiner is considered extirpated in one (i.e., North Fork of the Red River; Winston et al. 1991) of the 10 water bodies (10% of water bodies with an extirpation). As a measure of representation, Red River Shiners, at times, were the most abundant species within a site and water body, being rare (<5%) in 20% of the water bodies. Among the 50 species assessed by Faucheux et al. (In press), mean (± 1 SD) for estimates of the 3Rs were 3.2 ± 2.17 for number of independent drainages, 17.2 ± 14.25 for number of water bodies within independent drainages, $37\% \pm 22.9$ of water bodies with absences (i.e., potentially extirpated), and $70\% \pm 36.8$ of water bodies with rare abundances. Comparing 3R estimates of Red River Shiner to estimates for imperiled and common species provided by Faucheux et al. (2019), Red River Shiner was lower than average for redundancy (1 versus 3.2 independent drainages; 10 versus 17.2 water bodies), more resilient (10% versus 37% in absences), and with greater representation (20% versus 70% in rare abundances).

Discussion

Red River Shiners occurred in a variety of mesohabitats and generally at depths and current velocities available but were not ubiquitously distributed within upper Red River basin, found only in 40% of the water bodies surveyed. Habitat associations reported herein were similar to previous descriptions of Red River Shiner habitat associations, such as broad, shallow channels with sand and silt substrate (Gilbert 1980) and expands on habitat associations of sandy depressions, backwaters, and pools with salinities ranging between 0.4 to 21.7 ppt (up to 38,420 $\mu\text{S}/\text{cm} \sim 24.4$ ppt; this study) provided by Echelle et al. (1972). Red River Shiners were only detected in braided sand-bed prairie streams, such as western tributaries of the upper Red River basin, Red River mainstem, and one eastern tributary (i.e., Mountain Creek). Red River Shiners were not detected in the other eastern tributary streams, which consisted of entrenched banks and deeper, slower moving water.

Similar associations with braided sand-bed prairie streams are noted for introduced populations of Red River Shiners in the Cimarron River basin of Oklahoma and Kansas (Marshall 1978; Luttrell et al 1995) and South Canadian River of Oklahoma (Matthews 1988) and for several other fishes, such as Prairie Chub *Macrhybopsis australis* (Ruppel et al, In review), Smalleye Shiner (Moss and Meyer 1993), Sharpnose Shiner *Notropis oxyrinchus* (Moss and Meyer 1993), Arkansas River Shiner *N. girardi* (Cross 1953; Gilbert 1980), and Plains Minnow *Hybognathus placitus* (Cross et al. 1985). Affinities of species for braided, sand-bed prairie streams are not well understood. Prairie streams are often considered extreme environments with wide fluctuations in salinity, flows, turbidity, and water temperatures (i.e., Matthews 1988; Dodds et al.

2004). Extreme environments are thought to exclude and restrict many species from inhabiting braided, sand-bed rivers, thereby maintaining unique environments with lower competition and predation (Echelle et al. 1972; Gido et al. 1999), whereas prairie stream fishes, such as the Red River Shiner, have evolved tolerances to endure the extreme environments (Fausch and Bestgen 1997; Scudder 1989). However, it is unknown how and why prairie stream fishes are excluded and restricted from streams that are not braided, sand-bed prairie streams. Similar patterns of species being restricted to lower stream orders (i.e., upper reaches) of a drainage are reported (Craig et al. 2016). Temperature tolerances and temperature-mediated competition are thought to be primary mechanisms underlying segregation between coldwater forms (e.g., trout in upper reaches) and warmwater forms (e.g., cyprinids in lower reaches) in mountain to lowland river basins (Taniguchi et al. 1998; Quist et al. 2006), and temperature-mediated competition is thought to be a primary mechanism underlying segregation between stenothermal forms (e.g., spring-associated fishes in upper reaches) and eurythermal forms (e.g., riverine fishes in lower reaches) in karst spring to lowland rivers (Craig et al. 2019). However, temperature is an unlikely factor to explain why Red River Shiners are not found in non-prairie stream streams because of the lack of strong temperature gradients within drainages with prairie streams. A factor with a strong upstream to downstream gradient in the Red River drainage is salinity (115 to 49,968 $\mu\text{S}/\text{cm}$, this study; 622 to 5,667 $\mu\text{S}/\text{cm}$, Hargrave and Taylor 2010). Strong upstream to downstream gradients or areas of increased specific conductance exist in other Great Plains drainages (Canadian River, Pigg et al. 1999; Brazos River, Ostrand and Wilde 2002; Colorado River, Nance 2006), attributed to strata with salts deposited during the Permian age.

Similar to other headwater to lowland systems with segregation maintained by water temperature, salinity might also maintain segregation among the riverine fish communities, as suggested by Hargrave and Taylor (2010), and limit the distribution of Red River Shiner to other reaches of the drainage.

Red River Shiner is an early maturing, short-lived species, producing multiple batches of eggs in late spring through the summer and consuming benthic invertebrates and other fishes. Life history traits of Red River Shiner are consistent with opportunistic strategy, a strategy observed among many lineages of fishes and associated with widely fluctuating abiotic aquatic systems (Winemiller and Rose 2002). Selection pressures for opportunistic strategists within arid and semi-arid streams include extended periods of low flows, at times reducing stream habitats to isolated pools (Matthews 1988; Ostrand and Wilde 2002; Durham and Wilde 2009), and extended periods of high flows. During low flow periods, fishes avoid drying reaches by moving downstream towards more permanent water or remain in isolated pools (Ostrand and Wilde 2002) providing source populations when conditions become favorable (Lohr and Fausch 1997). Small body sizes enable persistence in isolated pools, and early maturation and multiple batch spawning enable rapid recolonization of areas following the return of flows (Schlosser 1987; Lohr and Fausch 1997). During high flow periods, multiple batch spawning is thought to be a bet hedging strategy, ensuring that at least some propagules are released during elevated flows (Durham and Wilde 2009). Progeny released during elevated flows are dispersed substantial distances downstream and are demonstrated to have higher survivability (Durham and Wilde 2009). With these selection pressures, life history traits of Red River Shiner tend to be more similar to those of other fishes in arid

southwest and southern Great Plains region, such as Tamaulipas Shiner *N. braytoni*, Smalleye Shiner, Chihuahua Shiner *N. chihuahua*, and Arkansas River Shiner (Burr and Mayden 1981; Bonner 2000; Durham 2007; Heard 2008) than the life history traits of closely related species (i.e., *Alburnops*) found farther east in the Mississippi River drainage and southeastern USA. Species found in the Mississippi River drainage and southeastern USA (e.g., River Shiner *N. blennioides*, Silverside Shiner *N. candidus*, Fluvial Shiner *N. edwarddraneyi*, and Coastal Shiner *N. petersoni*) have traits characteristic of an intermediate strategy (Winemiller and Rose 2002) with later maturation and longer life spans.

As a basin endemic, Red River Shiner has low redundancy but would have higher redundancy estimates if introduced populations were considered. This would be beneficial given that sustaining introduced populations can contribute to the long-term viability of a species (Osborne et al. 2013). We did not assess future conditions of the Red River Shiner in this study but threats within the upper Red River basin are likely to be similar this geographic area include natural and anthropogenically influenced effects of climate change, groundwater pumping, stream fragmentation and channelization, and introduction of non-native species (USFWS 1998; 2014). Currently, sodium chloride control management practices have been implemented to reduce specific conductance in order to provide better water quality for agricultural and municipal use among tributaries and mainstem reaches in the upper Red River (Wurbs 2002; USGS 2011). Considering that salinity might maintain segregation among the riverine fish communities in the braided sand-bed prairie streams (Hargrave and Taylor 2010), reducing specific

conductance levels could threaten the current fish community through displacement of less salinity tolerant species by removing the environmental filter.

Red River Shiner is grouped with a reproductive guild of minnows (i.e., pelagic broadcast spawning) that define the prairie streams of North America and with populations declining throughout the Great Plains this exemplify the need to balance water demand needs and needs of the unique fish communities (Worthington et al. 2018). Currently, pelagic broadcast spawning minnows represent 3% of all fish species listed as threatened or endangered by the USFWS. Among the pelagic broadcast spawning minnows listed by Worthington et al. (2018), one is extinct, 25% are listed as threatened or endangered, and others are listed on various states SGCN lists. As such, gathering basic life history and distribution information will provide a foundation for understanding how species are assembled in the natural environments and additionally will provide insight as to how anthropogenic effects can disrupt life cycles and sustainability of populations. Therefore, an intermediate step, quantification of a species redundancy, resiliency, and representation can identify those species that are more imperiled than others and enable prioritization of conservation actions.

Table 1.1. Percent volumes, occurrences, and relative abundances of food items in stomachs of Red River Shiners taken from February 2016 through January 2017.

Food Items	Volume (%)	Occurrence (%)	Relative Abundance (%)
Plant			
Algae	5	52	
Diatom	< 0.1	7	
Aquatic plant	0.1	2	
Grass Seed	2	6	4
Animal	79		
Aquatic invertebrates			
Crustacea		5	3
Copepoda		1	0.7
Isopoda		1	0.7
<i>Daphnia</i>		2	1
Trombidiformes			
Hydrachnidia		0.8	0.5
Coleoptera			
Dytiscidae		0.4	0.2
Hydrophilidae		1	0.7
Diptera			
Chironomidae		26	17
Chironomidae eggs		0.4	0.2
Simuliidae		0.4	0.2
Diptera pupa		0.4	0.2
Hemiptera		0.4	0.2
Neuroptera		0.4	0.2
Odonata		2	1
Gomphidae		3	2
Trichoptera		3	2
Hydropsychidae		0.4	0.2
Unidentifiable		23	15
Unidentifiable pupa		13	8
Invertebrate egg		5	3

Table 1.1. Continued.

Food Items	Volume (%)	Occurrence (%)	Relative Abundance (%)
Terrestrial invertebrates		13	9
Araneae		0.4	0.2
Cicadidae		1	0.7
Coleoptera		16	10
Scarabaeidae		0.4	0.2
Diptera		15	9
Ceratopogonidae		3	2
Hymenoptera		7	4
Apidae		0.4	0.2
Formicidae		3	2
Lepidoptera		0.8	0.5
Unidentifiable		13	9
Vertebrates			
<i>C. rubrofluvitalus</i>		0.4	0.2
Scales		2	1
otolith		0.4	0.2
Substrate			
Clay/Silt	13	63	
Sand	0.5	33	
Detritus	0.3	0.4	
Plastic	< 0.1	0.4	
Total N	261		

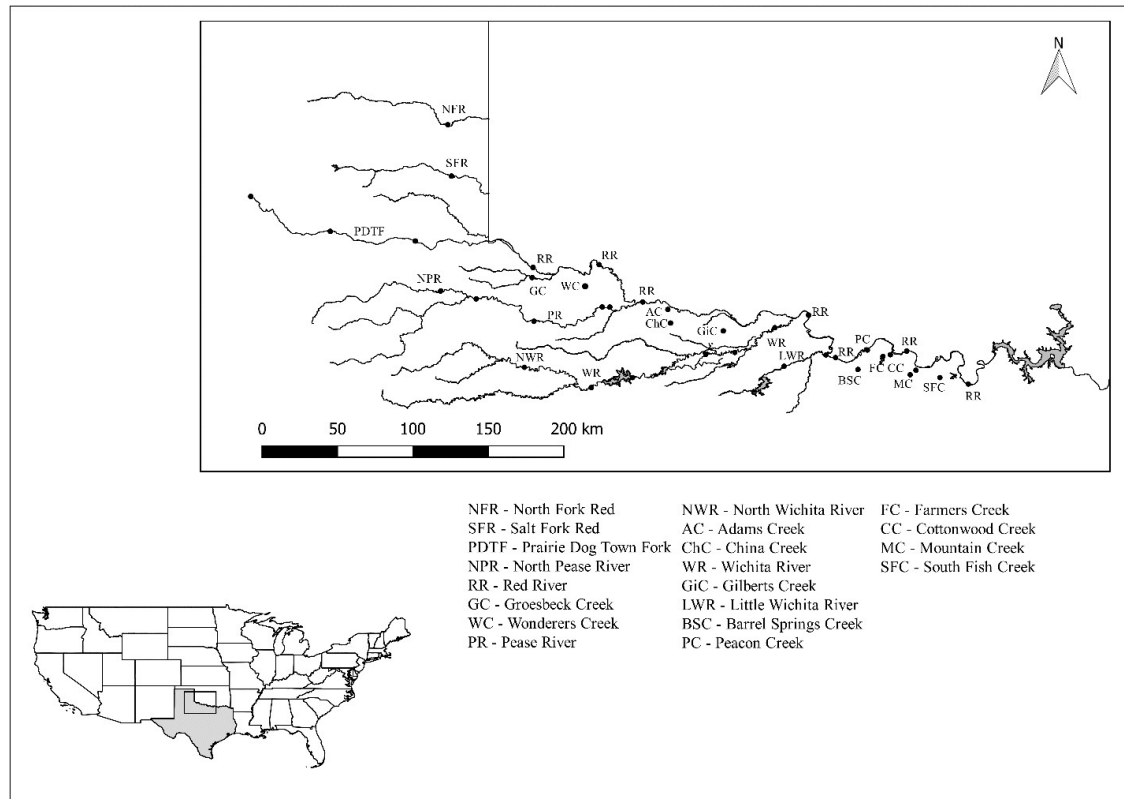


Figure 1.1. Site locations (N = 36, black dot) and water bodies (N = 20) for longitudinal surveys within the upper Red River basin of Texas and Oklahoma, September 2015 through September 2016. See Appendix 1 for georeferenced site locations

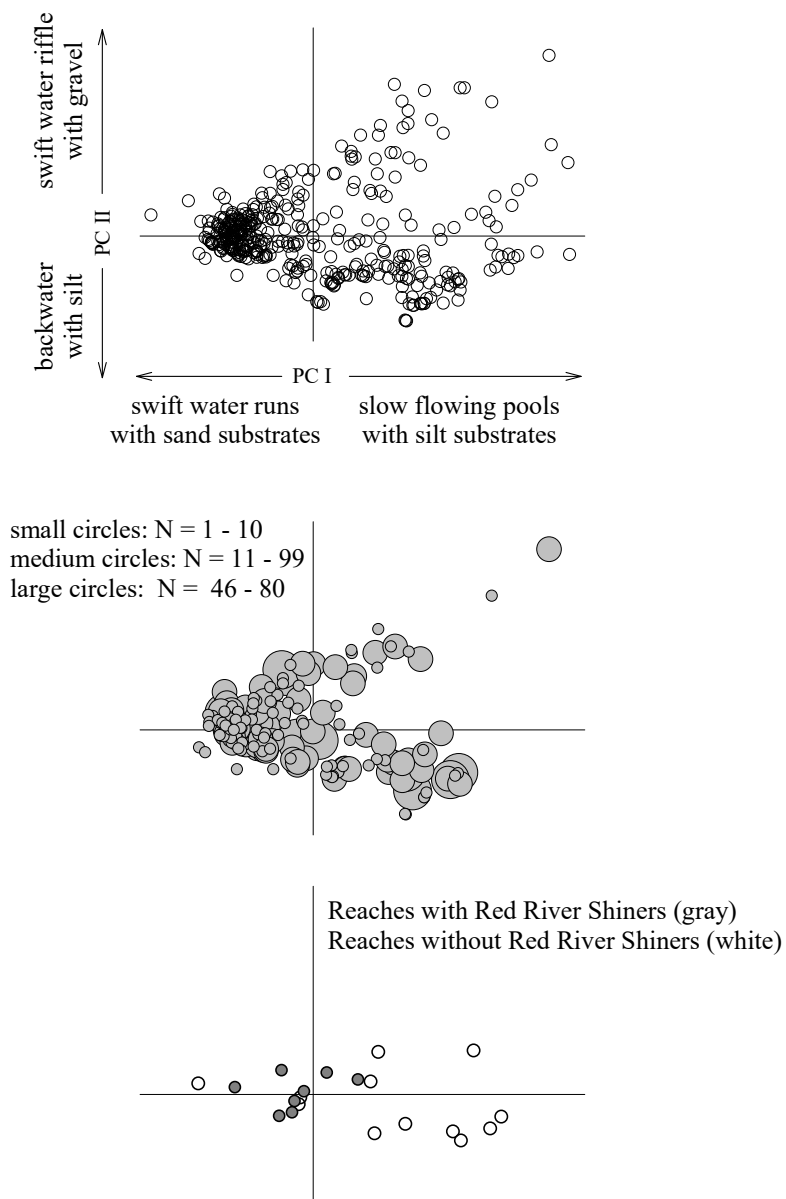


Figure 1.2. Circles represent each mesohabitat (N = 400) along PC I and PC II gradients (top panel). Shaded circles represent the number of Red River Shiners taken from each mesohabitat (middle panel) or reaches with Red River Shiner occurrences (bottom panel) from the upper Red River drainage.

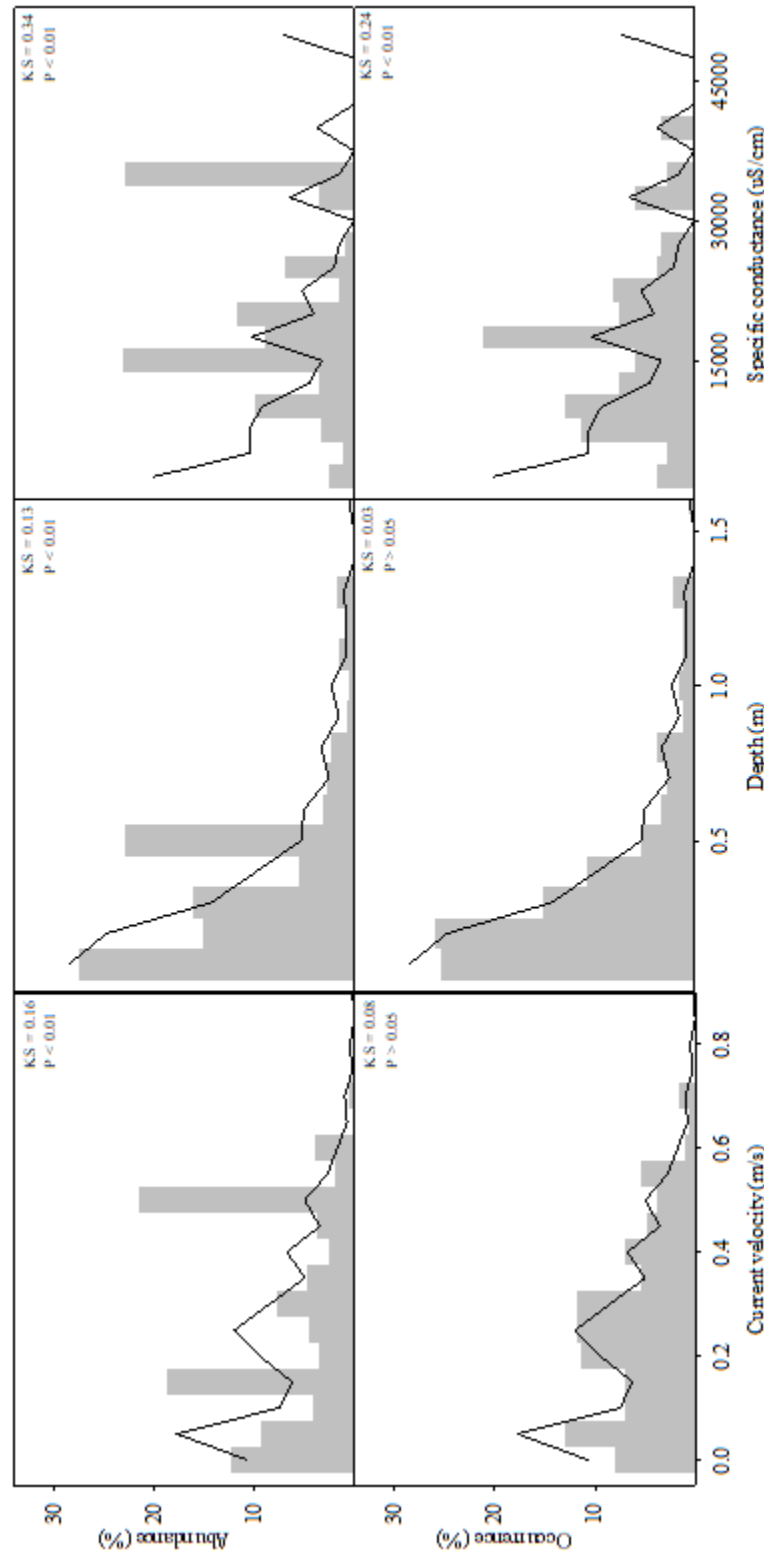


Figure 1.3. Frequency of abundances (top panel) and occurrences (bottom panel) of available habitats (line) and used habitats (bars) by Red River Shiners along current velocity, depth, and specific conductance gradients. Kolmogorov-Smirnov (KS) test statistic and associated P-value are provided.

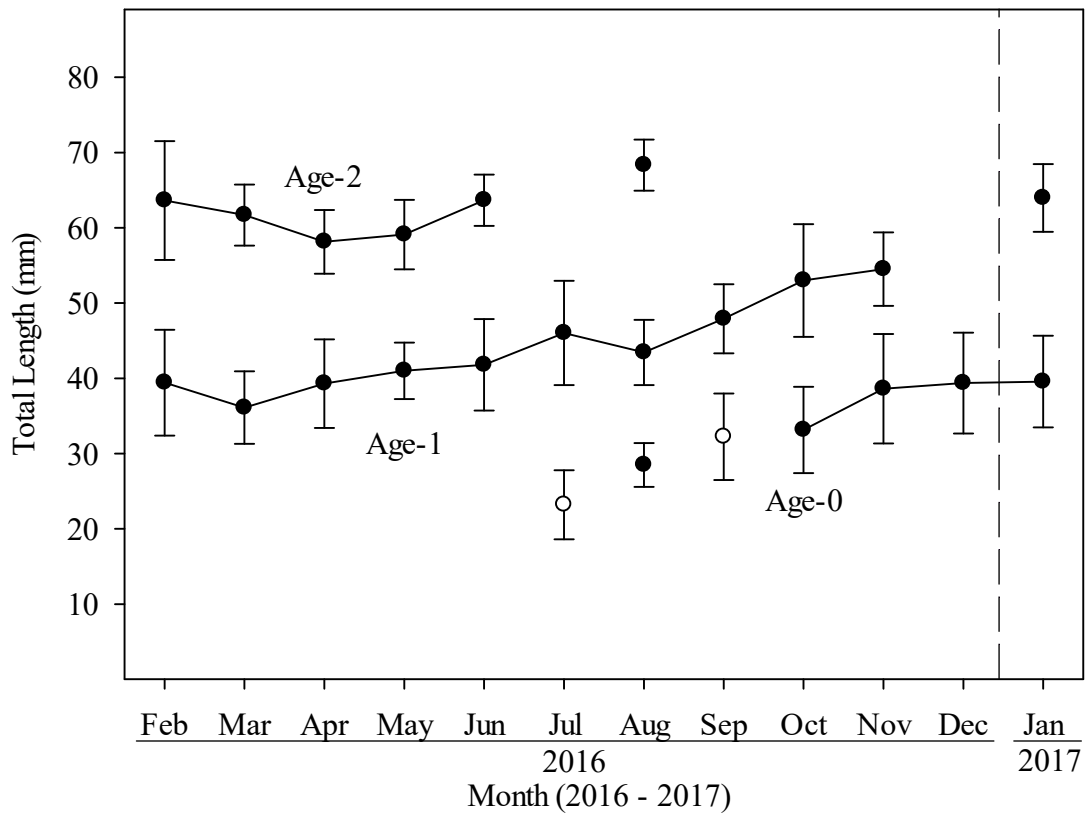


Figure 1.4. Mean ± 1 SD total lengths (black circles) for Age-0, Age-1, and Age-2 Red River Shiners taken monthly from February 2016 through January 2017. White circles represent mean and ± 1 SE of total lengths taken from ≤ 3 individuals within an age group per month. Dashed line indicates the transition into the next age class.

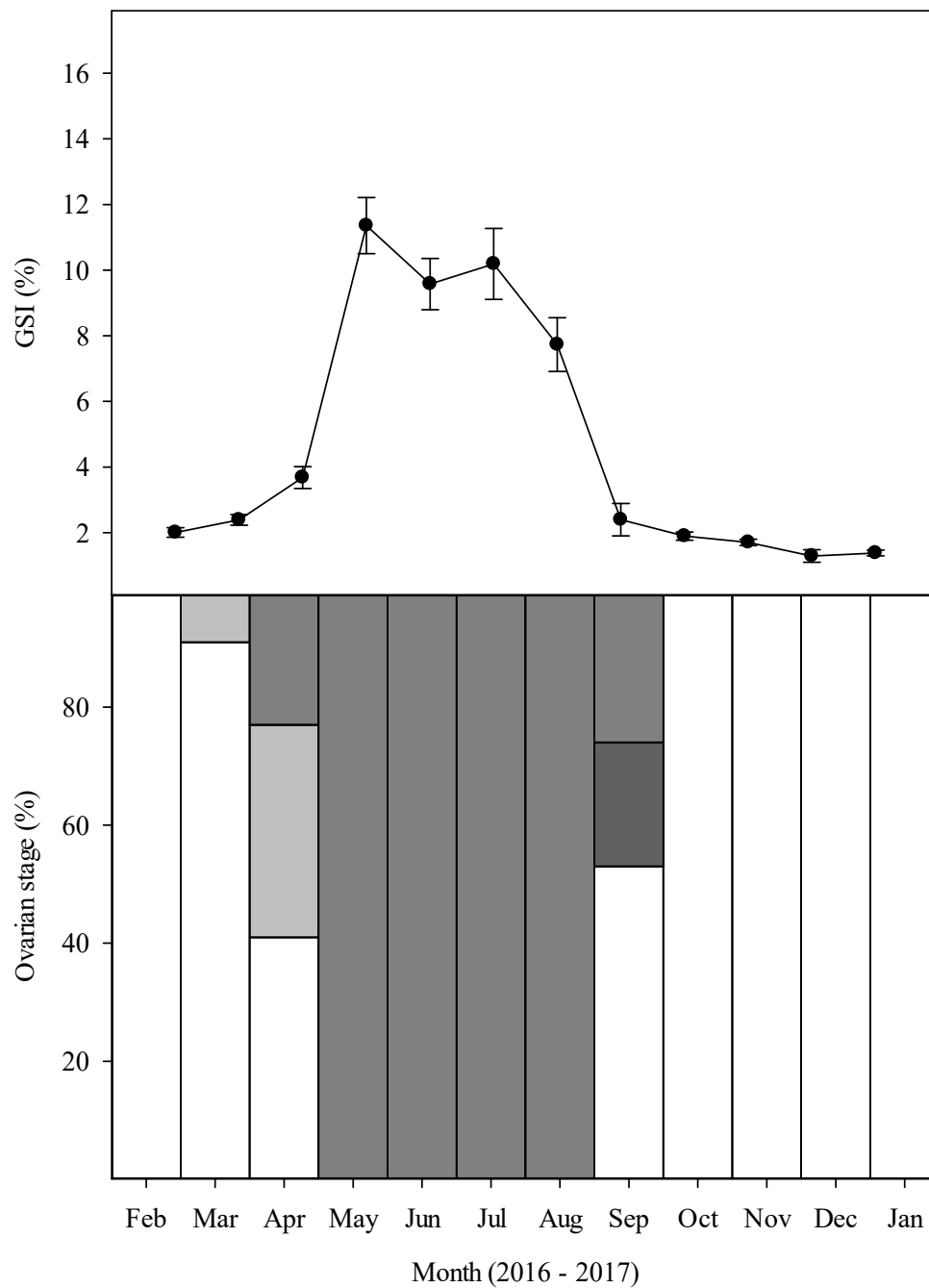


Figure 1.5. Mean (± 1 SE) monthly gonadosomatic index (GSI) for Red River Shiners taken from February 2016 through January 2017 (top panel). Percent ovarian stages by month for immature (white), developing (light gray), mature (gray), and spent (dark gray) females (bottom panel).

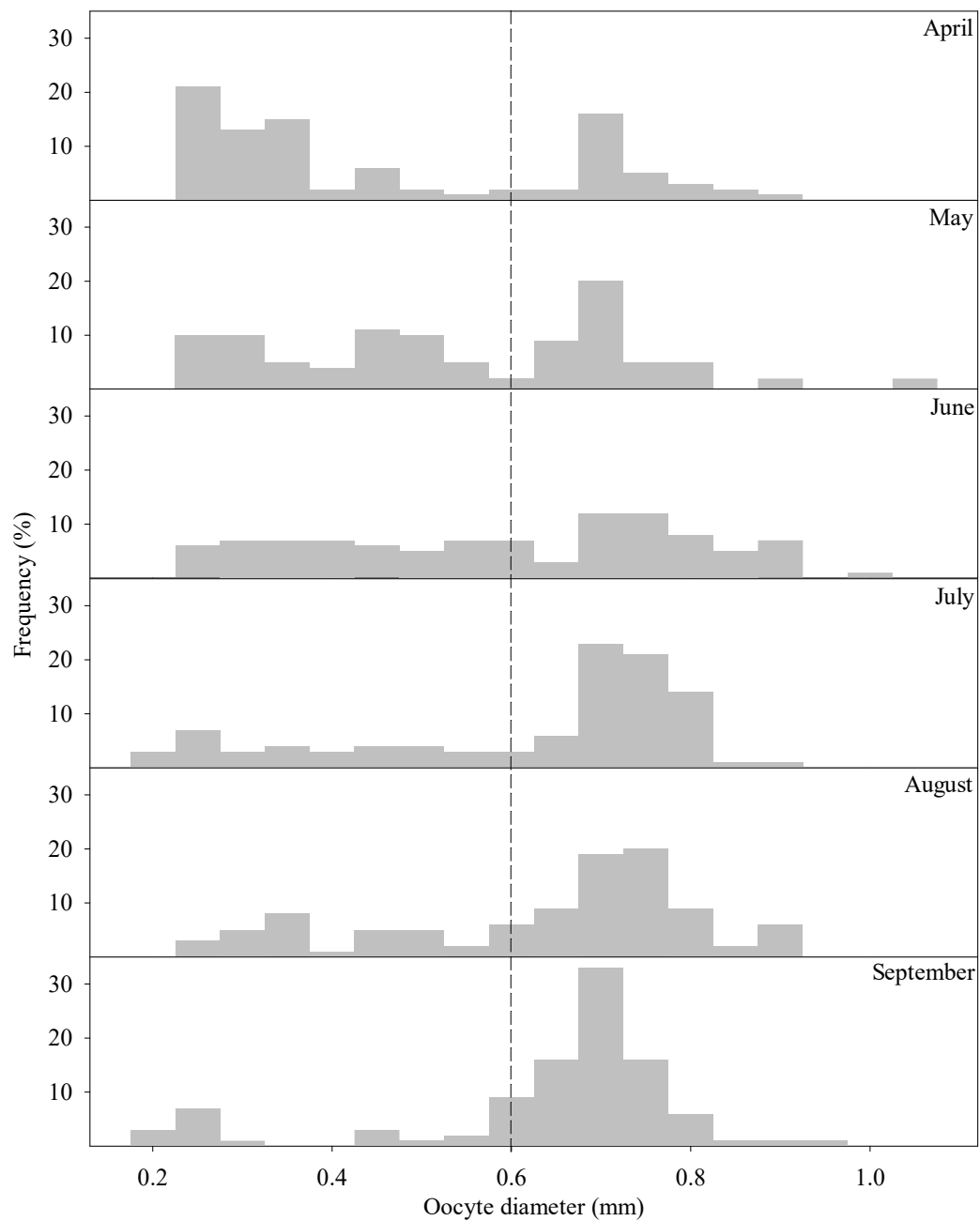


Figure 1.6. Frequency of oocyte size distribution in mature ovaries of Red River Shiner taken from May 2016 through September 2016. The dashed line indicates estimated size of late vitellogenic oocyte.

Literature Cited

- Arkansas Game and Fish Commission. 2015. The Arkansas Wildlife Action Plan. Editors, Allison Fowler and Jane Anderson. Little Rock, Arkansas.
- Association of Fish and Wildlife Agencies, Teaming with Wildlife Committee, State Wildlife Action Plan (SWAP) Best Practices Working Group. 2012. Best Practices for State Wildlife Action Plans—Voluntary Guidance to States for Revision and Implementation. Washington 389(DC): Association of Fish and Wildlife Agencies.
- Bonner, T.H. 2000. Life history and reproductive ecology of the Arkansas River Shiner and Peppered Chub in the Canadian River, Texas and New Mexico. PhD dissertation, Texas Tech University, Lubbock.
- Burr, B.M. and R.L. Mayden. 1981. Systematics, distribution and life history notes on *Notropis chihuahua* (Pisces: Cyprinidae). *Copeia* 1981:255-265.
- Craig, C.A., K. A. Kollaus, K. P. K. Behen, and T.H. Bonner. 2016. Relationships among spring flow, habitats, and fishes within evolutionary refugia of the Edwards Plateau. *Ecosphere* 7:1-13.
- Craig, C. A., J. D. Maikoetter, and T. H. Bonner. 2019. Temperature-mediated feeding between spring-associated and riverine-associated congeners, with implications for community segregation. *PeerJ* 6:e6144 <https://doi.org/10.7717/peerj.6144>
- Cross, F.B. 1953. A new minnow, *Notropis bairdi buccula*, from the Brazos River, Texas. *The Texas Journal of Science* 1953(2):252-259.
- Cross, F.B., O.T. Gorman, and S.G. Haslouer. 1983. The red river shiner, *Notropis bairdi*, in Kansas with notes on depletion of its Arkansas River cognate, *Notropis girardi*. *Trans. Kansas. Acad. Sci.* 86(2/3):93-98.
- Cross, F.B., R.E. Moss, and O.T. Collins. 1985. Assessment of dewatering impact on stream fisheries in the Arkansas and Cimarron Rivers. *Mus. Nat. Hist., Univ. Kansas, Lawrence*.
- Dodds, W. K., Gido, K., Whiles, M. R., Fritz, K. M., & Matthews, W. J. 2004. Life on the edge: the ecology of Great Plains prairie streams. *BioScience*, 54(3), 205-216.
- Durham, B.W. 2007. Reproductive ecology, habitat associations, and population dynamics of two imperiled cyprinids in a Great Plains river. Texas Tech University, Lubbock.

- Durham B.W. and G.R. Wilde. 2009. Effects of Streamflow and Intermittency on the Reproductive Success of Two Broadcast-spawning Cyprinid Fishes. *Copeia* 2009:21-28.
- Echelle, A.A., A.F. Echelle, and L.G. Hill. 1972. Interspecific interactions and limiting factors of abundance and distribution in the Red River pupfish, *Cyprinodon rubrofluviatilis*. *American Midland Naturalist* 88(1):109-130.
- Fausch, K.D. and K.R. Bestgen. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. 131p. In: F.L. Knopf and F.B. Samson (eds), *Ecology and conservation of Great Plains vertebrates*, Springer-Verlag, New York.
- Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. *Conservation Biology* 10(6):1500-1508.
- Gido, K.B., Schaefer, J.F., Work, K., Lienesch, P.W., Marsh-Matthews E., and Matthews, W.J. 1999. Effects of Red Shiner (*Cyprinella lutrensis*) on Red River Pupfish (*Cyprinodon rubrofluviatilis*). *Southwest Nat* 44:287–295.
- Gilbert, C.R. 1980. *Notropis bairdi* (Hubbs and Ortenburger), Red River shiner. p. 236. In: D. S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister & J. R. Stauffer, Jr. (eds.), *Atlas of North American freshwater fishes*, North Carolina State Museum of Natural History, Raleigh.
- Hargrave, C.W., C.M. Taylor. 2010. Spatial and temporal variation in fishes of the upper Red River Drainage (Oklahoma–Texas). *Southwestern Naturalist* 55(2):149-159.
- Heard, T. 2008. Spatial and temporal patterns in a Chihuahua Desert fish assemblage. M.S. Thesis, Texas State University, San Marcos.
- Hubbs, C.L., and A.I. Ortenburger. 1929. Further notes on the fishes of Oklahoma with descriptions of new species of Cyprinidae. *Publ. Univ. Okla. Biol. Surv.* 1(2):17-43.
- Leavy, T. 2004. Relationships among swimming ability, habitat use, and morphology of freshwater fishes in Texas and Louisiana. M.S. Thesis. Texas State University.
- Lohr, S.D. and K.D. Fausch. 1997. Multiscale analysis of natural variability in stream fish assemblages of a western Great Plains watershed. *Copeia* 1997:706-724.
- Luttrell, G.R., D.M. Underwood, W.L. Fisher, and J. Pigg. 1995. Distribution of the Red River shiner, *Notropis bairdi*, in the Arkansas River drainage. *Proc. Okla. Acad. Sci.* 75:61-62.

- Jelks H.L., Walsh S.J., Burkhead N.M., Contreras-Balderas S., Diaz-Pardo E., Hendrickson D.A., Lyons J., Mandrak N.E., McCormick F., Nelson J.S., Platania S.P., Porter B.A., Renaud C.B., Schmitter-Soto J.J., Taylor E.B., and Warren M.L. 2008. Conservation Status of Imperiled North American Freshwater and Diadromous Fishes. *Fisheries* 33:372–407.
- Marks, D.E. 1999. Life history characteristics of the Sharpnose Shiner (*Notropis oxyrhynchus*) and the Smalleye Shiner (*Notropis buccula*) in the Brazos River, Texas. M.S. Thesis. Texas Tech University.
- Marshall, C.L. 1978. The distribution of *Notropis bairdi* along the Cimarron River in Logan County, Oklahoma. *Proc. Okla. Acad. Sci.* 58:109.
- Matthews, W.J. 1988. North American prairie streams as systems of ecological study. *J N Am Benthol Soc* 7:387–409.
- Mayden, R.L. 1989. Phylogenetic studies of North American minnows, with emphasis on the genus *Cyprinella* (Teleostei: Cypriniformes). *Misc. Publ. Univ. Kans. Mus. Nat. Hist.* 80:1-189.
- Miller, R. J. and H. W. Robison. 2004. *Fishes of Oklahoma*. University of Oklahoma Press, Norman, OK.
- Moss, R.W. and K.B. Mayes. 1993. Current status of *Notropis buccula* and *Notropis oxyrhynchus* in Texas. *River studies report 8*, Texas Parks and Wildlife Department, Austin, TX.
- Nance, H. S., 2006, Tracking salinity sources to Texas streams: Examples from West Texas and the Texas Gulf Coastal Plain. *Gulf Coast Association of Geological Societies Transactions* 56:675-693.
- Oklahoma Department of Wildlife Conservation. 2005. Oklahoma comprehensive wildlife conservation strategy: a strategic conservation plan for Oklahoma's rare and declining wildlife. Oklahoma City, Oklahoma.
- Osborne, M.J., T.A. Diver, T.F. Turner. 2013. Introduced populations as genetic reservoirs for imperiled species: a case study of the Arkansas River Shiner (*Notropis girardi*). *Conservation Genetics* 14:637-647.
- Ostrand, K.G. and G. Wilde. 2002. Seasonal and spatial variation in a prairie stream-fish assemblage. *Ecology of Freshwater Fish* 11:137-149.
- Perkin, J.S., C.S. Williams, and T.H. Bonner. 2009. Aspects of Chub Shiner *Notropis potteri* life history with comments on native distribution and conservation status. *American Midland Naturalist* 162:276-288.

- Pigg, J., R. Gibbs, K.K. Cunningham. 1999. Decreasing abundance of the Arkansas River Shiner in the South Canadian River, Oklahoma. *Proc. Okla. Acad. Sci.* 79:7-12.
- Quist, M.C., M.R. Bower, W.A. Hubert, and F.J. Rahel. 2006. Spacial patterns of fish assemblage structure in a tributary system of the upper Colorado River basin. *Journal of Freshwater Ecology* 21:673-680.
- Robinson, H.W. and T.M. Buchanan. *Fishes of Arkansas*. The University of Arkansas Press, Fayetteville.
- Ruppel, D.S., V.A. Sotola, C.A. Craig, N.H. Martin, and T.H. Bonner. In review. Factors associated with instream movement of prairie stream fishes: a case study using *Macrhybopsis australis*. *Aquatic Ecology*.
- Scudder, G.E. 1989. The adaptive significance of marginal populations: a general perspective. *Can. Spec. Publ. Fish. Aquat. Sci.* 105:180-185.
- Scheffer, M., R. Vergnon, E. H. van Nes, J. G. M. Cuppen, E. T. H. M. Peeters, R. Leijds, and A. N. Nilsson. 2015. The evolution of functionally redundant species; evidence from beetles. *PLoS one* 10(10):1–10.
- Schlosser, I.J. 1987. The role of predation in age and size related habitat used by stream fishes. *Ecology* 68:651-659.
- Shaffer, M. L. and B.A. Stein. 2000. Safeguarding our precious heritage. In: B.A. Stein, L.S. Kutner, and J.S. Adams (eds) *Precious heritage the status of biodiversity in the United States*. pp 301-321 Oxford University Press, New York.
- Smith, D.R., N.L. Allen, C.P. McGowan, J.A. Szymanski, S.R. Oetker, and H.M. Bell. 2018. Development of a species status assessment process for decisions under the U.S. Endangered Species Act. *Journal of Fish and Wildlife Management* 9: 1-19.
- Taniguchi, Y., F.J. Rahel, D.C. Novinger, and K.G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Can. J. Fish. Aquat. Sci.* 55:1894-1901.
- Texas Parks and Wildlife Department. 2012. *Texas Conservation Action Plan 2012-2016: overview*. Editor, Wendy Connally, Texas Conservation Action Plan Coordinator. Austin, Texas.
- Thomas, C., T.H. Bonner, and B.G. Whiteside. 2007. *Freshwater fishes of Texas*. Texas A&M University Press, College Station.

- U.S. Fish and Wildlife Service. 1998. Endangered and threatened wildlife and plants; final rule to list the Arkansas River basin population of the Arkansas River Shiner (*Notropis girardi*) as threatened. Federal Register 63 FR 64772 64799, Arlington, TX.
- U.S. Fish and Wildlife Service. 2014. Determination of Endangered Status for the Sharpnose Shiner and Smalleye Shiner. Federal Register 79 FR 45273 45286, Arlington, TX.
- U.S. Fish and Wildlife Service. 2016. Long-term listing transformation and five guiding principles of the Unified Listing Team. Director's memorandum 16 March 2016, Washington, D.C. (Supplemental Material, Reference S9).
- U.S. Geological Survey. 2011. Chloride control and monitoring program in the Wichita River Basin, Texas, 1996-2009. Austin, TX.
- Warren, M.L., Jr., B.M. Burr, S.J. Walsh, H.L. Bart, Jr., R.C. Cashner, D.A. Etnier, B.J. Freeman, B.R. Kuhajda, R.L. Mayden, H.W. Robison, S.T. Ross, and W.C. Starnes. 2000. Diversity, Distribution, and Conservation status of the native freshwater fishes of the southern United States. *Fisheries* 25(10):7-29.
- Williams, C. S. and T. H. Bonner. 2006. Habitat associations, life history, and diet of the Sabine Shiner *Notropis sabiniae* in an east Texas drainage. *American Midland Naturalist* 155:84-102.
- Winemiller K.O. and K.A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Can J Fish Aquat Sci* 49:2196-2218.
- Winston, M.R., C.M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. *Trans. Amer. Fish. Soc.* 120:98-105.
- Worthington T.A., A.A. Echelle, J.S. Perkin, R. Mollenhauer, N. Farless, J.J. Dyer, D. Logue, and S.K. Brewer. 2017. The emblematic minnows of the North American Great Plains: a synthesis of threats and conservation opportunities. *Fish and Fisheries* 19:271-307.
- Wurbs, R.A. 2002. Natural salt pollution control in the Southwest. *Journal of American Water Works Association* 94:58-67.

II. FACTORS ASSOCIATED WITH INSTREAM MOVEMENT OF PRAIRIE STREAM FISHES: A CASE STUDY USING *MACRHYBOPSIS AUSTRALIS*

Abstract

Pelagic broadcast spawning cyprinids are a mobile group of fishes commonly found within semi-arid areas of the Great Plains of North America. Upstream movements of 50 to 200 km are reported for pelagic broadcast spawning cyprinids and associated with reproductive migration. However, fish migrations are also associated with feeding and refuge purposes. Goals of this study were to detect synchronous movements of a pelagic broadcast spawning cyprinid and relate movement to reproduction, feeding, and refuge. We used Prairie Chub *Macrhybopsis australis*, an endemic species in the Red River basin of Texas and Oklahoma, as our model organism. Objectives were to quantify habitat associations, reproduction, feeding, age structure, and movement of Prairie Chubs. Movement of Prairie Chubs was quantified by genetic differentiation by linear distances and temporal occurrences of breeding adults among multiple sites within two rivers. We found that Prairie Chubs were benthic invertivores, lived up to 2 years, and were multiple batch spawners over a 5-month period between May through September. Relationships between genetic differentiation and linear distances were not detected, suggesting a panmictic population. Movement was only detected among sites in one river and asynchronous. Movement was consistent with refuge migration, somewhat consistent with reproductive migration, and inconsistent with feeding migration. Our findings support an emerging theory on the life-history cycle of pelagic broadcast spawning cyprinids (i.e., upstream movement not related to

reproduction, drift of propagules not necessary) and contrasts the more established theory of upstream movement to compensate for downstream drift of propagules (i.e., drift compensation theory).

Introduction

Within semi-arid Great Plains region of North America (Omernik and Griffith 2014), fish communities are a result of historical species dispersion and isolation events with many species possessing or evolving an opportunistic life history strategy (Winemiller and Rose 1992) to persist in streams with variable flows and widely fluctuating turbidity, temperature, and specific conductance (Cross et al. 1986; Matthews 1988). A reproductive guild of fishes within the opportunistic life history strategy is the pelagic broadcast spawning cyprinids (Johnson 1999). Pelagic broadcast spawning cyprinids commonly inhabit Great Plains streams and are of an increasing conservation concern (Worthington et al. 2017). A key component of the conservation concern is fragmentation of river reaches by dams and the associated effects on pelagic broadcast spawning cyprinid life cycles, which includes large-scale (i.e., 50 to 200 km) upstream movements (Bestgen et al. 2010; Perkin and Gido 2011; Wilde 2016; Worthington et al. 2017). Upstream movement is supported by length frequency assessments and reproductive condition (Bonner 2000), catch rates and reproductive condition (Walters et al. 2014), visible implant elastomer tags (Wilde 2016), otolith microchemistry (Chase et al. 2015), and genetic assessments (Alò and Turner 2005). The purpose of large-scale upstream movements is presumed to be reproduction migration (Worthington et al. 2017).

Migration is defined as “synchronized movements by species that are large relative to the average home range of that species and which occur at a specific stage of the life cycle” (Lucas and Bara 2001) with three recognized purposes: 1) reproduction, 2) feeding, and 3) refuge (Northcote 1978, 1984). Reproductive migration is movement to complete a spawning cycle (Lucas and Bara 2001) in which individuals begin moving to spawning grounds prior to the onset of the spawning event (Irving and Modde 2000; Fredrich et al. 2003). Feeding migration is movement for resource acquisition and includes horizontal movement into floodplains and other areas to access newly available resources (Lucas and Bara 2001) and higher quality food (L’Abee-Lund and Vøllestad 1987). Refuge migration is movement from unfavorable abiotic conditions to more favorable abiotic conditions to enhance survival, conservation of energy, growth, and reproductive output (Lucas and Bara 2001). Movement is related to physiological preferences and tolerances of fishes (Edwards 1977) or leaving an area before complete drying of a stream reach (Cambray 1990). Identifying and quantifying the underlying purpose (i.e., reproductive, feeding, refuge) of observed upstream movements can provide greater insight into the basic behaviors of pelagic broadcast spawning cyprinids and facilitate management and threat assessments of Great Plains fishes.

One endemic Great Plains pelagic broadcasting spawning cyprinid, the Prairie Chub *Macrhybopsis australis*, is only found in upper Red River drainage of Texas and Oklahoma and likely migrates similar to other *Macrhybopsis* (Wilde 2016) within the “Speckled Chub” complex (Eisenhour 2004). Conservation status of the Prairie Chub is G2G3 (G2 = imperiled; G3 = vulnerable) by NatureServe (NatureServe 2018), vulnerable by the 2008 American Fisheries Endangered Species Committee (Jelks et al. 2008), and

species of greatest conservation need by Texas Parks and Wildlife Department (TPWD 2012) and Oklahoma Department of Wildlife Conservation (ODWC 2005). Life history information for the Prairie Chub (i.e., reproductive season and effort, age class structure, and diet) is lacking, and information is limited on distribution, abundance, and habitat associations (Taylor et al. 1996; Wilde et al. 1996; Eisenhour 2004). Life history information, current distributions, and habitat associations are necessary to assess the purpose of migration in the Prairie Chub.

Goals of this study were to detect synchronous movement of Prairie Chub at specific life stages and relate the movement to purposes associated with migration (i.e., reproduction, feeding, and refuge). Goals were addressed by four primary objectives. The first objective was to update current distribution, abundance, and habitat associations of Prairie Chubs within its historical range in Texas and the Red River of Oklahoma. This objective was necessary in order to quantify breadth in Prairie Chub habitat associations used to assess refuge migration and to identify river reaches with sufficient population sizes to sustain collections for population genetic, reproduction, diet, and age assessments. The second objective was to assess genetic isolation by distance among a subset of the river reaches and determine if the Prairie Chub population was panmictic or not (i.e., support for movement among sites or not). The third objective was to quantify monthly age class structure, reproductive pattern, and diet of Prairie Chubs at three, unimpeded sites on one river (i.e., Pease River) and two, unimpeded sites on another river (i.e., Wichita River). The fourth objective was to relate monthly changes in Prairie Chub occurrences and age structure at each site (i.e., synchronized movement by specific age groups) to reproductive status (i.e., gonadosomatic index, ovarian condition), feeding

(i.e., gut fullness, diet items and abundance), and habitat conditions. Based on previous literature, expectations were that Prairie Chubs would have a similar life history and habitat associations to other species within the *Macrhybopsis* “Speckled Chub” complex, specifically, Prairie Chubs will primarily consume benthic invertebrates, have a short life span, produce multiple clutches for three to five months based on latitude (Gotelli and Pyron 1991), and will be associated run and riffle habitats (Bonner 2000; Williams 2010; Perkin et al. 2013). We expected for the populations to be panmictic and genetic differences would not be related to linear geographic distances among sites similar to other prairie stream minnows (Alò and Turner 2005). Migrations of Prairie Chubs correspond with one or more of the purposes of migration: reproductive migration--movement during gonadal recrudescence but before egg release (Tyus 1990; Fredrich et al. 2003); feeding migration--movement into areas with greater food quality or quantity (L’Abee-Lund and Vøllestad 1987); or refuge migration--movement for physiological preference or intermittent drying (Edwards 1977; Cambray 1990).

Methods

Field Collections

Two longitudinal surveys, once during the non-reproductive season and once during the reproductive season, were conducted at 36 sites among 20 water bodies encompassing 730 river km (rkm) within the upper Red River drainage between September 2015 and September 2016 (Figure 2.1; Appendix 2.1). At each site, habitats (i.e., riffle, run, pool, backwater, and eddy) were delineated and sampled in proportion to their availability. Habitats were exhaustively sampled with single to multiple seine hauls,

using a standard seine (3 m x 1.8 m, mesh size = 3.2 mm) or bag seine (5 m x 1.8 m, mesh size = 3.2 mm). Length and width of area sampled were measured. Substrate (i.e., clay, silt, sand, gravel, cobble, boulder, and bedrock), woody debris, detritus, and aquatic vegetation were visually or tactilely estimated and represented as a percent coverage of the total habitat area. Mean water depth (m) and current velocities (m/s) were estimated from three to five-point estimates within a representative cross section of the habitat. Water temperature (°C) dissolved oxygen (mg/L), pH, and specific conductance (µS/cm) were measured at each site with a YSI 556 multi-probe sonde. Prairie Chubs were taken as available for genetic analysis, anesthetized in a lethal dose of tricane methanesulfonate (MS222), and preserved in 95% ethanol.

Five sites were selected for monthly collections of Prairie Chubs between February 2016 and January 2017 from three sites on the Pease River (i.e., FM 104, Hwy 6, Hwy 283) and two sites on the North Wichita-Wichita River (i.e., Hwy 6 and FM 1919). Sites on the Pease River and sites on the North Wichita-Wichita River were located within continuous river reaches but the two tributaries were separated by two reservoirs, Lake Kemp and Lake Diversion. On the Pease River, the upper site (i.e., FM 104) was located about 60 rkm upstream from middle site (i.e., Hwy 6), and the middle site was located about 60 rkm upstream from the lower site (i.e., Hwy 283). On the North Wichita-Wichita River, the upper site (i.e., Hwy 6) was located about 90 rkm upstream from the lower site (i.e., FM 1919). At each site and date, a minimum of 10 seine hauls were made to capture 10 Prairie Chubs (≥ 35 mm in total length; minimum length for sexual maturity in congeneric Peppered Chub *M. tetranema*, Bonner 2000). Total lengths (nearest mm) were measured on all Prairie Chubs and used for length

frequency assessment. Up to 10 Prairie Chubs were retained for life history assessment, anesthetized with a lethal dose of MS222, and fixed in 10% formalin.

Laboratory Techniques

Genetics

Genomic DNA was extracted from fin clips in 96-well format using Qiagen DNeasy blood and tissue extraction kits. For each individual, a reduced-complexity genomic library was prepared for genotyping by sequencing protocols modified from Meyer and Kircher (2010), Gompert et al. (2012), Parchman et al. (2012), Mandeville et al. (2015), and described in detail in Sotola et al (2019). DNA was digested using the enzymes EcoRI and MseI and the resulting fragments were labeled with 8-10 base pair barcodes. Two rounds of polymerase chain reaction (PCR) were performed on these restriction-ligation products using Illumina primers, and all samples were pooled into a single library and sent to the University of Texas Genomic Sequencing and Analysis Facility (Austin, TX, USA). After size selection between 300 and 400 base pairs, the library was sequenced on an Illumina HiSeq 4000 SR 150 platform.

After sequencing, PhiX contaminants, MseI adapters and barcodes were removed (Sotola et al. 2019, and a de novo assembly was performed using dDocent (Puritz et al. 2014). Unique reads were identified for each individual and those with fewer than four copies and shared by fewer than four individuals were removed from the dataset. The scaffolds obtained from this de novo assembly formed the basis of a subsequent reference-based assembly in which all sequenced reads were added (Li et al. 2009; Sotola et al. 2019). Variable sites (Single Nucleotide Polymorphisms - SNPs) were identified

and the Bayesian posterior probabilities that individual SNPs were variable were calculated (Li et al. 2009). For contigs containing more than one SNP, a single SNP was randomly chosen for subsequent analyses. SNP genotypes were not “called,” but rather likelihood estimates were calculated for each SNP across all individuals and used to determine population allele frequencies. SNPs with minor allele frequency of < 0.05 were excluded from the dataset. In all, genotype likelihood data were obtained for a total of 32,122 SNPs.

Reproduction

Up to five females fixed in formalin were randomly selected, measured to the nearest mm, and weighed to the nearest mg for each site and month. An incision was made from the urogenital opening to isthmus. The esophagus was severed, and the stomach, intestine, and ovaries were removed. Ovaries were weighed, and gonadosomatic index (GSI; $[\text{mass of ovaries} / \text{mass of fish}] \times 100$) was calculated for each fish. Ovaries were macroscopically categorized as 1) immature or resting ovaries with small, translucent oocytes; 2) developing ovaries with small (< 0.2 mm in diameter), translucent oocytes and small (< 0.5 mm) opaque oocytes indicating early stages of yolk deposition; 3) mature ovaries with small translucent oocytes, small opaque oocytes, and large (> 0.5 mm in diameter) vitellogenic oocytes; and 4) spent ovaries with small translucent oocytes and a few large vitellogenic oocytes (Williams and Bonner 2006). The left ovary of up to three females with mature ovaries were selected, and individual oocytes were separated by teasing oocyte mass apart and redistributed in a petri dish with a gentle swirl.

Diameters were measured for oocytes > 0.2 mm to the nearest 0.01 mm for the first 100 oocytes encountered in multiple fields of view with dissection microscope fitted with an ocular micrometer. Oocyte diameters were plotted by percent frequency of occurrence to estimate modalities of clutch production (i.e., single spawning or multiple batch spawning).

Diets

With the use of a dissecting scope, the stomach was separated from the intestine at the pyloric sphincter muscle. The stomach wall was cut longitudinally from the sphincter muscle to the esophagus, carefully exposing the gut contents. Stomach fullness (i.e., proportion of stomach filled by contents) was determined by two independent observers, assigning a number from 0 (empty) to 100 (full) in increments of 10. Stomach contents were sorted and identified. Percent volume was defined as the volume of algae, animal materials, substrates, and plastics comprising the total volume of stomach fullness. Percent occurrence was defined as the number of fish with a food item identified to the lowest practical taxonomic level. Animal materials were counted per lowest practical taxonomic level, and relative abundance was calculated for each item.

Data Analysis

Habitat Associations

Principal component analysis (PCA; SAS Institute, Cary, NC) was used to calculate linear combinations of habitat parameters and to assess variability among habitats. Qualitative parameters (e.g., habitat types) were denoted as dummy variables,

whereas quantitative parameters (e.g., percent substrate and current velocity) were z-transformed (Krebs 1999). Resulting PCA loadings of axes I and II were plotted to express similarities and differences among habitats. Loadings were averaged for habitats within a water body. Habitat associations were assessed from the PCA model developed for the longitudinal survey of upper Red River. Habitat PC axes I and II scores with Prairie Chub occurrences were compared to habitat PC scores without Prairie Chub occurrences using t-tests ($\alpha = 0.05$). Numbers of Prairie Chubs were $\log_{10}(N+1)$ transformed and regressed with habitat PC axes I and II scores (i.e., independent variables) to assess relationship between abundance and habitat gradients with linear regression. We additionally tested Prairie Chubs distributions among habitat types (i.e., run, riffle, pool, backwater) with Chi-Square test and tested habitat variables with Kolmogorov-Smirnoff (KS) test among depth, current velocity, and specific conductance gradients, because these variables were identified as factors associated with fish distributions within upper Red River drainage (Ruppel et al. 2017).

Genetics

A total of 32,122 SNPs were generated. Genetic differentiation, Nei's GST (Nei 1987), was calculated using Program R (R Core Team 2017) with allele frequencies, which were calculated from the mean genotype posterior probabilities from Entropy (Gompert et al. 2014; Mandeville et al. 2015, Sotola et al. 2018). Bayesian linear regressions were used to determine the degree to which linearized pairwise genetic distances ($GST/(1-GST)$) could be explained by pairwise geographic distance (measured as the rkm difference between two sites). Geographic distances were scaled and centered

prior to analysis. Program R and the RJAGS package were used to run MCMC models using the JAGS language (Plummer 2003). Because the Prairie Chub is hybridizing with the Shoal Chub *M. hyostoma* (Sotola et al. 2019), only sites and individuals with > 95% assignment probability to Prairie Chub clusters in Entropy were used (Gompert et al. 2014; Mandeville et al. 2015; Sotola et al. 2019). This included individuals from the Pease River, Wichita River, and upper Red River. Two separate linear regression models were assessed. The first regression model used pairwise linear genetic differentiation estimates taken from sites not separated by impoundments. The model consisted of 15 pairwise estimates among six, unimpeded sites on the Pease River and upper Red River, and one pairwise estimate between the two Wichita River sites separated from all other sites by an impoundment as the dependent variable. The second regression model used pairwise linear genetic differentiation estimates taken from all sites. The model consisted of 28 pairwise estimates including 12 pairwise estimates between sites separated by impoundments as the dependent variable. In total for each regression, four independent chains each were ran with 1,000 iterations, a 500 iteration burn-in and a thinning interval of 10. We specified vague Gaussian priors on the standardized scale for the regression coefficients ($\mu = 0$, $\sigma^2 = 0.01$). Significance was assessed via the 95% confidence intervals of the slope estimate; if they overlapped zero it was considered a non-significant slope (slope estimate did not differ from zero) estimate. Chains were checked for convergence using diagnostic plots and Gelman and Rubin's scale reduction factor to verify adequate chain mixing was calculated (value between 1 and 1.1 was acceptable; Gelman and Rubin 1992; Plummer et al. 2006).

Age classes

Length frequency histograms were constructed from monthly collections using 2-mm bin increments combined across sites to assess number of age groups and life span. Modal progression analysis (Bhattacharya's Method; Fish Stock Assessment Tools II; FiSAT II) was used to estimate the number of age groups and their sizes monthly between February 2016 and January 2017. Birth date follows conventional standard of January 1 (Jearld 1983). Age-0 fish were spawned in 2016, age-1 fish were spawned in 2015, and age-2 fish were spawned in 2014.

Results

Habitat associations — longitudinal surveys

Prairie Chubs (N = 486) were taken from 51 (13%) of 400 habitats, 16 (44%) of 36 sites, and six (30%) of 20 water bodies sampled within the upper Red River basin. Relative abundance of Prairie Chubs among all habitats, sites, and water bodies was 1.3% and ranged between 0.1% and 9.6% among sites where they occurred. Density of Prairie Chubs among all habitats, sites, and water bodies was 0.009 fish/m² and ranged between <0.01 fish/m² and 0.28 fish/m² among sites where they occurred. Habitats (N = 400) consisted primarily of runs (70%) and pools (12%). Habitats were generally shallow (mean depth $\pm$ 1 SE: 0.3 m $\pm$ 0.01) with moderate current velocities (0.21 m/s $\pm$ 0.009) and predominantly sand (57%), silt (30%), and gravel (9%) substrates. Mean woody debris, detritus, and aquatic vegetation ranged from 0.7% ($\pm$ 0.14) to 1.1% ($\pm$ 0.22). Water temperatures ranged between 5°C and 37°C, dissolved oxygen ranged between 2.6 to 15 mg/l, and pH ranged between 6.9 and 8.9. Specific conductance ranged between

115 and 49,968 $\mu\text{S}/\text{cm}$ with greater specific conductance observed in the western water bodies and lower specific conductance observed in eastern water bodies.

Principal component axes I and II explained 24% of the total variation among 400 habitats sampled. Axis I explained 13% of the total variation and represented habitat type and substrate gradient. Strongest loadings for PC axis I were pool (0.33), silt (0.30), run (-0.46), and sand (-0.45) (Figure 2.2A). PC Axis II explained 11% of the variation and represented a habitat type, substrate, and current velocity gradient. Strongest loadings for PC axis II were riffle (0.42), gravel (0.40), current velocity (0.39), and silt (-0.37).

Prairie Chub occurrences were not associated with PC axis I (t-test; $t_{0.05}(2, 398) = 0.42$, $P = 0.67$) or PC axis II ($t_{0.05}(2, 398) = 0.37$, $P = 0.67$). Likewise, Prairie Chub abundances were not associated with PC axis I (linear regression; $F_{1,398} = 0.14$, $P = 0.71$) or PC axis II ($F_{1,398} = 0.13$, $P = 0.72$) (Figure 2.2B). Six water bodies with Prairie Chubs did not differ among 14 water bodies without Prairie Chubs for PC axis I (t-test; $t_{0.05}(2, 398) = 1.80$, $P = 0.07$) but differed for PC axis II (t-test; $t_{0.05}(2, 398) = 3.25$, $P < 0.01$) (Figure 2.2C). Water bodies with Prairie Chubs generally consisted of swifter waters within braided, sand-bed prairie streams of the Red River and western tributaries, whereas water bodies without Prairie Chubs consisted of slow-moving pools with silt substrates within the entrenched eastern tributaries of the upper Red River drainage. However, Prairie Chubs were not taken from several braided, sand-bed prairie streams (i.e., negative water body averages on PC axis I), such as Prairie Dog Town Fork, Salt Fork Red River, North Fork Red River, Adams Creek, or Cottonwood Creek.

Habitats with Prairie Chubs differed from expected in habitat type, current velocity, depth, and specific conductance. Prairie Chubs were taken more often in run

(76%) and riffle (10%) habitats than available (70% runs, 9% riffles) and less often in pool (8%) and backwater (6%) habitats than available (12% pools, 9% backwater; Chi-square, $X^2 = 16.8$, $P < 0.01$). Prairie Chub occurrences among current velocities ranged between 0 and 0.6 m/s with 66% of Prairie Chubs captured between 0 and 0.2 m/s. Use of current velocities did not differ from expected for Prairie Chub occurrences (KS = 0.12, $P > 0.05$), but differed for abundances (KS = 0.24, $P < 0.01$) (Figure 2.3). Prairie Chub occurrences among water depths ranged between 0.04 and 1.2 m with 88% of Prairie Chubs captured between 0.1 and 0.4 m. Use of shallow water depths differed from expected for Prairie Chub occurrences (KS = 0.22, $P < 0.05$) and abundances (KS = 0.20, $P < 0.01$). Prairie Chub occurrences among specific conductance ranged between 2,215 and 26,408 $\mu\text{S}/\text{cm}$ with 77% of Prairie Chubs captured between 10,000 and 20,000 $\mu\text{S}/\text{cm}$. Use of moderately high specific conductance differed from expected for Prairie Chub occurrences (KS = 0.19, $P < 0.05$) and abundances (KS = 0.28, $P < 0.01$).

Genetics — longitudinal surveys

A total of 166 individuals from eight sites were used in the genetic analysis. Linear relationship was not detected (Npairwise comparisons = 16, slope: 0.015, 95% CI: -0.006 – 0.036; Figure 2.4A) between pairwise linear genetic differentiation (GST) and river distance (rkm) among sites not separated by an impoundment. Likewise, linear relationship was not detected (Npairwise comparisons = 28, slope: 0.002, 95% CI: -0.004 – 0.007; Figure 2.4B) between pairwise linear genetic differentiation (GST) and river distance (rkm) among all sites, including sites separated from another by an impoundment.

Reproduction, diet, and age— Pease and North Wichita-Wichita rivers

A total of 193 female Prairie Chubs were taken for reproductive assessments from Pease River (N = 87) and North Wichita-Wichita River (N = 106). Mean monthly GSIs were <2% from October through February, corresponding with females having immature or resting ovaries (N = 80 females; 39 – 63 mm in TL; Figure 2.5). Mean monthly GSIs were >2% from March through September, corresponding with females having developing ovaries between March and September (N = 27 females; 37 – 62 mm in TL) and with females having mature ovaries between May and September (N = 64 females; 38 – 66 mm in TL). Individual GSIs ranged between 0.9 to 8.8% for females with developing ovaries and ranged between 6.0% to 23% for females with mature ovaries. Oocyte diameters ranged from 0.3 mm to 1.2 mm in females with mature ovaries taken monthly from May through September (Figure 2.6). Non-vitellogenic and early vitellogenic oocytes occurred continuously among mature ovaries from May through September.

A total of 197 male and female Prairie Chubs were taken for gut content assessments from the Pease River (N = 89) and North Wichita-Wichita River (N = 108). Gut content by volume consisted primarily of animal materials (99%; Table 2.1). Mean (± 1 SD) monthly gut fullness ranged from 4.6% (± 7.6) in November 2016 to 65% (± 41.1) in May 2016. Frequency of empty stomachs was 4.5%. The most frequently occurring items were Chironomidae (88% occurrence), sand (37%), clay or silt (14%), and unknown Diptera pupa (11%). Chironomidae occurred in Prairie Chubs stomachs year-round with monthly occurrences ranging from 70% in December 2016 to 100% in

July 2016. Among animal material, Chironomidae was the most abundant food item (95%) followed by unknown Diptera pupa (2%). Other aquatic invertebrate taxa were consumed but at low ($\leq 0.1\%$) relative abundance. Likewise, terrestrial invertebrates and parts of vertebrates (i.e., fish scales and gills) were consumed but at low relative abundances.

Length measurements were taken from 1,295 Prairie Chubs (N = 569 from Pease River, N = 726 from North Wichita-Wichita River). Prairie Chubs consisted of three, estimated age classes: Age 0, Age 1, and Age 2 (Figure 2.7). Age-2 fish represented 11% of the adult population, were taken February through August 2016, and reached a maximum total length of 67 mm. Age-1 fish represented 89% of the adult population and were taken year-round. Age-0 fish were taken July through December 2016 and reached a mean total length of 40 mm (± 4).

Age group distributions among sites — Pease and North Wichita-Wichita rivers

Fish of sexually mature age (i.e., age 1 and age 2 adults) were less homogeneously distributed among sites on the Pease River from March 2016 through January 2017 and more homogeneously distributed between sites on the North Wichita-Wichita River from February 2016 through January 2017. Within the upper site (i.e., FM 104) of the Pease River, adult fish were present only June through August and in January (Figure 2.8). Within the middle (i.e. Hwy 6) site, adult fish were present every month, except in June. Within the lower site (i.e., Hwy 283), adult fish were present March through May and October through January. Age-0 fish were first detected in July and found at all sites from August through December, except at the upper site from October through

December. Within the upper site (i.e., Hwy 6) of the North Wichita-Wichita River, adult fish were present every month except in October (Figure 2.9). Within the lower site (i.e., FM 1919), adult fish were present every month, except in June. Age-0 fish were first detected in July and found consistently at both sites from August through December.

Heterogeneity in adult fish occurrences by site and month within the Pease River corresponded consistently more with a water quality (i.e., specific conductance) than with reproductive effort or with feeding. Adult fish were not detected at the upper Pease River site during or soon after periods of elevated specific conductance ($>26,408 \mu\text{S}/\text{cm}$, maximum levels for Prairie Chub observed in this study). Specific conductance decreased following elevated flows from precipitation events, April through June. With lower specific conductance in May and June, adult fish were observed at the upper site and not at the middle or lower sites. As specific conductance increased $>26,408 \mu\text{S}/\text{cm}$, adult or age-0 fish were no longer present at the upper site. Occurrences of adult fish at the upper site June through September corresponded with reproductive season (March – September) and spawning season (May – September), but after reproductive and spawning seasons were underway. Occurrences of adult fish in January did not correspond with the reproductive season. Occurrences of adult fishes at the upper site were not related to food quality or availability, given that mean ($\pm\text{SD}$) gut fullness was 15% (± 10) and the dominant diet item of adult Prairie Chubs at the upper site was Chironomidae (97%) and only consumed three food items. Gut fullness, dominant food items, and number of food items consumed was not noticeably different at the middle site (19% (± 27); Chironomidae, 95%; three food items) and lower site (11% (± 28); Chironomidae, 99%; two food items).

Discussion

Life history and habitat associations of the Prairie Chub were similar to those reported for other congeners within the *Macrhybopsis* “Speckled Chub” complex (Eisenhour 1997; Bonner 2000; Heard 2008; Perkin et al. 2013, Wilde 2016), such as a benthic invertivore (i.e., primarily chironomids), short-lived (i.e., up to age 2), multiple batch spawner over a 5-month period, inhabit run and riffle mesohabitats with sand to gravel substrates, and mobile (i.e., moving ≤ 60 km). Genetic differentiation was not related to linear geographic distances among sites, similar to findings for the Rio Grande Silvery Minnow *Hybognathus amarus* (Alò and Turner 2005). Patterns in age group distributions indicated movement within the Pease River but not in the North Wichita-Wichita River and were consistent with prediction of refuge migration, somewhat consistent with prediction of reproductive migration, and inconsistent with prediction of feeding migration.

Prairie Chubs were not homogeneously distributed among available habitats or among drainages of the upper Red River. Prairie Chubs were detected in runs and riffles of braided, sand-bed prairie streams comprised of shallower depths, moderate current velocities, sand and silt substrates, and specific conductance $< 26,408 \mu\text{S}/\text{cm}$ in the western extent of the study area and were not detected in more entrenched, slow-moving, and relatively deep tributaries in the eastern extent of the study area. Absence from entrenched slow-moving deep tributaries in the eastern extent of the study area could be linked to habitat specialization for braided sand-bed streams (Kehmeier et al. 2007) or driven by competition and predation (Echelle et al. 1972; Gido et al. 1999). Prairie Chubs were not detected in five braided, sand-bed prairie streams in the western extent of the

drainage (i.e., North Fork, Prairie Dog Town Fork, Salt Fork of the Red River, Adams Creek, Cottonwood Creek). Extirpation of Prairie Chubs in the North Fork were reported previously, attributed to predation and reproductive failures related to construction of Lake Altus (Winston et al. 1990). In Prairie Dog Town Fork, Prairie Chubs have been inconsistently reported since the 1920s (Wilde 1996; Hendrickson and Cohen 2015), and we attribute this lack of detection in this study to specific conductance $>40,000 \mu\text{S}/\text{cm}$ during the time of our surveys. In the Salt Fork of the Red River, specific conductance was $3,350 \mu\text{S}/\text{cm}$ during time of our surveys, but Prairie Chubs were not detected. Last record of Prairie Chubs in Salt Fork was in 1999 (Hendrickson and Cohen 2015). Lack of detection in Adams and Cottonwood creeks is speculative, but both systems are small sand-bed streams, prone to drying into isolated pools, and therefore likely ephemeral.

Significant relationships between pairwise GST and geographic distances were not detected among sampling sites, regardless of whether or not they were separated by impoundments. This lack of a significant relationship among the sites not separated by impoundments suggests that Prairie Chubs in the upper Red River basin are acting as one panmictic population (Wright 1943; Hutchison and Templeton 1999), which is consistent with the reported large-scale movement of prairie stream fishes. Lack of relationship among sites separated by impoundments since the 1920s (i.e., North Wichita-Wichita River) suggests that gene flow has continued between the North Wichita-Wichita River and the remaining Prairie Chub population of the upper Red River, which is unlikely given the height (i.e., 16 m for Lake Diversion Dam, 35 m for Lake Kemp Dam) and breadth (2.1 km for Lake Diversion Dam, 2.7 km for Lake Kemp Dam) of the instream dams. Alternatively, North Wichita-Wichita River population could be sufficiently large

to maintain their standing genetic variation, and therefore unaffected by genetic drift (Denier et al. 2007; Blanchet et al. 2010; Osborne et al. 2012; Gido et al. 2015). A large population size is supported by our surveys in the North Wichita-Wichita River (Prairie Chub densities: 0.08 – 0.28 fish/m²) in comparison to other sites with Prairie Chubs (<0.01 – 0.05 fish/m²). Therefore, genetic differentiation (this study) and genetic diversity (Sotola et al. 2019) of the North Wichita-Wichita River Prairie Chub population could be sufficiently robust to reduce the effects of genetic drift. Dams are associated with reduced genetic diversity and increased genetic differentiation between upstream and downstream fish populations (Hudman and Gido 2013; Gouskov et al. 2016; Sotola et al. 2017) in less than a decade (Yamamoto et al. 2004). Yet, our findings and interpretations are consistent with the lack of genetic differentiation and similar genetic diversity detected among pelagic broadcast spawning cyprinids separated by fragmented river reaches > 50 years, including genetic comparisons of Red Shiners *Cyprinella lutrensis* and Plains Minnows *Hybognathus placitus* taken from the same reaches as in our comparisons (Osborne et al. 2014).

We attributed heterogeneity in age-1 and age-2 fish among Pease River sites to upstream movement up to 60 km. If spatial patterns were wholly or partially attributed to fish movement in the Pease River, movement of age-1, age-2, and potentially age-0 fish, occurred within a period of a month, during reproductive and non-reproductive seasons, while having similar gut fullness and consuming similar food items as previous months, and once specific conductance at the upper site was < 26,408 μ S/cm. Adult riverine fishes, including broadcast spawning cyprinids, are reported to move upstream 30 to 200 km, including congener Peppered Chub moving at least 50 km (Wilde 2016), during the

reproductive season (Fredrich et al. 2003; Walters et al. 2014) or over a period of a year (Wilde 2016). Age-0 broadcast spawning cyprinids are also reported to move upstream > 50 km during the summer (e.g., Speckled Chubs *M. aestivalis*, Archdeacon et al. 2018) or during the fall (e.g., Pecos Bluntnose Minnows *Notropis simus pecosensis*; Chase et al. 2015), which could explain age-0 Prairie Chub summer occurrences within the upper reach of the Pease River. Alternatively, summer occurrences of age-0 Prairie Chub could be attributed to age-0 fish remaining in the upstream reaches after egg release and by resisting downstream drift (Hoagstrom and Turner 2013; Hoagstrom 2014). Without notable changes in diets among adult fish during the period of perceived movement, movement was not consistent with feeding migration. Upstream movement, in part, was consistent with reproductive migration as age-1 and age-2 fish moved upstream during spawning season, but also inconsistent with reproductive migration since one age-1 fish in January was taken at the upper Pease River site. Upstream movement was most consistent with refuge migration or something similar to refuge migration, with all age groups observed at the upper Pease River site during months where specific conductance was within their presumed tolerance (< 26,408 $\mu\text{S}/\text{cm}$).

We tested for three purposes of migration but did not strongly support evidence for migration based on our assessment. Based on the patterns of movement reported in this study and from other studies using broadcast spawning cyprinids, we suspect that movement of broadcast spawning cyprinids might be attributed to dispersal rather than migration, which has been noted and discussed previously (Hawkes 2009; Archdeacon et al. 2018). Migration is a synchronized movement among all or most individuals, extending upstream or downstream of the average home range, and at a specific stage of

the life cycle (Lucas and Bara 2001; Hawkes 2009). Dispersion can be defined as “any movement of individuals or propagules with potential consequences for gene flow across space” (Ronce 2007) but often generalized and not well-defined because dispersing organisms show a gradient of movement behaviors (Hawkes 2009). In this study, Prairie Chub movement was not synchronized (age-1 and age-2 fish remained in the lower two sites on the Pease River; movement was not detected in the North Wichita-Wichita River), and movement occurred among all age groups within and outside of reproductive season. In other studies, populations of Flathead Chubs *Platygobio gracilis* in Fountain Creek of the Arkansas River drainage only exhibited 18% of individuals moved either upstream or downstream during the reproductive season while 82% remained within 1 km of the release site (Walters et al. 2014). Likewise, movement of Arkansas River Shiners *N. girardi* (24% remained near release site) and Plains Minnow (64% remained near release site) in the Canadian River of Texas and New Mexico showed similar turnover rates (i.e., percentage of fish moving from an area; Schrank and Rahel 2006) during a period of a year (Wilde 2016). Defining broadcast spawning cyprinid movement as a presumed reproductive migration (Worthington et al. 2017) or dispersion (Archdeacon et al. 2018) is of less importance, although not trivial, than underlying mechanisms of the movement. Our study results indicate that Prairie Chub upstream movement was more consistent with periods of lower specific conductance (i.e., move downstream when specific conductance exceeded tolerance or optimum conditions and returning when conditions were favorable, similar to refuge migration; Lucas and Bara 2001) rather than periods of reproduction.

The life-history cycle of broadcast spawning cyprinids, specifically upstream movement of fishes to compensate for larval drift downstream (drift compensation theory; Fredrich et al. 2003), is explicably linked to the declines of pelagic broadcast spawning cyprinids related to river fragmentation that disrupt part or all of the life-history cycle (Dudley and Platania 2007; Perkin and Guido 2011; Wilde and Urbanczyk 2013). Fitness aspects of upstream movement and propagule drift is debated (Hoagstrom 2014; Wilde and Urbanczyk 2014), and along with findings of our work, identifies an alternative mechanism for upstream movement in addition to presumed reproductive migration (Worthington et al. 2017). As such, we provide two contrasting narratives on the life-history cycle of broadcast spawning cyprinids: 1) upstream movement and downstream drift are necessary in which, fragmented rivers disrupt this cycle Perkin and Guido 2011; Wilde and Urbanczyk 2014, 2) upstream movement is a consequence of movement towards suitable abiotic conditions (suggested by this study) and downstream drift is not necessary to maintain viable upstream populations (i.e., a sink in source-sink dynamics; Pulliam 1988; Hoagstrom 2014). At this time, we do not promote one narrative over the other given the results of this study. Instead, we use the results of this study and the perspectives of Hoagstrom (2014) to support the consideration of two contrasting narratives when contemplating processes that might explain the various patterns observed in broadcasting spawning cyprinids life histories, such as movement by age-0 fish (Chase et al. 2015; Archdeacon et al. 2018), adults (Wilde 2016) and sexually active adults (Walters et al. 2014), adult movement occurring with equal frequency upstream and downstream (Walters et al. 2014), variable turnover rates among species (18% - 76%; Walters et al. 2014; Wilde 2016) similar to those reported for resident

populations of stream salmonids (15% - 78%; Rodriguez 2002), and estimates of downstream drift distances of propagules (Dudley and Platania 2007) while accounting for diel patterns in larvae exiting the drift (Robinson et al 1998; Reichard et al. 2002; Reeves and Galat 2010).

Managers face a daunting task with future conservation efforts in semi-arid climates and with prairie stream fishes because current predictions of expanding aridity throughout the southern Great Plains region (Jones and Gutzler 2016). Future predictions of reduced precipitation and increased groundwater harvest are projected to further deplete aquifer levels (Milly et al. 2003; Taylor et al. 2013) resulting in the reduction of water quality and quantity (Ficke et al. 2007; Rahel and Olden 2008), which in turn, threaten existing fish communities (Perkin et al. 2017). Therefore, development of accurate life-history models through testing of contrasting narratives will aid in determining processes regulating populations of broadcast spawning cyprinids, which will enable conservation strategies to be more focused (Hoagstrom 2014) and incorporate more holistic management strategies (Perkin et al. 2014) for improved sustainment of freshwater resources.

Table 2.1. Percent volumes, occurrences, and relative abundances of food items in stomachs of Prairie

Chubs taken from three sites on the Pease River and two sites on the North Wichita-Wichita River,

February 2016 through January 2017.

Food Items	Volume (%)	Occurrence (%)	Relative abundance (%)
Plant			
Algae	0.2	8	
Animal	99		
Aquatic invertebrates			
Crustacea		0.5	< 0.1
Copepoda		0.5	0.1
Isopoda		0.5	< 0.1
<i>Daphnia</i>		0.5	0.1
Trombidiformes		0.5	< 0.1
Diptera			
Chironomidae		88	95
Pupa		11	2
Ephemeroptera		2	< 0.1
Odonata			
Gomphidae		0.5	< 0.1
Trichoptera		1	< 0.1
Hydropsychidae		0.5	< 0.1
Unidentifiable		3	< 0.1
Pupa		4	< 0.1
Invertebrate egg		1	1
Terrestrial invertebrates			
Diptera		1	< 0.1
Unidentifiable		0.5	< 0.1
Vertebrates			
Scales		0.5	< 0.1
Gill filaments		0.5	< 0.1
Substrate			
Clay/Silt	0.7	14	
Sand	0.1	37	
Plastic	< 0.1	2	
Total N	197		

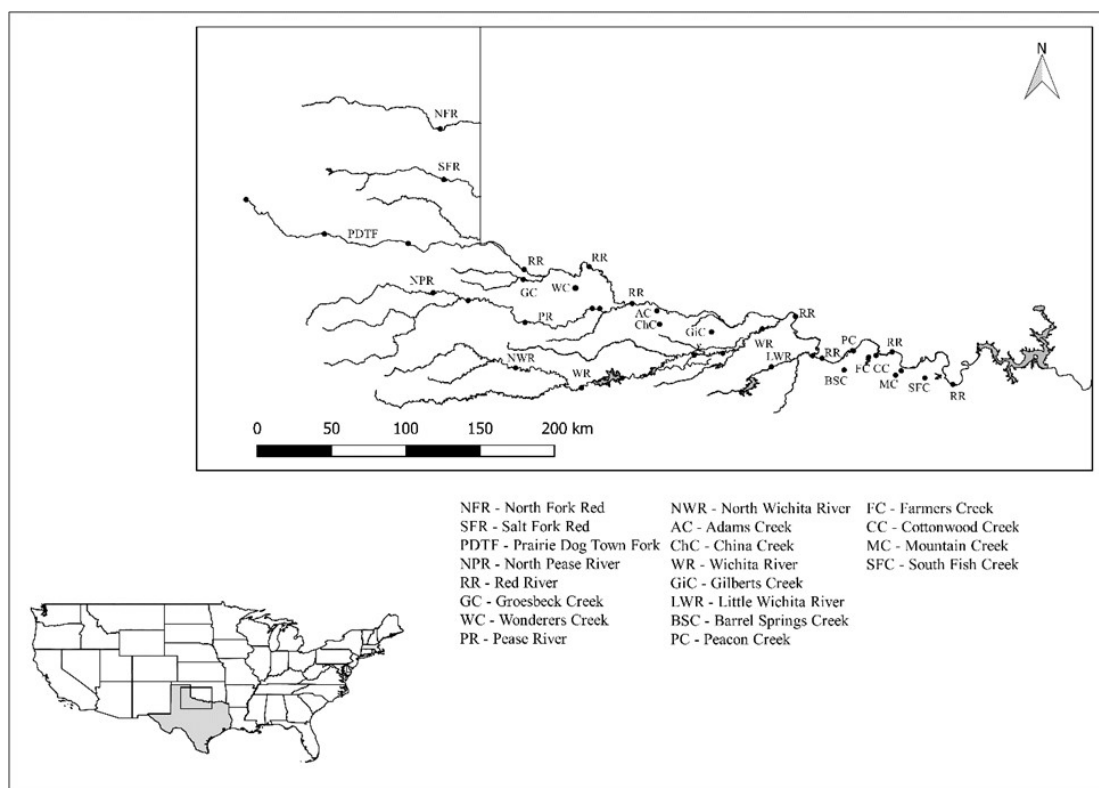


Figure 2.1. Site locations (N = 36, black dot) and water bodies (N = 20) for longitudinal surveys within the upper Red River basin of Texas and Oklahoma, September 2015 through September 2016. See Appendix 1 for georeferenced site locations.

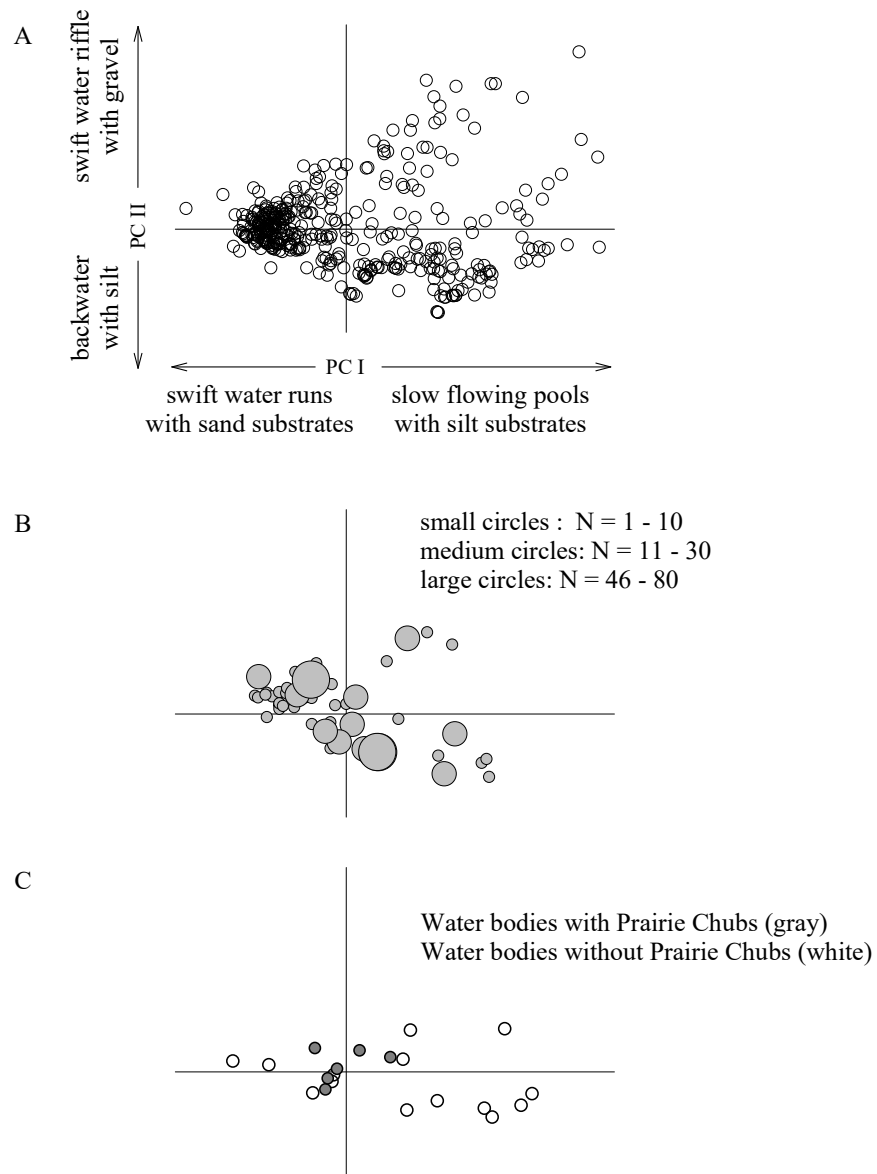


Figure 2.2. Circles represent all mesohabitats (N = 400) along PC I and PC II gradients sampled during the longitudinal surveys (A). Shaded circles represent the number of Prairie Chubs taken from each mesohabitat (B) and water bodies with Prairie Chub occurrences (C) from the upper Red River drainage.

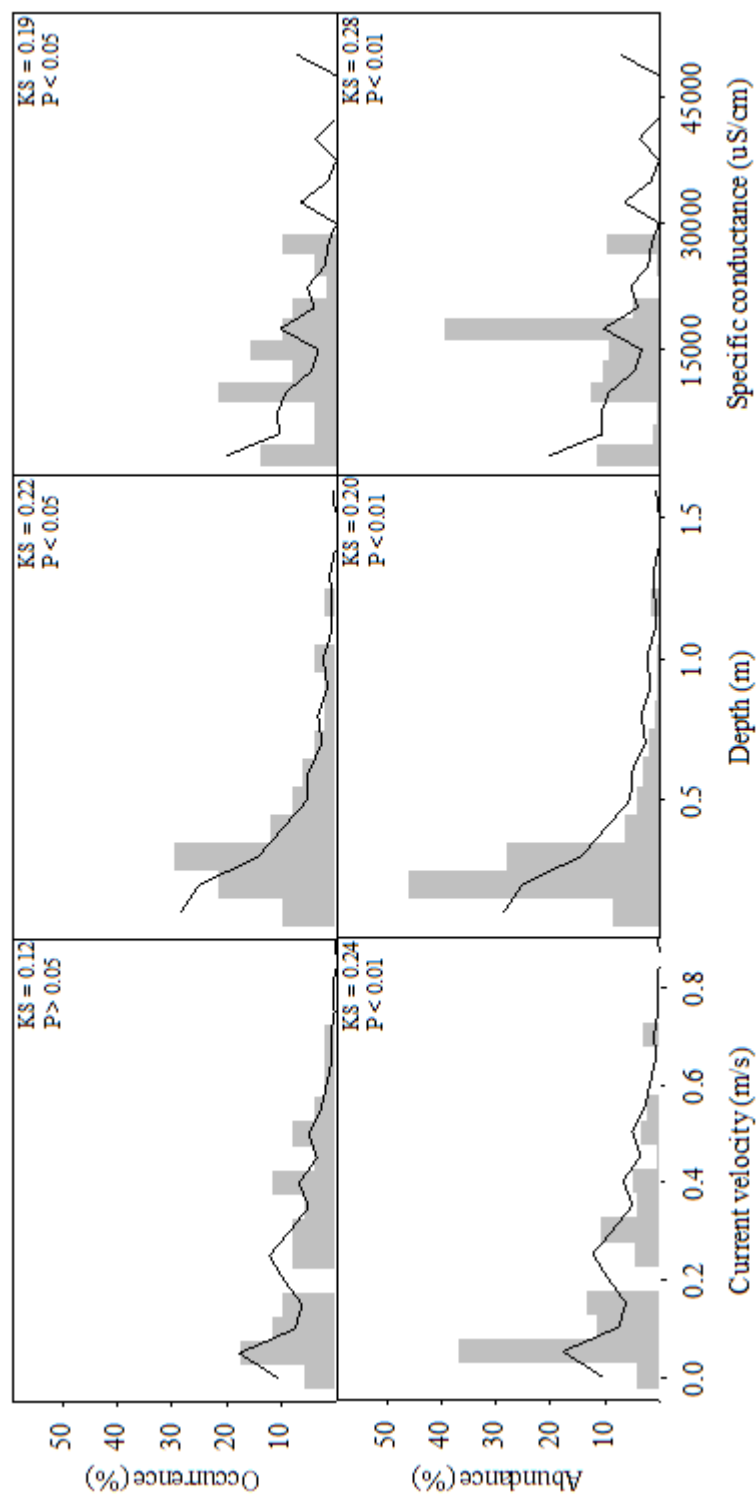


Figure 2.3. Frequency of occurrences and abundances of available habitats (line) and used habitats (bars) by Prairie Chub for current velocity, depth, and specific conductance. Kolmogorov-Smirnov (KS) test statistic and associated P-value are provided.

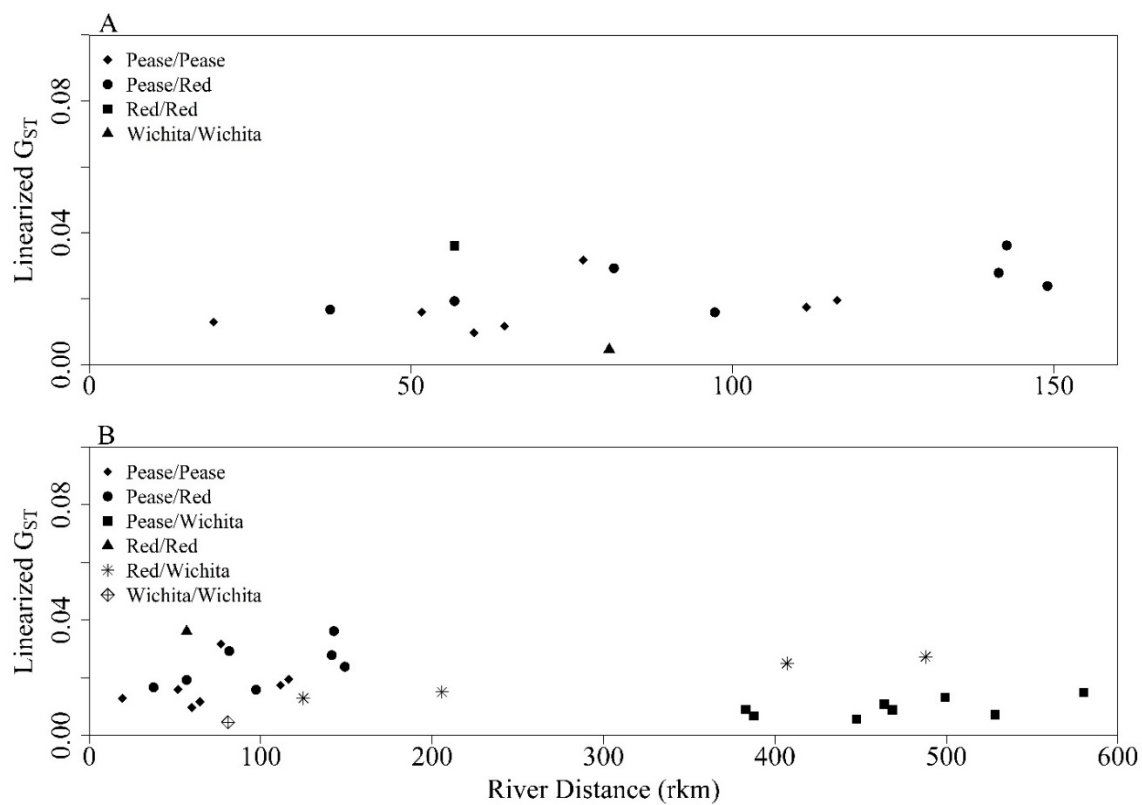


Figure 2.4. Scatter plot of linear genetic differentiation ($G_{ST}/(1-G_{ST})$) values among collection sites versus river distance between sites (rkm) not separated by dams (A) and between sites separated and not separated by dams (B).

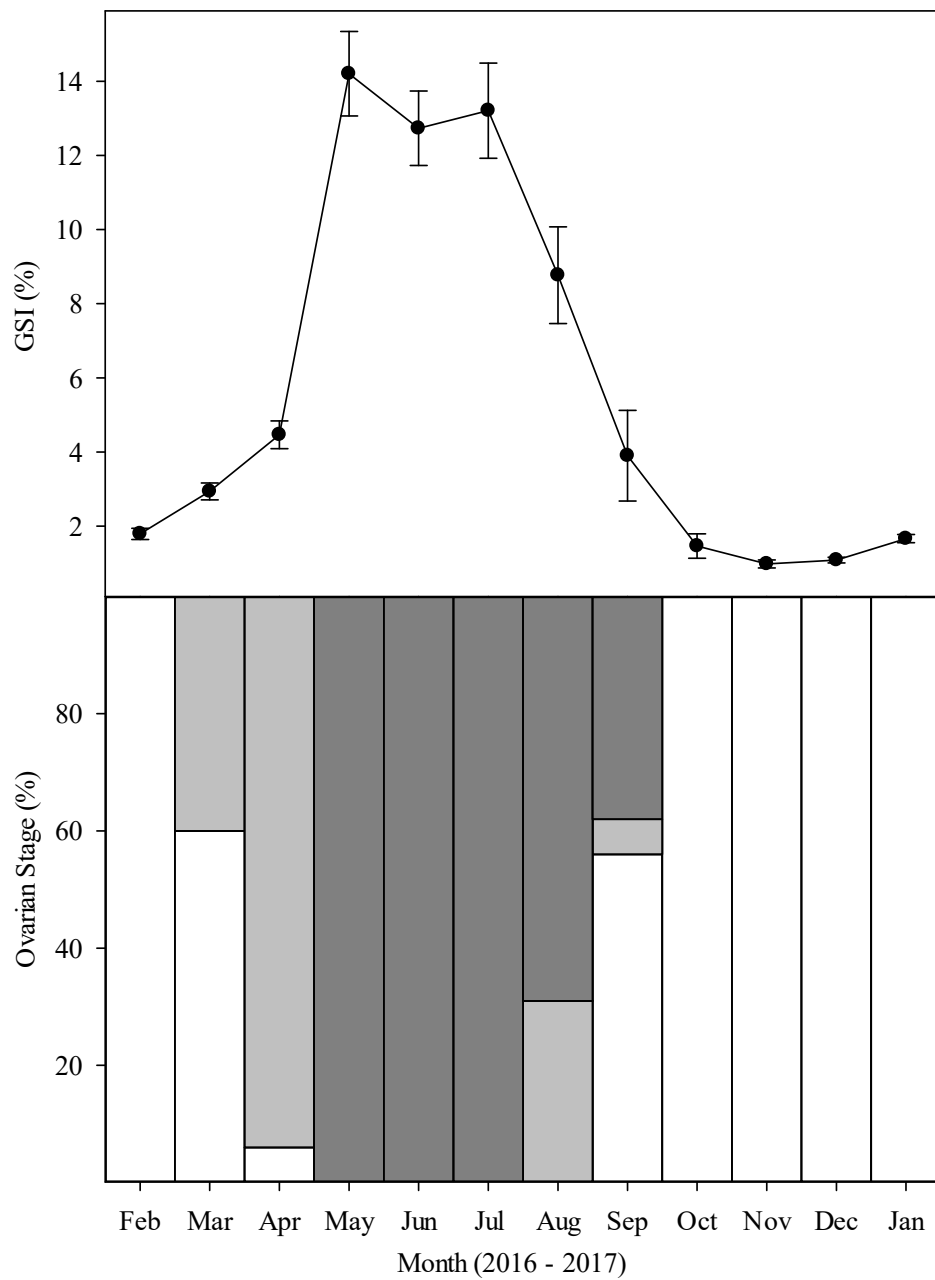


Figure 2.5. Mean (± 1 SE) monthly gonadosomatic index (GSI) for Prairie Chubs taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, February 2016 through January 2017, and corresponding ovarian stages (%) by month for immature (white), developing (light gray), and mature (dark gray) females.

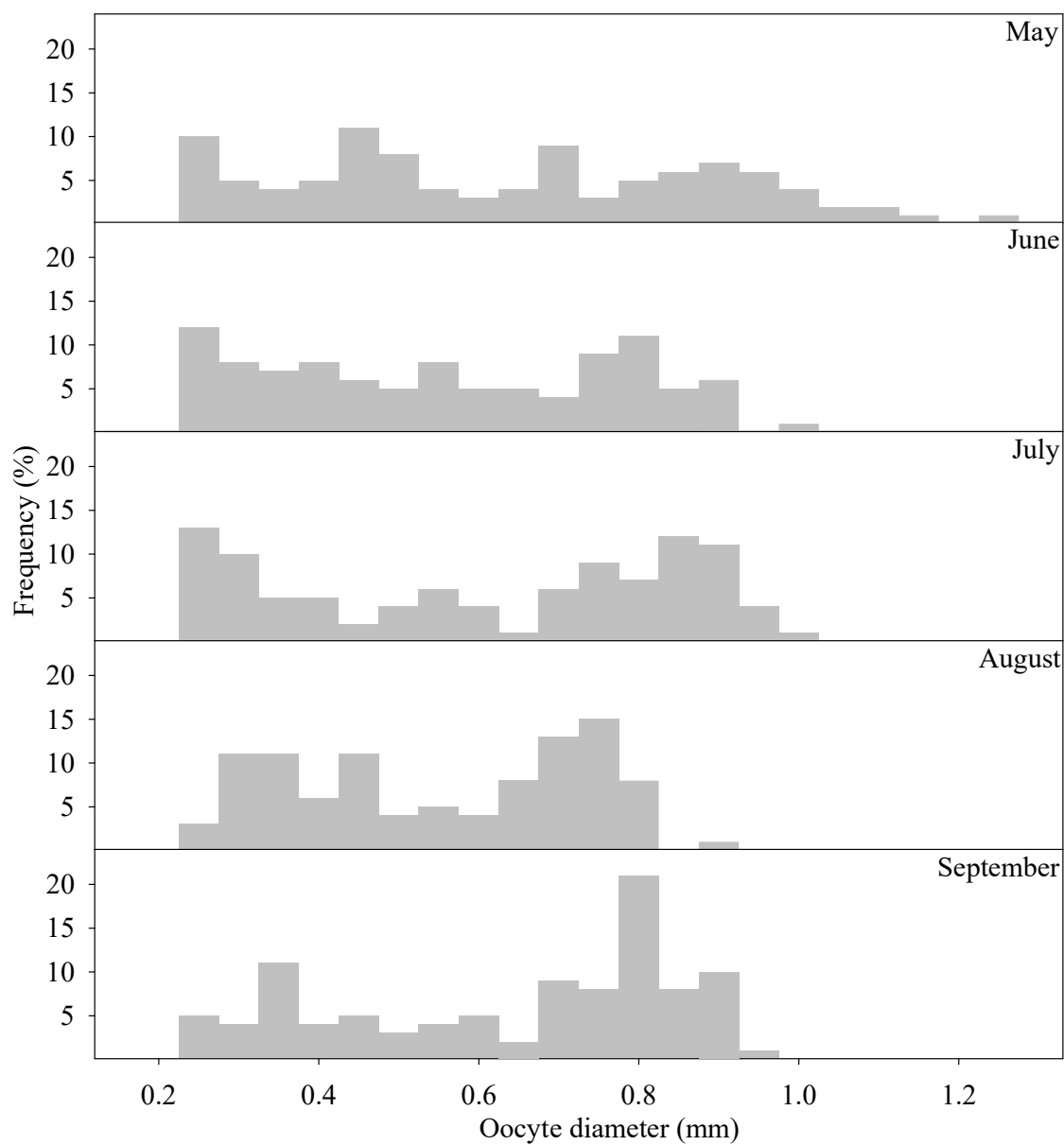


Figure 2.6. Frequency of oocyte size distributions in mature ovaries of Prairie Chubs taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, May 2016 through September 2016.

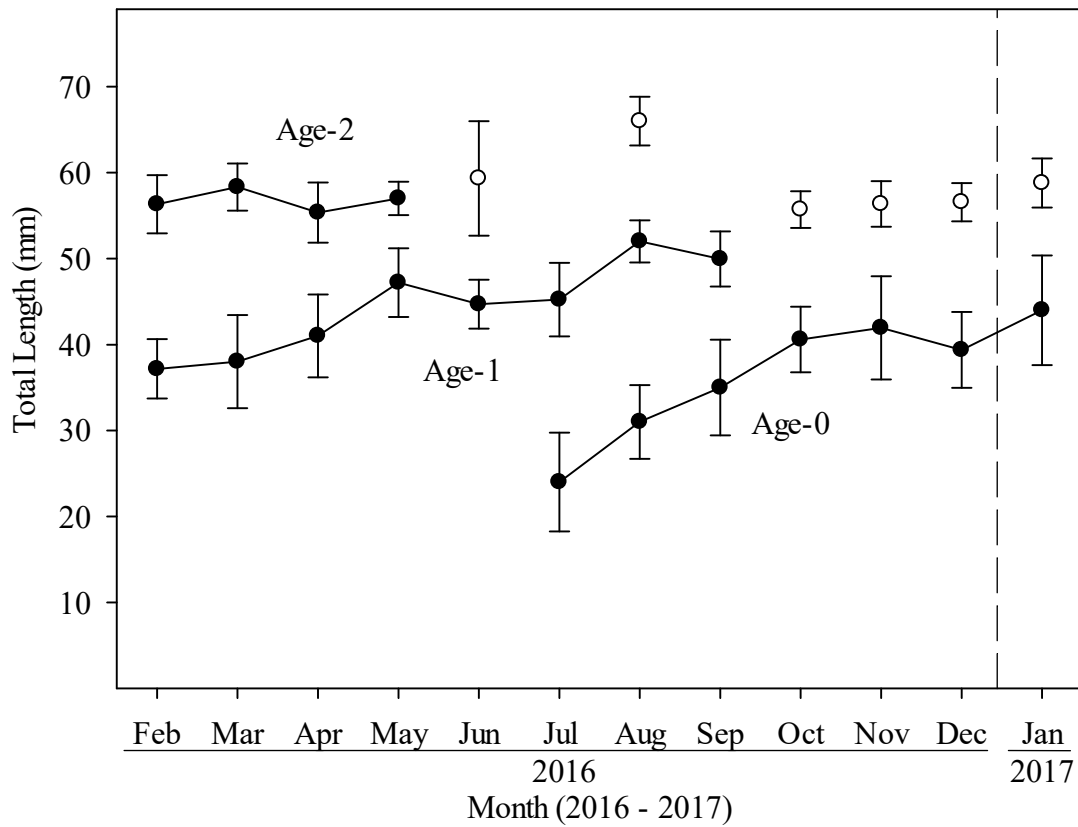


Figure 2.7. Mean $\pm$ 1 SD total lengths (black circles) for Age-0, Age-1, and Age-2 Prairie Chubs taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, February 2016 through January 2017. White circles represent mean and $\pm$ 1 SE of total lengths taken from ≤ 3 individuals within an age group per month. Dashed line indicates transition into the next age class.

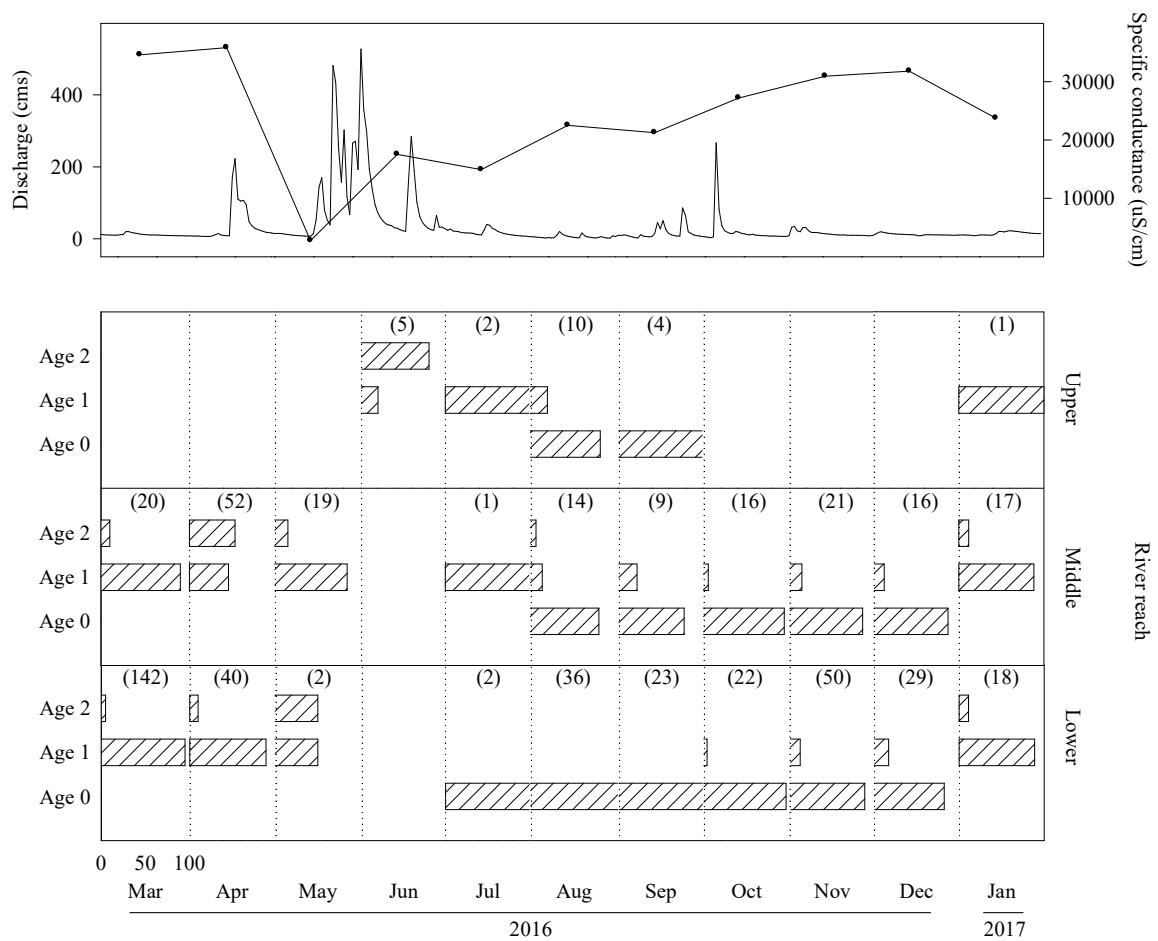


Figure 2.8. Daily flow (line; USGS Station 07308200) taken near Hwy 283 crossing on the Pease River, and monthly estimates of specific conductance (symbol and line) taken from FM 104 crossing on the Pease River. Bottom panels represent relative abundances of Prairie Chub age groups (denoted with shaded bars) among months within the upper site (FM 104), middle site (Hwy 6), and lower site (Hwy 283), March 2016 through January 2017.

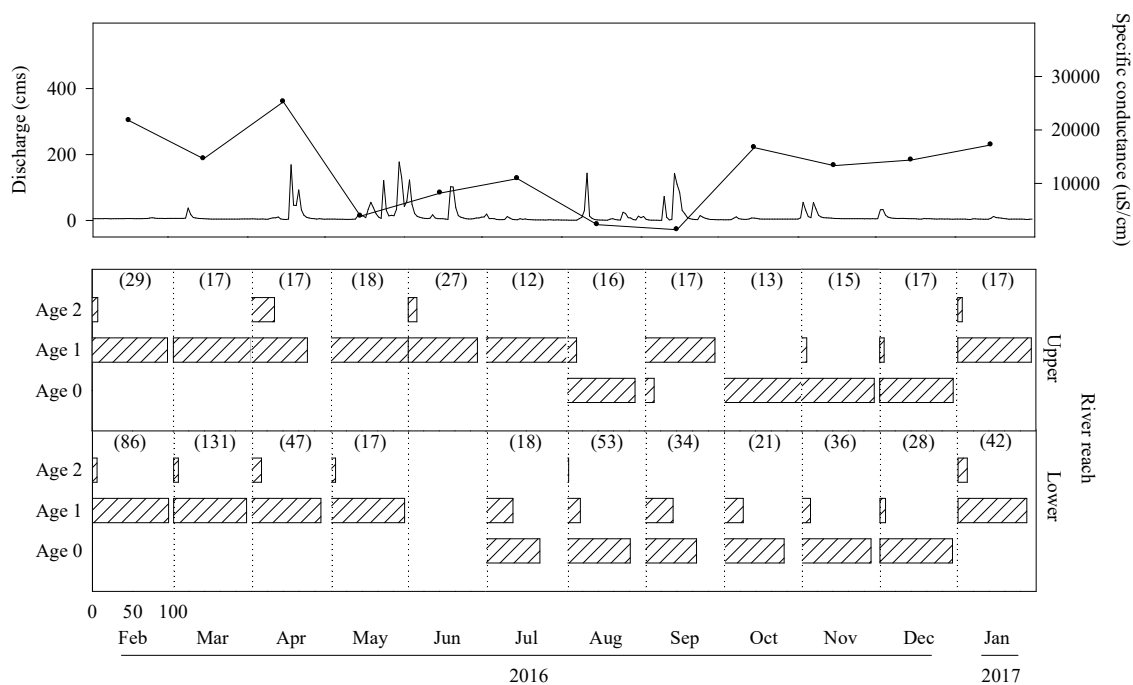


Figure 2.9. Daily flow (line; USGS Station 07311700) and monthly estimates of specific conductance (symbol and line) taken near Hwy 6 crossing on the North Wichita River. Bottom panels represent relative abundances of Prairie Chub age groups (denoted with shaded bars) among months within the upper site (North Wichita River, Hwy 6) and lower site (Wichita River, FM 1919), February 2016 through January 2017.

Appendix 2.1. Water body name, site location, site coordinates, specific conductance, and number of *Macrhybopsis australis* taken during longitudinal surveys and for life history and genetic assessments.

Number of <i>Macrhybopsis australis</i>								
Genetics	Diet	Repro- duction	Age class	Survey	Specific conductance	Coordinates	Site	Water body
					1,179 (48)	34.165007, -98.932641	TX 25	Adams Creek
					1,036	33.836776, -97.805088	Crain Rd	Barrel Springs Creek
					4,599	34.131392, -98.847801	Flippin Rd	China Creek
					1,529 (251)	33.895695, -97.607456	FM 2953	Cottonwood Creek
					1,743 (8)	33.919115, -97.618379	FM 103	Farmers Creek
					3,842	34.037321, -98.602167	FM 369	Gilberts Creek
					4,971 (994)	34.354671, -99.740408	Hwy 6	Grosebeck Creek
					488 (132)	33.826871, -98.240119	US 287	Little Wichita River
					4,153 (2,623)	33.894965, -97.989759	FM 2332	
		3			5,421 (531)	33.803474, -97.455165	FM 373	Mountain Creek
					895 (814)	33.776965, -97.489396	Childress Rd	Mountain Creek
				1	21,039 (1,340)	34.274520, -100.285651	US 83	North Pease River
22	45	44	185	18	15,867 (1,197)	34.094440, -99.730428	Hwy 6	Pease River
12	38	37	364		11,817	34.178947, -99.278430	US 283	
17				38	14,647	34.179708, -99.323546	US 287	
8	6	6	20	5	25,412 (8,849)	34.227642, -100.073801	FM 104	
					986	33.890599, -97.763585	FM 2849	Pecan Creek
					2,441	35.263180, -100.242297	US 83	North Fork
					3,350	34.957741, -100.220800	US 83	Salt Fork

Appendix 2.1. Continued.

Number of <i>Macrhybopsis australis</i>								
Genetics	Diet	Repro- duction	Age class	Survey	Specific conductance	Coordinates	Site	Water body
8					38,420	34.629331, -100.942459	Hwy 256	Prairie Dog Town Fork
					42,115 (9,322)	34.567450, -100.194678	US 83	
					15,675	34.837060, -101.416286	Hwy 207	
				2	26,048 (4,422)	34.414520, -99.735056	Hwy 6	Red River
				35	3,000 (1,570)	33.726830, -97.157504	I 35	
				15	6,832 (1,840)	34.132324, -98.092926	Hwy 79	
				2	6,863 (1,138)	33.878540, -97.933907	US 81	
				39	4,483 (2,857)	33.917562, -97.510006	FM 677	
4				50	11,740	34.209491, -99.081910	US 183	
				8	12,747 (653)	34.431235, -99.341510	US 283	
					663 (37)	33.760035, -97.312435	FM 411	South Fish Creek
29	59	58	200	74	19,131 (9,395)	33.820681, -99.786566	Hwy 6	North Wichita River
66					5,165 (1,642)	33.909172, -98.533858	Hwy 11	Wichita River
					5,677 (173)	33.760046, -99.142646	US 283	
				1	6,058 (1,124)	33.896929, -98.707103	FM 368	
				4	4,045 (479)	34.056307, -98.295166	FM 810	
				191	9,876 (3,623)	33.700198, -99.388808	FM 1919	
	49	48	526		2,614	34.346328, -99.421495	FM 2379	Wonderers Creek
166	197	193	1295	486				Total N

Literature Cited

- Alò D, and Turner TF (2005) Effects of habitat fragmentation on effective population size in the endangered Rio Grande Silvery Minnow. *Conserv Biol* 19:1138–1148. <https://doi.org/10.1111/j.1523-1739.2005.00081.x>
- Anbalagan T, Murugan A, Jawahar P, Vijayanand P, Saravanan R, and Veerappan N (2016) Age and growth of squirrel fish, *Sargocentron rubrum*, (Forsskal, 1775) from Cuddalore waters, southeast coast of India. *Indian J Geomarine Sci* 45:1742–1748. <http://nopr.niscair.res.in/handle/123456789/40538>
- Archdeacon TP, Davenport SR, Grant JD, and Henry EB (2018) Mass upstream dispersal of pelagic-broadcast spawning cyprinids in the Rio Grande and Pecos River, New Mexico. *West N Am Naturalist* 78:100–106. <https://doi.org/10.3398/064.078.0110>
- Bestgen KR, Mefford B, Bundy JM, Walford CD, and Compton RI (2010) Swimming performance and fishway model passage success of Rio Grande Silvery Minnow. *Trans Am Fish Soc* 139:433–448. <https://doi.org/10.1577/T09-085.1>
- Blanchet S, Rey O, Etienne R, Lek S, and Loot G (2010) Species-specific responses to landscape fragmentation: implications for management strategies. *Evol Appl* 3:291–304. <https://doi.org/10.1111/j.1752-4571.2009.00110.x>
- Bonner TH (2000) Habitat use and reproductive ecology of the Arkansas River Shiner and Peppered Chub in the Canadian River, New Mexico and Texas. Dissertation, Texas Tech University.
- Cambray JA (1990) Adaptive significance of a longitudinal migration by juvenile freshwater fish in the Gantoos River System, South Africa. *S Afr J Wildl Res* 20:148-156. https://hdl.handle.net/10520/AJA03794369_2219
- Chase NM, Caldwell CA, Carleton SA, Gould WR, and Hobbs JA (2015) Movement patterns and dispersal potential of Pecos Bluntnose Shiner (*Notropis simus pecosensis*) revealed using otolith microchemistry. *Can J Fish Aquat Sci* 72:1575–1583. <http://doi.org/10.1139/cjfas-2014-0574>
- Cross F, Mayden RL, and Stewart JD (1986) Fishes in the western Mississippi basin (Missouri, Arkansas and Red Rivers). In: Hocutt CH and Wiley EO (eds) *The Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, Inc, New York, pp 363-412
- Denier K, Garza JC, Coey R, and Gorman DJ (2007) Population structure and genetic diversity of trout (*Oncorhynchus mykiss*) above and below natural and man-made barriers in the Russian River, California. *Conserv Genet* 8:437–454. <http://doi.org/10.1007/s10592-006-9183-0>

- Dudley RK, and Platania SP (2007) Flow regulation and fragmentation imperil pelagic-spawning riverine fishes. *Ecol Appl* 17:2074–2086. <http://doi.org/10.1890/06-1252.1>
- Echelle AA, Echelle AF, and Hill LG (1972) Interspecific interactions and limiting factors of abundance and distribution in the Red River Pupfish, *Cyprinodon rubrofluviatilis*. *Am Midl Nat* 88:109–130. <http://doi.org/10.2307/2424492>
- Edwards RJ (1977) Seasonal migrations of *Astyanax mexicanus* as an adaptation to novel environments. *Copeia* 1977:770–771. <http://doi.org/10.2307/1443187>
- Eisenhour DJ (1997) Systematics, variation and speciation of the *Macrhybopsis aestivalis* complex (Cypriniformes: Cyprinidae) west of the Mississippi River. Dissertation, Southern Illinois University.
- Eisenhour DJ (2004) Systematics, variation, and speciation of the *Macrhybopsis aestivalis* complex (Cypriniformes: Cyprinidae) west of the Mississippi River. *Bull Alab Mus Nat Hist* 23:9–48.
- Ficke AD, Myrick CA, and Hansen LJ (2007) Potential impacts of global climate change on freshwater fisheries. *Rev Fish Biol Fish* 17:581–613. <http://doi.org/10.1007/s11160-007-9059-5>
- Fredrich F, Ohmann S, Curio B, and Kirschbaum F (2003) Spawning migrations of the chub in the River Spree, Germany. *J Fish Biol* 63:710–723. <http://doi.org/10.1046/j.1095-8649.2003.00184.x>
- Gido KB, Schaefer JF, Work K, Lienesch PW, Marsh-Matthews E, and Matthews WJ (1999) Effects of Red Shiner (*Cyprinella lutrensis*) on Red River Pupfish (*Cyprinodon rubrofluviatilis*). *Southwest Nat* 44:287–295.
- Gido KB, Whitney JE, Perkin JS, and Turner TF (2015) Fragmentation, connectivity and fish species persistence in freshwater ecosystems. In: Closs GP, Krkosek M, and Olden JD (eds) *Conservation of Freshwater Fishes*. Cambridge University Press, United Kingdom pp 292–316
- Gompert Z, Lucas LK, Buerkle CA, Forister ML, Fordyce JA, and Nice CC (2014) Admixture and the organization of genetic diversity in a butterfly species complex revealed through common and rare genetic variants. *Mol Ecol* 23:4555–4573. <https://doi.org/10.1111/mec.12811>
- Gompert Z, Lucas LK, Nice CC, Fordyce JA, Forister ML, and Buerkle CA (2012) Genomic regions with a history of divergent selection affect fitness of hybrids between two butterfly species. *Evolution* 66:2167–2181. <https://doi.org/10.1111/j.1558-5646.2012.01587.x>

- Gouskov A, Reyes M, Wirthner-Bitterlin L, and Vorburger C (2016) Fish population genetic structure shaped by hydroelectric power plants in the upper Rhine catchment. *Evol Appl* 9:394-408. <http://doi.org/10.1111/eva.12339>
- Hawkes C (2009) Linking movement behavior, dispersal and population processes: is individual variation a key? *J Anim Ecol* 78:894–906. <https://doi.org/10.1111/j.1365-2656.2009.01534.x>
- Heard T (2008) Spatial and temporal patterns in a Chihuahua Desert fish assemblage. Thesis, Texas State University
- Hendrickson DA and Cohen AE (2017, September 15) Fishes of Texas Project Database (Version 2.0). <http://doi.org/10.17603/C3WC70>
- Hoagstrom CW (2014) Drift versus retention: an alternative perspective to Wilde and Urbanczyk's relationship between river fragment length and persistence of two imperiled great plains cyprinids.' *J Freshwat Ecol* 29:449–452. <http://doi.org/10.1080/02705060.2014.908422>
- Hoagstrom CW and Turner TF (2013) Recruitment ecology of pelagic-broadcast spawning minnows: paradigms from the ocean advance science and conservation of an imperiled freshwater fauna. *Fish Fish* 16:282–299. <https://doi.org/10.1111/faf.12054>
- Hudman SP and Gido KB (2013) Multi-scale effects of impoundments on genetic structure of Creek Chub (*Semotilus atromaculatus*) in the Kansas River basin. *Freshwat Biol* 58:441–453. <https://doi.org/10.1111/fwb.12079>
- Hunter JR, Lo NCH, and Leong RJH (1985) Batch fecundity in multiple spawning fishes. NOAA Technical Report NMFS 36:67–77
- Hutchinson DW and Templeton AR (1999) Correlation of pairwise genetic and geographic distance measures: inferring the relative influences of gene flow and drift on the distribution of genetic variability. *Evolution* 53:1898-1914. <http://doi.org/10.1111/j.1558-5645.1999.tb04571x>
- Irving DB and Modde T (2000) Home-range fidelity and use of historic habitat by adult Colorado Pikeminnow (*Ptychocheilus lucius*) in the White River, Colorado and Utah. *West N Am Naturalist* 60:16-25.
- Jearld Jr A (1983) Age determination. In: Nielsen LA and Johnson DL (eds) *Fisheries techniques*. American Fisheries Society, Maryland

- Jelks HL, Walsh SJ, Burkhead NM, Contreras-balderas S, Diaz-pardo E, Hendrickson DA, Lyons J, Mandrak NE, McCormick F, Nelson JS, Platania SP, Porter BA, Renaud CB, Schmitter-Soto JJ, Taylor EB, and Warren ML (2008) Conservation Status of Imperiled North American Freshwater and Diadromous Fishes. *Fisheries* 33:372–407. <https://doi.org/10.1577/1548-8446-33.8.372>
- Johnston CE (1999) The relationship of spawning mode to conservation of North American minnows (Cyprinidae). *Environ Biol Fishes* 55:21-30. <http://doi.org/10.1023/A:1007576502479>
- Jones SM and Gutzler DS (2016) Spatial and seasonal variations in aridification across Southwest North America. *J Clim* 29:4637–4649. <http://doi.org/10.1175/JCLI-D-14-00852.1>
- Kehmeier JW, Valdez R, Medley C, and Myers OB (2007) Relationship of fish mesohabitat to flow in a sand-bed southwestern river. *N Am J Fish Manage* 27:750–764. <http://doi.org/10.1577/M06-016.1>
- Krebs CJ (1999) *Ecological Methodology*. Addison Wesley Longman, New York
- L'Abée-Lund JH and Vøllestad LA (1987) Feeding migration of roach, *Rutilus rutilus* (L.), in Lake Årungen, Norway. *J Fish Biol* 30:349-355. <https://doi.org/10.1111/j.1095-8649.1987.tb05759.x>
- Li H, Handsaker B, Wysoker A, Fennell T, Ruan J, Homer N, Marth G, Abecasis G, and Durbin R (2009) The sequence alignment/map format and SAMtools. *Bioinform* 25:2078–2079. <http://doi.org/10.1093/bioinformatics/btp352>
- Lucas MC and Baras E (2001) *Migration of freshwater fishes*. Blackwell Science Ltd, Iowa
- Mandeville EG, Parchman TL, McDonald DB, and Buerkle CA (2015) Highly variable reproductive isolation among pairs of *Catostomus* species. *Mol Ecol* 24:1856-1872. <http://doi.org/10.1111/mec.13118>
- Matthews WJ (1988) North American prairie streams as systems of ecological study. *J N Am Benthol Soc* 7:387–409. <http://doi.org/10.2307/1467298>
- Meyer M and Kircher M (2010) Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb Protoc* 2010.6: pdb-prot5448.
- Milly PCD, Dunne KA, and Vecchia AV (2005) Global pattern of trends in streamflow and water availability in a changing climate. *Nature* 438:347-350. <http://doi.org/10.1038/nature04312>

- Natureserve (2017, November 11) NatureServe Web Service. Arlington, VA. U.S.A.
Available <http://explorer.natureserve.org>
- Nei M (1987) Molecular evolutionary genetics. Columbia university press, New York City
- Northcote TG (1978) Migratory strategies and production in freshwater fishes. In: Gerking SD (ed) Ecology of Freshwater Production. Blackwell, Oxford, pp 326-359
- Northcote TG (1984) Mechanisms of fish migration in rivers. In: McCleave JD, Dodson JJ, and Neill WH (eds) Mechanisms of Migration in Fishes. Plenum, New York, pp 317-355
- Oklahoma Department of Wildlife Conservation. (2005) Oklahoma comprehensive wildlife conservation strategy: a strategic conservation plan for Oklahoma's rare and declining wildlife. Oklahoma City, Oklahoma
- Omernik JM and Griffith GE (2014) Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environ Manage* 54:1249–1266. <http://doi.org/10.1007/s00267-014-0364-1>
- Osborne MJ, Carson EW, and Turner TF (2012) Genetic monitoring and complex population dynamics: insights from a 12-year study of the Rio Grande Silvery Minnow. *Evol Appl* 5:553-574. <https://doi.org/10.1111/j.1752-4571.2011.00235.x>
- Osborne MJ, Perkin JS, Gido KB, Turner TF (2014) Comparative riverscape genetics reveals reservoirs of genetic diversity for conservation and restoration of Great Plains fishes. *Mol Ecol* 23:5663-5679. <http://dio.org/10.1111/mec.12970>
- Parchman TL, Gompert Z, Mudge J, Schilkey FD, Benkman CW, and Buerkle CA (2012) Genome-wide association genetics of an adaptive trait in lodgepole pine. *Mol Ecol* 21:2991-3005. <http://dio.org/10.1111/j.1365-294X.2012.05513.x>
- Perkin JS and Gido KB (2011) Feature: stream fragmentation thresholds for a reproductive guild of great plains fishes. *Fisheries* 36:37–41. <https://doi.org/10.1080/03632415.2011.597666>
- Perkin JS, Gido KB, Costigan KH, Daniels MD, and Johnson ER (2014) Fragmentation and drying ratchet down Great Plains stream fish diversity. *Aquat Conserv* 25:639-655. <http://doi.org/10.1002/aqc.2501>
- Perkin JS, Gido KB, Falke JA, Fausch KD, Crockett H, Johnson ER, and Sanderson J (2017) Groundwater declines are linked to changes in Great Plains stream fish assemblages. *Proc Natl Acad Sci U S A* 114:7373-7378. <https://doi.org/10.1073/pnas.1618936114>

- Perkin JS, Shattuck ZR, Gerken JE, and Bonner TH (2013) Fragmentation and drought legacy correlate with distribution of Burrhead Chub in subtropical streams of North America. *Trans Am Fish Soc* 142:1287–1298.
<http://doi.org/10.1080/00028487.2013.806352>
- Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using gibbs sampling JAGS: Just another gibbs sampler. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, (Dsc), March 20–22, Vienna, Austria. ISSN 1609-395X. <http://doi.org/10.1.1.13.3406>
- Plummer M, Best N, Cowles K, Vines K (2006) CODA: Convergence diagnosis and output analysis for MCMC. *RNews*, 5,7–11.
- Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132:652-661.
<https://doi.org/10.1086/284880>
- Puritz JB, Hollenbeck CM, and Gold JR (2014) dDocent: a RADseq, variant-calling pipeline designed for population genomics of non-model organisms. *PeerJ* (2:e431). <http://doi.org/10.7717/peerj.431>.
- Rahel FJ and Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. *Conserv Biol* 22:521–533. <http://doi.org/10.1111/j.1523-1739.2008.00950.x>
- Reeves KS and Galat DL (2010) Do larval fishes exhibit diel drift patterns in a large, turbid river? *J Appl Ichthyol* 26:571-577. <https://doi.org/10.1111/j.1439-0426.2010.01481.x>
- Reichard M, Jurajda P, and Ondračková M (2002) The effect of light intensity on the drift of young-of-the-year cyprinid fishes. *J Fish Biol* 61:1063-1066.
<http://doi.org/10.1006/jfbi.2002.2116>
- Robinson AT, Clarkson RW, and Forrest RE (1998) Dispersal of larval fishes in a regulated river tributary. *Trans Am Fish Soc* 127:772-786.
[https://doi.org/10.1577/1548-8659\(1998\)127<0772:DOLFIA>2.0.CO;2](https://doi.org/10.1577/1548-8659(1998)127<0772:DOLFIA>2.0.CO;2)
- Rodríguez MA (2002) Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology* 83:1-13. <http://doi.org/10.2307/2680115>
- Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu Rev Ecol Evol Syst* 38:231-253.
<https://doi.org/10.1146/annurev.ecolsys.38.091206.095611>
- Ruppel DS, Sotola VA, Gurbuz OA, Martin NH, and Bonner TH (2017). Endangered species, research projects for the Prairie Chub. Texas State University, San Marcos.

- Schrank AJ and Rahel FJ (2006) Factors influencing summer movement patterns of Bonneville Cutthroat Trout (*Oncorhynchus clarkii utah*). *Can J Fish Aquat Sci* 63:660-669. <http://doi.org/10.1139/f05-250>
- Schulz U and Berg R (1987) The migration of ultrasonic-tagged bream, *Abramis brama* (L), in Lake Constance (Bodensee-Untersee). *J Fish Biol* 31:409-414. <https://doi.org/10.1111/j.1095-8649.1987.tb05245.x>
- Sotola VA, Ruppel DS, Bonner TH, Nice CC, and Martin N (2019) Asymmetric introgression between fishes in the Red River basin of Texas is associated with variation in water quality. *Ecol Evol* 2019:1-13. <http://doi.org/10.1002/ece3.4901>
- Sotola VA, Schrey AW, Ragsdale AK, Whitley GW, Frankland L, Bollinger EK, and Colombo RE (2017) Genetic evidence of isolation by distance and impact of impoundments on genetic diversity of riverine Channel Catfish. *Trans Am Fish Soc* 146:1204-1211.
- Taylor RG, Scanlon D, Döll P, Rodell M, Van Beek R, Wada Y, Longuevergne L, Leblanc M, Famigliette JS, Edmunds M, Konikow L, Green TR, Chen J, Taniguchi M, Bierkens MFP, MacDonald A, Fan Y, Maxwell RM, Yechieli Y, Gurdak JJ, Allen DM, Shamsudduha M, Hiscock K, Yeh PJF, Holman I, and Tredel H (2013) Ground water and climate change. *Nat Clim Chang* 3:322-329. <http://dx.doi.org/10.1038/nclimate1744>
- Taylor CM, Winston MR, and Matthews WJ (1996) Temporal variation in tributary and mainstem fish assemblages in a Great Plains stream system. *Copeia* 1996:280-289. <http://doi.org/10.2307/1446844>
- Texas Parks and Wildlife Department (2012) Texas Conservation Action Plan 2012-2016: overview. Editor, Wendy Connally, Texas Conservation Action Plan Coordinator. Austin, Texas
- Tyus HM (1990) Potamodromy and reproduction of Colorado Squawfish in the Green River Basin, Colorado and Utah. *Trans Am Fish Soc* 119:1035-1047. [https://doi.org/10.1577/1548-8659\(1990\)119<1035:PAROCS>2.3.CO;2](https://doi.org/10.1577/1548-8659(1990)119<1035:PAROCS>2.3.CO;2)
- Walters DM, Zuellig RE, Crockett HJ, Bruce JF, Lukacs PM, and Fitzpatrick RM (2014) Barriers impede upstream spawning migration of Flathead Chub. *Trans Am Fish Soc* 143:17-25. <https://doi.org/10.1080/00028487.2013.824921>
- Wilde GR (2016) Migration of Arkansas River Shiner and other broadcast spawning fishes in the Canadian River, New Mexico-Texas. Texas Tech University, Lubbock

- Wilde GR and Urbanczyk AC (2013) Relationship between river fragment length and persistence of two imperiled great plains cyprinids. *J Freshwat Ecol* 28:445–451. <http://doi.org/10.1080/02705060.2013.785984>
- Wilde GR and Urbanczyk AC (2014) Speculation but no data: A response to Hoagstrom's drift versus retention perspective. *J Freshwat Ecol* 29:453–455. <http://doi.org/10.1080/02705060.2014.908791>
- Wilde GR, Weller RR, Smith CD, and Jimenez Jr R (1996) Review and synthesis of existing fish collection records for the upper Red River Basin upstream from Lake Texoma. Texas Tech University, Lubbock
- Williams CS (2010) Life history characteristics of three obligate riverine species and drift patterns of lower Brazos River fishes. Dissertations, Texas State University
- Williams CS and Bonner TH (2006) Habitat Associations, Life History and Diet of the Sabine Shiner *Notropis sabiniae* in an East Texas Drainage. *Am Midl Nat* 155:84–102. [http://doi.org/10.1674/0003-0031\(2006\)155\[0084:HALHAD\]2.0.CO;2](http://doi.org/10.1674/0003-0031(2006)155[0084:HALHAD]2.0.CO;2)
- Winemiller KO and Rose KA (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Can J Fish Aquat Sci* 49:2196–2218. <http://doi.org/10.1139/f92-242>
- Winston MR, Taylor CM, and Pigg J (1990) Upstream Extirpation of four minnow species due to damming of a prairie stream. *Trans Am Fish Soc* 120:98–105. [https://doi.org/10.1577/1548-8659\(1991\)120<0098:UEOFMS>2.3.CO;2](https://doi.org/10.1577/1548-8659(1991)120<0098:UEOFMS>2.3.CO;2)
- Worthington TA, Echelle AA, Perkin JS, Mollenhauer R, Farless N, Dyer JJ, Logue D, and Brewer SK (2017) The emblematic minnows of the North American Great Plains: a synthesis of threats and conservation opportunities. *Fish Fish* 19:271–307. <https://doi.org/10.1111/faf.12254>
- Wright S (1943) Isolation by distance. *Genetics* 28:114–138.
- Yamamoto S, Morita K, Koizumi I, and Maekawa K (2004) Genetic differentiation of White-spotted Charr (*Salvelinus leucomaenis*) populations after habitat fragmentation: spatial-temporal changes in gene frequencies. *Conserv Genet* 5:529–538. <http://doi.org/10.1023/B:COGE.0000041029.38961.a0>

III. FISH COMMUNITY STRUCTURE AND HABITAT ASSOCIATIONS OF THE UPPER RED RIVER OF TEXAS AND OKLAHOMA WITH A NOTE ON SPECIES OF GREATEST CONSERVATION NEED POPULATIONS

Abstract

Fishes within central and southern Great Plains of North America are subjected to a multitude of abiotic factors that shape community structure. Extreme temperatures, intermittent drying of reaches, and strong salinity gradients are common throughout Great Plains streams. Because of the uniqueness of these systems, many locally and regionally endemic fishes have life history traits suitable for extreme conditions and, therefore, persist within Great Plains streams. Several fishes are listed on the federal threatened and endangered species list, while others are listed as Species of Greatest Conservation Needs (SGCN) by state agencies. The upper Red River basin is unique in that the fish community is segregated between species that are tolerant or intolerant to high salinities. Additionally, eight SGCN species are documented in the upper Red River basin. The purpose of this study was to assess the contemporary fish community and factors influencing the community structure with a focus on the assessment of the eight SGCN species. Thirty-six sites were sample twice over a one-year period in order to quantify the contemporary fish community. Historical occurrence and abundance information (1950 – 1990) was gathered from reports and museum collections for eight SGCN species to assess current population status. The upper Red River fish community was segregated along a strong salinity gradient with species tolerant of high salinities having a strong affinity toward braided sand-bed river comprised of shallow depths and moderate current velocities. Two SGCN species (*Macrhybopsis australis*, *Notropis bairdi*) increased in occurrences and abundances through time, whereas two SGCN species (*N. potteri*,

Cyprinodont rubrofluviatilis) decreased in abundances through time. Updated information will provide natural resource managers with the necessary information needed to create conservation strategies which will benefit these organisms along with meeting societal needs for these aquatic resources.

Introduction

Fish communities are structured by abiotic and biotic factors, which exclude species that are less tolerant of existing conditions (Smith and Powell 1971; Jackson and Harvey 1989; Tonn 1990). Fish communities tend to segregate along longitudinal gradients because of physiological tolerance (Myrick and Cech 2000; Quist et al. 2006), abiotic mediated competition (Echelle et al. 1972; Craig et al 2019), and biotic interactions such as predation (Jackson et al. 1992; Chapleau et al. 1997). Regardless of the various factors influencing specific species, it is likely that a hierarchical series of factors affect the structure of a community.

River basins throughout the central and southern Great Plains region have high salt concentrations among many of the upper reaches (Wurbs 2002). Salt concentration in these basins derive from a strata layer which accumulated salt precipitation roughly 200 million years ago when this region was a large inland sea (Rought 1984). Upper reaches of several of the river basins have areas with salt concentrations exceeding that of seawater and, therefore, influence existing fish communities (Matthews 1988). Additionally, many of these reaches are subjected to high summertime temperatures and periods of intermittent drying (Ostrand and Wilde 2002), which selects for fishes that can tolerate high temperatures (Matthews 1987). Declining populations of several fishes

throughout the Great Plains region have prompted the U.S. Fish and Wildlife Service to list many species as threatened or endangered (USFWS 1998,2014) under the Endangered Species Act (1973), and state agencies have placed many others on Species of Greatest Conservation Need (SGCN) list.

The Red River basin of Texas and Oklahoma is one of several Great Plains rivers that demonstrates a west to east decreasing salinity gradient (Echelle et al. 1972). The fish community within the upper Red River basin is comprised of two distinct assemblages that are segregated among species with high to moderate salinity tolerances and species with low salinity tolerances (Echelle et al. 1972; Taylor et al. 1993; Higgins and Wilde 2005). Additionally, several fishes within this basin are SGCN species, and many have limited information known about their ecology, biology, or population status. Likewise, limited information is known about the entirety of the upper Red River community in Texas and Oklahoma, because previous studies sampled select tributaries of Oklahoma (Taylor et al. 1993, Starks et al. 2018), select tributaries of Texas (Higgins and Wilde 2005), or reported only the distributions of the most abundant fishes within the upper basin (Echelle et al. 1972).

The upper Red River basin is relatively unmodified by anthropogenic alterations (Hargrave and Taylor 2010) and provides an opportunity to gather contemporary information about the fish community and population status of SGCN species. The purpose of this study was to document the contemporary fish community, habitat associations, and factors influencing community structure in the upper Red River drainage in Texas and the mainstem in Oklahoma. The objectives were to quantify habitats factors at the reach scale (e.g., patterns in instream flow, unimpounded stream

length) and site scale (e.g., mesohabitat type, current velocity, depth, substrate) and to quantify factors influencing species distributions and community structure. Additionally, this study quantified population status of SGCN species using relative abundance and probability of occurrence within Red River mainstem and Texas tributaries upstream from Lake Texoma from historical data gathered from scientific reports and current information gathered from this study.

Methods

Longitudinal Surveys of upper Red River Fish Community and Habitats

Fish and habitat surveys of wadeable waters were conducted among 20 water bodies (i.e., named river or tributary) and 36 sites within the upper Red River drainage between September 2015 and September 2016 (Figure 3.1). Water bodies were selected based on accessibility and to represent the diversity of streams and habitats within the upper Red River drainage, such as small western tributaries (e.g., Groesbeck Creek), small eastern tributaries (e.g., South Fish Creek), small rivers (e.g., Pease River), and large rivers (e.g., Red River). Sites were selected based on accessibility within a reach and to capture upstream to downstream gradients in fish communities and habitats within small and large rivers. Therefore, only one site was sampled on most tributaries, and multiple sites were sampled on small and large rivers. Sites were sampled twice, once during the cool season (September through March) and again during the warm season (April through August), unless the stream was dry.

At each site, available habitats (i.e., riffle, run, pool, backwater, and eddy) were delineated and sampled in proportion to their availability. In smaller systems, passes were

made with a standard seine (3 m x 1.8 m, mesh size = 3.2 mm) or bag seine (5 m x 1.8 m, mesh size = 3.2 mm). Single passes were made within habitats that were constrained to small areas (i.e., shallow backwater habitat with sand or silt substrate and no woody debris) and multiple passes were made if few individuals were taken in complex habitats (e.g., deep backwater with cobble substrates and woody debris) or until no new species were taken (Rabeni et al 2009). In larger systems (e.g., lower Little Wichita River, Red River), up to three long (> 100 m) hauls were made with bag seines in run habitats. A minimum of two hours was spent at most sites, with up to five hours spent at larger systems. Fishes taken from habitats were identified to species, and the first 30 individuals of a species collected were measured (i.e., total length, nearest mm). Voucher specimens, small fishes, and individuals lacking certainty in identification were anesthetized with a lethal dose of tricane-methanesulfonate and fixed in 10% formalin. Length and width of area sampled (e.g., long seine hauls) or length and width of habitats were measured. Substrate (i.e., clay, silt, sand, gravel, cobble, boulder, and bedrock), vegetation, and woody debris were visually or tactilely estimated and represented as a percent coverage of the total habitat area. Water depth (m) and current velocities (m/s) were estimated from three to five-point estimates within a representative cross section of the habitat. Dissolved oxygen (mg/l), pH, specific conductance ($\mu\text{S}/\text{cm}$), and temperature ($^{\circ}\text{C}$) were measured at each site with YSI 556 multi-probe sonde.

Principal component analysis (PCA; SAS Institute, Cary, NC) was used to calculate linear combinations of habitat parameters for assessing variability among habitats. Qualitative parameters (e.g., habitat types) were denoted as binary numbers, whereas quantitative parameters (e.g., percent substrate and current velocity) were z-

transformed (Krebs 1999). Resulting PCA loadings of axes I and II were plotted to express similarities and differences among habitats, and loadings were averaged for habitats within a water body to express similarities and differences among water bodies. Renkonen similarity index (Renkonen 1938) was used to assess patterns in fish community similarities among water bodies and to identify species related to reach-level similarity. Bray-Curtis similarity matrices (Primer v6, Primer-E Ltd) was used to construct fish community similarity dendrogram by reach. Canonical correspondence analysis (CCA; Canoco 4.5) was used to assess patterns in habitat associations for upper Red River fishes. Total variation was partitioned into pure effects of physical parameters (i.e., qualitative and quantitative parameters used in PCA), season (i.e., cool and warm), and reach (Borcard et al. 1992), and Monte Carlo tests (1,000 permutations) were used to determine significance ($\alpha = 0.05$) of each pure effect.

SGCN population status

Contemporary collections were added to historical collections reported by Wilde et al. (1996) for 14 HUCs of upper Red River drainage. Analysis were spilt into two categories, SGCN species detected during our survey and SGCN species not detected during our survey. Population trends for eight SGCN species (i.e., Shovelnose sturgeon *Scaphirhynchus platyrhynchus*, Paddlefish *Polyodon spathula*, Goldeye *Hiodon alosoides*, Prairie Chub *Macrhybopsis australis*, Silver Chub *M. storeriana*, Red River Shiner *Notropis bairdi*, Chub Shiner *N. potteri* and Red River Pupfish *Cyprinodon rubrofluviatilis*) were assessed across decades (1950 to 2010; 2016 – 2017 data reported herein is represented in 2010). Effort for each decade was assumed from total number of

individuals captured across the decade: 1950s (N = 72,407), 1960s (N = 50,788), 1970s (N = 54,483), 1980s (N = 418,057), 1990s (N = 64,718). Relative abundances among each decade and HUC were log +1 transformed and assessed using a linear regression. Occurrences for each species was separated by among each decade and HUC and probability of occurrences were calculated using methods described by Perkin et al. (2014).

Results

Habitats

Thirty-six sites among 20 water bodies were sampled within the upper Red River drainage. Habitats (N = 400) among sites primarily consisted of runs (70%) and pools (12%). Mean ($\pm$ 1 SE) depths among sites was 0.3 ($\pm$ 0.3) m and ranged from 0.02 to 1.6 m. Mean current velocity among sites was 0.2 ($\pm$ 0.2) m/s and ranged from 0 to 0.9 m/s. Specific conductance ranged from 115 to 49,968 μ S/cm with greater specific conductance observed in the western portion of the study area and lower specific conductance observed in the eastern portion of the study area. Dominate substrate comprised of sand (57%), silt (30%), and gravel (9%). Woody debris, detritus, and aquatic vegetation were rare among habitats and sites.

Principal component axes I and II explained 24% of the variation among the 400 habitats. Axis I explained 13% of the variation and represented habitat type (i.e., pool and run) and substrate gradients. Strongest loadings for PC axis I were pool (0.33), silt (0.30), run (-0.46), and sand (-0.45) (Figure 3.2). Axis II explained 11% of the variation and represented a habitat type (i.e., riffle and backwater), substrate, and current velocity

gradients. Strongest loadings for PC axis II were riffle (0.42), gravel (0.40), current velocity (0.39), and silt (-0.37). Mean PC I scores, averaged across habitats and sites for each reach, ranged between -2.30 for North Fork Red River to 3.83 for Pecan Creek, contrasting prairie-type streams with shallow to moderate depths, flowing run and pool habitats with sand and silt substrates (negatively associated with PC I) versus more entrenched channel streams, common to eastern tributaries within the upper Red River drainage, with predominantly run and pool habitats with shallow to deep depths, sluggish current velocities except in riffle habitats, and silt and gravel habitats.

Fish community

A total of 36,211 fishes were taken, representing 14 families and 49 species of fishes. Most abundant family was Cyprinidae (71% in relative abundance), followed by Poeciliidae (8.9%), Cyprinodontidae (7.6%), and Fundulidae (3.6%). Most abundant species were Red Shiner *Cyprinella lutrensis* (26%), followed by Red River Shiner *Notropis bairdi* (18%), Plains Minnow *Hybognathus placitus* (14%), and Western Mosquitofish *Gambusia affinis* (9.0%) (Table 3.1). In addition to Red River Shiner, relative abundances of other Texas Species of greatest conservation need (SGCN) were 7.6% for Red River Pupfish *Cyprinodon rubrofluviatilis*, 1.3% for Prairie Chub *Macrhybopsis australis*, 0.01% for Silver Chub *M. storeriana*, and <0.01% for Goldeye *Hiodon alosoides*. Relative abundance was 0.3% for nonnative fishes (Common Carp *Cyprinus carpio*, Gulf Killifish *Fundulus grandis*, Striped Bass or hybrid *Morone saxatilis*, and Redbreast Sunfish *Lepomis auritus*).

Among 20 river water bodies, the most ubiquitously distributed fishes were Western Mosquitofish, taken from 19 water bodies, followed by Red Shiner (18 water bodies), Green Sunfish *Lepomis cyanellus* (13 water bodies), and Bluegill *Lepomis macrochirus*, Longear Sunfish *Lepomis megalotis*, and Largemouth Bass *Micropterus salmoides* (12 water bodies each) (Appendix 3.1). Ten species were taken only from one river reach. Among SGCN fishes, the most ubiquitously distributed fishes were Red River Shiner (8 water bodies), Red River Pupfish (8 water bodies), and Prairie Chub (6 water bodies). Mean ($\pm$ 1 SE) Renkonen similarity index (RSI) was 23.5% (1.59) among all pairwise comparisons. Greatest mean RSI was Adams Creek (36%), and lowest mean RSI was China Creek (4.3%). Adams Creek was dominated by the two most ubiquitously distributed fishes (i.e., Western Mosquitofish and Red Shiner), whereas China Creek was dominated by Bluegill and consisted of only two other species (i.e., Fathead Minnow *Pimephales promelas* and Common Carp *Cyprinus carpio*). Clustering based on Bray-Curtis dissimilarity separated water bodies into two primary groups (Group I and II; Figure 3.3). Fish communities within Group I consisted primarily of Red Shiners and Western Mosquitofish with no to rare occurrences of Red River Shiner, Prairie Chub, Plains Minnow, Plains Killifish, and Red River Pupfish. Three of seven streams had prairie-stream type habitats and all were consisted of specific conductance $< 3,500$ $\mu\text{S}/\text{cm}$. Fish communities within Group II usually consisted of Red Shiner and Western Mosquitofish, sometimes in great abundances as in Adams Creek and Groesbeck Creek, but typically consisted of Red River Shiner, Prairie Chub, Plains Minnow, Plains Killifish, and Red River Pupfish. Eight of the 10 water bodies had prairie-stream type

habitats and all but one reach (i.e., Mountain Creek) had specific conductance > 3,500 $\mu\text{S}/\text{cm}$.

Among 36 sites, most ubiquitously distributed fishes were Red Shiner (30 sites), Western Mosquitofish (30 sites), Red River Shiner (21 sites), and Green Sunfish (20 sites) (Appendix 3.2). Nine species were taken only from one site. In addition to Red River Shiner, numbers of occurrence for SGCN species were 16 sites for Prairie Chub, 14 sites for Red River Pupfish, and 1 site each for Goldeye and Silver Chub. Greatest mean (± 1 SE) relative abundances among sites were 28% (5.2) for Red Shiner, 13% (3.8) for Red River Shiner, 12% (3.7) for Western Mosquitofish, 7.8% (2.29) for Plains Minnow *Hybognathus placitus*, and 7.3% (3.7) for Red River Pupfish. Among remaining SGCN species, mean (± 1 SE) relative abundances among sites were 1.2% (0.51) for Prairie Chub and <0.01% (<0.01) for Goldeye and Silver Chub.

Fish-habitat associations

Axes I and II from CCA analysis explained 43% ($P < 0.01$) of the variability within the Red River fish community (Figure 3.4 & 3.5). Pure effects of reach explained 17% ($P < 0.01$), physical parameters explained 13% ($P < 0.01$), and season explained <1% ($P < 0.01$) of community variation. Shared effects (two- and three-way interactions) among reach, physical parameters, and season accounted for 13% of the community variation. Environmental parameters strongly associated with CCA axis I were specific conductance (-0.77), Prairie Dog Town Fork (-0.42), mean depth (0.48), and South Fish Creek (0.50). Environmental parameters strongly associated with CCA axis II were Red River (-0.41), specific conductance (0.41), and South Fish Creek (0.64). Among fishes

with >1% in overall relative abundance, Red River Pupfish and Plains Killifish were associated with greater specific conductance in Prairie Dog Town Fork and Pease River, and Red River Shiner, Plains Minnow, and Prairie Chub were associated with moderate specific conductance, run habitats with swifter current velocities, and sand substrates. Gizzard Shad, Red Shiner, Emerald Shiner, Ghost Shiner, Bullhead Minnow, and Mississippi Silverside, which collectively were numerically most abundant in Red River, Wichita River, and Little Wichita River, were associated with lower specific conductance, moderate current velocities, and deep-water habitats. Western Mosquitofish and Bluegill were associated with lower specific conductance, slack water, and pool habitats. Remaining fishes were generally associated with lower specific conductance, low to swift current velocities, and deeper habitats.

Specific conductance strongly influenced species segregation along CCA axes I and II. Mean (± 1 SD) specific conductance based on occurrence among all habitats was 17,700 (13,700) $\mu\text{S}/\text{cm}$. Mean (± 1 SD) specific conductance based on occurrence ranged between 14,900 (7,580) $\mu\text{S}/\text{cm}$ for Prairie Chub to 30,100 (12,890) $\mu\text{S}/\text{cm}$ for Red River Pupfish among fishes with > 1% in relative abundance and moderate to strong positive association with specific conductance (Figure 3.6). Mean (± 1 SD) specific conductance ranged between 6,700 (3,340) $\mu\text{S}/\text{cm}$ for Bluegill to 11,600 (8,580) $\mu\text{S}/\text{cm}$ for Western Mosquitofish among fishes with > 1% in relative abundance and moderate to strong negative association with specific conductance. Sites with specific conductance > 15,000 $\mu\text{S}/\text{cm}$ at the time of measurement were within Prairie Dog Town Fork, Red River (upper), Pease River (upper), North Pease River, North Wichita River water bodies. Collectively, these sites were within the western range of the study area also consisted of

swift to moderate current velocities with sand to silt substrates. Sites with specific conductance ≤ 3000 $\mu\text{S}/\text{cm}$ were within the Red River (e.g., I-35) and tributaries within the eastern range of the study area. However, three western range water bodies (i.e., Adams Creek, Wonderers Creek, and North Fork of Red River) have specific conductance of ≤ 3000 $\mu\text{S}/\text{cm}$. Sites and water bodies with specific conductance of ≤ 3000 $\mu\text{S}/\text{cm}$ consisted of a mix of swift water run and riffle habitats to slack water pools with silt, sand, and gravel substrates.

SGCN population status

For SGCN species detected during this survey, mean relative abundance (± 1 SE) among all water bodies was 1.7% (0.43; range: 0 – 12%) for Prairie Chub. Probability of occurrence (slope = 0.033; $P < 0.01$) and relative abundance (slope = 0.006; $P < 0.01$) for Prairie Chubs increased across decades (Figure 3.7). Mean relative abundance (± 1 SE) among all water bodies was 9.8% (1.8; range: 0 – 53%) for Red River Shiner (Figure 3.7 & 3.8). Probability of occurrence (slope = 0.012; $P = 0.03$) and relative abundance (slope = 0.009; $P < 0.01$) for Red River Shiner increased across decades. Mean relative abundance (± 1 SE) among all water bodies was 9.5% (2.5; range: 0 – 84%) for Red River Pupfish. Probability of occurrence for Red River Pupfish did not differ across decades, but relative abundance (slope = - 0.006; $P = 0.05$) decreased across decades (Figure 3.8). Mean relative abundance (± 1 SE) among all water bodies for Silver Chub and Goldeye was $<0.01\%$ (<0.01), ranging between 0 – 0.09% for Silver Chub and 0 – 0.16% for Goldeye. Probability of occurrence (slope = 0.020; $P < 0.01$) for Silver Cub increased across decades, but relative abundance did not differ across decades. For Goldeye, probability of

occurrence and relative abundance did not differ across decades. Among SGCN species that were not detected during our survey, Shovelnose Sturgeon and Paddlefish have not been reported in the upper Red River basin since the 1950's (Wilde et al. 1996) and therefore were not analyzed.

Discussion

Fishes were heterogeneously distributed within the upper Red River basin with general patterns of distribution segregated along habitat gradients and environmental parameters. The western portion of the upper Red River basin was dominated by fishes tolerant of highly saline water and associated with shallow runs habitats with moderate current velocities and sand or silt substrate, whereas fishes in the eastern tributaries were associated with deeper, slowing moving pool habitats with lower saline water. Segregation of fishes by environmental gradients has been documented before in the upper Red River basin (Echelle et al. 1972) and among major tributaries and forks in Texas (Higgins and Wilde 2005) and Oklahoma (Taylor et al. 1993), but this is the first study to comprehensively document distribution patterns among all fishes within major and minor tributary and three forks of the upper Red River basin of Texas and the mainstem Red River of Oklahoma. Additionally, we have documented distribution and abundance of one candidate species proposed for listing under the Endangered Species Act and four SGCN species for the state of Texas.

Our results support that salinity is the strongest factor influencing species spatial variation within the upper Red River basin and that regions were defined by high abundances of several fish species (Echelle et al. 1972; Taylor et al. 1993; Higgins and

Wilde 2005). Echelle et al. (1972) grouped Red Rive Pupfish and Plains Killifish among areas with the highest salinity ranges; Plains Minnow, Red River Shiner, Emerald Shiner, and Prairie Chub among areas with moderately high salinities; Red Shiner, Western Mosquitofish, Green Sunfish, Longear Sunfish, Fathead Minnow, and Bullhead Minnow among areas with moderate salinities. Taylor et al. (1993) reported similar findings but a few species varied among the salinity groupings, and Higgins and Wilde (2005) classified grouping of fishes by areas that had high, moderate, and low salinities. Overall, in this study, similar patterns were observed with Red River Pupfish and Plains Killifish being found among the highest salinity ranges, but a distinct assemblage associated with water bodies that had high salinities were comprised of Red River Pupfish, Plains Killifish, Red River Shiner, Prairie Chub, and Plains Minnow. Similarly, low salinity water bodies among eastern tributaries consisted of a distinct assemblage different from those in the western portion of the upper Red River but a conglomerate between the two assemblages were observed among mainstem sites on Red River downstream of the Wichita River confluence.

Variation in habitat gradients was also a significant factor contributing to the segregation of fishes within the upper Red River basin, but it is likely a combination of environmental and habitats parameters influencing the spatial variations of this system (Hargrave and Taylor 2010). Abundant species observed among highly saline water bodies were also associated with braided, sand-bed prairie streams dominated by shallow runs with moderate current velocities, whereas abundant species detected in lower salinity areas among eastern tributaries were associated with habitats that consisted of deeper, slow moving pool that had a variety of dominate substrates. Highly variable

flows and temperatures (Cross et al. 1995) in headwater reaches (Echelle et al. 1972; Matthews and Styron 1981; Ostrand and Wilde 2002) could explain why there was segregation among the assemblage. Alternatively, braided sand-bed rivers are only found among areas with higher salinities limiting intraspecific competition by reducing invasions of less tolerant species (Echelle et al. 1972; Winston et al. 1991). However, many of the saline tolerant species persist in downstream reaches of the mainstem Red River and other highly abundant species are members of the opportunistic life history guild. It is also uncertain why species such as Red River Shiner and Prairie Chub are only detected among braided sand-bed prairie streams and not among eastern tributaries. Segregation could be attributed to both abiotic and biotic interactions (competition, predations; Echelle et al. 1972; Gido et al. 1999) and the persistence of saline tolerant species downstream could be a consequence of species dispersing downstream when abiotic conditions in upper reaches become less favorable (Ruppel Chapter 2) and by extension, maintain a small population downstream. Additionally, the mainstem Red River could have a large enough diversity of habitats to minimize competition and allow for higher species richness (Hoagstrom and Berry 2008) which could allow the persistence of sand-bed associated species.

Estimating population status through time can be challenging given the limited information available from historical records but there are three primary methods use to assess this process: densities, relative abundance, and probability of occurrence (Runyan 2007; Perkin et al. 2015; Scanes 2016). However, historical records rarely provides effort or sampling area among collections making it impossible to compare densities between historical and contemporary datasets. Therefore, using relative abundances or probability

of occurrence would be more useful for comparing populations across decades. For two SGCN species, Prairie Chub, Red River Shiner, probability of occurrence and relative abundances increased across decades which indicates populations have been increasing in the upper Red River basin. In contrast to this study, Wilde et al. (1996) and Starks et al. (2018) reported the occurrences of Red River Shiner had been declining through the decades. However, Starks et al. (2018) primarily sampled major tributaries and forks of the Red River basin in Oklahoma which could have lower suitable habitats available compared to major tributaries in Texas. Red River Shiner was the second most abundant fish captured during the longitudinal surveys and had greater relative abundance and absolute abundance than was reported by Taylor et al. (1993). Silver Chub probability of occurrence has increased through the decades representing greater detection of this species among more locations within the upper Red River basin.

For the remaining SGCN species, based upon historical records it is likely that Paddlefish (i.e., last detected in the 1940s) and Shovelnose Sturgeon (i.e., last detected in the 1950s) no longer persist in the upper Red River basin. Differences were not detected for Goldeye through the decades because of limited number of individuals captured resulting in low detection rates. Decreases in Red River Pufffish relative abundance through the decades could be attributed to lower sampling efforts in upper reaches of the basin. Chub Shiner relative abundances declined through the decades even though Chub Shiner were captured among several sites with relative abundance ranging between 0.5% and 2.9% consistently from 1950s to the 1990s. However, Chub Shiner was not collected during recent surveys of the upper Red River and tributaries of Texas and Oklahoma (this study; Starks et al. 2018), except for one that was captured at the I-35 site while

collecting specimens for a genetic study (Sotola et al. 2019). Declining populations of Chub Shiner in the Brazos River (Runyan 2007) has been associated with increased fragmentation among the lower reaches (Perkin et al. 2009). However, it is unknown why there has been a sudden decline of Chub Shiner in the upper Red River considering that the Red River is free flowing upstream of Lake Texoma.

Braided sand-bed prairie streams within the Great Plains have been impacted through anthropogenic alterations and climate change over the past 150 years (Dodds et al. 2004; Hoagstrom et al. 2011; Perkin and Gido 2011) and many species have declined throughout this region, especially pelagic broadcast spawning cyprinids (PBSC; Worthington et al. 2016). The upper Red River basin has maintained a stable fish community compared with historical records (Echelle et al. 1972; Taylor et al 1993; Hardgrave and Taylor 2010) especially with PBSC. However, threats to the fish community are similar to threats in other basins throughout the Great Plains such as stream fragmentations, channelization, and ground water harvest (USFWS 1998; 2014; Perkin et al. 2017). Additionally, sodium chloride control project throughout this basin (Wurbs 2002; USGS 2011) could negatively impact the salinity tolerant species through increased competition (Echelle et al. 1972), predation (Gido et al. 1999), or genetic swamping (Sotola et al. 2019). Therefore, understanding factors that influence community structure and dynamics will play a vital role in the conservation and management of aquatic resources in arid and semi-arid systems.

Table 3.1. Common names, scientific names, species codes, and relative abundances for fishes taken among all sites within the upper Red River drainage from September 2015 through September 2016.

Common name	Scientific name	Code	Relative abundance (%)
Red Shiner	<i>Cyprinella lutrensis</i>	Cyp lut	26
Red River Shiner	<i>Notropis bairdi</i>	Not bai	18
Plains Minnow	<i>Hybognathus placitus</i>	Hyb pla	14
Western Mosquitofish	<i>Gambusia affinis</i>	Gam aff	9.0
Red River Pupfish	<i>Cyprinodon rubrofluviatilis</i>	Cyp rub	7.6
Emerald Shiner	<i>Notropis atherinoides</i>	Not ath	5.9
Plains Killifish	<i>Fundulus zebrinus</i>	Fun zeb	3.2
Gizzard Shad	<i>Dorosoma cepedianum</i>	Dor cep	2.7
Ghost Shiner	<i>Notropis buchanani</i>	Not buc	2.5
Mississippi Silverside	<i>Menidia audens</i>	Men aud	1.4
Prairie Chub	<i>Macrhybopsis australis</i>	Mac aus	1.3
Bullhead Minnow	<i>Pimephales vigilax</i>	Pim vig	1.2
Bluegill	<i>Lepomis macrochirus</i>	Lep mac	1.1
Blue Catfish	<i>Ictalurus furcatus</i>	Ict fur	0.91
Shoal Chub	<i>Macrhybopsis hyostoma</i>	Mac hyo	0.71
Green Sunfish	<i>Lepomis cyanellus</i>	Lep cya	0.46
Central Stoneroller	<i>Camptostoma anomalum</i>	Cam ano	0.41
Fathead Minnow	<i>Pimephales promelas</i>	Pim pro	0.38
Blackstripe Topminnow	<i>Fundulus notatus</i>	Fun not	0.36
White Crappie	<i>Pomoxis annularis</i>	Pom ann	0.31
Sunfish larvae	<i>Lepomis larvae</i>		0.22
Longear Sunfish	<i>Lepomis megalotis</i>	Lep meg	0.21
Orangespotted Sunfish	<i>Lepomis humilis</i>	Lep hum	0.20
Redbreast Sunfish	<i>Lepomis auritus</i>	Lep aur	0.17
Largemouth Bass	<i>Micropterus salmoides</i>	Mic sal	0.17
Suckermouth Minnow	<i>Phenacobius mirabilis</i>	Phe mir	0.16
Channel Catfish	<i>Ictalurus punctatus</i>	Ict pun	0.15
Sand Shiner	<i>Notropis stramineus</i>	Not str	0.11
Freshwater Drum	<i>Aplodinotus grunniens</i>	Apl gru	0.10
Smallmouth Buffalo	<i>Ictiobus bubalus</i>	Ict bub	0.09
Orangethroat Darter	<i>Etheostoma spectabile</i>	Eth spe	0.08
River Carpsucker	<i>Carpionodes carpio</i>	Car car	0.07
Common Carp	<i>Cyprinus carpio</i>	Cyp car	0.06
Bigscale Logperch	<i>Percina macrolepida</i>	Per mac	0.06
Threadfin Shad	<i>Dorosoma petenense</i>	Dor pet	0.04
Golden Shiner	<i>Notemigonus crysoleucas</i>	Not cry	0.04
Longnose Gar	<i>Lepisosteus osseus</i>	Lep oss	0.04
Striped Bass	<i>Morone saxatilis</i>	Mor sax	0.02

Table 3.1. Continued.

Common name	Scientific name	Code	Relative abundance (%)
Spotted Gar	<i>Lepisosteus oculatus</i>	Lep ocu	0.01
Blacktail Shiner	<i>Cyprinella venusta</i>	Cyp ven	0.01
Yellow Bullhead	<i>Ameiurus natalis</i>	Ame nat	0.01
Shortnose Gar	<i>Lepisosteus platostomus</i>	Lep plat	0.01
Silver Chub	<i>Macrhybopsis storeriana</i>	Mac sto	0.01
Brook Silverside	<i>Labidesthes sicculus</i>	Lab sic	0.01
Gar larvae	<i>Lepisosteus</i> larvae		0.01
Black Bullhead	<i>Ameiurus melas</i>	Ame mel	0.01
Logperch	<i>Percina caprodes</i>	Per cap	0.01
Goldeye	<i>Hiodon alosoides</i>	Hio alo	<0.01
Chub larvae	<i>Macrhybopsis</i> larvae		<0.01
Flathead Catfish	<i>Pylodictis olivaris</i>	Pyl oli	<0.01
Gulf Killifish	<i>Fundulus grandis</i>	Fun gra	<0.01
Redear Sunfish	<i>Lepomis microlophus</i>	Lep mic	<0.01
Richness			49
Total N			36,211

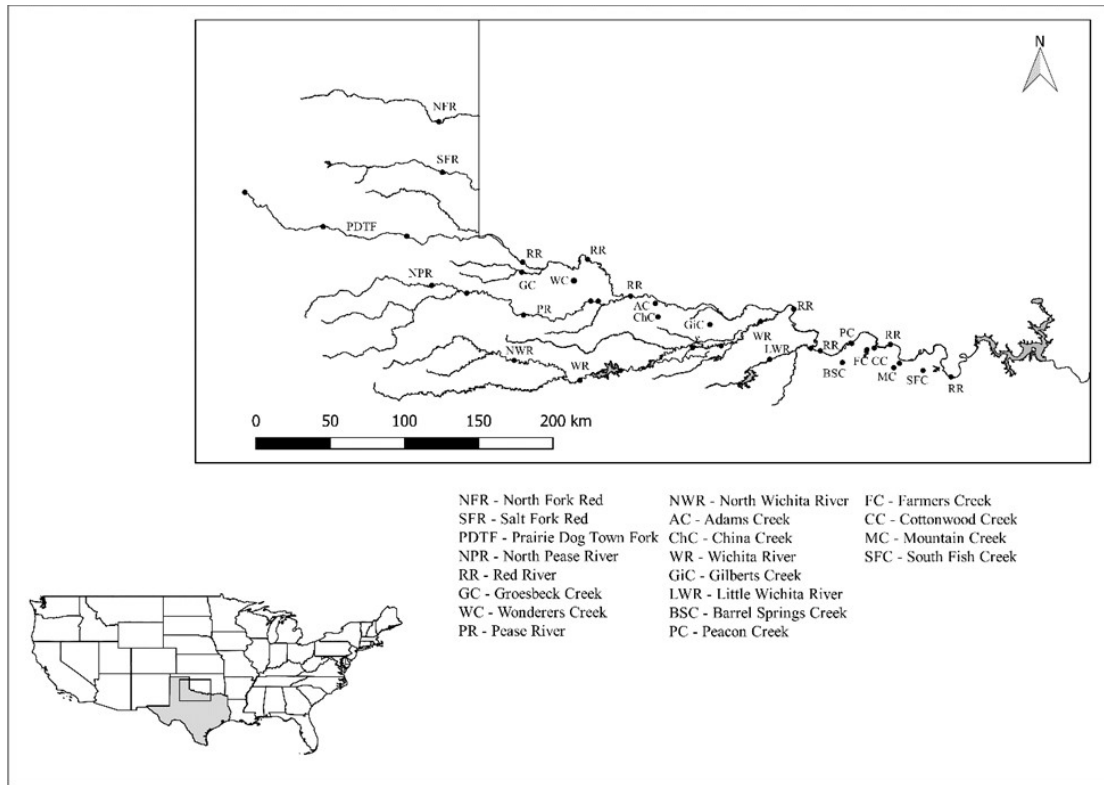
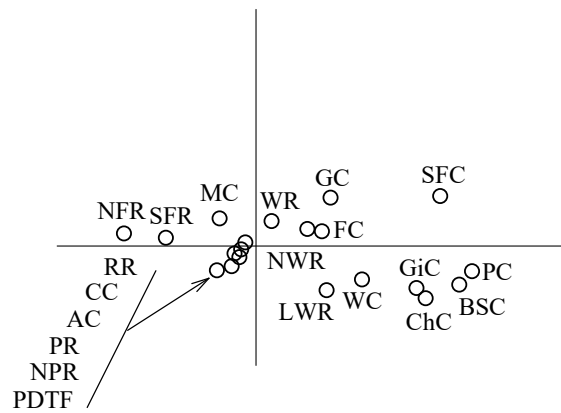
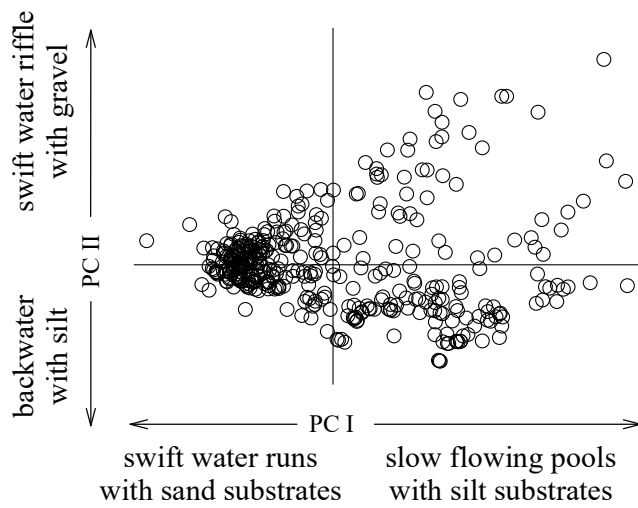


Figure 3.1. Site locations (N = 36, black dot) and water bodies (N = 20) for longitudinal surveys within the upper Red River basin of Texas and Oklahoma, September 2015 through September 2016. See Appendix 4.1 for georeferenced site locations.



- NFR North Fork Red
- SFR Salt Fork Red
- PDTF Prairie Dog Town Fork
- MC Mountain Creek
- NPR North Pease River
- PR Pease River
- AC Adams Creek
- CC Cottonwood Creek
- RR Red River
- WR Wichita River
- NWR North Wichita River
- FC Farmers Creek
- LWR Little Wichita River
- GC Groesbeck Creek
- WC Wonderers Creek
- GiC Gilberts Creek
- ChC China Creek
- SFC South Fish Creek
- BSC Barrel Springs Creek
- PC Pecan Creek

Figure 3.2. Circles represent each mesohabitat (N = 400) along PC I and PC II gradients (top panel). Circles represent water bodies (average PC I and PC II mesohabitat scores) along PC I and PC II gradients (bottom panel).

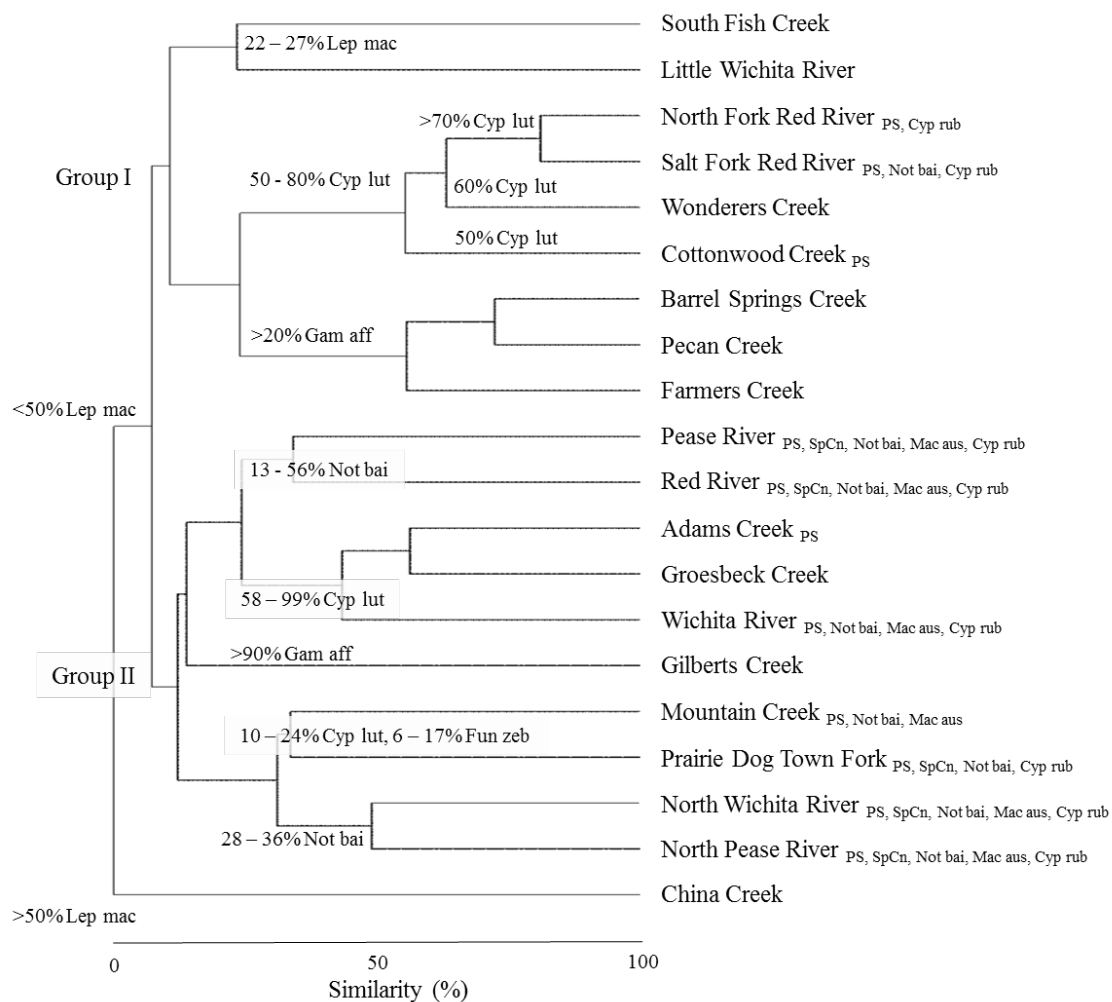


Figure 3.3. Fish community similarity groupings among water bodies explained by relative abundance of species in common between each reach. Water bodies classified as Prairie stream (PS) are annotated next to the reach. Water bodies with $> 3,500 \mu\text{S}\cdot\text{cm}^{-1}$ are annotated with specific conductance (SpCn). Genus and species are abbreviated to three characters.

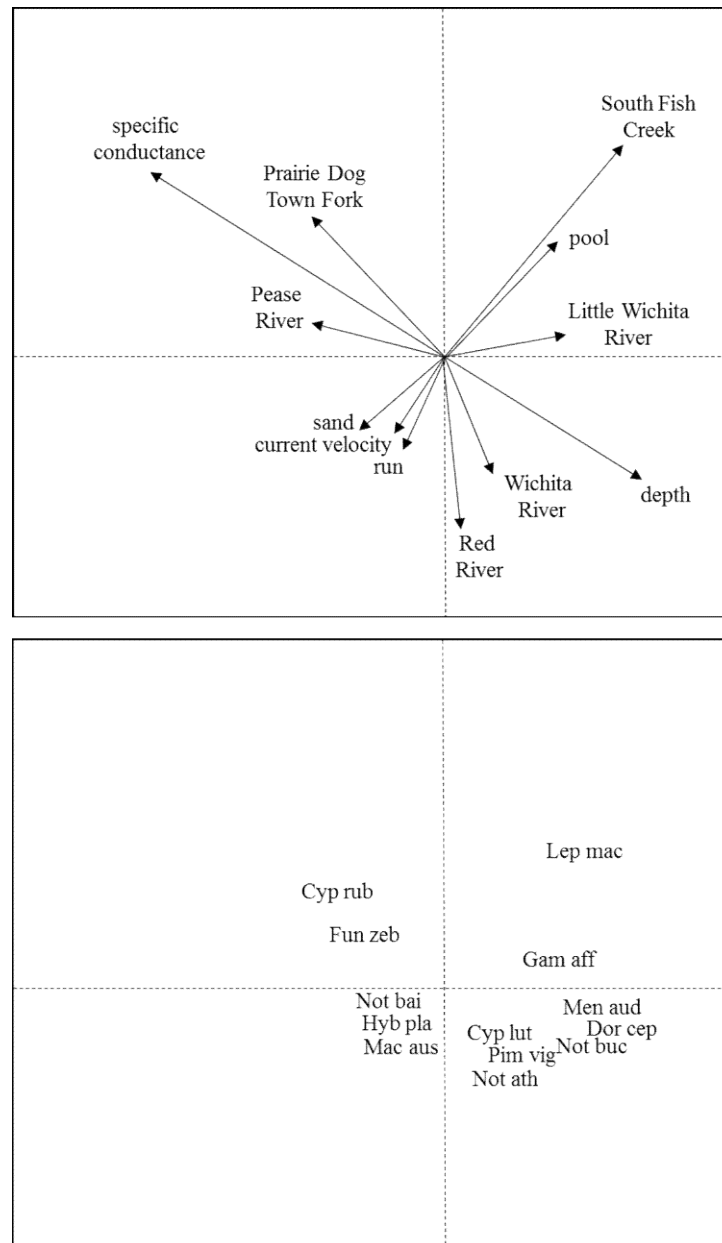


Figure 3.4. Fish-habitat associations between Canonical Correspondence Analysis (CCA) axis I (x-axis) and CCA axis II (y-axis) for fishes with >1% relative abundance in the upper Red River drainage. Genus and species are abbreviated to three characters.

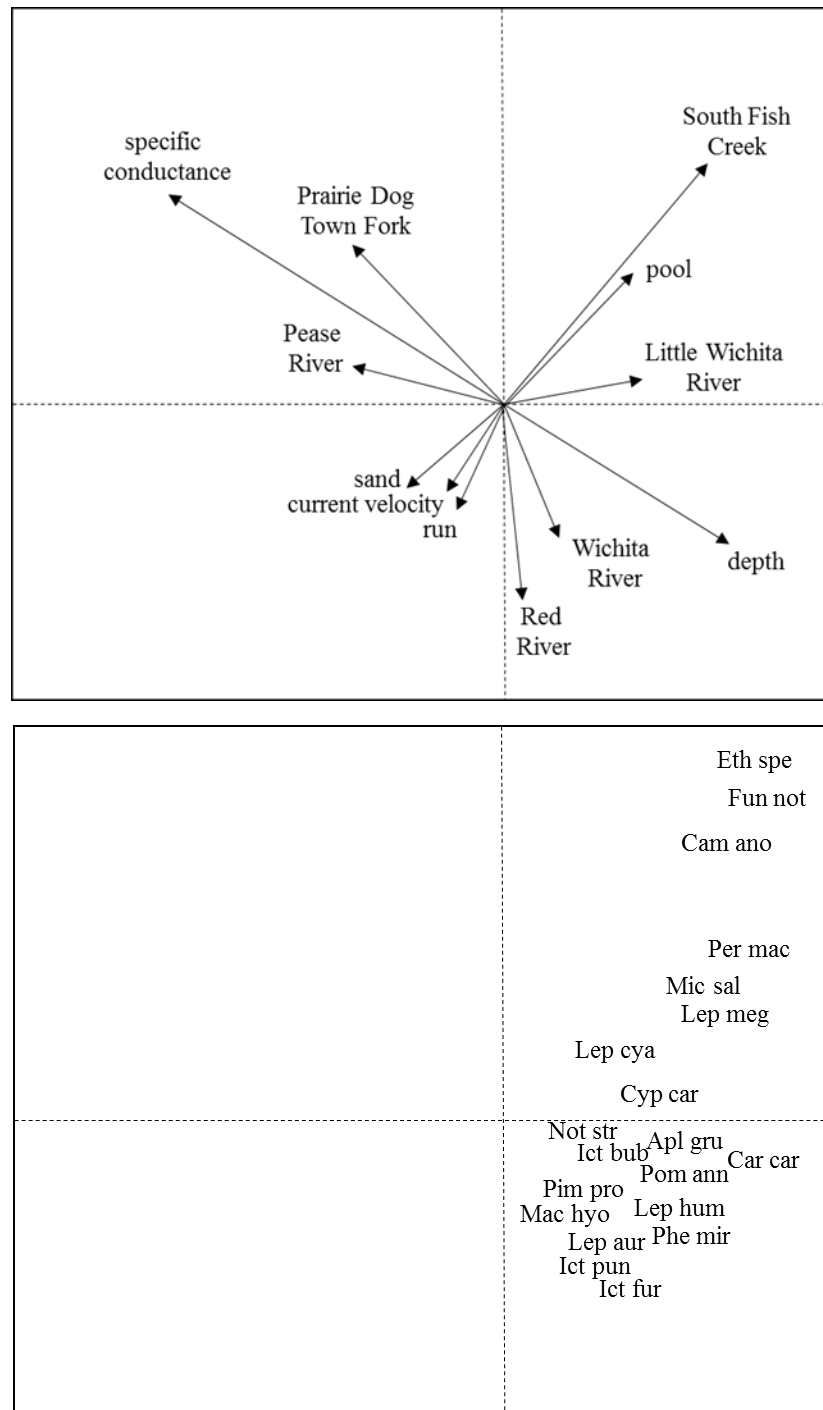


Figure 3.5. Fish-habitat associations between Canonical Correspondence Analysis (CCA) axis I (x-axis) and CCA axis II (y-axis) for fishes with <1% relative abundance in the upper Red River drainage. Genus and species are abbreviated to three characters.

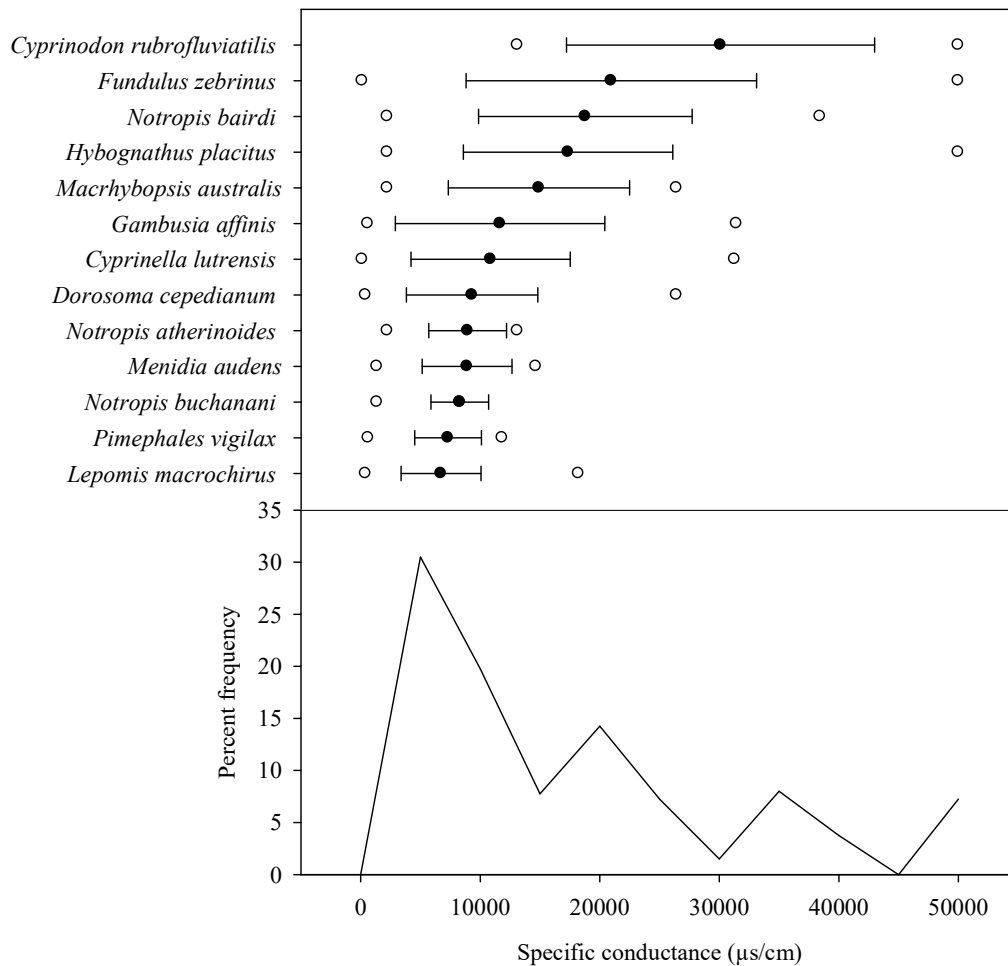


Figure 3.6. Mean (black circle), 1 SE (whisker), and minimum and maximum (open circle) specific conductance for fishes with >1% relative abundance within the upper Red River drainage (top panel). Amount of habitats available along specific conductance gradient (bottom panel).

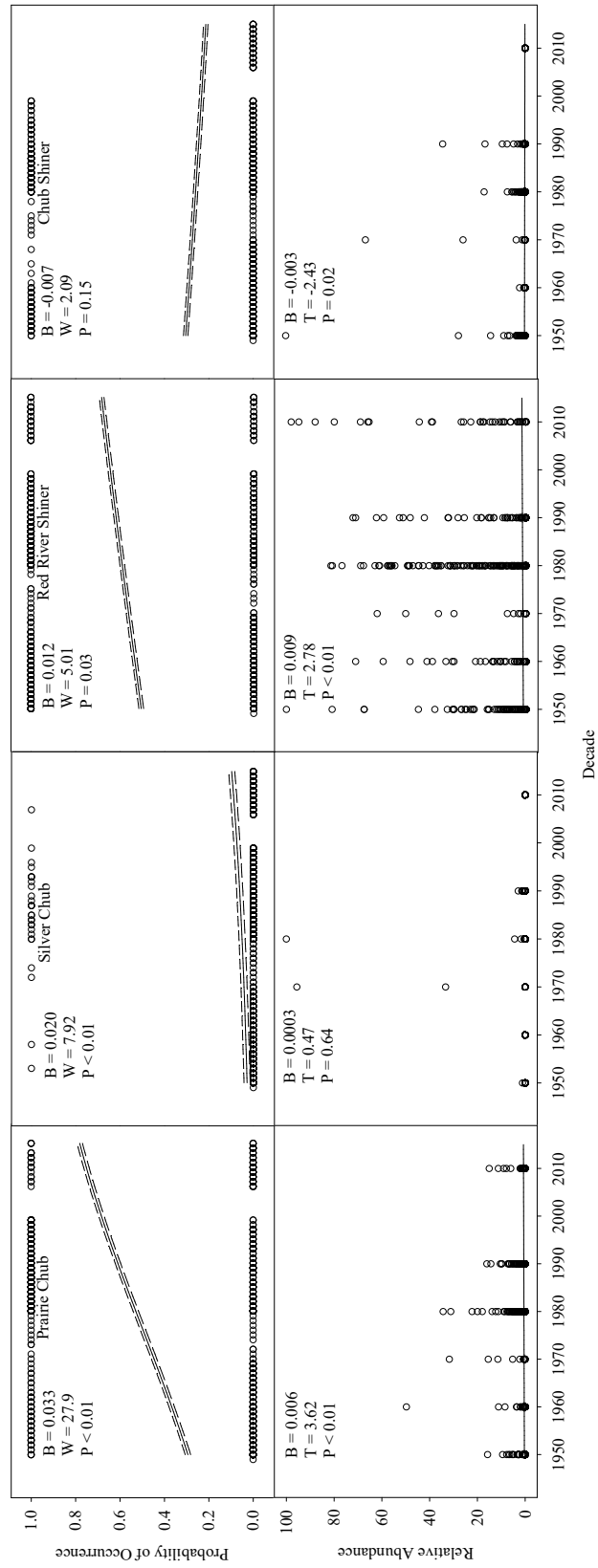


Figure 3.7. Probability of occurrence (Top) and relative abundance (Bottom) across decades (1950's - 2010's) for four Cyprinidae species that are classified as Species of Greatest Conservation Need in Texas

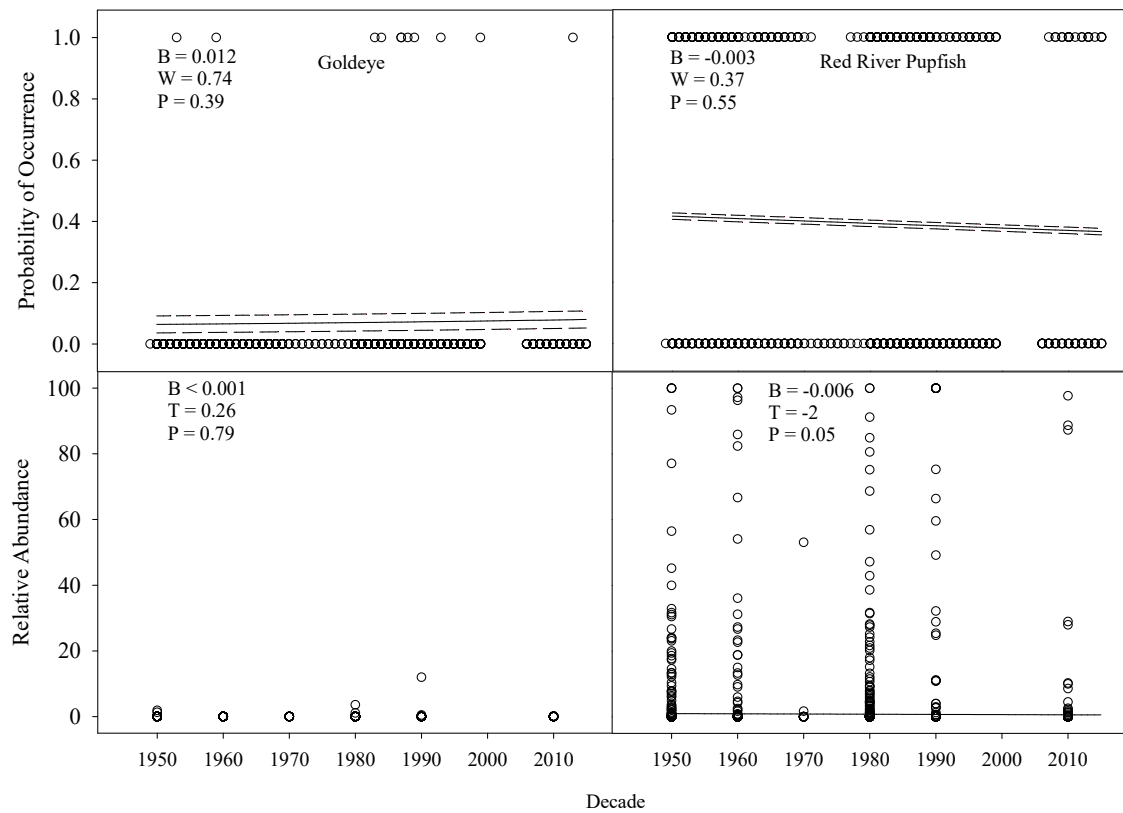


Figure 3.8. Probability of occurrence (Top) and relative abundance (Bottom) across decades (1950's - 2010's) for four non-Cyprinidae species that are classified as Species of Greatest Conservation Need in Texas

Appendix 3.1.1. Relative abundance of fishes by reach within the upper Red River drainage from September 2015 through September 2016. Reaches are list in order from upstream to downstream

Scientific Name	Prairie Dog Town Fork	Groesbeck Creek	Wonderers Creek	Red River	Salt Fork Red River
<i>Lepisosteus larvae</i>				0.02	
<i>Lepisosteus oculatus</i>				0.01	
<i>Lepisosteus osseus</i>		0.11		0.06	
<i>Lepisosteus platostomus</i>				0.02	
<i>Hiodon alosoides</i>				0.01	
<i>Dorosoma cepedianum</i>				6.59	
<i>Dorosoma petenense</i>				0.03	
<i>Campostoma anomalum</i>					
<i>Cyprinella lutrensis</i>	10.16	99.08	63.89	14.37	73.64
<i>Cyprinella venusta</i>					
<i>Cyprinus carpio</i>				0.01	
<i>Hybognathus placitus</i>	5.65			27.65	8.14
<i>Macrhybopsis larvae</i>				0.01	
<i>Macrhybopsis australis</i>				1.21	
<i>Macrhybopsis hyostoma</i>				2.03	
<i>Macrhybopsis storeriana</i>				0.03	
<i>Notemigonus crysoleucas</i>					
<i>Notropis atherinoides</i>				16.49	
<i>Notropis bairdi</i>	5.13			13.44	0.39
<i>Notropis buchanani</i>				4	
<i>Notropis stramineus</i>				0.04	1.55
<i>Phenacobius mirabilis</i>					
<i>Pimephales promelas</i>		0.49		0.07	
<i>Pimephales vigilax</i>		0.11	21.11	0.22	2.71
<i>Carpiodes carpio</i>				0.11	
<i>Ictiobus bubalus</i>				0.14	
<i>Ameiurus natalis</i>					
<i>Ameiurus melas</i>				0.02	
<i>Ictalurus furcatus</i>				2.6	
<i>Ictalurus punctatus</i>				0.19	0.39
<i>Pylodictis olivaris</i>					
<i>Labidesthes sicculus</i>					
<i>Menidia audens</i>				2.17	
<i>Fundulus notatus</i>					
<i>Fundulus grandis</i>					
<i>Fundulus zebrinus</i>	6.41			0.35	6.98
<i>Gambusia affinis</i>	0.57	0.05	9.44	5.81	4.65
<i>Cyprinodon rubrofluviatilis</i>	72.08			0.35	0.78

Appendix 3.1.1. Continued

Scientific Name	Prairie Dog Town Fork	Groesbeck Creek	Wonderers Creek	Red River	Salt Fork Red River
<i>Morone saxatilis</i>				0.04	
<i>Lepomis larvae</i>				0.02	
<i>Lepomis auritus</i>				0.47	
<i>Lepomis cyanellus</i>				0.14	0.78
<i>Lepomis humilis</i>		0.05		0.39	
<i>Lepomis macrochirus</i>			2.22	0.03	
<i>Lepomis megalotis</i>		0.05	3.33	0.03	
<i>Lepomis microlophus</i>					
<i>Micropterus salmoides</i>		0.05		0.03	
<i>Pomoxis annularis</i>				0.55	
<i>Percina caprodes</i>					
<i>Percina macrolepida</i>				0.01	
<i>Etheostoma spectabile</i>					
<i>Aplodinotus grunniens</i>				0.24	
Richness	6	8	5	37	10
Total N	2,106	1,841	180	12,437	258

Appendix 3.1.2. Continued

Scientific Name	North Fork Red River	North Pease River	Pease River	Adams Creek	China Creek
<i>Lepisosteus larvae</i>					
<i>Lepisosteus oculatus</i>					
<i>Lepisosteus osseus</i>					
<i>Lepisosteus platostomus</i>					
<i>Hiodon alosoides</i>					
<i>Dorosoma cepedianum</i>			0.34		
<i>Dorosoma petenense</i>					
<i>Campostoma anomalum</i>					
<i>Cyprinella lutrensis</i>	89.19	0.71	10.09	58.28	
<i>Cyprinella venusta</i>					
<i>Cyprinus carpio</i>					16.67
<i>Hybognathus placitus</i>		12.41	9.81		
<i>Macrhybopsis larvae</i>					
<i>Macrhybopsis australis</i>		0.12	0.89		
<i>Macrhybopsis hyostoma</i>					
<i>Macrhybopsis storeriana</i>					
<i>Notemigonus crysoleucas</i>					
<i>Notropis atherinoides</i>					
<i>Notropis bairdi</i>		27.78	56.1		
<i>Notropis buchanani</i>					
<i>Notropis stramineus</i>	2.7				
<i>Phenacobius mirabilis</i>				0.23	
<i>Pimephales promelas</i>			1.08	1.23	16.67
<i>Pimephales vigilax</i>	1.62		0.03	0.06	
<i>Carpionodes carpio</i>				0.12	
<i>Ictiobus bubalus</i>				0.18	
<i>Ameiurus natalis</i>					
<i>Ameiurus melas</i>					
<i>Ictalurus furcatus</i>					
<i>Ictalurus punctatus</i>			0.01	0.06	
<i>Pylodictis olivaris</i>					
<i>Labidesthes sicculus</i>					
<i>Menidia audens</i>			0.06		
<i>Fundulus notatus</i>					
<i>Fundulus grandis</i>					
<i>Fundulus zebrinus</i>	2.7	31.56	5.7		
<i>Gambusia affinis</i>	0.54	0.35	2.25	38.45	
<i>Cyprinodon rubrofluviatilis</i>	0.54	27.07	13.48		

Appendix 3.1.2. Continued

Scientific Name	North Fork Red River	North Pease River	Pease River	Adams Creek	China Creek
<i>Morone saxatilis</i>					
<i>Lepomis larvae</i>	0.54				
<i>Lepomis auritus</i>					
<i>Lepomis cyanellus</i>	0.54		0.04	0.99	
<i>Lepomis humilis</i>				0.06	
<i>Lepomis macrochirus</i>	0.54		0.01		66.67
<i>Lepomis megalotis</i>	0.54			0.29	
<i>Lepomis microlophus</i>					
<i>Micropterus salmoides</i>	0.54		0.09	0.06	
<i>Pomoxis annularis</i>					
<i>Percina caprodes</i>					
<i>Percina macrolepida</i>					
<i>Etheostoma spectabile</i>					
<i>Aplodinotus grunniens</i>					
Richness	10	7	15	12	3
Total N	185	846	6,838	1,714	6

Appendix 3.1.3. Continued

Scientific Name	Gilberts Creek	North Wichita River	Wichita River	Little Wichita River	Barrel Springs Creek
<i>Lepisosteus larvae</i>			0.02		
<i>Lepisosteus oculatus</i>					
<i>Lepisosteus osseus</i>			0.02	0.25	
<i>Lepisosteus platostomus</i>			0.02		
<i>Hiodon alosoides</i>					
<i>Dorosoma cepedianum</i>		0.39	0.1	9.23	
<i>Dorosoma petenense</i>			0.15		
<i>Campostoma anomalum</i>					
<i>Cyprinella lutrensis</i>	0.81	2.86	59.32	1.5	14.63
<i>Cyprinella venusta</i>			0.02		
<i>Cyprinus carpio</i>		0.13	0.17	0.12	
<i>Hybognathus placitus</i>		41.15	8.09		
<i>Macrhybopsis larvae</i>					
<i>Macrhybopsis australis</i>		9.64	3.74		
<i>Macrhybopsis hyostoma</i>			0.04		
<i>Macrhybopsis storeriana</i>					
<i>Notemigonus crysoleucas</i>					
<i>Notropis atherinoides</i>			1.26	1.5	
<i>Notropis bairdi</i>		36.72	4.14		
<i>Notropis buchanani</i>			3	32.42	
<i>Notropis stramineus</i>			0.02		
<i>Phenacobius mirabilis</i>			0.63		
<i>Pimephales promelas</i>		0.13	0.44		
<i>Pimephales vigilax</i>			6.36	0.25	
<i>Carpionodes carpio</i>				0.12	
<i>Ictiobus bubalus</i>			0.02		
<i>Ameiurus natalis</i>		0.13			
<i>Ameiurus melas</i>			0.02		
<i>Ictalurus furcatus</i>					
<i>Ictalurus punctatus</i>			0.42	0.12	0.81
<i>Pylodictis olivaris</i>					
<i>Labidesthes sicculus</i>					
<i>Menidia audens</i>			3.19	6.23	
<i>Fundulus notatus</i>					
<i>Fundulus grandis</i>			0.02		
<i>Fundulus zebrinus</i>		3.13	2.77		
<i>Gambusia affinis</i>	97.7	1.69	4.18	6.36	78.05
<i>Cyprinodon rubrofluviatilis</i>		3.65	0.32		

Appendix 3.1.3. Continued

Scientific Name	Gilberts Creek	North Wichita River	Wichita River	Little Wichita River	Barrel Springs Creek
<i>Morone saxatilis</i>					
<i>Lepomis larvae</i>			0.06	6.98	
<i>Lepomis auritus</i>			0.06		
<i>Lepomis cyanellus</i>	0.46		0.78	0.75	
<i>Lepomis humilis</i>	1.04	0.39	0.15	0.25	
<i>Lepomis macrochirus</i>			0.1	27.18	6.5
<i>Lepomis megalotis</i>			0.21	0.37	
<i>Lepomis microlophus</i>			0.02		
<i>Micropterus salmoides</i>			0.13	0.62	
<i>Pomoxis annularis</i>			0.02	4.86	
<i>Percina caprodes</i>					
<i>Percina macrolepida</i>					
<i>Etheostoma spectabile</i>					
<i>Aplodinotus grunniens</i>				0.87	
Richness	4	12	33	18	4
Total N	869	768	5,239	802	123

Appendix 3.1.4. Continued

Scientific Name	Pecan Creek	Farmers Creek	Cottonwood Creek	Mountain Creek	South Fish Creek
<i>Lepisosteus larvae</i>					
<i>Lepisosteus oculatus</i>	1.48	0.32			
<i>Lepisosteus osseus</i>					
<i>Lepisosteus platostomus</i>					
<i>Hiodon alosoides</i>					
<i>Dorosoma cepedianum</i>	11.33	4.17	9.09		
<i>Dorosoma petenense</i>		0.96			
<i>Campostoma anomalum</i>				1.83	26.71
<i>Cyprinella lutrensis</i>	11.33	17.63	53.33	24.85	
<i>Cyprinella venusta</i>		0.96	0.61		
<i>Cyprinus carpio</i>	2.46	0.32		0.37	
<i>Hybognathus placitus</i>				18.51	
<i>Macrhybopsis larvae</i>					
<i>Macrhybopsis australis</i>				0.37	
<i>Macrhybopsis hyostoma</i>				0.37	
<i>Macrhybopsis storeriana</i>					
<i>Notemigonus crysoleucas</i>	0.49	4.17			
<i>Notropis atherinoides</i>					
<i>Notropis bairdi</i>				4.51	
<i>Notropis buchanani</i>					
<i>Notropis stramineus</i>			4.24	2.19	
<i>Phenacobius mirabilis</i>		6.09		0.12	
<i>Pimephales promelas</i>					
<i>Pimephales vigilax</i>					0.8
<i>Carpionodes carpio</i>		2.24			
<i>Ictiobus bubalus</i>	3.45	0.96		0.24	
<i>Ameiurus natalis</i>				0.37	0.2
<i>Ameiurus melas</i>					
<i>Ictalurus furcatus</i>		2.56			
<i>Ictalurus punctatus</i>		1.28			
<i>Pylodictis olivaris</i>		0.32			
<i>Labidesthes sicculus</i>					0.8
<i>Menidia audens</i>		8.97			
<i>Fundulus notatus</i>					26.1
<i>Fundulus grandis</i>					
<i>Fundulus zebrinus</i>				17.17	
<i>Gambusia affinis</i>	48.28	27.88	7.27	26.8	4.22
<i>Cyprinodon rubrofluviatilis</i>					

Appendix 3.1.4. Continued

Scientific Name	Pecan Creek	Farmers Creek	Cottonwood Creek	Mountain Creek	South Fish Creek
<i>Morone saxatilis</i>		1.28			
<i>Lepomis larvae</i>	0.99	0.32			2.81
<i>Lepomis auritus</i>					
<i>Lepomis cyanellus</i>	3.94	3.53	16.36	1.95	2.81
<i>Lepomis humilis</i>					
<i>Lepomis macrochirus</i>	1.97	5.13	6.06		22.89
<i>Lepomis megalotis</i>	5.42	2.24	1.82	0.24	4.22
<i>Lepomis microlophus</i>					
<i>Micropterus salmoides</i>	8.87	1.92	1.21	0.12	1.81
<i>Pomoxis annularis</i>		0.96			
<i>Percina caprodes</i>		0.64			
<i>Percina macrolepida</i>		5.13			0.8
<i>Etheostoma spectabile</i>					5.82
<i>Aplodinotus grunniens</i>					
Richness	11	23	9	16	12
Total N	203	312	165	821	498

Appendix 3.2.1. Relative abundance of fishes by site within the upper Red River drainage from September 2015 through September 2016. Sites are list in order from upstream to downstream.

Scientific Name	Prairie Dog Town Fork			Groesbeck Creek	Wonderers Creek
	Hwy 207	Hwy 70	Hwy 83	Hwy 6	FM 2379
<i>Lepisosteus</i> larvae					
<i>Lepisosteus oculatus</i>					
<i>Lepisosteus osseus</i>				0.11	
<i>Lepisosteus platostomus</i>					
<i>Hiodon alosoides</i>					
<i>Dorosoma cepedianum</i>					
<i>Dorosoma petenense</i>					
<i>Campostoma anomalum</i>					
<i>Cyprinella lutrensis</i>	38.49		0.76	99.08	63.89
<i>Cyprinella venusta</i>					
<i>Cyprinus carpio</i>					
<i>Hybognathus placitus</i>	20.26		1.37		
<i>Macrhybopsis</i> larvae					
<i>Macrhybopsis australis</i>					
<i>Macrhybopsis hyostoma</i>					
<i>Macrhybopsis storeriana</i>					
<i>Notemigonus crysoleucas</i>					
<i>Notropis atherinoides</i>					
<i>Notropis bairdi</i>	15.29	1.33	1.97		
<i>Notropis buechanani</i>					
<i>Notropis stramineus</i>					
<i>Phenacobius mirabilis</i>					
<i>Pimephales promelas</i>				0.49	
<i>Pimephales vigilax</i>				0.11	21.11
<i>Carpiodes carpio</i>					
<i>Ictiobus bubalus</i>					
<i>Ameiurus natalis</i>					
<i>Ameiurus melas</i>					
<i>Ictalurus furcatus</i>					
<i>Ictalurus punctatus</i>					
<i>Pylodictis olivaris</i>					
<i>Labidesthes sicculus</i>					
<i>Menidia audens</i>					
<i>Fundulus notatus</i>					
<i>Fundulus grandis</i>					
<i>Fundulus zebrinus</i>	15.65	1	6.22		
<i>Gambusia affinis</i>			1.82	0.05	9.44
<i>Cyprinodon rubrofluviatilis</i>	10.31	97.68	87.86		

Appendix 3.2.1. Continued.

Scientific Name	Prairie Dog Town Fork			Groesbeck Creek	Wonderers Creek
	Hwy 207	Hwy 70	Hwy 83	Hwy 6	FM 2379
<i>Lepomis larvae</i>					
<i>Lepomis auritus</i>					
<i>Lepomis cyanellus</i>					
<i>Lepomis humilis</i>				0.05	
<i>Lepomis macrochirus</i>					2.22
<i>Lepomis megalotis</i>				0.05	3.33
<i>Lepomis microlophus</i>					
<i>Micropterus salmoides</i>				0.05	
<i>Pomoxis annularis</i>					
<i>Percina caprodes</i>					
<i>Percina macrolepida</i>					
<i>Etheostoma spectabile</i>					
<i>Aplodinotus grunniens</i>					
Richness	5	3	6	8	5
Total N	543	904	659	1,841	180

Appendix 3.2.2. Continued.

Scientific Name	Red River						I-35
	Hwy 6	Hwy 283	Hwy 183	Hwy 79	Hwy 81	Hwy 89	
<i>Lepisosteus</i> larvae						0.04	
<i>Lepisosteus oculatus</i>						0.02	
<i>Lepisosteus osseus</i>			0.36		0.16	0.09	
<i>Lepisosteus platostomus</i>						0.07	
<i>Hiodon alosoides</i>					0.16		
<i>Dorosoma cepedianum</i>		0.33	0.12	1.24	12.58	16.01	0.02
<i>Dorosoma petenense</i>							0.09
<i>Campostoma anomalum</i>							
<i>Cyprinella lutrensis</i>		67.8	59.95	22.31	7.92	11.71	0.7
<i>Cyprinella venusta</i>							
<i>Cyprinus carpio</i>		0.11					
<i>Hybognathus placitus</i>	9.96	2.75	2.88	15.7	0.78	13.02	60.5
<i>Macrhybopsis</i> larvae					0.16		
<i>Macrhybopsis australis</i>	0.24	0.88	6	6.2	0.31	0.86	0.79
<i>Macrhybopsis hyostoma</i>				4.55	2.64	2.83	2.18
<i>Macrhybopsis storeriana</i>							0.09
<i>Notemigonus crysoleucas</i>							
<i>Notropis atherinoides</i>		0.55	1.32	26.86	24.38	14.78	25.81
<i>Notropis bairdi</i>	79.23	14.84	17.51	19.01	39.75	6.58	2.9
<i>Notropis buchmanii</i>				3.72	2.02	10.39	0.02
<i>Notropis stramineus</i>						0.11	
<i>Phenacobius mirabilis</i>							
<i>Pimephales promelas</i>		0.66				0.07	
<i>Pimephales vigilax</i>					0.47	0.48	0.05
<i>Carpionodes carpio</i>					1.55	0.09	
<i>Ictiobus bubalus</i>		0.11			0.31	0.31	
<i>Ameiurus natalis</i>							
<i>Ameiurus melas</i>	0.24						
<i>Ictalurus furcatus</i>						0.86	6.44
<i>Ictalurus punctatus</i>		0.44	0.12	0.41	0.47	0.31	0.02
<i>Pylodictis olivaris</i>							
<i>Labidesthes sicculus</i>							
<i>Menidia audens</i>			2.64		1.09	5.24	0.05
<i>Fundulus notatus</i>							
<i>Fundulus grandis</i>							
<i>Fundulus zebrinus</i>	3.48	1.43	0.12				
<i>Gambusia affinis</i>	2.16	8.24	8.27		1.4	11.99	0.09
<i>Cyprinodon rubrofluviatilis</i>	4.68	0.33	0.12				

Appendix 3.2.2. Continued.

Scientific Name	Red River						I-35
	Hwy 6	Hwy 283	Hwy 183	Hwy 79	Hwy 81	Hwy 89	
<i>Lepomis</i> larvae						0.07	
<i>Lepomis auritus</i>						1.29	
<i>Lepomis cyanellus</i>		1.21	0.12			0.13	
<i>Lepomis humilis</i>		0.22			0.16	0.94	0.05
<i>Lepomis macrochirus</i>			0.12			0.07	
<i>Lepomis megalotis</i>		0.11				0.07	
<i>Lepomis microlophus</i>							
<i>Micropterus salmoides</i>						0.09	
<i>Pomoxis annularis</i>			0.24		3.57	0.9	0.07
<i>Percina caprodes</i>							
<i>Percina macrolepida</i>							0.02
<i>Etheostoma spectabile</i>							
<i>Aplodinotus grunniens</i>					0.16	0.53	0.11
Richness	7	16	16	9	20	29	19
Total N	833	910	834	242	644	4,561	4,413

Appendix 3.2.3. Continued.

Scientific Name	Salt Fork Red River Hwy 83	North Fork Red River Hwy 83	North Pease River Hwy 83
<i>Lepisosteus larvae</i>			
<i>Lepisosteus oculatus</i>			
<i>Lepisosteus osseus</i>			
<i>Lepisosteus platostomus</i>			
<i>Hiodon alosoides</i>			
<i>Dorosoma cepedianum</i>			
<i>Dorosoma petenense</i>			
<i>Campostoma anomalum</i>			
<i>Cyprinella lutrensis</i>	73.64	89.19	0.71
<i>Cyprinella venusta</i>			
<i>Cyprinus carpio</i>			
<i>Hybognathus placitus</i>	8.14		12.41
<i>Macrhybopsis larvae</i>			
<i>Macrhybopsis australis</i>			0.12
<i>Macrhybopsis hyostoma</i>			
<i>Macrhybopsis storeriana</i>			
<i>Notemigonus crysoleucas</i>			
<i>Notropis atherinoides</i>			
<i>Notropis bairdi</i>	0.39		27.78
<i>Notropis buchanani</i>			
<i>Notropis stramineus</i>	1.55	2.7	
<i>Phenacobius mirabilis</i>			
<i>Pimephales promelas</i>			
<i>Pimephales vigilax</i>	2.71	1.62	
<i>Carpionodes carpio</i>			
<i>Ictiobus bubalus</i>			
<i>Ameiurus natalis</i>			
<i>Ameiurus melas</i>			
<i>Ictalurus furcatus</i>			
<i>Ictalurus punctatus</i>	0.39		
<i>Pylodictis olivaris</i>			
<i>Labidesthes sicculus</i>			
<i>Menidia audens</i>			
<i>Fundulus notatus</i>			
<i>Fundulus grandis</i>			
<i>Fundulus zebrinus</i>	6.98	2.7	31.56
<i>Gambusia affinis</i>	4.65	0.54	0.35
<i>Cyprinodon</i>	0.78	0.54	27.07
<i>rubrofluvialis</i>			

Appendix 3.2.3. Continued.

Scientific Name	Salt Fork Red River Hwy 83	North Fork Red River Hwy 83	North Pease River Hwy 83
<i>Lepomis larvae</i>		0.54	
<i>Lepomis auritus</i>			
<i>Lepomis cyanellus</i>	0.78	0.54	
<i>Lepomis humilis</i>			
<i>Lepomis macrochirus</i>		0.54	
<i>Lepomis megalotis</i>		0.54	
<i>Lepomis microlophus</i>			
<i>Micropterus salmoides</i>		0.54	
<i>Pomoxis annularis</i>			
<i>Percina caprodes</i>			
<i>Percina macrolepida</i>			
<i>Etheostoma spectabile</i>			
<i>Aplodinotus grunniens</i>			
Richness	10	10	7
Total N	258	185	846

Appendix 3.2.4. Continued.

Scientific Name	Pease River			Adams Creek	China Creek	Gilberts Creek
	FM 104	Hwy 6	Hwy 283	TX 25	Flippin Rd	FM 369
<i>Lepisosteus</i> larvae						
<i>Lepisosteus oculatus</i>						
<i>Lepisosteus osseus</i>						
<i>Lepisosteus platostomus</i>						
<i>Hiodon alosoides</i>						
<i>Dorosoma cepedianum</i>		1.54	0.03			
<i>Dorosoma petenense</i>						
<i>Campostoma anomalum</i>						
<i>Cyprinella lutrensis</i>		1.68	18.54	58.28		0.81
<i>Cyprinella venusta</i>						
<i>Cyprinus carpio</i>					16.67	
<i>Hybognathus placitus</i>	0.39	25.84	8.21			
<i>Macrhybopsis</i> larvae						
<i>Macrhybopsis australis</i>	0.28	1.26	1.06			
<i>Macrhybopsis hyostoma</i>						
<i>Macrhybopsis storeriana</i>						
<i>Notemigonus crysoleucas</i>						
<i>Notropis atherinoides</i>						
<i>Notropis bairdi</i>	90.92	53.78	39.39			
<i>Notropis buchanani</i>						
<i>Notropis stramineus</i>						
<i>Phenacobius mirabilis</i>				0.23		
<i>Pimephales promelas</i>			2.06	1.23	16.67	
<i>Pimephales vigilax</i>			0.06	0.06		
<i>Carpionodes carpio</i>				0.12		
<i>Ictiobus bubalus</i>				0.18		
<i>Ameiurus natalis</i>						
<i>Ameiurus melas</i>						
<i>Ictalurus furcatus</i>						
<i>Ictalurus punctatus</i>			0.03	0.06		
<i>Pylodictis olivaris</i>						
<i>Labidesthes sicculus</i>						
<i>Menidia audens</i>			0.11			
<i>Fundulus notatus</i>						
<i>Fundulus grandis</i>						
<i>Fundulus zebrinus</i>	5.78	12.61	2.92			
<i>Gambusia affinis</i>	0.06	1.96	3.48	38.45		97.7
<i>Cyprinodon rubrofluviatilis</i>	2.59	1.26	23.86			

Appendix 3.2.4. Continued.

Scientific Name	Pease River			Adams Creek	China Creek	Gilberts Creek
	FM 104	Hwy 6	Hwy 283	TX 25	Flippin Rd	FM 369
<i>Lepomis larvae</i>						
<i>Lepomis auritus</i>						
<i>Lepomis cyanellus</i>			0.08	0.99		0.46
<i>Lepomis humilis</i>				0.06		1.04
<i>Lepomis macrochirus</i>		0.07			66.67	
<i>Lepomis megalotis</i>				0.29		
<i>Lepomis microlophus</i>						
<i>Micropterus salmoides</i>			0.17	0.06		
<i>Pomoxis annularis</i>						
<i>Percina caprodes</i>						
<i>Percina macrolepida</i>						
<i>Etheostoma spectabile</i>						
<i>Aplodinotus grunniens</i>						
Richness	6	9	14	12	3	4
Total N	1,818	1,428	3,592	1,714	6	869

Appendix 3.2.5. Continued.

Scientific Name	North Wichita River	Wichita River				
	Hwy 6	FM 1919	Hwy 283	Hwy 368	Hwy 11	Hwy 810
<i>Lepisosteus larvae</i>						0.05
<i>Lepisosteus oculatus</i>						
<i>Lepisosteus osseus</i>				0.14		
<i>Lepisosteus platostomus</i>						0.05
<i>Hiodon alosoides</i>						
<i>Dorosoma cepedianum</i>	0.39		0.85			0.14
<i>Dorosoma petenense</i>		0.3				0.19
<i>Campostoma anomalum</i>						
<i>Cyprinella lutrensis</i>	2.86	16.52	15.32	62.45	70.48	85.72
<i>Cyprinella venusta</i>						0.05
<i>Cyprinus carpio</i>	0.13		2.98		0.11	0.05
<i>Hybognathus placitus</i>	41.15	30.53		2.89		
<i>Macrhybopsis larvae</i>						
<i>Macrhybopsis australis</i>	9.64	14.47		0.14		0.19
<i>Macrhybopsis hyostoma</i>						0.1
<i>Macrhybopsis storeriana</i>						
<i>Notemigonus crysoleucas</i>						
<i>Notropis atherinoides</i>				0.14	0.34	2.99
<i>Notropis bairdi</i>	36.72	11.44		1.51	1.02	2.22
<i>Notropis buchanani</i>				7.43	6.67	2.12
<i>Notropis stramineus</i>						0.05
<i>Phenacobius mirabilis</i>				0.55	1.7	0.68
<i>Pimephales promelas</i>	0.13	0.15		2.61	0.11	0.05
<i>Pimephales vigilax</i>				19.12	14.14	3.33
<i>Carpionodes carpio</i>						
<i>Ictiobus bubalus</i>					0.11	
<i>Ameiurus natalis</i>	0.13					
<i>Ameiurus melas</i>			0.43			
<i>Ictalurus furcatus</i>						
<i>Ictalurus punctatus</i>				0.14	0.34	0.87
<i>Pylodictis olivaris</i>						
<i>Labidesthes sicculus</i>						
<i>Menidia audens</i>			61.7			1.06
<i>Fundulus notatus</i>						
<i>Fundulus grandis</i>				0.14		
<i>Fundulus zebrinus</i>	3.13	10.98				
<i>Gambusia affinis</i>	1.69	14.17	7.66	1.79	0.11	
<i>Cyprinodon</i>	3.65	1.29				
<i>rubrofluviatilis</i>						

Appendix 3.2.5. Continued.

Scientific Name	North Wichita River	Wichita River				
	Hwy 6	FM 1919	Hwy 283	Hwy 368	Hwy 11	Hwy 810
<i>Lepomis larvae</i>					0.34	
<i>Lepomis auritus</i>			1.28			
<i>Lepomis cyanellus</i>		0.08	4.26	0.14	3.05	0.1
<i>Lepomis humilis</i>	0.39		0.43	0.14	0.68	
<i>Lepomis macrochirus</i>			1.28		0.23	
<i>Lepomis megalotis</i>		0.08	0.85	0.41	0.57	
<i>Lepomis microlophus</i>			0.43			
<i>Micropterus salmoides</i>			2.55	0.14		
<i>Pomoxis annularis</i>				0.14		
<i>Percina caprodes</i>						
<i>Percina macrolepida</i>						
<i>Etheostoma spectabile</i>						
<i>Aplodinotus grunniens</i>						
Richness	12	11	13	18	15	18
Total N	768	1,320	235	727	884	2,073

Appendix 3.2.6. Continued.

Scientific Name	Little Wichita River		Barrel Springs Creek	Pecan Creek	Farmers Creek
	Hwy 287	FM 2332	Crain Rd	FM 2849	FM 103
<i>Lepisosteus</i> larvae					
<i>Lepisosteus oculatus</i>				1.48	0.32
<i>Lepisosteus osseus</i>	5.88				
<i>Lepisosteus platostomus</i>					
<i>Hiodon alosoides</i>					
<i>Dorosoma cepedianum</i>	2.94	9.51		11.33	4.17
<i>Dorosoma petenense</i>					0.96
<i>Campostoma anomalum</i>					
<i>Cyprinella lutrensis</i>		1.56	14.63	11.33	17.63
<i>Cyprinella venusta</i>					0.96
<i>Cyprinus carpio</i>	2.94			2.46	0.32
<i>Hybognathus placitus</i>					
<i>Macrhybopsis</i> larvae					
<i>Macrhybopsis australis</i>					
<i>Macrhybopsis hyostoma</i>					
<i>Macrhybopsis storeriana</i>					
<i>Notemigonus crysoleucas</i>				0.49	4.17
<i>Notropis atherinoides</i>		1.56			
<i>Notropis bairdi</i>					
<i>Notropis buchanani</i>		33.85			
<i>Notropis stramineus</i>					
<i>Phenacobius mirabilis</i>					6.09
<i>Pimephales promelas</i>					
<i>Pimephales vigilax</i>		0.26			
<i>Carpionodes carpio</i>		0.13			2.24
<i>Ictiobus bubalus</i>				3.45	0.96
<i>Ameiurus natalis</i>					
<i>Ameiurus melas</i>					
<i>Ictalurus furcatus</i>					2.56
<i>Ictalurus punctatus</i>	2.94		0.81		1.28
<i>Pylodictis olivaris</i>					0.32
<i>Labidesthes sicculus</i>					
<i>Menidia audens</i>		6.51			8.97
<i>Fundulus notatus</i>					
<i>Fundulus grandis</i>					
<i>Fundulus zebrinus</i>					
<i>Gambusia affinis</i>	5.88	6.38	78.05	48.28	27.88
<i>Cyprinodon rubrofluviatilis</i>					

Appendix 3.2.6. Continued.

Scientific Name	Little Wichita River		Barrel Springs Creek	Pecan Creek	Farmers Creek
	Hwy 287	FM 2332	Crain Rd	FM 2849	FM 103
<i>Lepomis larvae</i>		7.29		0.99	0.32
<i>Lepomis auritus</i>					
<i>Lepomis cyanellus</i>		0.78		3.94	3.53
<i>Lepomis humilis</i>	2.94	0.13			
<i>Lepomis macrochirus</i>	8.82	27.99	6.5	1.97	5.13
<i>Lepomis megalotis</i>		0.39		5.42	2.24
<i>Lepomis microlophus</i>					
<i>Micropterus salmoides</i>	2.94	0.52		8.87	1.92
<i>Pomoxis annularis</i>	64.71	2.21			0.96
<i>Percina caprodes</i>					0.64
<i>Percina macrolepida</i>					5.13
<i>Etheostoma spectabile</i>					
<i>Aplodinotus grunniens</i>		0.91			
Richness	9	15	4	11	23
Total N	34	768	123	203	312

Appendix 3.2.7. Continued.

Scientific Name	Cottonwood Creek	Mountain Creek		South Fish Creek
	FM 2953	Childress Rd	FM 373	CR 411
<i>Lepisosteus</i> larvae				
<i>Lepisosteus oculatus</i>				
<i>Lepisosteus osseus</i>				
<i>Lepisosteus platostomus</i>				
<i>Hiodon alosoides</i>				
<i>Dorosoma cepedianum</i>	9.09			
<i>Dorosoma petenense</i>				
<i>Campostoma anomalum</i>		7.85		26.71
<i>Cyprinella lutrensis</i>	53.33	34.03	22.06	
<i>Cyprinella venusta</i>	0.61			
<i>Cyprinus carpio</i>			0.48	
<i>Hybognathus placitus</i>			24.13	
<i>Macrhybopsis</i> larvae				
<i>Macrhybopsis australis</i>			0.48	
<i>Macrhybopsis hyostoma</i>			0.48	
<i>Macrhybopsis storeriana</i>				
<i>Notemigonus crysoleucas</i>				
<i>Notropis atherinoides</i>				
<i>Notropis bairdi</i>			5.87	
<i>Notropis buchmanii</i>				
<i>Notropis stramineus</i>	4.24	9.42		
<i>Phenacobius mirabilis</i>			0.16	
<i>Pimephales promelas</i>				
<i>Pimephales vigilax</i>				0.8
<i>Carpionotus carpio</i>				
<i>Ictiobus bubalus</i>			0.32	
<i>Ameiurus natalis</i>		1.57		0.2
<i>Ameiurus melas</i>				
<i>Ictalurus furcatus</i>				
<i>Ictalurus punctatus</i>				
<i>Pylodictis olivaris</i>				
<i>Labidesthes sicculus</i>				0.8
<i>Menidia audens</i>				
<i>Fundulus notatus</i>				26.1
<i>Fundulus grandis</i>				
<i>Fundulus zebrinus</i>		40.31	10.16	
<i>Gambusia affinis</i>	7.27		34.92	4.22
<i>Cyprinodon rubrofluviatilis</i>				

Appendix 3.2.7. Continued.

Scientific Name	Cottonwood Creek	Mountain Creek		South Fish Creek
	FM 2953	Childress Rd	FM 373	CR 411
<i>Lepomis</i> larvae				2.81
<i>Lepomis auritus</i>				
<i>Lepomis cyanellus</i>	16.36	6.28	0.63	2.81
<i>Lepomis humilis</i>				
<i>Lepomis macrochirus</i>	6.06			22.89
<i>Lepomis megalotis</i>	1.82	0.52	0.16	4.22
<i>Lepomis microlophus</i>				
<i>Micropterus salmoides</i>	1.21		0.16	1.81
<i>Pomoxis annularis</i>				
<i>Percina caprodes</i>				
<i>Percina macrolepida</i>				0.8
<i>Etheostoma spectabile</i>				5.82
<i>Aplodinotus grunniens</i>				
Richness	9	7	13	12
Total N	165	191	630	498

Literature Cited

- Chapleau, F., C.S. Findlay, and E. Szenasy. 1997. Impact of piscivorous fish introductions on fish species richness of small lakes in the Gatineau Park, Quebec. *Ecoscience* 4:259-268.
- Craig, C.A., K.A. Kollaus, K.P.K. Behen, and T.H. Bonner. 2016. Relationship among spring flow, habitats, and fishes within evolutionary refugia of the Edwards Plateau. *Ecosphere* 7.
- Cross, F.B., R.E. Moss, and O.T. Collins. 1985. Assessment of dewatering impact on stream fisheries in the Arkansas and Cimarron Rivers. *Mus. Nat. Hist., Univ. Kansas, Lawrence*.
- Dodds, W. K., K. Gido, M.R. Whiles, K.M. Fritz, and W.J. Matthews. 2004. Life on the edge: the ecology of Great Plains prairie streams. *BioScience*, 54(3), 205-216.
- Echelle, A.A., A.F. Echelle, and L.G. Hill. 1972. Interspecific interactions and limiting factors of abundance and distribution in the Red River Pupfish, *Cyprinodon rubrofluviatilis*. *The American Midland Naturalist* 88:109-130.
- Gido, K.B., J.F. Schaefer, K. Work, P.W. Lienesch, E. Marsh-Matthews, and W.J. Matthews. 1999. Effects of Red Shiner (*Cyprinella lutrensis*) on Red River Pupfish (*Cyprinodon rubrofluviatilis*). *The Southwestern Naturalist* 44:287-295.
- Hargrave, C.W. and C.M. Taylor. 2010. Spatial and temporal variation in fishes of the upper Red River drainage (Oklahoma-Texas). *The Southwestern Naturalist* 55:149-159.
- Higgins, C.L. and G.R. Wilde. 2005. The role of salinity in structuring fish assemblages in a prairie stream system. *Hydrobiologia* 549:197-203.
- Hoagstrom, C.W. and C.R. Berry. 2008. Morphological diversity among fishes in a Great Plains river drainage. *Hydrobiologia* 596:367-386.
- Hoagstrom, C.W., J.E. Brooks, and S.R. Davenport. 2011. A large-scale conservation perspective considering endemic fishes of the North American plains. *Biological Conservation* 144: 21-34.
- Krebs, C.J., 1999. *Ecological Methodology*. Addison Wesley Longman, New York, pp. 1-496.
- Jackson, D.A. and H.H. Harvey. 1989. Biogeographic associations in fish assemblages: local vs. regional processes. *Ecology* 70:1472-1485.

- Jackson, D.A., K.M. Somers, and H.H. Harvey. 1992. Null models and fish communities: evidence of nonrandom patterns. *American Naturalist* 139:930-943.
- Matthews, W.J. and J.T. Styron, Jr. 1981. Tolerance of headwater vs. mainstream fishes for abrupt physicochemical changes. *The American Midland Naturalist* 105:149-158.
- Matthews, W.J. 1988. North American prairie streams as systems of ecological study. *Journal of North American Benthological Society* 7:387-409. Brown, J.H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124:255-279.
- Myrick, C.A. and J.J. Cech, Jr. 2000. Temperature influences on California rainbow trout physiological performance. *Fish Physiology and Biochemistry* 22:245-254.
- Ostrand K. and G.R. Wilde. 2002. Season and spatial variation in a prairie stream-fish assemblage. *Ecology of Freshwater Fish* 11:137-149.
- Perkin, J.S., C.S. Williams, and T.H. Bonner. 2009. Aspects of Chub Shiner *Notropis potteri* life history with comments on native distribution and conservation status. *American Midland Naturalist* 162:276-288.
- Perkin, J.S. and K.B. Gido. 2011. Feature: stream fragmentation thresholds for a reproductive guild of great plains fishes. *Fisheries* 36:37-41.
- Perkin, J.S., K.B. Gido, K.H. Costigan, M.D. Daniels, E.R. Johnson. 2015. Fragmentation and drying ratchet down Great Plains stream fish diversity. *Aquatic Conservation Marine and Freshwater Ecosystems* 25:639-655.
- Perkin, J.S., K.B. Gido, J.A. Falke, K.D. Fausch, H. Crockett, E.R. Johnson, and J. Sanderson. 2017. Groundwater declines are linked to changes in Great Plains stream fish assemblages. *PNAS* 114:7373-7378.
- Quist, M.C., M.R. Bower, W.A. Hubert, and F.J. Rahel. 2006. Spatial patterns of fish assemblage structure in a tributary system of the upper Colorado River basin. *Journal of Freshwater Ecology* 21:673-680.
- Rabeni, C.F., J. Lyons, N. Mercado-Silva, and J.T. Peterson. 2009. Warmwater fish in wadeable streams. In. S.A. Bonar, W.A. Hubert, D.W. Willis (eds) *Standard Methods for Sampling North American Freshwater Fishes*. American Fisheries Society, Bethesda.
- Renkonen, O. 1938. Statisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. *Ann. Zool. Soc. Bot. Fenn. Vanamo* 6:1-231.

- Rought. B.G. 1984. The southwestern salinity situation: the Rockies to the Mississippi River. In: R.H. French (*ed*) Salinity in Watercourses and Reservoirs. Butterworth Publishers, Boston.
- Runyan, D. 2007. Fish assemblage changes in the Gulf Slope drainages; an historical perspective and occurrence and distribution of ag-0 fishes in the Rio Grande. M.S. Thesis. Texas State University, San Marcos.
- Ruppel D.S., V.A. Sotola, O.A. Gurbuz, N.H. Martin, and T.H. Bonner. 2017. Endangered species, research projects for the Prairie Chub. Texas State University, San Marcos.
- Scanes, C.M. 2016. Fish community and habitat assessments within an urbanized spring complex of the Edwards Plateau. M.S. Thesis. Texas State University, San Marcos.
- Smith, C.L. and C.R. Powell. 1971. The summer fish communities of Brier Creek, Marshall County, Oklahoma. American Museum Novitates 2458:1-30.
- Sotola, V.A., D.S. Ruppel, T.H. Bonner, C.C. Nice, and N. Martin. 2019. Asymmetric introgression between fishes in the Red River basin of Texas is associated with variation in water quality. Ecology and Evolution 2019:1-13.
- Starks, T.A., A.W. Rodger, D. King, and M. Skoog. 2018. Assessing temporal shifts in lotic fish community structure in the upper Red River basin, Oklahoma. Journal of Freshwater Ecology 1:129-138.
- Taylor, C.M., M.R. Winston, and W.J. Matthews. 1993. Fish species-environment and abundance relationships in a Great Plains river system. Ecography 16:16-23.
- Tonn, W.M. 1990. Climate change and fish communities: a conceptual framework. Transaction of the American Fisheries Society 119:337-352.
- U.S. Fish and Wildlife Service. 1998. Endangered and threatened wildlife and plants; final rule to list the Arkansas River basin population of the Arkansas River Shiner (*Notropis girardi*) as threatened. Federal Register 63 FR 64772 64799, Arlington, TX.
- U.S. Fish and Wildlife Service. 2014. Determination of Endangered Status for the Sharpnose Shiner and Smalleye Shiner. Federal Register 79 FR 45273 45286, Arlington, TX.
- U.S. Geological Survey. 2011. Chloride control and monitoring program in the Wichita River Basin, Texas, 1996-2009. Austin, TX.

- Wilde, G.R., R.R. Weller, C.D. Smith, and R. Jimenez, Jr. 1996. Review and synthesis of existing fish collection records for the upper Red River basin upstream from Lake Texoma, Lubbock, Texas.
- Winemiller K.O. and K.A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *The Canadian Journal of Fisheries and Aquatic Science* 49:2196-2218.
- Winston, M.R., C.M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. *Trans. Amer. Fish. Soc.* 120:98-105.
- Worthington T.A., A.A. Echelle, J.S. Perkin, R. Mollenhauer, N. Farless, J.J. Dyer, D. Logue, and S.K. Brewer. 2017. The emblematic minnows of the North American Great Plains: a synthesis of threats and conservation opportunities. *Fish and Fisheries* 19:271-307.
- Wurbs, R.A. 2002. Natural salt pollution control in the Southwest. *Journal of American Water Works Association* 94:58-67.

IV. DISTRIBUTION AND HABITAT ASSOCIATIONS OF FRESHWATER MUSSELS IN THE MAINSTEM COLORADO RIVER, TEXAS

Abstract

Quantification of freshwater mussel communities have been lacking compared to the quantification of other aquatic organisms, and most studies focus survey efforts over geographically small area. Within the Colorado River drainage of Texas, previous efforts to quantify freshwater mussel communities were focused on tributary reaches of the Edwards Plateau. Little information is available for the mainstem Colorado River. The purpose of this study was to conduct a longitudinal survey of the mainstem Colorado River in order to provide information to describe freshwater mussel communities and patterns associated with their distributions. Sampling was conducted over a one-year period and sites were grouped by similar surface geology. Patterns in mussel distribution were more related to georegion than to mesohabitats and substrate types. Therefore, factors, influenced by surface geology such as stream hydrology and water quality, appear to be influential in describing freshwater mussel distributions. This study provides baseline information regarding the natural variations of the Colorado River and give insight to resource managers how anthropogenic alterations could influence these organisms.

Introduction

USA has the highest diversity of freshwater mussels in the world with nearly 300 species. However, up to 65% of the species are thought to be extinct, endangered, or threatened (Haag and Williams 2014). Freshwaters of Texas support 52 mussel species with 31% (N = 16) of the mussels listed as Species of Greatest Conservation Needs

(SGCN) by Texas Parks and Wildlife, of which two (Ouachita Rock Pocketbook *Arkansia wheeleri* and Texas Hornshell *Popenaias popeii*) are listed as endangered and 12 are under consideration for listing by USFWS (Table 4.1; USFWS 2011b, USFWS 2016). In the central Texas province, which includes the Nueces-Frio, Guadalupe-San Antonio, Colorado, and Brazos basins, six endemic species are known to occur, four of which are pending review by the U.S. Fish and Wildlife Service (USFWS) for federal listing (USFWS 2011; Howells 2014). Three of the four candidate species (Texas Fatmucket *Lampsilis bracteata*, Texas Pimpleback *Cyclonaias petrina*, and Texas Fawnsfoot *Truncilla macrodon*) are found in the Colorado River drainage among different water bodies and habitats (Howells 2014). Several threats are thought to be associated with the decline of these taxa throughout Texas such as stream fragmentation, flow reduction, invasive species, habitat loss, and overharvest (Winemiller et al 2010).

Historically, 31 species of freshwater mussels occur in the Colorado River drainage, inhabit benthos of river water bodies and reservoirs, and associate among a range of current velocities and substrate types (Winemiller et al 2010, USFWS 2011b, Howells 2014). However, within the Colorado River basin, contemporary information about mussel communities, species, and distribution is limited and most recent studies on the unionid assemblages have focused on tributaries with less emphasis on the mainstem portions of these systems (Burlakova & Karatayev 2010; Randklev et al. 2017). Burlakova and Karatayev (2010) surveyed several sites on the mainstem Colorado River, but the assessments were limited to a few locations in close proximity to public access sites.

It is important to document the distribution and habitat association of freshwater mussel among the different regions within Colorado River basin to assist ongoing efforts by the U.S. Fish and Wildlife Service (USFWS) to quantify resiliency, representation, and redundancy for the three USFWS candidate species as well as other mussel species. The purpose of this study was to address gaps in information on the distribution of freshwater mussels in the Colorado River along with gathering habitat information among the different water bodies where they were detected. Freshwater mussel communities were assessed by regions that had similar surface geologies along the mainstem Colorado River. I used the georegion approach rather than ecoregion approach because ecoregions were delineated based upon terrestrial fauna which did not provide an appropriate representation of stream hydrology (e.g., flow, water permanency, gradient), substrate composition (e.g., sand, bedrock) and water quality (i.e., specific conductance) (Pfaff 2019). There were two primary objectives of this study. First objective was to quantify the distribution, occurrences, and abundances of freshwater mussels among the mainstem Colorado River, Texas by georegion. Second objective was to quantify habitat associations among all georegions of the Colorado River, Texas. Predictions were that mussel communities and species occurrences are likely not homogenously distributed within the basin because of the amount of heterogeneity in the basin geology and stream types (Strayer 1983, 1999, Baldio et al 2004).

Methods

Study Area

The Colorado River is the longest river in Texas that is completely confined within the state's border. The headwaters originate in Dawson County, Texas, of west Texas, and flows southeast through the Edwards Plateau, where it receives large contributions from several spring-fed rivers, such as the San Saba, Pedernales, and Llano Rivers. The river then transitions to a large alluvial system, as it flows through the Gulf Coastal Plain, eventually draining into Matagorda Bay (Dahm et al. 2005). Several mainstem reservoirs occur on the Colorado, most notably the Highland Lakes, a series of seven reservoirs (Lake Buchanan, Inks Lake, Lake LBJ, Lake Marble Falls, Lake Travis, and Lake Austin).

Mussel communities within the Colorado River basin were assessed by georegion. Georegions were delineated based on surface geology (US Geological Survey 2015). Perennial flows of the Colorado River mainstem begin on the western edge of the Llano Estacado. In a general southeast direction, the perennial flowing portion of the Colorado River main stem and tributaries bisects Carboniferous, Permian, and Triassic strata layers (Paleozoic Georegion), forming low gradient prairie streams with predominately silt substrates, although sandstones and limestones form a limited amount of rocky outcroppings and gravel to boulder substrates (Table 1). Streams common in this strata layer tend to be dominated by shallow runs, braided channels, and highly turbid, and of moderate to high salinity. The Colorado River then enters the Llano Uplift area with Precambrian and Cambrian strata (Llano Uplift Georegion; Latitude: 31.090572, Longitude: -98.463806; upstream from Colorado Bend State Park, San Saba County)

consisting primarily of granite but interspersed with some limestones, dolomites, and sandstones. The river and tributaries have less silt substrate and more gravel to boulder substrates and diversity in mesohabitats (e.g., run, riffle, pools), and are also characterized by their higher gradient, lower turbidity, and less saline waters. From the west, the Edwards Plateau with its Cretaceous limestone and karst aquifers (Edwards Georegion) contribute substantial spring flows to the Paleozoic Georegion (via Concho River) and Llano Uplift Georegion (via San Saba River, Llano River, and Pedernales River). From the Llano Uplift, the Colorado River enters another section of the Edwards Plateau and the Balcones Escarpment (Balcones Georegion; Lake Travis area, Travis County) before bisecting the gulf coastal plains of Cenozoic deposits (Cenozoic Georegion; Latitude: 30.200572, Longitude: -97.525748; upstream from Webberville Park, Travis County). Cenozoic deposits and stream substrates of the Cenozoic Georegion are dominated by sands and silts, but various sandstone strata layers occur in the lower Colorado River main stem.

Survey Design

To delineate survey sites within each georegion, I used aerial imagery to target areas with heterogeneous habitats. I chose sites within sections of each river with a mosaic of habitat types. Habitat types were divided into mesohabitats, which included riffles, runs, pools, and backwaters. Dividing habitat types with a mesohabitat scale is useful for investigating habitat associations because they can be easily identified (Frissell et al. 1986). Moreover, due to differences in mussel abundance between bank and mid-channel habitats observed in previous studies (Brown & Banks 2001; Brim Box et al.

2002), I partitioned runs and pools into sub-mesohabitats to increase resolution and identify potential differences within these mesohabitats. As a result, I separated each site by six potential mesohabitat types: run bank, run mid-channel, pool bank, pool mid-channel, riffle, and backwater.

Within each mesohabitat type, I used qualitative surveys via timed visual and tactile search methods. A qualitative survey approach is an efficient search method to establish a list of taxa, as well as increase the detection probability of rare species (Vaughn et al. 1997; Strayer and Smith 2003). At each site, I surveyed one of each mesohabitat type. If a mesohabitat type was absent within a site, I surveyed additional mesohabitat types present until a total of 6 mesohabitats were searched at each site. For each mesohabitat, areas with a maximum of 300 m² were marked off and initially surveyed for one person-hour (p-h). If no live mussels were detected, that mesohabitat was deemed completed. If live mussels were collected, I conducted a second p-h. If I collected a new species within the second p-h, a third p-h was conducted. I conducted additional one p-h searches until no new species were collected (Metcalf-Smith et al. 2000). Once sampling efforts were complete, all native freshwater mussels were identified and enumerated before being returned to the area of capture. I used retained the old nomenclature Smooth Pimpleback *Cyclonaias houstonensis* although Johnson et al. (2018) recently synonymized them with Pimpleback *C. pustulosa*.

Habitat Measurements

To avoid variation in flow parameters (i.e., depth, current velocity, and shear stress) among sampling dates, surveys were conducted under base flow conditions set by Texas Department of Environmental Quality (https://www.tceq.texas.gov/permitting/water_rights/wr_technical-resources/eflows/colorado-lavaca-bbasc-bbest). At each mesohabitat type, I estimated percent substrate composition based on the standard Wentworth particle size scale (Wentworth 1922). A Hach flowmeter and top-set wading rod was used to measure average depth (ft), mean water column velocity (ft/s), and benthic velocity (ft/s) at one point near the center of each mesohabitat. I used FST Hemispheres (Statzner et al. 1991) to quantify shear stress at one point within each mesohabitat. To measure substrate compaction (kg/cm^2), I took three readings from random points within the mesohabitat using a Humboldt soil penetrometer (Johnson & Brown 2000). Additionally, I recorded the percent coverage of other habitat parameters such as large woody debris, aquatic vegetation, and undercut banks. A HydroTech multiprobe water quality sonde was used to measure water quality parameters including temperature ($^{\circ}\text{C}$), dissolved oxygen (mg/L , % saturation), pH, specific conductance ($\mu\text{S}/\text{cm}$), and turbidity (NTU).

Data Analysis

Principal component analysis (PCA; Canoco 4.5, Microcomputer Power 2002) was used to assess linear combinations of habitat parameters. Mesohabitats were coded as dummy variables and quantitative data (e.g., current velocity column, current velocity bottom, depth) were z-transformed. Parameters with diel fluctuations (e.g., water

temperature) were omitted from the analysis. The resulting PCA loadings were plotted and grouped to assess habitat variability within and among basins and georegions. Canonical correspondence analysis (CCA; Canoco 4.5) was used to assess patterns in habitat associations among Colorado River mussel community independent of georegion. For univariate assessments, mesohabitat and species-substrate associations were determined from relative abundance by species using the ACFOR scale (Stiers et al. 2011): Abundant (75 – 100%), Common (50 – 74%), Frequent (25 – 49%), Occasional (5 – 24%), and Rare (>0 – 4%). Weighted means and standard deviations were calculated from relative abundance of a species by current velocity (mid-column, bottom), FST hemisphere, mean sheer stress, depth, and penetrometer among habitats observed. Visual comparisons of percent changes in relative abundance was calculated for mussels before and after Hurricane Harvey flood in the Cenozoic Georegion.

Results

Within the Colorado River basin, 527 mesohabitats from 84 sites consisted of riffle, run, pool, and backwater habitats with predominately silt, sand, gravel, cobble, boulder, and bedrock substrates (Table 4.2). Minimum water temperature was 22.3°C during surveys (Table 4.3). Principal component axis I explained 16% of the habitat variation and described a substrate and current velocity gradient (Figure 4.1). Principal component axis II explained 7% of the habitat variation and described primarily vegetation and specific conductance gradient. From upstream to downstream, central tendencies of mesohabitat scores within Paleozoic Georegion were negatively associated with PC I (i.e., slower current velocities, greater amounts of silt substrate) and positively

associated with PC II (i.e., greater amounts of vegetation and higher specific conductance). Central tendency of mesohabitat scores within Llano Uplift Georegion was negatively associated with PC I. Central tendencies of mesohabitat scores within Balcones Georegion was positively associated with PC I (i.e., swifter current velocities, greater FST values) and negatively associated with PC II (i.e., lower amounts of vegetation, lower specific conductance, greater amounts of sand substrates). Central tendency of mesohabitat scores within Cenozoic Georegion was negatively associated with PC II.

Sixteen species and 2,819 individuals were taken from the Colorado River (Table 4.4) with mussels occurring in 25 to 87% of the habitats sampled by georegion (Table 4.5). Abundances and occurrences of mussels differed among georegions. Paleozoic Georegion consisted of 10 species with Fragile Papershell (24% in relative abundance), Southern Mapleleaf (22%), and Tampico Pearlymussel (16%) being the most abundant, whereas Southern Mapleleaf (9.8% occurrence among habitats sampled), Yellow Sandshell (9.0%), Bleufer (6.8%), and Paper Pondshell (6.8%) were most widespread. Llano Uplift Georegion consisted of 11 species with Texas Pimpleback (37% in relative abundance), Pistolgrip (21%), and Southern Mapleleaf (6.5%) were most abundant, whereas Texas Pimpleback (7.1% occurrence among habitats sampled), Tampico Pearlymussel (6.2%), and Southern Mapleleaf (6.2%) were most widespread. Balcones Georegion consisted of seven species with Yellow Sandshell (33% in relative abundance), Giant Floater (33%), and Paper Pondshell (15%) were most abundant, whereas Tampico Pearlymussel (5.6% occurrence among habitats sampled) and Yellow Sandshell (5.6%) were most widespread. Cenozoic Georegion consisted of 14 species

with Threeridge (58% in relative abundance), Smooth Pimpleback (17%), and Yellow Sandshell (17%) were most abundant, whereas Threeridge (18% occurrence among habitats sampled), Yellow Sandshell (18%), and Smooth Pimpleback (15%) were most widespread.

Habitats explained 41% ($P < 0.01$) of the mussel community variation, partitioned among regional factors (i.e., georegion; 9%, $P < 0.01$) and local factors (i.e., habitats parameters; 22 %, $P < 0.01$) (Figure 4.2). Physical parameters and mesohabitats with strong loadings were Llano Uplift (habitat bi-plot score: 0.65), Paleozoic (0.54), cobble (0.45), run edge (-0.29), sand (-0.38), and Cenozoic (-0.97) on CCA axis I. Mussels with strong positive associations on CCA axis I (i.e., Llano Uplift georegion, Paleozoic georegion, cobble substrates) were Pistolgrip (species bio-plot score: 1.5), Texas Fatmucket (1.30), Southern Mapleleaf (1.18), and Paper Pondshell (0.92). Mussels with strong negative associations on CCA axis I (i.e., run edge habitats, sand substrates, Cenozoic georegion) were Pondhorn (-0.83), Texas Fawnsfoot (-0.82), and Threeridge (-0.72). Physical parameters and mesohabitats with strong loadings were Llano Uplift (0.53), FST (0.51), minimum bottom shear stress (0.48), Paleozoic (-0.50), and silt (-0.56) on CCA axis II. Mussels with strong positive associations on CCA axis II (i.e., Llano Uplift georegion, FST, greater minimum bottom shear stress) were Pistolgrip (1.48) and Texas Pimpleback (1.01). Mussels with strong negative associations on CCA axis II (i.e., Paleozoic georegion, silt substrates) were Lilliput (-1.32), Giant Floater (-1.27), and Pondhorn (-1.20).

Univariate estimates across georegions

Weighted mean (± 1 SD) habitat summaries were calculated for species within mussel communities across georegions. Texas Pimpleback and Pistolgrip had the swiftest mean current velocities (column and bottom), whereas Texas Lilliput, Texas Fatmucket, and Pondhorn had the lowest mean current velocities (Figure 4.3). Associated with current velocities (column and bottom), Texas Pimpleback and Pistolgrip had the greatest mean FST hemisphere and mean shear stress, whereas Texas Fatmucket, Pondhorn, and Lilliput had the lowest mean FST hemisphere and mean shear stress (Figure 4.4). Tampico Pearlymussel, Texas Lilliput, and Smooth Pimpleback had the deepest mean depths, whereas Texas Pimpleback, Texas Fatmucket, and Pistolgrip had the shallowest mean depths (Figure 4.5). Fragile Papershell, Pistolgrip, Paper Pondshell had the greater mean penetrometer estimate (i.e., greater substrate compactions), whereas Lilliput, Texas Lilliput, and Texas Fatmucket had the least mean penetrometer estimate (i.e., lesser substrate compaction).

Relative abundances of mussels ranged from absent to abundant among all mesohabitats (Table 4.6). Most species were taken pool-edge mesohabitats ($N_{\text{species}} = 15$), ranging in relative abundance scale from rare to abundant, and fewest species ($N_{\text{species}} = 8$) were taken from riffle habitats, ranging in relative abundance scale from rare to occasional. Majority of species (75%) were taken from mesohabitats consisting of all substrate types (Table 4.7). Mean percent silt was occasional to common for all species. Mean percent sand and gravel were rare to frequent for 88% of the species. Mean percent clay, cobble, boulder, and bedrock were rare to common for 81% of the species.

Cenozoic Georegion: pre and post hurricane community comparisons

Flows associated with Hurricane Harvey in August 2017 were estimated to exceed 4,600 cms (USGS stations 08161000) in the lower Colorado River. Previous to the high flow event, 179 mesohabitats were sampled (Table 4.8). The pre-hurricane community consisted of 14 species with Threeridge (59% in relative abundance), Yellow Sandshell (17%), and Pimpleback (16%) being most abundant. After high flows subsided, 66 mesohabitats were sampled. The post hurricane community consisted of 11 species with Threeridge (53%), Pimpleback (21%), and Yellow Sandshell (17%) being most abundant. Changes in relative abundances between pre- and post-hurricane ranged from - 5.9% for Threeridge to 4.7% for Pimpleback. Density estimates were 10.4 mussels per habitat pre-hurricane and 6.7 mussels per habitat post hurricane.

Discussion

Mussel communities were heterogeneously distributed among georegions within the Colorado River basin with a general increase in the number of mussel species from upstream to downstream, excluding the Balcones Georegion. Heterogeneity was attributed to species (i.e., Texas Fatmucket, Texas Lilliput, Texas Fawnsfoot, and Pondhorn) found only in one georegion, whereas others (i.e., Tampico Pearlymussel, Giant Floater, and Paper Pondshell) were found in all four georegions. Heterogeneity was also attributed to differences in species abundances. Most abundant species were Fragile Papershell, Southern Mapleleaf, and Tampico Pearlymussel (62% combined relative abundance) in Paleozoic Georegion, Texas Pimpleback, Pistolgrip, and Fragile Papershell (73%) in Llano Uplift Georegion, Yellow Sandshell and Giant Floater (66%) in Balcones Georegion, and Threeridge and Pimpleback (75%) in Cenozoic Georegion.

Similar patterns in freshwater mussel richness and abundances are linked to surface geology in other systems (Strayer 1983; McRae et al. 2004; Chambers and Woolnough 2018). Proximate processes of surface geology influencing mussel richness and abundances include stream hydrology, substrate composition, and water quality (McRae et al. 2004). An additional factor thought to be influential in mussel distributions is the mussel's fish host for glochidia development (Vaughn 1997; Wendell et al. 1998). Similar to mussel communities reported herein, fishes within the Colorado River basin (Pfaff 2019) and elsewhere in Texas (Hubbs 1957) are heterogeneously distributed among surface geology related to stream hydrology, substrate composition, and water quality.

Stream hydrology (e.g., flow, water permanency, gradient), substrate composition (e.g., sand, bedrock) and water quality (i.e., specific conductance) generally differed among georegions predictably (e.g., downstream increase in flows) but also uniquely (e.g., stream gradient, substrate sizes) attributed to surface geology. From upstream to downstream, low gradient, clay and sand substrates of Paleozoic strata with low volume and often saline alluvium aquifer contributions transition into higher gradient, larger substrates of the Llano Uplift and Balcones georegions, along with contributions from the Edwards Georegion, with high volume and fresh karst aquifer contributions, and transition back to a low gradient, small to large substrates in the Cenozoic Georegion with voluminous flows from alluvium aquifers and from flows upstream. Water permanency, flow magnitude and variability, and water quality (e.g., specific conductance) are among a suite factors that are related to mussel occurrences and abundances. Mussels differ in their ability to withstand desiccation (Mitchell et al. 2018),

which might influence occurrence and abundance of some species over others within georegions of lower water permanency. For example, Texas Pimpleback survived longer in desiccation experiments than Pimpleback and Threeridge (Mitchell et al. 2018), which corresponds with Texas Pimpleback greater abundance in Llano Uplift Georegion with lower water permanency (e.g., 1.4% zero flow days), and Pimpleback and Threeridge having greater abundance in Cenozoic Georegion with greater water permanency (e.g., 0% zero flow days). Flow magnitude and variability (i.e., flashiness) can destabilize substrate resulting in the dislodgment of some mussels (Arbuckle and Downing 2002, Vaughn and Taylor 1999). Water quality, specifically alkalinity (Neary and Leach 1992; Hincks and Mackie 1997) and salinity (Cvancara 1970), are known to influence distributions of mussels, although stressors caused by other water quality parameters such as dissolved oxygen, suspended solids, and nitrogenous compounds (Haney et al. 2018) could also play a role in distributional patterns.

Most mussel species were detected among all available mesohabitat types with exception of only a few species with low sample sizes (i.e., Lilliput, Texas Fatmucket, and Pondhorn) found only in one mesohabitats each. Likewise, most species were detected among a variety of different substrate types. Among five mussels (i.e. Tampico Pearlymussel, Fragile Papershell, Giant Floater, Southern Mapleleaf, Paper Pondshell) among all the georegions, ubiquitously distributed mussels were found more often in pool habitats with silt substrates, but it is likely these species are probably mesohabitat and substrate generalists. For example, Southern Mapleleaf highest abundance (5%) was reported from backwater habitats with sand and silt substrates in a tributary of the Brazos River (Randklev et al. 2014) and showed an association to run habitats with moderately

high current velocities in the Neches River (Glen 2017). Mussel associations with larger substrate sizes (i.e., gravel, cobble, boulder, bedrock) are linked to flow refuges (i.e., resist downstream displacement, Strayer 1999) more so than a preference for a particular habitat type (e.g., riffle habitats) correlating with the substrate sizes. Based on observations during field surveys in this study, mussels tend to be associated with habitats nearby large boulders, either within (quantified herein) or outside (not quantified herein) of delineated mesohabitats, especially in the lower reach of the Colorado River (Cenozoic Georegion). Post flood (i.e. Hurricane Harvey) site analysis from a companion study (A. Sotola, Texas State University, unpublished data) identified that areas with larger substrates (i.e., boulder and bedrock) maintained 20% of the original mussel community in total numbers and 67% of the species. Additionally, post flood surveys taken from European streams suggest larger substrates protect downstream displacement of mussels and the remaining population of mussels provides a source for recolonization (Hastie et al. 2001). Observations within this study and among other studies (Hastie et al. 2001; V.A. Sotola unpublished) suggest that the mechanism of mussel associations with larger substrate sizes is related to functionality of substrates as flow refuge, although additional work is needed to clearly understand the linkages.

Fourteen of our local factors explained 22% of the variation in the mussel community, whereas the four georegions explained 8%. However, the local factors are influenced by the georegion in a hierarchical fashion which is evident by the georegions having a higher loading on CCA axis I and II. Pfaff (2019) found that surface geology was a more powerful predictor of fish community structure rather than local habitat variables or other special delineations commonly used in aquatic community assessment

(e.g., stream order). Other studies have found similar patterns related to surface geology (macroinvertebrates; Neff and Jackson 2011, mussels; Strayer 1983; McRae et al. 2004; Chambers and Woolnough 2018, and fish; Hubbs 1957). However, understanding the mechanisms that drive heterogeneity among georegion are still elusive. Calculation of habitat associations independent of georegion showed patterns for a few species, but overall, most mussels were distributed among a variety of different habitat and substrate types. Therefore, future efforts could focus on determining the mechanisms of a georegion that influences the occurrence and abundances of mussels, along with additional considerations on fish-host relationships (Vaughn 1997; Haag and Warren 1998; Wendell et al. 1998), interspecific competition (Bronmark and Malmqvist 1982), or physiologic tolerances (Haney et al. 2018).

Benefits of the georegion approach, despite not clearly understanding the mechanisms, can be used in the process of applying the 3Rs concept through identification of the redundancy and resiliency of a species using methods purposed by Faucheux et al (2019). Species may occupy habitats that are less suitable to long term persistence of the species because reproduction does not offset mortality rate, but the population is maintained by a nearby source population (Pulliam 1988). The georegion approach provides information about natural tendency for a species among georegion and illustrates that mussel species are not equally abundant throughout all georegions, which can identify georegions as population sources and population sinks. Population sources would be more meaningful when quantifying the number of redundant populations and the species ability to withstand or rebound from stochastic events (i.e., resiliency), whereas population sinks could unnecessarily inflate the number of redundant

populations and deflate estimates of resiliency. Currently, concern for the management of freshwater mussels has increased because it is recognized that 65% of North American species are threatened (Strayer et al. 2004; Haag and Williams 2014). However, understanding levels of imperilment of these organisms has been challenging given the assessment of community structures has been at a small scale (Burlakova and Karatayev 2010; Randklev et al. 2017). Moving forward with the georegion approach will provide a more holistic management application by understanding large scale mussel distribution patterns influence by surface geology and habitat associations. Baseline information will provide information regarding the natural variations of the systems and give insight to resource managers how anthropogenic alterations are influencing these organisms.

Table 4.1. Surface geology, groundwater sources, stream gradient, and water quality and quantity estimates among georegions of the Colorado River basin.

	Georegions				
	Cenozoic	Balcones	Llano Uplift	Edwards	Paleozoic
Strata layer	Paleogene, Neogene, Pleistocene	Cretaceous	Pre-Cambrian, Cambrian	Cretaceous	Carboniferous, Permian, Triassic
Surface substrates	clay, silt, sand, sandstone	limestone, chalk, marl, dolomite, mudstone, clay, alluvial shale	granite, gneiss, schist, limestone, colluvium, dolomite	limestone, colluvium, dolomite, chalk, marl, mudstone	clay, sand, shale, sandstone, siltstone, mudstone, limestone, dolomite, gypsum, colluvium
Ecoregions	Texas Blackland Prairie, Central Texas Plains, Western Gulf Coast Plains	Balcones Canyonlands, Texas Blackland Prairie	Llano Uplift, Edwards Plateau Woodland	Semiarid Edwards Plateau, Edwards Plateau Woodland	Southwest Tablelands, Central Great Plains, Cross Timbers
Aquifer type	alluvium	karst	karst	karst	alluvium
Aquifers	Carrizo-Wilcox, Gulf Coast	Edwards-Trinity	Marble Falls, Ellenburger-San Saba	Edwards-Trinity	Ogallala, Dockum, Lipan
Groundwater type	fresh	fresh	fresh, some brackish	fresh, some brackish	fresh to saline
Dominant substrates	silt and sand with some boulders and bedrock	silt to gravel in mainstem, limestone in tributaries	silt to boulder	gravel to bedrock	sand and silt
Mean stream gradient (m/km)	0.27	1	1.6	1.7	0.56

Table 4.1. Continued

	Georegions				
	Cenozoic	Balcones	Llano Uplift	Edwards	Paleozoic
<u>Water quantity:</u>					
N of stations	4	5	3	8	9
Average flow (cfs)	2,297	366	274	59	103
Coefficient of variation	2.1	4.6	5.5	7.5	5.6
% zero flow days	0	19.9	1.4	15.9	4.7
% of stations with zero flow days	0	20	33	44	56
Base flow index	0.23	0.04	0.16	0.23	0.08
<u>Water quality</u>					
Mean dissolved oxygen (mg/l)	8.5	8.7	8.3	7.9	9
1 SD	1.9	2.27	2.33	1.98	3.55
Median pH	8.1	8	8.2	8	8
range of pH	2.9	2.78	3.25	2.4	3.89
Mean specific conductance (µS/cm)	588	556	653	741	4,030
1 SD	199.7	111.4	348.9	390.8	4,369.80
Mean water temperature (°C)	21.9	21.1	20.3	19.9	19.5
1 SD	6.68	6.33	6.9	6.78	7.95
Mean turbidity (NTU)	50.5	10.9	22.1	19.4	55.5
1 SD	73.55	22.15	28.71	75.43	49

Table 4.2. Total number, percent, and physical characterizations of habitats sampled within georegions of the Colorado River basin March through October 2017.

	Colorado River							
	Paleozoic		Llano Uplift		Balcones		Cenozoic	
N of habitats	132		114		36		245	
Habitat types (%)								
Riffle	11		15		19		11	
Run-channel	12		12		28		20	
Run-edge	6		12		19		22	
Pool-channel	25		26		6		15	
Pool-edge	37		27		22		22	
Backwater	10		8		6		11	
	<u>Mean</u>	<u>1</u> <u>SD</u>	<u>Mean</u>	<u>1</u> <u>SD</u>	<u>Mean</u>	<u>1</u> <u>SD</u>	<u>Mean</u>	<u>1</u> <u>SD</u>
Depth (m)	0.47	0.3	0.48	0.37	0.47	0.25	0.64	0.46
Current velocity column (m/s)	0.1	0.18	0.14	0.25	0.33	0.32	0.23	0.27
Current velocity bottom (m/s)	0.04	0.08	0.07	0.12	0.19	0.21	0.12	0.15
Penetrometer (kg/cm ²)	0.32	1.01	0.66	1.46	0.14	0.15	0.12	0.33
FST hemispheres	1.52	2.63	1.98	3.21	4.25	4.05	2.86	3.33
Minimum bottom shear stress (dyn/cm ²)	1.24	1.47	1.61	2.63	2.65	2.68	1.82	2.77
Specific conductance (uS/cm)	998	365	600	100	561	64	597	45
Substrate (%)								
Clay	3	10	7	17	3	12	5	15
Silt	26	28	23	27	16	30	21	28
Sand	9	15	6	11	30	23	38	30
Gravel	23	24	16	20	37	28	19	22
Cobble	26	25	23	27	14	25	9	18
Boulder	7	20	5	14			3	14
Bedrock	3	14	15	28			3	12
Detritus	3	9	5	13			1	5
Large woody debris (%)	3	10	4	11	1	2	3	7
Undercut bank (%)	1	5	1	4			1	5
Root wad (%)	<0.1	0.1	<0.1	0.2			0.4	2

Table 4.2. Continued

	Paleozoic		Llano Uplift		Balcones		Cenozoic	
Vegetation (%)	5	19	1	5	3	9	1	4
<i>Chara</i>	2	12						
<i>Ceratophyllum</i>								
Filamentous Algae	2	11	0.5	5				3
<i>Hydrilla</i>						1	0.1	1
<i>Justicia</i>								
<i>Nuphar</i>								
<i>Potamogeton</i>								
<i>Heteranthera</i>	1	10			3	9	0.4	3

Table 4.3. Water quality parameters (mean for temperature, dissolved oxygen, and turbidity, median for pH) for mesohabitats sampled within georegions of the Colorado River basin March through October 2017.

		Temperature (°C)	Dissolved oxygen (mg/L)	pH	Turbidity (NTU)
Georegion Paleozoic	Central tendency	28.7	8	8.3	96.2
	1 SD	2.52	2.01		51.67
	Minimum	24.3	3.6	7.2	19.5
	Maximum	34.5	14.1	10.9	152.2
Georegion Llano Uplift	Central tendency	28	8.5	8.3	76.4
	1 SD	2.52	1.57		44.56
	Minimum	22.3	5.4	6.9	20.6
	Maximum	32.5	12.8	10.2	152.2
Georegion Balcones	Central tendency	26.9	8.8	7.8	11.7*
	1 SD	2.65	11.04		25.78
	Minimum	23.4	5.2	7.6	0.49
	Maximum	34.4	73.1	7.9	339
Georegion Cenozoic	Central tendency	28.8	9	8.1	33.9
	1 SD	2.75	3.14		40.6
	Minimum	22.7	5.7	6.9	1.3
	Maximum	35.1	41	11.4	309.3

*Estimates obtained from waterquality.lcra.org, Site 12474 and Site 12466 (downstream of Lady Bird Lake to Webberville; period of record: 1998 – 2016).

Table 4.4. Mussel species and relative abundances (% of total N) taken from georegions within the Colorado River basin from March through October 2017.

Scientific Name	Common Name	Abundance (%)			
		Paleozoic Georegion	Llano Uplift Georegion	Balcones Georegion	Cenozoic Georegion
<i>Amblema plicata</i>	Threeridge		2.0		58
<i>Cyclonaias houstonensis</i>	Smooth Pimpleback	1.2	4.0		17
<i>Cyclonaias petrina</i>	Texas Pimpleback	2.4	37		1.3
<i>Cyrtonaias tampicoensis</i>	Tampico Pearlymussel	16	4.5	7.4	1.5
<i>Lampsilis bracteata</i>	Texas Fatmucket		0.8		
<i>Lampsilis teres</i>	Yellow Sandshell	11		33	17
<i>Leptodea fragilis</i>	Fragile Papershell	24	15	3.7	2.7
<i>Potamilus purpuratus</i>	Bleufer	4.5	3.6		0.7
<i>Pyganodon grandis</i>	Giant Floater	11	2.8	33	0.3
<i>Quadrula apiculata</i>	Southern Mapleleaf	22	6.5	3.7	0.2
<i>Toxolasma parvum</i>	Lilliput			3.7	0.1
<i>Toxolasma texasiense</i>	Texas Lilliput				1.5
<i>Tritogonia verrucosa</i>	Pistolgrip	0.8	21		
<i>Truncilla macrodon</i>	Texas Fawnsfoot				0.4
<i>Unio merus tetralasmus</i>	Pondhorn				0.04
<i>Utterbackia imbecillis</i>	Paper Pondshell	7.8	2.8	15	0.1
	Total N	245	247	27	2,300

Table 4.5. Mussel species and occurrences (% of total habitats sampled) taken from georegions within the Colorado River basin from March through October 2017.

Scientific Name	Common Name	Occurrence (%)			
		Paleozoic Georegion	Llano Uplift Georegion	Balcones Georegion	Cenozoic Georegion
<i>Amblema plicata</i>	Threeridge		1.8		18
<i>Cyclonaias houstonensis</i>	Smooth Pimpleback	1.5	2.7		15
<i>Cyclonaias petrina</i>	Texas Pimpleback	1.5	7.1		4.9
<i>Cyrtonaias tampicoensis</i>	Tampico Pearlymussel	6.0	6.2	5.6	4.9
<i>Lampsilis bracteata</i>	Texas Fatmucket		0.9		
<i>Lampsilis teres</i>	Yellow Sandshell	9.0		5.6	18
<i>Leptodea fragilis</i>	Fragile Papershell	13	21	2.8	11
<i>Potamilus purpuratus</i>	Bleufer	6.8	4.4		2.4
<i>Pyganodon grandis</i>	Giant Floater	12	4.4	2.8	1.6
<i>Quadrula apiculata</i>	Southern Mapleleaf	9.8	6.2	2.8	1.6
<i>Toxolasma parvum</i>	Lilliput			2.8	0.8
<i>Toxolasma texasiense</i>	Texas Lilliput				2.9
<i>Tritogonia verrucosa</i>	Pistolgrip	1.5	15		
<i>Truncilla macrodon</i>	Texas Fawnsfoot				3.3
<i>Unio merus tetralasmus</i>	Pondhorn				0.4
<i>Utterbackia imbecillis</i>	Paper Pondshell	6.8	5.3	2.8	1.2
	Total N of habitats	132	114	36	245
	Total % of habitats	68	75	25	87

Table 4.6. Mesohabitat associations by species using ACFOR scale (Stiers et al. 2011): Abundant (75 – 100% in a species relative abundance), Common (50 – 74%), Frequent (25 – 49%), Occasional (5 – 24%), and Rare (>0 – 4%). For example, Threeridge were taken rarely from riffle, occasionally from run-channel, pool-edge, and backwater, and frequently taken from run-edge and pool-channel habitats. Blank represents a species was not found in the mesohabitat.

Species	N	Riffle	Run-channel	Run- edge	Pool-channel	Pool- edge	Backwater
Threeridge	1,330	rare	occasional	frequent	frequent	occasional	occasional
Yellow Sandshell	421	rare	rare	frequent	occasional	frequent	occasional
Smooth Pimpleback	400	rare	frequent	occasional	frequent	occasional	rare
Fragile Papershell	160	rare	rare	frequent	occasional	frequent	occasional
Texas Pimpleback	127	rare	occasional	common	occasional	rare	occasional
Tampico Pearlymussel	86	rare		rare	common	occasional	occasional
Southern Mapleleaf	75	occasional	occasional	rare	abundant	occasional	rare
Pistolgrip	54	occasional	occasional	frequent	occasional	occasional	occasional
Giant Floater	49			rare	occasional	common	occasional
Bleufer	35				frequent	common	occasional
Texas Lilliput	34			occasional	occasional	common	
Paper Pondshell	33		occasional	occasional	occasional	frequent	occasional
Texas Fawnsfoot	9			common		frequent	occasional
Lilliput	3					abundant	
Texas Fatmucket	2				abundant		
Pondhorn	1						abundant

Table 4.7. Species-substrate associations using ACFOR scale (Stiers et al. 2011): Abundant (75 – 100% mean percent substrate), Common (50 – 74%), Frequent (25 – 49%), Occasional (5 – 24%), and Rare (>0 – 4%). For example, Threeridge were taken from substrates comprised, on average, rarely of cobble and detritus and occasionally of clay, silt, sand, gravel, boulder, and bedrock. Blank represents a substrate type where a species was not found.

Species	N	Clay	Silt	Sand	Gravel	Cobble	Boulder	Bedrock	Detritus
Threeridge	1,330	occasional	occasional	occasional	occasional	rare	occasional	occasional	rare
Yellow Sandshell	421	occasional	frequent	occasional	rare	rare	occasional	rare	rare
Smooth Pimpleback	400	rare	occasional	frequent	occasional	occasional	frequent	occasional	rare
Fragile Papershell	160	occasional	occasional	occasional	occasional	occasional	occasional	rare	rare
Texas Pimpleback	127	rare	occasional	frequent	occasional	occasional	occasional	rare	
Tampico Pearlymussel	86	rare	frequent	occasional	occasional	occasional	occasional	rare	rare
Southern Mapleleaf	75	rare	occasional	occasional	frequent	occasional	occasional	rare	rare
Pistolgrip	54	rare	occasional	occasional	occasional	frequent	occasional	occasional	rare
Giant Floater	49	occasional	common	occasional	occasional	occasional	occasional	rare	occasional
Bleufer	35	rare	frequent	frequent	occasional	occasional	occasional	rare	rare
Texas Lilliput	34	rare	frequent	rare	rare	rare	occasional	occasional	frequent
Paper Pondshell	33	rare	frequent	rare	occasional	occasional	rare	occasional	occasional
Texas Fawnsfoot	9	occasional	frequent	frequent	occasional	rare	occasional		
Lilliput	3		abundant	rare	rare				
Texas Fatmucket	2		common					common	
Pondhorn	1		abundant						

Table 4.8. Differences in mussel community relative abundances before and after Hurricane Harvey and >4,600 cm in Cenozoic Georegion. Relative abundances of mussel species pre and post Harvey, ranked by magnitude of percent change.

Species	Relative Abundance (%)		Change in percent
	Pre-Harvey	Post Harvey	
Threeridge	59	53	-5.91
Texas Lilliput	1.7	0.68	-0.99
Texas Pimpleback	1.4	0.91	-0.49
Tampico Pearlymussel	1.6	1.1	-0.48
Giant Floater	0.38		-0.38
Texas Fawnsfoot	0.43	0.23	-0.2
Paper Pondshell	0.16		-0.16
Pondhorn	0.05		-0.05
Yellow Sandshell	17	17	0.05
Lilliput	0.05	0.23	0.17
Southern Mapleleaf	0.11	0.45	0.35
Fragile Papershell	2.6	3.2	0.54
Bleufer	0.11	2.9	2.84
Smooth Pimpleback	16	21	4.71
N of mussels	1,859	441	
N of habitats	179	66	

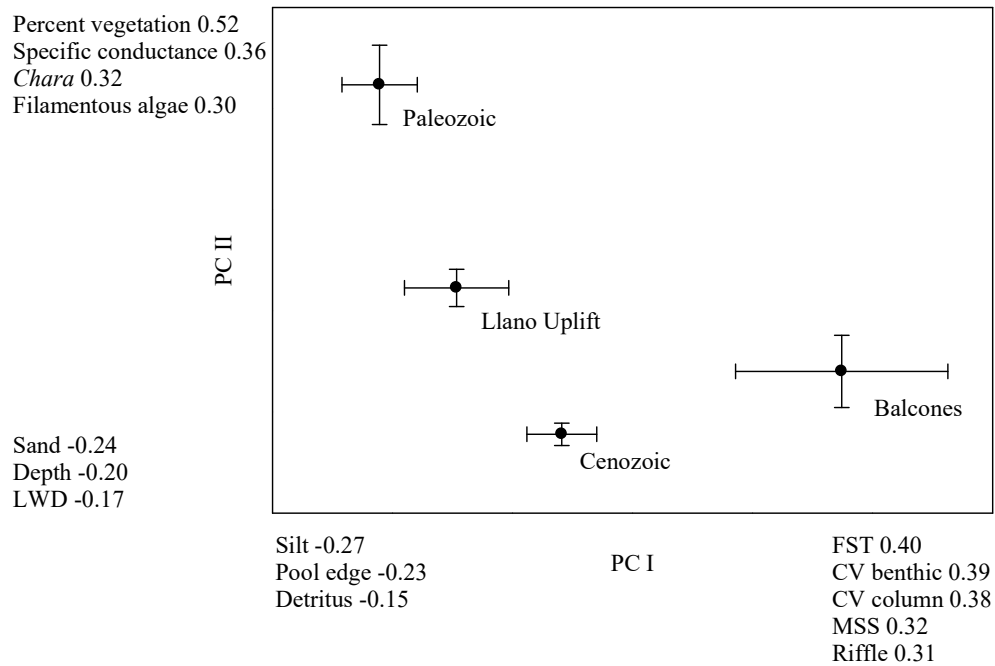


Figure 4.1. Plot of principal components axes I and II for physical characters of mesohabitats taken from Colorado River basins taken from March through October 2017. Black circles represent mean and whiskers represent 1 SD of mesohabitat scores grouped by basin, reach, or georegion.

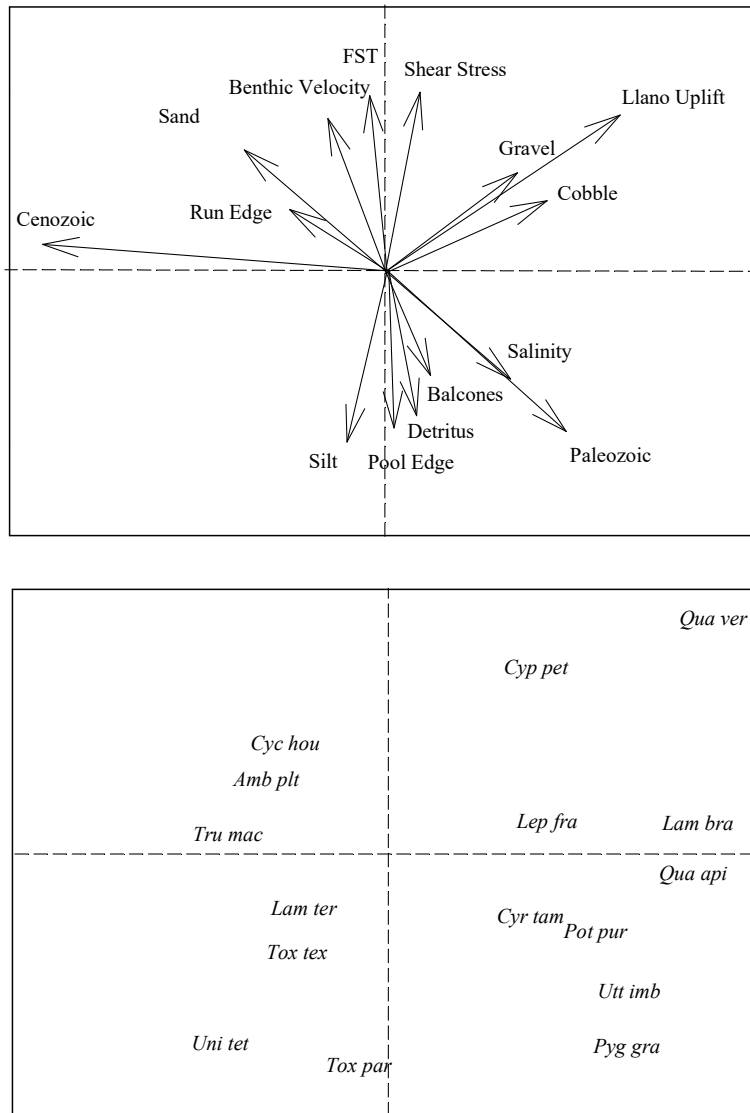


Figure 4.2. Plot of conical correspondence axes I and II for mesohabitats and their physical characters taken from the Colorado River basin from March through October 2017 (top panel). Arrow lengths indicate weight of mesohabitat and physical parameters along axes I and II. Centroid of species scores are represented by the first three letters of a species generic and specific epithets.

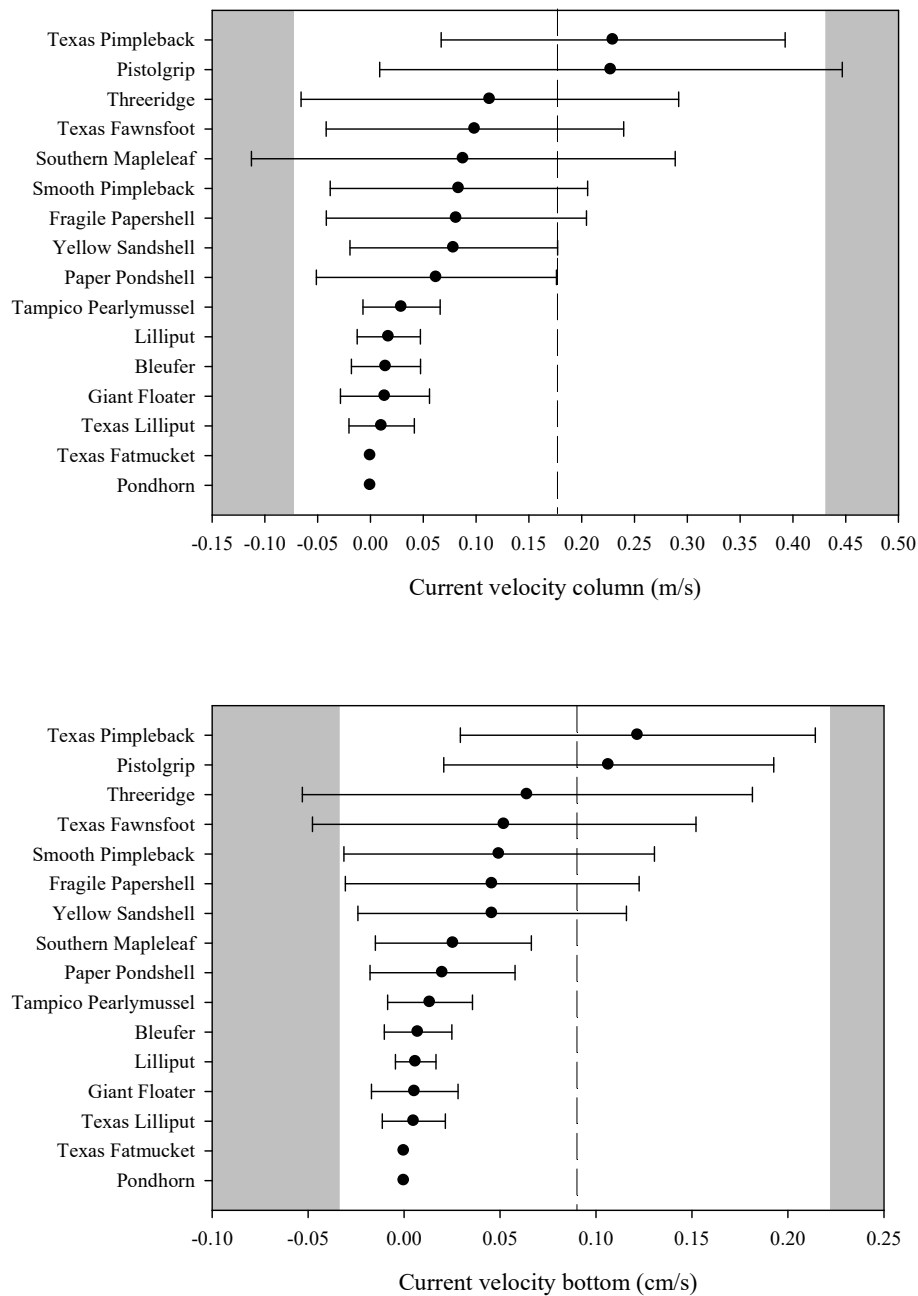


Figure 4.3. Weighted mean (black circle) and one SD (whiskers) of current velocities (column, top panel; bottom, bottom panel) for mussels taken from Colorado River from March through October 2017. Dashed vertical line represents mean of all available habitats, white area represents within 1 SD of all available habitats, and gray represents >1 SD of all habitats available. Total N for each species is provided in Table 6.

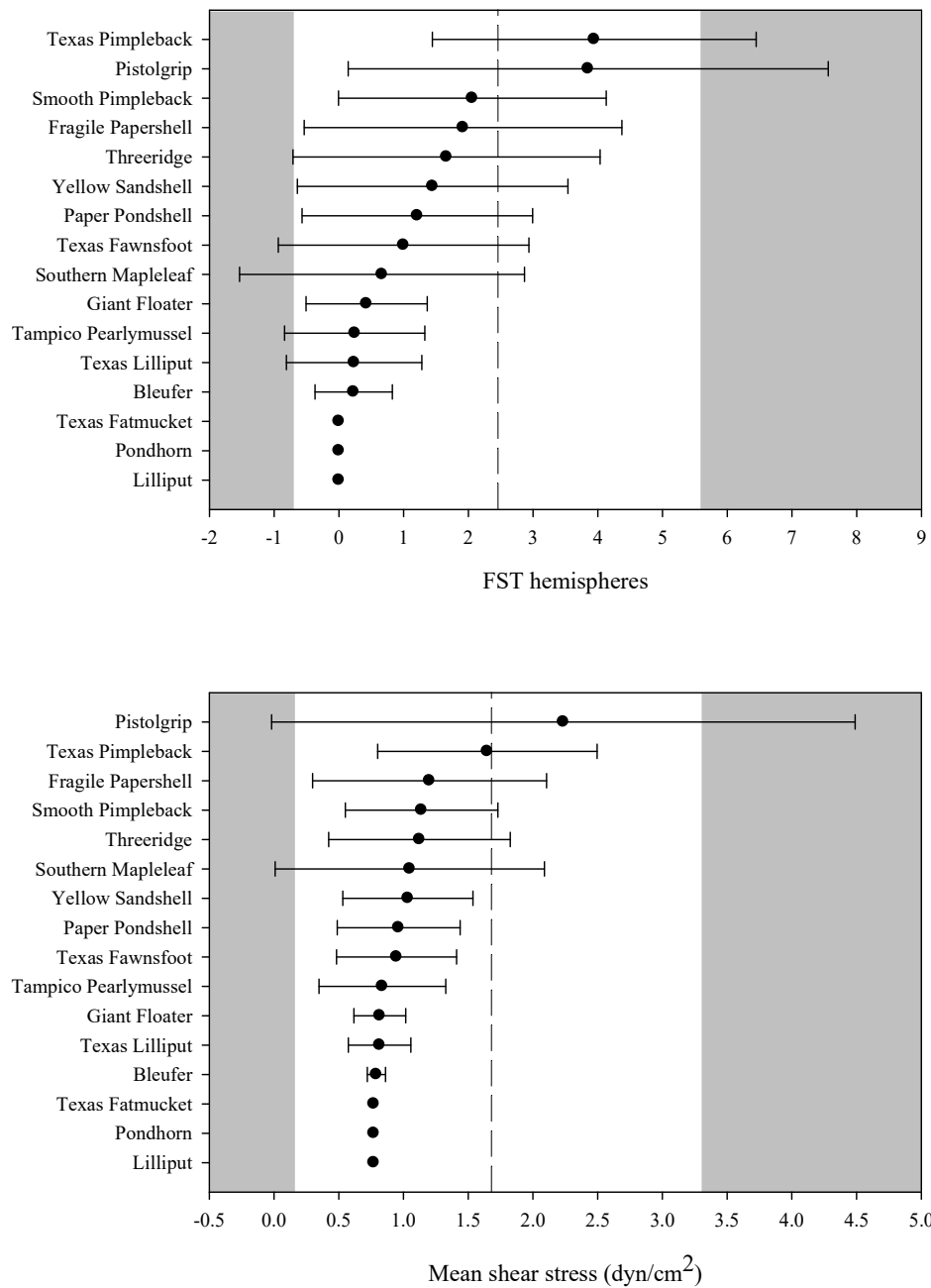


Figure 4.4. Weighted mean (black circle) and one SD (whiskers) of FST hemispheres (top panel) and mean shear stress (bottom panel) for mussels taken from Colorado River from March through October 2017. Dashed vertical line represents mean of all available habitats, white area represents within 1 SD of all available habitats, and gray represents >1 SD of all habitats available. Total N for each species is provided in Table 6.

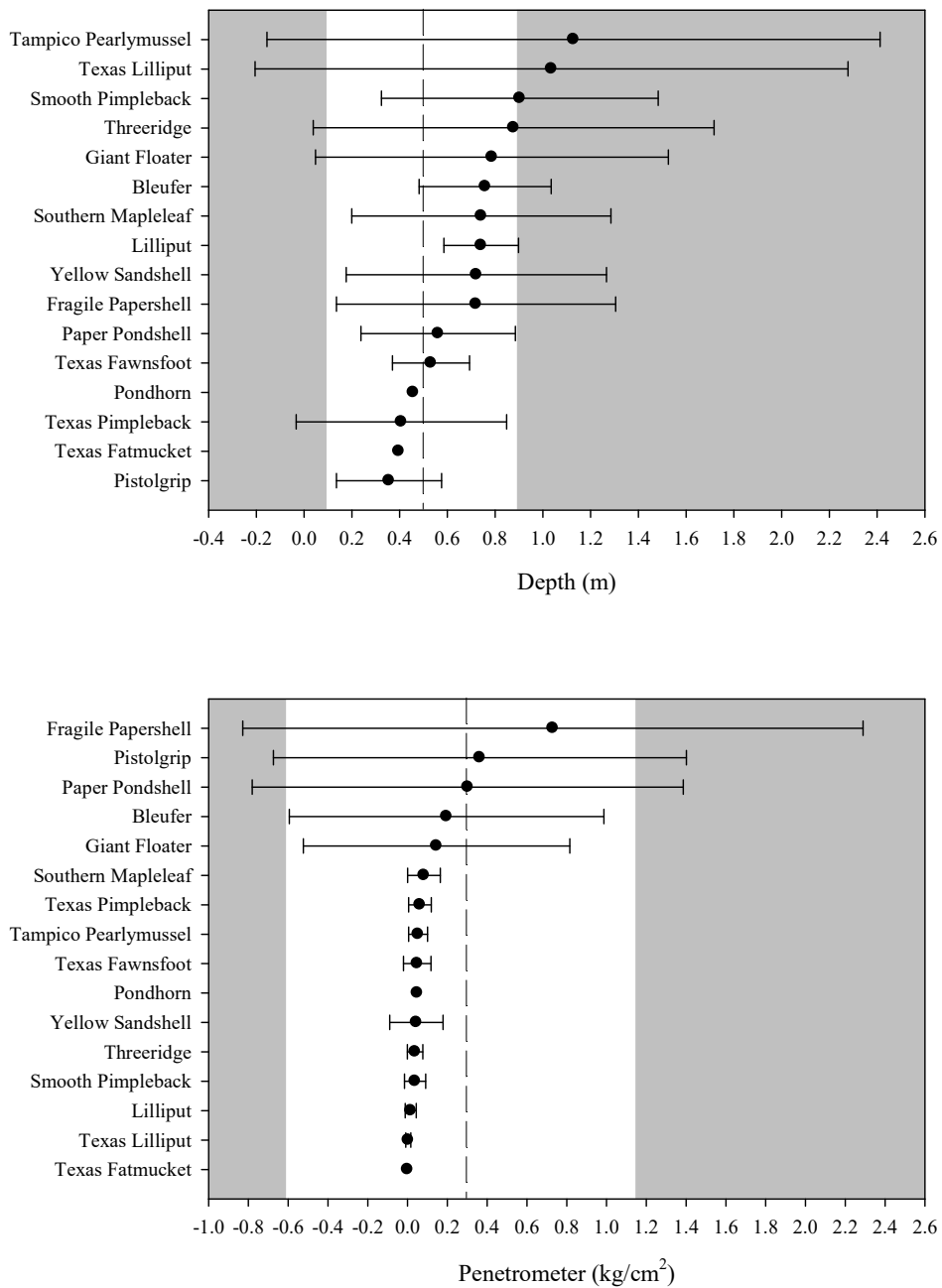


Figure 4.5. Weighted mean (black circle) and one SD (whiskers) of depth (top panel) and penetrometer (bottom panel) for mussels taken from Colorado River from March through October 2017. Dashed vertical line represents mean of all available habitats, white area represents within 1 SD of all available habitats, and gray represents >1 SD of all habitats available. Total N for each species is provided in Table 6.

Literature Cited

- Arbuckle, K. E., and Downing, J. A. 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. *Canadian Journal of Fisheries and Aquatic Sciences* 59:310-316.
- Avery-Gomm, S., J.S. Rosenfeld, J.S. Richardson, and M. Pearson. 2014. Hydrological drought and the role of refugia in an endangered riffle-dwelling fish, Nooksack dace (*Rhinichthys cataractae* ssp.). *Canadian Journal of Fisheries and Aquatic Sciences* 71:1625-1634.
- Baker, S.M., and J.S. Levinton. 2003. Selective feeding by three native North American freshwater mussels implies food competition with zebra mussels. *Hydrobiologia* 505:97-105.
- Brim Box, J., R.M. Dorazio, and W.D. Liddell. 2002. Relationships between streambed substrate Characteristics and freshwater mussels (*Bivalvia:Unionidae*) in Coastal Plain streams. *Journal of North American Benthological Society* 21:253-260.
- Brown, K.M., and P.D. Banks. 2001. The conservation of unionid mussels in Louisiana rivers: diversity, assemblage composition, and substrate use. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11:189-191.
- Burlakova, L.E., and A.Y. Karatayev. 2010. State-wide Assessment of Unionid Diversity in Texas. Final Performance Report to State Wildlife Grants Program. Federal Aid Grant T-43.
- Burlakova, L.E., A.Y. Karatayev, V.A. Karatayev, M.E. May, D.L. Bennett, M.J. Cook. 2011. Endemic species: Contribution to community uniqueness, effect of habitat alteration, and conservation priorities. *Biological Conservation* 144:155-165.
- Burlakova, L.E., B.L. Tulumello, A.Y. Karatayev, R.A. Krebs, D.W. Schloesser, D.T. Zanatta, W.L. Paterson, T.A. Griffith, M.W. Scott, and T. Crail. 2014. Competitive replacement of Invasive congeners may relax impact on native species: interactions among zebra, Quagga, and native unionid mussels. *PLoS ONE* <https://doi.org/10.1371/journal.pone.0114926>
- Chambers, A. J., and Woolnough, D. A. 2018. Discrete longitudinal variation in freshwater mussel assemblages within two rivers of central Michigan, USA. *Hydrobiologia* 810:351-366.
- Cummings, K. 2011. *Amphinaia pustulosa*. The IUCN Red List of Threatened Species 2011: e.T189523A8743529. <http://dx.doi.org/10.2305/IUCN.UK.2011-2.RLTS.T189523A8743529.en>

- Dahm, C.N., R.J. Edwards, and F.P. Gelwick. 2005. Gulf Cost Rivers of the Southwestern United States. Rivers of North America. Eslevier Academic Press, NY.
- Dascher, E.D., L.E. Burlakova, A.Y. Karatayev, D.F. Ford, A.N. Schwalb. 2017. Distribution of unionid freshwater mussels and host fishes in Texas. A study of broad-scale spatial patterns across basins and a strong climate gradient. *Hydrobiologia* DOI: 10.1007/s10750-017-3168-5
- Freshwater Mollusk Conservation Society (FMCS). 2016. A national strategy for the 108 conservation of native freshwater mollusks. *Freshwater Mollusk Biology and Conservation* 19:1-21.
- Gough, H.M., A.M. Gascho Landis, and J.A. Stoeckel. 2012. Behavior and physiology are linked in the responses of freshwater mussels to drought. *Freshwater Biology* 57:2356-2366.
- Haag, W. R. 2012. Life history variation in mussels. *North American Freshwater Mussels: Natural History, Ecology, and Conservation*. Cambridge University Press, NY.
- Haag, W.R., and J.D. Williams. 2014. Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels. *Hydrobiologia* 735:45-60.
- Haag, W. R., and Warren, Jr, M. L. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. *Canadian Journal of Fisheries and Aquatic Sciences* 55:297-306.
- Hakala, J.P., and K.J. Hartman. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. *Hydrobiologia* 515:203-213.
- Haney, A., R. Fluharty, H. Abdelrahman, R. Tucker, K. Fogelman, B. Helms, and J. Stoeckel. 2018. Potential factors limiting growth, survival, and reproduction of freshwater mussel species of interest. Multiple freshwater mussel species of the Brazos River, Colorado River, and Guadalupe River basins. CMD 1-6233CS.
- Howells, R.G. 2014. Field Guide to Texas Freshwater Mussels. BioStudies, Kerrville, TX.
- Hubbs, C. 1957. Distributional patterns of Texas fresh-water fishes. *The Southwestern Naturalist* 2: 89-104.

- Johnson, N.A., C.H. Smith, J.M. Pfeiffer, C.R. Randklev, J.D. Williams, and J.D. Austin. 2018. Integrative taxonomy resolves taxonomic uncertainty for freshwater mussels being considered for protection under the U.S. Endangered Species Act. *Scientific Reports* 8:15892.
- Johnson, P.D., and K.M. Brown. 2000. The importance of microhabitat factors and habitat stability to the threatened Louisiana pearl shell, *Margaritifera hembeli* (Conrad). *Canadian Journal of Zoology* 78:271-277.
- Karatayev, A.Y., L.E. Burlakoka, and D.K. Padilla. 2017. Can introduced species replace lost biodiversity? A test with freshwater molluscs. <https://doi.org/cmich.idm.oclc.org/10.1007/s10750-017-3135-1>
- McRae, S. E., D. Allan, J., and Burch, J. B. 2004. Reach-and catchment-scale determinants of the distribution of freshwater mussels (*Bivalvia*: *Unionidae*) in south-eastern Michigan, USA. *Freshwater Biology* 49:127-142.
- Metcalf-Smith, J.L., J. Di Maio, S.K. Station, and G.L. Macki. 2000. Effect of sampling effort on the efficiency of the timed search method for sampling freshwater mussel communities. *Journal of North American Benthological Society* 19:725-732.
- Mitchell, Z. A., McGuire, J., Abel, J., Hernandez, B. A., and Schwalb, A. N. 2018. Move on or take the heat: Can life history strategies of freshwater mussels predict their physiological and behavioural responses to drought and dewatering?. *Freshwater Biology* 63:1579-1591.
- Pfaff, P. 2019. Influence of surface and near-surface geology on fish assemblages in the Colorado River basin of Texas. M.S. Thesis, Texas State University, San Marcos.
- Randklev, C.R., B.J. Lundeen, R.G. Howells, and J.H. Kennedy. 2009. First Account of a Living Population of Texas Fawnsfoot, *Truncilla macrodon* (*Bivalvia*: *Unionidae*), in the Brazos River, Texas. *The Southwestern Naturalist* 55:297-298.
- Randklev, C.R., M.S. Johnson, E.T. Tsakiris, S. Rogers-Oetker, K.J. Roe, S. McMurray, C. Robertson, J. Groce, and N. Wilkins. 2012. False Spike, *Quadrula mitchelli* (*Bivalvia*: *Unionidae*) is not extinct: first account of a live population in over 30 years. *American Malacological Bulletin* 30:327-328.
- Randklev, C.R., M.S. Johnson, E.T. Tsakiris, J. Groce, and N. Wilkins. 2013. Status of freshwater mussel (Family: *Unionidae*) fauna in mainstem of the Leon River, Texas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 23:390-404.

- Randklev, C.R., M. Cordova, J. Groce, E. Tsakiris, and B. Sowards. 2014. Freshwater mussel (Family: Unionidae) data collection in the middle and lower Brazos River. Institute of 109 Renewable Natural Resources, Texas A&M University. Texas Parks and Wildlife Contract No. 424520.
- Randklev, C. R., N. A. Johnson, T. Miller, J. M. Morton, J. Dudding, K. Skow, B. Boseman, M. Hart, E. T. Tsakiris, K. Inoue, and R. R. Lopez. 2017. Freshwater Mussels (Unionidae): Central and West Texas Final Report. Texas A&M Institute of Renewable Natural Resources, College Station, Texas.
- Rose, D.R., and A.A. Echelle. 1981. Factor Analysis of Associations of Fishes in Little River, Central Texas, with an Interdrainage Comparison. *The American Midland Naturalist* 106:379-391.
- Sietman, B.E., M.A. Furman, and F.A. Pursell. 1999. Colonization of Bedrock by Freshwater Mussels (Bivalvia: Unionidae). *American Midland Naturalist* 141:209-211.
- Statzner, B., F. Kohmann, and A.G. Hildrew. 1991. Calibration of FST-hemispheres against bottom shear stress in a laboratory flume. *Freshwater Biology* 26:227-231.
- Strayer, D. 1983. The effects of surface geology and stream size on freshwater mussels (Bivalvia, Unionidae) distribution in southeastern Michigan, U.S.A. *Freshwater Biology* 12:253-264.
- Strayer, D. 1983. The effects of surface geology and stream size on freshwater mussel (Bivalvia, Unionidae) distribution in southeastern Michigan, USA. *Freshwater Biology* 13:253-264.
- Strayer, D.L. 2008. *Freshwater Mussel Ecology: Multifactor Approach to Distribution and Abundance*. University of California Press, CA.
- Strayer, D.L. and D.R. Smith. 2003. *A Guide to Sampling Freshwater Mussel Populations*. Bethesda, Maryland.
- Stiers, I., N. Crohain, G. Josens, L. Triest. 2011. Impact of three aquatic invasive species on native plants and macroinvertebrates in temperate ponds. *Biological Invasions* 13:2715-2726.
- Texas Parks and Wildlife (TPWD). 2010. Threatened and Endangered Nongame Species. *Texas Register* 35:249-251.

- Texas Parks and Wildlife (TPWD). 2014. 2014 Fisheries Management Survey Report: Belton Reservoir. Inland Fisheries Division Monitoring and Management Program.
- Tsakiris, E.T., and C.R. Randklev. 2016. Distribution and habitat associations of freshwater mussels (Bivalvia: Unionidae) in the lower Guadalupe River, Texas. Texas A&M Institute of Renewable Natural Resources, College Station, Texas.
- Tsakiris, E.T., and C.R. Randklev. 2016. Structural changes in freshwater mussel (Bivalve: Unionidae) assemblages downstream of Lake Somerville, Texas. *American Midland Naturalist* 175:120-127.
- U.S. Fish and Wildlife Service (USFWS). 2011. Endangered and threatened wildlife and plants: 90-day finding on petitions to list nine species of mussels from Texas as threatened or 110 endangered with critical habitat. *Federal Register*. 2011 74:66260–66271.
- U.S. Fish and Wildlife Service (USFWS). 2016. U.S. Fish and Wildlife Service Species Assessment and Listing Assignment Form.
https://ecos.fws.gov/docs/candidate/assessments/2016/r2/F04G_I01.pdf
- Vaughn, C.C., M. Taylor, and K.J. Eberhard. 1997. A comparison of the effectiveness of timed Searches vs. quadrat surveys. *Conservation and Management of Freshwater Mussels II: Proceedings of a UMRCC Symposium* 157-162.
- Vaughn, C.C. 2017. Ecosystem services provided by freshwater mussels.
<https://doi.org/10.1007/s10750-017-3139-x>
- Vaughn, C. C. (1997). Regional patterns of mussel species distributions in North American rivers. *Ecography* 20:107-115.
- Vaughn, C. C., and Taylor, C. M. 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conservation Biology* 13:912-920.
- Wentworth, C.K. 1922. A scale grade and class terms for clastic sediments. *Journal of Geology* 30:377-392.
- Williams, J.D., A.E. Bogan, R.S. Butler, K.S. Cummings, J.T. Garner, J.L. Harris, N.A. Johnson, and G.T. Watters. 2017. A Revised List of Freshwater Mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada. *Freshwater Mollusk Biology and Conservation* 20:33-58.